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**Soil moisture gradients and climate change:
predicting growth of a critical boreal tree species**

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Abstract

Understanding the complex relationships between climate, tree growth and water availability is key for predicting the performance of environmentally and economically salient tree species like *Pinus banksiana*. Ecologically, *P. banksiana* occupies the extreme habitats of soil moisture gradient, from very sandy dry soils to waterlogged bogs. However, little is known about how its growth may be affected by future climate in these two habitats. We assessed the effect of climatic variability on this species growth under different moisture conditions (sandy-dry and bogs). Trees in the bog site had the highest growth rates. Individuals in all sites responded positively to increased spring temperature, whereas those in the bog site showed the highest response to increased summer moisture. However, in dry years growth response in the bog site declined by 17%, while in the two drier sites growth declined between 1 and 9.8%, equalizing growth rates across sites. Further, the decline in growth associated with drier summers eliminated the benefits of warmer springs at the bog site. Sites near bogs are currently associated with high growth performance and are commonly planted with this species. Yet, under the projected climate for the region, trees growing in these sites will likely lose their advantage.

Key words: drought, dendrochronology, hierarchical Bayes, jack pine, tree rings

Introduction

Predictions of global climate patterns call for higher average temperatures, more variable precipitation, and an increase in the frequency and intensity of severe weather events (IPCC 2014). In the past, similar climatic shifts occurred at more gradual 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 trends 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 is essential to assess their performance and adequate management. Suitable habitats for tree species are 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 (e.g., Elliott et al. 2015; Peters et al. 2015). 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 (Woodward 1987). But, other physical factors including soils, elevation, aspect, and slope, shape that performance and determine the outcome at the local level. Furthermore, accounting for site conditions substantially explains varying growth responses when assessing productivity as a function of climatic variables (Forrester et al. 2013; Beauregard and de Blois 2014; Mina et al. 2018).

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 (Rudolph and Laidly 1990; Fig. 1). *Pinus 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 its most southern distributional range

(Fig. 1), provide critical nesting habitat for the endangered Kirtland's Warbler (*Setophaga kirtlandii*) (Probst and Hayes 1987). Further, wood production from this species substantially contributes to local economies, accounting for approximately 8% of saw logs in our study region (Haugen et al. 2014). *Pinus banksiana* typically grows in pure, even-aged stands on extensively well-drained loamy-sands, but it has been found growing in a variety of soil types (Yarranton and Yarranton 1975; 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); and, in Maine, *P. banksiana*, grows on sandy, well-drained, thin soils and in coastal bogs and wetlands (Barton and Grenier 2008). In our study area, upper Midwest of the USA (Fig. 1), this species grows naturally in well-drained sandy soils, but it is also planted in nearby bogs; there, both types of stands are harvested for commercial purposes (DNR 2018).

The objective of this study is to assess the effect of annual variability on climatic conditions on the growth and performance of *P. banksiana* stands growing under different soil moisture conditions. We address the following questions: 1) how different is the growth response to annual variability on environmental conditions of *P. banksiana* stands located on bogs and intermittent wetlands from those in stands with well-drained sandy soils? 2) How will the future growth of individuals be affected by the forecasted climate for the region? And, 3) should *P. banksiana* continue to be planted across these soil moisture gradients in the future? Answers to these questions will shed light about how sensitive *P. banksiana* are to forecasted climatic conditions, and allow for assessment of performance under anticipated climate shifts.

Methods

The study area is located in the center of Michigan's northern lower peninsula, USA (Fig. 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. Annual precipitation varies between 770-850 mm, most of which falls between May and October (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 *P. strobus*) and oaks (*Quercus*), while excessively drained sites are dominated by *P. banksiana* (Barnes and Wagner 1981).

Forest sites for this study were selected from an assortment 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 Michigan Department of Natural Resources (DNR) data, three forest stands were identified on the Camp Grayling National Guard Military Reservation that fit the environmental criteria listed above, i.e., they have similar features and mainly differ in their soil moisture content (Table 1).

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* (Table 1). The first stand, BOG was planted along the edge of an intermittent wetland/bog. The second stand, DRY 1, and the third stand, DRY 2, were located on sandy well drained uplands, both dry stands were recorded as being naturally regenerated (DNR 2018).

Field and Laboratory Methods

Field work was completed between May and August 2018. At each stand, five 10x10 m plots were randomly established 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 (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 (top 15 cm) was determined by recording values at 1.5 m in each cardinal direction from each tree sampled 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. Diameter at breast height (DBH) of each tree was recorded using a circumference tape. Two tree cores, one from the north and one from the south side, were extracted at breast height (1.37m) from each tree using a 4.3mm Haglof increment borer. Standard methods for preparing tree increment cores were used (Stokes and Smiley, 1968; Phipps 1985); and 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 (Holmes 1983). Of the 180 increment cores collected 155 were used in the final analysis (25 cores were either broken, damaged, or we were unable to accurately cross-date them). After being cross-dated, north and south ring width measurements were averaged to determine annual radial growth for each tree (Fig. 2a).

Climate Data and Analysis

Climate data from 1972 to present was retrieved from the National Oceanic and Atmospheric Administration weather station located in Grayling, Michigan (NOAA 2018a). Palmer Drought

Severity Index (PDSI; Palmer 1965) data was also retrieved from the NOAA divisional time series from 1972 to present (NOAA 2018b). We carried out exploratory data analysis and model selection to assess the relationship between growth and multiple combinations of spring temperature, variable determining the beginning of the growing season, and of summer precipitation and PDSI, variables determining water constraints. In particular PDSI, as it accounts for both temperature and precipitation, is a well suited measured of water availability in these well-drained sandy soils. The model with the best fit (based on deviance information criterion, DIC [Spiegelhalter et al. 2002]; see Supplementary File 1 for model comparisons) included April temperature and July PDSI from the current year (separate assessments for each stand showed same trends; Fig. 2b).

The natural log of diameter was included in the analysis to account for growth variation as a function of size (age) (i.e., detrending; Fig. 2a; Fritts 1976; Cook et al. 1990). Because growth and climatic conditions from previous years can affect current growth through lag effects (Peltier et al. 2016), the growth 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.). Differences in soil moisture across the sites were then factored into the model by estimating all parameters at the stand level. Growth increments for tree i in year y ($G_{i,y}$; ring width in mm) were modeled using a normal likelihood limited to positive values:

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

with process model:

$G_{i,y}$

$$= \alpha_i + \beta_1 \ln(DBH_{i,y}) + \beta_2 (\omega_1 \text{stand}(i) \text{Growth}_{i,y-1} + \omega_2 \text{stand}(i) \text{Growth}_{i,y-2}) + \beta_3 \text{AprilTemp}_y + \beta_4 \text{JulyPDSI}_y$$

Because the variance of the growth data changed with diameter, we estimated the variance of the model (σ^2) as a function of DBH with the following parameter model: $\sigma_{i,y}^2 = a_{\text{stand}(i)} + b_{\text{stand}(i)} DBH_{i,y}$ (Lines et al., 2012). Weights for the effect of previous growth, ω parameters, were added to determine which year of previous growth is more influential. A Bayesian framework was used to estimate parameter values (see Supplementary File 2 for detailed description).

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 estimated for the range of April average temperatures (1-12.5°C) and July PDSI (-5 to 4) found in the data. Growth lag effects were included by using a growth rate of 2 mm (average across the data) and tree size of 13 cm DBH (average across 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 (see code in Supplementary File 3). Once convergence was reached, chains were run for 50,000 iterations more to estimate posterior parameter means, standard deviations, and 95% credible intervals.

Results

Canopy cover and basal area were approximately the same across all three sites (Table 1). The BOG site had more variable soil moisture. Average tree diameter ranged from 16.2 to 21.4 cm; individuals in the BOG site being both the largest and youngest (Table 1; Fig. 2). The final model fit (R^2 representing goodness of fit between observed and predicted data) was 0.70 (Supplementary File 4). Parameter values can be found in Supplementary File 5.

As expected, increasing diameter had a statistically significant negative effect on the growth of all individuals in each of the three stands (Fig. 2b declining trend), parameter β_1 was -0.27 $\pm$ 0.08 (mean $\pm$ SD) and -0.59 $\pm$ 0.09 in DRY 1 and DRY 2, and -3.61 $\pm$ 0.41 in the BOG. Previous years' growth had a significantly positive effect on the current year growth, parameter β_2 was 0.41 $\pm$ 0.05 (mean $\pm$ SD) in the BOG, and 0.75 $\pm$ 0.03 and 0.58 $\pm$ 0.04 in DRY 1 and DRY2. Growth during the previous year had a much stronger effects than two years prior (parameters ω_1 were always larger than parameters ω_2 ; see Supplementary File 5).

Increasing average temperature in April had a statistically significant positive effect on the growth of individuals in all three forest sites (parameter β_3 ; Fig. 3). Increasing summer moisture, measured by July PDSI, had a statistically significant positive effect on the growth of individuals in the BOG and DRY 2, but was not significant in DRY 1; this effect was significantly different between the BOG and DRY 1 (parameter β_4 ; Fig. 3).

The growth simulations show how growth rates increase with higher temperature and decrease with drier conditions (Fig. 4; Supplementary File 6). When comparing current average conditions (April temperature 5°C, July PSDI 0) to different scenarios we found that: under warmer springs (April temperature 12°C, July PSDI 0) growth rates will increase 15.8% in the BOG and 18.7 and 19.6% in DRY 1 and DRY 2 (Fig. 4a); in drought years (April temperature 5°C and July PDSI -5) growth rates decrease by 17% in the BOG, and 1 and 9.6% in DRY 1 and DRY 2 (not shown); and under both warmer and dry conditions growth in the DRY 1 and DRY 2 sites still increase 17 and 10%, while growth in the BOG decreases by 1.3% (Fig. 4b; Supplementary File 6).

Discussion

Global warming is rapidly changing the conditions under which plants are growing (IPCC 2014, Ballantyne et al. 2017). As tree populations cope with these changes, understanding how their growth may be differently impacted across areas in the landscape becomes critical for assessing their future productivity and well-being. In this study, we determined how climatic shifts could affect growth in even-aged *P. banksiana* stands differing in their soil moisture conditions. Individuals in all of the sites responded positively to increased April temperature while those in the bog site showed the highest positive response to increased July moisture. As expected, average growth rates were highest in the bog, indicating higher productivity under wet conditions. However, the simulations also showed that under predicted drier summer conditions the growth response in the bog 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 shifts in regional climate.

As with most tree species, growth rates of *P. banksiana* can be strongly influenced by the availability of water (Green and Grigal 1979; Hamilton and Krause 1985). This trend was evident in these sites. Individuals in the BOG had the largest average diameter by age, indicating consistently higher growth rates and overall productivity (Fig. 2). This indicates a gradient of productivity driven by site-specific conditions which may be best explained by moisture availability during the growing season. Soil moisture is associated with *P. banksiana* population productivity (Beland and Bergeron, 1996); and, as our results show, it is essential for assessing growth variation between these forest stands.

When first assessing the effects of climatic fluctuations on tree growth, our exploratory analysis, i.e., correlations between tree growth and climatic variables (see Supplementary File 1),

did not show a clear picture of how these may be related. That is likely due to the fact that tree growth is also strongly influenced by other intrinsic factors, i.e., age related growth rates and lag effects from previous years performance (Szeicz and MacDonald 1994; Anderegg et al. 2015). Our analysis shows the well-established pattern that as trees age (increase in size) they allocate more energy towards storage and maintenance than to radial growth (Cook et al. 1990). The positive trend shown from previous year's growth illustrates how growth performance along consecutive years are related (Ibáñez et al. 2018). In this case, the positive association is likely a reflection of continuous gain in resources that can then be allocated to growth. Only by accounting for these two factors we were able to discern the relationship between growth and environmental conditions.

We found a positive response to higher April average temperatures across all stands, these results followed previous findings indicating that warmer spring temperatures correspond with a longer growing season and consequently higher radial growth of *P. banksiana* (Genries et al. 2012; Subedi and Sharma 2013). Although the responses were not statistically different along stands, 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. In warmer springs, trees in the BOG 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.

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 (Fig. 3). 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 reported on multiple occasions (Despland and Houle 1997; Hofgaard et al. 1999; Huang et al. 2010; Dietrich et al. 2016). In drier sites, carbon allocation to radial growth may stop earlier in the season than in wetter sites, thus the weaker association we document.

Climate in our study area is predicted to change in the future; expectations being that average spring temperatures will increase between 0.9 and 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 (Fig. 4b). While individuals in the BOG are currently experiencing higher growth performance, our predictions show that they may be most affected under the forecasted conditions (growth declining by 17% with respect to current average conditions) and show growth rates similar to those in dry sites where growth might increase by 1 and 10%. This agrees with results of a review that illustrate a positive impact of global warming on plant growth only when water is not limited (Boisvenue and Running 2006).

Local adaptations to drought have been explained within wide-ranging species by wood hydraulic traits and stomatal regulation (O'Neill et al. 2008; Isaac-Renton et al. 2018). 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 (Tjoelker et al. 2009; Peltier and Ibáñez 2015). Due to the excessively drained sandy soils and similar climate, the recorded responses in the DRY sites may be attributed to

274 stomatal regulation, explaining the lower productivity in those sites (Isaac-Renton et al. 2018).
275 Hence, the effects of moisture variability between years is less palpable in their growth rates, as
276 these are always low. However, our simulations may have underestimated this effect as the
277 duration of droughty conditions could have an even more pronounced negative impact on
278 unacclimated individuals, depleting stored carbohydrates to maintain growth to the detriment of
279 long-term survival (Mitchell et al. 2013). Furthermore, lag effects were stronger in the drier sites,
280 meaning reductions on tree growth will have a larger effect at these sites.

281

282 Understanding the physical factors that most substantially influence a tree population's
283 sensitivity to climate fluctuations is particularly important for the development of effective
284 management strategies for economically and environmentally important tree species. Both
285 Kirtland Warbler habitat and the lumber industry in the region rely on the successful and
286 continual health of *P. banksiana* populations. Managers seeking short term yield benefits may
287 consider available sites near bogs and intermittent wetlands. While growth in these sites will
288 continue to be as high or higher than those in the drier areas, we expect that the benefits gained
289 from moister locations to quickly decline under predicted drier conditions. This study illustrate
290 the relevance of assessing tree growth across resource gradients in the landscape, as those will
291 determine differences in plant performance under changing environmental conditions.

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References

Aitken, S.N., Yeaman, S., Holliday, J.A., Wang, T., and Curtis-McLane, S. 2008. Adaptation,
migration or extirpation: climate change outcomes for tree populations. *Evol. Appl.* **1**: 95–111.

- Anderegg, W.R.L., et al. 2015. Pervasive drought legacies in forest ecosystems and their implications for carbon cycle models. *Science* **349**: 528–532.
- Ballantyne, A., et al. . 2017. Accelerating net terrestrial carbon uptake during the warming hiatus due to reduced respiration. *Nature Climate Change* **7**:148-152.
- Barnes, B.V., and Wagner, W.H. 1981. *Michigan Trees: A guide to the Trees of Michigan and the Great Lakes Region*. University of Michigan Press, Ann Arbor.
- Barton, A.M., and Grenier, D.J. 2008. Dynamics of jack pine at the southern range boundary in downeast Maine. *Can. J. For. Res.* **38**: 733–743.
- Beauregard, F., and De Blois, S. 2014. Beyond a climate-centric view of plant distribution: Edaphic variables add value to distribution models [online]. *PLoS One* **9**.
<https://doi.org/10.1371/journal.pone.0092642>.
- Beland, M., and Bergeron, Y. 1996. Height growth of jack pine (*Pinus banksiana*) in relation to site types in boreal forests of Abitibi, Quebec. *Can. J. For. Res.* **26**: 2170–2179.
- Boisvenue, C., Running, S.W. 2006. Impacts of climate change on natural forest productivity – evidence since the middle of the 20th century. *Glob. Chang. Biol.* **12**(5): 862-82.
- Brzostek, E.R., et al. 2014. Chronic water stress reduces tree growth and the carbon sink of deciduous hardwood forests. *Glob. Chang. Biol.* **20**: 2531–2539.
- Cook, E., Briffa, K., Shiyatov, S., Mazepa, V., and Jones, P.D. 1990. Data Analysis, in: Cook, E.R., Kairiukstis, L.A. (Eds.), *Methods of Dendrochronology: Applications in the Environmental Sciences*. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 97-153.
- Davis, M.B., and Shaw, R.G. 2001. Range Shifts and Adaptive Responses to Quaternary Climate Change. *Science* **292**: 673–679.

- Department of Natural Resources (DNR), 2018. Michigan State Forest Cover type. <https://gis-midnr.opendata.arcgis.com/datasets/michigan-state-forest-covertime> (accessed 3 May 2018).
- Despland, E., and Houle, G. 1997. Climate Influences on Growth and Reproduction of *Pinus banksiana* (Pinaceae) at the Limit of the Species Distribution in Eastern North America. *Am. J. Bot.* **84**: 928–937.
- Dietrich, R., et al. 2016. Climatic sensitivity, water-use efficiency, and growth decline in boreal jack pine (*Pinus banksiana*) forests in Northern Ontario. *J. Geophys. Res. Biogeosci.* **121**: 2761–2774.
- Elliott, K.J., Miniati, C.F., Pederson, N., and Laseter, S.H. 2015. Forest tree growth response to hydroclimate variability in the southern Appalachians. *Glob. Chang. Biol.* **21**(12): 4627–41.
- Forrester, D.I., Kohnle, U., Albrecht, A.T., and Bauhus, J. 2013. Complementarity in mixed-species stands of *Abies alba* and *Picea abies* varies with climate, site quality and stand density. *For. Ecol. Manage.* **304**: 233–242.
- Fritts, H.C., 1976. *Tree Rings and Climate*. Academic Press, New York.
- Genries, A., Drobyshev, I., and Bergeron, Y. 2012. Growth-climate response of jack pine on clay soils in northeastern Canada. *Dendrochronologia* **30**: 127–136.
- Green, D.C., and Grigal, D.F. 1979. Jack pine biomass accretion on shallow and deep soils in Minnesota. *Soil Sci. Soc. Am. J.* **43**: 133–1237.
- Hamilton, W.N., Krause, H.H. 1985. Relationship between jack pine growth and site variables in New Brunswick plantations. *Can. J. For. Res.* **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., and 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., and Bergeron, Y. 1999. Dendroclimatic response of *Picea mariana* and *Pinus banksiana* along a latitudinal gradient in the eastern Canadian boreal forest. Can. J. For. Res. **29**: 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., and 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. Glob. Chang. Biol. **16**: 711–731.
- Ibáñez, I., Zak, D.R., Burton, A.J., and Pregitzer, K.S. 2018. Anthropogenic nitrogen deposition ameliorates the decline in tree growth caused by a drier climate. Ecology **99**: 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., and Treydte, K. 2018. Northern forest tree populations are physiologically maladapted to drought. Nat. Commun. **9**: 1–9.

- Larsson, L. A. 2018. Cybis CooRecorder v9.3.1, Cybis CDendro v9.3.1. Cybis Elektronik and Data AB, Saltsjobaden, Sweden. www.cybis.se/forfun/dendro/index.htm (accessed 18 June 2018).
- Lines, E.R., Zavala, M.A., Purves, D.W., and Coomes, D.A. 2012. Predictable changes in aboveground allometry of trees along gradients of temperature, aridity and competition. *Glob. Ecol. Biogeogr.* **21**: 1017–1028.
- Lunn, D., Spiegelhalter, D., Thomas, A., and Best, N. 2009. The BUGS project: Evolutions, critique and future directions. *Stat. Med.* **28**: 3049–3067.
- Mina, M., Huber, M.O., Forrester, D.I., Thürig, E., and Rohner, B. 2018. Multiple factors modulate tree growth complementarity in Central European mixed forests. *J. Ecol.* **106**: 1106–1119.
- Mitchell, P.J., O’Grady, A.P., Tissue, D.T., White, D.A., Ottenschlaeger, M.L., and Pinkard, E.A. 2013. Drought response strategies define the relative contributions of hydraulic dysfunction and carbohydrate depletion during tree mortality. *New Phytol.* **197**: 862–872.
- NOAA a National Centers for Environmental Information, Climate Data Online: Station Details published May 2018. <https://www.ncdc.noaa.gov/cdo-web/datasets/GSOM/stations> (accessed 7 October 2018).
- NOAA b National Centers for Environmental information, Climate at a Glance: Divisional Time Series, published December 2018. <https://www.ncdc.noaa.gov/cag/> (accessed 30 January 2019).
- O’Neill, G.A.O., Hamann, A., and Wang, T. 2008. Accounting for population variation improves estimates of the impact of climate change on species’ growth and distribution. *J. Appl. Ecol.* **45**: 1040–1049.

- Palmer, W. 1965. Meteorological Drought. United States Department of Commerce, Washington D.C., Office of Climatology, U.S. Weather Bureau Research Paper No. 45.
- Pellerin, S., and Lavoie, C. 2003. Recent expansion of jack pine in peatlands of southeastern Québec: A paleoecological study. *Ecoscience* **10**: 247–257.
- Peltier, D.M.P., Fell, M., and Ogle, K. 2016. Legacy effects of drought in the southwestern United States: A multi-species synthesis. *Ecol. Monogr.* **86**: 312–326.
- Peltier, D.M.P., and Ibáñez, I. 2015. Patterns and variability in seedling carbon assimilation: Implications for tree recruitment under climate change. *Tree Physiol.* **35**: 71–85.
- Peters, R.L., Groenendijk, P., Vlam, M., and Zuidema, P.A. 2015. Detecting long-term growth trends using tree rings: a critical evaluation of methods. *Glob. Chang. Biol.* **21**(5): 2040-54.
- Phipps, R. L. 1985. Collecting, preparing, crossdating, and measuring tree increment cores. USDI Geological Survey. Water Res. Invest. Rep. **85**: 4148.
- Probst, J.R., and Hayes, J.P. 1987. Pairing Success of Kirtland's Warblers in Marginal vs. Suitable Habitat. *The Auk* **104**(2): 234-41.
- Rudolph, T.D., and Laidly, P.R. 1990. *Pinus banksiana* Lamb. (jack pine), in: Burns, R.M., Honkala, B.H. (Eds.), *Silvics of North America I. Conifers*. USDA For. Serv. Agric. Handb. 654, pp. 280-293.
- Spiegelhalter D.J., Best, N.G., Carlin, B.P., van der Linde, A. 2002. Bayesian measures of model complexity and fit (with discussion). *Journal of the Royal Statistical Society* **64**: 583-639.
- Stokes, M.A., and Smiley, T. L. 1968. *An Introduction to Tree-Ring Dating*. University of Chicago Press, Chicago.
- Subedi, N., and Sharma, M. 2013. Climate-diameter growth relationships of black spruce and jack pine trees in boreal Ontario, Canada. *Glob. Chang. Biol.* **19**: 505–516.

- Szeicz, J.M., and MacDonald, G.M. 1994. Age-dependent tree-ring growth responses of subarctic white spruce to climate. *Can. J. For. Res.* **24**: 120–132.
- 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 Phytol.* **181**: 218–229.
- University of New Hampshire. 2018. CanopyApp (1.0.3) [Mobile application software] <https://itunes.apple.com/us/app/canopyapp/id926943048?mt=8> (accessed 4 May 2018).
- U.S. Climate Data. 2018. Temperature – Precipitation – Sunshine – Snowfall. <https://www.usclimatedata.com/climate/grayling/michigan/united-states/usmi0349/2018/1> (accessed 24 January 2019).
- Wilmking, M., Juday, G.P., Barber, V.A., and Zald, H.S.J. 2004. Recent climate warming forces contrasting growth responses of white spruce at treeline in Alaska through temperature thresholds. *Glob. Chang. Biol.* **10**: 1724–1736.
- Woodward FI. 1987. *Climate and plant distributions*. Cambridge: Cambridge University Press.
- Yarranton, M., Yarranton, G.A. 1975. Demography of a jack pine stand. *Can. J. Bot.* **53**: 310–314.

Supplementary File

Supplementary File 1 Model selection

Supplementary File 2 Parameter estimations – Model prior distributions

Supplementary File 3 Analysis code

Supplementary File 4 Model Fit

Supplementary File 5 Parameter values

Supplementary File 6 Growth predictions

Table 1: List of forest sites sampled. Sampling sites were assessed and data collected in May and August 2018.

Site	DNR	Lat/ Long	Origin Year	BA m ² /ha	Elevation m a.s.l.	Average DBH cm mean±sd	Canopy Cover % mean±sd	Moisture % mean±sd May August	
BOG	20	44.6781° N 84.7689° W	1979	24.2	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	26.5	368-375	16.2 ± 2.2	52.0 ± 9.9	10.7 ± 2.1	6.7 ± 1.4
DRY 2	36	44.7503° N 84.5669° W	1976	25.5	375-378	20.1 ± 1.8	54.3 ± 9.4	NA*	3.05 ± 0.63

* We were unable to collect soil moisture measurements at DRY 2 in May due to restricted access on military training land.

Figure 1: Distributional range of *Pinus banksiana* in North America highlighted in green (Little 1971). Location of the study area with selected forest sites within Crawford County, Michigan (star). https://upload.wikimedia.org/wikipedia/commons/e/ec/Pinus_banksiana_USGS_range_map.png. Elbert L. Little, Jr., U.S. Department of Agriculture, Forest Service, and others / Public domain.

Figure 2: Summary of data used in the analysis. **a)** Stand mean ($\pm 2SD$) diameter (DBH) along the years data was gathered, based in reconstructions using tree ring widths. **b)** Stand mean ($\pm 2SD$) annual tree ring growth, temporal variability indicates both changes in growth rate as a function of age (decline trend) and as a function of annual climatic conditions (year to year variability).

Figure 3: 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. Credible intervals that do not cross zero are considered statistically significant (shown with an asterisk). Letters indicate statistically significant differences among coefficients between stands.

Figure 4: Simulations of radial tree growth (mean+SD). **a)** Predicted growth for current average July PDSI (0) along the gradient of April average temperature represented in the data (1.5 to 12 °C). **b)** Predicted growth along of a gradient of July moisture conditions (PDSI 4 to -5) under the highest April temperatures recoded in the data (12 °C).

Figure 1.

Figure 2.

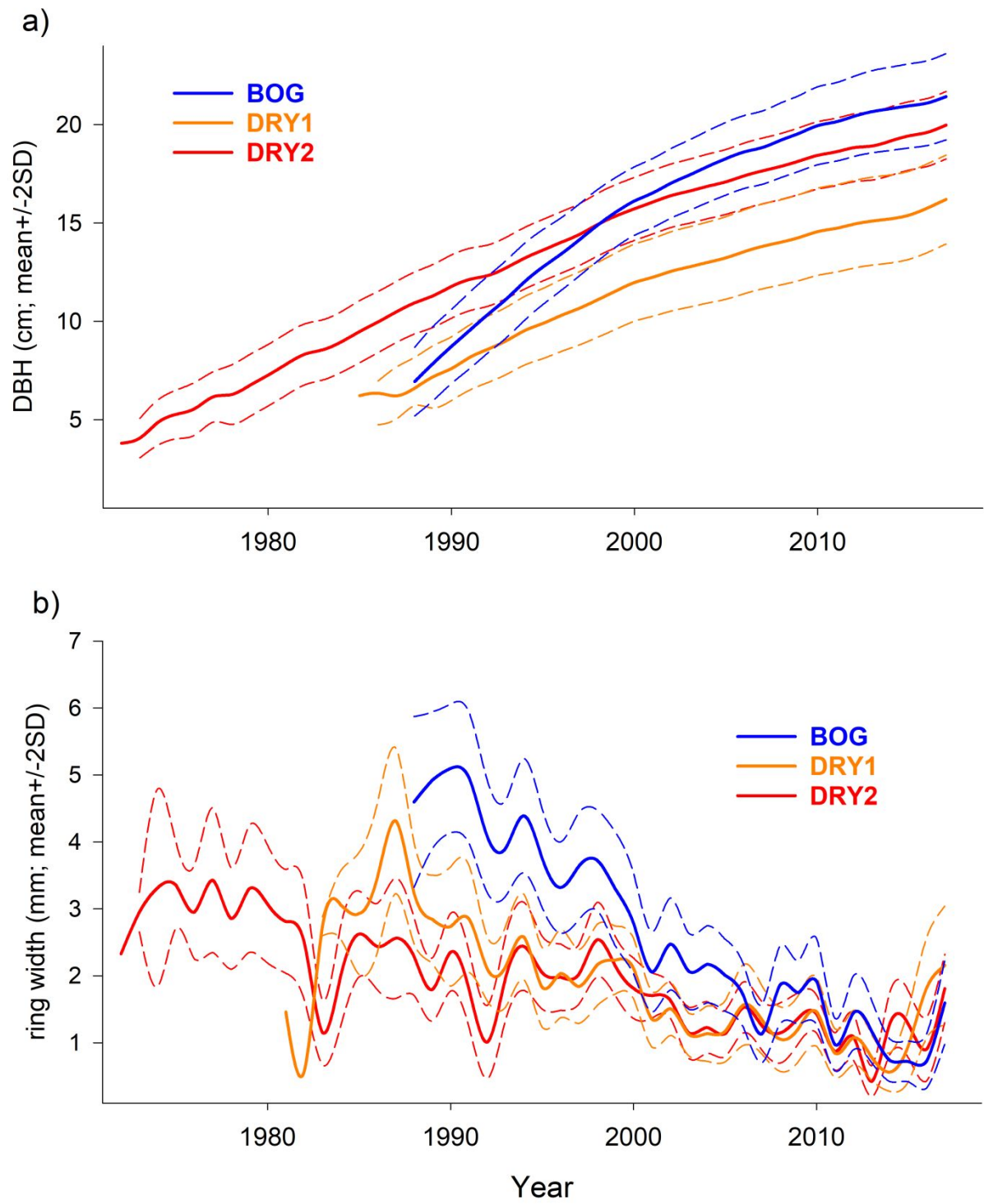


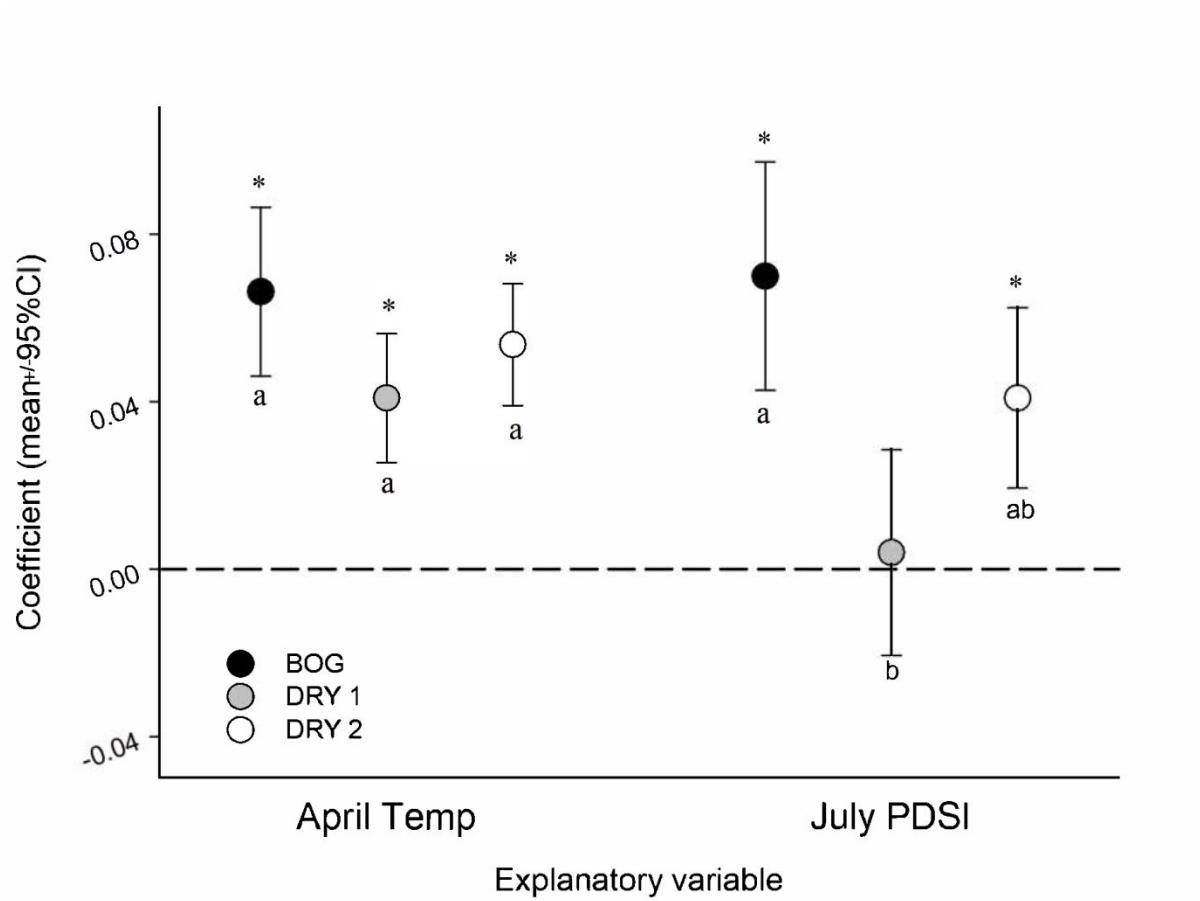
Figure 3.

Figure 4.

