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**Dendroclimatic analysis of red pine affected by Diplodia shoot blight
in different latitudinal regions in Michigan**

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Abstract

Drought and intraspecific competition in red pine stands in Michigan have been implicated as predisposing factors for increased shoot blight risk caused by *Diplodia pinea*. The overall objective of the study is to examine the interactive effects of drought, other climatic factors, and biotic factors (intraspecific competition) on productivity and growth of red pine forests (*Pinus resinosa*) affected by *Diplodia* (*Diplodia pinea*) shoot blight. This study incorporates a dendroclimatic approach that allows the retrospective examination of past annual diameter growth in relation to historical climate, and to assess the potential impacts of future climate change. A total of 20 red pine stands were sampled in two latitudinal regions (the Upper Peninsula (UP) and the Lower Peninsula (LP) region) of Michigan across two levels of initial stand density (low vs. high) and two levels of forest health condition (healthy vs. *D. pinea* affected). The full dendroclimatic relationships revealed in this study indicated that other climatic factors, in addition to summer drought stress, impacted red pine radial growth. Overall, red pine radial growth was generally more affected by precipitation and moisture index than solely temperature variables. The radial growth response to climate depended on latitudinal region since summer moisture stress was more influential in the LP; cold spring and early summer temperatures negatively impacted growth more in the UP; and the degree of winter harshness was more of a factor in the UP region. Crown damage caused by winter damage may have predisposed red pine stands to *D. pinea* affection by providing an easier entry point for fungal infection. Negative relations with precipitation in *D. pinea* affected stands may be due to increased dispersal of spores in *D. pinea* affected stands with significant rain and any increased storm and wind activity. Projections of radial growth under future scenarios of climate change indicated that climate warming has the potential to increase growth mainly in red pine stands in the UP region where growth has historically been limited by cool temperatures early in the

growing season. Under the moisture index model, growth of red pine under the drier (A2) climate change scenario, only the *D. pinea* impacted high density stands in the LP region are projected to show a significant decrease in growth by the middle (2041-2070) and final (2071-2100) projection periods. Model based projections of forest growth in Michigan generally do not account for forest health issues such as invasive pathogens. The current study therefore provides a new understanding of the role of forest pathogens under future climate change.

Keywords: climatic resiliency, dendrochronology, *Diplodia pinea*, forest pathology, *Pinus resinosa*, shoot blight, stand density

Draft

Introduction

Diplodia pinea (Desm.) is one of the most common and widespread fungal pathogens to infect pines and is widespread geographically in the United States, occurring in 30 eastern and central states as well as California and Hawaii, and impacts more than 20 pine species (Peterson 1997). Symptoms of infection include shoot blight, stem cankers, branch dieback, dead tops, death, and blue staining on dead wood (Munck et al. 2009). *D. pinea* sporulates on or in pine cones from asymptomatic trees, and is able to persist in the overstory as conidia in cones in mature trees (Munck et al. 2009). After spore germination, the fungus penetrates the stomata of needles and can penetrate directly through the surface of young or wounded stems (Munck and Stanosz 2008). Conidia are released during wet weather and throughout the growing season (Munck and Stanosz 2008). As a result, pine species host an abundant source of inoculum, threatening current stands as well as regeneration in understory and adjacent areas (Munck et al. 2009). The fungus can persist asymptotically on or in red pines for at least a year, which could explain the rapid onset of disease in apparently healthy pines that are exposed to stressful conditions, such as high temperatures and low moisture (Stanosz et al. 2001; Blodgett et al. 2003; Stanosz et al. 2007). In nursery studies, red pine seedlings contained *D. pinea* more often and had higher rates of mortality in drier regimes (Stanosz et al. 2001). Solar radiation also increases pine susceptibility to symptomatic infection as indicated by Normalized Insolation index measurements on Austrian pine (*Pinus nigra* Arn.) shoots in Italy (Maresi et al. 2007). Drought and intraspecific competition in pine stands have been implicated as predisposing factors for increased shoot blight risk caused by *D. pinea* (MDNR 2008, 2009; Gilmore & Palik 2005).

The instrumental climatic record has indicated that global average surface temperatures have increased by 0.74°C over the period of 1906-2005 (IPCC 2007). Projections of future

climate change based on models and different emission scenarios of greenhouse gases indicate that temperatures will warm further by 1.1°C–6.4°C by the end of the 21st century (2090-2099) relative to 1980-1999 (IPCC 2007). Regional climate forecasts for the state of Michigan and the Great Lakes Region indicate that average temperatures will rise 3-11°C in the summer and 3-7°C in the winter (Kling et al. 2003; Handler et al. 2014). While annual average precipitation is expected to show little change, higher temperatures are expected to lead to increased rates of evapotranspiration and temperature-induced drought stress in plants. Climate is generally considered an important factor that can predispose trees to secondary factors (e.g., insects and fungal diseases) eventually leading to forest decline (Manion 1991; Desprez-Loustau et al. 2006).

Red pine is a shade-intolerant native conifer that covers approximately 769,000 ha of forest land in Michigan (Gilmore and Palik, 2005). Red pine is economically important in the Great Lakes region and has a variety of uses such as pulpwood, saw timber, and utility poles. In Michigan, the southern distributional range of red pine occurs in the northern Lower Peninsula region while the central range of red pine occurs in the Upper Peninsula region according to the range map in Rudolf (1990). Changes in future climate are predicted to shift the range of red pine (*Pinus resinosa* Ait.) by as much as 600 to 800 km northeast and result in a decrease in the total distribution range of red pine (Flannigan and Woodward 1994). Prior studies of red pine have noted the sensitivity of red pine radial growth to climate factors in the Great Lakes region (Graumlich 1993; Kipfmüller et al. 2010) and in Michigan (Kilgore and Telewski 2004; Magruder et al. 2012; Magruder et al. 2013). Forest management techniques may promote resiliency to climatic stress by controlling the intensity of tree competition for environmental resources (e.g., light and water) and thus help maintain tree and stand-level productivity (Laurent et al. 2003; Magruder 2012; Magruder et al. 2012; Magruder et al. 2013). Low initial stand

density (Magruder et al. 2012) and thinning from below to a moderate density of 21 m² ha⁻¹ (Magruder et al. 2013) were shown to increase resiliency of red pine to climatic stress.

The overall objective of the study is to examine the interactive effects of drought, other climatic factors, and biotic factors (intraspecific competition) on productivity and growth of red pine forests (*Pinus resinosa*) affected by Diplodia (*Diplodia pinea*) shoot blight. This study incorporates a dendrochronological approach that allows the retrospective examination of past annual diameter growth rates and allows relating these parameters to meteorological records of the study region, and to assess the potential impacts of future climate change. Detailed annual tree-ring measurements also have the potential to provide a method for early detection of forest health threats before external symptoms are readily perceptible (Siegert et al. 2010). Overall, this research will potentially help limit economic losses in the pine resources in the Great Lakes region due to climate change and *Diplodia*-induced tree mortality and losses in forest productivity. The specific questions that will be addressed in this project include:

- 1) Is drought stress the sole abiotic factor that predisposes red pine stands to Diplodia shoot blight or can other climatic factors (such as summer heat stress) in different latitudinal regions influence susceptibility of red pine to *Diplodia*?
- 2) To what degrees does intraspecific competition (as reflected in tree stand density) for resources influence the radial growth response of red pine to climate and susceptibility to *Diplodia*?
- 3) How will future regional climate change influence the productivity of red pine forests across different categories of forest health condition (*Diplodia*-infected vs. healthy reference), stand density, and latitudinal region?

Methods

Study site and field sampling

Plantation stands (pole sized) were selected along a latitudinal climate gradient from the northern Lower Peninsula (LP) to the Upper Peninsula (UP) region of Michigan (Fig. 1). In each region, stands were selected across two categories of forest health condition: healthy reference vs. affected by *D. pinea*. Selected healthy reference stands had $\leq 5\%$ (mean = 4.6 %, standard deviation = 1.3 %) signs of visual crown dieback while *Diplodia*-affected stands had at least 15% crown dieback (mean = 22.5 %, standard deviation = 4.9 %) (Table 1). Infection with *Diplodia* was confirmed based on visual symptoms of crown dieback and by culturing pine needles in standard mycological agar media (Munck et al. 2009). Furthermore, smears of black fruiting bodies (pycnidia) found on pine needles were placed on microscope slides and examined under a compound microscope to identify the presence of *D. pinea* spores. Half of the total number of sites that were selected in this study were originally planted at low density (<988 trees per ha) while the other half of the study sites were planted at higher density (>1977 trees per ha) to examine the effect of stand density and intraspecific tree competition. In the Huron National forest, intermediate stand tending of red pine is uniformly managed by initially cutting with row thinning (cut two rows, leave two rows). After the row thinning treatment, subsequent stand entries involve free thinning conducted approximately every 15 years to a residual basal area of 21 m² per ha (K. Lazda, US Forest Service, personal communication) to remove individuals with poor form and/or disease (Gilmore and Palik 2005).

In the UP region of Michigan (Fig. 1a), site selection and field sampling was accomplished in the Hiawatha National Forest in a total of 8 sites and included (Table 1): 4 healthy reference stands and 4 *Diplodia*-affected red pine stands. In the LP region of Michigan (Fig. 1b), site selection and field sampling was accomplished in the Huron National Forest in a total of 12 sites and included (Table 1): 6 healthy reference stands and 6 *Diplodia*-affected red

pine stands. Furthermore, for either region, half of the number of either healthy reference or *Diplodia*-affected stands was selected with low stand density and the other red pine stands had high stand density.

At each site, a forest stand inventory was conducted by first establishing a circular plot with the plot center in each stand being a randomly selected focal tree. High initial density stands were sampled with a circular plot radius of 7.99 m (0.02 ha), while low initial density stands had a radius of 9.78 m (0.03 ha). Each plot was a minimum of 30 m from the stand's boundary. Trees that were closest to the halfway point of the radius of the plot along the compass bearings of NE, SE, SW and NW were selected for sampling. For each of the selected trees, total height, height to live crown, and diameter at breast height (DBH) were measured. Two cores were sampled from each tree with an increment borer at breast height (1.37 m) from the north and south side of each tree. In addition, DBH was measured on the remaining trees in the plot. Each of the selected stands was managed by the US Forest Service and stand age was obtained from US Forest Service inventory records.

Climate data (mean monthly temperature and total monthly precipitation) were obtained from the spatial climate data set developed by Oregon State University's PRISM Climate Group (<http://prismmap.nacse.org/nn/>) (Daly et al. 2008). Climate data were obtained for each of the sites by inputting each site's geographical coordinates (i.e., latitude and longitude). The climate data at each site were based on a spatially weighted estimate derived from neighboring meteorological climate data. A Climate Moisture Index (CMI) was also calculated and is defined as precipitation minus potential evapotranspiration (PET) where PET is a function of temperature and provides an effective measure of net water balance (Hogg 1997). Thus, CMI is a synthetic variable that combines the effect of both precipitation and temperature in characterizing moisture regimes of the site. Climate conditions for the climate normal period of 1971-2000 varied in

terms of mean annual temperature being generally higher in the LP sites (mean range of 6.4-6.8°C) compared to the UP sites (mean range of 5.1-5.2°C) (Table 2). Total annual precipitation did not vary significantly between LP and UP sites (Table 2). CMI was generally similar amongst sites in the LP and amongst sites in the UP. Both the UP sites in the Hiawatha National Forest and LP sites in the Huron National Forest are located in the Northern Lakes and Forests ecological region according to the ecological classification system devised by the U.S. Environmental Protection Agency (EPA) (2013).

Sample Processing, Cross-Dating and Tree-Ring Measurement

Field samples from the 20 sampled sites were processed using standard dendrochronological techniques (Stokes and Smiley 1996). All increment cores were mounted onto grooved boards and then sanded with successive grades of sandpaper up to 600 grit to provide visual clarity of the annual rings. All samples were visually crossdated under a binocular microscope to account for any missing and/or false double rings by using the list method to accurately assign a calendar date to each tree ring by identifying patterns of narrow marker rings (Yamaguchi 1991). All samples were digitally scanned at an optical resolution of 1200 d.p.i.. Ring widths were subsequently measured using the software programs Coorecorder and CDendro (Cybis Elektronik & Data AB, Saltsjöbaden, Sweden). A stage micrometer (Velmex: Bloomfield, New York, NY, USA) was also used as a supplemental tool to measure portions of cores with very narrow rings that were difficult to discern in the scanned image. Additional statistical quality control and verification of the visual crossdating of annual rings was provided through the use of the program COFECHA (Holmes 1983). COFECHA identifies tree core samples that should be checked for potential cross-dating errors based on a poor

correlation between an individual ring widths series and an average chronology of the other tree ring series at the site.

Growth-climate analyses

Annual DBH (cm yr^{-1}) and height growth (m yr^{-1}) was determined by dividing total DBH and total height by their respective stand ages. The slenderness coefficient is a dimensionless value that is calculated as tree height divided by the DBH in the same units (m). Greater values of the slenderness coefficient indicate a taller and narrower tree, and trees with values over a threshold of 80 are particularly prone to wind-induced stem breakage (Rudnicki et al. 2004). Crown ratio represents the ratio of the crown length to the total height of a tree. All collected measures of tree-level productivity (DBH, total height, crown ratio, slenderness coefficient) for the four trees in a sampling plot were treated as sub-samples and averaged before being subjected to a one-way analysis of variance in conjunction with multiple comparisons using Fisher's Least Significant Difference (LSD) test to compare between the 8 treatment groups representing the possible combinations of latitudinal region (UP and LP), forest health condition (healthy reference and affected by *D. pinea*) and initial stand density (low and high) using the program SYSTAT (version 10.2) (2002). Furthermore, stand-level productivity (on a per hectare basis) was also compared between the treatment groups using a one-way analysis of variance followed by multiple comparisons using Fisher's LSD test. A p-value that was less than 0.05 was considered statistically significant.

Ring widths were detrended to generate a radial growth index through the statistical program ARSTAN using a 40-year cubic smoothing spline (Cook 1985; Holmes 1994). Ring widths were detrended to standardize the raw ring width measurements though the removal of size and age related effects on radial growth. A 40-year cubic spline preserves 99% of the

variation in each ring-width series at a wavelength of about 13 years. The common trends (1-13 years) in radial growth that are shared between trees due to stand-wide effects like climate and stand management practices are still preserved (Biondi, 1999). The radial growth index of each tree and year was averaged to create a standard chronology for each site. Radial growth data were further summarized by averaging the standard chronology for all sites sharing the same forest health condition class and initial stand density class for each region.

Based on the monthly climate data from Oregon State University's PRISM Climate Group (Daly et al. 2008), seasonal 3-month climate variables were also determined for mean temperature, total precipitation, and Climate Moisture Index (CMI) to examine the extent of seasonal climatic effects on radial growth. Temperature variables were averaged during 3-month periods, and precipitation and CMI variables were summed during 3-month periods. Monthly and season climate data was further summarized by averaging the climate data for all sites sharing the same forest health condition class and initial stand density class for each region. The climate data for each treatment combination were combined by first converting the raw climate data at each site into anomalies in °C (mean temperature), mm (total precipitation), and cm (CMI) from their respective mean for the reference period of 1971-2000 (Jones and Hulme 1996). The climate variables of all 20 sites expressed as anomaly values were then averaged together for all sites in each treatment group.

Relationships between annual ring-width and past climate records (both monthly and seasonal variables) were assessed using a step-wise multiple linear regression technique (full details of this dendroclimatic modeling approach can be found in Chhin 2008, Chhin et al. 2008, and are also applied in Chhin et al. 2010) across all possible combinations of the two levels of forest health condition, the two levels of initial stand density, in each study region. The function *stepAIC* (package *MASS*) in the program R was used to conduct the multiple regression analysis

(Venables and Ripley 2002) and involves minimizing the value of Akaike's information criterion (AIC) (Burnham and Anderson 2002). A dendroclimatic regression model was selected for each climate variable set (TAV, PPT, and CMI) and across both monthly and seasonal climate scale. The regression analyses were conducted over two growing seasons from April of the prior year (t-1) to October of the current year (t)) and over a 41 year period (1971-2011). Standardized (β) partial regression coefficients were also calculated to help determine the relative importance of the predictor variables in the dendroclimatic regression models (Zar 1999).

Future Climate Change Scenarios

The predicted change in climate (primary climate variables include mean temperature and precipitation) under two different scenarios and for three periods in the 21st century (2011-2040, 2041-2070, and 2071-2100) relative to the climatic normal (CN) period of 1971-2000 were obtained for each of the 20 red pine sites using a web-based portal (http://gmaps.nrcan.gc.ca/cl_p/climatepoints.php) co-developed by the Canadian Forest Service and the US Forest Service (Joyce et al. 2011). Estimates for each site are based on a spatial interpolation procedure that utilizes the sites geographic location (latitude and longitude) at a spatial resolution of 5 arcminutes (0.0833°) longitude and latitude. Climate change forecasts were obtained from the output of the general circulation model developed by the National Center for Atmospheric Research (NCAR) called Community Climate System Model version 3.0 (CCSM3) (Vertenstein et. al 2004). The two climate change scenarios considered here were based on NCAR-CCSM3 forced with two different IPCC (2007) emission scenarios: A2 and B1. The emission scenarios assume different socioeconomic parameters. The B1 emission scenario is characterized by a slower human population growth rate and more emphasis on environmental protection and sustainability. In contrast, the A2 emission scenario is characterized by a more

divided world with regionally independent economies and a continually increasing population. Consequently, less greenhouse gas emissions are produced resulting in less warming under the B1 scenario compared to A2. The climate change variables of the 20 sites were averaged together by treatment group.

The regression model for each treatment group was applied to the regional climate change variables to project radial growth for the three periods in the 21st century under the two climate change scenarios (full details of this approach can be found in Chhin 2008 and Chhin et al. 2008). The projected radial growth was based on the regression models for temperature, precipitation and CMI applied separately to the future climate scenarios. The significance of the projected growth estimates were examined in comparison to a 95% confidence interval of the mean expected radial growth index for the period of 1971-2000. Projected radial growth for the climate scenario periods were also expressed as percentage change relative to the mean radial growth for the climate normal period of 1971-2000.

Results

Growth and Chronology Characteristics

In the Upper Peninsula region, total DBH and annual DBH increment did not differ significantly amongst treatment groups (all $p > 0.05$) (Table 2). In the Lower Peninsula region, *D. pinea* affected high density stands (LP-D-H) had significantly smaller total diameters than the other treatment groups (all $p < 0.05$), but this pattern was not significant in terms of annual diameter. Total height, annual height growth, crown ratio, and slenderness did not differ significantly amongst the treatment groups in either the UP or LP regions. In the Upper Peninsula region, stand-level basal area was significantly smaller in healthy low density stands

(UP-R-L) compared to higher basal area in *D. pinea*-affected high density stands (UP-D-H) ($p < 0.05$)

In the Upper Peninsula region, there were few significant correlations between the treatment group combinations (Table 3 and Figure 2a). Growth chronologies of red pine were significantly positively correlated ($p < 0.05$) between all treatment group combinations in the Lower Peninsula region and therefore showed stronger growth synchrony compared to the Upper Peninsula region (Table 3 and Figure 2b). The lowest correlation in the LP region was between the healthy low density treatment group (LP-R-L) and the *D. pinea*-affected high density (LP-D-H) treatment group. In either region (UP or LP), the highest correlation between treatment groups was between the low density treatment groups: UP (UP-R-L and UP-D-L) or LP (LP-R-L and LP-D-L).

Growth-Climate Relationships

Dendroclimatic relationships indicated that other climatic factors, in addition to summer drought stress, impacted red pine radial growth. Red pine responded to temperature mainly in the Upper Peninsula compared to weaker or lack of association in the Lower Peninsula region (Figure 3a). Healthy stands (UP-R-L, UP-R-H) and *D. pinea*-affected stands at low density (UP-D-L) were positively correlated with spring temperature. In *D. pinea*-affected stands (UP-D-L, UP-D-H), red pine was negatively associated with temperature in summer (June) or fall (October) of the prior year ($t-1$).

Except for healthy low density stands in the Lower Peninsula (LP-R-L), all the other treatment categories showed a stronger growth response to precipitation compared to mean temperature as reflected in the values of the adjusted coefficient of determination (R^2) (Figure 3b). Red pine radial growth was positively associated with summer precipitation in all treatment

groups except UP-D-H and LP-R-L. In three of the treatment groups in the LP (LP-R-H, LP-D-L, and LP-D-H), summer precipitation in June of the current year (t) was the principal variable in the multiple regression models according to the higher values of the standardized (β) partial regression coefficients (Table 4). Growth was also affected more by winter precipitation (i.e., snow) in many of the UP stands (UP-R-H, UP-D-L, UP-D-H) compared to the LP region (only LP-D-H). Low density stands in the UP (UP-R-L, UP-D-L) were negatively associated with fall (t and/or t-1) moisture index, while in low density stands in the LP, precipitation was negatively correlated with late summer (LP-R-L) or early summer (LP-D-L) growth.

Growth responses to moisture index (CMI) were generally similar to the growth response to precipitation, except the explanatory power of the CMI models (i.e., adjusted R^2 values) were slightly lower for most of the treatment groups, except for treatment LP-C-H for which the CMI regression model had slightly higher explanatory power than the precipitation model (Fig. 3c). For Upper Peninsula sites that were *D. pinea*-affected and low density (UP-D-L), the influence of summer CMI became the primary independent variable influencing growth, whereas it was only the third most important precipitation variable impacting growth. The negative association between growth and precipitation either no longer existed (as was the case for LP-R-L), or the weaker independent variables (i.e., smaller β partial regression coefficients) dropped out of existence when comparing to the corresponding regression model between radial growth and CMI (as was the case for UP-D-L, LP-D-L, LP-D-H).

Future Climate Change Scenarios and Growth Projections

Under the A2 climate change scenario, annual temperatures increased similarly between sites in the UP and LP and rose by 5.0°C and 4.9°C, respectively for each region, by the 2071-2100 time period (Table 5). The rate of warming was greater over the winter compared to the

summer. Output from the A2 climate scenario also indicated an increase in precipitation and that by 2071-2000 the increase would be similar in the summer and winter in the UP region but appreciably more in the summer compared to the winter in the LP region. Moisture index values (CMI) showed a general trend of drying from the initial projection period of 2011-2040 to the final projection period of 2071-2100 with the LP region ending up drier compared to the UP region. Compared to the A2 scenario, future climatic patterns under the B1 climate change scenario showed a milder increase in temperature; a lower increase in precipitation; and comparatively higher CMI values (Table 5).

Under the A2 climate change scenario, and based on the regression models with temperature, growth of healthy stands of red pine in the UP region (UP-R-L and UP-R-H) showed a significant increase in growth by the middle (2041-2070) and final projection (2071-2100) periods compared to reference period of 1971-2000 (Fig. 4a). High density *D. pinea*-affected stands in the UP region (UP-D-H) as well as healthy low density stands in the LP region (LP-R-L) showed a decrease in growth by the middle and final projection periods. Based on the regression models with precipitation, growth of red pine showed a decrease in growth by the final projection period in UP-R-L, and a decrease in growth by the middle and final projection period in UP-D-H (Fig. 4b). Growth was low for LP-R-L stands for all projection periods and high for LP-R-H for all projection periods. The projected decline in growth for LP-D-H was registered in the first projection period but not the subsequent two projection periods. In terms of the regression models with moisture index, growth only showed a decline in the middle and final projection periods for high density *D. pinea*-affected stands in both regions (UP-D-H and LP-D-H) (Fig. 4c).

Compared to the A2 scenario, growth projections under the B1 scenario and temperature-based regression models were not as strong (Fig. 4d). Growth projections under the

precipitation-based model were generally similar except that there is no longer a significant decrease in growth for the UP-D-H and LP-D-H treatment groups and there is a significant increase in growth for the final period for the UP-D-L treatment group (Fig. 4e). Prior declines present under the A2 scenario disappear under the B1 scenario for UP-D-H and LP-D-H (Fig. 4f). Further, significant increases in growth now register for the final period of the UP-R-L stands and the final two projection periods for the LP-R-H stands.

Discussion

Growth-Climate Relationships

Summer drought stress in red pine stands has been implicated as a predisposing factor for increased shoot blight risk caused by *D. pinea* (MDNR 2008, 2009; Blodgett et al. 2001; Gilmore & Palik 2005), which is further confirmed by our study. A summer moisture stress signal was detected in most of the *D. pinea*-affected treatment groups (i.e., UP-D-L, LP-D-L, and LP-D-H). Red pine radial growth was positively associated with summer precipitation, which indicates that growth is affected by summer moisture stress. Although this summer moisture stress effect was prevalent in many of the treatment groups in both regions, it was only a secondary or tertiary variable in the UP region treatment groups, while it was the primary variable having the most influence on growth in the LP treatment groups. While precipitation and moisture index (CMI) values were not statistically different between LP and UP treatment groups, the LP region did have drier conditions, which could increase the vulnerability of red pine stands in the LP region to this climatic stress factor. Sensitivity to summer moisture stress has also been reported in other populations of red pine in the Great Lakes forest region (St. George et al. 2008; Kipfmüller et al. 2010). In contrast, Kilgore and Telewski (2004) found no significant correlation between growth and precipitation.

The full dendroclimatic relationships revealed in this study indicated that other climatic factors, in addition to summer moisture stress, impacted red pine radial growth. Growth was also affected more by winter precipitation (i.e., snow) in many of the UP stands (UP-R-H, UP-D-L, UP-D-H) compared to the LP (only LP-D-H) which was expected given the higher snowfall levels in the UP. Higher snowfall levels have been linked to increased strain on tree crowns leading to crown damage (Havranek and Tranquillini 1995; Vaganov et al. 2006). From an ecophysiological perspective, damaged crowns elicit increased allocation of reserves to repair the photosynthetic apparatus while the lower stem region has lower priority for resource allocation (Everham and Brokaw 1996; Scott and Huff 1996; Peterson 2000). It was inferred from the dendroclimatic relationships that *D. pinea* stands were potentially impacted by the degree of winter harshness and that crown damage may have predisposed these stands to *D. pinea* infection by providing an easier entry point for fungal infection.

Radial growth responses of red pine to climate did differ between different stand density levels. In particular, radial growth in low density stands in the UP (UP-R-L, UP-D-L) was negatively associated with fall (t-1) precipitation and moisture index compared to their high density counterparts. The explanation for this difference is that October is a time of major storm activity in Michigan and the accompanying high winds can have a bigger impact in the low density stands since the trees are less sheltered. Furthermore, a potential ecophysiological explanation for the negative relationship with precipitation in *D. pinea* affected stands (i.e., UP-D-L, LP-D-H) may be due to increased dispersal of spores in *D. pinea* affected stands with significant rain and any increased storm and wind activity. This falls within the spore dispersal period for *D. pinea* which is between March and October during which moist conditions are needed for Diplodia infection (Munck and Stanosz 2008). Although spore dispersal rates were not explicitly measured in this study, this could be examined directly in follow-up studies.

Red pine responded positively to increasing temperature mainly in the Upper Peninsula compared to weaker or no associations in treatment groups in the Lower Peninsula region. This result was expected given the generally colder climatic conditions in the UP region compared to the LP region. Growth in healthy reference stands (UP-R-L, UP-R-H) and *D. pinea* affected stands at low density (UP-D-L) was positively correlated with spring and early summer temperature, which suggests that a potential ecophysiological explanation could be that cold temperatures delay the timing of the start of the growing season (Fritts 1976; Vaganov et al. 2006). The fact that this dendroclimatic response persisted until early summer strongly suggests that late spring frosts can have a negative impact on red pine growth. A positive response to warm spring temperatures has also been reported in other red pine populations in the Great Lakes region (Graumlich 1993; Kilgore and Telewski 2004). Phenological radial growth data were not collected in the current study but future studies might examine the environmental controls on radial growth initiation in the early growing season.

In *D. pinea*-affected stands (UP-D-L, UP-D-H), growth in red pine was negatively associated with temperature in summer or fall of the prior year ($t-1$), which suggests that heat stress impacted growth. High temperature can lead to higher respiration rates, which in turn could deplete carbohydrate storage reserves for subsequent growing seasons (Pallardy 2007). The negative impact of high summer temperatures has also been reported in other populations of red pine near the Great Lakes forest region (St. George et al. 2008; Kipfmüller et al. 2010).

Growth Projections under Future Climate Change Scenarios

Growth was projected under the B1 and A2 emissions scenarios. The B1 scenario is underpinned with environmental sustainability and therefore less greenhouse gas emissions are generated. The B1 scenario also generates a lower rate of climatic warming compared to A2

which is characterized by a continually increasing human population (IPCC 2007). Healthy reference stands in the Upper Peninsula region (UP-R-L and UP-R-H) are forecasted to greatly benefit from climate warming under the A2 emission scenario particularly by the middle (2041-2070) and final reporting periods (2071-2100). This is mainly because these treatment groups in the UP region have historically been limited by cold temperatures early in the growing season. Although climate warming under the A2 and B1 emission scenario is expected to have a negative impact on high density stands affected by *D. pinea* in the UP region (UP-D-H) and low density healthy stands in the LP region (LP-R-L), the explanatory power of the regression model that these projections are based on are very low (adjusted R^2 less than ≤ 0.11) which adds uncertainty to these projected declines.

Under both emission scenarios (A2 and B1) and the precipitation regression models, growth was projected to significantly increase by the final reporting period in UP-R-L and LP-R-H. UP-R-L and LP-R-H, however, no longer show a significant increase under the A2 scenarios based on the moisture index model, and the degree of increase is not as strong under the B1 scenario and moisture index model. Projections of growth under the moisture index model is more realistic from a net water balance perspective since it is widely expected that climatic warming will lead to increased rates of evapotranspiration, which can negate any future increases in precipitation (Kling et al. 2003). Under the A2 scenario and moisture index model, only the *D. pinea*-impacted high density stands are projected to show a significant decrease in growth by the middle and final projection period.

Model based projections of forest types in Michigan generally do not account for forest health issues such as invasive pathogens (Handler et al. 2014). The current study therefore provides new understanding of the role of forest pathogens under predicted future climate change.

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Table 1. List and characteristics of 20 red pine study sites sampled in the Lower Peninsula (LP) and Upper Peninsula (UP) regions of Michigan across different forest health condition and initial stand density. There are two levels of forest health condition (healthy reference vs. affected by *D. pinea*) and two levels of initial stand density (low stand density stands were initially planted at <988 trees per ha; and high density stands were initially planted at >1977 trees per ha).

Site	Region	Forest Health	Crown		Lat. (°N)	Long. (° W)	Elev. (m)	Group ID
			Dieback (%)	Stand Density				
RPC51	UP	Reference	5	Low	46.1877	84.7852	221	UP-R-L
RPC64	UP	Reference	5	Low	45.8471	86.9458	206	UP-R-L
RPC59	UP	Reference	5	High	46.3153	84.9909	335	UP-R-H
RPC65	UP	Reference	5	High	45.8392	86.9545	179	UP-R-H
RPD62	UP	Diplodia	15	Low	46.3185	85.0323	298	UPDL
RPD67	UP	Diplodia	20	Low	45.8018	86.9610	200	UPDL
RPD60	UP	Diplodia	20	High	46.3113	84.9994	296	UPDH
RPD66	UP	Diplodia	15	High	45.8270	86.9475	188	UPDH
RPC03	LP	Reference	5	Low	44.5715	83.9673	355	LP-R-L
RPC04	LP	Reference	5	Low	44.6589	84.0781	295	LP-R-L
RPC06	LP	Reference	1	Low	44.4974	83.5937	267	LP-R-L
RPC05	LP	Reference	5	High	44.6588	84.0495	278	LP-R-H
RPC07	LP	Reference	5	High	44.5156	83.6176	267	LP-R-H
RPC09	LP	Reference	5	High	44.4832	83.6389	256	LP-R-H
RPD11	LP	Diplodia	25	Low	44.4976	83.6904	272	LPDL
RPD17	LP	Diplodia	25	Low	44.4289	83.6979	255	LPDL
RPD19	LP	Diplodia	25	Low	44.4118	83.6270	259	LPDL
RPD01	LP	Diplodia	25	High	44.6552	84.2502	328	LPDH
RPD09	LP	Diplodia	25	High	44.5950	84.0881	387	LPDH
RPD16	LP	Diplodia	30	High	44.5584	83.5829	254	LPDH

Table 2. Average (standard deviation) tree level and stand level productivity of red pine in Michigan from different latitudinal regions, forest health condition, and initial stand density class. Climatic characteristics of each site grouping is also provided over the climate normal period of 1971-2000: TAV = mean annual temperature, PPT = total annual precipitation, CMI = climate moisture index. Group abbreviations: UP = Upper Peninsula, LP = Lower Peninsula, R = healthy reference, D = *Diplodia*-affected, L = low initial stand density, H = high initial stand density. Slend. = slenderness coefficient. Different letters denote significant differences between groups ($p < 0.05$) whereas no letters indicate that groups are not statistically significant ($p \geq 0.05$).

Group	DBH (cm)	Total Height (m)	Annual DBH (cm)	Annual Height (m)	Crown Ratio	Slend.	Basal Area (m ² ha ⁻¹)	Stand Age (yrs)	TAV (°C)	PPT (mm)	CMI (cm)
UP-R-L	28.7 (2.9) abc	20.0 (3.8) ab	0.39 (0.04) ab	0.27 (0.05)	0.501 (0.204)	68.6 (6.2) ab	26.6 (6.0) a	74 (0) ab	5.2 (0.6) a	783.9 (50.7)	75.5 (5.2) ab
UP-R-H	21.6 (4.6) bc	15.5 (5.3) ab	0.38 (0.07) ab	0.26 (0.01)	0.491 (0.004)	66.5 (9.8) a	42.1 (13.7) ab	59 (23) ab	5.2 (0.5) a	790.6 (60.2)	76.2 (6.1) b
UP-D-L	35.5 (4.5) bc	23.0 (3.3) bc	0.47 (0.04) b	0.30 (0.03)	0.365 (0.031)	63.2 (2.3) a	45.3 (13.5) ab	76 (4) ab	5.1 (0.6) a	786 (67.7)	75.8 (6.7) ab
UP-D-H	23.8 (8.4) bc	15.5 (9.5) ab	0.47 (0.10) b	0.28 (0.02)	0.508 (0.039)	63.7 (23.4) a	54 (29.8) bc	54 (30) a	5.2 (0.6) a	788.7 (57.5)	76 (5.8) b
LP-R-L	25.4 (1.5) bc	19.5 (2.9) ab	0.37 (0.05) ab	0.29 (0.07)	0.430 (0.204)	74.4 (10.6) ab	36.3 (7.2) ab	69 (8) ab	6.5 (0.2) b	718.2 (35.2)	67.9 (3.6) a
LP-R-H	20.0 (1.5) bc	15.8 (1.0) ab	0.34 (0.07) a	0.27 (0.03)	0.313 (0.107)	78.9 (4.5) ab	41.7 (4.4) ab	59 (9) ab	6.6 (0.1) b	717.9 (27)	67.9 (2.7) a
LP-D-L	24.6 (2.3) b	18.9 (0.7) ab	0.31 (0.03) a	0.24 (0.01)	0.440 (0.029)	70.6 (3.8) ab	36.2 (5.2) ab	79 (4) bc	6.8 (0.1) b	733.5 (3.5)	69.4 (0.3) ab
LP-D-H	17.6 (1.7) a	13.5 (0.8) a	0.36 (0.06) ab	0.27 (0.06)	0.472 (0.047)	85.2 (0.9) bc	44.2 (4.2) b	50 (10) a	6.4 (0.2) b	717.5 (17.8)	67.9 (1.8) ab

Table 3. Correlations statistics between radial growth chronologies of red pine in the Upper Peninsula and Lower Peninsula regions of Michigan. Group abbreviations: UP = Upper Peninsula, LP = Lower Peninsula, R = healthy reference, D = *Diplodia*-affected, L = low initial stand density, H = high initial stand density. * denotes correlation coefficients which are statistically significant ($p < 0.05$).

Group	UP-R-L	UP-R-H	UP-D-L	UP-D-H	LP-R-L	LP-R-H	LP-D-L	LP-D-H
UP-R-L	1							
UP-R-H	0.089	1						
UP-D-L	0.565*	0.358*	1					
UP-D-H	0.038	0.141	0.287	1				
LP-R-L	0.111	0.120	0.118	0.020	1			
LP-R-H	0.063	0.245	0.182	0.122	0.758*	1		
LP-D-L	0.232	0.243	0.075	0.068	0.785*	0.756*	1	
LP-D-H	0.008	0.602*	0.278	0.035	0.398*	0.547*	0.641*	1

Table 4. Coefficients of regression models relating radial growth of red pine sampled from different latitudinal regions, forest health condition, and initial stand density to different climatic variables. Group abbreviations: UP = Upper Peninsula, LP = Lower Peninsula, R = healthy reference, D = *Diplodia*-affected, L = low initial stand density, H = high initial stand density.

Group	C	V1	V2	V3	V4
a) Temperature					
UP-R-L	1.012	0.348 (0.0317)			
UP-R-H	0.964	0.340 (0.0362)	0.301 (0.0283)		
UP-D-L	1.012	0.350 (0.0480)	0.314 (0.0458)		
UP-D-H	0.974	0.320 (0.0268)			
LP-R-L	0.963	0.363 (0.0697)			
LP-R-H	n.s.				
LP-D-L	n.s.				
LP-D-H	n.s.				
b) Precipitation					
UP-R-L	1.037	0.513 (0.0031)	0.379 (0.0016)	0.299 (0.0021)	
UP-R-H	0.964	0.443 (0.0020)	0.401 (0.0024)	0.316 (0.0016)	
UP-D-L	1.038	0.413 (0.0046)	0.409 (0.0026)	0.370 (0.0016)	0.296 (0.0019)
UP-D-H	0.973	0.395 (0.0017)			
LP-R-L	0.950	0.332 (0.0020)			
LP-R-H	0.963	0.471 (0.0042)	0.400 (0.0024)		
LP-D-L	1.002	0.397 (0.0025)	0.290 (0.0017)		
LP-D-H	0.983	0.646 (0.0054)	0.423 (0.0052)	0.298 (0.0023)	
a) Climate Moisture Index					
UP-R-L	1.034	0.517 (0.0290)	0.347 (0.0112)	0.264 (0.0142)	
UP-R-H	0.966	0.465 (0.0208)	0.375 (0.0184)	0.306 (0.0137)	
UP-D-L	1.019	0.403 (0.0222)	0.380 (0.0221)	0.322 (0.0358)	
UP-D-H	0.973	0.384 (0.0165)			
LP-R-L	n.s.				
LP-R-H	0.968	0.474 (0.0348)	0.423 (0.0193)		
LP-D-L	0.993	0.433 (0.0227)			
LP-D-H	0.980	0.581 (0.0382)	0.289 (0.0357)		

Note: The first term in the regression model is the constant (C). The regression terms (V1-V4) are listed in descending order according to the ranking of the absolute values of the standardized (β) regression coefficients (Zar, 1999), and values in parentheses represent the corresponding partial regression coefficients (cf. Figure 3).

Table 5. Change in climate characteristics for 3 periods in the 21st century (2011-2040, 2041-2070, 2071-2100) under two climate change scenarios (CCS: A2 and B1) averaged across red pine study sites in the Upper Peninsula (UP) and Lower Peninsula (LP) regions of Michigan.

CCS/Climate/Region	2010-2040			2041-2070			2071-2100		
	Sum.	Win.	Ann.	Sum.	Win.	Ann.	Sum.	Win.	Ann.
A2									
Temperature (°C)									
UP	1.1	2.8	1.7	2.4	4.5	3.3	3.7	6.8	5.0
LP	1.2	2.6	1.6	2.6	4.2	3.2	3.9	6.3	4.9
Precipitation (mm)									
UP	50.7	32.7	121.4	44.2	44.2	129.0	71.3	69.8	190.3
LP	92.4	19.0	158.5	94.6	20.5	173.0	102.1	43.3	199.2
CMI (cm)									
UP	4.0	2.0	8.4	0.4	2.3	2.6	0.7	3.1	2.2
LP	6.4	0.4	9.2	3.1	-0.6	2.4	0.5	-0.5	-3.1
B1									
Temperature (°C)									
UP	0.9	2.8	1.7	1.4	3.6	2.2	1.4	3.8	2.3
LP	1.0	2.3	1.7	1.6	3.2	2.2	1.5	3.3	2.2
Precipitation (mm)									
UP	31.4	19.3	59.7	63.8	40.4	161.6	72.0	37.4	132.8
LP	55.5	11.8	89.5	86.2	20.2	170.2	103.0	15.9	173.7
CMI (cm)									
UP	2.2	0.9	1.9	4.8	2.4	11.1	5.6	2.0	7.4
LP	2.6	-0.1	1.6	4.9	0.1	8.2	6.5	-0.6	8.0

Note: Climate variables are expressed as anomalies relative to the normal reference period of 1971-2000. Summer (sum.) is defined as the 4-month period of May-August; winter (win.) is defined as 4-month period of November-February; and annual (ann.) is the 12-month period of January-December.

Figure Captions

Figure 1. Regional context of Michigan in the mid-west and northeastern United States. Study sites were selected in the Hiawatha National Forest in the Upper Peninsula and the Huron National Forest in the Lower Peninsula region of Michigan (National Forests are shaded in dark grey).

Figure 2. Radial growth chronologies of red pine in a) Upper Peninsula and b) Lower Peninsula regions Michigan over a common overlapping time period of 1970-2011. Group abbreviations: UP = Upper Peninsula, LP = Lower Peninsula, R = healthy reference, D = *Diplodia* affected, L = low initial stand density, H = high initial stand density.

Figure 3. Relationships between red pine growth and monthly and seasonal a) mean temperature, b) precipitation, and c) Climate Moisture Index examined via multiple regression analysis. For each regression model, predictor climate variables having a positive relationship with growth are denoted by light gray boxes, and predictor climate variables having a negative relationship with growth are denoted by darker gray boxes. All climate variables in each of the regression models are statistically significant ($p < 0.05$). Group abbreviations: UP = Upper Peninsula, LP = Lower Peninsula, R = healthy reference, D = *Diplodia*-affected, L = low initial stand density, H = high initial stand density. For groups that were significantly associated with more than 1 climate variable, these variables were ranked according to the absolute value of standardized regression coefficient. A rank of 1 indicates the climate variable which has the strongest influence on growth.

Figure 4. Projected percent change of growth variables across different latitudinal regions, forest health condition, and initial stand density for 3 future periods in the 21st century under two climate change scenario (A2 and B1). The projected estimates are based on applying separately the regression models for temperature (TAV, Table 4), precipitation (PPT, Table 4), and moisture index (CMI, Table 4) to the future climate scenarios. The lower and upper limits of a 95% confidence interval of mean radial growth for the control period (1971-2000) and growth projections for the climate scenario periods are expressed as percentage change relative to the mean growth for the control period. Group abbreviations: UP = Upper Peninsula, LP = Lower Peninsula, R = healthy reference, D = *Diplodia*-affected, L = low initial stand density, H = high initial stand density.

Figure 1
304x189mm (300 x 300 DPI)

Figure 2
148x183mm (300 x 300 DPI)

a) Temperature

b) Precipitation

c) Climate Moisture Index (CMI)

Figure 3
155x183mm (300 x 300 DPI)

Figure 4
161x205mm (300 x 300 DPI)