

Article

Dendroclimatic Response of Jack Pine (*Pinus banksiana*) Affected by Shoot Blight Caused by *Diplodia pinea*

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Abstract: The overall objective of our study was to examine the influence of climatic factors and tree-based competition on the radial growth of jack pine (*Pinus banksiana*) forests affected by the fungal pathogen, *Diplodia pinea*. Our study utilized dendroclimatic techniques to examine how past annual diameter growth can be influenced by the historical climate of the region. Twenty jack pine sites were sampled in Michigan within the Upper Peninsula (UP) and the Lower Peninsula (LP) region. Furthermore, two condition levels of forest health (*D. pinea*-affected vs. healthy reference stands) were considered between two levels of stand density (i.e., high vs. low density). The relationships between radial growth and climate identified in this study indicated that jack pine radial growth was typically affected by the climatic moisture index, whereas the response to temperature variables was weak to non-existent. In the Upper Peninsula region, crown damage likely sustained during harsh winters could have made jack pine stands prone to *D. pinea* by facilitating a point of entry for infection; furthermore, higher-density stands infected by *D. pinea* were influenced by moisture stress that occurred during the summer of the prior year. In the LP region, regardless of stand density, *D. pinea* was sensitive to moisture stress in the summer of the prior growing season; furthermore, negative relationships with precipitation in the spring may have improved spore dispersion in *D. pinea*-affected stands. Overall, our study provides improved understanding of the interactive role of climatic stress and forest pathogens on jack pine productivity.



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Keywords: climatic resiliency; dendroecology; *Diplodia pinea*; diseases; forest pathology; *Pinus banksiana*; shoot tip blight; stand density

1. Introduction

Diplodia pinea (Desm.) J.Kickx f. (Ascomycota, Botryosphaeriaceae) is widespread in the United States and impacts over 20 pine species in at least 30 states [1]. Infection symptoms include stem cankers, shoot blight, branch dieback, dead stem tops, blue staining, and tree mortality [2]. Fungal spores are typically shed during wet weather conditions, as well as throughout the growing season [3]. Consequently, host pine species can already be an abundant source of inoculum, which can threaten current stand health and hinder understory regeneration [2]. The fungus can occur asymptotically in pine stands, which can lead to a quick outbreak of disease in seemingly healthy stands which are actually predisposed to infection due to biotic or abiotic factors, such as increasing temperatures and decreasing moisture availability [4,5]. There is concern that drought and competition in pine stands are potential predisposing factors that can increase the potential risk of *D. pinea* infection [6,7]. Fire has not been considered as a predisposing factor, but the potential for fire risk could increase in stands affected by fungal pathogens [8].

Future projections of climate change indicate that global surface temperatures will increase under all future climate change scenarios [9]. These emission scenarios are called

Shared Socio-economic Pathways (SSPs) and are governed by the socio-economic characteristics and the radiative forcing and warming levels resulting from each scenario [9]. Compared to that in 1850–1900, the global temperature in 2081–2100 is expected to increase by anywhere from 1.0 °C to 5.7 °C depending on the SSPs [9]. Regional climate forecasts for the Great Lakes states, including Michigan, show that temperatures may rise by 3–11 °C in summer and 3–7 °C in winter [10,11]. Higher temperatures would likely result in increased evapotranspiration and, therefore, temperature-induced vegetative drought stress. Climatic conditions can predispose tree species to secondary disturbances (e.g., insects and pathogens), which can lead to forest decline [12,13].

Young pine stands are particularly susceptible to *Diplodia* shoot blight [4]. Unfortunately, young jack pine (*Pinus banksiana* Lamb.) stands in the northern Lower Peninsula region of Michigan provide a crucial summer nesting habitat for the Kirtland's warbler (*Dendroica kirtlandii* S.F.Baird) [14]. The Kirtland's warbler was listed under the U.S. Endangered Species Act in 1973; fortunately, this bird species was delisted in 2019 due to successful conservation efforts [15]. According to the International Union for the Conservation of Nature (IUCN) [16], this bird species' conservation status is currently classified as near-threatened. Therefore, to assist with protecting the Kirtland's warbler, it is imperative to safeguard jack pine stands against *Diplodia*. Jack pine is intolerant of shade and therefore typically regenerates via stand-replacing fires [17,18].

Management of jack pine can be challenging in the presence of *D. pinea*. For instance, Ostry et al. [19] observed increased mortality in jack pine plantations due to *D. pinea* presence after a variable retention harvesting regime. Nonetheless, forest management practices can help promote resiliency to climatic stress factors by reducing tree competition for limited resources. This in turn can help with tree growth and stand-level yield [20–22]. For example, thinning smaller crown classes (i.e., from below) to a moderate level of residual stand density of 21 m² ha^{−1} increased the resiliency of red pine (*Pinus resinosa* Ait.) to climate-related variables [22].

The objective of our study is to quantify the interaction between climatic variables and tree competition on the radial growth of jack pine (*Pinus banksiana*) forests infected by *Diplodia pinea*-induced shoot blight.

2. Methods

2.1. Study Area, Site Selection, and Field Sampling

Pole-sized plantation stands of jack pine were sampled along a latitudinal range from the northern Lower Peninsula (LP) region to the Upper Peninsula (UP) region in the state of Michigan (Figure 1). In each region, stands were selected to represent two different categories of health status: reference control stands that were healthy vs. stands affected by *D. pinea*. Healthy reference stands had ≤5% signs of crown dieback, while *Diplodia*-infected stands had a minimum of 15% crown dieback (Table 1). Confirmation of *Diplodia* infection was based on visual observation of crown dieback, which was then followed by culturing pine needles in agar media, which allowed us to isolate the pathogen from the infected trees [2]. Furthermore, for each geographic location sampled, 5 needles were randomly selected; on each needle, a single black fruiting body (pycnidia) was selected and all pycnidia were placed as a single smear on microscope slides and the presence of *D. pinea* spores was observed under a compound microscope. Half of the selected study sites were originally planted in a square planting grid at a higher density (>1977 trees per ha) while the other half of the study sites were planted at a lower density (<988 trees per ha) to examine the effect of stand density and competition between trees.

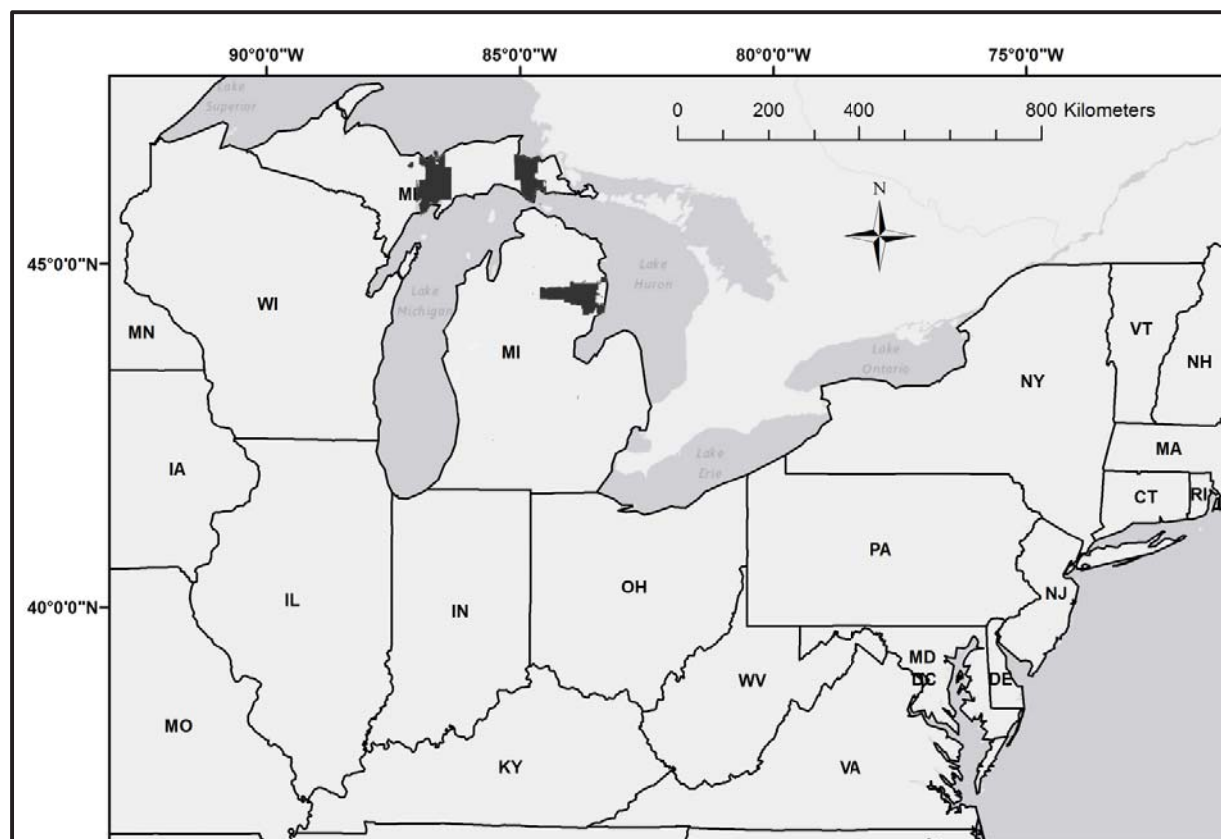


Figure 1. The study was conducted in Huron National Forest in the Lower Peninsula region and in Hiawatha National Forest in the Upper Peninsula region of Michigan (MI). Note: National Forests are indicated by dark gray shading.

Table 1. Treatment groupings and geographical characteristics of the 20 jack pine study sites. These sites were sampled in the Upper Peninsula (UP) and Lower Peninsula (LP) regions of Michigan. In addition, sites were selected from different categories of forest health status and initial stand density. Under consideration were two levels of forest health status (healthy reference vs. infected by *D. pinea*) and two levels of initial stand density (low density vs. high density).

Site ID	Region	Forest Health	Stand Density	Lat. (°N)	Long. (°W)	Elev. (m)	Group ID
JPC75	UP	Reference	Low	−86.6163	46.3019	273	L-R-UP
JPC81	UP	Reference	Low	−84.9866	46.2881	268	L-R-UP
JPC74	UP	Reference	High	−84.9790	46.3023	281	H-R-UP
JPC80	UP	Reference	High	−86.9738	45.8475	193	H-R-UP
JPD72	UP	<i>Diplodia</i>	Low	−84.9694	46.2126	267	L-D-UP
JPD77	UP	<i>Diplodia</i>	Low	−86.9615	45.8485	201	L-D-UP
JPD71	UP	<i>Diplodia</i>	High	−85.0044	46.2320	267	H-D-UP
JPD79	UP	<i>Diplodia</i>	High	−86.3902	46.1565	220	H-D-UP
JPC03	LP	Reference	Low	−84.0307	44.6542	294	L-R-LP
JPC05	LP	Reference	Low	−84.4482	44.6454	364	L-R-LP
JPC06	LP	Reference	Low	−84.5333	44.6110	363	L-R-LP
JPC01	LP	Reference	High	−84.3678	44.5355	367	H-R-LP
JPC02	LP	Reference	High	−84.3521	44.5351	372	H-R-LP
JPC04	LP	Reference	High	−83.9006	44.6619	303	H-R-LP
JPD01	LP	<i>Diplodia</i>	Low	−84.5260	44.6479	349	L-D-LP
JPD07	LP	<i>Diplodia</i>	Low	−84.5366	44.6162	379	L-D-LP
JPD14	LP	<i>Diplodia</i>	Low	−84.3692	44.5364	364	L-D-LP
JPD09	LP	<i>Diplodia</i>	High	−84.3703	44.5341	371	H-D-LP
JPD13	LP	<i>Diplodia</i>	High	−83.9118	44.6709	303	H-D-LP
JPD16	LP	<i>Diplodia</i>	High	−84.3719	44.5458	361	H-D-LP

The site selection protocol was based on a geographic information system (GIS)-based analysis in which jack pine plantation sites meeting the density categories were randomly selected from both the healthy and *Diplodia*-affected sites. Sample size was based primarily on sampling efficiency and on financial limitations on field sampling. Nonetheless, the regression modeling described later in Section 2.3 provides the statistical rigor of ensuring that only the statistically significant relationships between growth and climate are interpreted.

Site selection and field sampling of eight sites was conducted in the Hiawatha National Forest in the Michigan UP and included four reference stands which were healthy and four jack pine stands affected by *Diplodia* (Figure 1 and Table 1). Twelve sites were sampled in the LP region of Michigan within the Huron National Forest and included six reference stands which were healthy and six jack pine stands affected by *Diplodia* (Figure 1 and Table 1). Additionally, for both regions, half of either the healthy reference or *Diplodia*-affected jack pine stands were selected as being either low or high stand density. These sampled stands were overseen by the US Forest Service and their inventory records were used to determine stand age.

At each site, the stand inventory was conducted by randomly selecting a focal tree to be the center of a circular plot. The plot radius for high-density stands was 7.99 m (0.02 ha), while low-density stands had a radius of 9.78 m (0.03 ha). Each plot was at least 30 m from the stand's boundary in order to provide a buffer. At the halfway point of the plot radius along the compass bearings of NW, SW, SE, and NE the closest tree was selected for a total of 4 trees per plot. Each of the four trees were cored twice with an increment borer at breast height (1.37 m) and a core was obtained from the north and south side of each tree.

Mean monthly temperature and total monthly precipitation data were downloaded from a spatially based climate data set provided by the PRISM Climate Group developed by Oregon State University (<https://prism.oregonstate.edu/explorer/>, accessed on 27 October 2014) [23]. Climate data were obtained by inputting the latitudinal and longitudinal coordinates of each site. A climate moisture index (CMI) was then calculated by taking precipitation values and subtracting potential evapotranspiration (PET) [24]. CMI is a calculated variable that couples the effect of both temperature and precipitation in representing net moisture availability of a region. Climate conditions for 1971–2000 varied; the mean annual temperature was generally higher in the LP sites (mean range of 5.9–6.2 °C) compared to the UP sites (mean range of 5.0–5.2 °C) (Table 2). CMI was generally drier in LP compared to the UP. Based on the U.S. Environmental Protection Agency (EPA) [25] classification of ecological regions, both the Hiawatha National Forest (UP) and the Huron National Forest (LP) are located in what is known as the Northern Lakes and Forests ecological region.

Table 2. Climatic conditions for each treatment grouping for the climate reference period of 1971–2000 for sites sampled from two latitudinal-based regions in Michigan, two types of forest health condition, and two types of initial stand density. Note: TAV = mean annual temperature, PPT = total annual precipitation, CMI = climate moisture index. Treatment group abbreviations are as follows: UP = Upper Peninsula region, LP = Lower Peninsula region, R = reference stands that are healthy, D = *Diplodia*-affected, L = low density, H = high density.

Group	TAV (°C)	PPT (mm)	CMI (cm)
L-R-UP	5.0	854.8	32.7
H-R-UP	5.2	786.9	27.8
L-D-UP	5.2	786.1	27.5
H-D-UP	5.1	827.7	30.0
L-R-LP	6.1	767.0	15.5
H-R-LP	6.2	754.9	13.7
L-D-LP	5.9	803.8	20.0
H-D-LP	6.2	758.3	14.2

2.2. Increment Core Processing and Measurements

Increment core samples obtained from the 20 sampled sites were processed using dendrochronological techniques [26]. All increment cores were glued onto grooved core holders and sanded with successively finer grades of sandpaper up to 600 grit. A binocular microscope was used to visually cross-date all samples to account for any false or missing rings. We used the list method to assign a calendar year to each tree ring by identifying unique patterns of narrow rings [27]. A flatbed bed scanner (EPSON, South Jakarta, Indonesia) was used to digitize all increment core samples using a 1200 d.p.i optical resolution. Ring widths were measured using the CooRecorder (Version 9.0) and CDendro (Version 9.0) software (Cybis Elektronik & Data AB, Saltsjöbaden, Sweden). For cores with rings that were difficult to see in the digitally scanned image, a stage micrometer (Velmex: Bloomfield, NY, USA) was also used for tree ring measurement. We also used the program COFECHA (Version 6.06P) as a statistical quality control tool to verify the cross-dating accuracy [28].

2.3. Growth–Climate Analyses

Ring widths were detrended using a 40-year cubic smoothing spline to generate a radial growth index (RGI) by using the program ARSTAN (Version 6.05P) [29]. The rationale for this was that the ring widths were standardized in order to eliminate size- and age-related effects on ring widths. The 40-year cubic spline was characterized to preserve 99% of the variation in each ring-width series. This method preserved the trends in jack pine radial growth shared between trees due to stand-wide effects like climate and stand management. A standard chronology was created for each site by averaging the RGI of each tree and year. Additional summarization involved averaging the standard chronology for all sites sharing the same treatment grouping of the combination of each forest health condition, initial stand density, and latitudinal region.

Based on the monthly climate data [23], we calculated seasonal (3-month) climate variables for CMI and meant temperature to examine the influence of seasonal climatic effects on radial growth. The temperature variables were averaged during the 3-month seasonal periods, while the CMI variables were summed during the 3-month seasonal periods. For the same treatment grouping of the same forest health condition class and density level for each region, monthly and seasonal climate data were also averaged for all sites.

Radial growth–climate relationships between annual ring-width and past climatic conditions (both monthly and seasonal variables) were evaluated using a stepwise multiple linear regression approach (for full details of this modeling approach, see the work of Chhin et al. [30]). This regression modeling was carried across all combinations of the two levels of *Diplodia* infection status, the two levels of stand density, and each latitudinal region. The multiple regression analysis was carried out using the function *stepAIC* (package MASS) in the program R (Version 3.1.2), which involves minimizing the value of Akaike’s information criterion (AIC) [31,32]. A regression model was selected for each climate variable set (TAV and CMI) on monthly and seasonal climate scales. The regression analyses were conducted for a 26-year period (1986–2011) and over two growing seasons starting from April of the year prior to ring formation ($t - 1$) and ending in October of the current year (t) of ring formation. To identify the relative ranking of importance of each of the predictor variables in the regression models, standardized (β) partial regression coefficients were calculated [33].

3. Results

3.1. Growth and Chronology Characteristics

There were fewer significant correlations for the chronologies of jack pine radial growth among the different treatment groups within the UP region in comparison to the LP region during 1986–2011 (Table 3 and Figure 2). In the UP region, the two healthy reference groups showed a significant positive correlation with one another ($p < 0.05$), while the two

Diplodia-affected groups were not significantly correlated ($p \geq 0.05$) (Table 3 and Figure 2a). In the UP region, the radial growth chronologies for treatment groups with different health conditions and densities ((L-R-UP and H-D-UP), as well as (H-R-UP and L-D-UP)), also showed significant positive correlations ($p < 0.05$) (Table 3 and Figure 2a). Within the LP region, with the exception of the L-R-LP and H-D-LP (i.e., healthy reference low-density group and *Diplodia*-affected high-density group), all treatment groups were significantly positively correlated with one another ($p < 0.05$) (Table 3 and Figure 2b). Additionally, the radial growth chronologies for all of the UP region *Diplodia*-affected treatment groups showed statistically significant positive correlation with the LP region *Diplodia*-affected grouping ($p < 0.05$), with the exception of the two high-density groups, which did not show positive correlation with one another ($p \geq 0.05$) (Table 3 and Figure 2). Finally, the treatment groups (L-R-UP and H-D-LP), (H-D-UP and L-R-LP), and (H-D-UP and L-D-LP) also showed significant positive correlations between the different radial growth chronologies ($p < 0.05$) (Table 3 and Figure 2).

Table 3. Correlations analysis statistics between the radial growth chronologies of jack pine in the Upper Peninsula and Lower Peninsula regions of Michigan for the analysis period of 1986–2011. Treatment group abbreviations are as follows: UP = Upper Peninsula region, LP = Lower Peninsula region, R = reference stands that are healthy, D = *Diplodia*-infected, L = low density, H = high density. * indicates correlation coefficients that are statistically significant ($p < 0.05$).

Group	L-R-UP	H-R-UP	L-D-UP	H-D-UP	L-R-LP	H-R-LP	L-D-LP	H-D-LP
L-R-UP	1							
H-R-UP	0.639 *	1						
L-D-UP	0.345	0.442 *	1					
H-D-UP	0.434 *	0.310	−0.085	1				
L-R-LP	0.215	0.034	−0.005	0.419 *	1			
H-R-LP	0.053	0.114	0.300	0.125	0.503 *	1		
L-D-LP	0.567 *	0.278	0.451 *	0.428 *	0.412 *	0.398 *	1	
H-D-LP	0.155	0.131	0.589 *	0.120	0.348	0.727 *	0.557 *	1

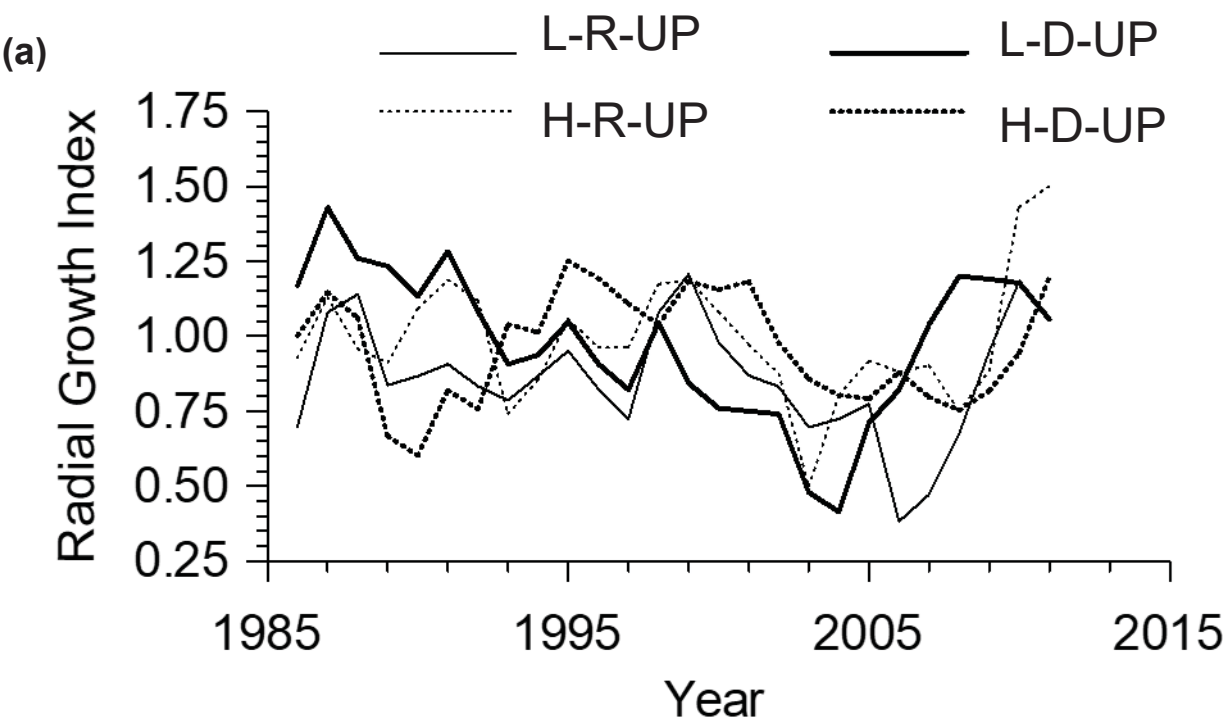


Figure 2. Cont.

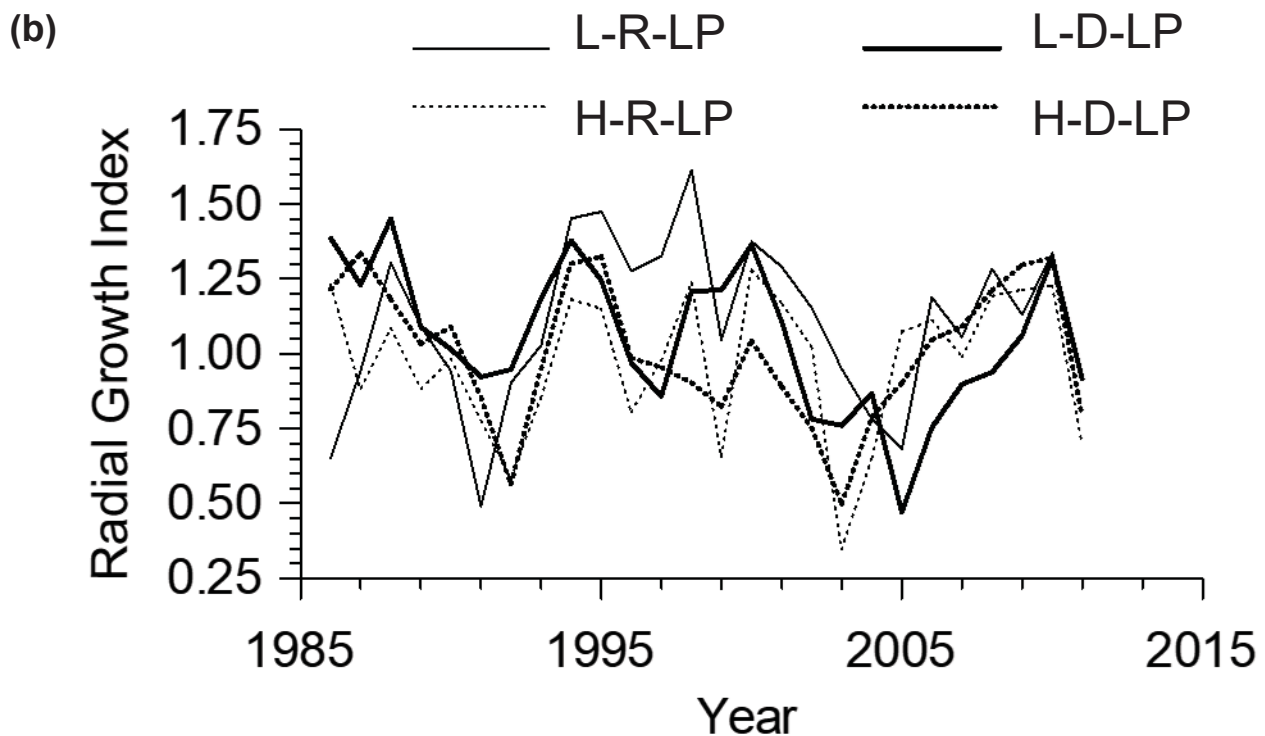


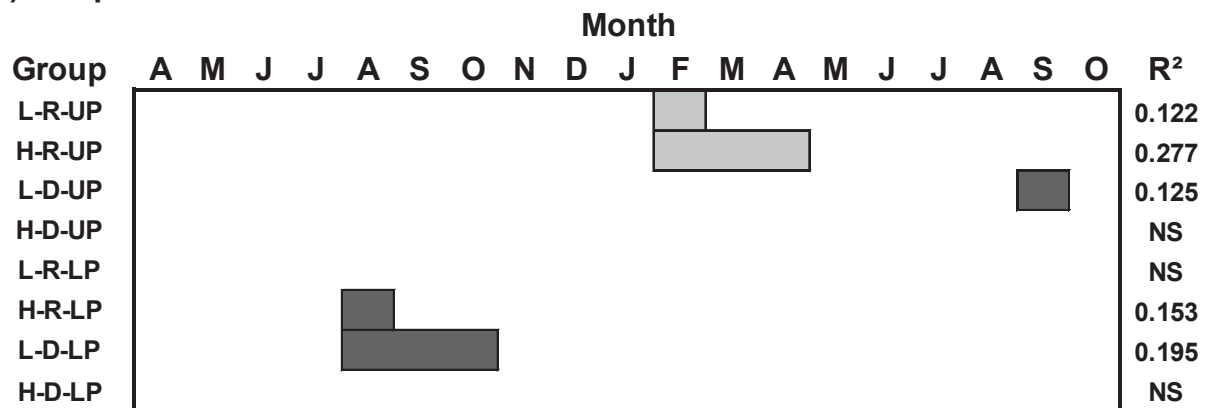
Figure 2. Chronologies of jack pine growth based on sampling in Michigan’s (a) Upper Peninsula region and (b) Lower Peninsula region for 1986–2011. Treatment group abbreviations are as follows: UP = Upper Peninsula region, LP = Lower Peninsula region, R = reference stands that are healthy, D = *Diplodia* present, L = low density, H = high density.

3.2. Growth–Climate Relationships

Based on stepwise multiple regression modeling, jack pine radial growth was shown to be statistically influenced by additional climatic factors, as well as summer drought stress in Michigan (Figure 3 and Table 4). For both the UP and LP regions, the radial growth relationships with temperature were typically weak (as reflected by the adjusted R^2 values) or not significant ($p \geq 0.05$) (Figure 3a). The UP region healthy reference groups had positive relationships with temperature in the current year (t) in either February (L-R-UP) or February through April (H-R-UP) (Figure 3a). Negative relationships with temperature and radial growth were observed for the UP low-density *Diplodia*-affected group (L-D-UP) in September of the current year (t), in the LP healthy reference high-density group (H-R-LP) in August of the previous year ($t - 1$), and in the LP *Diplodia*-affected low-density group (L-D-LP) in August through October of the previous year ($t - 1$) (Figure 3a).

Except for the LP healthy reference high-density treatment group (LP-R-H), all treatment groups in this study had at least one monthly or seasonal significant relationship with the climate moisture index (CMI) (Figure 3b). The adjusted R^2 values were typically higher compared to the values associated with temperature, indicating a stronger radial response due to CMI (Figure 3). While there was a seasonal positive relationship with CMI in the summer of the previous year ($t - 1$) (L-R-UP, H-D-UP, L-D-LP, and H-D-LP), summer CMI in the current year (t) only had a significant positive influence on radial growth for the UP low-density healthy reference group (L-R-UP) (Figure 3b). Negative seasonal relationships between radial growth and CMI were also observed during October through December of the previous year ($t - 1$) (L-R-UP, H-D-UP, and L-R-LP), March through May of the current year (t) (L-R-UP, L-D-LP, and H-D-LP), and August through October of the current year (t) (L-R-LP) (Figure 3b). Monthly negative relationships between radial growth and CMI were observed during May of the previous year ($t - 1$) (L-D-LP), August of the previous year ($t - 1$) (H-R-UP), and February of the current year (t) (L-D-UP) (Figure 3b).

a) Temperature



b) Climate Moisture Index (CMI)

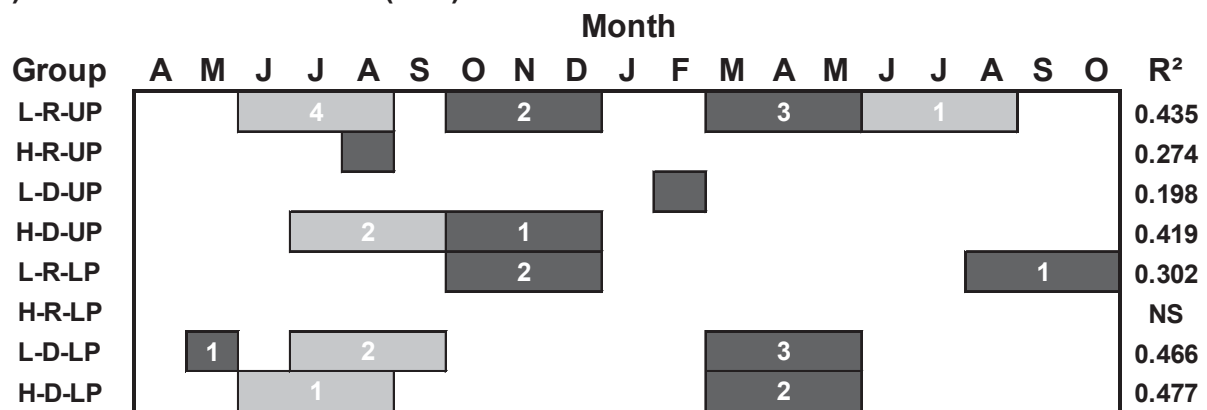


Figure 3. Jack pine growth responses to monthly and 3-month seasonal (a) mean temperature and (b) climate moisture index. In each regression model, lighter gray boxes highlight climatic variables as having a positive association with radial growth, while darker gray boxes showcase climatic variables as having a negative association with radial growth. All climatic relationships presented in each model are significant statistically ($p < 0.05$). Treatment group abbreviations are as follows: UP = Upper Peninsula of Michigan, LP = Lower Peninsula of Michigan, R = reference sites that are healthy, D = *Diplodia*-present, L = low density, H = high density. For treatment groups that have more than 1 significant climate variable in the regression model, these variables in turn were ranked, and variables ranked as 1 had the strongest influence on radial growth.

Table 4. Coefficients of the multiple regression models which relate jack pine radial growth to climate variables sampled from two different latitudinal-based regions, two fungal infection statuses, and two levels initial plantation density. Treatment group abbreviations are as follows: UP = Upper Peninsula of Michigan, LP = Lower Peninsula of Michigan, R = healthy reference control, D = *Diplodia*-present, L = low initial plantation density, H = high initial plantation density.

Group	C	V1	V2	V3	V4
(a) Temperature					
L-R-UP	1.101	0.397 (0.0304)			
H-R-UP	1.130	0.553 (0.0675)			
L-D-UP	2.046	−0.4 (0.0765)			
H-D-UP	NS				
L-R-LP	NS				
H-R-LP	2.447	−0.432 (0.0794)			
L-D-LP	2.861	−0.477 (0.1374)			
H-D-LP	NS				

Table 4. Cont.

Group	C	V1	V2	V3	V4
(b) Climate Moisture Index					
L-R-UP	1.310	0.439 (0.0148)	−0.340 (0.0107)	0.318 (0.0107)	−0.318 (0.0102)
H-R-UP	1.118	−0.551 (0.0399)			
L-D-UP	1.228	−0.48 (0.0879)			
H-D-UP	1.280	−0.541 (0.0160)	0.516 (0.0169)		
L-R-LP	1.442	−0.429 (0.0191)	−0.541 (0.0195)		
H-R-LP	NS				
L-D-LP	1.172	−0.405 (0.0251)	0.341 (0.0098)	−0.323 (0.0130)	
H-D-LP	1.285	0.543 (0.0200)	−0.511 (0.0199)		

Note: The first term in the regression model consists of the constant (C). The other regression terms (V1–V4) are listed in descending order of importance based on the ranking of the absolute values of the standardized (β) regression coefficients [34], while the values in parentheses are the corresponding partial regression coefficients (cf. Figure 3). NS = regression model not significant ($p \geq 0.05$).

4. Discussion and Conclusions

The observed radial growth relationships showed that jack pine (*P. banksiana*) growth was typically more influenced by moisture availability, as reflected in the moisture index, compared to weaker or no response to temperature variables. Regression models between radial and temperature variables, if significant, only contained a single influential independent variable, and had lower explanatory power (Figure 3). In contrast, dendroclimatic responses to the moisture index had between 1 and 4 significant independent climatic variables with higher values of explanatory power for radial growth, as reflected in the higher coefficient of determination (R^2) (Figure 3). Chhin and O’Brien [34] also noticed that red pine, in Michigan, was influenced more by moisture-related climatic variables than by temperature. Iturrutxa et al. [35] also confirmed that Monterey pine (*Pinus radiata* D. Don) plantations in Spain were primarily affected by moisture conditions, especially in the summer. *P. nigra* J.F. Arnold stands in the eastern Spanish Pyrenees were more impacted by *Diploдия* tip blight in the warmest and driest areas [36].

The dendroclimatic response of jack pine in our study varied by latitudinal region. In the UP region, the results suggest that crowns were damaged by harsh winters and that this may have made jack pine stands prone to *D. pinea* by allowing an entry point for infection. In particular, it is likely that the harsh winter mechanism is due to heavy winter snowfall accumulations that caused branch breakage of jack pine in the UP region (c.f., Table 2 and Figure 3b). The potential effect of crown damage being linked to harsh winters was also inferred by Chhin and O’Brien [34] in their study of red pine (*P. resinosa*) in Michigan. Our results indicated that lower-density healthy stands were affected by summer moisture stress primarily in the summer of the current year of ring formation, but also in the summer of the previous year. Higher-density stands sampled in the Upper Peninsula which were affected by *D. pinea* were also influenced by moisture stress, but only in the summer of the previous year.

In the LP region, regardless of stand density, *D. pinea*-affected stands were sensitive to moisture stress in the summer of the previous growing season. Furthermore, negative relations with precipitation in the spring suggests these climate conditions can increase the likelihood of spore dispersal. Chhin and O’Brien [34] also interpreted a similar mechanism of easier spore dispersal connected to wet climatic conditions in stands of red pine (*P. resinosa*) in Michigan. In stands of *P. nigra* and *Pinus sylvestris* L. in France, the presence of *D. pinea* in the cones of these tree species was positively correlated with summer rain conditions [37]. Furthermore, Brodde et al. [38] observed that spore deposition was higher in *P. sylvestris* stands in connection with high precipitation. The dendroclimatic response of Jack pine in reference stands at low density suggested stormy weather associated with precipitation events in late summer to early fall in the current year and fall to early winter in the previous year negatively impacted radial growth. We believe this is mechanistically

plausible, since wind is a major driver of minor disturbances in this region [39,40]. In other stands of jack pine with clay soils, poor drainage has also led to negative associations with excess precipitation [41]. Kidd et al. [42] determined that frost ring formation due to spring frosts was more prevalent in young jack pine trees and trees of smaller diameter in Michigan's northern LP region.

Globally, *Diplodia* shoot blight also affects areas in Europe. For instance, in France, it has been present since the late 19th century, but it started to cause serious forest decline issues for pine species in the early 1990s (i.e., *P. nigra* and *P. sylvestris*) [37]. In Spain, many diseases affect Monterey pine (*P. radiata*) plantations, including *D. pinea* [35]. Furthermore, in Spain, *Diplodia* affects the productivity of *P. radiata* plantations, and this was attributed to the high genetic diversity of the different strains of *Diplodia sapinea* [43]. *Diplodia* shoot blight caused by *D. sapinea* (Fr.) Fuckel impact *P. nigra* stands in the eastern Pyrenees of Spain, primarily in the warmest and driest areas [36]. *D. sapinea* affected *P. sylvestris* stands that had previously been damaged by hailstorms [8]. Solar radiation has been found to increase the vulnerability of Austrian pine (*P. nigra*) to fungal infection in Italy [44]. In an arboretum in Germany, *Diplodia* tip blight was found to be temperature-dependent in that warmer temperatures negatively affected Scots pine (*P. sylvestris*) [45]. Similarly, *Diplodia* tip blight has had a negative impact on Scots pine in Sweden [38,46].

In our study, healthy reference stands of jack pine still showed some sensitivity to climate (cf. Figure 3). For each latitudinal region, the healthy reference stands of jack pine showed a weaker response to temperature in the lower-density stands compared to the higher-density stands, as indicated by the lower coefficient of determination of the regression models (R^2). Other studies of other pine species (i.e., *P. resinosa*) in the Great Lakes region have also confirmed that thinning stands can ameliorate the impact of a harsh regional climate [21,22]. However, the growth response to climate differed in our study in terms of relationships with the climate moisture index (CMI), since lower-density stands appeared more responsive to CMI compared to the higher-density stands (cf. Figure 3). It is unclear why this is the case, but we speculate that healthy high-density stands likely still contained a strong competitive signal, which in turn could obscure the climate signal.

While this study focused on how climate factors can cause predisposition to a fungal pathogen, other studies have examined the role of climate stress leading to insect pest issues in jack pine forest types. For instance, Mamet et al. [47] found that mortality of jack pine in the southern boreal forest of Canada was linked to both drought and insect outbreaks. Furthermore, Robson et al. [48] found a link between dry summers and cool May temperatures and infestation with budworm defoliation on jack pine in Canada.

Overall, the above radial growth responses of jack pine to climate indicate that climate stress potentially plays a role in predisposing jack pine stands to *D. pinea*. Further field-based experimental studies are still required to definitively confirm this potential causal connection, which was inferred via retrospective tree ring-based analysis. Future studies should also examine how different climate change scenarios could impact the future productivity of jack pine. It is expected that, based on climate change projections for the Great Lakes region [10,11], jack pine could potentially be negatively impacted by higher intensities and longer duration of hot, dry summers, which could in turn predispose jack pine to further *Diplodia* infection. This research will also help safeguard important wildlife habitat for the Kirtland's warbler. Models of vulnerability to climate change for different forest types in Michigan and the Great Lakes region generally do not consider forest health-related issues, including fungal infections [11]. This study helps provide climate adaptation options in the context of forest health threats.

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