

Climate-growth relationships for yellow-poplar across structural and site quality gradients in the southern Appalachian Mountains



Tara L. Keyser^{a,*}, Peter M. Brown^{b,1}

^aUSDA Forest Service, Southern Research Station, Bent Creek Experimental Forest, 1577 Brevard Rd., Asheville, NC 28806, United States

^bRocky Mountain Tree Ring Research, Inc., 2901 Moore Ln., Fort Collins, CO 80526, United States

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ABSTRACT

Forecasted changes in climate across the southeastern US include an increase in temperature along with more variable precipitation patterns, including an increase in the severity and frequency of drought events. As such, the management of forests for increased resistance or resilience to the direct and indirect effects of climate change, including decreased tree- and stand-level productivity, is of interest to natural resource practitioners. Because the sensitivity of tree growth to climate can be moderated by competition, manipulating stand density through silvicultural activities may mitigate the negative effects climate change may have on tree growth and productivity. In this paper, we utilized dendrochronology data, along with long-term forest inventory data, from 134 plots established and subsequently thinned between 1960 and 1963 to analyze the effects of climate on annual tree growth for yellow-poplar (*Liriodendron tulipifera* L.) across a broad stand structural and site productivity gradient in the southern Appalachian Mountains.

Annual basal area increment (BAI) was most related to the Palmer Drought Severity Index (PDSI) during the months of May, June, and July (PDSI_{MJJ}) relative to that of the annual or growing season when structural and site productivity variables were included in the analysis. Annual BAI of trees growing in stands of lower density responded to increases in PDSI_{MJJ} at a faster rate than trees growing in stands of greater density. Conversely, those same trees experienced proportionally greater decreases in BAI at lower values of PDSI_{MJJ} compared to trees in stands of greater density. Annual BAI was positively related to site productivity, as quantified by site index, with BAI more sensitive to changes in PDSI_{MJJ} on plots of progressively higher site index. Results suggest stand structure as well as measures of productivity should be considered when quantifying climate-growth relationships for forest tree species. Such information could not only aid in the identification of stands most susceptible to reduced growth, but also be used to develop site- or stand-specific silvicultural prescriptions focused on promoting resilience or resistance under a changing climate.

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1. Introduction

The southern Appalachian Mountains encompasses ~14.97 million hectares in the southeastern US (Southern Appalachian Man and Biosphere, 1996) and contain some of the most productive and diverse temperate forests in North America. Forecasted changes in climate across the southeastern US include an increase in temperature along with more variable precipitation patterns, including an increase in the severity and frequency of drought events (McNulty et al., 2013). More frequent and extreme weather events have the potential to affect forest productivity through a

variety of mechanisms, including increasing tree mortality (Klos et al., 2009; Allen et al., 2010), reducing tree- and stand-level growth (Elliott and Swank, 1994; Boisvenue and Running, 2006; D'Amato et al., 2013), and amplifying complex insect and/or disease interactions (Lawrence et al., 2002; Negrón et al., 2009; Vose et al., 2012). The specific response of tree- and stand-level growth to climate varies across species (Pan et al., 1997), tree size (Mérian and Lebourgeois, 2011), age (Copenheaver et al., 2011), stand structures (Linares et al., 2010; D'Amato et al., 2013), edaphic or productivity gradients (Orwig and Abrams, 1997; Leonelli et al., 2008), and genetic variability across populations (McLane et al., 2011). Because the sensitivity of tree growth to climate has been shown, for some species, to be moderated by intra- (Piutti and Cescatti, 1997; Cescatti and Piutti, 1998; Linares et al., 2010) and

* Corresponding author. Tel.: +1 828 667 5261x102; fax: +1 828 667 9097.

E-mail addresses: tkeyser@fs.fed.us (T.L. Keyser), pmb@rmtrr.org (P.M. Brown).

¹ Tel.: +1 970 229 9557.

inter-specific competition (Lebourgeois et al., 2013; Forrester, 2014), manipulating stand density and/or species composition through silvicultural activities may prove a useful strategy that mitigates some of the negative effects climate change may have on growth and productivity.

Thinning has been suggested as a potential management activity that may increase the resilience of individual trees, stands, and forests to the direct and indirect effects of a changing climate, including potential decreases in growth and productivity (Bréda and Badeau, 2008; Klos et al., 2009; Vose et al., 2012). Reductions in stand density via thinning increases growing space and may result in decreased competition for water, nutrients, and light among residual trees (Martín-Benito et al. 2010). Soil moisture availability is also indirectly increased through decreased rainfall interception and reduced stand-level transpiration (Morikawa et al., 1986; Stogsdiil et al., 1989; Bréda and Granier, 1996; Bréda et al., 1996), with the degree of increase varying with stand density (Della-Bianca and Dils, 1960; Butcher, 1977; Mitchell et al., 1993). Due to the interaction among density and soil moisture, tree-level response to periods of soil moisture deficit can vary with stand structure. For example, Misson et al. (2003a,b) report growth of plantation-origin Norway spruce (*Picea abies* (L.) Karst.) in heavily thinned stands was less affected by drought than in higher density stands. Likewise, D'Amato et al., (2013) report stand density, as modified through repeated thinnings, altered the climate-growth relationships of plantation-origin red pine (*Pinus resinosa* Ait.), with trees in high density stands more susceptible to reductions in growing season precipitation than trees in low density stands. Although information related to how stand structure interacts with climate to modify tree growth for naturally-regenerated, deciduous tree species is less abundant, similar effects have been observed. For example, both increased temperature and increased moisture deficit were found to decrease growth of European beech (*Fagus sylvatica* L.) to a greater extent in high density than low density stands (Piutti and Cescatti, 1997).

Although stand structure can influence the effects of climate on tree growth, other factors such as site productivity can interact with climate to further affect growth. For example, studies suggest trees growing on mesic high-quality sites often experience proportionally greater growth reductions during periods of reduced soil moisture availability than trees growing on xeric, low quality sites (Fekedulegn et al., 2003; Orwig and Abrams, 1997). Dendrochronological climate-growth relationships have been developed for many eastern US tree species, including oak (*Quercus*) and hickory (*Carya*) species (Orwig and Abrams, 1997; Speer et al., 2009; LeBlanc and Terrell, 2011; White et al., 2011) and a subset of the prominent mixed-mesophytic species [e.g., yellow-poplar (*Liriodendron tulipifera* L.), black cherry (*Prunus serotina* Ehrh.), sugar maple (*Acer saccharum* Marsh.)] (Orwig and Abrams, 1997; Pan et al., 1997; Fekedulegn et al., 2003). Lacking, however, is information about how competition and site quality interact with climate to influence tree growth for some of these ecologically and economically important tree species.

Yellow-poplar is a mesophytic species common to moderate to highly productive sites throughout the southern Appalachian region and is the most abundant individual tree species (in terms of volume) in the southern Appalachian Mountains (Thompson, 1998; Schweitzer, 1999; Brown, 2003). Although yellow-poplar is most often found in areas of relatively high soil moisture holding capacity where moisture does not generally limit growth (Beck and Della-Bianca, 1981), yellow-poplar is susceptible to decreased growth and increased mortality during drought events (Elliott and Swank, 1994; Orwig and Abrams, 1997; Klos et al., 2009). Past studies linking tree growth with climate for eastern US tree species have often failed to consider the interacting effects competition and site quality may have with variations in tree growth affected

by annual changes in climate. This likely over-simplifies climate-growth relationships and the potential effect of climate change on both tree- and stand-level productivity. The primary goal of this study was to examine the effect of climate on the growth of a prominent tree species in the southern Appalachians, yellow-poplar, across broad structural and site quality gradients. Specifically, based on the literature, we hypothesize the negative effects of reduced soil moisture availability on annual tree growth will be exacerbated as stand density, site quality, and tree size increase. Such quantitative information regarding climate-growth relationships under varying stand structures and across environmental gradients will (1) determine if altering the competitive environment via silvicultural thinning does, in fact, mitigate some of the deleterious effects of climate on tree growth, and (2) provide information that will aid in the identification of stands most susceptible to drought-induced reductions in growth.

2. Materials and methods

2.1. Study area

This study was conducted in the Blue Ridge Mountains and Northern Ridge and Valley Physiographic provinces of the southern Appalachian Mountains. Study sites were located in northern Georgia, western North Carolina, and southwestern Virginia. Soils were either ultisols or inceptisols, and encompassed six major soil series (Tusquitee, Brevard, Ashe, Haywood, Watuga, and Porters), indicating a range of site productivity. Soils were well-drained, coarse or fine-loamy in texture. Temperatures in the intermountain basin of Asheville, NC, which is centrally located within the geographic study area, ranged from 2.3 °C in January to 22.3 °C in July (McNab et al., 2004). Elevations of the study sites range from approximately 340–1150 m. Average annual precipitation, which increases with elevation, is evenly distributed throughout the year and ranges from 1000 mm to 1500 mm (but can be as high as 2500 mm in some areas) across the study sites (McNab, 2011). As a reference, in the Asheville Basin, which is approximately 600 m elevation, annual precipitation averages 1200 mm (McNab et al., 2004).

2.2. Experimental design and data collection

Between 1960 and 1963, 141 – 0.1 ha permanent plots were established in yellow-poplar stands throughout the study area. This study utilized 133 of the original 141 plots, as some plots were mistakenly harvested. All plots were established in naturally regenerated, even-aged stands in which yellow-poplar comprised >75% of the overstory basal area. Plots were located on north and east aspects and ecologically mapped as primarily rich cove forests (Simon et al., 2005). Rich cove forests possess high levels of biodiversity (tree and herbaceous layers) and are located on protected landscapes characterized by gentle slopes (Simon et al., 2005). At the time of plot establishment, all live trees greater than 11.4 cm in diameter at breast height (DBH; 1.37 m above ground line) within each plot were tagged, and species, DBH (cm), and total height (m) were recorded. Increment cores were extracted from five of the most dominant trees on each plot. Using age data obtained from the increment cores and height data, site index (base-age 50) was calculated for each of the five trees per plot (Beck, 1962), with site index (SI; m) calculated as the average SI of the five sample trees.

Within a one to two months following the initial inventory (1960–1963), plots were thinned to a randomly assigned basal area (BA; m² ha⁻¹). Post-thinning BA corresponded to residual relative densities (RD) ranging from 12% to 56% calculated as plot-level

SDI_{observed}/SDI_{maximum} (Reineke, 1933). Thinning was accomplished via low thinning. After the second inventory cycle (1965–1968) was completed, the majority of plots were thinned from below for a second time to the originally assigned basal area. Re-measurement of DBH of all live tagged trees occurred during the dormant season every five years following plot establishment up through 2003.

Between October and December 2009, one increment core was collected at 1.37 m above groundline from five randomly selected dominant/co-dominant yellow-poplar trees from each of the 133 plots. Cores were dried, mounted, and sanded with progressively finer sandpaper until cell structure was clearly visible. Rings were visually crossdated against other trees in each plot. Radial growth was then measured to the nearest 0.001 mm using a linearly controlled stage and microscope attached to a digital encoder (Velmex, Inc.). Accuracy of visual crossdating was supported statistically using the program COFECHA (Holmes, 1983). Crossdated ring-width chronologies were converted to chronologies of annual inside bark basal area increment (BAI; cm² yr⁻¹) assuming circularity for each sample tree. Specifically, BAI was calculated as:

$$\text{BAI} = \pi(r_t^2 - r_{t-1}^2)$$

where r is the radius of the tree and t is the year of ring formation. The use of BAI in lieu of radial growth eliminates variation in growth due to the negative correlation between ring width and tree circumference (Biondi and Qeadan, 2008). Estimates of diameter inside bark at breast height (DIB; cm) were obtained from the BAI chronologies.

2.3. Statistical analysis

We used mixed-effects linear modeling to explore the relationship among annual BAI and various structural and environmental variables, including density, climate, and productivity variables. Growth is a function of tree size, competition, and various factors related to site productivity (Wyckoff, 1990). Therefore, we modeled variability in BAI due to tree size, density, and site index, which is an indirect measure of site productivity (Skovsgaard and Vanclay, 2008). Preliminary examination of data revealed a pattern in BAI associated with the number of years since thinning (YST). A cubic function that described the effect of YST on BAI was, therefore, included in the model. Specifically, BAI was modeled as:

$$\ln\text{BAI} = \beta_0 + \beta_1(\text{YST}) + \beta_{24}(\text{YST}^2) + \beta_3(\text{YST}^3) + \beta_4(\ln\text{DIB}) \\ + \beta_5\left(\frac{\text{DIB}}{\text{Dq}}\right) + \beta_6(\text{RD}) + \beta_7(\text{SI})$$

where $\ln\text{BAI}$ is \log_e of annual BAI for each tree, YST is years since thinning, $\ln\text{DIB}$ is \log_e diameter inside bark at breast height reconstructed from BAI chronologies (cm), Dq is quadratic mean diameter of the plot (cm), RD is plot-level relative density, and SI is plot-level estimate of site index (m). Basal area increment was \log_e -transformed to stabilize variance and approximate normality.

After fitting this 'base' model, we formulated 15 a priori hypotheses (i.e., models) that described the potential effects of climate, tree size, density, site quality, and relevant interactions on annual BAI (Table 1). We chose to use a single variable, Palmer Drought Severity Index (PDSI), to describe annual climate during the 45 years post-thinning. Palmer Drought Severity Index describes moisture conditions and is calculated using precipitation and temperature data along with available soil moisture content (Palmer, 1965; Alley, 1984). The time periods encompassed by the PDSI values were based, in part, on past literature linking the growth of yellow-poplar to precipitation and/or temperature (e.g., Beck, 1985; Pan et al., 1997; Tryon et al., 1957), and included: (a) PDSI_{ANNUAL} (average PDSI from October of the previous year

through September of the current year); (b) PDSI_{GROW} (average PDSI from April of the current year through the end of September of the current year); or (c) PDSI_{MJJ} (average PDSI from May of the current year through the end of July of the current year). The PDSI data were obtained from the National Climatic Data Center (<http://www.ncdc.noaa.gov/cag/time-series/us>), with PDSI values varying based on each plot's location within its respective State and Climate Division.

All models were developed to test the null hypothesis that tree size, site productivity, density, and climate had no significant effect on BAI over the time period encompassed by this study. Models, therefore, should be considered descriptive rather than predictive. Akaike's information criterion (AICC) was utilized to determine which models most parsimoniously fit the data. Models were considered the best-fitting model when ΔAICC between any two models was >2.0 (Burnham and Anderson, 2002). Akaike weights were calculated to provide information regarding the strength of evidence for each model (Burnham and Anderson, 2002). The hierarchical structure of the data was accounted for by incorporating individual trees and plots as random effects. A linear effect of YST was included as an additional random effect at both the plot- and tree-level. Autocorrelation was modeled using a first-order autoregressive covariance structure (ar(1)). All analyses were conducted using the PROC MIXED procedure in SAS v. 9.3 (SAS Institute, 2011).

3. Results

The thinning treatment and subsequent differences in tree growth among plots created a wide variety of stand structures. The results presented here are applicable to the range of tree- and plot-level attributes presented in Table 2. Tree size (i.e., DIB), DIB/Dq, which describes the competitive position of the individual tree within the stand, and SI were all positively associated with annual BAI while RD had a negative effect on annual BAI (Table 1). Basal area increment peaked during the immediate years post-thinning, with BAI slowly decreasing between 11 and 37 years since thinning (YST) and then increasing slightly between 38 and 45 YST.

Although the addition of PDSI_{ANNUAL}, PDSI_{GROW}, or PDSI_{MJJ} to the base model improved model performance, as evidenced by the reduction in AICC model (Table 1, Models 1, 6, 11), the addition of PDSI_{GROW} resulted in the best single PDSI factor model (AICC = 19415.5). In all cases, the coefficients for PDSI in the single-factor PDSI models indicated PDSI had a positive effect on annual BAI. Relative to the single-factor PDSI models, the addition of interactions between PDSI and RD or PDSI and DIB improved model performance (Table 1). Based on AICC, the models containing YST (years since thinning), YST², YST³, DIB, DIB/Dq, RD, SI, and PDSI along with interactions PDSI * RD, PDSI * DIB, and PDSI * SI were the best performing models utilizing PDSI_{ANNUAL} (Model 5), PDSI_{grow} (Model 10), and PDSI_{MJJ} (Model 15). Among these, Model 15, which utilized PDSI_{MJJ}, produced the lowest AICC value, with a corresponding Akaike weight of 1.000. Consequently, we limit the presentation of results to those associated with Model 15.

Similar to the Base model, in Model 15 DIB, DIB/Dq, and SI were positively correlated with BAI while increases in RD were associated with reductions in BAI. Not only did trees growing in plots with higher RD have lower BAI, but BAI of trees growing in plots of greater RD was less responsive to the positive effects of PDSI_{MJJ} (i.e., significant RD * PDSI_{MJJ} interaction, Table 1). Holding all other independent variables at their mean values, the difference in annual BAI 23 years after thinning between PDSI_{MJJ} values of -5.14 (extreme drought) and 5.36 (extremely wet) for trees in low (RD = 0.19), moderate (RD = 0.39), and high (RD = 0.62) density plots was 8.4, 4.5, and 1.7 cm² yr⁻¹, respectively (Fig. 1). For tree size, a significant negative

Table 1

A-priori models and associated parameter estimates (SE) describing the effects of years since thinning (YST), tree size (lnDIB), competitive position within the plot (DIB/Dq), density (RD), site index (SI), and Palmer Drought Severity Index (PDSI). ΔAICC refers to the change in AICC compared to the best overall model (i.e., the model corresponding to the lowest AICC).

Model	Intercept	YST	YST ²	YST ³	lnDIB	DIB/Dq	RD	SI	PDSI	PDSI * RD	PDSI * lnDIB	PDSI * SI	AICC	ΔAICC	Akaike weights
Base	-2.4314 (0.2896)	0.0116 (0.0036)	-0.0020 (0.0002)	0.000031 (0.000002)	1.5452 (0.0747)	0.2488 (0.0764)	-1.1339 (0.1447)	0.0097 (0.0082)					19974.3	675.7	0.000
PDSI_{ANNUAL}															
1	-2.2072 (0.2921)	0.0132 (0.0035)	-0.0019 (0.0002)	0.000029 (0.000002)	1.4020 (0.0747)	0.3924 (0.0771)	-1.4630 (0.1473)	0.0168 (0.0084)	0.0232 (0.0013)				19637.2	338.6	0.000
2	-2.1970 (0.2918)	0.0125 (0.0035)	-0.0018 (0.0002)	0.000029 (0.000002)	1.3945 (0.0746)	0.4037 (0.0770)	-1.4583 (0.1470)	0.0169 (0.0084)	0.0590 (0.0043)	-0.0860 (0.0099)			19563.3	264.7	0.000
3	-2.1985 (0.2917)	0.0124 (0.0035)	-0.0018 (0.0002)	0.000029 (0.000002)	1.3933 (0.0746)	0.4112 (0.0770)	-1.4526 (0.1470)	0.0169 (0.0084)	0.2169 (0.0171)		-0.0525 (0.0046)		19510.7	212.1	0.000
4	-2.2052 (0.2920)	0.0132 (0.0035)	-0.0019 (0.0002)	0.000029 (0.000002)	1.4023 (0.0747)	0.3922 (0.0771)	-1.4560 (0.1437)	0.0166 (0.0084)	0.0539 (0.0127)			-0.0001 (0.0004)	19633.3	334.7	0.000
5	-2.1912 (0.2915)	0.0117 (0.0035)	-0.0018 (0.0002)	0.000028 (0.000002)	1.3852 (0.0745)	0.4233 (0.0769)	-1.4580 (0.1468)	0.0172 (0.0084)	0.2132 (0.0185)	-0.0838 (0.0102)	-0.0546 (0.0049)	0.0015 (0.0004)	19444.2	145.6	0.000
PDSI_{GROW}															
6	-2.3367 (0.2920)	0.0109 (0.0035)	-0.0018 (0.0002)	0.000030 (0.000002)	1.4824 (0.0744)	0.3045 (0.0762)	-1.2929 (0.1452)	0.0131 (0.0083)	0.0227 (0.0010)				19415.5	116.9	0.000
7	-2.3234 (0.2918)	0.0104 (0.0035)	-0.0018 (0.0002)	0.000029 (0.000002)	1.4811 (0.0744)	0.3074 (0.0762)	-1.2905 (0.1451)	0.0131 (0.0083)	0.0361 (0.0032)	-0.0326 (0.0075)			19398.7	100.1	0.000
8	-2.3086 (0.2916)	0.0103 (0.0035)	-0.0018 (0.0002)	0.000029 (0.000002)	1.4723 (0.0743)	0.3203 (0.0762)	-1.2929 (0.1450)	0.0131 (0.0083)	0.1268 (0.0130)		-0.0282 (0.0035)		19353.4	54.8	0.000
9	-2.3258 (0.2920)	0.0109 (0.0035)	-0.0018 (0.0002)	0.000030 (0.000002)	1.4821 (0.0744)	0.3049 (0.0762)	-1.2926 (0.1452)	0.0131 (0.0083)	0.0257 (0.0095)			-0.0001 (0.0003)	19417.4	118.8	0.000
10	-2.3139 (0.2916)	0.0097 (0.0035)	-0.0018 (0.0002)	0.000028 (0.000002)	1.4731 (0.0743)	0.3205 (0.0761)	-1.2939 (0.1449)	0.0134 (0.0083)	0.1173 (0.0141)	-0.0360 (0.0077)	-0.0313 (0.0037)	0.0011 (0.0003)	19332.1	33.5	0.000
PDSI_{MJJ}															
11	-2.3137 (0.2920)	0.0094 (0.0035)	-0.0018 (0.0002)	0.000029 (0.000002)	1.4851 (0.0744)	0.2934 (0.0763)	-1.2952 (0.1453)	0.0130 (0.0084)	0.0201 (0.0009)				19474.8	176.2	0.000
12	-2.3038 (0.2917)	0.0085 (0.0035)	-0.0017 (0.0002)	0.000028 (0.000002)	1.4825 (0.0744)	0.2958 (0.0762)	-1.2859 (0.1451)	0.0129 (0.0083)	0.0397 (0.0030)	-0.0477 (0.0070)			19430.8	132.2	0.000
13	-2.2702 (0.2917)	0.0079 (0.0035)	-0.0017 (0.0002)	0.000028 (0.000002)	1.4673 (0.0743)	0.3099 (0.0761)	-1.2974 (0.1451)	0.0133 (0.0083)	0.1619 (0.0122)		-0.0384 (0.0033)		19342.0	434.4	0.000
14	-2.3088 (0.2919)	0.0094 (0.0035)	-0.0018 (0.0002)	0.000029 (0.000002)	1.4834 (0.0744)	0.2956 (0.0763)	-1.2939 (0.1453)	0.0129 (0.0083)	0.0356 (0.0089)			-0.0005 (0.0003)	19473.7	175.1	0.000
15	-2.2688 (0.2915)	0.0068 (0.0035)	-0.0016 (0.0002)	0.000027 (0.000002)	1.4674 (0.0743)	0.3085 (0.0761)	-1.2910 (0.1449)	0.0134 (0.0083)	0.1556 (0.0132)	-0.0468 (0.0072)	-0.0410 (0.0035)	0.0011 (0.0003)	19298.6	0.0	1.000

Table 2

Individual tree and plot-level attributes.

Variable	Mean	Min	Max	Standard deviation
Diameter inside bark (DIB; cm)	39.8	7.5	83.1	10.8
Site index (m)	31.9	22.9	40.2	3.3
Quadratic mean diameter (Dq; cm)	43.8	15.9	76.3	10.3
Relative density	0.39	0.09	0.74	0.13
DIB/Dq	0.92	0.22	1.84	0.17
PDSI _{ANNUAL}	-0.04	-4.30	3.93	1.67
PDSI _{GROW}	-0.12	-5.09	5.31	1.91
PDSI _{MJJ}	-0.09	-5.14	5.36	2.02

PDSI_{MJJ}*DIB interaction was observed, meaning BAI of larger trees was less responsive to increased PDSI_{MJJ} than smaller diameter trees. For example, the increase in annual BAI between PDSI_{MJJ} values of -5.14 and 5.36, holding all other variables constant, for small (DIB = 22.6 cm) diameter trees was 4.1 cm² yr⁻¹ compared to only 2.1 cm² yr⁻¹ for large (DIB = 58.2 cm) diameter trees 23 years after thinning (Fig. 2). A significant positive PDSI_{MJJ} * SI interaction was also observed. For trees located in a plot with SI = 25.6 m, and holding all other variables at their mean value, this translates into an increase in BAI of 2.8 cm² yr⁻¹ between PDSI_{MJJ} values of -5.14 and 5.36 compared to 6.0 cm² yr⁻¹ in a plot where SI = 36.9 m 23 years after thinning (Fig. 3).

4. Discussion

The development of adaptation strategies that promote the resistance or resilience of forest stands and landscapes to the

negative effects of climate change is of ecological and economic importance (Vose and Klepzig, 2013). The direct and indirect effects of climate change, all of which have the potential to strongly affect ecosystem structure, function, and composition, are numerous (Dale et al., 2001; Allen et al., 2010; Vose et al., 2012). For tree growth and productivity, an increase in frequency, severity, and extent of drought events will likely manifest in decreased tree- and stand-level growth (Magruder et al., 2013). In this study, we sought to identify whether manipulating stand density through forest thinning activities modulates the response of individual tree growth to climate in temperate deciduous forests of the southern Appalachian Mountains – an area containing some of the most diverse and productive temperate forests in North America (Trani Griep and Collins, 2013).

When interactions between PDSI and structure and productivity variables were included in the growth models (i.e., hypotheses), we found moisture availability during the months of May, June, and

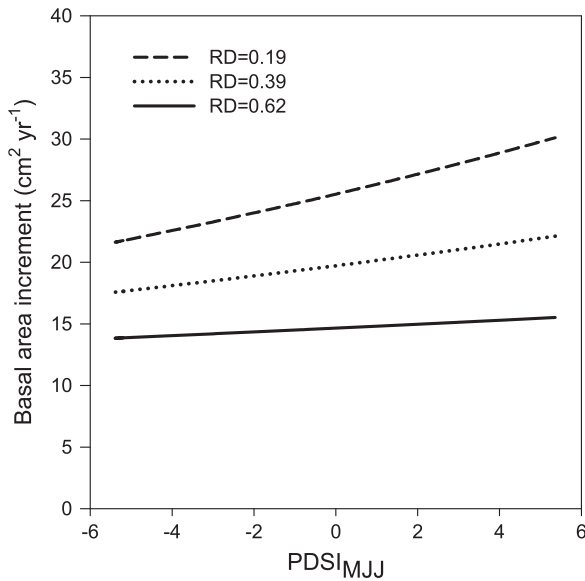


Fig. 1. Annual basal area increment (BAI) relative to changes in $PDSI_{MJJ}$ based on Model 15 (23 years post-thinning, i.e., mean years since thinning) for trees from low (relative density (RD) = 0.19, i.e., 5th percentile), moderate (RD = 0.39, i.e., mean), and high (RD = 0.62, i.e., 95th percentile) density plots. All other independent variables (i.e., diameter inside bark, site index, and diameter inside bark/quadratic mean diameter) were held constant at their mean values.

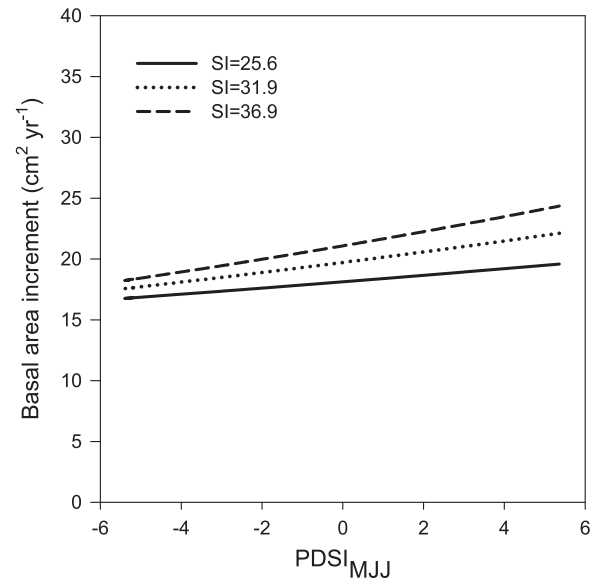


Fig. 3. Annual basal area increment (BAI) relative to changes in $PDSI_{MJJ}$ based on Model 15 (23 years post-thinning, i.e., mean years since thinning) for trees from low (site index (SI) = 25.6 m, i.e., 5th percentile), moderate (SI = 31.9 m, i.e., mean), and high (SI = 36.9 m, i.e., 95th percentile) productivity plots. All other independent variables (i.e., relative density, diameter inside bark, diameter inside bark/quadratic mean diameter) were held constant at their mean values.

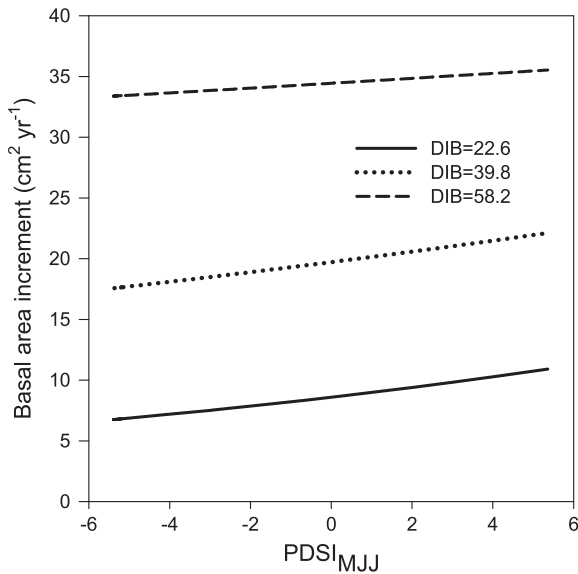


Fig. 2. Annual basal area increment (BAI) relative to changes in $PDSI_{MJJ}$ based on Model 15 (23 years post-thinning, i.e., mean years since thinning) for small (diameter inside bark (DIB) = 22.6 cm, i.e., 5th percentile), medium (DIB = 39.8 cm, i.e., mean), and large (DIB = 58.2 cm, i.e., 95th percentile) diameter trees. All other independent variables (i.e., relative density, site index, diameter inside bark/quadratic mean diameter) were held constant at their mean values.

of longer-term moisture patterns, the intensity of drought during the summer months is dependent on cumulative patterns from previous months. A greater dependency of yellow-poplar on soil moisture during the summer suggests that, in addition to potential declines in precipitation (McNulty et al., 2013), changes in the seasonality of precipitation have the potential to affect the annual growth of yellow-poplar.

Confirming the results from plantation-origin conifer forests in North America (D'Amato et al., 2013; Magruder et al., 2012, 2013) and Europe (Pérez-del-Lis et al., 2011; Kohler et al., 2010; Misson et al., 2003a,b), we found that stand density significantly interacts with climate to influence annual tree growth. The mechanisms by which this happens include increased resources, in particular water availability, on a per-tree basis and decreased above- and below-ground competition (Martín-Benito et al., 2010). In this study, BAI of trees growing in stands of lower relative density (RD), with all other factors (i.e., DIB, DIB/Dq, SI) equal, responded to increases in $PDSI_{MJJ}$ at a faster rate than trees growing in stands of greater RD (Fig. 1). According to McDowell et al. (2006), tree-level structural attributes often observed in high density stands, including small root systems (Litton et al., 2003) and low sapwood permeability brought about, in part, by narrower growth rings (Shelburne et al., 1993; Reid et al., 2003), may limit the ability of trees in high density stands to respond to increased soil moisture availability (e.g., Gea-Izquierdo et al., 2009; Kohler et al., 2010).

Thinning increases individual tree growth, with the magnitude and longevity of increase greater with increasing thinning intensity (Keyser and Brown, 2014; Latham and Tapeiner, 2002; Harrison et al., 1986; Beck and Della-Bianca, 1975). The results of this study suggest as tree diameter increases, the sensitivity of BAI to moisture availability, as inferred by PDSI, decreases (Fig. 2). In other words, relative to smaller trees, the rate of increase in BAI of larger trees in response to increased moisture availability was less than that of smaller diameter trees. D'Amato et al. (2013) reported low density red pine stands, characterized by larger trees resulting from heavy and repeated thinnings, experienced substantially greater reductions in stand-level growth in response to drought than high density stands characterized by small diameter trees.

July ($PDSI_{MJJ}$) during the current year of ring formation had more influence on annual BAI of yellow-poplar than average moisture availability throughout the year ($PDSI_{ANNUAL}$) or growing season ($PDSI_{GROW}$) of ring formation (Table 1). Our results using $PDSI_{MJJ}$ confirm results from previous studies that suggest moisture availability during the summer months, including July (Pan et al., 1997), May through June (Tryon et al., 1957), and June through July (Beck, 1985) were the most important climatic factors influencing the growth of yellow-poplar in the southern and central Appalachian Mountains. Since PDSI is a measure of the duration and intensity

The authors suggest the greater leaf area maintained by larger trees in these low density stands, and their correspondingly high moisture requirements, confers increased susceptibility to reduced growth during periods of moisture deficit. In addition, an increase in maintenance respiration of root and sapwood tissue (McDowell et al., 2008; Amthor, 2000), both of which often increase with tree size (Martin et al., 1998; Vogt et al., 1995; Bolte et al., 2004) during periods of moisture deficit may further exacerbate declines in tree growth. For yellow-poplar, leaf area increases with tree size (Martin et al., 1998). However, unlike the coarse-textured soils (Powers et al., 2010) characterizing the study site utilized by D'Amato et al., (2013), the soils in our study locations possess high soil water holding capacity (Beck and Della-Bianca, 1981), possibly buffering large trees, and their associated high water requirements, from more substantial reductions in growth during drought events.

The positive relationship between site productivity and tree- and stand-level growth is well established (Knoebel et al., 1986; Carmean, 1972). As expected, BAI was greatest for trees located in plots of progressively greater SI. Basal area increment, however, was more sensitive to changes in PDSI_{MJJ} for trees growing on plots of progressively higher SI (Fig. 3). Many studies have documented an increased sensitivity to declining growth under drought conditions as site productivity improves. For example, yellow-poplar located on more mesic sites has been shown to experience greater reductions in radial growth during drought events than yellow-poplar located on more xeric sites (Fekedulegn et al., 2003; Orwig and Abrams, 1997). Similarly, Leonelli et al., (2008) reported the growth of trembling aspen (*Populus tremuloides* Michx.) was more sensitive to climate as SI increased. Orwig and Abrams (1997) suggests the lower allocation of biomass to roots on higher productivity sites (Keyes and Grier, 1981) limits a tree's access to soil moisture during drought. Given decreased sapwood permeability may limit the ability of trees in high density stands to respond to increased soil moisture (McDowell et al., 2006), sapwood permeability, which can be reduced in low versus high productivity sites (Shelburne et al., 1993), may, in combination with differential patterns of root biomass, be partly responsible for the lower sensitivity of trees to changes in PDSI_{MJJ} in sites of low SI.

5. Conclusions

In these even-aged, pure yellow-poplar forests, adaptation strategies for climate change are focused on increasing resilience or resistance to disturbance and stressors, including an increase in the frequency, severity, and extent of drought. Due to the competitiveness of yellow-poplar on these productive sites, altering species composition to favor more drought-resistant species, such as oak species (Abrams, 1990), another possible climate change adaptation strategy (Millar et al., 2007), is problematic (Loftis, 1990; Beck and Hooper, 1986). Results from this study suggest modifying stand structure through forest thinning activities can alter the response of yellow-poplar to variations in soil moisture availability, with moisture in the months of May, June, and July exerting the most influence over tree growth. Specifically, thinning to low densities can result in a significant, and often long-term (Keyser and Brown, 2014) increases in tree growth during periods favorable to growth (i.e., ample moisture or high PDSI values) and creates a structure in which competition is low enough such that trees maintain absolute growth rates above those observed in higher density stands during periods of moisture deficit (i.e., low PDSI). This study confirms stand structure, as well as measures of productivity should be considered when quantifying climate-growth relationships for forest tree species. Such information could not only aid in the identification of stands – low versus high

density; high versus low productivity – most susceptible to the negative impacts (e.g., reduced growth) of climate change, but also be used to develop site- or stand-specific silvicultural prescriptions focused on promoting resilience or resistance under a changing climate. Furthermore, although the models (i.e., hypotheses) we present address the effects of historical climate and not forecasted climate, our results do suggest climate variables along with their interactions with site and structural variables be evaluated and considered during the development of climate-sensitive growth and yield models (e.g., Crookston et al., 2010).

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