



A comparison of the climate response of longleaf pine (*Pinus palustris* Mill.) trees among standardized measures of earlywood, latewood, adjusted latewood, and totalwood radial growth

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Abstract

Key message Longleaf pine radial growth is primarily driven by late summer moisture availability, latewood and adjusted latewood are more sensitive to climate than either earlywood or totalwood, and there is a high level of agreement spatially in growth/climate responses.

Abstract Our objective was to examine broadly the climate–growth responses of longleaf pine (*Pinus palustris* Mill.) on the Coastal Plain province of North and South Carolina to temperature, precipitation, and drought severity. We compared the responses between standardized earlywood, latewood, adjusted latewood, and totalwood radial tree growth. We sampled mature longleaf pine growing in open-canopy savanna environments and developed six tree-ring chronologies using standard dendroecological techniques. We used a combination of Pearson correlation, moving interval correlation, and Fisher r – z tests to determine which monthly and seasonal variables were most closely related to radial growth, the temporal stability of the dominant growth/climate relationship, and whether earlywood and latewood growth provide significantly different climate responses. Our results show that the strongest relationships with climate are with adjusted latewood growth and that rainfall in the later parts of the growing season (i.e., July–September) is the primary control of radial growth. Spatially, we found that growth/climate responses were similar throughout the Coastal Plain region encompassing the six study sites. Temporally, we found that July–September precipitation produced significant ($p < 0.05$) relationships with radial growth for extended annual intervals, but there were shorter periods when this relationship was non-significant. In general, growth/climate relationships were stronger for latewood compared to earlywood, and these responses were significantly ($p < 0.05$) different at about half of our study sites. Our findings are congruent with prior research in this region showing that short-duration precipitation events are a critical component for radial growth. Further, these results emphasize the importance of latewood growth—particularly adjusted latewood growth—in capturing interannual climate/growth responses.

Keywords Longleaf pine · Growth/climate relationships · Earlywood · Latewood · Tree rings

Introduction

Longleaf pine (*Pinus palustris* Mill.; LLP) has been long recognized as a valuable biorecorder of climatic conditions. The first analyses of relationships between radial growth of LLP and climate date to the 1930s (Lodewick 1930; Coile 1936). Radial growth of LLP has been examined in studies focused on: (1) seasonal and monthly growth climate relationships (Henderson and Grissino-Mayer 2009; Mitchell et al. 2019a, 2020), (2) comparisons across physiographic (Patterson et al. 2016; Mitchell et al. 2019b) and hydrologic gradients (Foster and Brooks 2001), (3) relationships with ecological disturbances (Devall et al. 1991; Pederson et al. 2008), (4) relationships to cone production (Patterson and

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Knapp 2018), (5) the impacts of competition (Meldahl et al. 1999) and prescribed burns on radial growth (Zahner 1989; Ames et al. 2015), (6) climate–growth relationships at the latitudinal margins of the range (Bhuta et al. 2009), and (7) multi-century climatic reconstruction of rainfall from tropical cyclones (Knapp et al. 2016, 2020). The utility of LLP in various subdisciplines of ecology and climate science (e.g., dendroecology, dendroclimatology, dendromastecology) is thus well established, despite the limited number of old growth stands minimally impacted by human agency (Varner and Kush 2004).

Longleaf pine is climatically sensitive to different periods of seasonal precipitation, but there has been no systematic comparison of which radial growth measurement (e.g., earlywood, latewood) most effectively captures interannual variability of climate. LLP totalwood was positively associated with previous June–current August precipitation in the Coastal Plain of central Florida (Schumacher & Day 1939), with February–May precipitation in the southern Georgia Coastal Plain (Coile 1936), and with precipitation during August in the southern Mississippi Coastal Plain (Devall et al. 1991). Additionally, totalwood was best associated with March–October precipitation (+) in the southern Alabama Coastal Plain (Meldahl et al. 1999) and positively associated with current winter temperature and precipitation while negatively associated with previous August PDSI near the species northern range limit in southeastern Virginia (Bhuta et al. 2009). LLP earlywood is positively associated with 2-year lagged March PHDI and negatively associated with maximum temperature during February–April (current year) in Southern Alabama (Meldahl et al. 1999). LLP LW is most strongly influenced by late summer precipitation (Henderson and Grissino-Mayer 2009; Knapp et al. 2016; Patterson et al. 2016, and Mitchell et al. 2019a) and typically exhibits strong mean sensitivity (e.g., Meldahl et al. 1999; Henderson and Grissino-Mayer 2009).

LLP forests provide critical habitat and conservation efforts have been initiated to restore altered ecosystems (McIntyre et al. 2018). The historic range of LLP has declined from ~37 million ha to 1.75 million ha since European settlement, particularly due to land-use changes, deforestation, and fire suppression (Frost 2007). Given the

ecological importance of these forests as biologically rich habitats (Means 1996), including endangered species (e.g., the eastern indigo snake (*Drymarchon couperi*, Means 1996) and the red cockaded woodpecker (*Dryobates borealis*, Kaiser et al. 2020)), management efforts are in place to increase the area of LLP-dominated ecosystems by 1.5 million ha by 2025 (McIntyre et al. 2018). Additionally, because of the longevity of LLP (Earle 2020) coupled with the slow decay rates of remnant stumps, the species serves as a valuable data source for ecological (e.g., Cippolini et al. 2019; Patterson 2020), dendroclimatic (e.g., Henderson and Grissino-Mayer 2009; Patterson et al. 2016) and dendroecological studies (e.g., Devall et al., 1991; White and Harley 2016; Rother et al. 2018; Kaiser et al. 2020).

In a previous study (Knapp et al. 2016) using data from two of the sites included in this study, LLP had an exceptionally strong relationship ($r=0.71$, $p<0.01$) with precipitation specifically delivered from tropical cyclones. Here, we investigate more fully the relationship between climate and radial growth by including measures of LLP earlywood (EW), latewood (LW), adjusted latewood (LWA) and totalwood (TW), and relate these measures to monthly and seasonal values of temperature, precipitation, and drought severity. Our specific objectives are to: (1) determine the primary climatic drivers of radial growth for LLP growing within portions of the Coastal Plain province of North and South Carolina, (2) determine whether significant differences in growth/climate relationships exist between EW and LW radial growth, and (3) determine the long-term temporal stability of the strongest growth/climate relationships.

Methods

We collected samples from LLP at six sites in the Coastal Plain region of eastern North and South Carolina (Table 1, Fig. 1). All locations were low elevation (<20 m for all sites except MBL which is <60 m) open-canopy savannas with either old growth remnants or mature trees evolving in the post-naval stores industry era. The sites are sandy uplands typically surrounded by pocosin bogs, with the dominant tree in the bogs being pond pine (*Pinus serotina* Michx).

Table 1 Site chronology statistics for the LW chronologies and relationships (via Pearson r values) between EW and LW radial growth (all r values significant at $p<0.01$) across the six sites

3-Letter Site code	# of samples in full chronology	Interseries correlation	Minimum EPS 1905–end year	Year chronology ends	r value EW/LW
CFL	40	0.51	0.91	2018	0.71
MRL	40	0.56	0.89	2017	0.65
HSL	49	0.52	0.91	2016	0.55
GSL	42	0.54	0.91	2017	0.63
LOL	36	0.49	0.81	2017	0.55
MBL	29	0.4	0.73	2017	0.54

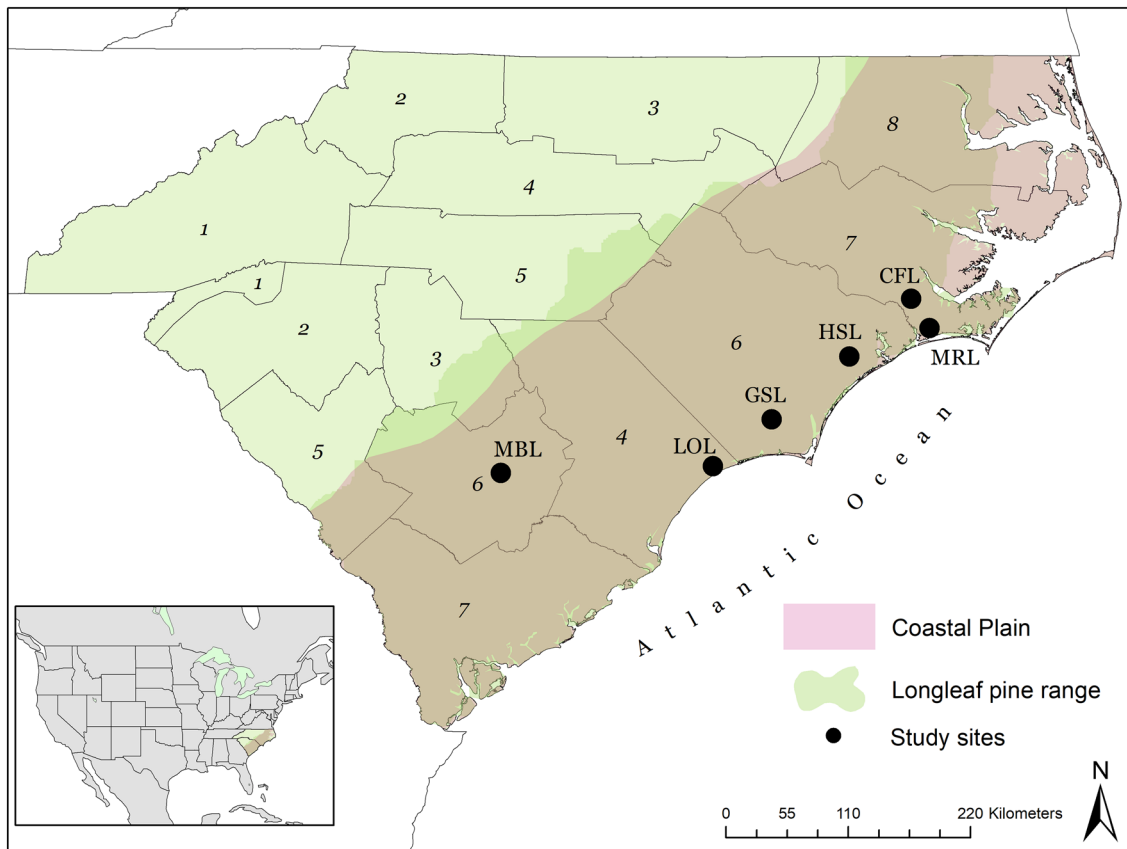


Fig. 1 Location of the six study sites, climatic division boundaries, and current range of longleaf pine in North and South Carolina. The intersection of the Coastal Plain region and longleaf pine range is shaded brown. (created using ArcMap)

Four of the sites (CFL, MRL, HSL, GSL) are located on Carolina Bay rims (Lide et al. 1995), and the longleaf pine grow on deep, sandy soil profiles (NRCS 2019) that are elevated (0.5–1 m) above the pocosin bogs that frequently contain standing water. Wiregrass (e.g., *Aristida stricta* Michx.) is common and facilitates frequent surface fires (Frost 2007) and charred wood remnants were present at all sites. While high winds and fire are a component of Coastal Plain longleaf ecosystems, crown fires are rare due to the open-canopy conditions (Platt et al. 1988) and, where present, surrounding pocosin bogs that serve as fuel breaks. Ames et al. (2015) found that while fire can cause declines in LLP radial growth, this influence was short term, only impacting current year growth.

The climate of the region is humid subtropical, and there is minimal variability in climatic conditions among the four climatic divisions where our study sites are located (Fig. 2). North Carolina division seven is the coldest and wettest, with a mean annual temperature of 16.2 °C and annual precipitation of 130 cm. The warmest and driest conditions are in the only division without an Atlantic Ocean boundary, South Carolina division six (17.4 °C, 118 cm). At all four divisions, precipitation is maximized during the summer

(June–September), and precipitation delivered to the region specifically from tropical cyclones (Bregy et al. 2020) has been shown to be a significant driver of longleaf pine radial growth (Knapp et al. 2016, 2020). LLP are resilient to winds generated by landfalling hurricanes (Provencher et al. 2001). Thus, in the absence of human disturbance, stands develop with live trees > 300 years of age (Knapp et al. 2020).

At each site, we sampled live trees using 5.15-mm diameter increment borers. We obtained two core samples per tree to account for asymmetrical tree growth and to improve the climate signal (Fritts 2012) from 30+ trees per site by sampling approximately 1 m above ground level. If there was any canopy overlap between two trees, we excluded them from the sample. Further, we also excluded trees that had any visual signs of damage from lightning strikes, wind, or pathogens. We placed all collected samples in paper straws to air dry. In some cases, we also used chainsaws to obtain sections from stumps and included these data in the final chronologies. We followed standard laboratory procedures for processing the core samples (Stokes and Smiley 1996). Specifically, we glued the cores to wooden mounts and used a progression of finer sandpaper grits to reveal the cellular structure under magnification.

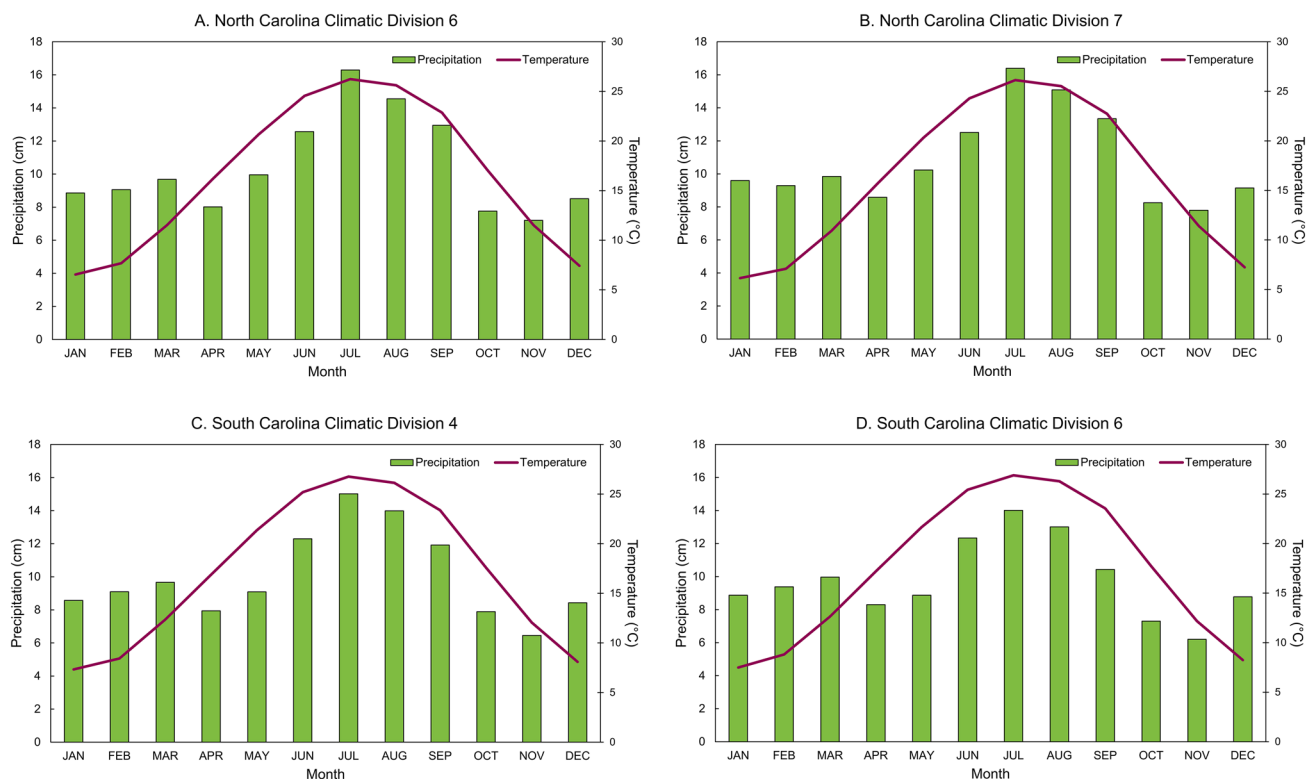


Fig. 2 Climographs showing mean monthly temperatures (C) and total precipitation (cm) for the four climatic divisions where our study sites are located. Climatic divisional data from: <https://psl.noaa.gov/cgi-bin/data/timeseries/timeseries1.pl>. (created using Microsoft Excel)

Prior work in this region established that the most accurate crossdating of samples occurred with the LW portion of growth (Knapp et al. 2016, 2020). We experimented with crossdating using the EW, LW, and TW record, and found the LW growth, because of its higher interannual variability, provided the most reliable results. Thus, we used the LW portion of the radial growth data in association with the list method (Yamaguchi 1991) to crossdate samples from each site and quality controlled the crossdating with the computer program COFECHA (Holmes 1983). We then included the same mix of core samples in the EW and TW chronologies for each site. We created measurement files of EW, LW, and TW widths using the program WIND-ENDRO (Regent Instruments 2013). Longleaf pine radial growth contains intra-annual density fluctuations (IADFs, Mitchell et al. 2019c) that may complicate ring measurements. This includes Type E+, which represents a transition between EW and the beginning of LW, and Type L+, which is characterized by EW-like growth near the end of LW (*c.f.* Campelo et al. 2007). For rings with IADFs, we consistently measured LW by excluding E+ widths, but including L+ widths, thus ensuring accurate and consistent measurements. We standardized all radial growth files (*i.e.*, EW, LW, TW) using ARSTAN (Cook and Holmes 1996) and the spline-fitting Friedman super smoother with a tweeter

sensitivity of five (Friedman 1984). The super smoother is an adaptive smoothing regression that is ideal for removing the higher-frequency variance of growth related to disturbance while retaining the lower frequency variance of growth associated with climate (Friedman 1984). Detrending also removes the biological growth trend associated with a tree getting bigger through time. For each site, we used the results from the standard chronology to search for relationships between EW, LW and TW radial growth and climatic conditions. Further, to account for the potential inertia influence of EW on LW, we created an adjusted LW index (LWA; Meko and Baisan 2001).

We examined Pearson correlation values between EW/LW/TW/LWA and monthly (seasonal) precipitation, mean temperature, and Palmer Drought Severity Index (PDSI) variables using climatic division data (<https://psl.noaa.gov/cgi-bin/data/timeseries/timeseries1.pl>; NC 7 for CFL and MRL; NC 6 for HSL and GSL; SC4 for LOL; SC6 for MBL; Fig. 1) during 1905–2016, –2017 or –2018. We also examined the relationship between EW and LW using Pearson correlation. Although the climatic division data extend to 1895, the early portion of the record can be volatile due to a lack of stations contributing to the divisional data (Keim et al. 2003). To avoid this potential volatility, we began our analyses in 1905. From the climate/growth correlation analyses, we present

monthly patterns of climate/growth relationships graphically to compare among the six study locations. From each site, we used the Fisher r to z transformation test to determine if EW or LW has a significantly stronger relationship with the monthly mean temperature, total precipitation, and PDSI variables most closely aligned with radial growth. We also used a 24-year moving interval correlation from the program Dendroclim2002 (Biondi and Waikul 2004) on the variable with the consistently strongest relationship with radial growth at each site to determine the temporal stability of the strongest growth/climate relationship. For each of the four climate divisions, we tested for the presence of long-term trends of July–September total precipitation using Kendall's Tau correlation.

Results

Results from the LW crossdating produced moderately strong interseries correlation values ranging from 0.4–0.56 (Table 1). While each chronology extends to at least the early portion of the nineteenth century, we are basing our climate/growth relationships on the period 1905–2016, –2017, or –2018, and over this time period the express population signals (Wigley et al. 1984; Buras 2017) are generally strong, ranging from 0.73 to 0.91 (Table 1). Relationships between EW and LW radial growth were positive, significant ($p < 0.01$), and moderately strong at all sites (Table 1).

Across the six sites, the weakest climate/growth relationships occur with mean temperature (Fig. 3). During

winter and into late spring, the impact of temperature on radial growth is generally positive, but this switches to a negative relationship beginning in June at all six sites, with the strongest negative relationships found in either July or August. For precipitation, the strongest signal across the six sites is that radial growth is positively and most strongly related to mid- to late summer (July–September; JAS) total precipitation, with the growth primarily manifested in the LW bands (Fig. 4). Weaker positive relationships exist across most sites in both midwinter (February) and early spring (April). Another pattern that emerges is for precipitation to have a negative impact on radial growth in autumn, with the strongest negative relationships in November.

The PDSI is a water balance-based measure of drought severity and includes both the impacts of supply (precipitation) and demand (temperature) of water over multi-month periods (Palmer 1965). Across the six sites, radial growth is positively related to the PDSI from March–December, with the strongest relationships generally observed in September (Fig. 5). This pattern is logical, as the relationship between late summer (August) mean temperature and precipitation is negative within the four climatic divisions (Fig. 1) containing the study sites (NC 7—CFL & MRL, $r = -0.17$, $p < 0.07$, $n = 114$; NC 6—HSL & GSL, $r = -0.26$, $p < 0.01$, $n = 114$; SC4—LOL, $r = -0.34$, $p < 0.001$; SC6—MBL, $r = -0.33$, $p < 0.001$). Thus, warmer/drier summers (i.e., negative PDSI) result in reduced radial growth and wetter/cooler summers result in enhanced radial growth.

Overall, we find that the growth/climate relationships are generally stronger for LW than EW, and most of the



Fig. 3 Monthly relationships (Pearson r) between earlywood (EW), latewood (LW), totalwood (TW), and adjusted latewood (LWA) ring widths and mean monthly temperature for **a** CFL, **b** MRL, **c** HSL, **d**

GSL, **e** LOL, and **f** MBL. r values > 0.185 (< -0.185) are significant at $p < 0.05$. Created using Microsoft Excel



Fig. 4 Monthly (seasonal) relationships (Pearson r) between earlywood (EW), latewood (LW), totalwood (TW), and adjusted latewood (LWA) ring widths and mean monthly precipitation for **a**

CFL, b MRL, c HSL, d GSL, e LOL, and f MBL. r values > 0.185 (< -0.185) are significant at $p < 0.05$. Created using Microsoft Excel



Fig. 5 Monthly relationships (Pearson r) between earlywood (EW), latewood (LW), totalwood (TW), and adjusted latewood (ADJ) ring widths and the Palmer Drought Severity Index (PDSI) for **a**

CFL, b MRL, c HSL, d GSL, e LOL, and f MBL. r values > 0.185 (< -0.185) are significant at $p < 0.05$ (Created using Microsoft Excel

strongest relationships are with LWA and JAS precipitation (Fig. 4). Relative to LW, LWA improved the strength of the relationship via Pearson correlation by an average of 0.05. At four of our six sites, there is a significantly stronger relationship between LW and precipitation than between EW and precipitation based on the monthly or seasonal variable producing the strongest precipitation/growth relationship

(Table 2). For the PDSI, LW has a stronger (positive) relationship than EW at all sites, and this is significant at half of the study sites.

The moving interval correlations reveal that the relationships between late summer (JAS) precipitation and LWA have substantial temporal and spatial variability. Across the four North Carolina sites, we found most of the strongest and

Table 2 Results from Fisher r to z transformation test to determine if EW or LW has a stronger relationship with the climate variable producing the strongest climate/growth relationship for precipitation, temperature, and PDSI at each study site for the full period of record (1905–end)

		Fisher r to z transformation test results					
		Precipitation		Temperature		PDSI	
		EW	LW	EW	LW	EW	LW
CFL							
Variable	July–Sept			March		Sept	
r value		0.07	0.382	0.129	0.203	0.221	0.395
p value		0.01		0.28		0.08	
MRL							
Variable	April			May		August	
r value		0.289	0.183	– 0.026	0.231	0.128	0.306
p value		0.2		0.03		0.08	
HSL							
Variable	July–Sept.			March		Sept	
r value		0.125	0.423	0.211	0.229	0.208	0.359
p value		0.01		0.44		0.11	
GSL							
Variable	July–Sept.			August		Sept	
r value		0.168	0.486	– 0.93	– 0.241	0.178	0.392
p value		0.01		0.13		0.04	
LOL							
Variable	July–Sept.			December		Sept	
r value		0.034	0.297	0.179	0.033	– 0.011	0.238
p value		0.02		0.14		0.03	
MBL							
Variable	April			March		Sept	
r value		0.171	0.313	0.096	– 0.203	0.062	0.344
p value		0.13		0.21		0.02	

Relationships significantly stronger at $p < 0.05$ are boldfaced

significant relationships during the 1950s–1970s (Fig. 6). The relationships became weaker and non-significant in at least a portion of the late 1980s to early 1990s, and then were significant again in the 2010s. For the two South Carolina study sites, the relationships were strongest and significant from the 1950s/60s until the late 1990s but have generally weakened since then. We found no long-term (i.e., 1905–end of record) trends in July–September total precipitation within the four climatic divisions containing our study sites (NC 7—CFL & MRL, $r = 0.02$, $p > 0.84$; NC 6—HSL & GSL, $r = 0.02$, $p > 0.75$; SC4—LOL, $r = 0.01$, $p > 0.94$; SC6—MBL, $r = -0.08$, $p > 0.18$).

One of our primary findings is that LLP LW bands are generally more sensitive to climatic variability than either the EW band or TW. Thus, although EW comprises the majority (average of 56%) of radial growth in any calendar year, they express comparatively less interannual variability than LW, hence their lower correlations with climate variables. Conversely, LW radial growth is significantly more sensitive to climatic variability for LLP growing in the Coastal Plain province of North and South Carolina. More

specifically, when the influence of EW is removed (i.e., when using LWA), the strongest relationships (with JAS precipitation; Fig. 4) emerge, suggesting that even though the climate–growth relationships with EW are generally weaker with contemporaneous climate variables, whatever conditions that favor EW positively affect LW through some inertia process. Wider EW supports wider LW widths as seen by both the significant, positive relationships between EW and LW (Table 1) and the general improvement in the strongest growth/climate relationships with LWA (Fig. 4). Thus, once we remove the influence of EW on LW (i.e., LWA), the true LW signal emerges.

Across the six sites, we found the consistently strongest growth/climate relationships with late summer moisture, measured either directly with JAS precipitation or through September PDSI, which accounts for both supply and demand for moisture throughout the growing season. Using PDSI, a more complete understanding of the growth/climate relationships emerges. LLP responds negatively to high summer temperature, thus years with low soil moisture due to reduced supply (low rainfall) and/or increased

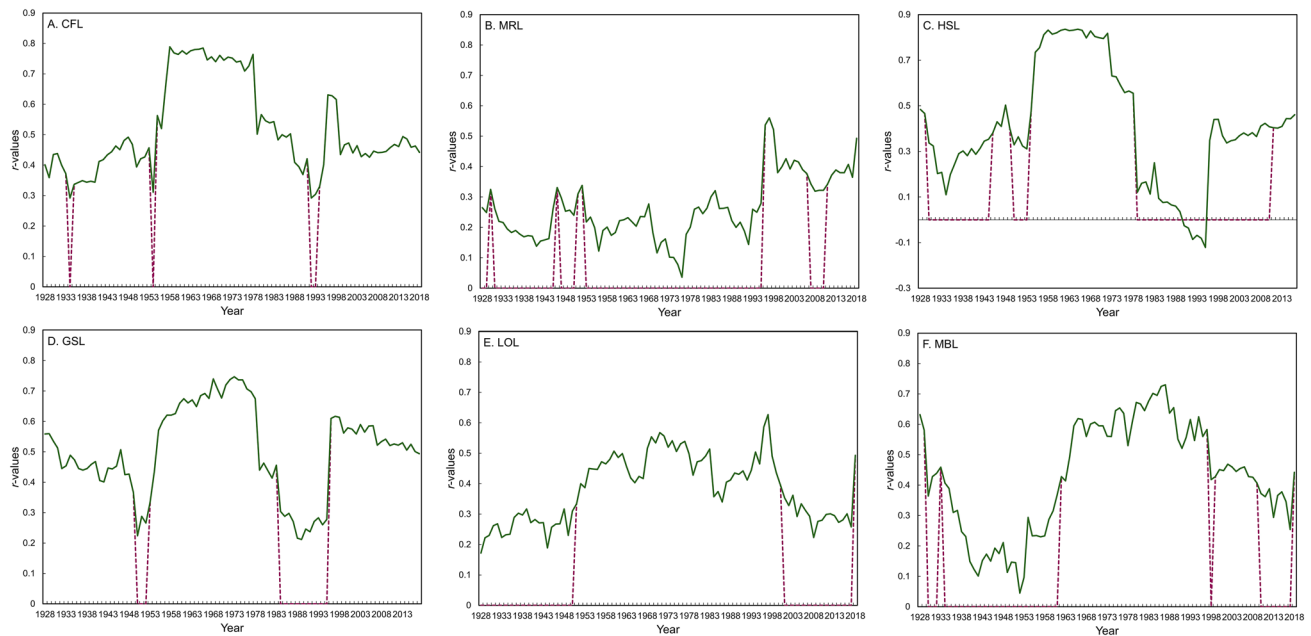


Fig. 6 24-year moving-interval correlations between adjusted latewood and total July–September precipitation for **a** CFL, **b** MRL, **c** HSL, **d** GSL, **e** LOL, and **f** MBL. When the purple dashed line falls

to zero, the relationship is not significant ($p > 0.05$). C Created using Microsoft Excel

demand (high temperature) are associated with low radial growth and vice-versa, as reflected in the strong positive relationships between LLP LW and LWA radial growth and late summer PDSI.

Discussion

Our primary growth/climate findings of positive growth with late summer moisture concur with prior studies of growth/climate relationships for LLP throughout the broad range of this species (Meldahl et al. 1999; Foster and Brooks 2001; Henderson and Grissino-Mayer 2009; Patterson et al. 2016; Mitchell et al. 2019a). Whereas other studies (e.g., Devall et al. 1991; Meldahl et al. 1999; Foster and Brooks 2001; Henderson and Grissino-Mayer 2009; Mitchell et al. 2019a) have demonstrated that LLP radial growth is most sensitive to climatic conditions during the portion of the growing season associated with LW bands (June to October; Lodewick 1930), by testing for significant differences in the relationships between EW and LW (Table 2), we are able to statistically demonstrate that LW radial growth patterns, particularly post-adjustment (i.e., LWA) are more sensitive to climatic variations than EW, despite being consistently narrower.

Our study is the first, to our knowledge, to examine the temporal stability of growth/climate relationships for LLP. Using moving interval analyses, we demonstrate that the

climatic drivers of radial growth exhibit significant temporal variability (Fig. 6). Specifically, at all sites there are extended periods when the relationship between JAS precipitation and LWA radial growth was significant, and generally shorter periods (with an exception at MRL) when the relationships remained positive but were non-significant ($p < 0.05$). We are unsure why the growth/climate relationships exhibit this degree of temporal variability. At CFL (NC Climatic Division 7), GSL and HSL (NC Climatic Division 6) the temporal pattern of relationships between LWA radial growth (Fig. 6) and July–September total precipitation appear to weakly mirror the temporal patterns of precipitation, as periods with significant relationships (e.g., 1950s–1970s and the 2010s) are concurrent with periods of greater total precipitation. While this might lead to a conclusion that JAS precipitation, as a driving force for radial growth, is stronger during extended wetter periods of late summer precipitation, the same pattern is not evident at the two South Carolina study sites (LOL and MBL) or at MRL. Thus, this seems an unlikely explanation given the high degree of interannual variability in precipitation.

In summary, for LLP growing in the Coastal Plain region of North and South Carolina, there is a high level of agreement spatially in growth/climate responses. Late summer moisture is the primary driving force for radial growth, and this is most strongly expressed in the LW bands. This finding matches the growth/climate response found in many areas within the natural range of LLP (Devall et al. 1991;

Henderson and Grissino-Mayer 2009; Patterson et al. 2016; Mitchell et al. 2019a). Our results support the work of Knapp et al. (2016, 2020) who used data from some of the sites in this study for multi-century climate reconstructions of tropical cyclone precipitation. They found precipitation delivered by tropical cyclones to be a significant component of late summer moisture in the region and more strongly associated with interannual variability in LW radial growth than what we present here. Further, they found that summer droughts inferred from narrow LW bands were years with minimal tropical cyclone precipitation, but not necessarily less summer precipitation, suggesting caution in interpretation of dendroclimatically derived drought years.

The strong relationship between LW and tropical cyclone precipitation has been examined in the context of microelevational variability by Montpellier et al. (2020), who found that elevational changes of under one meter resulted in significant increases in climate/growth relationships for LLP. They posit that rising water tables associated with tropical cyclone precipitation result in growth increases late in the growing season, which is congruent with our finding of the strongest relationships between LWA and late summer precipitation. Additionally, we find that EW generally does not correlate as strongly as LW with any of the commonly used climate variables used in dendrochronology. These findings suggest that EW has generally less sensitivity to climate variability than LW for LLP and are congruent with the hypothesis that short-duration, high-intensity precipitation events associated with tropical cyclones are a primary driver of radial growth for this tree species within the Coastal Plain province of the Carolinas (Knapp et al. 2016, 2020).

We conclude that the primary climatic drivers of radial growth for LLP growing within portions of the Coastal Plain province of North and South Carolina are JAS precipitation regardless of site and this relationship is best expressed using LWA. Further, we found that radial growth/precipitation relationships are significantly greater for LW compared to EW at four of our six sites. Temporally, while radial growth/precipitation relationships are typically significant and positive for extended periods, there are shorter intervals when these relationships become non-significant, potentially because of variability in precipitation delivery associated with landfalling hurricanes in the late summer period concurrent with LW growth. Finally, our results suggest the value of using LW chronologies for crossdating longleaf pine may be applicable to other southern pines (e.g., shortleaf pine, *Pinus echinata* Mill.) that also express considerable interannual variability in LW and are responsive to summer rainfall events. Specifically, because LWA accounts for the biological inertia effect of EW growth on LW it can improve the strength of the relationship with summer precipitation.

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Author contributions PTS, PAK, and JTM contributed to the study conception and design. Data collection and material preparation were performed by PTS, PAK, JTM, and TJM. Data analyses were performed by PTS, PAK, and JTM. TJM created the graphics. The first draft of the manuscript was written by PTS and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Availability of data and material Tree-ring chronologies are available from the corresponding author upon request.

Compliance with ethical standards

Conflict of interest/competing interests None declared.

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