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The Relationships between Climate, Tree-Ring Growth, and Cone Production in Longleaf Pine

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Abstract: Historically abundant longleaf pine (*Pinus palustris* Mill.) trees were once a leading source of profit and ecosystem services across the southeastern United States. The widespread decline in longleaf numbers following European colonization has prompted substantial restoration efforts, though much is still not understood about longleaf growth and reproductive processes. In this study, we used Pearson and regression correlation analysis to quantify the relationship between cone production, radial growth, and climate signals in longleaf pine trees at three sites across their range. We documented a high amount of intersite variability; trees at all three sites experienced significant relationships between reproduction, radial growth, and climate, though in different and sometimes contrasting ways. We found a roughly equivalent number of significant cone growth and climate correlations with extreme climate events (e.g., heat stress, hurricane frequency) as with average climate conditions, and highlight the need to consider both over multiple spans of time. This study provides a new understanding of how climate variables relate to the relationship between growth and reproduction in longleaf pine trees.

Keywords: longleaf pine; cone production; radial growth; resource allocation; climate; dendrochronology

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1. Introduction

Climate plays a crucial role in plant growth and forest health [1,2], and anthropogenic climate change is expected to pose a significant threat to many ecosystems [3,4]. In the Southeast United States, we can expect a continued increase in temperatures over time, as well as high variation in precipitation linked to extreme events such as hurricanes [5–9]. Another key climate variable is the el niño southern oscillation (ENSO) cycle, characterized by alternating periods of cold and wet (La Niña), then hot and dry (el niño) conditions [10]. ENSO cycles are known to significantly impact plant physiology due to close ties to climate variables such as precipitation and temperature [11,12], yet are becoming increasingly less predictable than before [13]. However, a changing climate may affect each plant taxon differently on short- and long-term scales [3,14–16]. While many traditional studies have examined the impact of mean temperature and precipitation, recent studies have highlighted the importance of extreme weather events such as intense rain or prolonged heat stress, which can directly impact plant physiological processes [17–19]. Yet how each taxon responds to extreme events is not fully known.

Structural adaptations of plants, as well as their interactions with climate, often relate to whole-plant success, and individual plants must acclimate to their given environment for survival [20–22]. When resources are limited, the principle of resource allocation suggests that plants must choose how to divide energy between different structures [23,24]. However, plant expression of resource allocation can vary over species, location, and time, and plants often change strategies in response to changing climate conditions [25–29]. Key among these is the frequently negative relationship between tree growth and reproductive effort [30]. However, relationships can be complex in longer-lived species; multiple studies have documented varied no-year to multiyear time lags in tree responses to changing climate conditions, the strength of which at times varied with the climate regime [25,31–34]. Yet, the exact resource allocation or other mechanisms behind these delays provide much potential for research.

Before European colonization, longleaf pine (*Pinus palustris* Mill.) savannas were the dominant ecosystem over 60–90+ million acres across the southeastern United States, yet now occupy less than 5% of their historical range due to factors such as overharvesting, fire suppression, and land-use change [35,36]. Despite the high levels of fragmentation and the poor quality of the remaining stands, longleaf forests still hold much ecological, environmental, and commercial value, and are the focus of substantial restoration efforts [35–38]. One factor that complicates reproductive success in longleaf pine is that cone production is temporally variable [35,39]. Weak masting cycles vary across the range and occur over 3–10-year cycles, though it is argued whether longleaf pine is a true masting species [40–42]. Masting, the regionally synchronized cycles of high and low seed production, is postulated to have evolved as a response to seed predators, limited resources, inefficient pollination, and climate conditions, or some combination thereof [12,32]. Yet if or how longleaf seed production relates to each of these factors is not fully understood [43].

Historical study of longleaf pine reproduction establishes that weather patterns such as precipitation influence early reproductive-structure success, and that mismatched favorable conditions between male (catkin) and female (conelet) structures can lead to heavy losses before fertilization [40,44]. Longleaf pines are wind-pollinated and monoecious [44]. The reproductive cycle is over two years from the time reproductive strobili begin to form until seed dispersion occurs [42]. Recent studies have revealed correlations between climate factors, sex allocation ratios, and the time of peak pollen shedding [45,46]. However, the bulk of long-term studies regarding reproductive output in longleaf pine rely on long-term annual cone data from mature trees at various Forest Service sites [33,41,42,47–50]. Climate–cone studies are often complicated by findings that correlations between climate and cone production are typically localized; there is not a strong or universal link between cone production and climate [39,41,42]. Yet, it was recently supported that climate factors alone may have a greater impact on cone production of longleaf pine than all other nonclimate factors combined [5]. However, few details are known about the intrinsic resource-allocation dynamics between reproduction and tree growth, or how climate impacts them.

Much about the relationship between climate and the growth of longleaf trees comes from correlative studies using dendrochronological records [51–53]. Longleaf pine trees can grow close to year-round in the southernmost part of their range and have been posited to grow from April through October in the northernmost areas [52–55]. Historically, many longleaf studies relied on radial totalwood (TW) growth, though recent papers have documented climate connections between latewood (LW, produced in the summer and fall) growth and late summer/early fall correlations with precipitation and temperature (+ and −, respectively) [52,53]. Earlywood (EW, produced in the spring) growth is generally held to be less sensitive to climate and is not often used [33,52,53]. Yet, many studies are geographically limited, even though results can vary widely even within the same state or region [33,52–54]. Several recent studies have successfully linked ENSO signals to longleaf pine radial growth with significant results [33,52]. Two commonly used ENSO signals include sea surface temperature (SST) and southern oscillation index (SOI), which are based on fluctuating temperatures and pressures, respectively [10]. One study [12] recently correlated ENSO data to reproduction in masting trees in NW America with significant results, though it is not clear whether there is a similar trend in longleaf pine.

In longleaf pine trees, there is a documented weak negative correlation between cone production and radial growth, though this relationship is largely overshadowed by the influence of other variables such as stand density [33,50]. Yet, these studies do not include an examination of specific climate variables other than drought [33,50]. One study [33] recently acquired cores from longleaf cone-count trees at multiple sites in the Central Southeastern US and correlated each individual's growth with its cone production. One key finding was a significant impact of bumper years, classified as $\geq$100 cones per tree [33].

When they categorized cone-crop years (i.e., bumper, good, fair, etc.) in growth–cone correlations, their results suggested that the relationship between BAI and cone production was almost exclusively influenced by the few bumper years of extreme cone production.

Here, we seek to combine the three processes of longleaf pine radial growth, cone production, and climate signals at three widespread sites across the southeast. Our objectives are to (1) quantify longleaf pine radial growth and cone production with monthly, seasonal, and yearly precipitation, temperature, SOI, SST, drought, wet, and extreme heat and cold, as well as to (2) quantify and compare the relationship between cone production and yearly radial growth under these climate regimes at each site. We hypothesize that these climate variables significantly correlate to radial growth and cone production, though the time of year may differ. However, we also hypothesize that relationships between growth and reproduction will be complex, owing to potentially mismatched influences of resource allocation versus similar optimal climate conditions.

2. Materials and Methods

2.1. Site Selection

We selected three established USDA Forest Service research sites for both their geographical spread and length of cone-count histories (Table 1):

1. Escambia Experimental Forest in Southern Alabama (hereafter Escambia)
2. Kisatchie National Forest in Louisiana (Kisatchie)
3. Bladen Lakes State Forest in Eastern North Carolina (Bladen Lakes)

Table 1. Location and description of longleaf pine study sites.

	Escambia	**Kisatchie**	**Bladen Lakes**
Latitude, longitude	31.0091, −87.0825	31.0249, −92.6359	34.7290, −78.5315
Elevation (approx. m.)	40	90	30
Average air temperature (°C)	19.8	19.5	17.6
Average precipitation (cm)	153.8	145.4	121.8
Average sampled tree age (years)	68.0	59.7	88.3
Number of available cone count years	64	53	41

2.2. Reproductive Data

We obtained long-term cone-count data from research scientists at the Southern Research Station of the United States Department of Agriculture—Forest Service. Through multiple decades, they have collected annual cone-count data for the same 10 or more trees at each of these sites across the longleaf pine range. Counts were completed on green cones in mid-to-late April. Additional details on procedures and findings for cone-count data can be found in the references [42,47,48].

2.3. Dendrochronological Data

At each site, we collected tree ring (“cookie”) data from close by stands of similar age and density to the associated cone-count stand. We felled three trees per site for a total of nine trees. From each tree, we collected thin (<10 cm.) cookies at the tree bottom and increased visibility on the cookie surface using an electric planar. As found by other longleaf studies [52,55], the transition from EW to LW growth was distinct each year, and there were relatively few unclear/partial rings. Then we took a high-resolution digital scan of each cookie. We used ImageJ to measure basal area increment (BAI) (BAI) for EW and LW growth for each year. After measuring BAI, we crossdated the trees using the list method to match years of narrow bands to other narrow band years, first by site, then between all sites using standard dendrochronology methods [56].

2.4. Climate Data

At each of the three sites, we used the National Oceanic and Atmospheric Administration's (NOAA) GIS mapping tool to locate and obtain available monthly climate data from the nearest weather stations to each site. Due to the incompleteness of each station's records, it was necessary to compile climate data from multiple nearby stations per site to obtain a complete record to match the length of tree ring data. For mean climate data, we included mean air temperature and precipitation; for extreme events, we included the total number of days over 32.2 °C or below 0 °C, as well as standardized precipitation index, drought, and wet categorizations (five NOAA categories from abnormal to exceptional all weighted equally). We also obtained NOAA 3.4 southern oscillation index (SOI) and sea surface temperature (SST) monthly indices (the standard region of ENSO used in climate studies), which began in 1951 and 1982, respectively. Additionally, we used NOAA's historical hurricane and tropical storm mapping tool to compile the number of hurricanes and tropical storms each site experienced each year using the site's default buffer zone.

2.5. Data Analysis

Before analyzing tree-ring data, we removed the pith and earliest five years of growth for more accurate detrending. We then converted collected basal area increment values (circular area in mm^2 to ring width in mm) to radial and detrended each site by age using ARSTAN software (natural log, negative exponential curve with any k (the constant level of growth that is by definition positive in old conifers; in young/variably-aged trees such as ours, a constant positive or negative level cannot be assumed)). Using bivariate correlations in SPSS v. 25, we used a Pearson correlation analysis to establish correlations between each applicable climate variable for both tree growth and cone production at monthly, seasonal, and yearly levels. We used a linear regression analysis to correlate cone data with annual radial growth from four years prior to the cone count through one year after (i.e., an April 2020 cone count was correlated with 2017, 2018, 2019, 2020, and 2021 radial-growth values). To test previous findings regarding bumper years of at least 100 cones [33], we then removed all bumper year data from the datasets and reran the analysis between cone production and radial growth. We considered significance at the $p < 0.05$ level.

Since longleaf pine natural processes do not coincide exactly with the standard calendar and can vary across the range, we modified the standard calendar year's climate data to match the natural growth and seasonal cycles of the trees. In formatting climate data to pair with the growth data, we considered a year's growth as the start of March of year x to the end of February of year x + 1. For example, we correlated 2020 radial growth with climate conditions from March 2020 through February 2021. Since cone production is almost a 3-year process with multiple significant dates in the year, we simply considered a year as the 12 months directly including and preceding the cone-count month of April. Since cone formation is a long process and environmental influences may not be expressed immediately, we considered cone production with all climate variables going back four full years from the cone count. For example, the site-specific cone count for 2020 was correlated with monthly and yearly climate data from May 2019–April 2020 (year 1; seasons: spring, summer, and fall 2019 with winter 2019/2020), May 2018–April 2019 (year 2), May 2017–April 2018 (year 3), and May 2016–April 2017 (year 4), while 2020 radial growth was correlated with monthly, seasonal, and yearly data from March 2020–February 2021.

3. Results

Our three study sites exhibited relatively similar climate regimes based on visual evaluation of annual temperature and precipitation trends (Figure 1). While cycles in radial growth appeared strongly linked between the three sites, trends in cone production were not as clear (Figure 1). EW and LW growth were strongly positively associated with each other ($p < 0.01$ at all three sites).

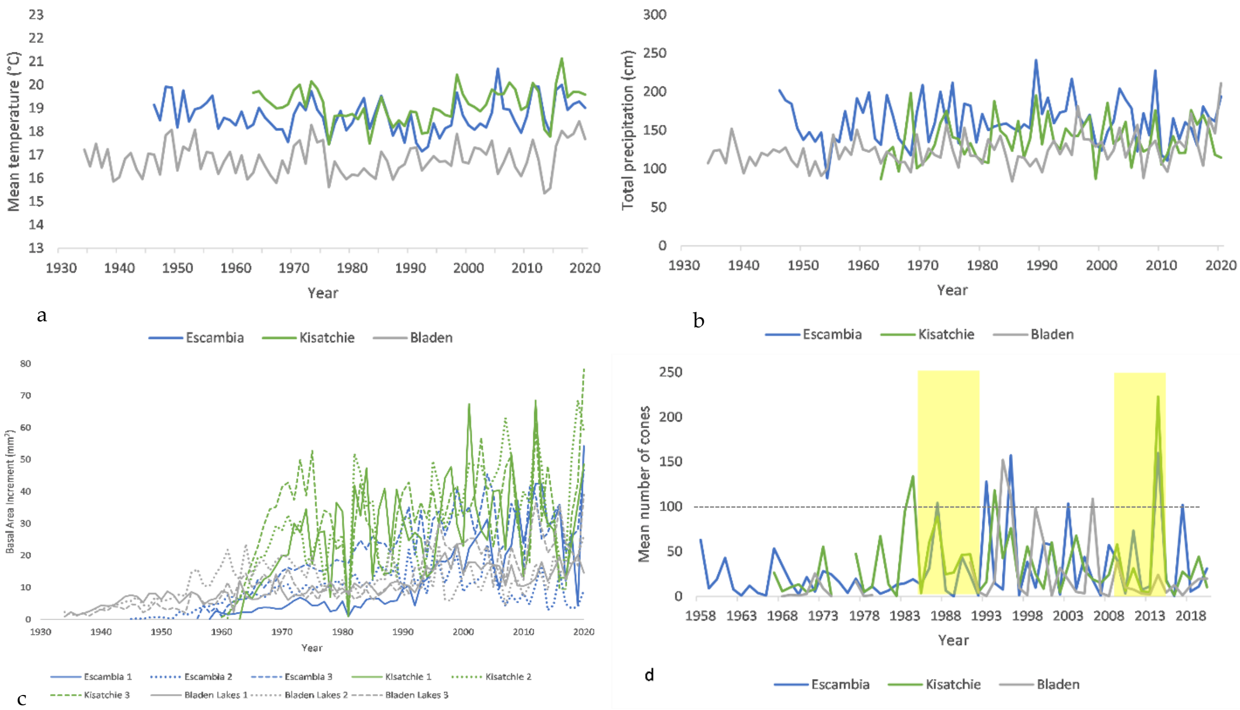

Figure 1. Overall climate, growth, and cone data at three longleaf pine sites. (**a**) is the annual mean temperature (°C), (**b**) annual total precipitation (cm), (**c**) raw tree-ring growth data for each sampled tree, and (**d**) mean annual cone production. (**d**) Areas highlighted in yellow indicate the years of the most synchronized cone production between all sites and values above the dashed line indicate bumper crop years.

3.1. Radial Growth and Mean Climate Signals

Our results indicate a greater number of significant growth–climate correlations with EW and TW, with substantially fewer significant LW correlations present (Table 2). There were multiple varied significant correlations between temperature/precipitation and EW, LW, and TW. However, monthly correlations were needed to demonstrate variability in temperature and precipitation correlations throughout the year, as sign changes occurred frequently (Figure 2). All SOI and SST correlation coefficients with TW at the monthly level were negative and positive, respectively. Yet, correlations were only significant during certain months, with SOI experiencing a larger and longer significant trend (Figure 2). While Escambia and Bladen Lakes had a similar number of significant ENSO–monthly TW correlations, Kisatchie had notably fewer significant correlations and tended to have higher p values than the other two sites. Yearly SOI was not significantly correlated to LW at any of the sites but was negatively correlated with TW at Kisatchie, and both EW and TW growth at Bladen Lakes and Escambia (Table 2). Yearly SST was only correlated positively with TW at Escambia and Bladen Lakes.

3.2. Radial Growth and Extreme Climate Signals

Annual ring width and extreme climate correlations, varied by site and sign changes, were present over time (Figure 3). The most consistent of the results was a largely negative correlation between radial growth and drought stress (Figure 3c). The only significant correlation between annual growth and any of the seasonal temperature extremes of the same year was a negative relationship between growth and the number of days over 32.2 °C during the summer at Kisatchie (p = 0.047). A comparison with the monthly analysis demonstrates the influence of June in this finding (Figure 3, p = 0.010). We found no significant correlations between any wet season and radial growth, though seasonal drought was significantly negatively correlated to TW growth during the spring, winter, and year at Kisatchie (p = 0.049, 0.046, and 0.014, respectively), and during the winter at Escambia (p = 0.014). Escambia EW, LW, and TW growth were all correlated with the current and previous year's number of hurricanes (negatively and positively, respectively), yet only EW and LW were significant (p = 0.013 and 0.013 for EW and LW in the same year, p = 0.033 and 0.040 for EW and LW for the year before). Hurricane or tropical storm frequency was not significantly correlated with tree-ring growth at Kisatchie or Bladen Lakes.

Table 2. Seasonal and yearly earlywood, latewood, and totalwood Pearson correlation coefficients (top) and p values (bottom) with longleaf pine radial growth at three sites. Significant values ($p < 0.05$) are in bold. The year was considered as March–February of the following year. (Spr.: Spring, March–May; Sum.: Summer, June–August; Fall: September–November; Win.: Winter, December–February; Tem.: Temperature; Pre.: Precipitation).

						Escambia						
	Earlywood				Latewood				Totalwood			
	Tem.	Pre.	SOI	SST	Tem.	Pre.	SOI	SST	Tem.	Pre.	SOI	SST
Spr.	0.067	**−0.333**	−0.217	0.262	0.026	−0.176	−0.155	0.051	0.069	**−0.235**	−0.231	0.267
	0.568	**0.004**	0.071	0.107	0.826	0.132	0.200	0.758	0.555	**0.043**	0.055	0.101
Sum.	−0.010	−0.042	**−0.304**	0.306	−0.066	−0.024	−0.168	0.212	−0.080	0.042	**−0.313**	**0.364**
	0.935	0.721	**0.010**	0.058	0.574	0.836	0.164	0.195	0.497	0.722	**0.008**	**0.023**
Fall	−0.042	−0.151	−0.211	0.241	−0.091	−0.146	−0.154	0.174	−0.076	−0.026	**−0.269**	0.313
	0.720	0.197	0.080	0.140	0.439	0.213	0.203	0.290	0.516	0.825	**0.024**	0.052
Win.	−0.117	0.062	−0.167	0.166	−0.201	0.110	−0.119	0.121	−0.122	0.157	−0.228	0.238
	0.317	0.596	0.167	0.312	0.083	0.347	0.325	0.464	0.299	0.179	0.057	0.144
Year	−0.066	**−0.262**	**−0.255**	0.270	−0.166	−0.143	−0.171	0.164	−0.099	−0.057	**−0.302**	**0.337**
	0.573	**0.023**	**0.033**	0.096	0.155	0.221	0.156	0.318	0.400	0.625	**0.011**	**0.036**
						Kisatchie						
	Earlywood				Latewood				Totalwood			
	Tem.	Pre.	SOI	SST	Tem.	Pre.	SOI	SST	Tem.	Pre.	SOI	SST
Spr.	0.005	−0.074	−0.254	0.255	0.017	−0.069	−0.251	0.290	−0.039	−0.039	**−0.261**	0.248
	0.970	0.579	0.054	0.117	0.899	0.608	0.057	0.074	0.770	0.772	**0.048**	0.129
Sum.	−0.243	**−0.279**	−0.250	0.231	−0.255	0.231	**−0.267**	0.239	**−0.306**	**0.305**	**−0.260**	0.293
	0.066	**0.034**	0.058	0.157	0.053	0.082	**0.042**	0.142	**0.019**	**0.020**	**0.048**	0.070
Fall	−0.082	−0.039	−0.145	0.157	−0.063	−0.075	−0.184	0.153	−0.111	−0.069	−0.230	0.226
	0.540	0.771	−0.278	0.338	0.638	0.576	0.167	0.353	0.405	0.608	0.083	0.167
Win.	−0.120	0.110	−0.138	0.075	−0.134	0.081	−0.147	0.072	−0.116	0.087	−0.229	0.146
	0.371	0.410	0.303	0.648	0.317	0.545	0.270	0.663	0.385	0.517	0.083	0.374
Year	−0.158	0.112	−0.219	0.209	−0.158	0.060	−0.238	0.195	−0.198	0.118	**−0.285**	0.252
	0.238	0.403	0.098	0.208	0.237	0.656	0.072	0.234	0.136	0.377	**0.030**	0.122
						Bladen Lakes						
	Earlywood				Latewood				Totalwood			
	Tem.	Pre.	SOI	SST	Tem.	Pre.	SOI	SST	Tem.	Pre.	SOI	SST
Spr.	−0.011	−0.004	−0.199	0.213	−0.077	−0.063	−0.196	0.169	0.017	−0.009	**−0.246**	0.277
	0.919	0.967	0.099	0.194	0.480	0.561	0.104	0.303	0.877	0.933	**0.040**	0.088
Sum.	−0.117	−0.109	**−0.254**	0.296	−0.147	−0.138	−0.080	0.052	−0.143	−0.061	**−0.304**	**0.389**
	0.282	0.316	**0.034**	0.067	0.174	0.201	0.510	0.754	0.185	0.572	**0.010**	**0.014**
Fall	−0.136	0.010	−0.207	0.268	−0.180	0.004	−0.085	0.015	−0.104	−0.053	**−0.262**	**0.320**
	0.208	0.930	0.086	0.099	0.095	0.973	0.482	0.930	0.340	0.624	0.028	0.047
Win.	−0.117	**0.274**	−0.199	0.175	−0.157	0.089	−0.045	−0.053	−0.077	**0.301**	−0.231	0.246
	0.281	**0.010**	0.098	0.287	0.146	0.414	0.714	0.749	0.479	**0.005**	0.054	0.132
Year	−0.156	0.060	**−0.250**	0.270	**−0.226**	−0.057	−0.110	0.032	−0.118	0.058	**−0.302**	**0.350**
	0.150	0.583	**0.037**	0.096	**0.035**	0.601	0.364	0.846	0.278	0.593	**0.011**	**0.029**

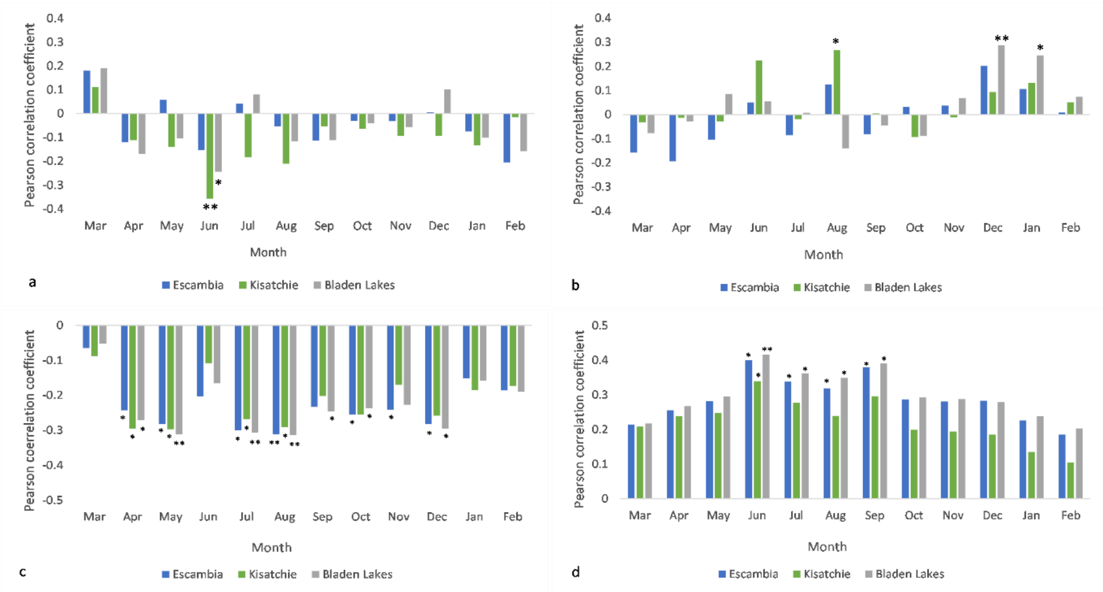

Figure 2. Monthly mean longleaf pine radial growth. Pearson correlation coefficients with monthly climate variables during the year of growth at three sites. Asterisks denote significance at $p = 0.05$ (*) and $p = 0.01$ (**) levels; (**a**) is the monthly mean temperature, (**b**) the monthly mean precipitation, (**c**) the monthly mean southern oscillation index, and (**d**) the monthly mean sea surface temperature. One year's growing season was considered as March–February.

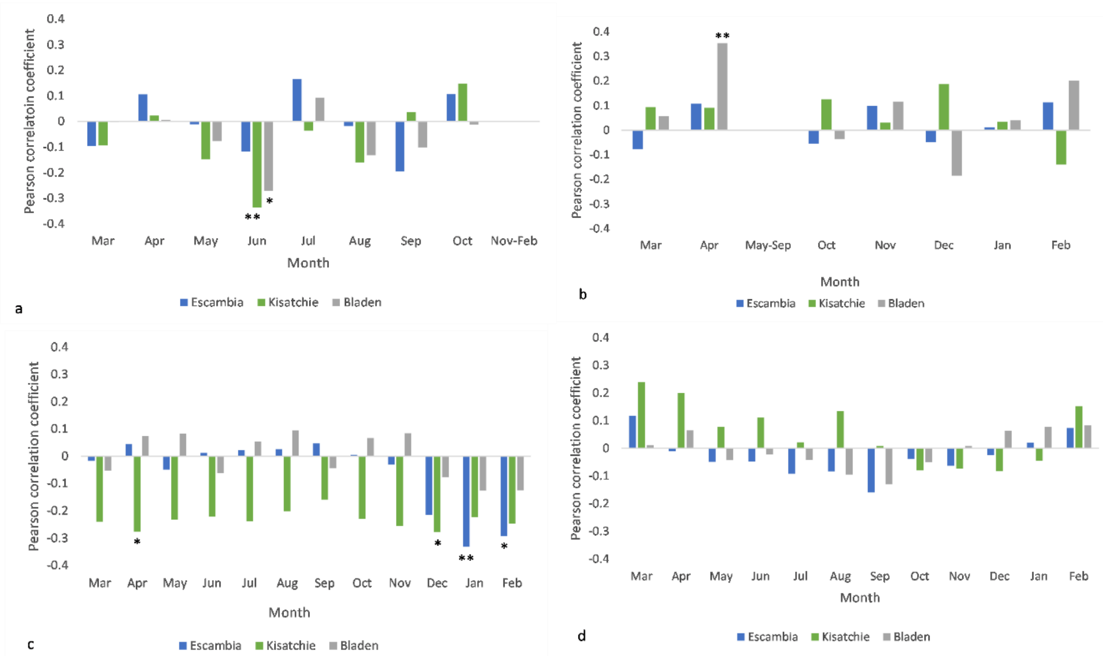

Figure 3. Monthly extreme climate Pearson correlation coefficients with longleaf pine growth at three sites. Asterisks denote significance at $p < 0.05$ (*) and $p < 0.01$ (**) levels; (**a**) is the number of days above 32.2 °C (climate data insufficient for analysis November–February due to seasonality of the region), (**b**) the number of days below 0 °C (climate data insufficient for analysis May–September due to seasonality of the region), (**c**) all standard precipitation index (SPI) categories of drought (equally weighted), and (**d**) all SPI categories of wet (equally weighed). One year's growing season was considered as March–February.

3.3. Cone Production and Mean Climate Signals

Correlations between cone production and mean climate variables varied considerably between and among years; only two alike results were found between Escambia and Kisatchie with temperature (Figure 4). Only three (negative) significant correlations exist for seasonal SOI, and all were at Bladen Lakes. We found no significant relationships between seasonal SST and cone production at any site. Yearly correlations of each variable were all insignificant except for Kisatchie temperature in year one (negative, $p = 0.007$) and Bladen Lakes precipitation in year three (positive, $p = 0.004$).

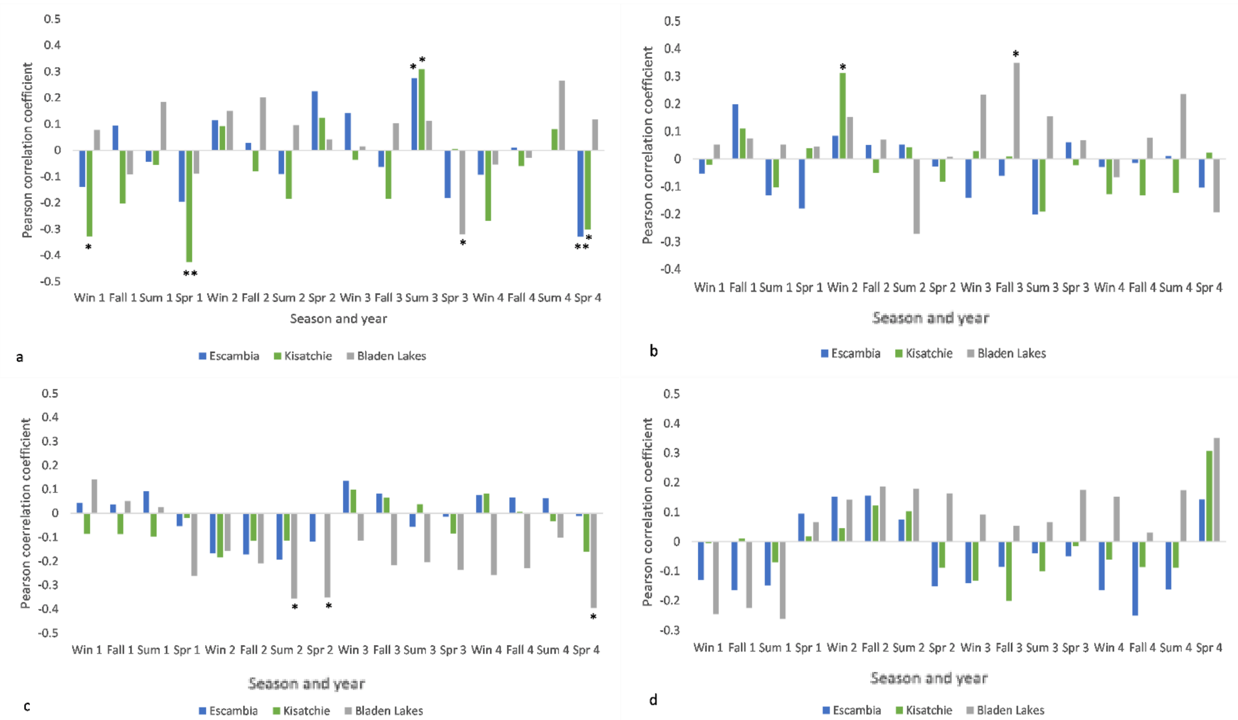

Figure 4. Seasonal climate Pearson correlation coefficient with annual longleaf pine green cone production at three sites. Asterisks denote significance at $p < 0.05$ (*) and $p < 0.01$ (**) levels; (**a**) is the mean seasonal precipitation, (**b**) the mean seasonal temperature, (**c**) the mean seasonal southern oscillation index, and (**d**) the mean seasonal Sea Surface Temperature. Each year was considered as spring–winter of each year directly preceding the April cone counts.

3.4. Cone Production and Extreme Climate Signals

Analysis of cone production and extreme climate metrics yielded a similar overall number of significant correlations as mean climate variables and intersite variability were again evident (Figure 5). Conflictingly, cone production was significantly positively correlated with drought at least once at Escambia and Kisatchie, while Bladen Lakes experienced multiple significant positive correlations with wet conditions. Yearly cone correlations with extreme events produced a greater number of significant correlations than with the mean climate conditions, though none at Bladen Lakes were found. The number of days over 32.2 °C was significantly negative at Escambia in years two and four ($p = 0.021$ and 0.017, respectively), and drought was significantly positive in year four at Escambia ($p = 0.030$). The number of days below freezing was significant in year one at both Escambia and Kisatchie, though the correlation was negative in the former ($p = 0.028$) and positive in the latter ($p = 0.020$). The number of hurricanes and tropical storms was not significantly correlated to cone production at Escambia or Bladen Lakes. Kisatchie cone production was significantly correlated with both the number of hurricanes (positive, $p = 0.014$) and the combination of hurricanes and tropical storms (positive, $p = 0.007$) in year two (the year before the year preceding the cone counts).

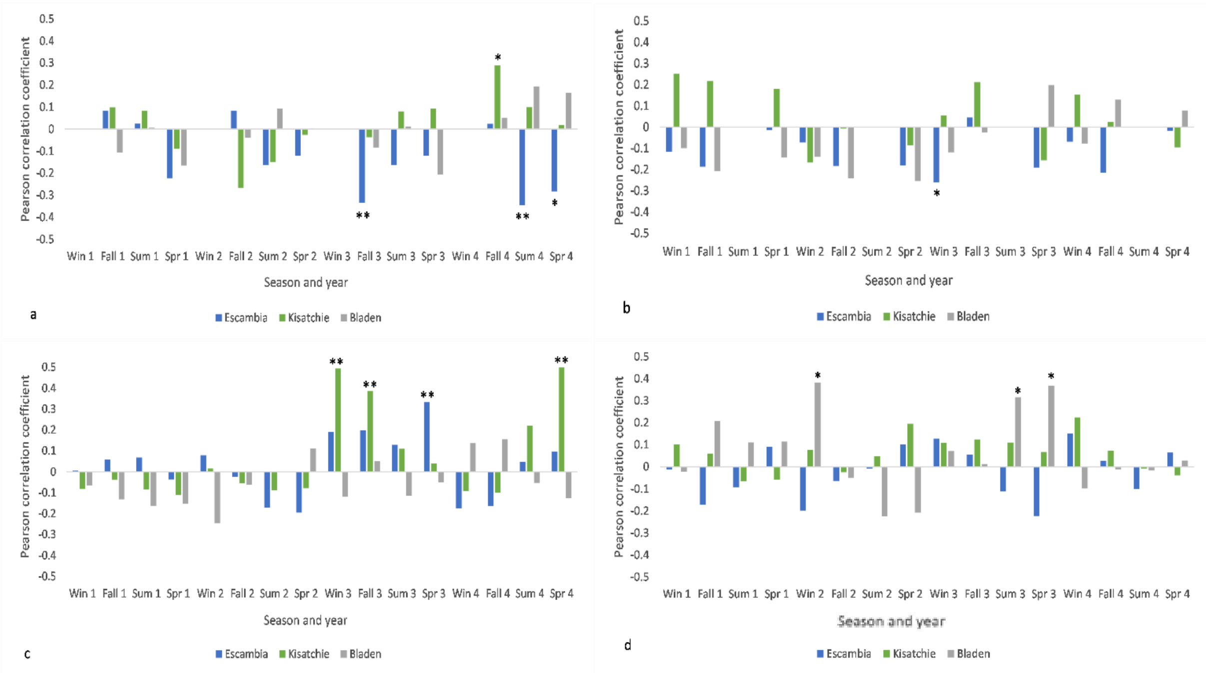

Figure 5. Monthly extreme climate Pearson correlation coefficients with annual longleaf pine green cone production at three sites. Asterisks denote significance at $p < 0.05$ (*) and $p < 0.01$ (**); (**a**) is the number of days above 32.2 °C, (**b**) the number of days below 0 °C, (**c**) all standard precipitation index categories of drought (equally weighted), and (**d**) all SPI categories of wet (equally weighed). The year was considered as spring–winter of each year directly preceding the April cone counts.

3.5. Cones and Radial Growth

Cone production and radial growth two years prior to the cone counts were significantly associated at all three sites; both Escambia and Kisatchie had positive relationships ($p = 0.030$ and 0.026, respectively), though Bladen Lakes was contrastingly negative ($p = 0.033$) (Figure 6a). No other significant associations were found, except for a strong positive correlation in year four at Bladen Lakes ($p = 0.009$). Overall, these correlations were not influenced more by EW vs. LW growth (Table 3). A deeper analysis of data revealed a potential skewing of data from the influence of bumper years (Figure 6b–d). When bumper years (defined as having a mean of ≥100 cones) were removed from the data, only two significant negative associations were found; a retained negative correlation in year two at Bladen Lakes ($p = 0.037$), and a new negative correlation in year one at Escambia ($p = 0.006$) (Figure 6e).

Table 3. Longleaf pine earlywood and latewood Pearson correlation coefficients (top) and associated *p* values (bottom) with cone production at three sites without removing bumper-crop years. Significant values ($p < 0.05$) are in bold. The year was considered as spring–winter of each year directly preceding the April cone counts.

	Escambia		Kisatchie		Bladen Lakes	
	Earlywood	Latewood	Earlywood	Latewood	Earlywood	Latewood
Year 1	0.099 0.440	0.104 0.416	−0.117 0.408	−0.095 0.501	0.057 0.729	0.011 0.945
Year 2	0.236 0.060	0.178 0.160	**0.281** **0.044**	0.270 0.053	**−0.340** **0.029**	**−0.402** **0.009**
Year 3	−0.098 0.441	−0.089 0.482	0.150 0.289	0.106 0.455	0.013 0.937	−0.068 0.671
Year 4	−0.083 0.516	−0.031 0.810	−0.167 0.237	−0.200 0.155	**0.408** **0.008**	**0.449** **0.003**

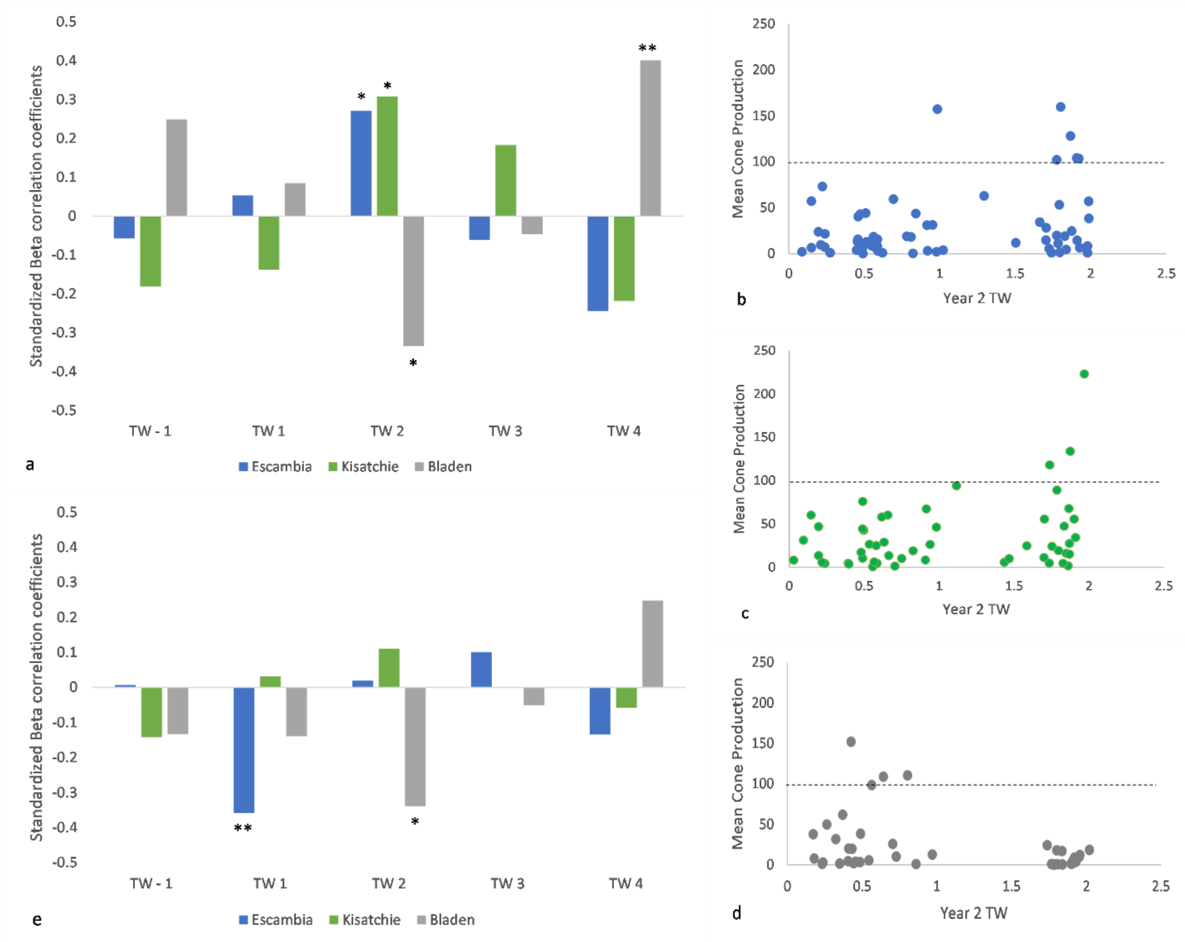

Figure 6. Left: longleaf pinecone production linear regression association with the current and previous 4 years totalwood (TW) growth; (**a**) contains bumper crop years, (**e**) does not. (**b**–**d**) Longleaf pinecone production vs. year 2 TW (including bumper years), significantly correlated at all three sites (Escambia $p = 0.030$, Kisatchie $p = 0.026$, and Bladen Lakes $p = 0.033$). TW-1 corresponds to the growth year following the cone counts, TW-1 to the growth year immediately preceding cone counts, TW-2 to 2 years preceding cone cones, and so on. Points above the dashed lines indicate bumper crop years. * indicates statistically significant at $p < 0.05$ while ** indicates statistically significant at $p < 0.01$.

4. Discussion

We present here an exploratory study of longleaf pine trees sourced from across their native range. Since we were limited in our tree sample size by practical considerations, we suggest that these data may provide a framework for factors necessary to include in future analysis. Contrary to several other studies (e.g., [52,53]), we found a greater-than-expected number of significant correlations between EW growth and climate, as well as an inconsistent relationship between cone production and the previous years' radial growth between sites. These results may be taken as a first step in understanding broad-scale and likely highly variable relationships. As a whole, we neither fully supported nor rejected our initial hypothesis that each climate variable significantly impacted longleaf growth and cone production; some resulted in stronger or more frequent significant correlations than others, though none yielded a significant relationship all year round.

4.1. Intersite Variability

Perhaps the most prominent of our findings was that there was a considerable amount of intersite variation; no two sites experienced the same correlations between climate and tree-ring growth or cone production as each other. This echoes the results of similar work [33], yet we demonstrated even larger differences throughout a larger geographical scale. Further investigation is required to determine how much of this is due to site factors versus random variation between individuals. High levels of variability are not unexpected among conifers; varied relationships have been documented between radial growth and factors such as seasonal precipitation or cosmic radiation, yet cone–growth relationships can vary by species and even tree size [57–59]. Thus, it is common that tree-ring growth may only correlate with some monthly climate variables, while other processes (e.g., radiation) may play a significant role in tree growth. Long-term monitoring of trees and the environment for longleaf pine is necessary to understand its growth.

4.2. Mean Climate vs. Extreme Events

Our results support the importance of considering both mean climate conditions and extreme events alike to understand longleaf pine processes. Superficial inspection of mean vs. extreme climate–cone relationships, for example, reveals a similar number of significant correlations between the two sets of four factors (Figures 4 and 5). Yet the limited number of certain extreme events may cause sample-size-related difficulties in the analyses. For example, the relationship between tree function and the most severe drought categories may differ from relationships with mild drought, though the limited number of extreme droughts makes it problematic to individually analyze by each category. Hurricane frequency is a relatively unexplored avenue for longleaf pine climate analysis, though each site typically only experiences zero to two hurricanes a year. Therefore, it may be interesting to note that the number of hurricanes in a year can produce significant results where simple wet conditions do not, as is the case here with Escambia growth and Kisatchie cones. Yet, with limited datasets, this could simply be a result of combined small sample sizes. Others [60] have posited that intense rainfall events such as cyclones positively influence tree growth by raising the water table to a considerable enough level for trees to increase water uptake. Therefore, analysis that considers intense rather than cumulative rainfall events over time may produce the most reliable results [19,60]. Yet, further analysis, including water-table data, must be conducted to test this idea.

To understand how both general and extreme climate trends impact longleaf pine production, known physiological processes of the species must be considered. For example, Kisatchie and Bladen Lakes TW growth were both significantly negatively correlated with the average temperature in the month of June (Figure 2), though this could be explained by several possibilities, such as more efficient growth on somewhat cool days or a lessened ability to grow in extreme heat. The negative correlation between growth and the number of days over 32.2 °C at each site in the same month (Figure 3) suggests the latter. This makes sense, as cambial cell division is the ultimate source of wood formation, and the rate of division and, thus, the density of the formed wood controls the distinction between EW and LW in conifers [61,62]. The cambial division is affected directly by temperature; experimental manipulation of temperatures has been shown to induce changes in wood type [61,62]. This may relate to the significance of June temperatures in our findings, as previous United States literature has indicated that June is the pivotal month for the earlywood–latewood radial growth transition [57,63]. However, trees in the coastal-plain pine system may differ in the timing of this transition [55]. In longleaf pine, short-term increment ("punch") cores have been used to document an average late-May–late-June transition time, though only in the southern extent of the longleaf pine range; more studies are needed to determine if this is consistent geographically, especially in more northern latitudes [55]. Thus, we suggest the continued exploration of these and other methods across the longleaf pine range, as changes in climate during the earlywood–latewood transition period may affect the tree-ring growth and cone production variably at different locations.

4.3. The Importance of Scale in Climate-Longleaf Analysis

Each climate variable was different in how growth and cones were affected at each site, though not generally in the time span at which the clearest correlations were found.

For example, at all three sites, the correlation between TW growth and SOI was evident at the seasonal level, and monthly correlations did not provide much detail except to demonstrate that these correlations were consistent throughout each season (Figure 2). Yet, monthly temperature correlations with growth displayed a high level of irregularity within seasons, with only a few months (e.g., June) found to be significant (Figure 2). Thus, it is important to test correlations at multiple time scales to understand how climate relates to tree function over short-and long-term spans. We suggest that a key next step for this species is to use dendrometer bands to measure and correlate short-term changes in radial growth with microclimate site data. To date, we have only encountered one study that utilized dendrometer data in longleaf pine trees [55], though it was limited geographically to Florida and the very southern part of Georgia. The inclusion of a greater number of more temporally variable datasets may thus allow us a much deeper insight into the climate–physiological relationships of this species.

Although each site correlated differently with each climate variable, the time span of the impact of each variable did not appear to differ as much (e.g., cone production is particularly sensitive to climate variables 2–3 years before green cones form), perhaps alluding to universal physiological processes of the trees. In many cases, yearly or even seasonal data was insufficient; we often had to consider monthly data to provide the best context for understanding climate–growth relationships. Although it is impractical to include monthly relationships throughout the entire time span of cone formation, seasonal correlations provide substantial insight into the timing of peak sensitivity of cone production to climate (Figures 3 and 5). This result is consistent with Guo et al. [42], in that there is no clear and consistent link between climate events and cone production across longleaf sites, though some months are more significant. Species' life-history traits may represent an adaptive response of species to disturbance and are an information legacy, which could become an ecological memory [64]; however, legacies and memories can be lost or diminished as environmental disturbance regimes and climate conditions change while the species still are extant [65].

4.4. Climate and Cone Production

Cone–climate correlations are bound to be complex given the long reproductive cycles in longleaf pine. For example, during the short time surrounding fertilization, even a single hot day or cold night can be fatal to reproductive success for many plant species [66]. Interestingly, although cone production was generally most sensitive to climate two to four years preceding cone counts, each site was significantly correlated with different variables (Figures 3 and 5). For example, of all the extreme conditions tested, Escambia cones were mostly correlated to temperature extremes, Kisatchie cones to drought, and Bladen Lakes cones to wet conditions (Figure 5). Sign differences between and among sites were also common (Figures 3 and 5). These combined indicate that multiple climate factors complexly influence cone production at each site.

Our findings may support that climate variables relate to cone formation at key points throughout the reproductive cycle. For example, the only significant correlations found within the one year preceding cone counts both occurred at Kisatchie with the winter and spring average temperatures (Figure 3). This period includes a few significant points in cone formation: conelets are fertilized the month before green cones form, while pollination occurs in the spring before that. During year two, we found no significant correlations between cone production and temperature, though a few were between SOI (−) and wet (+) conditions at Bladen Lakes during the spring and summer (Figures 3 and 5). These are the seasons directly before and in which pollen cones (M, July) and seed conelets (F, August) begin to form [42]. Ergo, at Bladen Lakes, early cone formation, whether directly or mediated through a covariate such as tree growth, is selected for during wetter conditions. The number of significant correlations preceding the beginning of the reproductive cycle support resource accumulation or other delaying factors are present. A key example here is the four highly significant positive correlations between cone production and drought in the 3–4 years preceding cone formation at Kisatchie and Escambia. Although seemingly counterintuitive, this could be explained by the sometimes-negative relationship between drought and radial growth at each site (Figure 4, Table 2). If drought conditions impede tree growth, and resource accumulation in the years before cone formation influences later cone production, we would expect to see a positive relationship between drought and cone production, even outside of the time that cones are forming. A similar argument has been made regarding substantially time-lagged site- and age-specific associations between cone production and previous weather conditions in *Araucaria Araucana*, which the authors argued was potentially related to the slow process of carbon cycling important to long-lived conifers [67].

As far as we can tell, this is the first attempt at correlating ENSO data with longleaf cone production, and we did support others' research involving strong TW–ENSO relationships (Figure 2) [52]. Yet ENSO is only one of many climate cycles; a recent study [68] found that the tree-ring width of a tropical legume-tree species (*Prioria copaifera* Griseb.) is significantly related to the oceanic niño index, Pacific decadal oscillation, and the southern oscillation index. Interestingly, cone production was only significantly correlated with SOI at Bladen Lakes, while Kisatchie had the weakest ENSO-growth correlations of the three sites. This could perhaps be explained by Bladen Lakes' position as closest to the Atlantic Ocean and Kisatchie's as the farthest. Given its relatively higher latitude, trees at Bladen Lakes may also experience a slightly shorter growing season than the other two sites. Ties to precipitation and temperature regimes should not be ignored as well: ENSO events usually bring strong temperatures and precipitation extremes to longleaf pine trees.

4.5. Cone Production and Tree-Ring Growth

As with individual climate correlations, our most notable result from cone–growth analysis is the amount of variation between sites. Bladen Lakes differed in sign from our other two sites, as well as the six others previously studied in the southern-central southeast sites [33], where all but two of which (not significant) were found to have a significantly positive relationship between TW growth and cone production two years before cone formation. More research is needed to understand why Bladen Lakes experienced a significantly negative correlation during the same time, though it could relate to how Bladen Lakes is the farthest geographically and latitudinally from South Alabama. It is possible that a different climate regime may partially explain this finding. For example, unlike at Kisatchie or Escambia, cone production at Bladen Lakes is significantly negatively correlated to yearly SOI conditions (Figure 3, Table 3). The finding that growth and cone production is thus supported by similar climate conditions during this period would perhaps augment the expression of resource allocation between reproduction and growth, as both would be supported and limited at the same time as each other. It is also important to note, however, that Bladen Lakes has fewer years of cone-count data available than the other two sites (Table 1), so additional caution should be used in interpreting these results. Regardless, these findings provide many potential research avenues surrounding how a hypothetically negative resource-allocation relationship between reproduction and growth is expressed when optimal climate conditions for each system fall on a spectrum between matched and mismatched.

Studying relationships between tree-ring growth and mean cone-production data in longleaf pine provides many valuable insights. It is known that there is great variability between cones produced by each tree at each site [33], and here we use the mean number of cones at each site with the average tree-ring growth, which may not necessarily represent each individual tree. Yet, masting should be based on the regional synchronization of reproductive cycles. Thus, our results are more representative of trends by site rather than an individual tree. One study [33] documented a substantial influence of bumper years on the correlation between BAI and cone production in individual trees at six close sites in the center of the longleaf range and suggests that bumper crops are the only significant influence on radial growth. Alternatively, we used radial data from trees near the cone-count trees in similar stands, rather than the cone-count trees themselves. The similarity of our Escambia results to their (nearby) sites may suggest that our method of using average cone data for the analysis of trees nearby to the cone-count trees is valid. The strong significance between cones and ring growth four years before cone formation in bumper years at Bladen Lakes (Figure 6) may suggest that bumper crops rely on stored resources from previous years. Our results found that year two correlations between tree-ring growth and cone production became insignificant after removing bumper years at Kisatchie and Escambia, though not Bladen Lakes, where the correlation was negative (Figure 6). Thus, our results echo the argument of [33] that bumper-crop years may be the most significant influence on longleaf pine cone–radial growth relationships. However, we would challenge the strength of this argument, as it is clear that bumper-crop years are statistically much less common than others. At our sites combined, for example, only twelve years could be classified as bumper years, half of which were at Escambia. Although it does appear there could be a skewing of relationships by these bumper crops (Figure 6b–d), we are again limited in the surety of our analysis by the amount of data available to us. More difficult to interpret is how the removal of bumper years caused a new, highly significant, negative correlation in year one at Escambia. However, yearly reproduction in trees is complexly linked to many individuals and interacting biotic and abiotic factors [69], and we here investigated only a limited number of possible influences on longleaf pine reproductive cycles. Thus, we argue that a more holistic view of ecological mechanisms is necessary to develop adaptive forest-management strategies for longleaf pine. Furthermore, the gaps in, and questions raised, by our analyses suggest that much larger datasets are needed on this endangered species to understand intrinsic links between fundamental life processes.

5. Conclusions

Longleaf pine forests are an important ecosystem in the southeastern United States, but their sporadic seed production often prohibits successful restoration. It is necessary to study the responses of longleaf pine to current climate-change conditions. We present here a deep look at the association between common climate metrics and longleaf pine reproductive output and radial growth. Although the results were widely varied, all three sites experienced significant correlations within the interconnected relationship between cone production, radial growth, and climate. Notably, extreme climate conditions such as drought and extreme heat had roughly the same number of significant correlations with longleaf growth and cone production as mean temperature and precipitation during the same times. Whether due to geographical location, physical-stand factors, or some combination thereof, it is clear that climate impacts the connection between growth and reproductive success differently at each of our three sites. This alone provides many gaps in the literature that should be addressed with further study, including the known influence of stand variables (e.g., tree size, soil conditions, etc.) on tree growth. Only long-term intensive monitoring at different scales for longleaf pine trees may provide an understanding of their ecological mechanisms.

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