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Characterizing the dynamics of cone production for longleaf pine forests in the southeastern United States

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ABSTRACT

Longleaf pine (*Pinus palustris* Mill.) forests are historically and ecologically important and also endangered ecosystems in the southeastern United States. In addition to extensive exploitation and land use conversion, one characteristic which contributed to their dramatic decline and presents a continuing challenge to their future recovery is the sporadic timing of their seed production. In this study, about 60 years of cone production data for longleaf pine forests at four different sites were quantitatively characterized from different perspectives. Results indicated that longleaf pine was different from masting species and there was no general trend of increasing coefficient of variation (CV) in cone production through time. On a decade scale, there was a significantly positive correlation between the CV of cone production and CV of average annual air temperature, but the CV of annual precipitation was negatively correlated with the CV of cone production at the Escambia (AL) and Blackwater (FL) sites. Phase coupling of cone production with a strength of approximately 0.4 existed only between the Escambia and Blackwater sites and no significant phase coupling was found between other sites. The implications of these results for forest management are discussed from a perspective of spatial and temporal complexity.

1. Introduction

Longleaf pine (*Pinus palustris* Mill.) forests were historically among the most important ecosystems in the southeastern United States, because of their ecological and economic value and large natural range (Brockway et al., 2005; Jose et al., 2006; Hodges, 2006). These ecosystems dominated the southern coastal plain for thousands of years (Watts, 1971; Delcourt and Delcourt, 1987). However, extensive exploitation and land use conversion during the 19th and 20th centuries dramatically reduced the extent of these ecosystems, to < 5% of their original occupancy (Outcalt and Sheffield, 1996; Frost, 2006), from 38 million ha before European settlement to only 1 million ha in 1995. Longleaf pine forests are among the most endangered ecosystems in the United States (Noss et al., 1995). One characteristic that also contributed to their decline is the sporadic timing of their seed production, which limits the effectiveness of their natural regeneration and presents a continuing challenge for their restoration (Brockway et al., 2006). Analyzing the various spatial and temporal dynamics of cone production in longleaf pine forests is therefore prudent and may provide useful insights into their unique behavior.

Annual variation in longleaf pine cone production is thought to be mainly related to variable weather conditions (Pederson et al., 1998). However, Guo et al. (2016) concluded that the response of cone production to climate is complex, after comparing cone production and local weather condition across its natural range. In order to quantitatively characterize the sporadic cone production, entropy (means lacking of prediction or order) at multiple scales, which can show the complexity (or irregularity) of cone production along different lengths of time, was used for analyzing the long-term data of cone production in longleaf pine forests across the southeastern region (Chen et al., 2016a). Those results indicated that the overall patterns for the complexity of cone production, with the change of time scale, were similar among sites, except for one location in Florida. There were high correlations between the entropy of cone production and entropy of annual mean air temperature or annual total precipitation at all sites. It was also found that the dynamics of information entropy (irregularity in the information of cone production), at all sites, was within the upper and lower boundaries set by the joint entropy, with maximum and minimum values (Chen et al., 2016b). Recently, it was also found that the sporadic cone production, at multiple sites across its range, followed power laws

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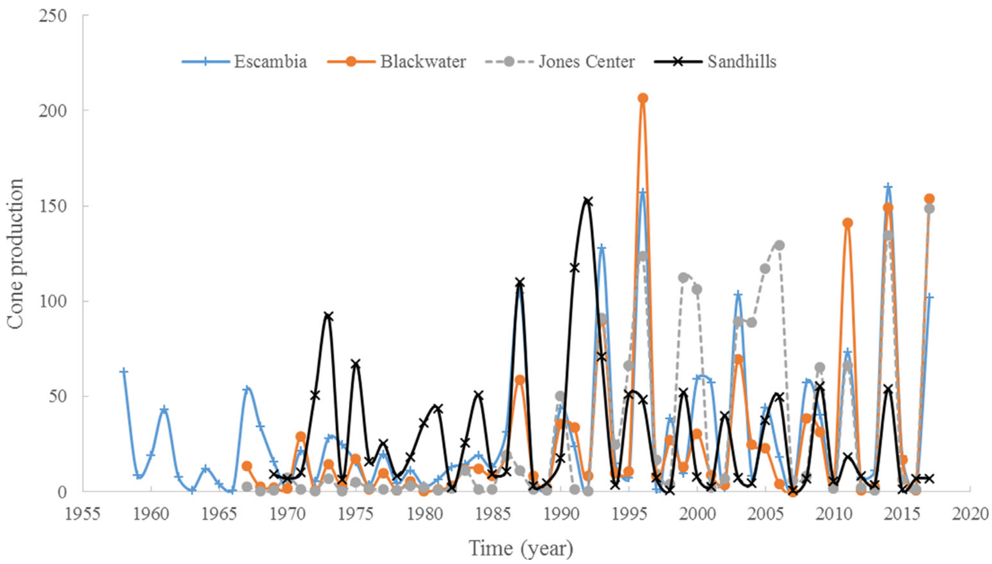

Fig. 1. Annual cone production for the population of longleaf pine forest at four sites.

(frequent power law and Taylor's power law), which are considered as ubiquitous in life forms and nature (e.g., Bak, 1996), but the scaling exponents varied among sites (Chen et al., 2017). These results, from a computational approach, have provided important information about the emergent behavior of cone production in longleaf pine forests at varied spatial and temporal scales.

Some hypotheses related to weather and resources have been proposed to explain inter-annual variation in the seed crops of perennial plants (Kelly et al., 2013; Pearse et al., 2016). Guo et al. (2017) discovered that climate fluctuation may affect sex allocation in longleaf pine forests and that an optimal sex allocation ratio may exist for promoting cone production. After analyzing 1086 datasets of plant seed production throughout the world during 1900–2014, Pearse et al. (2017) found that inter-annual variation in seed production, as a whole, increased through time with a decrease in the long-term mean of seed production. It is not known whether the cone production of longleaf pine follows similar dynamics.

Furthermore, when the dynamics of cone production for longleaf pine forests at different sites were compared, similar common features of complexity were found, such as the entropy change and power laws in cone production (Chen et al., 2016a, 2016b; 2017). However, the relationships (such as synchrony) between cone production behaviors at different sites were not obvious (Guo et al., 2016). Masting has been defined as the synchronous production of seed at long intervals by a population of plants (Janzen, 1976), or as synchronously highly variable seed production among years by a population of plants (Kelly, 1994), or as high inter-annual variability in seed crops and high levels of synchronization in seed production at the population- and community- levels, over large geographical areas (Kelly and Sork, 2002). Thus, spatial synchrony, which means correlated population fluctuations over a wide geographic area, is often used to characterize masting behavior in many plant species (Kelly, 1994; Kelly and Sork, 2002). Numerous studies indicate that regional stochasticity, species dispersal, and mobile natural enemies are the possible mechanisms for spatial synchrony (e.g., Ims and Steen, 1990; Chen et al., 2006). Usually the synchrony in plants across large areas is associated with similar climate, where variable weather provides important resources and stimuli to form spatial patterns of reproduction (Schauber et al., 2002; Post, 2003). Haydon et al. (2001) suggested phase coupling should be tested before spatial synchrony is measured, because phase effects are confounded by the amplitudes within the collected data in time-series. That is, if the amplitudes are not uniform or highly correlated, phase correlation can break down. For phase coupling in the cone production of longleaf pine forests, it is not clear how large an area, how strong the relationship and how long a time interval are pertinent. It is necessary to examine phase coupling in the dynamics of cone production among different longleaf pine forest sites. It will also be interesting to know whether there are spatial interactions (phase coupling) among these separated longleaf pine forests within a large area.

Therefore, the goal of this study is to test the above hypotheses and characterize the spatial and temporal dynamics of cone production for longleaf pine forests at several sites in the Southeast. The specific objectives include determining (1) whether inter-annual variation in cone production at different sites increased through time and the mean of seed production decreased; whether climate correlated with variation in cone production; and (2) whether the results from the correlation method and phase coupling method were consistent; whether phase coupling existed in the dynamics of cone production among different longleaf pine forest sites. Answers to these questions could enhance our understanding of the dynamics of cone production across sites, from new and different perspectives, which may be used for developing improved management approaches for these forest ecosystems at a regional level.

2. Material and methods

2.1. Data

As part of a long-term regional monitoring study, cone production data for longleaf pine were collected by scientists at the USDA Forest Service, Southern Research Station, by counting the number of green cones present in tree crowns during the spring of each year. At least 10 trees were sampled in stands at each site. The mean number of green cones on all sampled trees was used to estimate the average production at each site. Additional details can be found in Chen et al. (2016a, 2016b) and Guo et al. (2016, 2017). From this broad-scale study, four sites having the most complete data were selected for further analysis. These four sites include the (1) Escambia Experimental Forest in southern Alabama (short name: Escambia), (2) Blackwater River State Forest in the western panhandle of Florida (Blackwater), (3) J.W. Jones Ecological Research Center in southwestern Georgia (Jones Center), and (4) Sandhills State Forest in northeastern South Carolina (Sandhills). Cone production at these sites is shown in Fig. 1. Climate data were obtained from nearby weather stations.

2.2. Variation in cone production

So that these results could be readily compared with previous research (Pearse et al., 2017), the same method was applied. The coefficient of variation (CV, standard deviation/mean) for cone production of longleaf pine population at each site during different time periods was calculated, to facilitate comparisons among the sites. Time periods included all time intervals from the beginning of observations to 2017, such as 1958 to 2017 for the Escambia site. The first 10 years of data were used for data accumulation (such as from 1958 to 1967 at Escambia). The average and standard deviation were calculated for each year, from the 11th year to 2017, and for the decade periods (1970s, 1980s…2010s). For the 2010s, only data from 2010 to 2017 were included.

2.3. Phase coupling

The phase, $\phi_{i,t}(0\le\phi_{i,t} < 1)$, of the population at the *i*th site ($i = 1\ldots n$) at time *t* can be considered as the proportion of the orbit circumscribed by time *t* as measured relative to the position on the orbit of the last cyclic trough (Haydon et al. 2001). Phase coupling is expressed as a link between the overall mean phase ($\bar{\phi}_t$) across two sites and the phase at each site. It has the effect of drawing back the cone production that lead the overall average and pulling forward the cone production lagging behind the overall phase. The method from Haydon and Greenwood (2000) and Haydon et al. (2001) was applied, here listing only some of the main steps for this calculation.

The cone production (*X*) of a longleaf pine forest at site (*i*) and time (*t*) can be considered as:

$$X_{i,t+1} = f(X_{i,t}) + \varepsilon_{i,t}$$

The phase field $\{\phi_{i,t}\}$ corresponds to a set of cone production in the dynamic field $\{X_{i,t}\}$. The circumference, $\Psi_{\tau_{i,k}}$,of a cyclic orbit can be the sum:

$$\Psi_{\tau_{i,k}} = \sum_{j=\tau_{i,k}}^{\tau_{i,k+1}-1} [(X_{i,j+1}-X_{i,t})^2 + (X_{i,j+2}-X_{i,j+1})^2]^{1/2}$$

The phase of the cone production *X* at site *i* at any time *t* can be the fraction of this current completed orbit.

$$\phi_{i,t} = \frac{1}{\Psi_{\tau_{i,k}}} \sum_{j=\tau_{i,k}}^{\tau_{i,k+1}-1} [(X_{i,j+1}-X_{i,j})^2 + (X_{i,j+2}-X_{i,j+1})^2]^{1/2}$$

$$(\tau_{i,k} \leqslant t \leqslant \tau_{i,k+1}-1)$$

Phase coupling strength (*c*) can be estimated from the following, if it is constant during the time period. From the regression, *1-c* can be estimated by the slope.

$$\Delta(\phi_{i,t+1},\bar{\phi}_{t+1}) = (1-c)\Delta(\phi_{i,t},\bar{\phi}_t) + \eta_{i,t}$$

Where $\eta_{i,t}$ is a noise term. The coupling parameter *c* is 0 in the absence of any coupling, which means the change in $\Delta(\phi_{i,t}, \bar{\phi}_t)$ from *t* to $t + 1$ is random. When $c > 0$, it indicates coupling of phase. Correlation analysis was performed by using the least-squares technique by SAS software (Cary, NC). The statistical test was considered significant at $P < 0.05$.

3. Results

Fluctuations in the CV values of cone production were observed at each site (Fig. 2). However, there was no general trend of increasing CV values through time. Sudden breaks did occur in the dynamics of CV values. In comparing CV values during different decades from 1960s to 2010s, there was no general trend of increasing CV and also decreasing average of cone production (Fig. 3). There was significantly positive correlation between the CV values of cone production and CV values of average annual air temperature on a decade scale (Fig. 4). The CV values of annual precipitation during decades negatively correlated with the CV values of cone production at the Escambia ($y = -11.243x + 3.0296$, $R^2 = 0.6023$, $p < 0.05$) and Blackwater sites ($y = -7.2273x + 2.4178$, $R^2 = 0.6734$, $p < 0.05$), but positively correlated at the Jones Center ($y = 4.4873x + 0.2507$, $R^2 = 0.5607$, $p < 0.05$). No correlation was apparent at the Sandhills site ($y = 0.0861x + 1.0674$, $R^2 = 0.0003$, $p > 0.05$).

Phase coupling, with coupling strength of approximately 0.4, existed between cone production at the Escambia and Blackwater sites during the overall time span (Fig. 5), but this phase coupling was significant only during the 1990 s ($y = 0.5435x + 0.0066$, $R^2 = 0.8391$, $p < 0.05$). Cone production at Escambia and Blackwater was significantly correlated for the overall time period and during different decades ($p < 0.05$) except for the 1970s. Phase coupling for cone production among other sites was not significant. Although phase coupling between the Sandhills and Escambia sites during the overall time period was not significant (Fig. 5), it was significant during the 1980s ($y = 0.0131x - 0.0084$, $R^2 = 0.7263$, $p < 0.05$). Cone production was significantly correlated ($p < 0.05$) at the Sandhills and Escambia sites during the 1980s, Blackwater and Jones Center during the 2010s, and Blackwater and Sandhills during the 1980s.

4. Discussion

The dynamics of cone production for longleaf pine forests at four sites in the southeastern United States did not support the findings of Pearse et al. (2017), which indicated that inter-annual variation in seed production as a whole increased through time with a decrease in the long-term mean of seed production. On a decade scale, there existed a positive correlation between the CV in cone production and CV in average annual air temperature at three sites. R^2 values were low (0.54–0.63), indicating that other factors also influenced these relationships. The variation of annual precipitation had a differing relationship with variation in cone production at several sites (Escambia, Jones Center, and Sandhills). This correlation was negative at the Escambia and Blackwater sites, but positive at the Jones Center, with no correlation at the Sandhills site. Increasing temperature may be an advantage for cone production at a decade scale, but precipitation can affect the result. It would be interesting to ascertain how precipitation can enhance the effect of increasing temperature. Such information may be useful in the restoration of longleaf pine forests. Perhaps the varied microclimate, landscape, hydrology, and soils at each site across the region and the way in which each plant community has adapted to these factors may be the cause for the complicated relationship between cone production and climate. Although the cone production of longleaf pine is high variable, a previous study found no global correlation between annual cone production and annual weather, such as monthly temperature and precipitation (Guo et al., 2016). The pattern for longleaf pine cone production also did not support the view that plants with the most variable seed production often respond strongly to inter-annual differences in weather (Kelly et al., 2008). Based on results here and also our previous results, showing that the entropy of cone production was significantly correlated with the entropy of average annual air temperature or precipitation (Chen et al., 2016a), it can be said that cone production for longleaf pine is related to climate, but in a complex way. Our results support the “climate variability hypothesis.” Increases in the CV for air temperature and precipitation may lead to varied, and perhaps difficult to predict, results for cone production among different sites at a decade scale.

Results from the phase coupling method and correlation method for cone production were not consistent. The correlation method found more cases than the phase coupling method. This outcome confirms a limitation for the correlation method, as being influenced by amplitudes. In this study, cone production varied from a value approximating 0 to more than 100, with higher cone production values contributing

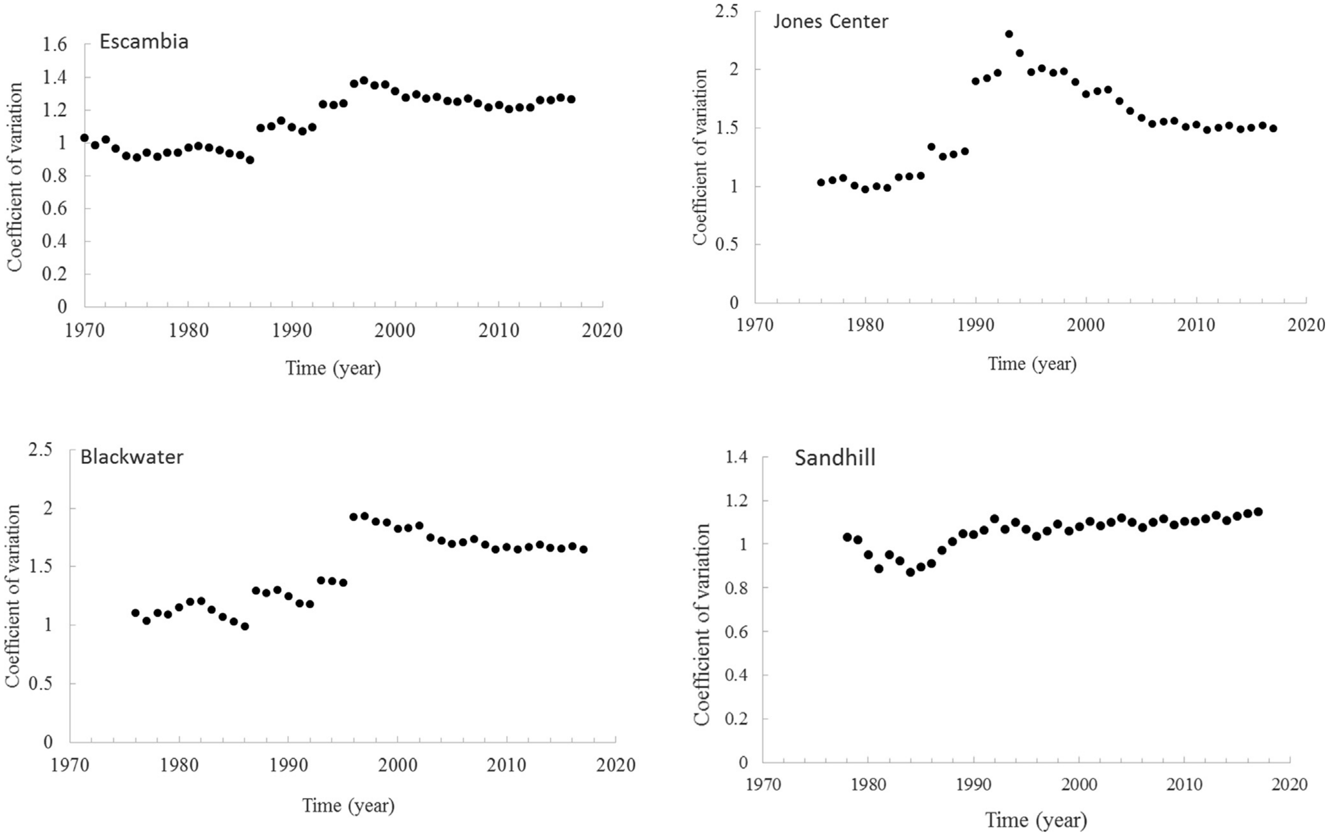

Fig. 2. Coefficient of variation of cone production for the population of longleaf pine forest with time from the beginning of observation at four sites.

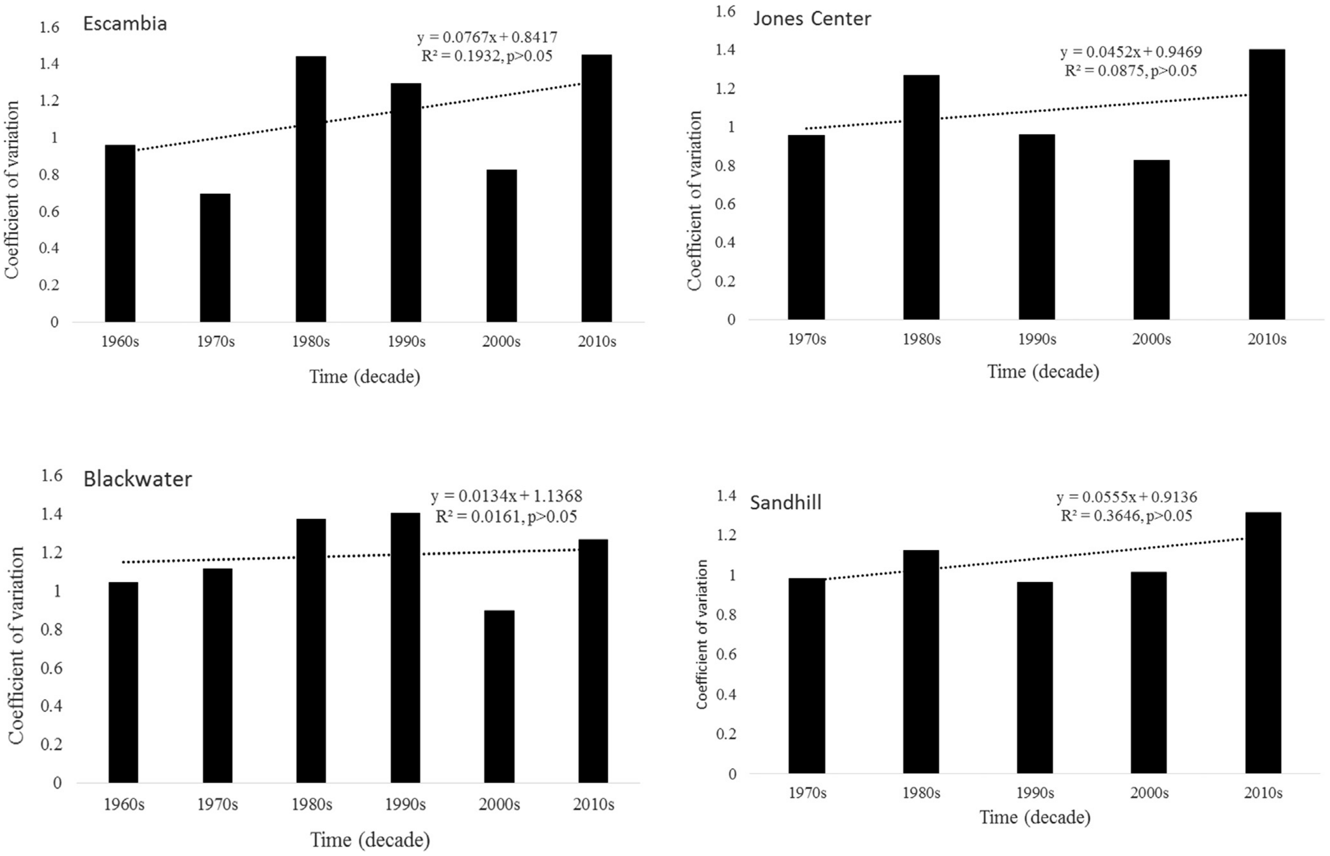

Fig. 3. Coefficient of variation of cone production for the population of longleaf pine forest during different decades at four sites.

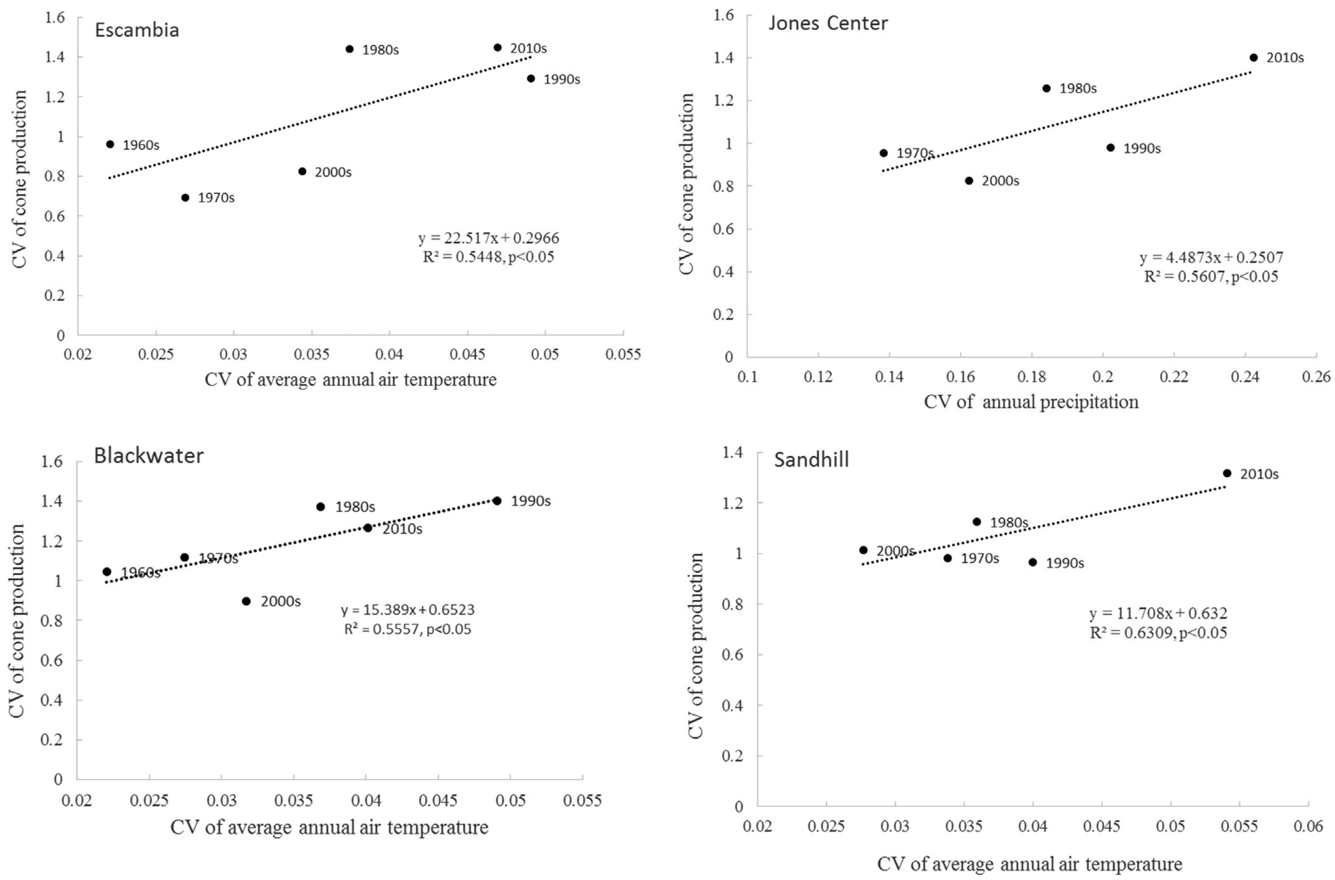

Fig. 4. Correlation between coefficient of variation of cone production and coefficient of variation of average annual air temperature on a decade scale at four sites (each dot represents one decade).

more to the correlation. If data in the time series are fairly uniform or highly correlated, phase correlation may be measurable by the correlation method; otherwise, that method may not work and phase coupling should be used (Haydon et al., 2001). There was no significant phase coupling in the cone production of longleaf pine among the four sites, although weak phase coupling existed between the Escambia and Blackwater sites (significant only in the 1990s) or between the Sandhills and Escambia sites during the 1980s. Thus, longleaf pine is not a strong masting tree species. The advantage of no phase coupling is that longleaf pine at each site works as an independent population and will not simultaneously respond to some factors (e.g., climate). Mooney et al (2011) found that synchrony of seed production in ponderosa pine was high within individual populations, but quickly became asynchronous with the increasing distance. Inter-annual variation in temperature and precipitation had differing influences on seed production for ponderosa pine at Boulder County and Manitou in Colorado. This characteristic may enhance population persistence or stability of the species from an evolutionary perspective (Blüthgen et al., 2016). When a year with low cone production occurs at some sites, it will not be a catastrophe for cone production across the entire range of a species. Absence of significant phase coupling may be related to factors such as (i) local environment playing a major role in cone production for longleaf pine at each site and (ii) longleaf pine at these sites may have already formed its own biological character or genetic constitution resulting from historical and prevailing natural disturbances regimes (e.g., recurrent fire, damaging windstorms, insects, pathogens) and/or human management activities (e.g., prescribed burning, stand thinning, timber harvest).

5. Conclusion

The cone production of longleaf pine was quite variable and lacked strong synchrony among the four study sites. Although cone production in longleaf pine forests was correlated with average annual air temperature and precipitation on a decade scale, forests at each site appear to have evolved their own unique character relative to their local environment. Our results support the view that cone production in longleaf pine forests across the southeastern United States is a complex process, likely influenced by environmental factors at local scales. These findings point toward important implications for the conservation and management of longleaf pine forests, across their extensive natural range.

Longleaf pine forests at different sites have very likely already developed their own distinctive attributes, through many centuries of interactions with natural disturbances and more recent management regimes. Longleaf pine forests exist across a vast landscape containing a wide variety of local environmental conditions to which they are adapted. In developing effective strategies and avoiding the pitfalls of a “one size fits all” approach, prudent forest managers will strive to understand the unique characteristics of longleaf pine sites in their locale. A broad-scale influence, such as climate change, may cause quite heterogeneous effects on longleaf pine forests across the region. Longleaf pine at some locations may be more sensitive to the stress of change than those growing at other locations. A narrowly-focused management strategy may prove ineffective for the vast array of site types encompassed by the complex of longleaf pine forest ecosystems spanning from Texas to Florida to Virginia. Emerging knowledge from a variety of different disciplines is best considered when formulating management strategies. The detailed mechanisms of these reproductive characteristics in longleaf pine forests deserve further exploration.

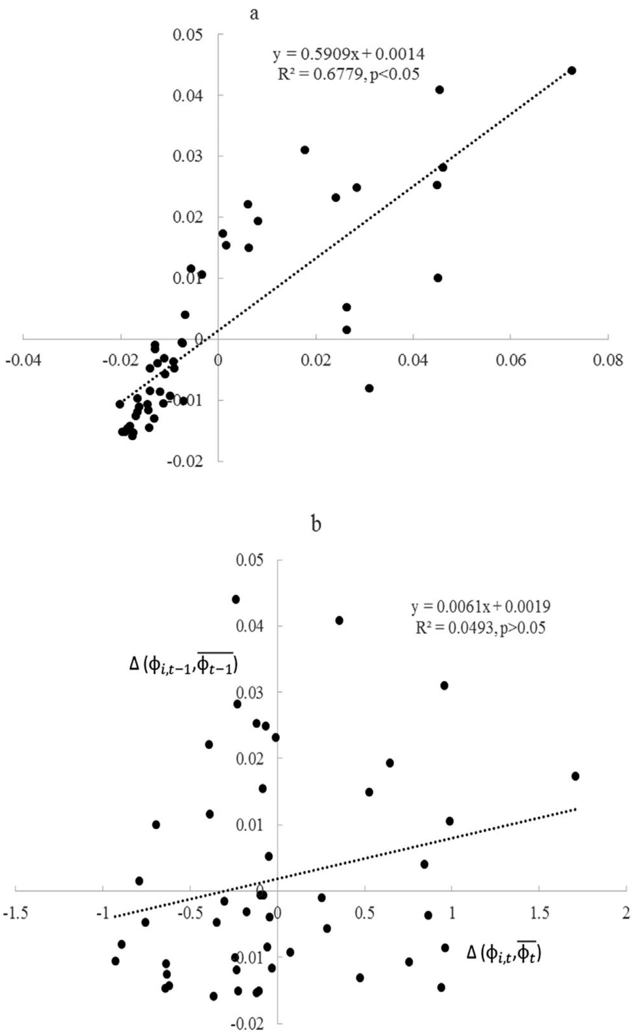

Fig. 5. Phase change in cone production as populations between time *t-1* and *t* at Escambia and Blackwater sites (a) and Escambia and Sandhills sites (b).

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.foreco.2018.06.014.

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