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Assessing the influence of climate on cone production of longleaf pine forests

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ABSTRACT

Longleaf pine (*Pinus palustris* Mill.) forests have been identified as a societal, economical, and ecological resource in the southeastern United States. One major factor inhibiting contemporary efforts to restore native forests is the sporadic cone production of longleaf pine. It is difficult to evaluate the climate contribution to seed production since the reproduction process is lengthy and complicated. Here, we utilize a quantitative method previously applied to understanding complex systems to assess the influence of climate on longleaf pine cone production at five long-term monitoring sites in the southeastern United States. Our results indicate that climatic factors (annual air temperature and annual precipitation) have a stronger influence on cone production than non-climatic factors. However, the contribution of climate to cone production varied with time at each site. Greater contribution of climate was related to low cone production at three of five sites. However, the scaling relationship between climate and cone production is not statistically significant. The potential maximum cone production can be estimated by this method, such as 250 cones per tree for Blackwater River State Forest and 150 cones for Jones Center. Our results provide a new understanding of cone production in longleaf pine forests and can be utilized to identify stands with high natural regeneration potential.

1. Introduction

Longleaf pine (*Pinus palustris*) forests were historically among the most important ecosystems in the coastal areas of the southeastern United States because of their social, ecological, and economic value (Brockway et al., 2006; Hodge, 2006; Jose et al., 2006). Such as, longleaf pine forests could provide quality timber (e.g., the net present value is about $150–500 per acre, McIntyre et al., 2006) and related forest products (such as tar, pitch, and rosin) while also serving as excellent wildlife habitats (Hodges, 2006; Jose et al., 2006). From a conservation perspective, longleaf pine forests are often targeted by conservation efforts for their abundant biodiversity, as their discontinuous canopy and frequent surface fire regime create a heterogeneous resource environment (Rother et al., 2020; Platt et al., 2006). These forests represent one of the most unique and biologically diverse ecosystems in the world. Indeed, they support an estimated 900 plant species, 100 bird species, 36 mammal species, and 170 species of reptiles and amphibians. Some endangered species are dependent on this ecosystem, such as the red-cockaded woodpecker (*Picoides borealis*), gopher tortoise (*Gopherus polyphemus*), and black pine snake (*Pituophis melanoleucus*), and a variety of carnivorous plants (*Sarracenia* spp.) (NRCS, 2020). In addition, longleaf pine forests have significant potential for carbon storage, as trees can reach heights of more than 40 m and diameters approaching 91 cm, and have a lifespan of up to 450 years and the belowground allocation strategy (Samuelson et al., 2017; Boyer, 1990; Platt et al., 1988). However, following the extensive exploitation and land use conversion during the 19th and 20th centuries after European settlement, longleaf pine forests are now among the most endangered ecosystems in the United States (Noss et al., 1995). Consequently, maintaining longleaf pine woodlands is critical for many contemporary natural resource objectives.

After depletion, due to land-use change and fire suppression (Carter et al., 2015; Van Lear et al., 2005; Fox et al., 2007), the extent of longleaf forest ecosystems reduced dramatically to only less than 5% of their original occupancy, which once covered a broad area of about 37 million ha along the coast from southeastern Virginia to eastern Texas across many diverse landscapes (Frost, 2006). Based on forest inventory and analysis data in 1995, only about 1.02 million ha of longleaf pine forests remained (Outcalt and Sheffield, 1996). Government agencies and private landowners have renewed interest in restoring longleaf pine forests

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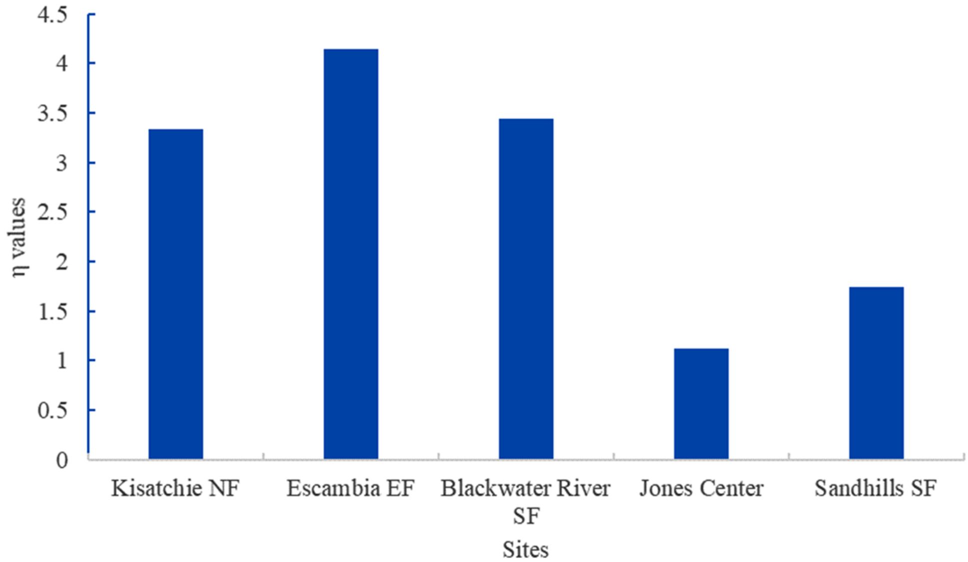

Fig. 1. The attribution of climate (η values) on cone production at different sites.

for their high-value wood products, pine straw production, wildlife and biodiversity benefits, and carbon sequestration for climate change (Diop et al., 2009). There is financial support through various governmental incentives for longleaf pine restoration. Also, the financial risk of growing longleaf pine is lower than that of other southern pines. Land expectation values with environmental amenities of longleaf pine forests range between $3,254 and $3,793/ha (Paudel and Dwivedi, 2021). Currently, the total area of longleaf pine forests reaches about 1.9 million ha (Matthew et al., 2020).

Restoring longleaf pine forests has become a management priority in the southeastern United States (Gordon et al., 2020; Guldin, 2019). Unfortunately, silvicultural efforts to regenerate longleaf pine woodlands are often confronted with several factors that complicate the restoration process (Willis et al., 2021; Lavoie et al., 2011; Varner et al., 2007). The sporadic seed production was a significant cause of the decline and limited the natural regeneration of longleaf pine forests (Brockway et al., 2006; Pederson et al., 1998). This irregular cone production is considered to be related to the complex interactions between climate fluctuation and their reproduction processes (Chen et al., 2016, 2018; Guo et al., 2016). From a biological perspective, the major stages of the reproductive process, which take about three years, include the development of male and female strobili, pollination of conelets, fertilization in the ovary, cone maturation, and seed production. Because of the differential in favorable conditions for each sex, conelet losses can be extensive, such as frequently more than half senescing before maturity (e.g., McLemore, 1975; Boyer, 1973). There exists a weak burstiness in cone production (Chen et al., 2020). From a climate perspective, complicated relationships exist between climate and cone production of longleaf pine forests. Cone production is determined before the final year of seeding, and precipitation explains 48.6% of annual cone crop variation while average monthly temperature explains 33.7% (Pederson et al., 1998). The frequency of high cone production does not match the frequency of high annual precipitation, limited pollen production, and male-female sex allocation (Guo et al., 2017).

There are significant correlations between the entropy of cone production and entropy of both annual mean air temperature and annual total precipitation at different sites (Chen et al., 2016). From a management perspective, silvicultural practices for longleaf pine forests, such as prescribed fires and thinning, may impact tree growth and eventually cone production (Kuehler et al., 2006; Croker, 1973). The exact mechanisms which cause variation in cone production are still not entirely known, especially with respect to climate change (Bowman and Chen, 2022). However, cone production could be considered a complex system (Chen et al., 2017), which has many interacting factors; its emergent properties are hard to infer from the components, and the fluctuations in the external conditions systematically obscure the mechanisms that control the system's internal dynamics (Bar-Yam, 2002). Complex systems have distinct properties that arise from these relationships among components, such as nonlinearity, emergence, spontaneous order, adaptation, and feedback loops.

Modern techniques have been developed to separate the importance of internal and external factors in complex systems based on time series from many components that interact with each other (De Menezes and Barabási, 2004). This method has been successfully applied to determine the dynamics of some ecological systems. For example, Chen and Li (2007) used this method to reanalyze the long-term monitoring data of Soay sheep population fluctuation and climate variation on Hirta Island, UK. Their results indicated that the climate conditions had a higher impact than internal factors on the fluctuations of the sheep population, of which detailed knowledge of internal factors was not known. They also found a scaling relationship between the size of the sheep population and external and internal factors. This method has also been used to evaluate the climate and non-climate (e.g., human activities) contribution to global vegetation dynamics at the continental level (Chen and Li, 2010) and indicate the increasing influence of human activities on continental NDVI dynamics.

This study aims to apply this method to assess the climate and non-climate influence on the longleaf pine cone production at five geographically distinct sites across the southeastern United States. The detailed objectives include (i) determining whether this method can be used to analyze the dynamics of cone production; (ii) assessing the relative importance of climate and non-climate factors on cone production of longleaf pine forests; (iii) evaluating and comparing the importance of climate on cone production at different periods based on the long-term cone data; (iv) determining whether there is a scaling relationship between climate and cone production; and (v) estimating whether there exists a threshold of cone production at each site. These results will greatly improve our understanding of cone production in longleaf pine and provide a practical approach for estimating the upper limits of cone crop potential.

2. Material and methods

2.1. *Longleaf pine cone data and study sites*

Cone production data for longleaf pine have been collected since the

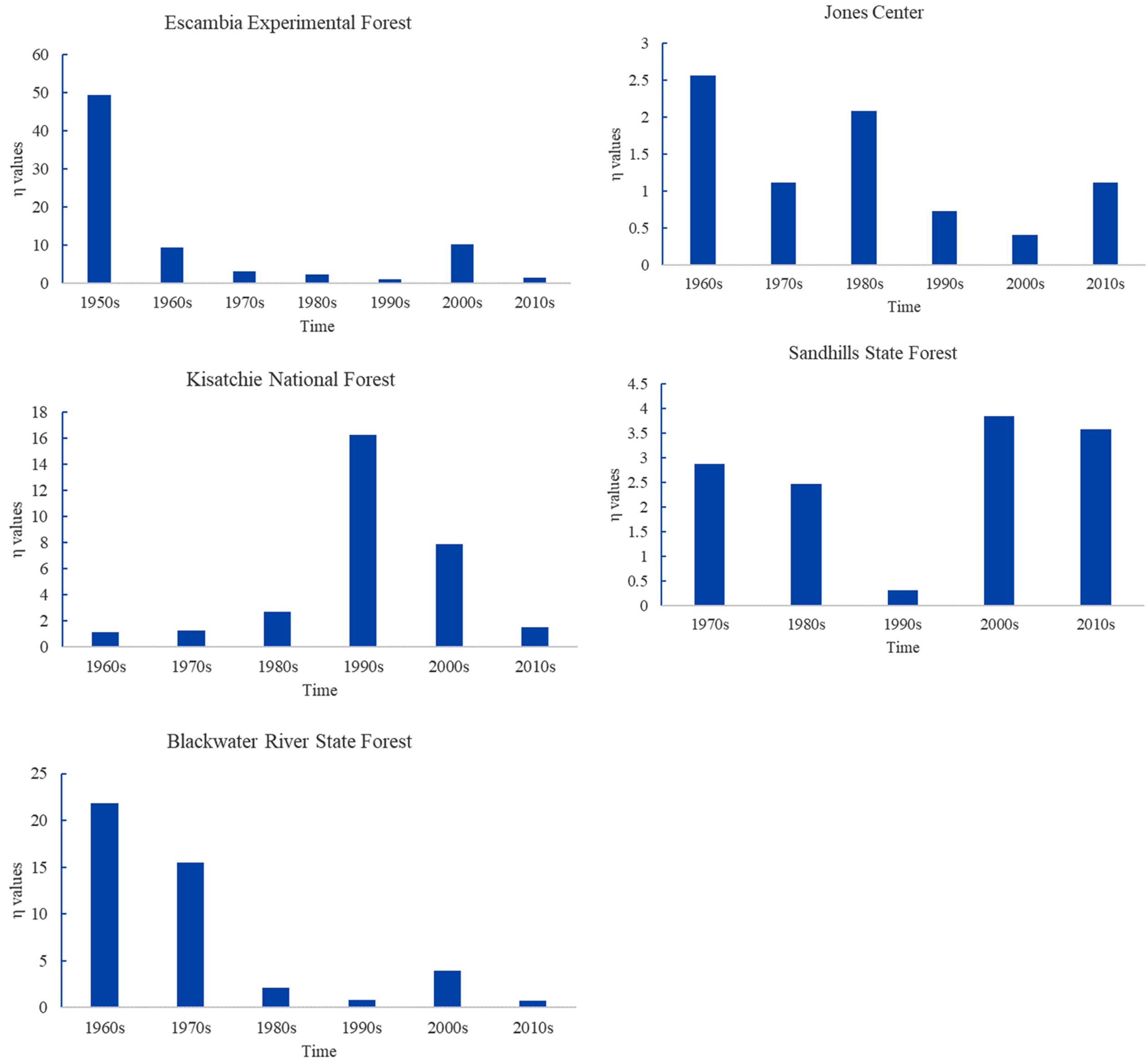

Fig. 2. The attribution of climate (η values) on cone production at sites in different periods.

1960s as part of a long-term monitoring effort conducted by scientists at the Southern Research Station of the US Department of Agriculture Forest Service. Observers use binoculars (8–10 ×) each spring at different sites across the southeastern region to count and record the number of green cones in the crowns of mature longleaf pine trees growing in low-density stands. At least 10 trees were investigated in stands at each site. The average number of cones on all investigated trees is used to represent cone production for each site. Detailed information can be found in Chen et al. (2016) and Guo et al. (2016). In this study, five sites with the longest monitoring of cone production are selected. These five sites are (a) Escambia Experimental Forest in southern Alabama, (b) Blackwater River State Forest in the western panhandle of Florida, (c) Jones Center in southwestern Georgia, (d) Sandhills State Forest in northeastern South Carolina, and (e) Kisatchie National Forest in Louisiana. Climate information, including annual mean air temperature and total precipitation, was acquired from the public weather stations near each study site.

2.2. The method for comparing the climate and non-climate contributions

According to the study of the complex system (De Menezes and Barabási, 2004), without detailed knowledge, the fluctuations of the longleaf pine cone production system can be attributed to two general factors: (i) climatic factors, such as air temperature and precipitation (drought is considered as the joint force of temperature and precipitation); and (ii) non-climatic factors, such as biological factors (tree growth), prescribed burning, soil nutrients, diseases, etc. We can separate the two general contributions from each site (i) as the following:

$$f_i(t) = f_i^{\text{climate}}(t) + f_i^{\text{non-climate}}(t)$$

If only non-climatic fluctuations contribute to the activity at site i, at any moment t the amount of fluctuation to go through the site i is estimated by the product A_i and the total fluctuation in the system at time t follows:

$$f_i \text{ non-climate}(t) = A_i \sum f_i(t)$$

and

$$A_i = \frac{\sum_{t=1}^{T} f_i(t)}{\sum_{t=1}^{T}\sum_{i=1}^{N} f_i(t)}$$

then

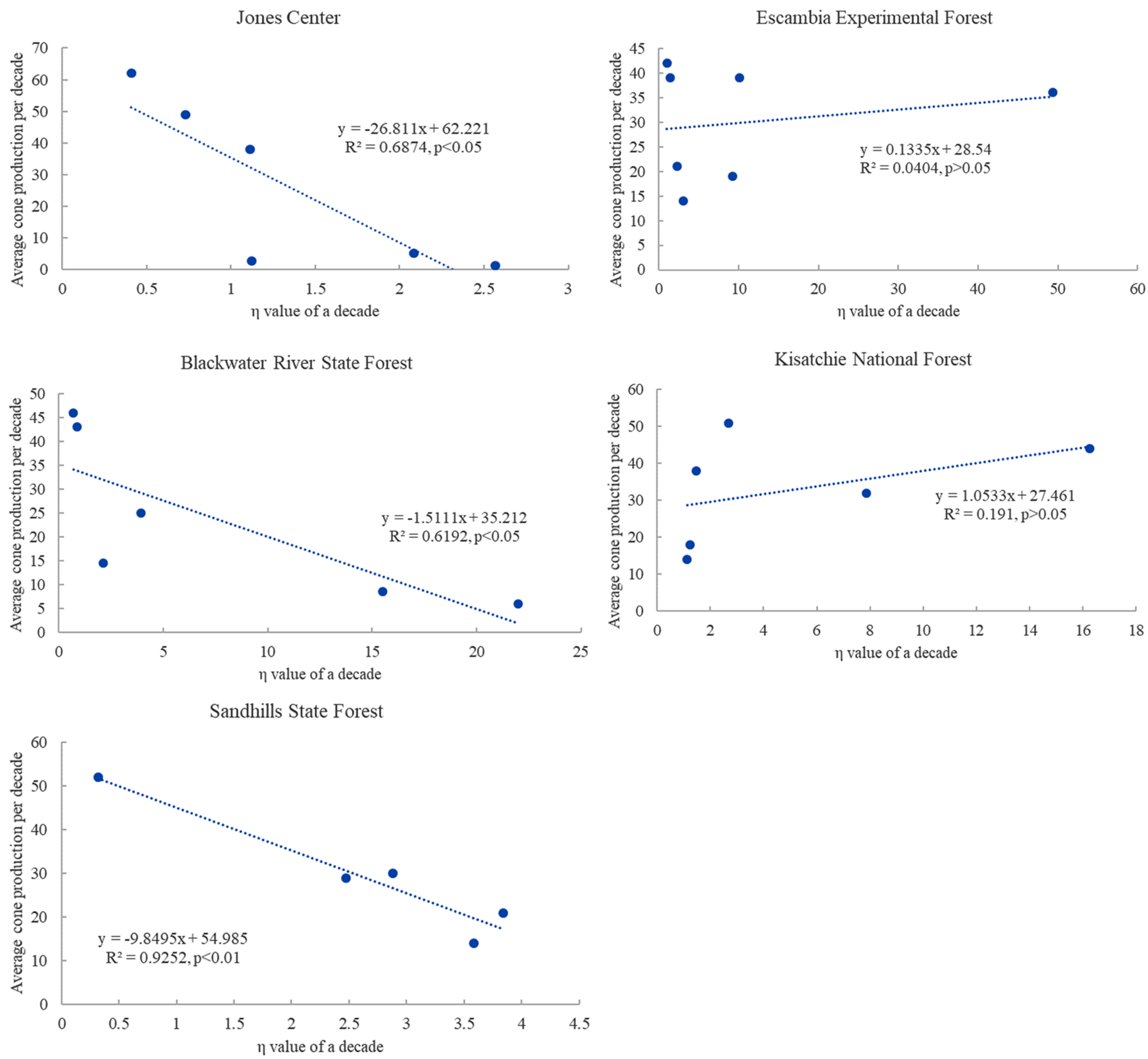

Fig. 3. The relationship between η values and average cone production at a decade level.

$$f_i^{climate}(t) = f_i(t) - A_i \sum f_i(t)$$

For each recorded signal, the climate and non-climate standard deviations ($\sigma_i^{climate}$ and $\sigma_i^{non\text{-}climate}$) and their ratio ($\eta_i$) can be calculated,

$$\eta_i = \sigma_i \text{ climate} / \sigma_i \text{ non} - \text{climate}$$

When $\eta_i >> 1$, climate fluctuations dominate the dynamics, while for $\eta_i << 1$ the system's non-climate fluctuation dominates over the imposed changes (De Menezes and Barabási, 2004).

2.3. Scaling comparison

For each recorded signal, the time average $<f_i>$ and the standard deviation σ_i from climate and non-climate influences should obey the scaling law $\sigma_i \sim <f_i>^{\alpha}$. If the climate and non-climate contributions follow the same scaling, the systems' climate fluctuations should have a strong impact on the overall dynamics of the system (De Menezes and Barabási, 2004).

Spearman's correlation analysis of SAS software was conducted between η values and average cone production and the scaling relationship between climate and cone production. Statistical significance was considered at $p < 0.05$.

3. Results and discussion

Climatic factors (annual air temperature and annual precipitation) influence cone production because overall η_i are more than 1 at different sites (Fig. 1). Some sites have high η values (e.g., Escambia Experimental Forest in Alabama and Kisatchie National Forest in Louisiana), while Jones Center in Georgia has a relatively low η value. The sites with high η vales indicate a relatively stronger contribution from climate to cone production, while the sites with low η vales may be influenced more by non-climatic factors (e.g., soil nutrients, prescribed burning, thinning, and diseases). With frequent inter-annual climate change in this region (Chen et al., 2022), it is reasonable to assume that cone production of longleaf pine could be impacted by climate factors.

η values at different decades varied for each site (Fig. 2). It appears that this value changes with time. Some sites had low η values during some periods, such as Blackwater River State Forest and Sandhills State Forest had low values in the 1990s. The change of η values might indicate the relative contribution of climate and non-climate factors to cone production at different periods. The possible reason may be that cone

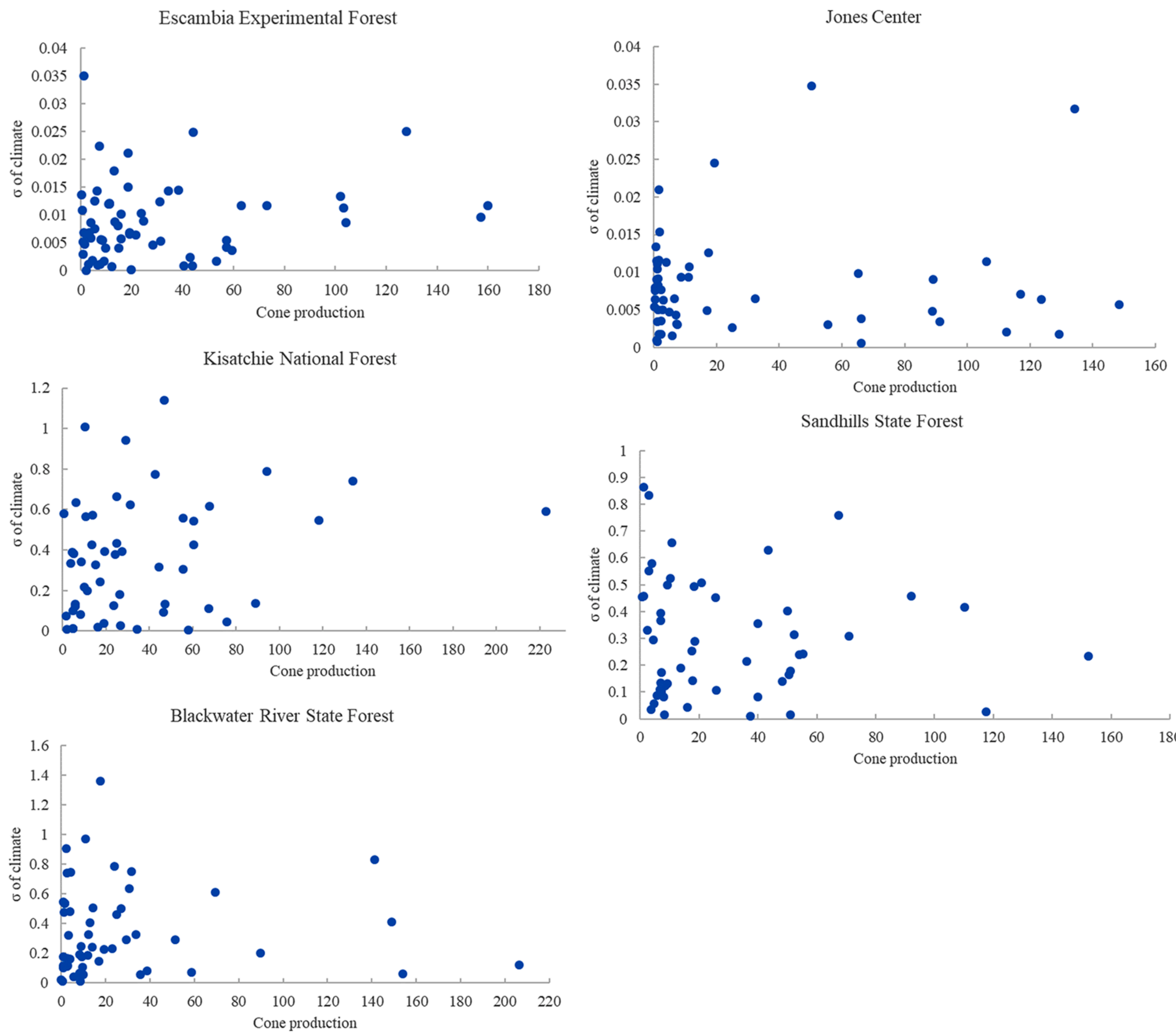

Fig. 4. The scaling relationship between climate and cone production at different sites.

production in longleaf pine is a lengthy process extending over three calendar years. It may confirm that there is heterogeneity in the reproductive investment of populations (or individuals) over time scales (Patrick et al., 2022).

High cone crop years are unpredictable, but usually occur every 5–7 years in this region (Pederson et al. 1998). Also, prescribed burning is a necessary practice (every 3–5 years) to control the competition of hardwood trees in longleaf pine forests (Willis et al., 2021; Gordon et al., 2020; Brockway et al., 2006). Prescribed burning can also be used to control insects and diseases (e.g., brown spot-needle blight), promote biodiversity in the understory, and change the growth of longleaf pine trees (Kuehler et al. 2006; NRCS, 2020; Sayer et al., 2020). We cannot discount the potential impact of prescribed fire on cone production since prescribed fire is typically applied every 2–5 years in the southern region. However, to our knowledge, no studies have examined this possibility with longleaf pine or any other southern pine species (Willis et al. 2021; Addington et al. 2015; Brockway et al. 2006; Outcalt 1994). There is a trend of decreasing contribution from climate factors across sites except for Sandhills State Forest. Since there are complicated relationships between climate and cone production at different periods at each site (Guo et al., 2017; Chen et al., 2016), the η values at different periods may be used to monitor the integrated conditions of longleaf pine forests.

A significantly negative correlation exists between η values and average cone production at the decade time scale for Jones Center, Blackwater River State Forest, and Sandhills State Forest (Fig. 3). This result means that high climate influence (high η values) may relate to a low cone production. It is partially consistent with the fact that longleaf pine trees have intermittency in cone production and need time for energy accumulation (Chen et al., 2020). It is not clear why this negative relationship did not appear at Escambia Experimental Forest and Kisatchie National Forest. The detailed processes still need to be investigated.

The scaling relationship between the stand deviation of climate (air temperature + annual precipitation) and cone production was not statistically significant at each site ($p > 0.05$) (Fig. 4). This result is a surprise because there were significant scaling relationships in previous studies (Chen and Li, 2007, 2010). The possible reason may be that climate factors influence many ecological processes (growth, diseases and etc) through the complicated biological/ecological processes, but they may still be not significant in comparison with other factors. This may be consistent with the previous finding that air temperature and precipitation might have an opposite influence on cone production at some sites (Chen et al., 2018). But in this study, even though the annual air temperature and precipitation were separated, their scaling relationships were still not significant. Suppose the outlier points are used for the estimation of the potential maximum cone production by the site. In this case, Blackwater River State Forest may have a maximum of 250 cones/tree, Jones Center may have a maximum of 150 cones/tree, Escambia Experimental Forest may have 170, Sandhills State Forest may have 180, and Kisatchie National Forest may have up to 230. This result may be helpful for selecting seed orchards at potentially more productive sites. These estimated maximum cone numbers are close to the historical highest cone production at each site. Thus, it is possible to estimate the potential maximum production with limited information, but it is not clear how often this maximum can occur.

Based on a simple model from the physics of complex systems, our results highlight salient aspects of longleaf pine cone production and have important implications for the restoration of longleaf pine forests. First, climate dominates the overall process of cone production. Thus, climate change will likely have strong implications for future cone production and the natural regeneration dynamics of longleaf pine. While we cannot say whether climate change will increase or decrease cone production, proactively developing management strategies to mitigate the potential negative effects of climate change on cone production would be a prudent step given our level of uncertainty. Manipulative studies examining the influence of silvicultural practices such as seasonal prescribed fire, prescribed fire frequency, or fertilization impact on longleaf pine cone production are currently lacking to guide such efforts. Second, climatic influence varies across sites. This result suggests that management efforts to promote or conserve cone production should be tailored more to local conditions than regional recommendations. Third, the scaling relationship between climate and longleaf pine cone production may change with time and location. This insight corresponds with a previous report demonstrating that air temperature and precipitation have different relationships with cone production and highlights the complexity of the cone production process (Chen et al., 2018). Finally, the complex system method examined in this study can be used to estimate maximum cone production potential. This function has utility in identifying stands that have inherently high-or-low natural regeneration potential, which would be useful in identifying sites with favorable natural regeneration potential. Moreover, the methods examined here could be used to identify stands that would be ideal candidates for cone collections to support future artificial regeneration efforts.

4. Conclusion

Sporadic cone production is a major limitation in longleaf pine restoration. Many studies have indicated that cone production in longleaf pines is a complicated process, which creates a challenge in assessing the attribution of climate. With the help of a general physics method based on the complex system theory, here we assess the climatic and non-climatic influence on cone production. Without knowing detailed knowledge of underlying processes at each site, the result indicates that overall climatic factors (annual air temperature and precipitation) have influenced cone production in longleaf pine forests more than non-climatic factors. However, at different times, the influence of climatic and non-climatic factors varied among sites. Our results indicate that strong climatic influence is significantly correlated to low cone production on a decadal scale at three sites (Jones Center, Blackwater River State Forest, and Sandhills State Forest). The scaling relationship between climate and cone production is not significant at each site. By this method, the maximum cone production at each site can be estimated, which is close to known historical data at each site. It is necessary to test these results and explore more information from this method. While limited to just five sites with long-term cone monitoring history, our results indicate the potential utility of applying a complex system approach to irregular ecological processes.

Declaration of Competing Interest

The authors declare that they have no competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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