Forest Ecology and Management 429 (2018) 1–6

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

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

Xiongwen Chen[a,b,*], Dale G. Brockway[c], Qinfeng Guo[d]

[a] Department of Biological and Environmental Sciences, Alabama A & M University, Normal, AL 35762, USA
[b] Department of Landscape and Art, Jiyang College of Zhejiang A & F University, Zhuji 311800, PR China
[c] USDA Forest Service, Southern Research Station, 521 Devall Drive, Auburn, AL 36849, USA
[d] USDA Forest Service, Eastern Forest Environmental Threat Assessment Center, Research Triangle Park, NC 27709, USA

ARTICLE INFO

Keywords:
Coefficient of variation
Phase coupling
Regime
Management

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

* Corresponding author at: Department of Biological and Environmental Sciences, ARC 139, Alabama A & M University, Normal, AL 35762, USA.
E-mail address: xiongwen.chen@aamu.edu (X. Chen).

https://doi.org/10.1016/j.foreco.2018.06.014
Received 23 March 2018; Received in revised form 6 June 2018; Accepted 10 June 2018
0378-1127/

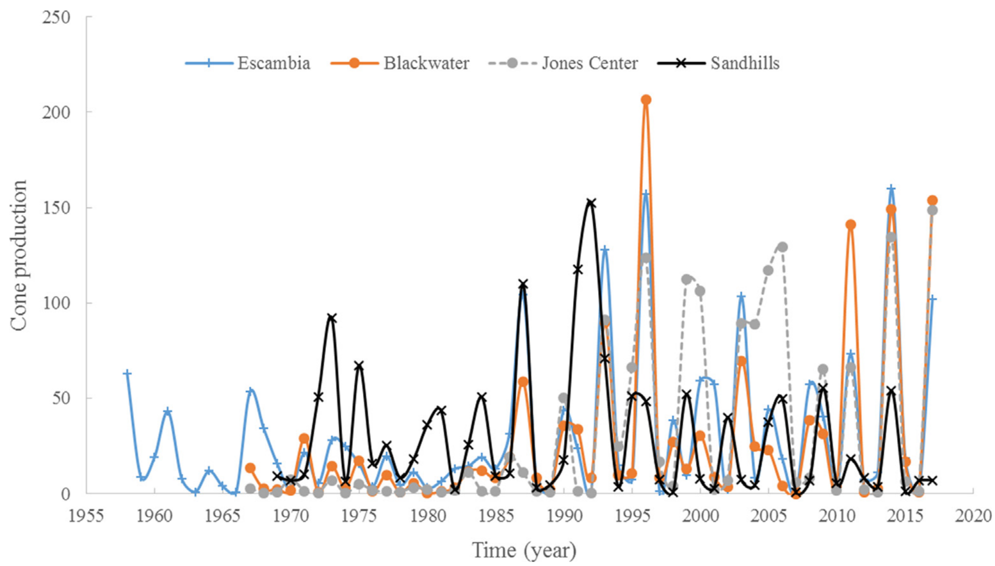

Fig. 1. Annual cone production for the population of longleaf pine forest at four sites.

(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.