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Longleaf pine cone–radial growth relationships in the southeastern U.S.A.

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ABSTRACT

Longleaf pine (*Pinus palustris* Mill.) cones have been counted annually by the United States Forest Service (USFS) at eleven locations throughout the species' range since 1958. These data have been useful for understanding spatiotemporal patterns in longleaf pine cone production, and are beneficial in timing regeneration efforts. Variations in annual mast (i.e. seed crop) are known to influence ring widths in numerous tree species, yet this relationship is poorly understood for longleaf pine. This research examines the relationship between longleaf pine cone data and tree-ring growth from trees sampled in the multi-decadal USFS cone-crop study. We examined cone–radial growth relationships using individual tree-ring data and proprietary cone data for each tree from six sites in four locations in the southeastern USA. We found that longleaf pine cones were correlated with basal area increment growth (BAI) over the three-year cone-development cycle. Low BAI years were more frequently associated with above-average cone crop and BAI during years that coincided with the largest cone-crop class (bumper, > 100 cones per tree) were statistically less than any other cone class. We prepared linear models that predicted radial growth using PDSI and cones as predictors, and found that including cones in the models did not improve adjusted R^2 values. We conclude that while cone production is inversely related to radial growth, the combination of infrequent bumper years and the concentration of cone production by a few trees per stand, creates an environment where radial-growth chronologies assembled from longleaf pine for dendroclimatic purposes are unlikely to be significantly influenced by reproductive strain.

1. Introduction

Longleaf pine forests once spanned an estimated 37 million hectares (Frost, 1993) of the coastal plain and piedmont physiographic regions of the American Southeast. A fraction of this forested landscape remains (1.74 million hectares, Oswalt et al., 2012) following centuries of fire suppression, deforestation, domestic livestock grazing, and other land-use changes (Frost et al., 2006). Currently, a reversal in longleaf forest decline is underway largely due to replanting. Roughly 25% of all living longleaf today has been planted and 84% of these planted stands are less than 20-years old (Gouldin et al., 2017). Reforestation strategies for longleaf pine include planting containerized seedlings on either clear-cut tracts or thinning techniques that remove unwanted vegetation and preserve adult trees capable of producing their own seed source (Brockway et al., 2006). The success of reforestation is dependent on the variable nature of cone crop production (Brockway et al., 2006). Due to the infrequent (i.e., once every five-to-seven years) nature of adequate longleaf cone crops (Wahlenberg, 1946), reforestation techniques that utilize local seed trees need be timed with productive cone years to ensure sufficient seed stock for germination success.

In an effort to better understand the frequency of longleaf pine crops, cone production has been monitored throughout its range as part of a long-term regeneration study called the "Longleaf Regeneration Trials" (Connor et al., 2014). Beginning in 1958 at the Escambia Experimental Forest in southern Alabama, annual cone counts have expanded to 11 sites across the geographic range of longleaf pine from North Carolina to Louisiana (Brockway, 2017). At each stand the number of green cones and conelets, indicative of the upcoming year's cone crop, are counted during February–April for ≥ 10 trees and reported as an annual stand-average cone crop. These results are published each spring and disseminated to foresters to help guide management techniques (e.g. natural regeneration) dependent on expected seed release from the cones during autumn. Longleaf pine cone crops exhibit significant interannual and spatial variability (Boyer, 1987). The 52-year regional average cone production is 28 cones per tree (Brockway, 2017). Half of all years since 1966 have produced > 25 cones per tree, and > 50 cones per tree for roughly one tenth of all years (Brockway, 2017). Similarly, sites nearest the Gulf coast typically

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produce fewer cones per tree relative to more inland sites (Boyer, 1993, 1998). These values are important due to the number of cones needed for successful regeneration: 750–1000 cones per acre depending on stocking density (40–75 cones per tree (Boyer, 1993, 1997).

Genetics principally influence the number of cones produced for individual trees, yet tree size, canopy status, stand density, and site quality are all important (Brockway et al., 2006; Haymes and Fox, 2012). Conversely, the effect of weather on longleaf masting cycles is equivocal. Some variation in longleaf pine cone crop is believed to be influenced by interannual climatic conditions; however, since the cones develop during a three-year process determining explicit linkages between weather variables and cone production is difficult (Guo et al., 2016). Pederson et al. (1999) examined monthly weather variables as they pertain to cone crop at the Escambia Experimental Forest, and more recently this research has expanded to all sites (Leduc et al., 2015; Chen et al., 2016b; Guo et al., 2016). While longleaf cone production is complex, warmer and wetter conditions during the three years of cone development have a positive influence on cone crop (Shoulders, 1967; Pederson et al., 1999; Leduc et al., 2015; Guo et al., 2016).

Despite a general understanding regarding the frequency of productive cone years and the variables that influence longleaf pine cone crops, less understood is how variations in annual cone crop influence internal growth dynamics such as radial-growth rings and the extent of intra-site variability in a cone crop. As longleaf pine is a commonly used species for dendrochronology studies (e.g. Crockett et al., 2010; Knapp et al., 2016; Harley et al., 2017), understanding the influence of cone-crop variability on radial growth is necessary to improve confidence in using this species as a proxy data source (i.e. is ring-width variability influence by cone-crop variability?).

Several studies have examined the influence annual seed production (i.e. mast) has on annual, radial growth rings of trees (Holmsgaard, 1958; Eis et al., 1965; Woodard et al., 1994; Koenig and Knops, 1998; Hacket-Pain et al., 2015, 2017). As trees trade-off resources from radial growth in the trunk to reproduction in the canopy, negative relationships between annual mast crop and annual radial growth are commonly observed. Speer (2001) and Drobyshev et al. (2014) have explored these relationships and used oak (five *Quercus* spp.) and beech (*Fagus sylvatica*) tree-ring data to produce multi-century reconstructions of annual mast. Hacket-Pain et al. (2015) combined beech mast with climate data to better explain variance in growth rings, and Hacket-Pain et al. (2017) found interactive relationships between summer drought and beech mast that significantly reduced radial growth. These studies provide evidence for the feasibility of time series analysis of mast on tree rings yet are limited to hardwood species. Woodard et al. (1994) examined relationships between mast, climate, and radial growth of subalpine fir and mountain hemlock finding above-average mast crops had a greater reduction in radial growth than below-average crops for these conifer species. In a synthesis on mast and tree rings, Hacket-Pain et al. (2016) underscore the importance for understanding how trees allocate resources to reproduction, and in particular how mast imprints growth rings in ways similar to climate extremes (i.e. drought). At present, research that incorporates mast with climate–radial-growth analyses are limited in part due to the paucity of multidecadal mast datasets. However, if available, these data can be useful to interpret variations in radial growth not attributable to interannual climate variations.

Research examining longleaf pine cone–tree-ring relationships suggests larger cone crops are associated with decreased in radial growth (Patterson and Knapp, 2016). Based on data from two USFS cone-count sites in North and South Carolina, Patterson and Knapp (2016) identified a negative relationship between annual, average longleaf pine cone production and radial growth of the year previous to the cone year. The North Carolina cone site was thinned to a lower stocking density, which improved annual cone production yet temporarily ameliorated cone/radial growth relationships. While limited in scope, this previous research showed a relationship exists between longleaf pine cone production and radial growth that is sensitive to changes in stand density.

Annual growth rings of longleaf pine are principally influenced by temperature and precipitation from mid- to late- growing season with much of the variability present in latewood growth (Devall et al., 1991; Foster and Brooks, 2001; Henderson and Grissino-Mayer, 2009; Knapp et al., 2016; Patterson et al., 2016). The fidelity between longleaf pine growth rings and climate has been useful for developing tree-ring based reconstructions of tropical cyclone precipitation (Knapp et al., 2016), drought (Ortegren, 2008), and streamflow (Crockett et al., 2010; Harley et al., 2017). Not evaluated in these studies are how variations in annual cone production may influence these climate-growth relationships. To this end, this research examines longleaf pine cone production–radial-growth relationships at six sites in four locations to determine: 1) how annual cone production influences radial growth at USFS cone count sites in Alabama, Florida, and Georgia; and 2) if linear models that use climate variables to predict variations in ring growth benefit from the inclusion of cone data. Herein, we present six newly developed chronologies from the exact trees whose cones are counted annually, and pair these data with proprietary cone data from each individual tree.

2. Material and methods

2.1. Cone count sites

As of 2018, the USFS counts annual cone production at 11 locations in the longleaf pine range from North Carolina to Louisiana. We selected four locations for this study based on data completeness and recommendations (Dale Brockway pers. comm. October 2015) that included: The Escambia Experimental Forest in Escambia County, Alabama; Blackwater River State Forest in Santa Rosa County, Florida; Eglin Air Force Base (AFB) in Okaloosa County, Florida; and the Joseph W. Jones Ecological Research Center in Baker County, Georgia (Fig. 1, Table 1). The Escambia Experimental Forest, located in southern Alabama, is managed by the USFS through a 99-year lease with the T.R. Miller Mill Company. The 1214-acre forest was established in 1947 to study various longleaf regeneration and management methods (Connor et al., 2014). Cone-production inventories were initiated in 1958 and later expanded to 10 similar shelterwood stands throughout the longleaf pine range beginning in 1966 (Connor et al., 2014). At Escambia, two cone-count sites were sampled: the “Farm Forty” stand and the “Croker Pond” stand, which are approximately 2 km apart. Similar to Escambia, we sampled from two stands (“Rattlesnake Road” and “Boondocks”) at Eglin AFB that are roughly 20 km apart. Both the Blackwater River State Forest (hereafter Blackwater River) and the Joseph W. Jones Ecological Research Center (hereafter Jones Center) contained one cone-count site. Therefore, each stand was treated as a separate site for a total of six sites from four locations.

2.2. Sampling procedures

All fieldwork was completed in December 2015. Four of the stands contained ten trees, whereas there were 11 trees at the Jones Center and 12 trees at Farm Forty. Therefore, in total we sampled from 63 trees. We exclusively sampled from trees in the multi-decadal cone-count study, which were labeled 1–12 with paint or metal ID tags. Two core samples were obtained from opposing sides of each tree using 5.15 mm increment borers. Each tree was georeferenced and trunk diameter (cm) at breast height (DBH) and crown height (m) were obtained using a DBH tape and a digital laser rangefinder respectively.

2.3. Laboratory procedures

Tree-ring samples were processed using standard dendrochronological techniques (Stokes and Smiley, 1996) to reveal ring

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