

2025, vol. 93, 98-107

https://doi.org/10.12657/denbio.093.007

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Characterizing the growth of *Pinus palustris* and the relationship with cone production at the individual tree level

Received: 12 February 2025; Accepted: 16 April 2025

Abstract: Regenerating longleaf pine (LP) (*Pinus palustris* Mill.) is essential for sustaining the production of high-value wood products and ecological benefits. Understanding the relationship between LP growth and cone production is critical for this effort, as both processes contribute to natural regeneration. In this study, we tracked the growth and cone production of individual LP trees at three sites across the natural range of LP over six-decades. Our results indicate that diameter growth increased linearly with time on a yearly scale before sampling, though the radius increments at tree bases varied from 0.5 mm to 8.0 mm each year. Basal area increment had no significant correlations with annual precipitation or average air temperature. Tree height growth generally slowed after 30~40 years. Cone production had no significant relationship with basal area increment, and their variance dynamics differed. During the cone monitoring period, the basal area increments of each tree followed power laws. A significant relationship existed between radii (basal areas or stem volumes) and the accumulated cone production. These results provide helpful information on the growth characteristics and functional tradeoff between growth and reproduction at individual trees.

Keywords: Basal area increment, height, radius, restoration, reproduction scaling

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Introduction

The longleaf pine (*Pinus palustris* Mill.) ecosystem, which once covered an expansive area along the coast from southeastern Virginia to eastern Texas in the United States (Frost, 2006) (Fig. 1), provides important social, ecological, and economic value to communities (Jose et al., 2006). For example, longleaf pine forests could provide quality timber (McIntyre et al., 2006) and related forest products (e.g., resin, turpentine, and straw), alleviating rural poverty.

Long needles (one foot long) were popularly used in ancient crafts, such as coiled baskets and are now valued as a landscaping material. The longleaf pine seeds are expansive, but raw or roasted seeds can be served as food. From a cultural perspective, the longleaf pine tree is a cultural symbol of the southeastern United States (Gordon et al., 2020), such as it serves as the state tree in Alabama. Longleaf pine forests are often conserved for the habitats of abundant biodiversity. Longleaf pine woodlands also represent one of the most biologically diverse ecosystems in



Fig. 1. Longleaf pine range and three research sites (The base map is from the USDA)

the world as they support 900 plant species, 100 bird species, 36 mammal species, and 170 species of reptiles and amphibians. Some endangered species live in this community, such as the red-cockaded woodpecker (Picoides borealis), gopher tortoise (Gopherus polyphemus), and black pine snake (Pituophis melano*leucus*), and a variety of threatened carnivorous plants (e.g., Sarracenia spp.) (NRCS, 2020). In addition to promoting biodiversity, longleaf pine forests have significant potential for carbon storage, as longleaf pine can survive up to 450 years with heights of 40 m and diameters at breast height (DBH) of 91 cm and also significant belowground carbon storage (Samuelson et al., 2017). However, following an era of exploitative logging, fire suppression, and land use conversion (including urbanization) during the 19th and 20th centuries, the extent of longleaf forest ecosystems reduced dramatically from 37 million ha to less than 5% of their original occupancy (Outcalt & Sheffield, 1996).

The longleaf pine ecosystem is among the most endangered ecosystems in the United States (Noss et al., 1995). As such, the sustainability of longleaf pine ecosystems and their ecological services remain in question. Thus, maintaining and restoring longleaf pine woodlands is critical for many current natural resource objectives. Government agencies and private landowners expressed interest in restoring the important infrastructure of the longleaf pine ecosystem for its high-value wood products, pine straw production, wildlife, biodiversity benefits, carbon sequestration potential, and deep cultural connection to human society (Gordon et al., 2020). Natural regeneration is essential to landowners seeking to maintain existing longleaf pine forests. Thus, understanding the characteristics of tree growth and its trade-off with cone production is important for the long-term sustainability of restoration efforts, especially on private land because of their limited land size but large number of holdings (Chen, 2020). Previous studies developed various tree growth models under different conditions (Goelz & Leduc, 2002). However, it is necessary to indicate additional attributes in the growth of longleaf pine across their natural range to investigate the potential thresholds in ecological function. For example, critical slowing down (abrupt shift in the state of system) has been observed in cone production at different sites (Chen

et al., 2023). Yet, it is unknown whether growth (e.g., basal area increment) followed critical slowing down, indicated by the sudden increase in variance and autocorrelation. This is important because critical slowing down may affect natural regeneration potential. A previous study showed the existence of power laws (nonlinear relationship between cone production and the frequency) in cone production (Chen et al., 2017). However, it is still being determined whether similar laws simultaneously regulated tree growth. Although it is rare to find trees near their biological maximum lifespan, it is still helpful to characterize the growth at the decade-to-century scale, which is relevant to ecosystem conservation.

Silvicultural efforts to regenerate longleaf pine woodlands often confront several factors that complicate restoration (Willis et al., 2021). However, in most years, natural regeneration is limited by insufficient cone production (Pederson et al., 1998). Irregular cone production is related to complex interactions between climate fluctuation and reproduction processes (Chen et al., 2018). For example, tropical cyclone winds and precipitation stimulate cone production (Cannon et al., 2024).

Height and diameter growth are similarly crucial for gaining a prominent canopy position, which is beneficial for preventing shade-induced mortality (Curtin et al., 2020). Based on long-term monitoring data of tree diameter change and standardized tree ring index, no statistically significant relationships were found between tree diameter (or basal area) growth and cone production among trees across sites (Bowman & Chen, 2023; Chen & Willis, 2023). However, calculating a standardized tree ring index may obscure the unique growth features of individual trees (Peltier et al., 2020). Therefore, further effort from other perspectives is needed to establish the relationship between tree growth and cone production at an individual tree level.

This study explores tree growth characteristics and their relationship with cone production for longleaf pine at the tree level across three sites within its historical range. Specific objectives included determining (i) growth features of individual longleaf pine trees, (ii) whether tree growth (e.g., basal area increment) followed critical slowing down, whether power laws existed in the basal area increment during the cone record period, and (iii) the relationship between tree growth and cone production; whether there is a relationship between tree growth and accumulated cone production (total cone production at the current year and before). Understanding this information will improve our fundamental knowledge of longleaf pine resource allocation strategy and provide valuable information to aid efforts to restore and sustain this imperiled ecosystem.

Materials and methods

Study sites

Scientists at the USDA Forest Service have monitored longleaf pine cone production and growth at multiple sites across the southeastern United States for over six decades (Willis & Brockway, 2022). In this study, we used data from three monitoring sites (Fig. 1): (1) Bladen Lake State Forest in North Carolina (short name as Bladen) (34.72°N, 78.56°W), which is close to the northeastern range, (2) Escambia Experimental Forest in southern Alabama (Escambia) (31.01°N, 87.08°W), which is near the south-central range, and (3) Kisatchie National Forest in central Louisiana (Kisatchie) (31.05°N, 92.64°W), which is close to the southwestern edge of the natural range. At each site, 10-17 trees in mature longleaf pine forests with low density have been monitored for cone production each spring. Staff scientists used binoculars (8 to $10\times$) to count the number of green cones in the crown of each monitoring tree. The average cone number on these sampled trees represents the annual cone production on each tree at the site. Climate information for each site was collected from nearby weather stations. Annual precipitation refers the sum of monthly precipitation. Average air temperature is the average of all monthly air temperatures in a year. A more detailed description of the site and cone-counting protocol can be found in previous research (Bowman & Chen, 2023; Chen et al., 2018; Chen & Willis, 2023).

Standardized precipitationevapotranspiration index (SPEI)

The SPEI provides drought information, which often affects tree growth. SPEI is statistically robust and easily calculated with a straightforward procedure (Keyantash & Dracup, 2002). An important advantage of SPEI over other drought indices is its multi-scalar characteristics of potential evapotranspiration on different drought types. The global SPEI database offers long-term, reliable information on drought conditions at a global scale with 0.5 degrees spatial resolution and monthly time resolution. This drought index is based on monthly precipitation and potential evapotranspiration from the University of East Anglia Climatic Research Unit. In this study, the global SPEI data at each region from the 1900s were used since there was no local climate information during the earliest years of the sample trees' lifespan. SPEI>0 means precipitation was more than evapotranspiration, while SPEI<0 means precipitation was less than evapotranspiration.

Tree ring analysis

We harvested three mature (\sim 90 years old) longleaf pine trees at each site from stands adjacent to our cone counting stands. Each tree occupied the dominant growing position in the canopy with the access of full sunlight within low density woodlands (e.g., 50–62 trees per ha). From each harvested tree we obtained small thin sections ("cookies") near the base of the tree, at breast height, at 2 m height, and then every subsequent 2 m interval (e.g., 4, 6, 8) up to 30 m. The "cookies" were polished and then scanned at high resolution. Basal area increments (BAI), the increase of stem area from the year (ring) *n* to the year (ring) n+1, were measured through ImageJ software, and the corresponding tree ring radii of circles with the same area each year were calculated since the tree ring interfaces were not perfect circles. Height growth was estimated from tree ring counts at different heights. Cone production was classified as bumper (>100 cones per tree), good (50–100), fair (25–50), and poor (< 25) (Chen & Willis, 2023). BAI in different cone production years were compared. The variance dynamics in BAI and cone production were compared to check whether they shared a similar regime (e.g., starting time and duration). BAIs during the cone count period were tested for possible power laws like $N = BAI^x$, where the occurrences (N) of BAI under different thresholds ($\leq 5.0 \text{ cm}^2$, $\leq 10.0 \text{ cm}^2$, $\leq 15.0 \text{ cm}^2$... $\leq 30.0 \text{ cm}^2$) on each tree were counted. The correlation between log (BAI) and log (N) was then tested.

Statistical analysis

Linear regression and correlation analysis were performed using the least-squares technique by SAS software (Cary, NC, USA). A t-test was used to compare the average BAI during the different phases of the production years. The statistical test was considered significant at p < 0.05.

Results and Discussion

The radii at the tree base area (hereafter referred to as the ground level) increased linearly over time for each tree (p < 0.01) (Fig. 2a, b, c). Radial growth increments at the base area varied from 0.5 mm to 8.0 mm annually but typically ranged from 2.0–3.0 mm annually. Tree heights stabilized after $30\sim40$ years (Fig. 2d, e, f). A second-order polynomial fit tree height growth (p < 0.01). The observed growth rate is lower than that observed from longleaf pine in South Carolina (Cram et al., 2010), where trees reached an average radius of 5.9 cm and a height of 11.7 m after 15 years. Usually, longleaf pine takes 100

to 150 years to reach maximum size (Boyer, 1990). Thus, longleaf pine is not a fast-growing tree species compared to other southern pine species (Willis et al., 2024). The slow growth is part of the reason why longleaf pine woodlands were replaced by loblolly pine (Pinus taeda) monoculture. However, longleaf pine can add radial growth continuously for a century. This slow, continuous growth characteristic may infer an intrinsic ability to sustain itself over an extended period of time. Due to its slow growth, longleaf pine restoration across its historical range will mainly depend on human interventions, such as herbicide application and prescribed burning. The relatively low growth rate may also be advantageous to maintain its sustainability under unfavorable environmental conditions since the species are not easily changed by climate (Bartelme, 2009). Similar results were also observed in Chinese Torreya (Torreya grandis) with a lifespan of a thousand years (Chen & Niu, 2020).

In this study, the BAI of individual trees was no significantly correlated with annual precipitation or average air temperature. Average BAI was not significantly affected in relatively wet or dry years. However, if we combined the BAI of these trees at each site and local drought conditions (SPEI), there was a "triangle" pattern at the Bladen and Escambia sites (Fig. 3). Most high BAI occurred in years with moderate precipitation. This result corresponds with observed patterns of cone production and ecosystem water consumption (Chen et al., 2023). The relationship between tree growth and air temperature and precipitation may be modified by longleaf pines' natural tolerance to drought. Since longleaf pines have well-developed root systems, they can absorb water in a deep soil profile (Heyward, 1933). Longleaf pine is also known to reduce water loss during drought by closing its stomata (Samuelson et al., 2019). Microsite conditions may also obscure the effects of temperature and moisture on growth at the tree level. Future research needs to acquire more data for further exploring growth dynamics under drought conditions.

Annual BAI varied dramatically among trees after 10–20 years (Fig. 4). Tree heights were approximately 10–15 m at that time. Fluctuation in BAI can be caused by several factors that influence canopy interception of light including windstorms and pest outbreaks. Limitations in our sample size prevented us from investigating this phenomenon at the stand-level; however, we cannot rule out the possibility that disturbances may have impacted BAI after canopy closure.

High cone production events occurred in years with both low and high BAI. Likewise, cone production did not significantly change the average BAI. Critical slowing down also existed in the BAI. However, the variance dynamics in BAI (e.g., starting time and duration) and cone production were quite



Fig. 2. The growth patterns of three longleaf pine trees in radius and height at Bladen (a, d), Escambia (b, e), and Kisatchie (c, f). Each Roman number corresponds with the individual tree number. In (a), the fitting line of tree I is $y_1 = 2.1154x_{1-}4074.0$, $R^2 = 0.9912$, p < 0.01; the fitting line of tree II is $y_2 = 2.4601x_{2-}4735.6$, $R^2 = 0.9700$, p < 0.01; the fitting line of tree III is $y_3 = 1.5867x_{3-}3065.1$, $R^2 = 0.9964$, p < 0.01. In (b), the fitting line of tree I is $y_1 = 3.0827x_{1-}6053.2$, $R^2 = 0.9584$, p < 0.01; the fitting line of tree II is $y_2 = 3.0940x_{2-}6016.4$, $R^2 = 0.9916$, p < 0.01; the fitting line of tree III is $y_3 = 2.5104x_{3-}4904.1$, $R^2 = 0.9971$, p < 0.01. In (c), the fitting line of tree I is $y_1 = 4.9059x_{1-}9622.3$, $R^2 = 0.9859$, p < 0.01; the fitting line of tree II is $y_2 = 4.0090x_{2-}7831.2$, $R^2 = 0.9767$, p < 0.01; the fitting line of tree III is $y_3 = 4.1791x_3 - 8177.5$, $R^2 = 0.9807$, p < 0.01



Fig. 3. The combined BAI of three trees and regional drought conditions (SPEI) at Bladen (a), Escambia (b), and Kisatchie (c)



Fig. 4. Patterns of basal area increment and cone production in three longleaf pine trees at Bladen (a, b, c), Escambia (d, e, f), and Kisatchie (g, h, i)



Fig. 5. Variance dynamics of BAI and cone production in three longleaf pine trees at Bladen (a, b, c), Escambia (d, e, f), and Kisatchie (g, h, i). Cone/10 and Cone/100 represent the variance of cone production divided by 10 or 100

different (Fig. 5). This result further indicates that there was no significant relationship between regimes of BAI and cone production. Our finding that cone production did not influence BAI runs contrary to previous thinking (Patterson & Knapp, 2018). Power laws existed in these dramatically changed BAI during the cone monitoring period (Fig. 6), indicating that BAI followed a stochastic process with a long-range correlation. This result is consistent with the previous research (Bowman & Chen, 2023; Chen & Willis, 2023). The relationship between tree growth and cone production was still insignificant even if the tree stem volume was used. Thus, systematic monitoring is required to understand the tree energy allocation (Chen & Willis, 2023).

There was a significant correlation between tree radii (or basal areas or stem volumes) and the accumulated cone production, although it varied among individuals (Fig. 7). For example, a longleaf pine tree with a base diameter of 30 cm (in bark) might have produced \sim 500 cones. This pattern is confirmed by the diameter (outside bark) and cone data on individual trees at Kisatchie from 2009 to 2022 (Chen & Willis, 2023), where data were available each year

(data not shown here). Our study is the first to report this scaling relationship. This result provides a quantitative relationship between tree growth (diameter) and cone production, which can be used to reflect changes in fecundity and vigor over time (e.g., growth and reproduction). This relationship means that a large tree could produce more cones overall than a small tree over its lifetime although it might produce fewer cones in some periods. It is consistent with the biological processes that large-diameter trees support greater leaf area than small trees, providing resources for more cone production. Thus, at least some mature trees should be preserved for cone production during regeneration harvest. This result may also indicate that longleaf pine trees might use previously stored carbon (or energy) to produce recent cones, similar to redwood sprouts after wildfires (Stokstad, 2023). Where would the longleaf pine store energy for later use? Longleaf pine is known to maintain large carbohydrate reserves in its roots, trunk, and stems (Samuelson et al., 2017; Johnsen, 2021). Monitoring the dynamics of the root system, resin, and hormones may be a good start. Further experimental research in this field is needed to discover the biological mechanisms.



Fig. 6. Power laws in the basal area increments during cone monitoring periods in three threes at Bladen (a, b, c), Escambia (d, e, f), and Kisatchie (g, h, i). The fitting line information is in the following: (a) y = 1.4401x-0.7591, R² = 0.9574, p < 0.01; (b) y = 0.8179x + 0.4487, R² = 0.8784, p < 0.01; (c) y = 0.9109x + 0.4796, R² = 0.8750, p < 0.01; (d) y = 1.2741x - 0.8107, R² = 0.9467, p < 0.01; (e) y = 1.0764x-0.1703, R² = 0.8643, p < 0.01; (f) y = 2.0556x-1.4743, R² = 0.9252, p < 0.01; (g) y = 1.2485x-0.7407, R² = 0.9265, p < 0.01; (h) y = 1.8887x-1.8186, R² = 0.8062, p < 0.01; (i) y = 1.3511x-0.8881, R² = 0.9310, p < 0.01



Fig. 7. Relationships between radius (within bark) and accumulated cone production for three trees at Bladen (a, b, c), Escambia (d, e, f), and Kisatchie (g, h, i). The fitting line information is in the following: (a) y = 14.501x - 1876.7, $R^2 = 0.9198$, p < 0.01; (b) y = 18.308x - 2992.9, $R^2 = 0.9233$, p < 0.01; (c) y = 11.519x - 752.1, $R^2 = 0.9406$, p < 0.01; (d) y = 8.6215x - 447.6, $R^2 = 0.9724$, p < 0.01; (e) y = 12.483x - 1403.5, $R^2 = 0.9443$, p < 0.01; (f) y = 17.32x - 1435.0, $R^2 = 0.9912$, p < 0.01; (g) y = 9.0238x - 748.78, $R^2 = 0.9916$, p < 0.01; (h) y = 12.041x - 1296.8, $R^2 = 0.9873$, p < 0.01; (i) y = 10.943x - 1017.2, $R^2 = 0.9884$, p < 0.01

Conclusions

Although the sample size was limited, our results demonstrated that interesting patterns in longleaf pine growth and cone production. Notably, our results confirm that restoration of longleaf pine ecosystems on cutover sites will require extensive time because of the slow growth and sporadic cone production. Longleaf pine height growth stabilized after 30–40 years, but its diameter growth increased for at least 100 years. Stem growth had no significant correlation with annual precipitation or average air temperature at an individual tree level, but drought could affect the basal area increment at the population (or stand) level. Basal area growth is a stochastic process with variations that generally follow power laws. No clear relationship was found between the annual basal area increment and cone production in individual trees, although both exhibited the critical slowing down. However, a significant positive correlation existed between the stem diameters or accumulated basal area increments and accumulated cone production, which means longleaf pine may use previously accumulated energy or matter for cone production.

This result can help to estimate cone production for individual longleaf pine trees based on their sizes. Further research on the mechanisms of tree growth and cone production is needed to understand the functional ecology of this iconic tree species.

Author contribution statement

XC: conceptualization, field sample, data analysis, writing; JLW: writing, data providing, permission; Both authors contributed to the discussion of results.

Acknowledgments

Thanks to the people for their assistance in the fieldwork, which include Dr. Dale G. Brockway, Dr. Mary Anne Sword Sayer, Jacob Floyd, and Alan Springer at Southern Research Station of the USDA Forest Service, Hans Rohr at Bladen Lake State Forest, and Kimberly Bowman, Jeremy Whigham at AAMU. This paper was written and prepared in part by a U.S. government employee on official time, and therefore, it is in the public domain and not subject to copyright. The findings and conclusions in this

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publication are those of the authors. They should not be construed to represent an official USDA, Forest Service, or United States Government determination or policy.

Funding

This study was partially supported by the USDA National Institute of Food and Agriculture Capacity Building Program, McIntire Stennis project, 1890COE NREE, and the USDA Forest Service.

Data availability

The data supporting this study's findings are available upon request from the authors.

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