forests

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Individuals' Behaviors of Cone Production in Longleaf Pine Trees

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Abstract: The sporadic cone production of longleaf pine (*Pinus palustris* Mill.) challenges the restoration of the longleaf pine ecosystem. While much has been learned about longleaf pine cone production at the stand level, little information exists at the tree level regarding cone production and energy allocational strategy. This study aims to analyze cone production and diameter growth of approximately ten sampled longleaf pine trees at seven sites across the southeastern USA over the past twenty years. The results indicate that three-year cycles dominated the cone production dynamics, but longer cycles (four years and more) also occurred. The dynamics of entropy in cone production varied among trees. Taylor's law, which describes the correlation between average and variance, existed in cone production for the majority of trees. Lagged cone production at one and two years was not autocorrelated among trees across sites. No significant relationships existed between tree diameter (or basal area) growth and cone production among trees across sites. This study provides new information on cone production at the individual tree level and narrows down the possible mechanisms. The results will be helpful in developing strategies for the management and modeling of longleaf pine cone production.

Keywords: cycle; entropy; intensive monitoring; resource allocation; Taylor's law; pine trees

Citation: Chen, X.; Willis, J.L. Individuals' Behaviors of Cone Production in Longleaf Pine Trees. *Forests* **2023**, *14*, 494. https://doi.org/10.3390/f14030494

Academic Editor: Brian Tobin

Received: 6 February 2023
Revised: 25 February 2023
Accepted: 27 February 2023
Published: 2 March 2023

1. Introduction

Longleaf pine (*Pinus palustris* Mill.) forests are among the most economically and culturally valued ecosystems in the southeastern United States [1,2]. Before European settlement, longleaf pine forests occupied 37 million hectares ranging from eastern Texas to southeastern Virginia [3]. Currently, the longleaf pine ecosystem is fragmented and covers about 1.9 million ha after decades of timber exploitation, fire suppression, and forest conversion [4–6]. Thus, the longleaf pine ecosystem has become critically threatened [7]. Longleaf pine forests are capable of producing quality timber and related forest products, and thus provide job opportunities to local communities [1,2,5,8]. These forests are also characterized as one of the North America's most biologically diverse ecosystems [9], supporting approximately 900 plant species, 100 bird species, 36 mammal species, and 170 species of reptiles and amphibians. Some endangered species include the red-cockaded woodpecker (*Picoides borealis*), gopher tortoise (*Gopherus polyphemus*), black pine snake (*Pituophis melanoleucus*), and carnivorous plants [10]. Furthermore, longleaf pine forests have the potential for significant carbon storage, as trees can live up to 450 years and reach heights of more than 40 m and diameters approaching 91 cm [11–13].

One of the essential factors contributing to the restoration difficulties of longleaf pine forests is sporadic seed production, which limits longleaf pine restoration, regeneration, and management [3]. The longleaf pine cone production cycle is a lengthy physiological process that can extend over three years [10,14]. If cone production is insufficient to support natural regeneration, longleaf pine will gradually be replaced by more prolific seeding species such as loblolly pine (*P. taeda* L.). Cone production variability is thought to be related to biological factors and climatic conditions, although the exact mechanisms are unknown [11,15]. Previous results noted episodes of high seed production once every

5–7 years or longer (8–10 years) based on location [16,17]. Recent studies have shown that there were 3-year and 4-year cycles (Sandhills) in the long monitoring data of the longleaf pine population across its range based on wavelet analysis [18]. Due to data limitations, these estimations are mainly based on the average observational data at the stand scale rather than on individual trees.

Recently, power laws were found in the scaling of cone production of longleaf pine populations, although the scaling exponents differed among sites [19]. However, invariant scaling properties were found in seed output for 28 tree species with 148 reproductive time series in Europe [20,21]. Entropy (e.g., Shannon entropy) is an efficient dynamical indicator of information order in plant growth [22]. The entropy of cone production for each longleaf pine population was relatively stable at each site (e.g., Escambia) and highly correlated with the local climate [23,24]. As a minimum unit of self-organization, each tree may have a similar power law or entropy in its cone production.

One hypothesis of tree seed variation over time is related to energy accumulation and resource allocation trade-offs between seed production and biomass growth [25]. For example, large trees may produce more cones due to their biomass or energy accumulation potential. Relatedly, small trees may allocate fewer resources toward diameter growth during years of heavy cone production. These resource-matching hypotheses could be supported by a positive correlation between tree growth and cone production within individual trees over time. However, this theory has seldom been supported by evidence [26]. On the contrary, negative correlations between cone production and tree growth are more common [27,28]. Hypotheses regarding trade-offs between reproduction and growth have largely been developed for species with strong masting habits, which may not apply to longleaf pine given its weak masting behavior [29].

In addition to allocational patterns, plants often exhibit lagged autocorrelation, a tendency for low-seed years to follow high-seed years and vice versa [30–32]. The normalized tree ring growth in longleaf pine in North Carolina was found to have a negative correlation when the cone production lagged one year from radial growth (i.e., cone production of year X with radial growth of year X-1) [33]. However, these relationships were not significantly correlated in the same year.

This study aims to test the above results and hypotheses at the individual tree level.

Specifically, the objectives are to investigate whether: (i) longleaf pine trees have 3-year cycles for cone production; (ii) consistent power law or entropy exists in cone production; (iii) cone production among years is autocorrelated; (iv) there are trade-offs between tree growth and cone production. The results from this study may provide insights into the functional ecology of longleaf pine cone production.

2. Materials and Methods

2.1. Study Sites

As a long-term regional monitoring study, scientists at the USDA Forest Service monitor longleaf pine cone production at multiple sites across the southeastern United States each spring. These 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) Eglin military base in western Florida (Eglin), (4) the Jones Center at Ichauway in southwestern Georgia (Jones Center), (5) Bladen Lake State Forest in North Carolina (Bladen), (6) Sandhills State Forest in northeastern South Carolina (Sandhills), and (7) Kisatchie National Forest in central Louisiana (Kisatchie). At each site, approximately ten trees were sampled. Tree diameter (DBH) and green cone counts on each sampled tree were measured at each site [18,23,24]. Six sites with complete data in the past twenty years were selected for analysis in this study. Detailed information about each site is listed in Table 1. Some site information (e.g., latitude, longitude, and climate conditions) can be found in the reference [18]. The data set included some years with missing data due to some problems (e.g., COVID-19). We skipped the missing year in the calculation to address missing data if only a single measurement was missing. However, for continuous missing data, that period or the tree was excluded from the relevant analysis. All analyses in this study were based on measurements.

Table 1. Year of cone count initiation and average tree diameter at the study sites.

Sites	Included Time	Average DBH at the Start of Analysis (cm)
Escambia	2002–2019	43
Blackwater	2005–2019	41
Eglin	1999–2019	39
Jones Center	2005–2019	45
Bladen	1996–2018	34
Sandhills	1996–2019	38
Kisatchie	2000–2022	52

2.2. Methods

(i) Taylor's law between average and variance

The logarithm of the variance of the density (individuals per area or volume) of populations was approximately a linear function of the logarithm of the mean density for many species [34]. This relationship is known as Taylor's law. This law has been verified in the cone production of longleaf pine populations [24]. In this study, Taylor's law can be expressed in the following way:

$$V = a \times M^b$$

So that

$$\log(V) = \mathrm{Log}(a) + b\ \mathrm{Log}(M)$$

with V as the variance of cone production and M as the average cone production in each tree. With the time increase of 2, 3 … to n years from the early time, the relationship between the variance and average cone production was estimated for each tree.

(ii) Entropy

Entropy is defined as the Shannon entropy. H(x) of cone production of each tree at different time scales of ε (length of years) is the following:

$$H_\varepsilon(x) = -\Sigma p_\varepsilon(x) \times \mathrm{Log}(p_\varepsilon(x)), p(x) = x_i/\Sigma x_i$$

where p (x) is the probability of cone production (x) in the ith year measured using samples of ε units in size (see the diagram below). The time scale of ε includes 1, 2, … , n years.

(iii) Increase in diameter and basal area

$$\text{Increase in diameter} = \text{DBH}_{t2} - \text{DBH}_{t1,}$$

$$\text{Increase in basal area} = \text{Basal area}_{t2} - \text{Basal area}_{t1,}$$

where t1 and t2 are different times, DBH is the diameter at breast height, and the basal area is equal to $3.14 \times (\text{DBH}/2)^2$.

(iv) Autocorrelation in cone production

One-year lag autocorrelation was calculated between the cone production $X_1 \ldots X_t$ and $X_2 \ldots X_{t+1}$ and two-year lag autocorrelation was calculated between $X_1 \ldots X_t$ and $X_3 \ldots X_{t+2}$. Correlation analysis was performed using the least-squares technique by SAS software (Cary, NC, USA). The statistical test was considered significant at $p < 0.05$.

3. Results and Discussion

There were variations in cone production of each longleaf pine tree. Three-year intervals were the most common cone production cycle among sampled trees (Figure 1), but longer cycles (four, five, or more than five years) were observed. Synchrony and asynchrony in cone production were observed over time. For the past 20 years, the frequency of a bumper crop (more than 100 cones per tree) has varied among individuals at different sites.

Usually, after a bumper crop, there is a low cone production year. However, most trees typically had low annual cone production (e.g., 2–5 cones) in most years. Additionally, some trees were always poor cone producers.

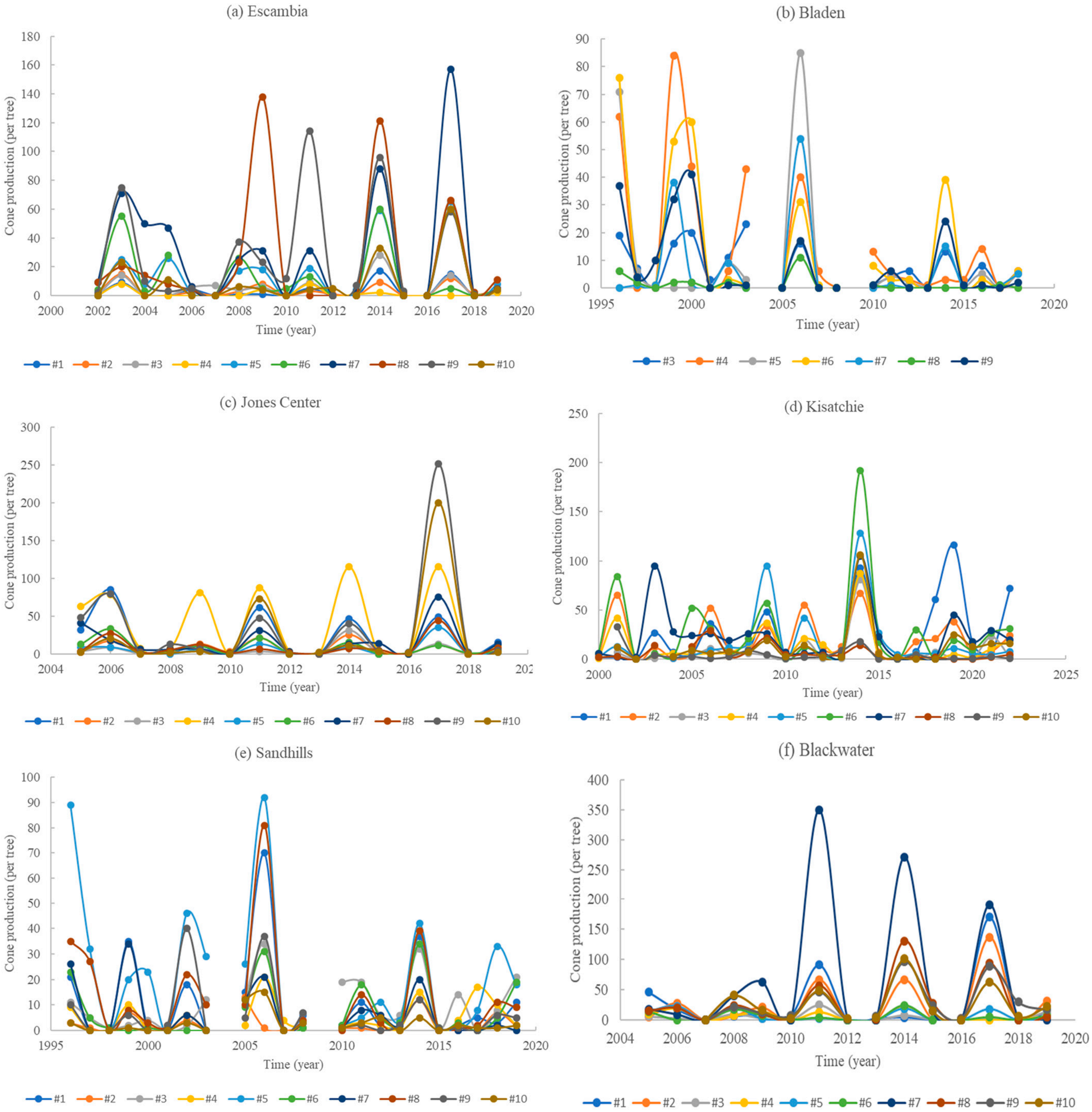

Figure 1. Cycles of cone production of individual trees at different sites (#1, 2 … 10 represent 10 sampled trees).

The result of three-year or longer cone production cycles at the individual tree level is consistent with the cone production at the population level, which is based on the average of the sampled trees [18]. There were frequent very low or no cone production events for individual trees. However, at the population level, the low cone production might be mitigated by some high cone producers in any given year [35], which could create localized regeneration pockets within the stand but overall low regeneration throughout.

The relationships among sampled trees may affect the dynamics of cone production at the population level. For example, at least three of the ten sampled trees (e.g., #4, #6, and #8) at Escambia had no significant correlation in cone production with other trees (Table 2). The heterogeneity in cone production among trees might affect the synchrony of cone production (e.g., magnitude and cycle) at the population level. Since the sampled trees were of similar DBH, the effect of tree size on cone production remains unknown. The cycle of cone production in longleaf pine is considered to be related to the reproduction process, which is approximately three years from pollen to seed [14]. It is not clear how the reproduction duration affects the cone production cycle. Nevertheless, longer reproduction duration may be worse because more things can go wrong. Cone production variability (such as four-year cycles or longer) might be related to climate and environmental conditions [18]. Although there are several assumptions related to the cycle of tree seed production [25], it is still unclear what exactly determines the length of the cone production cycle.

Table 2. Correlation of cone production between sampled trees at Escambia.

Tree ID	#1	#2	#3	#4	#5	#6	#7	#8	#9	#10
#1		Yes	Yes	No	Yes	No	Yes	No	Yes	Yes
#2			Yes	No	No	No	Yes	No	No	Yes
#3				No	Yes	No	No	No	Yes	No
#4					No	No	No	No	No	No
#5						No	Yes	No	No	Yes
#6							No	No	No	No
#7								No	No	Yes
#8									No	No
#9										No

The entropy of cone production of each tree generally increased with time (Figure 2), but the entropy dynamics varied among trees. The sudden increase in cone production could bring down the entropy. Some trees had large deviations (e.g., #6 and #7 at Escambia). The increase in entropy on each tree with time is consistent with the previous results at the population level [23,24]. However, the dynamics of entropy varied among trees. The multiscale entropy of cone production was highly related to the biological regime [24]. This difference in regime at the individual tree level might be related to their varied microenvironmental conditions (e.g., soil water and nutrients) since these sites are across the southeastern region and have different climatic regimes. Intensive monitoring is needed to study the entropy dynamics at the individual and population levels [23].

For most trees, a significant correlation existed between variance and average cone production over the past 20 years ($p < 0.05$) (Table 3). This pattern occurred in a tree before death (Eglin #9 in 2016). However, this relationship was also insignificant for some living trees ($p > 0.05$) (e.g., Jones Center #2, #5, #7). The percentage of trees following Taylor's law was the lowest (50%) at Blackwater. Taylor's law was found in cone production at the population level [19], and it still existed at the individual tree level. However, some trees did not follow Taylor's law in this study. This breakdown of Taylor's law might be related to the health conditions of these trees. Previous studies indicated that parasitism or epidemic infection could alter the exponents of Taylor's law [36–38]. However, a tree (Eglin #9) was found to follow Taylor's law in cone production even before its death in 2016. This result may be related to the possible cause of tree death, such as wind damage. Further research on Taylor's law, cone production, and tree health may be needed at the individual tree level.

There was no significant autocorrelation between cone production and their 1-year or 2-year lagged data for each tree across sites ($p > 0.05$). In addition, there were no significant relationships between diameter growth (or basal area increase) and cone production among trees across sites (Figure 3). A significant negative correlation between cone production and 1-year lagged diameter growth (or basal area increase) was not observed.

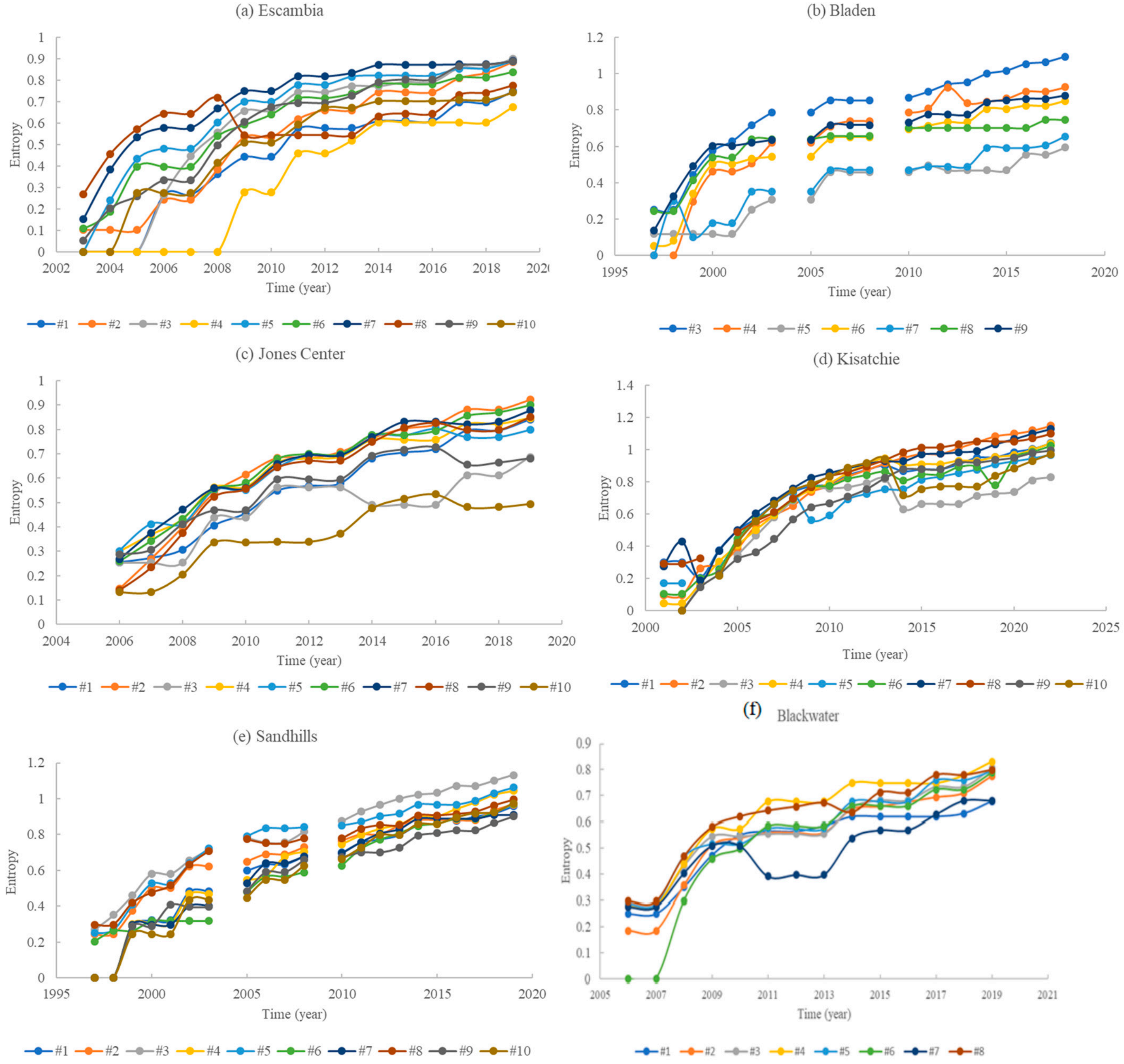

Figure 2. The entropy of cone production of each tree with time (#1, 2 . . . 10 represent 10 trees).

Table 3. Taylor's law in the cone production of ten monitored longleaf pine trees at different sites (y = log(variance), x = log(average)).

Trees	Escambia	Blackwater	Jones Center	Kisatchie	Eglin
#1	$y = 1.773x + 0.556$ $R^2 = 0.895$, $p < 0.01$	$y = 1.643x + 0.762$ $R^2 = 0.391$, $p > 0.05$	$y = 0.699x + 2.034$ $R^2 = 0.595$, $p < 0.05$	$y = 1.82x + 0.374$ $R^2 = 0.636$, $p < 0.05$	$y = 1.499x + 0.577$ $R^2 = 0.896$, $p < 0.01$
#2	$y = 1.805x + 0.308$ $R^2 = 0.613$, $p < 0.05$	$y = 2.658x - 0.538$ $R^2 = 0.902$, $p < 0.01$	$y = 1.499x + 0.521$ $R^2 = 0.555$, $p > 0.05$	$y = 1.684x + 0.267$ $R^2 = 0.347$, $p > 0.05$	$y = 2.926x - 0.61$ $R^2 = 0.758$, $p < 0.05$
#3	$y = 2.007x + 0.303$ $R^2 = 0.93$, $p < 0.01$	$y = 3.138x - 0.605$ $R^2 = 0.464$, $p > 0.05$	$y = 2.459x + 0.061$ $R^2 = 0.601$, $p < 0.05$	$y = 3.294x - 0.629$ $R^2 = 0.907$, $p < 0.05$	$y = 1.699x + 0.351$ $R^2 = 0.969$, $p < 0.01$
#4	$y = 2.003x + 0.492$ $R^2 = 0.901$, $p < 0.01$	$y = -0.410x + 2.164$ $R^2 = 0.205$, $p > 0.05$	$y = -3.746x + 9.268$ $R^2 = 0.725$, $p < 0.05$	$y = 2.04x + 0.207$ $R^2 = 0.603$, $p < 0.05$	$y = 2.949x - 0.387$ $R^2 = 0.836$, $p < 0.05$
#5	$y = 2.069x + 0.284$ $R^2 = 0.952$, $p < 0.01$	$y = -0.213x + 2.162$ $R^2 = 0.064$, $p > 0.05$	$y = 2.353x - 0.225$ $R^2 = 0.316$, $p > 0.05$	$y = 2.702x - 0.614$ $R^2 = 0.979$, $p < 0.01$	$y = 2.211x + 0.043$ $R^2 = 0.964$, $p < 0.01$
#6	$y = 2.51x + 0.024$ $R^2 = 0.955$, $p < 0.01$	$y = 0.692x + 1.257$ $R^2 = 0.253$, $p > 0.05$	$y = 0.875x + 1.209$ $R^2 = 0.823$, $p < 0.05$	$y = 7 \times 10^{-5}x + 1.337$ $R^2 = 0.697$, $p < 0.05$	$y = -1.069x + 4.799$ $R^2 = 0.196$, $p > 0.05$

Table 3. *Cont.*

Trees	Escambia	Blackwater	Jones Center	Kisatchie	Eglin
#7	$y = 1.905x + 0.538$ $R^2 = 0.802, p < 0.05$	$y = 0.303x - 0.291$ $R^2 = 0.994, p < 0.01$	$y = 0.585x + 1.716$ $R^2 = 0.189, p > 0.05$	$y = 3.188x - 1.528$ $R^2 = 0.982, p < 0.01$	$y = 2.022x + 0.111$ $R^2 = 0.477, p > 0.05$
#8	$y = 2.542x - 0.297$ $R^2 = 0.924, p < 0.01$	$y = 3.663x - 2.109$ $R^2 = 0.619, p < 0.05$	$y = 1.779x + 0.414$ $R^2 = 0.824, p < 0.05$	$y = 0.797x + 1.131$ $R^2 = 0.788, p < 0.05$	$y = -2.289x + 5.064$ $R^2 = 0.343, p > 0.05$
#9	$y = 2.267x - 0.021$ $R^2 = 0.963, p < 0.01$	$y = 2.338x - 0.272$ $R^2 = 0.927, p < 0.01$	$y = 0.286x - 0.255$ $R^2 = 0.997, p < 0.01$	$y = 1.924x + 0.441$ $R^2 = 0.949, p < 0.01$	$y = 1.675x + 0.568$ $R^2 = 0.984, p < 0.01$
#10	$y = 2.069x + 0.451$ $R^2 = 0.961x, p < 0.01$	$y = 2.234x - 0.126$ $R^2 = 0.849, p < 0.01$	$y = 2.471x + 0.077$ $R^2 = 0.939, p < 0.01$	$y = 5.336x - 3.299$ $R^2 = 0.946, p < 0.01$	$y = 1.483x + 1.091$ $R^2 = 0.772, p < 0.05$
Percentage of trees following Taylor's law (%)	100	50	70	90	70

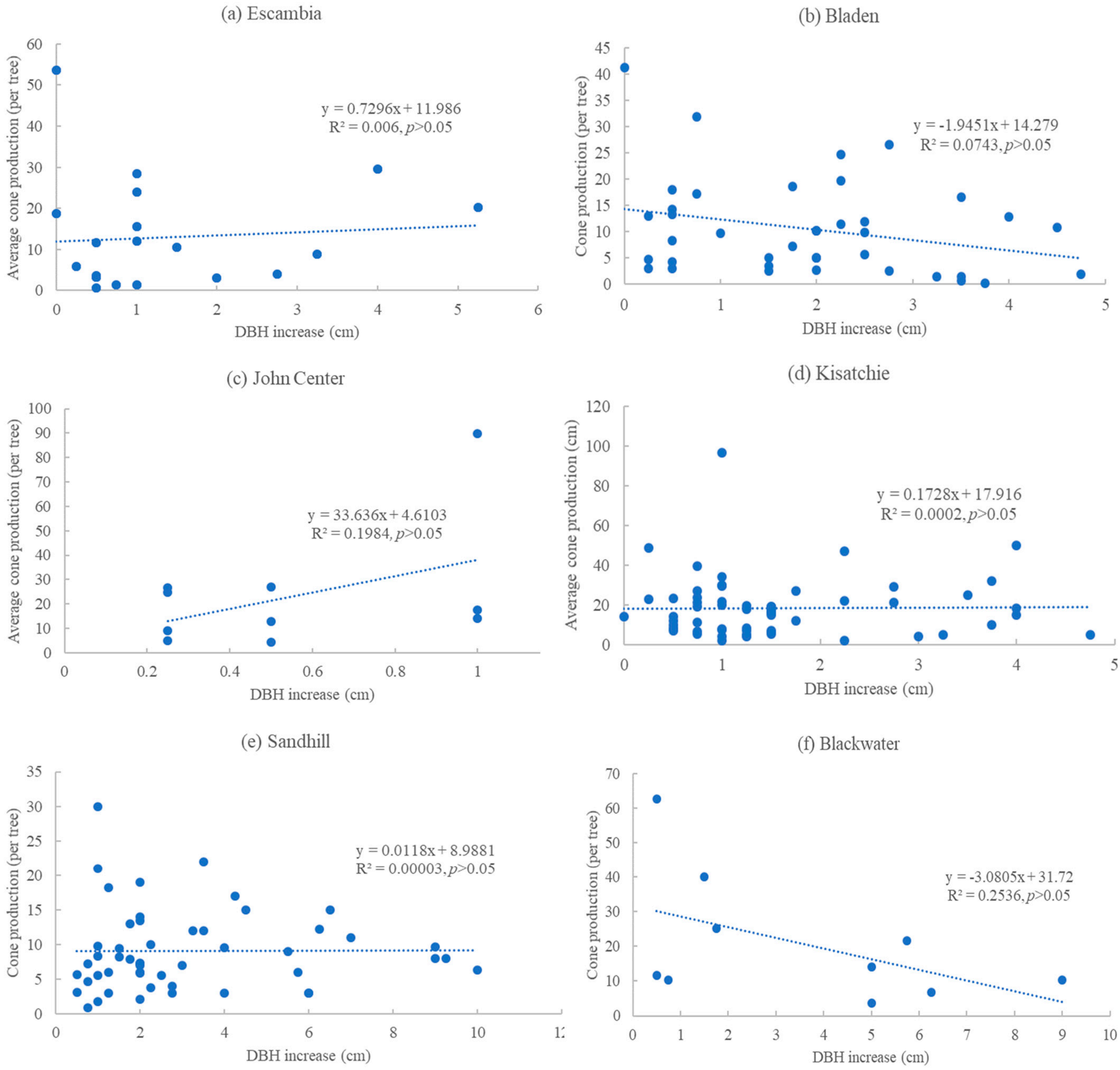

Figure 3. Relationships between diameter growth and the corresponding average cone production over time across sites.

From an energy balance perspective, it is reasonable to assume that trees would decrease their growth (such as DBH) while they allocate resources (e.g., carbohydrates, nitrogen, phosphorus) towards cone production [25]. However, the question is in what year would the lag occur over the three-year cycle. The result of this study indicated no significant correlation between diameter or basal area growth and cone production in longleaf pine trees over two decades across multiple sites. This result neither supports the positive correlation between growth and reproduction nor the negative correlation hypotheses [27,28]. The positive correlation was never confirmed [25,26]. In order to study resource allocation, it is better to know how much energy is devoted to different parts of a tree (such as needles, branches, stems, and roots). Otherwise, only the information of DBH and cone production may not be sufficient since trees may not follow the same allometric relationship while under stress [39]. Annual precipitation may be related to the relationship between tree height and DBH for longleaf pine [40]. The result of this study also did not show an autocorrelation in cone production with one- or two-year lagged data in individual trees. Recently, autocorrelation in the variance of cone production was observed at stand level [41]. The resource budget model suggests that a plant has to reach the threshold necessary for a full crop; otherwise, the plant does not invest, or invests very little, in reproduction [25]. Obviously, the results of this study do not support this view because longleaf pine makes at least some investment in cone production even in poor years. The results from this study also differed from a strong negative correlation [31]. That study was based on retrospective tree ring analysis, while here the growth measurements were obtained from living trees. However, tree ring data may be biased [42], because trees are long-lived and their growth in tree rings is complex with lagged responses from diverse factors [43], which are not well-captured by correlation methods [44]. Other factors, such as the hormones abscisic acid and ethylene, may affect resource allocation through interactions [25,45]. It is difficult to conduct precise annual DBH measurements for many living trees considering tree bark properties.

The results of this study provide implications for longleaf pine management and research. First, cone production has a high degree of heterogeneity among individual trees. This may lead to spatial differences in cone production within populations across landscapes. Any population with a high producer may obscure the general low production at the stand level. For cone monitoring, mature longleaf pines with different sizes (DBH) should be included. Second, there was no significant correlation between tree growth in DBH and cone production. Further studies on energy allocation at the individual tree level of longleaf pine should be carried out. Third, precise measurements of tree DBH for the monitoring of trees should be conducted annually. Due to the rough tree bark, care has to be taken to record tree DBH. Wet and dry weather and fires may affect precise measurements due to bark expansion and shrinking. Other measurements that can characterize tree growth, such as leaf area index and height, should also be recorded for the monitored trees. Fourth, if possible, intensive monitoring of trees and their microenvironment should be established at some research sites. These steps would significantly benefit future studies examining the trade-offs between longleaf pine growth and cone production.

4. Conclusions

There were heterogeneous behaviors (e.g., cycle, amplitude) of cone production among longleaf pine trees. Although three-year cycles were dominant, four-year cycles and longer also occurred. The regime of cone production, which was characterized by entropy and Taylor's law, also differed among trees. This study found neither a significant autocorrelation in cone production with one-year or two-year lagged data nor a significant relationship between cone production and DBH (or basal area) growth. The cone production in longleaf pine trees seems to be a complicated and subtle process. This study tested and narrowed down some relevant hypotheses on cone production in longleaf pine. The results also raise questions surrounding energy allocation and storage for cone production. Long-term intensive monitoring of tree growth and microenvironment with precise measurements may help uncover the underlying mechanisms.

Author Contributions: Conceptualization, X.C.; methodology, X.C.; formal analysis, X.C.; investigation, X.C. and J.L.W.; writing-original, X.C.; data curation, J.L.W.; writing-editing, J.L.W. All authors have read and agreed to the published version of the manuscript.

Funding: This research was supported by the USDA National Institute of Food and Agriculture Capacity Building Program (2021-38821-34596) and the McIntire Stennis project (7001918) and by the USDA Forest Service.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: Data are available upon request to JLW.

Acknowledgments: We thank Dale Brockway for his suggestions.

Conflicts of Interest: The authors declare no conflict of interest.

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