

Article

Longleaf Pine Growth Divergence Increases over Time Across Its Geographic Range

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Abstract

The “divergence problem” in recent decades is a tendency for trees in high latitudes to lose climate sensitivity. Growth divergence has been reported for certain tree species in alpine or northern latitude locations but has yet to be found in species with southern distributions. This retrospective study used tree ring data collected from longleaf pine trees (*Pinus palustris* Mill.) in natural stands and a young plantation to test whether divergence exists in this important southeastern tree species. Our results demonstrate that a growth divergence in basal area increment (BAI) occurred among individual longleaf pines within stands. The BAI of each tree followed Taylor’s law but with differing exponents, which varied from 0.75 to 6.4. Divergence of BAI among trees increased with time, and it might be related to the local drought, as the highest BAI divergence occurred when the SPEI (standardized precipitation-evapotranspiration index) was approximately 0 (−0.3–0.3). Hourly dendrometer measurements confirmed growth divergence among individuals. Collectively, our study provides new information about the growth characteristics of longleaf pine, which may partially explain how this species persists and thrives in southeastern environments. Our current management strategy on longleaf pine forests, such as prescribed burning and genetics improvement efforts, needs to be adapted.

Keywords: basal area increment (BAI); growth divergence; standardized precipitation evapotranspiration index (SPEI); natural forest; plantation



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1. Introduction

Tree rings are important in characterizing tree growth. They are also used as a proxy for reconstructing historical climate conditions [1,2], which is known as the science of dendrochronology. Some recent tree-ring studies have demonstrated the “divergence problem” in northern latitude forests, where tree growth becomes less responsive to the mean temperature over time [3,4]. Divergence-related studies show a reduction in tree ecophysiological response to climate in some high-latitude and temperature-limited areas [4]. This phenomenon is found in two ways: first, there is a response-related divergence between tree ring-based reconstructed temperatures and actual measured temperatures, and second, there is a “growth divergence” that has been reported for some high-latitude and high-elevation sites, where formerly homogeneous sites show diverging tree growth patterns among emergent subpopulations [5,6]. Potential explanations for this phenomenon include (i) temperature-induced summer drought stress [3,7,8]; (ii) complex growth responses to

local climatic and environmental changes [5,9,10]; and (iii) air pollution [11,12]. It was found that growth declines were widespread in tree-ring records from eight alpine and high-latitude tree-line sites in Alaska, especially in the warmer and drier locations [7]. Currently, the growth-divergence phenomenon has not been reported in lower latitude areas because of higher average temperatures [4,8,11]. Since temperature and precipitation have fluctuated in the southern region of the U.S. [13], growth divergence may exist among southern tree species.

Longleaf pine (*Pinus palustris* Mill.) is an important tree species in the southeastern United States due to its social, ecological, and economic value [14,15]. Longleaf pine forests provide quality timber and related forest products (such as tar, pitch, pine straw, and rosin) and contribute to wildlife habitat [14–16]. From a conservation perspective, restoration efforts (e.g., planting, prescribed burning, and thinning) often target longleaf pine forests for their biodiversity [17,18]. The longleaf pine forest ecosystem in this region supports an estimated 900 plant species, 100 bird species, 36 mammal species, and 170 species of reptiles and amphibians. Some threatened and 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.) [19]. Indeed, the longleaf pine ecosystem represents one of the world's most unique and biologically diverse ecosystems. Furthermore, longleaf pine forests have significant potential for carbon storage, as trees can reach heights of more than 40 m, diameters approaching 91 cm, and have a lifespan of up to 450 years [20–22]. However, following an era of exploitative logging, fire suppression, and land use conversion (including urbanization) during the 19th and 20th centuries, the extent of the longleaf pine ecosystem reduced dramatically from 37 million ha to less than 5% of its original range, extending from Virginia to Texas (Figure 1) [23]. It is important to study the growth of longleaf pine trees for the long-term sustainability of this imperiled ecosystem. Our previous investigations on tree growth in longleaf pine include radial growth (e.g., basal area increment, BAI) followed by critical slowing down, indicated by the sudden increase in variance and autocorrelation in BAI, and the existence of power laws (nonlinear relationship between tree growth and the frequency) [24]. Therefore, further research on longleaf pine tree growth dynamics is needed.

This study aims to explore whether there is divergence in longleaf pine growth at different locations within its geographic range. Our hypothesis was that tree growth and its regime (e.g., fluctuations) would be consistent among individual trees within the same stand. Specific objectives include (i) comparing radial growth in longleaf pine and testing whether the basal area increment (BAI) follows a similar regime within and across stands in the geographic range; (ii) determining whether radial growth divergence existed in individual trees at the same sites and between sites; and (iii) exploring the relationship between drought and radial growth. These results will provide new insights into how longleaf pine adapts its growth strategy to varying climatic conditions, which will improve our ability to predict growth dynamics.

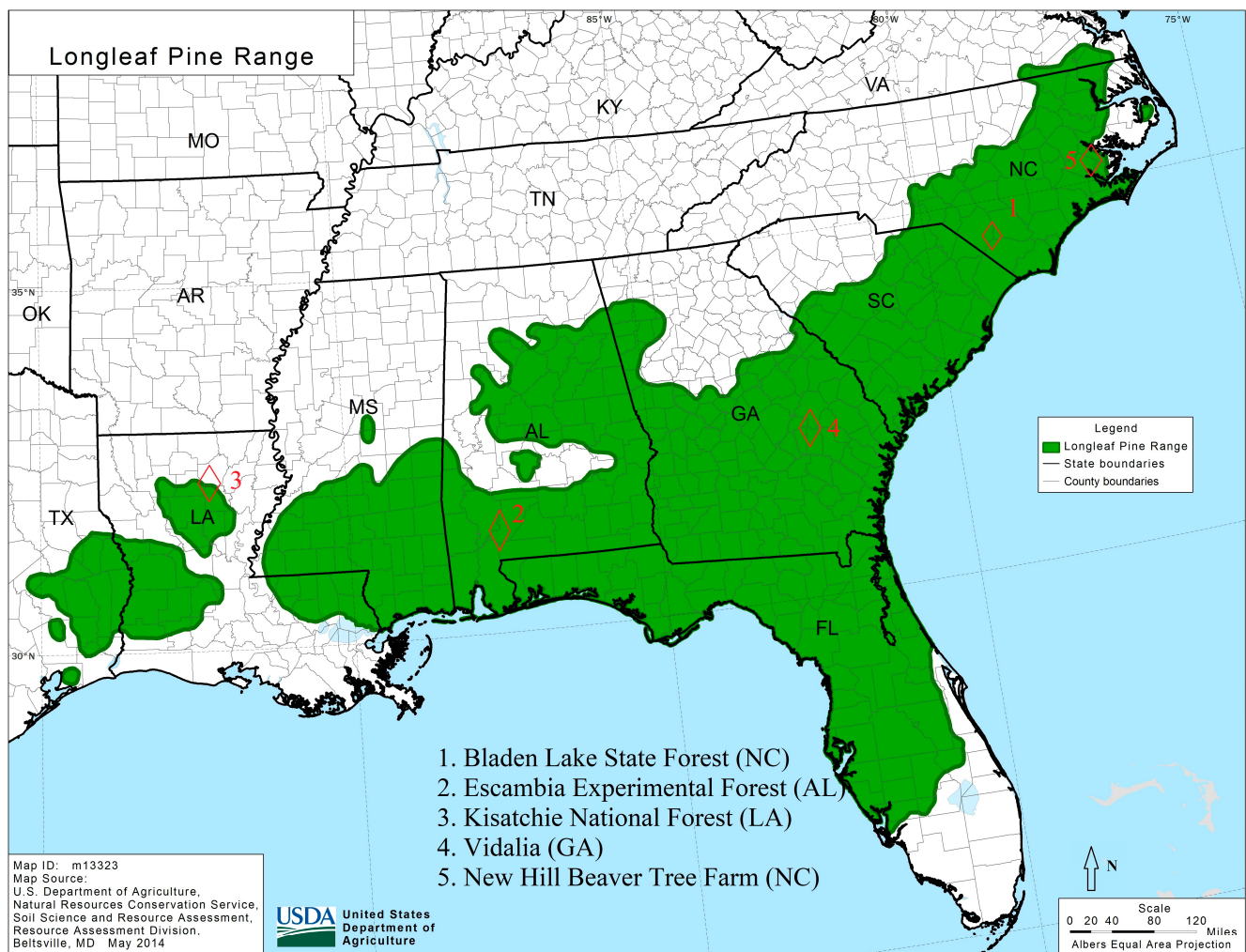


Figure 1. Five study sites in the longleaf pine historical range (the base map was developed by the USDA).

2. Materials and Methods

2.1. Study Sites

For over six decades, scientists at the USDA Forest Service have monitored longleaf pine growth at multiple sites across its geographic range in the southeastern United States. In this study, we selected three of their monitoring sites: (1) Bladen Lake State Forest in North Carolina (short name as Bladen) (34.72° N, 78.56° W) (Figure 1), which is close to the northeastern edge of the range; (2) Escambia Experimental Forest in southern Alabama (Escambia) (31.01° N, 87.08° W), which is near the south-central extent of the range; (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. The longleaf pine forests on these sites are uneven-aged and naturally regenerated with a maximum age of about 100 years. In addition, we included a fourth site at the University of Georgia's Vidalia Onion and Vegetable Research Center (Vidalia) (32.02° N, 82.22° W). This site is a 12-year-old, even-aged longleaf pine plantation planted on former agricultural land. The fifth site is at New Hill Beaver Tree Farm, NC (NHF, 35.65° N, -78.88° W) from the International Tree Ring Data Bank (NOAA Paleoclimatology Program, National Centers for Environmental Information), which included tree ring information of seventeen longleaf pine trees from 1903 to 1975 to match the time of drought information.

2.2. Tree Ring Analysis

We harvested three mature longleaf pine trees with similar diameters at three sites (Bladen, Escambia, and Kisatchie). Each tree occupied the dominant crown class position in the canopy within low-density woodlands (e.g., 50–62 trees ha^{−1}). The forest at Vidalia (1226–1686 trees ha^{−1}) was impacted by Hurricane Helene in September 2024, and many trees were uprooted. Five uprooted (i.e., tipped over) but still living trees in this young plantation were chosen for this study. From all harvested trees, thin sections (“cookies”) were acquired near the base (~20 cm from the ground). The “cookies” were polished and then scanned at high resolution. Basal area increments (BAI) with an accuracy of 0.1 mm were calculated from the increase of stem area from the year (ring) n to the year (ring) $n + 1$, which was measured through ImageJ software (version 1.43c) since the tree ring interfaces were not always perfect circles. The growth data were cross-dated among trees at the same stand. Detailed information on ring width information on seventeen longleaf pine trees (during 1903–1975) was contributed by Barefoot, A.C., in 2002 to the International Tree Ring Data Bank. The ring width data were transferred to tree radii and basal area increments with the assumption that tree rings are perfect circles.

2.3. Taylor’s Power Law

In ecological research, for many species, the logarithm of the variance of density (individuals per area or volume) of populations was approximately a linear function of the logarithm of mean density. This relationship is known as Taylor’s Law (Taylor, 1961) [25]. Taylor’s Law is one of ecology’s most widely verified empirical relationships. It has been verified in hundreds of species, including trees [26,27]. For our study, Taylor’s Law can be expressed in the following way:

$$V = a \cdot M^b,$$

with V as the variance of BAI, M as the average of BAI, and a and b as coefficients. After logarithm, $\log(V) = \log(a) + b \cdot \log(M)$. With the time increase of 1, 2 ... to n years from the radial growth, the scaling exponents (b) between the variance and average of BAI were estimated.

2.4. Divergence in Radial Growth

The divergence in radial growth can be quantified by the following:

$$D = \Sigma \sqrt{(x - y)^2} / N,$$

where x and y represent BAI for different trees along a time series. N is the total number of tree pairs (C_n^2). Due to limited old longleaf pine trees and cost prohibition, three to five similar trees were sampled in this study, which may represent the minimum divergence at each site. The total number of pairs for Bladen, Escambia, and Kisatchie was three, while 10 pairs were made from the five trees at Vidalia. The unit of divergence is mm², which is the same as with BAI.

2.5. Standardized Precipitation-Evapotranspiration Index (SPEI)

The SPEI provides drought information. An important advantage of SPEI over other drought indices is its multi-scalar characteristics of potential evapotranspiration on different drought types [28]. The global SPEI database offers long-term (from 1900), reliable information on drought conditions with 0.5 degrees spatial resolution and monthly time resolution. This drought index, which was developed by the University of East Anglia Climatic Research Unit [29], is based on monthly precipitation and potential evapotranspiration. We used the SPEI data at each location over the lifespan of the sampled trees since

there was no local climate information during the early developmental years. $SPEI > 0$ means precipitation was more than evapotranspiration, while $SPEI < 0$ means precipitation was less than evapotranspiration.

2.6. Dendrometer Measurements

Three dendrometers (ICT International, Armidale, Australia) were set up on mature longleaf pine trees at Escambia in early 2022. The recording time is every hour, and the measurement unit is mm. In this study, the overlaid time of these dendrometers was before July 2022.

2.7. Statistical Analysis

After the data were tested for normality, simple linear regression and correlation analysis were performed using the least-squares technique by SAS software (version 9.3) (Cary, NC, USA). The statistical test was considered significant at $p < 0.05$.

3. Results

3.1. BAI Divergence

The change of BAI at the individual longleaf pine tree level was a dynamic process (Figure 2a,b). BAI was maximized at Escambia and Kisatchie, reaching 8000–10,000 $\text{mm}^2 \text{yr}^{-1}$. It even reached about 12,888 $\text{mm}^2 \text{yr}^{-1}$ at NHF in 1955 (Figure 2b). Usually, individual trees increase their BAI fluctuation after the first 20 years. The change of BAI occurred in cycles of 3–5 years, but trees at the same site may or may not change consistently (e.g., direction and magnitude). With the exception of one tree (tree #5) at Vidalia and another one (NHILLF051) at NHF, the BAI values of each tree followed Taylor's Law at these sites but with different exponents (Table 1). The exponents for most mature trees ranged from 1.8 to 6.4, but the exponents of young trees at Vidalia ranged from 0.7 to 2.7, while some trees at NHF had higher values (>5).

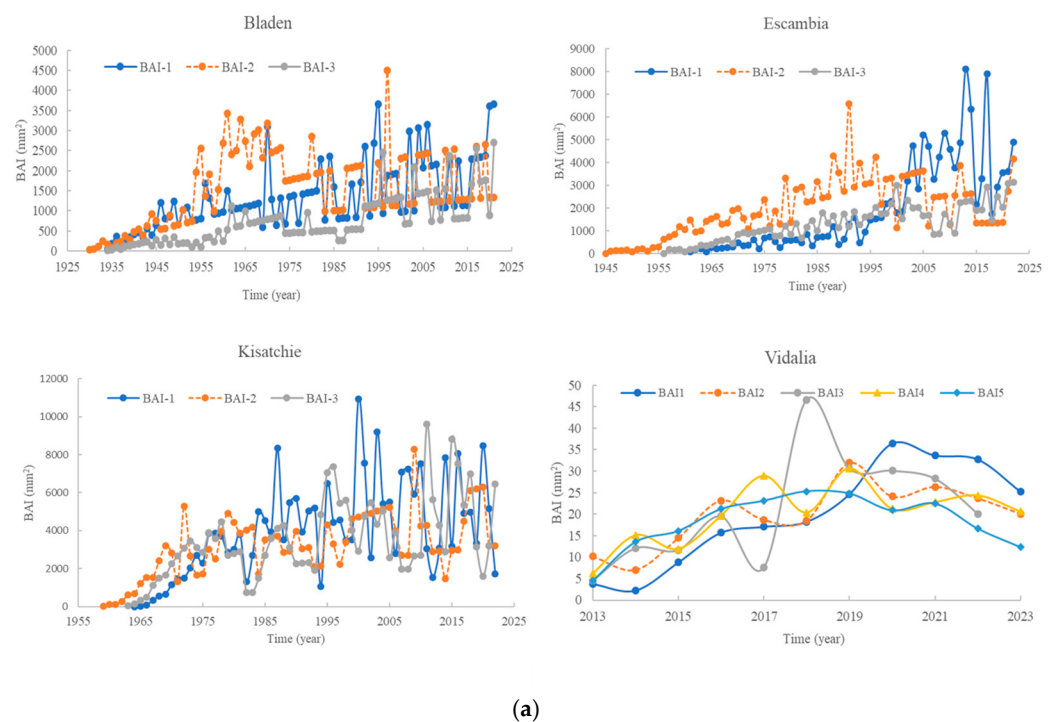


Figure 2. Cont.

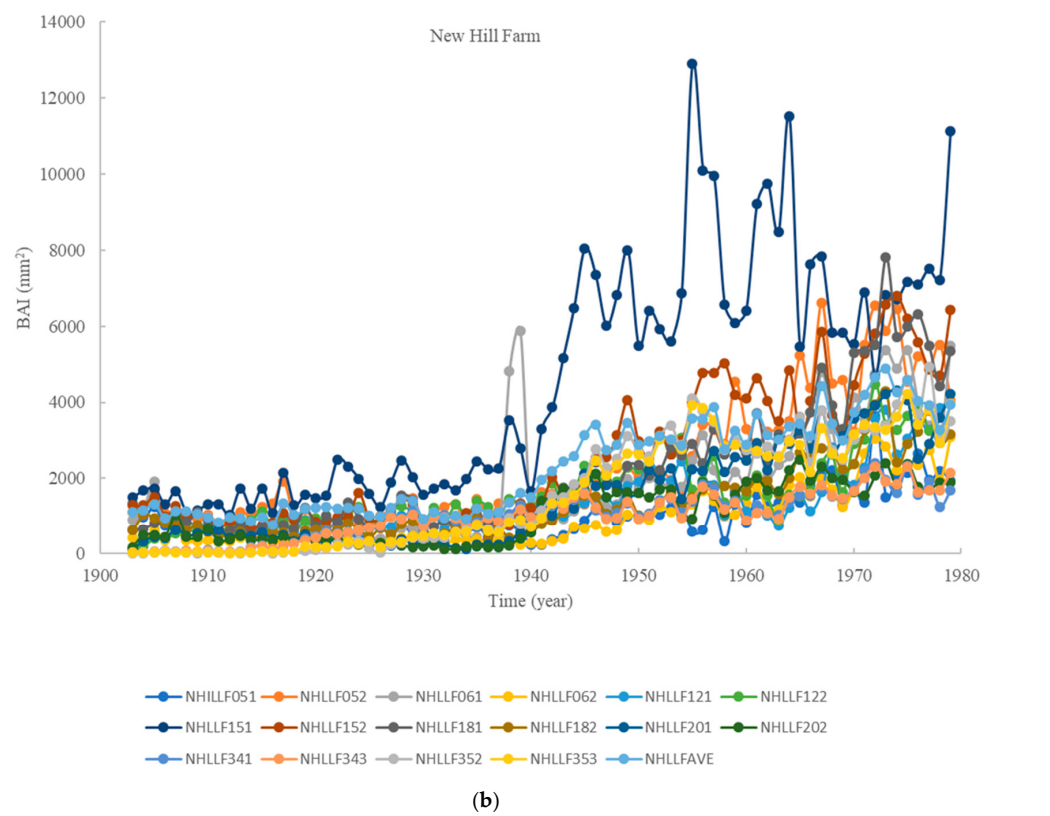


Figure 2. Comparing basal area increment (BAI) dynamics in individual longleaf pine trees at four sites (BAI-1 . . . n represents Tree 1 . . . n) (a) and New Hill Farm (b) (The tree names, such as NHILLF051, are used to be consistent with the original information in the International Tree Ring Data Bank).

Table 1. Taylor’s power law in the BAI’s of radial growth among individual longleaf pines at five sites.

Sites	Trees	Linear Fitting Equation for $\log(V) = b \cdot \log(M) + \log(a)$	R ²	p
Bladen	Tree #1	$y = 1.8818x - 0.0992$	0.976	<0.01
	Tree #2	$y = 2.0217x - 0.3243$	0.9711	<0.01
	Tree #3	$y = 2.1948x - 0.7831$	0.9681	<0.01
Escambia	Tree #1	$y = 2.7985x - 2.5056$	0.9901	<0.01
	Tree #2	$y = 2.0397x - 0.3923$	0.9727	<0.01
	Tree #3	$y = 1.8797x - 0.0843$	0.9781	<0.01
Kisatchie	Tree #1	$y = 1.7691x + 0.4529$	0.9898	<0.01
	Tree #2	$y = 1.6532x + 0.7477$	0.9406	<0.01
	Tree #3	$y = 1.7181x + 0.538$	0.9746	<0.01
Vidalia	Tree #1	$y = 2.3498x - 0.7555$	0.9401	<0.01
	Tree #2	$y = 2.7717x - 1.7201$	0.8689	<0.01
	Tree #3	$y = 2.6982x - 1.218$	0.8847	<0.01
	Tree #4	$y = 1.3007x - 0.1279$	0.6018	<0.05
	Tree #5	$y = 0.7544x + 34.901$	0.1261	>0.05
NHF	NHILLF051	$y = 1.1097x + 1.7618$	0.1123	>0.05
	NHILLF052	$y = 5.5497x - 12.061$	0.7445	<0.05
	NHILLF061	$y = 3.4442x - 4.728$	0.5956	<0.05
	NHILLF062	$y = 5.259x - 9.548$	0.942	<0.01
	NHILLF121	$y = 2.0701x - 0.9439$	0.678	<0.05
	NHILLF122	$y = 1.9109x - 0.3969$	0.869	<0.01
	NHILLF151	$y = 4.7994x - 10.237$	0.9154	<0.01

Table 1. Cont.

Sites	Trees	Linear Fitting Equation for $\log(V) = b \cdot \log(M) + \log(a)$	R ²	p
	NHILLF152	$y = 5.0763x - 10.569$	0.57	<0.05
	NHILLF181	$y = 5.2092x - 10.602$	0.8642	<0.01
	NHILLF182	$y = 4.9798x - 9.557$	0.9022	<0.01
	NHILLF201	$y = 3.469x - 4.5928$	0.8812	<0.01
	NHILLF202	$y = 3.089x - 3.4024$	0.8582	<0.01
	NHILLF341	$y = 2.2158x - 0.8736$	0.9471	<0.01
	NHILLF343	$y = 2.2438x - 0.9342$	0.939	<0.01
	NHILLF352	$y = 2.2435x - 0.6069$	0.985	<0.01
	NHILLF353	$y = 2.5019x - 1.3833$	0.9688	<0.01
	NHILLFAVE	$y = 6.4933x - 15.275$	0.8696	<0.01

The divergence of BAI among longleaf pine trees increased with time even at the same sites (Figures 3 and 4). The divergence at different sites varied from about 100 to 5400. The standard deviation of divergence is 482, 834, 1213, 342, and 613 for Bladen, Escambia, Kisatchie, Vidalia, and NHF, respectively. With the increase of sample size (e.g., 3, 8, and 17 trees) at NHF, the divergence pattern (e.g., behavior and time) did not change dramatically (Figure 4a–c), but the magnitude varied.

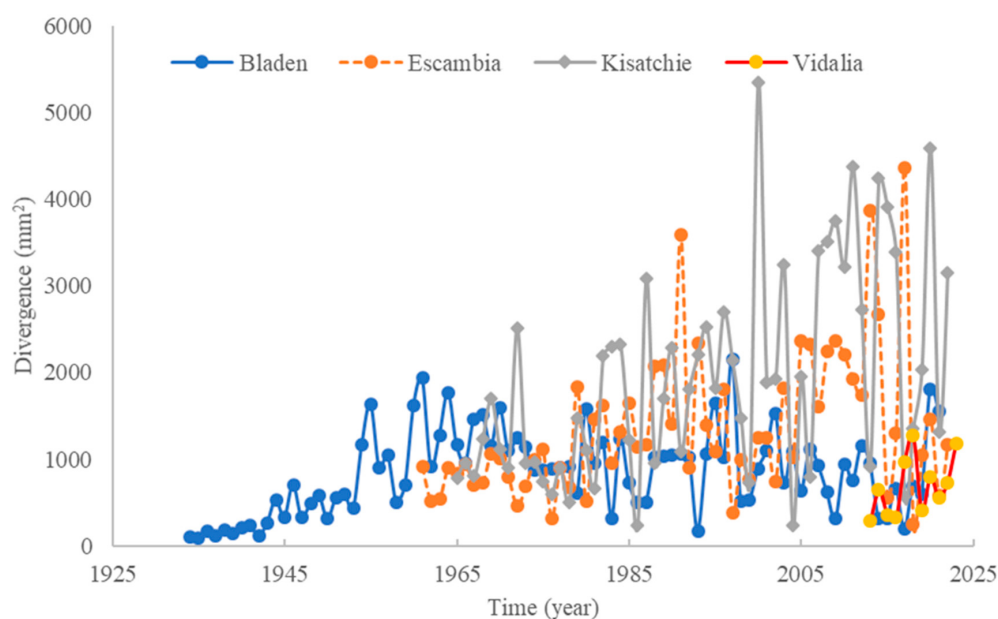


Figure 3. Dynamics of BAI divergence in individual trees at four sites.

3.2. BAI Divergence and SPEI

Divergence in BAI might be related to the regional moisture availability (Figure 5a,b). The highest BAI divergence occurred when the SPEI was approximately 0 (−0.3–0.3). With the increase of moisture or drought conditions, the divergence of BAI decreased. Under two continuous years of highly wet or drought conditions, the divergence of BAI decreased (Figure 6a,b), while under two continuous years of slightly dry or wet conditions (−0.3~0.3), the divergence of BAI increased. The nonlinear relationship between SPEI and BAI divergence looks like a “triangle”.

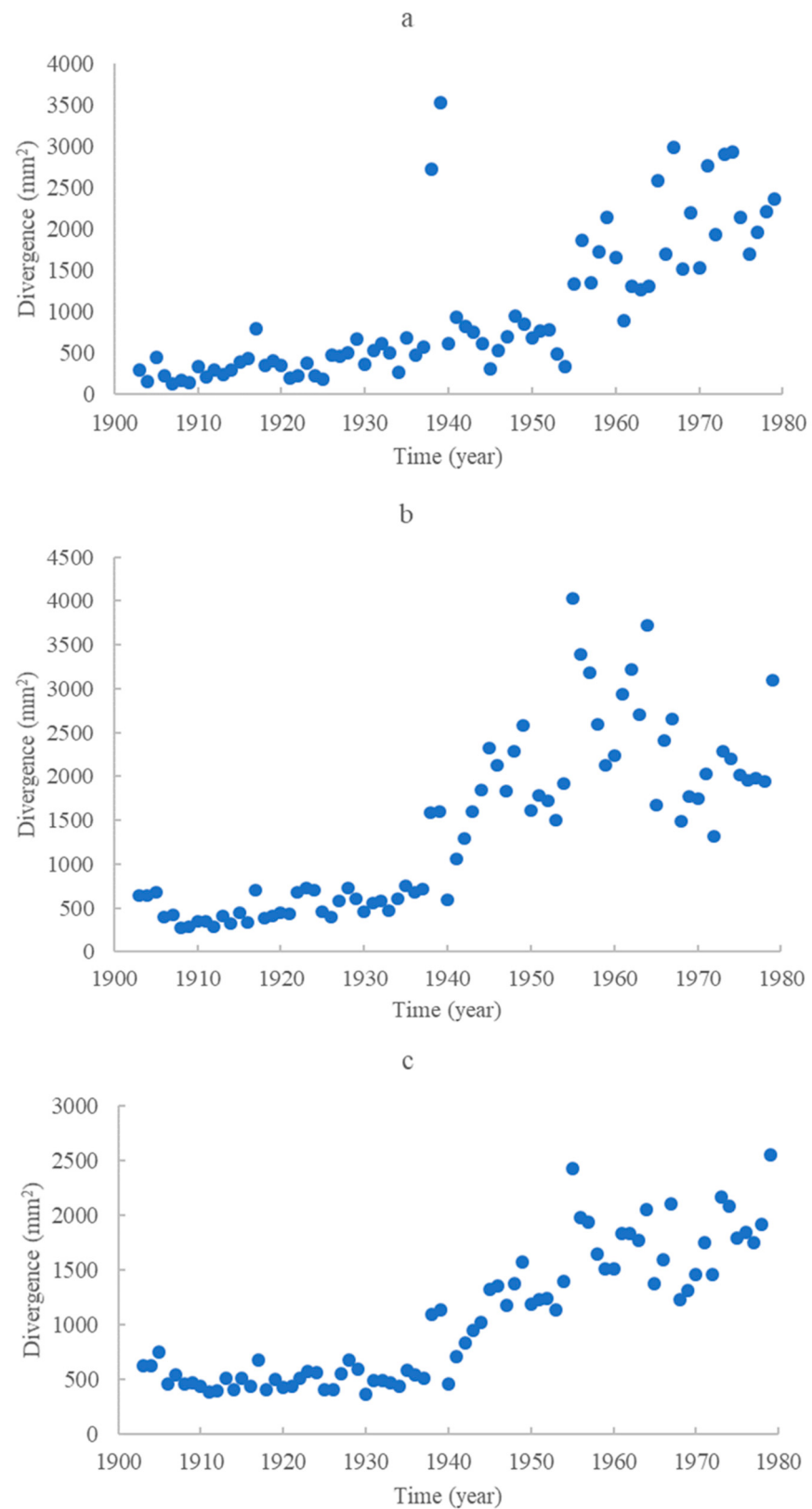


Figure 4. The pattern of BAI divergence with different sample sizes at New Hill Farm. (a) Three trees; (b) Eight trees; and (c) Seventeen trees.

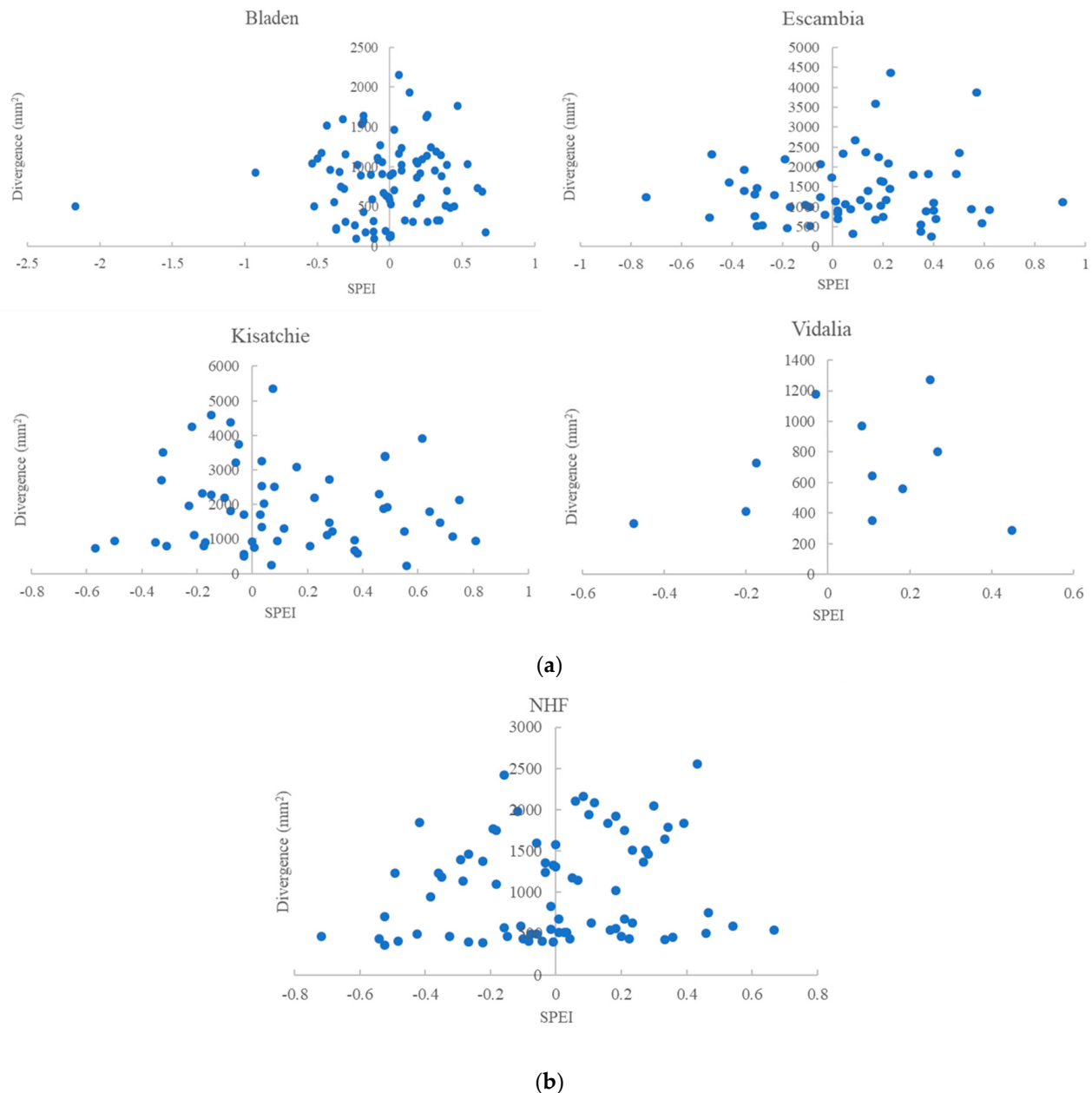


Figure 5. The triangle-shaped relationship between drought index (SPEI) and BAI divergence at four sites (a) and NHF (b).

3.3. Dendrometer Measurements at Escambia

The dynamics of hourly tree growth in three mature longleaf pine trees followed two distinct patterns (Figure 7). Tree 8 was very active, demonstrating several peaks and valleys from April until June. In contrast, trees 3 and 7 demonstrated little growth over the same period. Radial growth initiated at the end of March or early April for each tree.

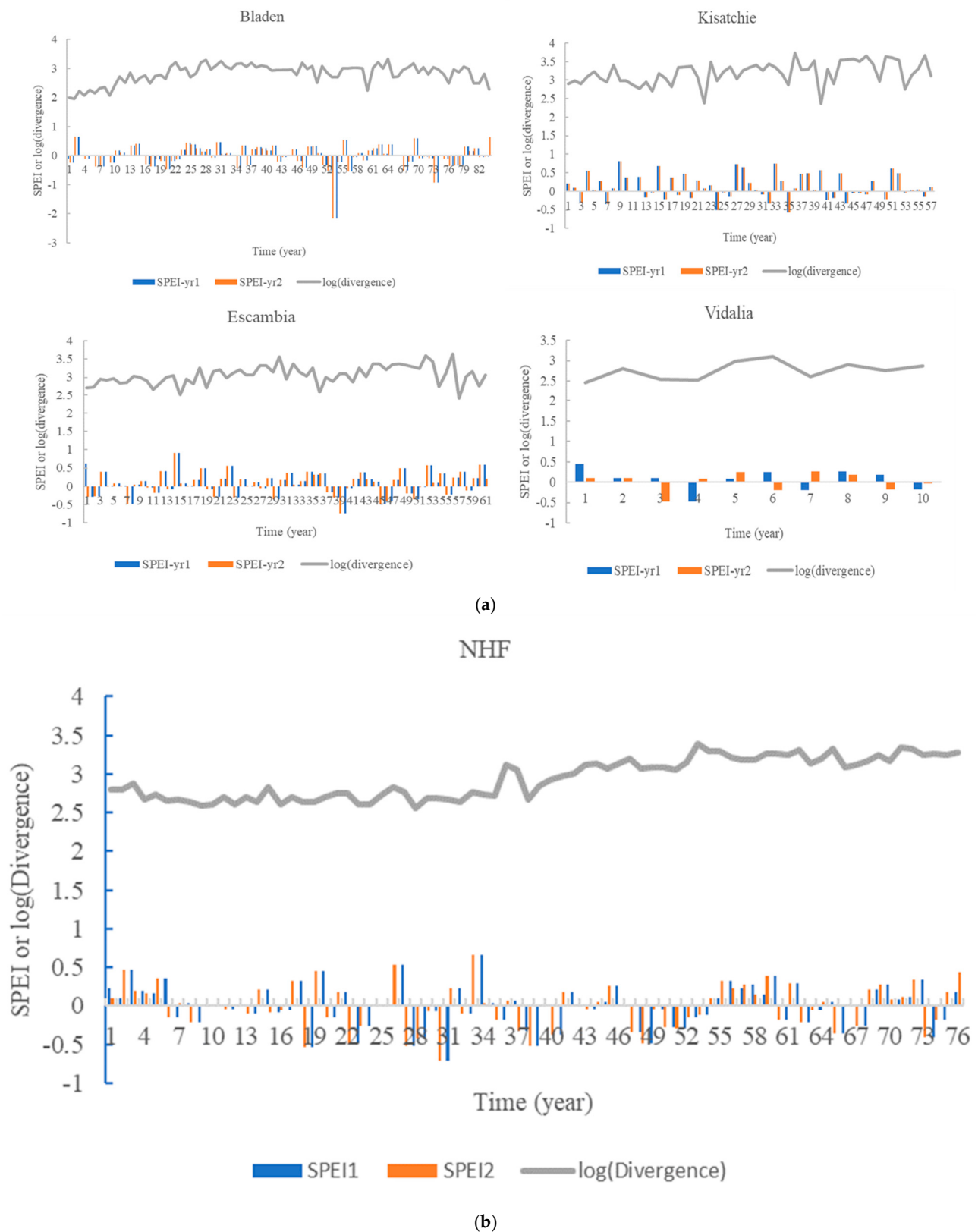


Figure 6. Dynamics of two continuous years' SPEI and the BAI divergence at four sites (a) and NHF (b) (SPEI-yr1 and SPEI-yr2 represent SPEI in the first and second years).

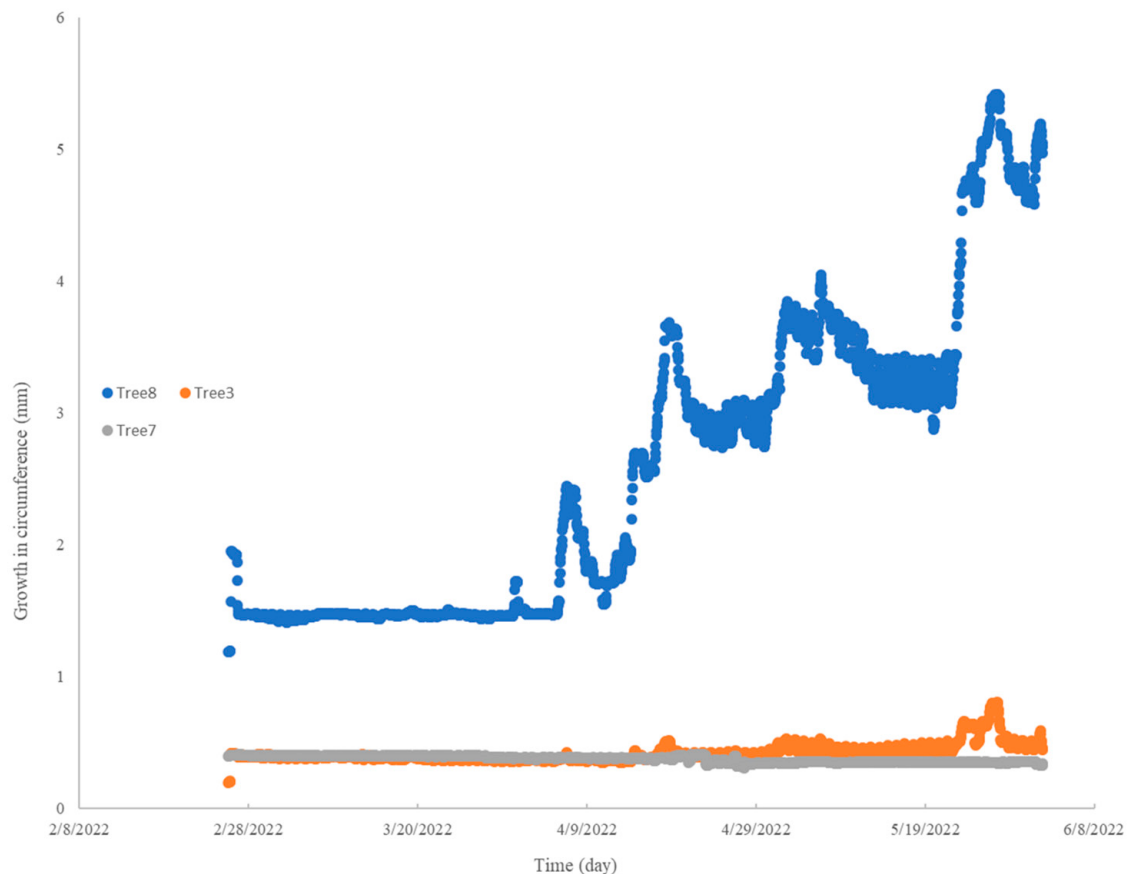


Figure 7. Hourly dendrometer measurements in three mature longleaf pine trees at Escambia.

4. Discussion

Although it is complicated in BAI dynamics of individuals, our results demonstrated some interesting patterns in longleaf pine radial growth. Sample size at NHF did not change the pattern of growth divergence. Since these selected trees were in similar diameters, their divergence may represent the minimum in the stand. BAI dynamics among trees within the same site were heterogeneous in terms of changing time, magnitude, and exponents of Taylor's power law. Usually, the exponents are within the extent of [1,3]. Here, one tree (#5) from Vidalia and another one from NHF had no significant relationship ($p > 0.05$), which might indicate these trees were stressed since trees under stress (e.g., diseases or high intraspecific competition) may not follow Taylor's Law [27]. When the exponent approaches 1, it is considered to represent stochastic processes [30]. When the exponent exceeds 2, it may propose deterministic and exponential growth [27,31]. Tree growth is a self-organized process. Power laws are thought to characterize information in a system from disorder to order [32]. Similar to Taylor's power laws in BAIs, it may be proposed that intrinsic biological traits (e.g., hormones or other chemical growth regulators) may be responsible for the tree growth patterns [33]. This result may be related to the entire micro-environmental conditions (e.g., soil water, nutrients, light, and disturbances) [34] where the tree was located even though all sampled trees were at a similar location (e.g., within 20 m) within the same stand at the first four sites. Small differences in soil water or nutrient availability may lead to different radial growth rates despite the fact that longleaf pine is a drought-tolerant species [35]. The high fluctuation in BAI after ~20 years in natural forests may be affected by tree canopy conditions because canopy closure usually is completed around that age. Any changes in canopy conditions, such as an increase of leaf area index or a decrease of light access, may affect the photosynthate production and subsequent tree

growth [36]. Cone production in longleaf pine has a similarly complicated relationship with tree growth [24]. Furthermore, the frequency and seasonality of prescribed burning, which is necessary to maintain longleaf pine forests, may interact with temperature and moisture availability at each location in ways that can complicate the impact of climatic factors on tree growth [37,38]. Although mature longleaf pine trees are resistant to frequent, low-intensity surface fire [39,40], growth may decline in the aftermath of fire if the crown or vascular tissues are damaged by fire.

A standardized tree ring index is often used on long-term tree ring data. However, calculating a standardized tree ring index through averaging may obscure the unique growth features of individual trees [41], which is obvious in this study. Thus, further effort at the individual level is needed to understand more on growth. In addition, increasing divergence in BAI could weaken the relationship between the standardized tree ring index and temperature, as divergence may be expressed as a loss of temperature sensitivity or divergence in trend [2–5,8,42,43].

A single weather factor, such as air temperature or precipitation, may be insufficient to indicate the integrated thermal environment for a tree because other factors, including soil moisture and evapotranspiration, also exert influence [3,44,45]. However, acquiring all micro-environmental information for individual trees is difficult. In this study, we used the SPEI, a regional index, to accomplish the task. However, this index provides important information that the BAI divergence reached its highest when SPEI was close to 0 ($-0.3 \sim 0.3$) because limited moisture available near the threshold (e.g., $\text{SPEI} = 0$) may play a significant role. When SPEI is too big or small (too much water or drought), individual trees have a similar growth response. This study also shows two continuous wet/drought years ($\text{SPEI} > 0$ or $\text{SPEI} < 0$), which may cause BAI divergence to increase or decrease. Longleaf pine trees respond to prolonged drought or abundant moisture. With drought frequency increasing in the Southeast (such as $\text{SPEI} -0.5 \sim -1.0$) [46], the divergence of tree growth in longleaf pine could intensify [47]. Analysis of radial growth can give insight into how drought will impact long-term tree growth (e.g., carbon storage in woody biomass) and how ongoing growth divergence could impact the longleaf forest response to future environmental change in this region. Further research on other tree species in this region should be conducted.

The radial growth dynamics in three mature longleaf pine trees from dendrometers at Escambia showed different patterns. One tree was very active, while the others were not. The short time difference (e.g., hourly) might lead to growth divergence in a long time (e.g., yearly). Since these trees were within 20 m distance in the same stand and shared the same topography (minimal slope), the internal biological characteristics may play an important role here, such as plant hormones and genetics. However, we do not have long-term (e.g., a couple of years) dendrometer measurements. It is unknown how long this pattern will continue. Otherwise, the active tree would grow much bigger than the others. Some previous studies reported “seasonal flush” in longleaf pine growth [45,48]. This pattern is also similar to longleaf pine cone production at the individual level, which shows some trees were more productive than others [49]. An integrated monitoring effort of individual longleaf pine growth is needed to uncover potential mechanisms.

The divergence of radial growth among individual trees has implications for current longleaf pine management practices. First, each longleaf pine tree may have a unique growth trajectory due to the complicated interactions between its internal biology and external environments. Their responses to environmental change may also be divergent. Managing longleaf pine forests should emphasize an individual-based approach, which considers the individual tree level due to the growth divergence. However, it would be challenging to make this approach operational due to the high amount of information.

Some functional groups (trees with similar growth responses) may be developed for management operations. Second, the climate-tree growth method may be biased due to their unstable relationship and varied sensitivity. A multi-factor relationship should replace the single-factor relationship. The average approach (e.g., BAI) may not reflect the high divergence in tree growth. Third, the current prescribed burning, which is conducted to control competition from other tree species and promote understory herbaceous diversity, could also affect the growth of longleaf pine (e.g., thermal pruning, fine root consumption, etc.) [50], especially when trees are small or have low branches [51]. Longleaf pine may recover from damaged canopies (e.g., scorch and/or needle/bud consumption), but this could take time and slow the growth. Also, prescribed burning may bring survival uncertainties for some trees recovering from drought or stress. Some alternative methods should be considered for vegetation management during that time, such as herbicides or mechanical treatments. Furthermore, some trees may have genetic adaptations, such as being more productive or highly adaptive (e.g., disease resistance), especially those in areas with frequent changes in SPEI.

5. Conclusions

Tree growth divergence, an anomalous reduction in forest growth indices and temperature sensitivity, has been detected in tree-ring records from many northern latitude sites due to a variety of factors. In this study, we used the tree rings from the minimum sampled (3 or 5 trees) longleaf pine trees at four locations and 17 trees at New Hill Farm, NC, across the geographic range of longleaf pine to study tree radial growth in mature natural forests and a young plantation. Despite potentially needing more samples from different areas, our results indicated that radial growth in longleaf pine trees was quite divergent at the individual level within stands. Forest trees are a self-organized system, and the BAI values of each tree followed Taylor's power law but with different organizing regimes. The divergence of BAI among trees increased with tree age. The BAI divergence might also be related to drought, as the highest BAI divergence occurred when the SPEI was around 0 (−0.3–0.3), while the divergence of BAI decreased under drought conditions or abundant moisture availability. The radial growth divergence was also observed in the dendrometer measurements in several months from three intensively measured nearby mature longleaf pine trees. Our results indicate that radial growth in longleaf pine at the individual level is quite heterogeneous. The mechanisms of tree growth divergence should be studied on-site for the adaptation of longleaf pine under the changing environment.

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Data Availability Statement: Tree data at NHF are available at the International Tree Ring Data Bank. Other tree data will be available under request.

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

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