

Article

Growth-Climate Relationships and Long-Term Growth Trends of the Tropical Forest Tree *Choerospondias axillaris* (Anacardiaceae) in East-Central Thailand

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Abstract: Tropical forests play important roles in global carbon cycling. Tree-ring analysis can provide important information for understanding long-term trends in carbon-fixation capacity under climate change. However, tree-ring studies in tropical regions are limited. We carried out a tree-ring analysis to investigate the dendrochronological potential of the tropical forest tree *Choerospondias axillaris* (Anacardiaceae) in east-central Thailand. Our study focused on growth-climate relationships and long-term growth trends. A chronology was constructed covering the period from 1932 to 2019. The tree-ring width index of *C. axillaris* was positively correlated with precipitation in June, July, and October. Furthermore, growth of *C. axillaris* was positively correlated with the Standardized Precipitation-Evapotranspiration Index (SPEI) from July to October, indicating that growth of *C. axillaris* is mainly limited by moisture availability in the late monsoon season. Moving correlation analysis further revealed the consistency and temporal stability of the relationship of tree growth with monsoon season precipitation and SPEI during the period under study. There was a significant increasing trend in long-term growth from 1932 to 2002 (slope = 0.017, $p < 0.001$); however, long-term growth decreased from 2003 to 2019 (slope = −0.014, $p < 0.001$). Our study provides important insight into the growth-climate correlations of a broad-leaved tree species in a dry evergreen forest in tropical Asia.

Keywords: *Choerospondias axillaris*; growth-climate response; long-term growth pattern; Mo Singto Forest dynamic plot; Thailand; tree rings; tropical broad-leaved forests

1. Introduction

Climate change has major impacts on natural ecosystems worldwide. The most significant evidence for climate change is rising temperatures and the increasing frequency of extreme events, such as extreme drought, violent storms, and severe flooding [1]. Climate change and related increases in climate extremes have affected tree growth and forest productivity globally [2,3], including in tropical regions [4,5], the Himalayas [6,7] and Europe [8,9]. Tree-ring analysis can provide important information on climate change [10]. Tree rings provide a long-term record of past climates, and record environmental signals over the entire lifespan of a tree, both directly and indirectly [11]. The physiological mechanisms underlying variation in tree radial growth are complex, and are affected by climatic factors (e.g., precipitation and temperature), mean site conditions, and species characteristics [5,7]. The sensitivity of tree growth to climate may change over time, depending on the severity of climate change [8]. Positive and negative effects of climatic factors can be read from the relative width of the rings [12,13].

Tropical forests are known biodiversity hotspots. They have an important role in the global carbon cycle and are important for natural solutions to mitigate climate change [14,15]. The main factors that influence tropical tree growth in addition to climatic factors are soil factors (texture, structure, moisture, and nutrients) and topographic factors (elevation, slope, and aspect) [12,13]. Dendrochronology is the scientific method of the dating of trees and investigating tree growth-climate relationships [16]. There are no strong limiting climatic factors for tree growth in tropical regions, so cross-dating is a challenge for tropical trees. Several techniques can be used to study the responses of tropical tree species to climate variation, including analysis of tree-ring width, cambial activity, wood anatomy, and stable isotopes (^{13}C and ^{18}O) [17].

Increasing numbers of tree species in tropical regions have been found to form clear ring boundaries and have dendrochronological potential [11,13,18–20]. The growth of tropical tree species is positively correlated with precipitation and negatively correlated with temperature [2]. Climate change was not found to stimulate growth in tropical tree species across Cameroon, Bolivia, and Thailand [3]. However, most studies have thus far focused on conifer species; it is important to expand our knowledge in tropical broad-leaved species, as these species tend to play more important roles in tropical ecosystems.

Choerospondias axillaris (Anacardiaceae) is a deciduous tree with semi-ring porous wood [21]. It is widely distributed in tropical Asia [22] and is economically important in Southeast Asian countries [23]. Tree-ring boundaries in *C. axillaris* are very distinct (Figure S1). This trait forms the basis for this first dendroclimatic study on *C. axillaris*, which focused on the Mo Singto ForestGEO plot in Khao Yai National Park, east-central Thailand. The aim of this study was to use tree-ring width measurement to: (1) establish a tree-ring width chronology for *C. axillaris*, (2) determine the relationships between tree-ring width and climatic factors, and (3) reveal the long-term growth patterns of this tree species. We hypothesized that moisture availability during growing season is the main climatic factor controlling the radial growth of *C. axillaris*, and increased year-to-year variability and rapid climate change will have negative impacts on tree-growth trend in recent decades.

2. Materials and Methods

2.1. Study Area and Climate

The study was conducted in the Mo Singto ForestGEO plot in Khao Yai National Park, east-central Thailand (latitude 101°22' E, longitude 14°26' N, elevation 725 to 815 m above sea level). The plot is located in broad-leaved, seasonal evergreen forest in which some species are briefly deciduous (Figure 1) [24]. The annual mean temperature and total annual

precipitation of the study area for the period of 1994 to 2019 were 22.5 °C and 2002 mm, respectively. The mean monthly temperature of the warmest month was 23.9 °C (May), and of the coldest month was 19.8 °C (January). The monsoon season was from the middle of May to the middle of November. September was the month with highest precipitation (approx. 350 mm). Since only a relatively short period of climate data (1994 to 2019) were available from the Mo Singto (Khao Yai National Park) station, we supplemented it with gridded monthly precipitation, temperature (maximum, mean, and minimum), and Standardized Precipitation-Evapotranspiration Index (SPEI) derived from the Climate Research Unit Time Series (CRU TS4.04; <https://crudata.uea.ac.uk/cru/data/>, accessed on 21 November 2021) [25]. We extracted data for the period 1932 to 2018 at latitude 14°26' N to 14°27' N and longitude 101°21' E to 101°22' E. The mean annual temperature and total annual precipitation for the CRU TS data were 27.3 °C and 1702 mm, respectively. The mean monthly maximum temperature of the warmest month (April) was 35.4 °C and the minimum temperature of the coldest month (January) was 18.4 °C. The long-term trends for climate in the CRU TS data and the Mo Singto area had similar patterns (Figures 2 and S2). However, the Mo Singto climate data were more variable than the CRU TS climate data. Precipitation in Mo Singto was higher and the mean annual temperature was lower than in the CRU TS data (Figure S2). These differences were likely due to the fact that the official provincial weather stations that the CRU TS data rely on are located in the lowlands (<400 m msl) that surround the mountain that Khao Yai National Park encompasses.

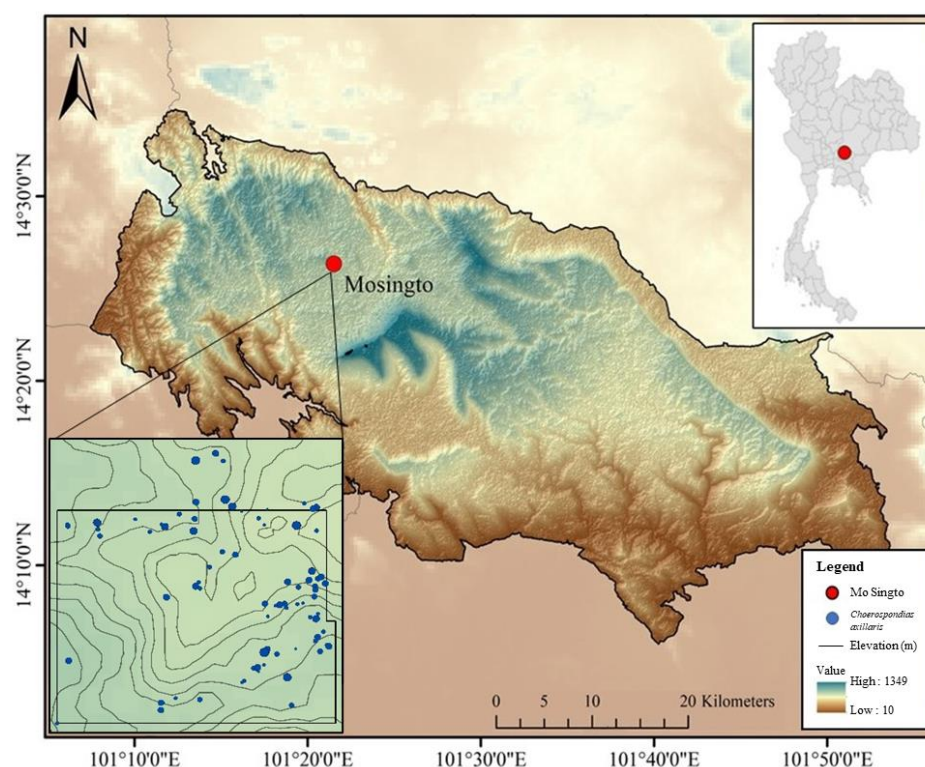


Figure 1. Map of the study area showing topography and the sampling location of *Choerospondias axillaris* trees (blue circles) in Mo Singto ForestGEO, Khao Yai National Park, Thailand. The distance between the contour lines is 10 m.

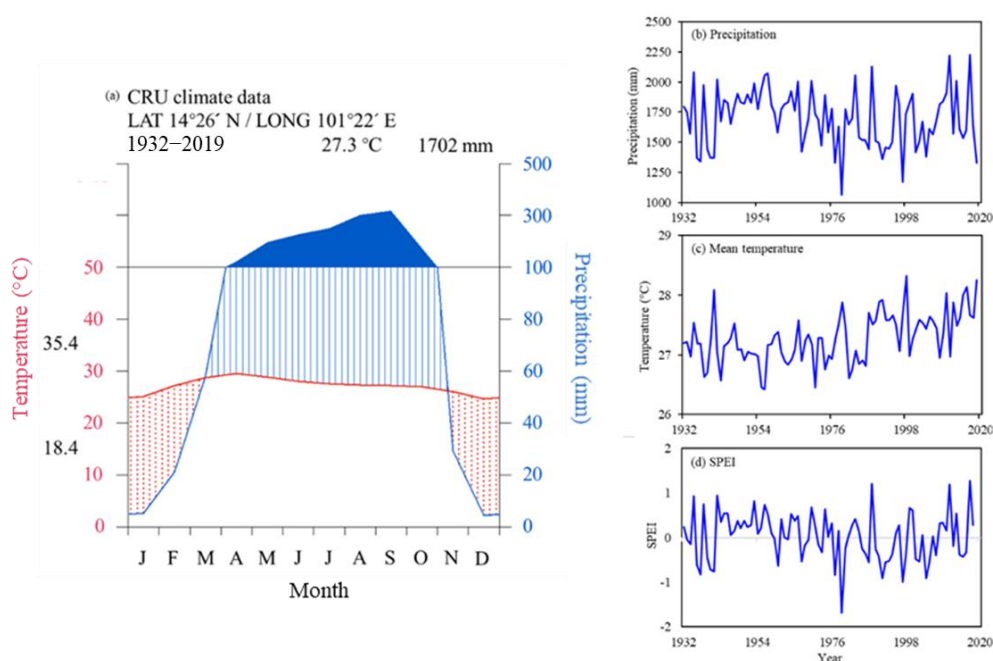


Figure 2. Climatic Research Unit Time Series (CRU TS) gridded climate data for the study area. (a) Walter and Lieth CRU climograph showing monthly temperature (red line) and precipitation (blue line). Red dots, vertical blue lines, and dark blue shape indicate dry period, humid period, and wet period, respectively. At the top are the mean annual temperature and mean annual precipitation. Mean monthly maximum temperature of the warmest month (April) and mean minimum temperature of the coldest month (January) are shown in black on the left. Blue lines show long-term climate trends for (b) precipitation, (c) mean temperature, and (d) Standardized Precipitation-Evapotranspiration Index (SPEI) covering the analysis period 1932 to 2019.

2.2. Study Species

Choerospondias axillaris (Roxb.) Burt & Hill (Anacardiaceae), commonly known as Nepali Hog Plum, is widely distributed in tropical and subtropical Asia, mainly in China, Nepal, India, Japan, and the Indochina peninsula region [26]. It is a common canopy species in the Mo Singto plot with a density of about 5.6 trees ha⁻¹ for trees at least 10 cm in diameter at breast height (DBH) [24]. The main canopy species at Mo Singto are *Illex chevalieri*, *Sloanea Sigun*, and *Dipterocarpus gracilis*, which together comprise 17.7% of the individuals in the plot. The basal area of *C. axillaris* is ranked third in the plot. Live, standing *C. axillaris* at the Mo Singto plot can reach 112 cm DBH, and 30 m height [24]. It is a fast-growing deciduous tree species in secondary forest, and usually grows on heavy clay or sandy clay soils [27]. The flowering period of *C. axillaris* in Mo Singto is January to March, while fruiting is June to November [28]. The cambium of *C. axillaris* is most active during the transition from dry to wet season (March) [29]. *Choerospondias axillaris* is a shade-intolerant, successional species that is used in forest restoration projects [30]. The species has a unimodal size distribution on the Mo Singto plot and is not regenerating in the old-growth forest of the plot (Figure S4). The fruit of *C. axillaris* is an important food for gibbon in the Mo Sinto plot.

2.3. Sampling, Sample Preparation, Tree Ring-Width Measurement and Cross-Dating

We collected 258 cores from 133 trees, with one to three cores per tree at breast height (1.30 m above the ground), using an increment borer (Haglöf Sweden). Samples were collected in January 2020. Samples were dried at ambient temperature in the laboratory and then mounted into wooden core frames. The dried cores were polished using progressively finer grades of sandpapers until the ring boundaries were clearly visible, following standard dendrochronological techniques [31]. Tree-ring width was measured at a precision of 0.001 mm under a stereomicroscope connected to a digital positioning table (LINTAB™

6, Rinntech, Heidelberg, Germany). Cores of *C. axillaris* showed distinct ring boundaries with ring-porous to semi ring-porous anatomical features. The early wood had larger vessels, compared to smaller vessels in late wood (Figure S1). The cross-dating of tree-ring width to calendar year of formation was done by visual growth pattern matching and statistical tests (sign test, *t*-test, and cross-date index) using TSAP-Win software (Rinn, 2003). The quality of cross-dating was further assessed with COFECHA software [32]. We removed cores with indistinct ring boundaries and cores that only covered a short period of time. Finally, 100 cores from 56 *C. axillaris* trees were successfully cross-dated and used for further analyses.

Raw tree-ring width data were standardized using cubic smoothing splines with a 50% frequency cut-off equal to two-thirds of the series length [33] using the “dplR” package [34] in R software [35]. We averaged all of the de-trended series into a mean standard chronology by computing the bi-weight robust mean. Average radial growth rate (AGR, mm year^{−1}) was calculated for the raw ring-width series, while mean sensitivity (MS) was calculated for the standard chronology. Mean sensitivity, ranging from 0 to 1, indicates year-to-year variation in tree-ring width. Mean sensitivity would approach 0 as tree rings became more similar in width, while mean sensitivity would approach 1 as rings became absent [11,36]. The inter-series correlation (Rbar) and the expressed population signal (EPS) were calculated with 30-year moving windows and 15-year overlaps. Rbar indicates the common signal strength (i.e., the growth synchrony) across the chronology, while EPS is an arbitrary threshold of shared population variance among the individual tree-ring series used to assess the quality of the derived chronology. A value of 0.85 is often used as an appropriate threshold for dendroclimatological purposes [37,38].

2.4. Growth-Climate Relationships

Growth-climate analyses were done using residual chronologies, since residual chronologies excluding tree-level autocorrelation are likely to contain more climate information [12]. Growth-climate relationships were analyzed by computing Pearson’s correlation coefficients between ring-width residual chronologies for *C. axillaris* and the extracted monthly CRU TS climate data using SPSS [39]. A 17-month window from the previous August to the current December was used for each year over the period 1932 to 2019. We did moving correlation analysis (30-year moving windows) to determine the temporal stability of growth-climate relationships using the package “treeclim” [40] in R [35].

2.5. Long-Term Growth Trends

Basal area increment (BAI) was calculated from the raw measurements of ring width using the “bai.out” function in the “dplR” package [41], assuming each ring was uniform and represented a circular cross-section of the tree. The BAI was calculated according to the following equation [42]:

$$BAI = \pi (R^2_t - R^2_{t-1}) \quad (1)$$

where *R* is the tree radius at breast height and *t* is the year of tree ring formation.

Changes in long-term growth trends of *C. axillaris* were identified by analyzing the break points in BAI for each individual tree using the “segmented” package in R [43]. The year 2003 had the highest frequency of break points according to the density distribution for break points (Figure S5). Therefore, we split the BAI into two sub-periods (1932 to 2002 and 2003 to 2019), and the growth trend for each of these sub-periods was analyzed separately. The trends in BAI were analyzed using linear mixed-effect models by using “Year” as the fixed effect and “TreeID” as the random effect in the “lme4” package in R [44].

$$BAI = Year + (1 | Year/TreeID) \quad (2)$$

3. Results

3.1. Characteristics Tree-Ring Chronology for *Choerospondias axillaris* at Mo Singto

The tree-ring width chronology of *C. axillaris* at Mo Singto spanned the period 1932 to 2019 (88 years). The AGR was $3.79 \text{ mm year}^{-1}$ (Table 1). Mean sensitivity was 0.412, and Rbar was 0.297. The EPS value (0.968) for the chronology surpassed the recommended criteria of 0.85 for the period 1932 to 2019, indicating that the entire 88-year chronology was acceptable for dendroclimatic analysis (Figure 3).

Table 1. Sampling site characteristics and chronology statistics for *Choerospondias axillaris* at Mo Singto, Khao Yai National Park, east-central Thailand.

Latitude (°N)	Longitude (°E)	Elevation (m asl)	Cores/Trees	Time Span	AGR (mm year^{-1})	MSL (yr)	MS	Rbar	EPS
14.26	101.22	725–815	100/56	1932–2019	3.79	65	0.412	0.297	0.968

Note: AGR, Average growth rate; MSL, Mean segment length; MS, Mean sensitivity; Rbar, Inter-series correlation; EPS, Express population signal. AGR was calculated from the raw series, while MS, Rbar, and EPS were calculated after de-trending.

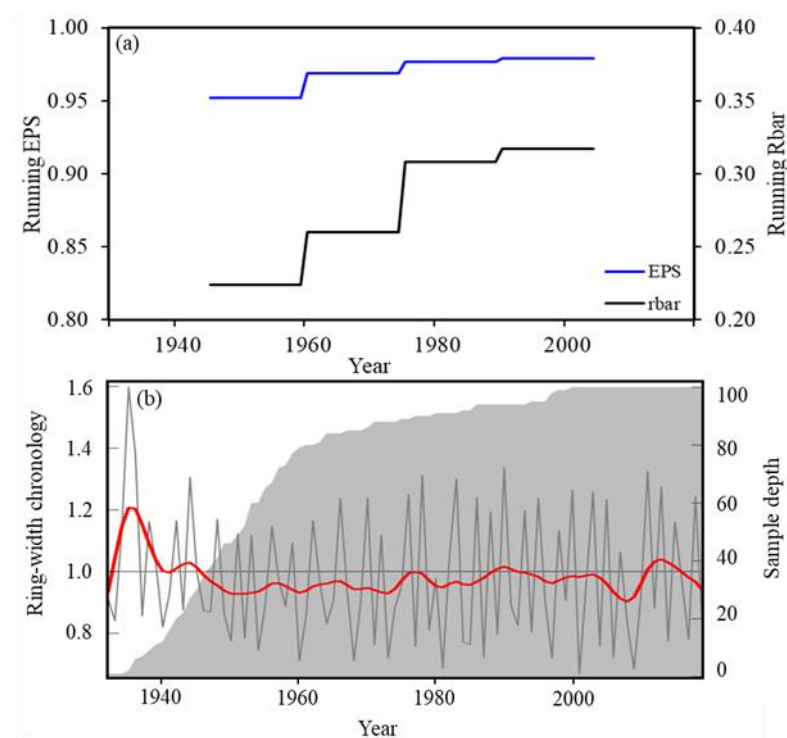


Figure 3. The residual chronology of *Choerospondias axillaris* at Mo Singto, Khao Yai National Park, east-central Thailand. (a) Running Expressed Population Signal (EPS) and running inter-series correlation (Rbar), and (b) *C. axillaris* residual chronology (grey line) with 10-year low pass filter (red line) and sample depth (grey area).

3.2. Growth-Climate Relationships

The tree-ring width index for *C. axillaris* was significantly and positively correlated with precipitation in June, July, and October. Similarly, tree-ring width index positively responded to SPEI during the monsoon season (July to October). However, there were no significant correlations between the tree-ring width index and mean temperature throughout the year (Figure 4). Moving correlation analysis revealed the consistency and temporal stability of tree growth with precipitation and SPEI during the study period. There were significant and positive correlations between tree-ring width index and precipitation in the late monsoon season (July to October) over the analysis period (1932 to 2019); the correlation was weaker during the earlier part of the analysis period, and gradually strengthened

over more recent decades. Conversely, the correlation between tree-ring width index and precipitation in June was significant during the early period, but became non-significant in more recent decades. The tree-ring index of *C. axillaris* was significantly and negatively correlated with SPEI during the second half of the year (July to December), and this correlation became stronger in the recent decades (Figure 5). However, correlations between mean temperature and tree growth were not stable throughout the analysis period.

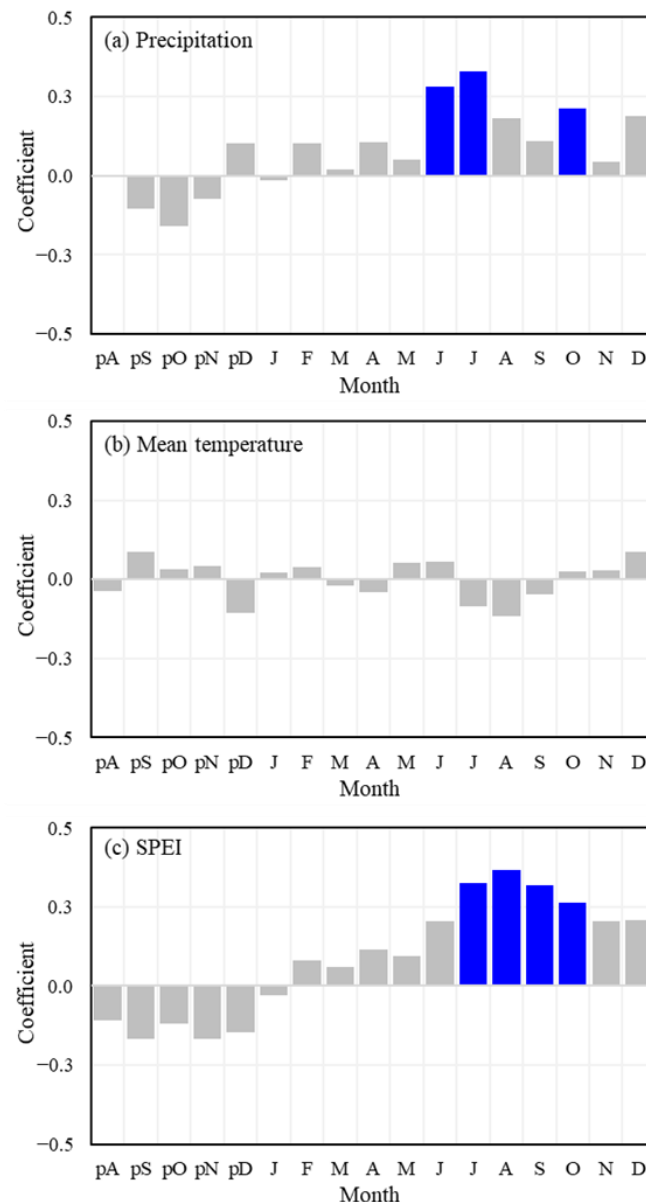


Figure 4. Correlation coefficients for *Choerospondias axillaris* tree-ring width index with monthly mean climate data. (a) Precipitation, (b) mean temperature, and (c) Standardized Precipitation–Evapotranspiration Index (SPEI). Blue and grey bars indicate statistically significant ($p < 0.05$) and non-significant ($p > 0.05$) correlations, respectively. *p*, month in the previous year.

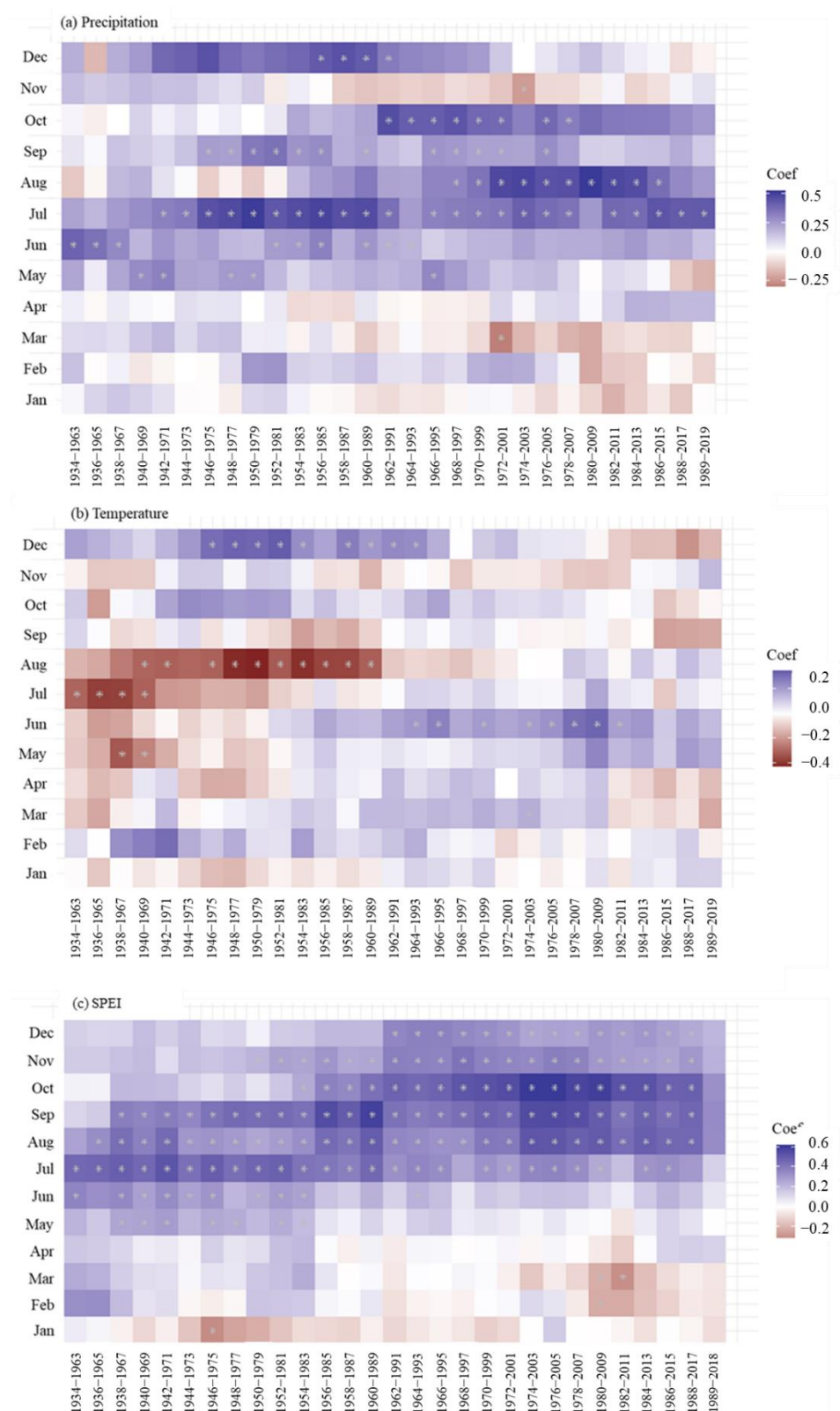


Figure 5. Moving correlation analysis of tree-ring width index for *Choerospondias axillaris* with (a) precipitation, (b) mean temperature, and (c) Standardized Precipitation-Evapotranspiration Index (SPEI). The correlation coefficients were computed from CRU TS climate data during the period of 1934 to 2019 for 30-year moving windows with a two-year offset. Color represents the scale of correlation coefficients ranging from positive (purple) to negative (brown). Significant correlation coefficients at 95% confidence level are indicated by white asterisks.

3.3. Long-Term Growth Trend and Climate Responses

The long-term growth of *C. axillaris* had a continually increasing trend from 1932 to 2002 (slope = 0.017, $p < 0.001$). However, growth had a significantly declining trend from 2003 to 2019 (slope = -0.014 , $p < 0.001$) (Figure 6).

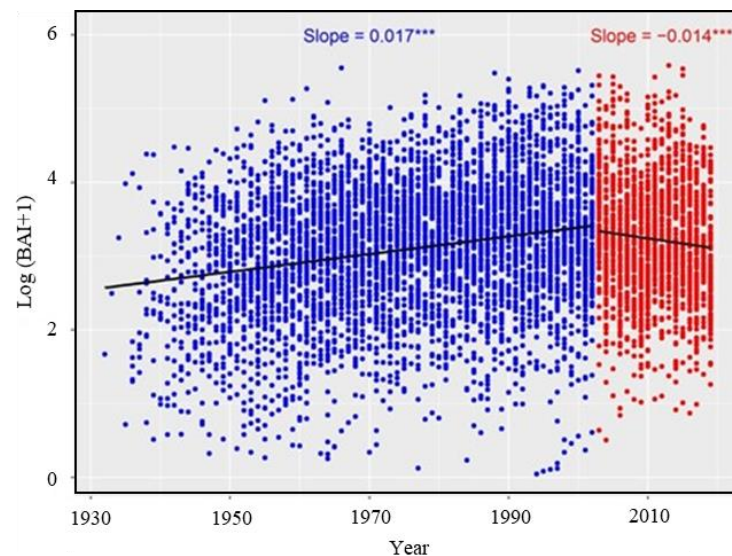


Figure 6. Long-term trends for basal area increment in *Choerospondias axillaris* at Mo Singto during the period 1932 to 2002 (blue) and 2003 to 2019 (red). Black lines represent growth trends modeled using linear mixed-effects models with “Year” as fixed factor, and “treeID” as a random factor. The slope of the fixed effect “Year” and the significance level from 1932 to 2002 and from 2003 to 2019 are given at the top (***, $p < 0.001$).

4. Discussion

4.1. *Choerospondias axillaris* Chronology Characteristics

Our study established a new tree-ring chronology for *C. axillaris* spanning from 1932 to 2019. Since only a few broad-leaved tree species have been studied in tropical regions, our study provided important information about the growth-climate relationships of tropical trees. Mean sensitivity (MS = 0.412) of this species was comparable to existing dendroclimatic studies for broad-leaved species from the tropics of Southeast Asia [45–48], indicating that growth of *C. axillaris* was highly responsive to year-to-year climatic variation. The Rbar was higher after 1985, indicating that the environmental influence on growth became stronger during recent decades. The EPS (0.968) of this chronology indicated that this species was reliable for dendroclimatic analysis [11].

We found that the tree-ring width chronology of *C. axillaris* had a rather high short-term variation, which may relate to the impact of fruit production. There is usually an inverse relationship between radial growth and fruit production [49,50]. Chanthorn and Brockelman (2008) observed that fruit production in the year 2004 was high (with abundant seeds in the field), whereas fruit production in the year 2005 was low (with fewer seeds in the field) [28]. High fruit production in 2004 corresponded to a narrower ring width index (0.76), whereas low fruit production in 2005 corresponded to a wider ring-width index (1.23). However, since long-term fruit production data were lacking, the relationship between radial growth and fruit production requires further study.

4.2. Growth–Climate Relationships

Our study found that the growth of *C. axillaris* was mainly limited by moisture availability in the monsoon season. Monsoon precipitation was found to limit the growth of teak (*Tectona grandis*) in Myanmar [45]. However, moisture availability during the dry season, or dry-to-wet season transition, was found to be the main limiting factor for tree

growth in tropical regions [48]. Pumijumnong and Buajan found that precipitation during March was the main factor influencing cambial activity of *C. axillaris* at the Mo Singto plot [29]. Although the cambial activity of tree species is related to climate in the transition season, maximum radial growth of tropical tree species occurs mainly in the late monsoon season (July to October) [51]. Our study found that the growth of *C. axillaris* was positively correlated with SPEI from July to October, which further confirmed that growth was limited by moisture availability in the late monsoon season.

Previous studies found that radial growth of tropical tree species was negatively correlated with temperature in the dry season and dry-to-wet transition in seasonally dry forests [48,52]. A higher temperature in the dry season increased evapotranspiration and induced water deficit [53], which further limits tree growth. However, we did not find a significant correlation between the radial growth of *C. axillaris* and temperature. It is possible that the mean temperature at this site was sufficiently low that evapotranspiration had not induced water deficit. The correlation between tree growth and July-to-October precipitation became stronger in recent years, which was similar to studies on *Pinus latteri* in Northeastern Thailand [54] and *Pinus sylvestris* in Poland [55].

Individual genetic variation and topographic variables (slope, aspect, and elevation) will also impact tree growth-climate relations [13]. The relationships between fruit production and wood radial growth may also impact the growth-climate relationships for *C. axillaris*. Mund et al. (2020) [49] found that fruit production was negatively correlated with May precipitation, whereas wood growth was positively correlated with May precipitation. A precise understanding of climate-growth correlations needs to include long-term monitoring of fruiting.

4.3. Long-Term Growth Trends of *Choerospondias axillaris*

Our study revealed that the growth of *C. axillaris* in the Mo Singto plot had a continually increasing trend early in the analysis period, but that growth rate declined in recent decades, especially after the year 2003. These results were consistent with a previous study in which the growth trend of *P. latteri* in Thailand had an increasing trend from 1951 to 1984, but a decreasing trend from 1985 to 2017 [54,56]. Growth over time also decreased for four broad-leaved tree species in Thailand [57]. The decreasing growth trend for *C. axillaris* in recent years could be related to increasing temperature and/or the decreasing trend in precipitation at the study site. Changes in temperature and precipitation may have affected tree growth in the last decades more widely [58]. Battipaglia et al. (2015) showed that decreasing growth for three tropical tree species from Central Africa was related to the increase in local temperature [59]. van der Sleen et al. (2015) found that there was no growth stimulation with the increase of water-use efficiency across three tropical forests worldwide [5]. The decrease in growth for *C. axillaris* in recent decades may also be related to the aging of the individual plants. The population of *C. axillaris* at Mo Singto was dominated by a cohort of aging individuals that were seeded around 90 years ago, and this species showed poor regeneration (i.e., recruitment failure) over time. Such recruitment failure over time alters the tree demography of the *C. axillaris* population, which has the potential to induce spurious negative growth trends in recent decades [60]. Therefore, multiple methods to detect growth trends and more robust analyses should be used to better understand the drivers of long-term trends in tree growth.

5. Conclusions

This study provided a new tree-ring chronology (spanning 1932 to 2019) for a tropical broad-leaved species, *Choerospondias axillaris*, from the Mo Singto Forest dynamic plot, Khao Yai National Park, east-central Thailand. The growth of *C. axillaris* was mainly limited by moisture availability in the late monsoon season during July to October. The long-term growth of *C. axillaris* had an increasing trend early in the chronology that transitioned into a decreasing growth trend during the two most-recent decades. Our study thus contributes a new broad-leaved species for dendrological studies in the tropics, where the number

of species targeted for tree-ring analysis needs to be increased to better understand and quantify the ecosystem services provided by tropical trees.

Supplementary Materials: The following are available online at <https://www.mdpi.com/article/10.3390/f12121655/s1>, Figure S1: Scanned image (a) and microscopic images from different sides, (b) cross section, (c) tangential section and (d) radial section of a wood core sample from *Choerospondias axillaris*. Black triangles indicate ring boundaries, while the year indicates calendar year of ring formation; Figure S2: Climate diagram according to Walter & Lieth for Mo Singto for the period from 1994 to 2019; Figure S3: Comparison of temporal pattern in annual climate between CRU TS data (blue line, 1932–2019) and Mo Singto station data (black line, 1994–2019) for (a) Precipitation, (b) Maximum temperature, (c) Mean temperature, and (d) Minimum temperature. ‘r’ indicates the correlation between CRU TS data and Mo Singto climate data for the period 1994 to 2019; Figure S4: Number of sampled trees classified according to DBH class. Figure S5: Density plot of break points for all in-dividual trees of *Choerospondias axillaris*, calculated by the package ‘segmented’ in R. Dashed line indicates the highest frequency of break points, which was in the year 2003.

Author Contributions: P.F., N.P. and W.Y.B. conceived and designed the research; W.Y.B., Y.C., W.C., P.T.-n. and A.N. coordinated the permission for doing this study in the Khao Yai National Park; W.S. and S.B. performed the experiments; W.S., P.F. and S.P. analyzed the data; W.S., P.F. and N.P. wrote the draft; S.B., Z.F., P.M.F. and Y.Z. revised the draft. All the authors appraised the research, reviewed and edited the draft. All authors have read and agreed to the published version of the manuscript.

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Conflicts of Interest: The authors declare no competing financial and any other potential conflict of interests.

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