

Monsoon climatic signal is stronger in wood anatomical traits than in ring widths of *Fokienia hodginsii* in central Vietnam

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ABSTRACT

Dendrochronological studies conducted in tropical regions in recent decades revealed that some species exhibit annual rings. In Southeast Asia, several ring-width chronologies of *Fokienia hodginsii* (Dunn) A. Henry & H. H. Thomas were established to reconstruct past climatic conditions.

Nevertheless, despite the strong correlations with meteorological data, the climate signal in the ring-width chronologies is robust for the shoulder season of the monsoon. For those interested in intra-annual climate signals, other parameters might prove useful. Information on intra-annual variability is crucial for understanding tree growth processes and climate dynamics in tropical regions. In this study, we explore the potential of wood anatomical parameters for climate reconstruction and for gaining a better understanding of the current climate of Southeast Asia. Microslides from cores of *F. hodginsii* in central Vietnam were analyzed. Notably, average lumen perimeter and lumen length demonstrated the most robust climate signals. They exhibit stronger correlations than ring width with maximum temperature, precipitation, and the Standardized Precipitation Evapotranspiration Index. The highest correlation ($r = 0.5$) was observed between lumen area and October–November–December precipitation. Furthermore, earlywood parameters show higher correlations with precipitation than whole ring parameters. The growth of earlywood in *F. hodginsii* appears to be influenced by climatic conditions during September–October–November of the previous year and April of the current year. Thus, earlywood is generally produced around April, whereas latewood grows during or after April–May–June. This study is the first attempt to use anatomical parameters to reconstruct climate in Southeast Asia and provides valuable insights into the intra-annual growth dynamics of tropical tree rings.

1. Introduction

In Southeast Asia, several rapidly industrializing countries are grappling with resource scarcity. Many of these nations rely heavily on agriculture, forests, and fisheries for their resources, making water management crucial. However, meteorological data are sparse in terms of both spatial coverage and temporal resolution. While dendrochronological studies have been able to reconstruct past climatic conditions in the region (Pumijumnong, 2013; Buckley et al., 2007, 2010, 2014, 2017, 2019; Sano et al., 2009), the tropical climate poses challenges for accurately identifying and dating tree rings. Despite this limitation, or

perhaps because of that, there is a growing recognition of the potential of wood anatomical analyses to enhance our understanding of intra-annual climate variability.

Vietnam, situated along the eastern Asian coast with the Red River (Song Hong) in the north and the Mekong River in the south, faces significant challenges due to its reliance on coastal ecosystems for agriculture and fisheries, and the impact of sediment discharge and pollution on both (Vien, 2011). Climate change is expected to disproportionately impact less developed countries like Vietnam, which has limited capacity to adapt (Adger, 1999). Changes in hydrological conditions (Van et al., 2012), including precipitation patterns, seasonal

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periodicity, flood distribution, and salinity intrusion threaten socio-economic systems (e.g., Quinn et al., 2010). Protecting Vietnam’s coastal environment is crucial for biodiversity and forest conservation and for maintaining fishery productivity (Thanh et al., 2004). However, the expected increase in the frequency and intensity of typhoons and floods (Van et al., 2012) poses significant risks to coastal populations and the economy.

Vietnam’s climate, characterized by tropical to subtropical conditions, is heavily influenced by the Asian Summer Monsoon (ASM; Buckley et al., 2017). Understanding the patterns and dynamics of monsoon activity is essential for the region’s social and economic development (Liu et al., 2019), as vital sectors like agriculture, forestry, and fishing depend on it (Buckley et al., 2014; Nguyen-Le et al., 2014). While tree-ring based climate reconstructions could provide valuable insights into the ASM’s relationship with global atmospheric patterns over the past decades and centuries, the difficulty in identifying tree-ring boundaries in tropical trees has been a significant challenge. However, recent advancements in tree-ring related techniques offer promise in overcoming these obstacles (Wang et al., 2022).

Dendrochronological studies rely on annual ring formation, which is challenging in the tropics and subtropics, which lack clear seasonality. Nonetheless, certain climatic factors such as precipitations patterns can induce annual ring formation even in these regions. By analyzing vessel size variations in Andean walnut trees (*Juglans neotropica* Diels-Juglandaceae) Rodríguez-Ramírez et al. (2023) managed to detect South American Monsoon System (SAMS) precipitation signals in the Peruvian tropical montane cloud forest. *Fokienia hodginsii* (Dunn) A. Henry & H. Thomas, a conifer species found in tropical Asia, has been identified as suitable for dendroclimatological studies due to its annual tree rings, longevity, and sensitivity to moisture (Buckley et al., 2017). While several previous studies have successfully reconstructed climatic parameters with annual resolution using *F. hodginsii* ring-width chronologies (Buckley et al., 2010; Buckley et al., 2017; Buckley et al., 2019; Sano et al., 2009; Sano et al., 2012) only few have addressed the intra-annual variability of the rings analyzed (Buckley et al., 2018).

Despite ring-width measurements, there are numerous more sophisticated approaches to allow analyzing the response of woody plants to environmental conditions. Among these approaches are isotope analyses (Huang et al., 2024), blue intensity measurements (Mundo et al., 2024), wood anatomy (Balzano et al., 2024), and all related measurements possible as e.g., anatomical density (Björklund et al., 2019). Within all tree-ring related research approaches, wood anatomical techniques evolved significantly in recent years (e.g., Gärtner et al., 2024) and are nowadays to be seen as a standard in many dendroecological studies (Edwards et al., 2021; Zhirnova et al., 2022).

This study explores the potential of Blue Intensity and wood anatomical measurements in reconstructing past climatic patterns in Vietnam using *F. hodginsii*. By conducting a qualitative and quantitative analysis of the anatomical structure of *F. hodginsii* wood and correlating the results to meteorological data, we seek to determine if wood anatomical characteristics provide a stronger climate signal than ring width alone in tropical regions. The study’s objectives include identifying the main anatomical characteristics of *F. hodginsii*, analyzing the impact of climatic conditions on these characteristics, and assessing whether wood anatomical characteristics serve as better proxies for climate variability.

2. Materials and methods

2.1. Sampling

This research is based on cores of 20 *F. hodginsii* trees from the Quang Nam core collection (Buckley et al., 2017, 2018). The samples were obtained from a mixed evergreen broadleaved-coniferous forest in the Tay Giang Protection Forest, located in the mountains of Quang Nam Province in central Vietnam (15°09’ N, 107°41’ E; 1350 m asl). These

cores have already undergone analysis, with their ring widths measured (RW1), cross-dated, and analyzed for RW and Blue Intensity (BI) at the Lamont-Doherty Earth Observatory (LDEO, Columbia University, Palisades NY, USA) (Buckley et al., 2017, 2018). For this study, the samples were cross dated again with the result that missing rings had to be added to some of the core chronologies (RW2).

In central Vietnam, where the sample site is located, the ASM behaves differently than in most of Southeast Asia because the wet season starts in autumn (September–November), rather than in summer. This difference is attributed to the orography of central Vietnam, as well as cold surges and tropical disturbances over the South China Sea in early winter. During the summer, the climate in central Vietnam tends to be dry due to warm winds, which are caused by the ASM. Most rainfall occurs on the windward slopes in Laos and Cambodia. The autumn rain originates from the South China Sea and is transported to central Vietnam by winter monsoon westerlies (Nguyen-Le et al., 2014).

2.2. Blue Intensity measurements

Blue Intensity data were used derived from measurements done by Buckley et al. (2018). The rings were digitized using a flat bed scanner and the resulting images were then imported into CooRecorder where an area of analysis was defined over the latewood portion of each ring. For the ongoing measurement the blue component of the reflected light was analyzed. Within each analyzed area all pixels were ranked in order of the measured amount of blue on a color-depth scale that is based on an 8-bit encoding where every channel is resolved with 256 possible values that range from 1 (=complete absorption of visible blue light and high density) to 256 (= total reflection of blue light and low density) (Buckley et al., 2018).

2.3. Wood anatomical analyses

Microsections were obtained by cutting cores of four of the 20 trees sampled using a WSL Lab-microtome (Gärtner et al., 2015). A non-Newtonian solution was prepared by mixing cornstarch with water until the desired consistency was achieved (Schneider and Gärtner, 2013). This solution was applied directly onto the freshly cut samples to prevent cell walls from breaking during cutting. The samples were then sliced to a thickness of about 15 µm. All microsections were stained with a 1:1 mixture of Safranin (which stains lignified parts red) and Astra-blue (which stains non-lignified parts blue). The stained and dehydrated sections were then embedded in Euparal. Images of the final microsections were digitalized using a Zeiss Axio Scan Z1 automatic digital slide scanning system.

WinCELL 2020a (Regent Instruments Inc., Canada) was utilized for the anatomical analysis. Five filter variables, determined by applying a preliminary test measurement to the samples, were added to the original settings to enhance cell detection (area < 100 µm², minimum length/width < 0.15, max. length > 200 µm, max. width > 170 µm, max.

Table 1
Wood anatomical parameters. The letters "e" or "l" before the abbreviation indicate that the parameter is measured only in EW ("e") or only in LW ("l") cells, respectively.

Parameter	Acronym	Unit of measurement
Ring width	RW2	µm
Percent total lumen area	%LA	%
Average lumen area	ALA	µm ²
Average lumen width	ALW	µm
Average lumen length	ALL	µm
Average cell length	ACL	µm
Average lumen perimeter	ALP	µm
Average lumen form coefficient	AFC	(µm ² /µm ²)
Average lumen length/width	ALLW	(µm/µm)
Average wall thickness	AWT	µm

length/width > 4.5). For each individual ring, ring width and various anatomical parameters were measured (Table 1). All measured rings were cross-dated, and the resulting core chronologies were then cross-dated with existing ring-width chronologies from the same site (RW1) (Buckley et al., 2017, 2018). Earlywood (EW) and latewood (LW) cells were differentiated according to the standard Mork's index (Denne, 1989; Mork, 1928). Subsequently, all anatomical parameter series were detrended with a 30-year spline using the R package dplR. Finally, the average of the detrended data for each parameter for each year was calculated to obtain one chronology for each parameter. In the context of this study, the blue intensity (BI) data were detrended with a 30-year spline before being correlated with the anatomical parameters. We chose the 30-year spline to preserve the high-frequency signal.

The wood anatomical parameters were analyzed using the KNMI Climate Explorer (<https://climexp.knmi.nl>; Trouet and Van Oldenborgh, 2013) to calculate spatial correlations with the climatic data. Meanwhile, R was used to correlate the time series of anatomical parameters with the climatic data. The climatic dataset comprises monthly maximum temperature (1901–2018; CRU TS4.04, Harris et al., 2020), monthly precipitation data measured at three climate stations in the region from 1980 to 2006, and monthly SPEI data (Global SPEI database <https://spei.csic.es/database.html>).

3. Results

3.1. Anatomical characteristics of *F. hodginsii*

The rings of *F. hodginsii* exhibit distinct ring boundaries, with a clear transition from the last row of latewood cells to the first earlywood cells, as typically observed in coniferous species. The ring structure is characterized by a wide EW section and a narrow band of LW cells. The transition from EW to LW is sharp, although a wider LW results in a less distinct transition. Axial parenchymatic cells are abundant in *F. hodginsii*. These parenchyma cells are arranged both diffusely and tangentially, and they are present in both EW and LW (Fig. 1).

To understand the presence and distribution of axial parenchyma bands over time, tree rings from five samples formed between 1946 and 2013 were visually analyzed. In only six years were axial parenchyma bands found in three different samples. For most years, only one sample analyzed showed bands of axial parenchyma cells. The analysis revealed that from 1946 to 1980, the bands were mainly found in LW (86 % of the bands), while from 1981 to 2013, they were predominately located in EW (64 % of the bands).

3.2. Blue intensity

Earlywood blue intensity (EW-BI), latewood blue intensity (LW-BI), and Δ BI (difference between EW-BI and LW-BI) correlate ($r = -0.56$, 0.22 , 0.70 ; all $P < 0.05$) with RW1 better than with anatomical

parameters. However, BI shows very similar correlations to RW1 and anatomical parameters when calculated only for EW or for the whole ring. Only the anatomical parameters EW-AFC, AFC, and EW-AWT do not correlate significantly with EW-BI.

The correlations for Δ BI with anatomical parameters (calculated for only EW and for the whole ring) are slightly lower than with RW1. However, they are all significant, except for the correlations between Δ BI and EW-ALW, EW-AFC, AFC, and EW-AWT. Among all parameters, ALL and eALL show the highest correlations with EW-BI and Δ BI.

LW-BI exhibits the lowest correlations (correlation coefficient < 0.220) with the anatomical parameters. No significant correlation between LW-BI and anatomical parameters was found.

3.3. Wood anatomical data and precipitation

Wood anatomical parameters demonstrate higher correlations with precipitation than ring width does.

The strongest correlation between ring width and rainfall is with the sum of the rain that fell in the previous November–December–January (NDJ) months ($r = 0.41$).

Wood anatomical chronologies calculated for the entire ring show coefficients of correlation of up to 0.50 between lumen area (LA) and October–November–December (OND) precipitation. LA exhibits significant and high correlation only in the two periods September–October–November (SON) and OND. In the following three-month periods, the correlation coefficients tend to decrease. In the period OND of the year prior to the year in which the ring was formed, when LA shows the highest correlation, four out of seven wood anatomical parameters have significant correlations with precipitation.

Earlywood (EW) anatomical parameters display higher correlations with precipitation than parameters calculated for the whole ring. The highest correlation found is between EW-LA and rainfall over the months of SON of the year prior to the year in which the ring was formed (0.54). Similar to ALA, the correlation coefficients between EW-ALA and precipitation tend to decrease during the year. Four parameters (EW-ALA, EW-ALL, EW-ACL, and EW-ALP) show correlations higher than 0.44 only for the months of the previous autumn (SON or OND), while ALW, AFC, ALLW, and AWT generally exhibit lower correlations than the other parameters.

The correlation coefficient between precipitation and the latewood (LW) anatomical chronologies are lower than those found for earlywood (EW). Only one correlation coefficient is higher than 0.44 (IALA and AMJ precipitation). In the case of LW, the correlation coefficient of LW-LA changes during the year in a different way than those of the parameters LA and EW-LA. In the case of LW-LA, the highest peak occurs in the spring (especially in the months of April–May–June (AMJ)), while the trend over the rest of the year is not clear.

IALA, IALL, IACL and IALP are the parameters that have the highest correlations, with coefficients higher than 0.30 almost exclusively with

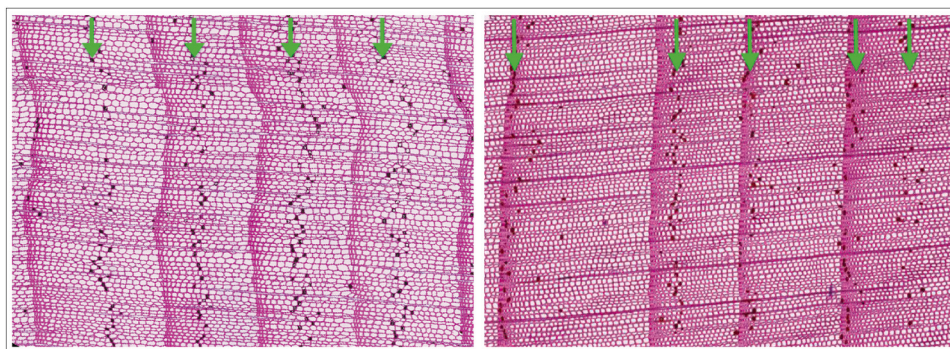


Fig. 1. Tangential axial parenchyma bands are marked with green arrows. On the left, the bands occur predominately in the earlywood, while on the right we show bands occurring more in the latewood.

the sum of rainfall during AMJ. The only two significant correlations between precipitation and LW anatomical parameters are those between lALA and AMJ precipitation, and lALL and AMJ precipitation. Even in this case, the parameters ALW, AFC, ALLW, and AWT show low correlations with precipitation.

Years with particularly high or low rainfall occur at regular intervals. The extreme events in the early years of the reconstruction (until 1733) may be amplified since they are based on only one core. In the medium to long term, no trend is observed due to the type of detrending applied to the anatomical data, which preserved only the high-frequency signal.

3.4. Wood anatomical data and standardized precipitation evapotranspiration index

The anatomical parameters exhibit low correlations ($r < 0.25$) with the monthly Standardized Precipitation Evapotranspiration Index (SPEI) data for the period 1911–2012. However, an exception is noted for the SPEI data for April, which show higher correlations (Table 2). The ALP parameter shows the strongest correlation with April SPEI data ($r = 0.4704$), which is considerably higher than that between April SPEI data and RW1 ($r = 0.3137$). Almost all correlations between April SPEI data and parameters of the whole ring or EW are significant; however, those with the LW parameters are significant for only three anatomical parameters.

The April SPEI data were reconstructed using a linear model based on the correlation with ALP. The linear model is characterized by a median residual equal to -0.03748 and an R^2 of 0.221 .

Observations for the period 1670–2013 show similar trends to those observed in the reconstruction of SON precipitation. Due to the detrending of the eALP data, medium- or long-term trends are not observable, but frequent variations from year to year are noted.

3.5. Wood anatomical data and maximum temperature

High correlations between the maximum monthly temperature and the anatomical parameters were found almost exclusively in April, akin to the results observed between April SPEI data and wood anatomical parameters. Correlation coefficients higher than 0.30 were found only by comparing anatomical data with maximum temperatures in April. Most of these correlations are highly significant. The maximum correlation coefficient ($r = -0.43$) is between maximum temperature in April and eALP, surpassing the correlation between maximum temperature in April and RW1 ($r = -0.29$, Table 2Table 2).

When correlating the maximum temperature data averaged over three months, correlations slightly exceeding 0.30 were obtained even at other times of the year. However, the highest correlations, even when analyzing averaged climate data, are observed for the spring period (months MAM). The eALP parameter is confirmed to be the climate parameter that best correlates with maximum temperature.

Similarly, the maximum temperatures of April were reconstructed

using a linear model based on the best correlation with an anatomical parameter – in this case, eALP. The median residual is 0.00778 , and R^2 is 0.19 . Similar observations to those made for the other two reconstructions are valid. Due to the detrending of the eALP parameter, no medium- or long-term trends are recognizable, but frequent and important variations from year to year are observed.

4. Discussion

4.1. Wood anatomical characteristics of *F. hodginsii*

The visual analysis conducted does not demonstrate the formation of tangential axial parenchyma bands filled with starch or other substances in the same years across different samples, which might have been explained by environmental conditions inducing them. Plavcová and Jansen (2015) have shown that tropical trees grown under similar conditions accumulate starch in parenchyma cells to varying degrees. Differences are also observed within different parts of the same tree. Moreover, these substances could potentially have been mobilized or consumed between their formation and the time of sample extraction, and those found may not coincide with those produced in the year of cell formation. However, our analysis has some more limitations: the sample size is very small, and not all axial parenchyma cells are distinguishable from tracheids (if not filled with starch). Consequently, it cannot be conclusively stated that axial parenchyma cell bands are not induced by certain climatic or environmental conditions.

The mobilization and consumption of the contents of parenchyma cells may challenge the notion that the content of axial parenchyma cells is formed under specific environmental conditions in the year of cell formation, and only a portion of it remains in the cells.

Tangential parenchyma bands remain relatively unexplored in terms of their chemical and functional properties. To date, features related to the supportive and storage functions of parenchyma cells have not been thoroughly studied. This is true of *F. hodginsii* and many other species, although these features may provide insights into environmental conditions (Eckstein, 2013). In the case of *F. hodginsii*, questions such as what substance fills the axial parenchyma cells, their role, and whether parenchyma cells are formed regularly or in result to specific climatic conditions remain unclear.

Another open question pertains to the position of axial parenchyma bands (i.e., at the beginning of the ring, in the middle of the EW, between the EW and the LW, or in the LW). Our visual analysis indicates that during the period 1946–1980, the bands are mainly found in LW, while in the period 1981–2013, they are predominately located in EW. The cause of this distribution is unclear, but if induced by climatic conditions, it might suggest a shift in seasonality over time.

O'Brien et al. (2014) demonstrated that the storage of non-structural carbohydrates (NCSS) positively impacts tropical trees' resistance to and resilience during drought. This category of substances, which includes sugars and starches, is mostly stored in parenchyma (Plavcová and

Table 2

Correlation coefficients of the anatomical parameters with the April Standardized Precipitation Evapotranspiration Index (SPEI) data of the sampling site (1911–2012) and with the April maximum temperature (1902–2013). Significant correlations ($P < 0.05$) are marked by asterisks.

	Correlations with April SPEI			Correlations with April max. temperature		
	Entire ring	Earlywood	Latewood	Entire ring	Earlywood	Latewood
RW1	0.3137 *			−0.2897 *		
RW2	0.2981 *			−0.2960 *		
%LA	0.4241 *			−0.3719 *		
ALA	0.4450 *	0.4050 *	0.0476	−0.3925 *	−0.4145 *	−0.0229
ALL	0.4313 *	0.4107 *	0.0963	−0.3677 *	−0.3960 *	−0.0982
ALW	0.2868 *	0.2348 *	−0.1791	−0.2445 *	−0.2748 *	0.2666 *
ACL		0.3601 *	0.1637		−0.3600 *	−0.1915 *
ALP	0.4704 *	0.4124 *	0.2016 *	−0.4218 *	−0.4342 *	−0.1879 *
AFC	−0.1658	−0.2684 *	−0.4029 *	0.1775	0.2694 *	0.4238 *
ALLW	0.2884 *	0.2541 *	0.2362 *	−0.2555 *	−0.1961 *	−0.2769 *
AWT		−0.2358 *	0.1699			

Jansen, 2015). If the substances contained in *F. hodginsii* cells are NCSs, it would be interesting to examine how the distribution of full axial parenchyma cells varies over very long-term scales or in relation to particularly dry years.

4.2. Blue intensity

Blue intensity (BI) is commonly used as a proxy for tree-ring density (Buckley et al., 2018). The anatomical parameter that could theoretically better reflect tree-ring density is %LA, which expresses the percentage of the area occupied by lumens in a ring. Therefore, the difference between %LA and 100 % corresponds to the percentage of area occupied by cell walls. However, to obtain the density of the tree-ring wood, the specific weight of the cell wall, i.e., its density, must also be considered. The latter depends on the content of the relative abundance of the three macromolecular classes (celluloses, hemicellulose and lignin) but it is considered to be more or less constant among tree species (approximately 1.5 g/cm³, Björklund et al., 2019). Nevertheless, the correlation between the three BI parameters measured by Buckley et al. (2018) and the percentage of LA is lower than expected, possibly due to the fact that %LA was measured only for the whole ring, not separately for EW and LW. Similarly, the BI data were not measured for the whole ring but for EW and LW separately (plus the difference between these two data), which likely influences the correlations.

Buckley et al. (2018) suggest the possibility that other anatomical features, in addition to cell wall density, contribute to BI variability, particularly for earlywood blue intensity (EW-BI), such as the lumen diameter (Buckley et al., 2018). Correlations between EW-BI, latewood blue intensity (LW-BI), Δ BI (difference between EW-BI and LW-BI), and anatomical parameters show a correlation with lumen diameter (ALL or ALW) of up to -0.562 (equal to the r between ALL and EW-BI). Surprisingly, the correlation coefficient of EW-BI and ALL is slightly higher than that of EW-BI and eALL (-0.533).

The fact that Buckley et al. (2018) assessed BI by measuring only a portion of all pixels of the EW and LW may explain why the final BI value does not correspond to the average value of all pixels. This in turn affects correlations with the wood anatomical parameters, which are calculated either on the area of the whole tree ring or only on EW or LW.

By correlating intra-annual (e.g., monthly) climate data with BI data, it is possible to obtain a signal that refers to the period in which lignification takes place or a period in which a pre-conditioning necessary for lignification occurs. This signal may differ from a signal obtained from wood anatomical data, which refers to the period of cell formation or the period in which a pre-conditioning necessary for cell formation takes place.

4.3. Wood anatomical parameters and climate

The analysis of correlation coefficients between monthly precipitation data and detrended anatomical parameters of EW and LW cells reveals that the highest correlations occur in EW, the strongest correlations are observed in the months of SON and OND. This finding aligns with the correlations identified by Buckley et al. (2018) between EW-BI and Δ BI of the same *F. hodginsii* samples and precipitation: these BI parameters exhibit significant correlations for the preceding October and November, albeit lower than those obtained in our study with anatomical parameters (particularly EW-ALA and ALA). Thus, the hypothesis of a pre-conditioning effect on soil moisture by autumn rainfall, posited by Buckley et al. (2018), is supported by the results of this study. The heavy rains in central Vietnam during autumn may alleviate the effects of the subsequent dry season (January–April).

In contrast, fewer significant correlations between cell parameters and precipitation were found for LW. The stronger correlation between AMJ precipitation and lALA suggests that LW is influenced by precipitation in late spring. Buckley et al. (2018) did not report any significant correlation between LW-BI and climatic parameters. This therefore

marks the first indication of intra-annual growth in the LW cells of *F. hodginsii*.

The parameters that most strongly correlate with precipitation are ALA and ALL (in the EW, LW, or in the entire ring): water availability in the previous autumn positively relates to lumen area and length.

The analysis of correlations with monthly Standardized Precipitation Evapotranspiration Index (SPEI) data or maximum monthly temperature confirms the significance of April, as discussed by Buckley et al. (2017, 2018). Anatomical parameters exhibit better and more significant correlations with April SPEI than ring width does. Similarly, correlations with maximum monthly temperature reveal that the best correlation with anatomical parameters occurs in April. The parameters that correlate most strongly are ALP (for the entire ring), eALP (for EW), and AFC (for LW), exactly the same ones that correlate best with April SPEI data.

During the MAM months, the Intertropical Convergence Zone moves north through Southeast Asia, leading to increased temperature and humidity. As a result, April is one of the warmest months in Southeast Asia. For most of Southeast Asia (except central Vietnam), April precedes the onset of the monsoon and thus represents a period of potential atmospheric drought (Buckley et al., 2018) (Fig. 2).

These correlations between climatic data and wood anatomical parameters confirm previous findings (Buckley et al., 2017) and provide insights into intra-annual ring growth. While growing and dormancy seasons are well defined in temperate zones, this knowledge remains unclear and highly variable in tropical regions. The growth of EW in *F. hodginsii* appears to be influenced by the SON of the previous year and April, suggesting that it likely occurs during or after this month, while LW grows during or after the AMJ months. It remains unclear whether precipitation during AMJ acts as a conditioning factor in advance of or during cell growth.

Our climatic reconstructions do not allow for conclusions regarding medium- or long-term trends in SON precipitation, April maximum temperature, and April SPEI due to the 30-year spline used to detrend anatomical parameters. However, other conclusions can be drawn. The linear models used for climate reconstructions yield R^2 values between 0.18 and 0.22, explaining 18 %–22 % of the data variance. While this may appear low, it aligns with the results obtained for the April SPEI reconstruction made by Buckley et al. (2017), where the model explained 23.3 % of the variance.

In other studies of *F. hodginsii*, the percentage of variance explained was considerably higher. For example, Buckley et al. (2010) explained 35 % of the Palmer Drought Severity Index variance, Buckley et al. (2018) explained 37 % of the December–April maximum temperature variance, and Buckley et al. (2019) explained 57 % of the Interdecadal Pacific Oscillation variance.

The reconstructions exhibit significant inter-annual variability and regularity in the occurrence of extreme climatic conditions. An analysis of the 12 years with the most extreme climatic conditions for each reconstruction reveals that maximum temperatures in April were particularly low in 1844–1845 and 1892–1893, while the SON rainfall was very high. These characteristics are not reported in other studies.

A comparison between the April SPEI reconstruction of Buckley et al. (2017) and our study shows clear similarities, with strong correspondence between minimum and maximum peaks (Fig. 3). Years with very dry conditions (negative SPEI) align particularly well in both reconstructions (1905, 1926, 1941, 1966, 1975, 1983, and 1990). According to the reconstruction of SON precipitation, all years with particularly low April SPEI data also experienced very low SON precipitation (< 4000 mm).

5. Conclusions

This study demonstrates that wood anatomical parameters as cell lumen length and area are promising proxies for climate reconstructions in tropical regions. For *F. hodginsii*, these parameters exhibit stronger

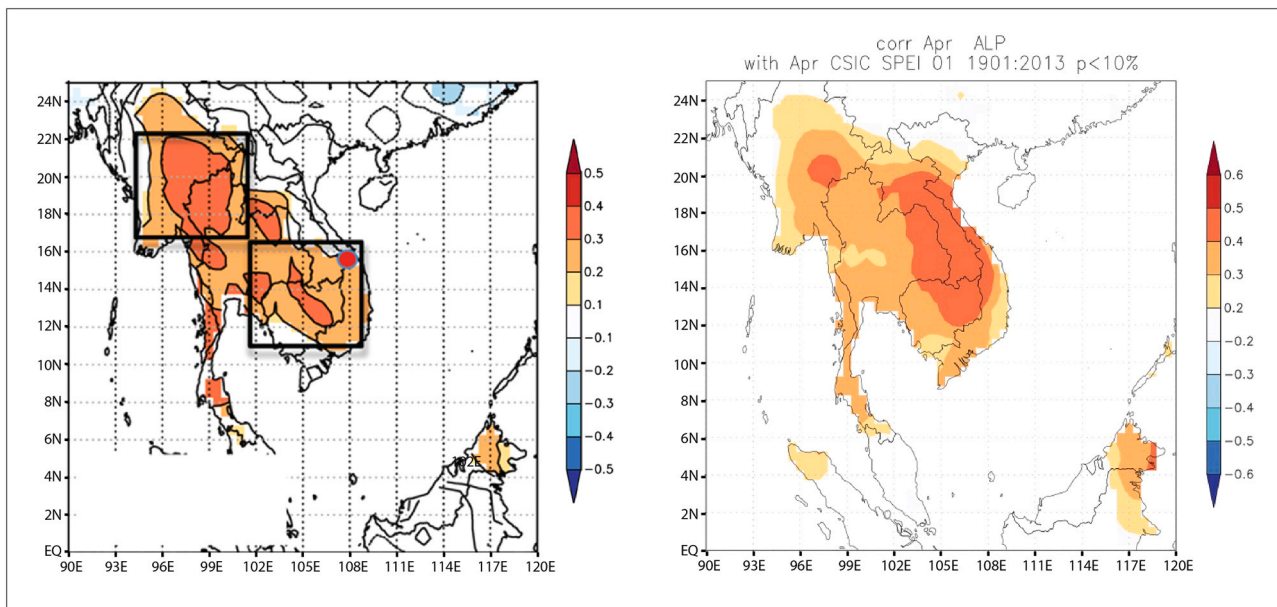


Fig. 2. Comparison of the spatial correlations between April Standardized Precipitation Evapotranspiration Index (SPEI) data and ring width (on the left, from Buckley et al. [2017]) and ALP (on the right). The color scale is different for the two images.

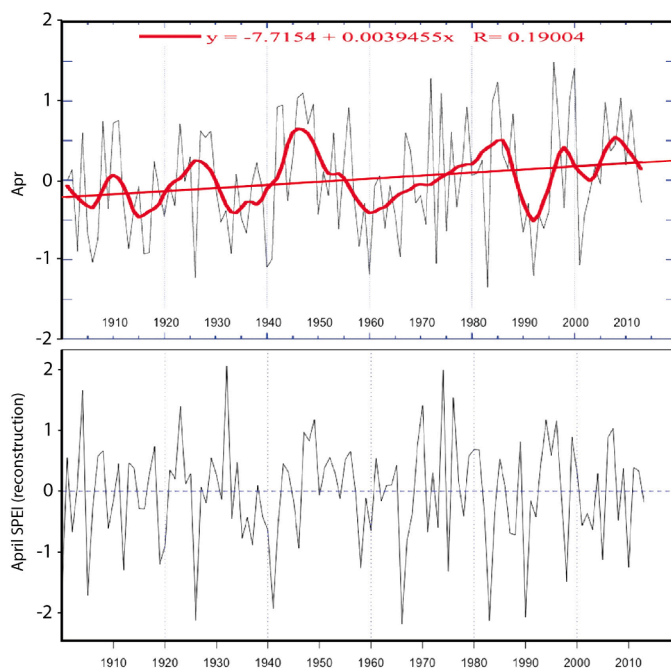


Fig. 3. Reconstruction of the April SPEI data by Buckley et al. (2017); graph and equation in the upper image and of this study (lower image). The upper image is stretched to facilitate comparison with the lower image.

correlations with meteorological data compared to ring width. The findings support the hypothesis of a pre-conditioning effect of the previous autumn's precipitation and highlight the significance of April for tracheid formation in *F. hodginsii* in central Vietnam. By analyzing earlywood and latewood cells separately, this study also discerned on an intra-annual scale which climatic conditions influence the formation of these cell types.

The primary limitation of this study is the small sample size, which is the result of the complex and time-consuming sample preparation process. A second limitation arises from the extremely small size of *F. hodginsii*'s LW cells, which WinCELL, the software used, sometimes

fails to recognize. Consequently, there may be misidentification of cells as LW in EW and vice versa, as well as undetected LW cells. This issue slightly reduces the reliability of LW data compared to EW data.

Future research should investigate, with a larger sample size, the relationships between climate and anatomical parameters as cell size, cell wall thickness and lumen area for *F. hodginsii* in other regions of Vietnam and Southeast Asia. Additionally, exploring the relationship between climate and wood anatomical parameters in other tropical tree species is warranted. Finally, a chemical and functional analysis of axial parenchyma cells is crucial for understanding if they form due to specific climatic conditions.

In regions like Southeast Asia, where climate change will have a significant impact on millions of people's daily lives, understanding past climatic variability is vital to predict the magnitude of future changes and to adopt adequate management measures. Studying the response of tropical trees to climate is also important for developing effective conservation policies to preserve tropical forests. Given the lack of regularly spaced meteorological stations and long-term data, it is necessary to reconstruct climate using proxies such as ring width or wood anatomical parameters. Wood anatomical traits hold promise as valuable climatic proxies.

Keymessage

Anatomical parameters exhibit stronger correlations than ring width with maximum temperature, precipitation, and the Standardized Precipitation Evapotranspiration Index.

CRedit authorship contribution statement

Silvia Passardi: Writing – original draft, Methodology, Formal analysis, Data curation. **Holger Gärtner:** Writing – original draft, Methodology, Conceptualization. **Nam Le Cahn:** Investigation, Data curation. **Brendan M. Buckley:** Supervision, Formal analysis, Conceptualization. **Paolo Cherubini:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation, Data curation, Conceptualization.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

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