



Climatic influences on intra-annual stem radial variations and xylem formation of *Toona ciliata* at two Asian tropical forest sites with contrasting soil water availability

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ABSTRACT

Climate extremes will increasingly influence ecosystem productivity of tropical forests, but little is known about their effects on tree stem radial growth, a major component of forest productivity. To analyze the role of climatic drivers and local site differences on tree growth at sub-annual timescales, we studied the timing, magnitude and climatic drivers of stem growth and xylem formation at two tropical forest sites with contrasting soil water availability in southwestern China. We combined high-resolution point dendrometer recordings and microcoring to investigate intra-annual stem radius variation and xylem formation of *Toona ciliata* over three consecutive years (2018–2020). Stem radial increment of *T. ciliata* derived from dendrometer data showed distinct seasonal patterns, with growth mainly occurring during March to October. The start day of stem radial growth coincided with the occurrence of the cell enlarging phase, and its end day occurred concomitantly with the cessation of cell enlarging as identified from microcores. *Toona ciliata* trees at the tropical ravine rainforest site with higher soil water availability showed higher mean annual stem radial increment, higher daily growth rates, and longer duration of xylem productivity than that at the tropical karst forest site. Weekly stem radial growth rates increased with precipitation and air temperature at the wetter ravine rainforest site, while relative humidity had a positive effect at the drier karst forest site. Our findings indicate that drought stress advances and shortens the growing season for *T. ciliata*. Our study highlights the strong influence of soil water capacity mediating the impact of climate, so response to drought is site-specific, which should be considered in growth models.

1. Introduction

Tropical forests harbor a high biodiversity and play an important role in global carbon and water cycle (Bonan, 2008; Pan et al., 2011). Changes of carbon stocks of tropical forests has major impacts on the global carbon cycling and is mainly caused by shifts in growth and mortality of large trees (Gora & Esquivel-Muelbert, 2021), thus the responses of tropical forest to future environmental changes will influence the pace of climate change. In recent decades, changes in temperature and precipitation in tropical regions have caused impacts on forest structure and deposition (Deb et al., 2018). Rapidly decrease in tropical

lowlands tree longevity (Locosselli et al., 2020) reduces carbon stocks and wood productivity (Sullivan et al., 2020) and tree growth reduction (Su et al., 2017). Moreover, the temporal fluctuations in ecosystem productivity of tropical forests are closely linked to temporal variations in climatic conditions and contribute to the climate-driven inter-annual variability in the carbon land sink (Le Quéré et al., 2018). Yet, a better understanding of the climatic conditions that drive tree growth and mortality is urgently needed to develop reliable models of tropical forest productivity under future environmental conditions (Zuidema et al., 2013).

Many studies analyzed tree growth-climate relationships in tropical

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regions by correlating ring-width chronologies with monthly climate parameters (Pumijumnong et al., 2014; Rahman et al., 2017; Rakthai et al., 2020). Total ring width is an integrative parameter that summarizes radial tree growth over a whole vegetation period. However, xylem production rates may strongly vary under contrasting climatic conditions and similar amounts of radial growth can be achieved with different combinations of growth rate and duration during the vegetation period (Duchesne et al., 2012). Empirical evaluations of these drivers at tropical forests are still limited, particularly at intra-annual timescales (Wagner et al., 2016). Therefore, better knowledge on the response of tree growth to short-term climate extremes (e.g., droughts) is of high relevance, because the timing of climate extremes within the course of the growing season defines their impact on tree growth (Scharnweber et al., 2020). Continuous monitoring of stem cambial activity and radial increments of tropical trees may help clarifying the physiological mechanisms and climatic drivers of tropical tree growth at daily to seasonal level (Krepkowski et al., 2011; Butz et al., 2017). Such insights are also important to benchmark vegetation models that simulate stem productivity in forests at daily timescales (Zuidema et al., 2018; Babst et al., 2021).

High-resolution dendrometers continuously monitor stem radius variation and are an important aide to quantify daily to annual rates of tree growth (Deslauriers et al., 2007; De Swaef et al., 2015; Zweifel et al., 2020; Knüsel et al., 2021). Dendrometer measurements are increasingly applied in temperate and subtropical forests (e.g., Deslauriers et al., 2007; Wang et al., 2015; Zweifel et al., 2020) and are especially valuable in the tropics where periodicity of tree-ring formation is often lacking (O'Brien et al., 2008). However, understanding of intra-annual tree growth patterns and their climatic drivers is very limited for tropical species. Studies conducted so far yielded insights into the role of precipitation and vapor pressure deficit on stem radial growth in East Africa (Krepkowski et al., 2011) and South America (Volland-Voigt et al., 2011; Raffelsbauer et al., 2019). Another study in South America found that high air temperatures reduce radial increment in tropical dry forests, likely due to increased vapor pressure deficit and enhanced transpiration rates (Mendivelso et al., 2016).

However, dendrometer data contain signals of both irreversible tree volume growth of xylem and phloem and reversible water-related expansion and shrinkage (Zweifel et al., 2016). Thus, the dendrometer method cannot detect the precisely xylem growth, especially in drier habitat (Mendivelso et al., 2016). It is promising to combine both dendrometer and xylogenesis methods to quantify the radial growth of tropical trees more precisely (Cocozza et al., 2016). While wood anatomical studies of xylogenesis quantify xylem growth without being affected by the tree water status, albeit at a much lower temporal resolution. Most of these studies have been conducted in cold and dry environments (Rossi et al., 2016; Zhang et al., 2018). These studies have shown that intra-annual cambial activity is driven by both of temperature and soil water status, while the onset of xylem formation is mainly determined by temperature, whereas soil water potential can predict the total amount of xylem formation and termination (Cabon et al., 2020). Seasonal timing and duration of xylem formation is linked to temperature variability in cold environments (Moser et al., 2010; Li et al., 2016), but more closely associated with moisture conditions in warm environments. Huang et al. (2020) found that the onset of xylem formation in northern Hemisphere conifers was triggered by photoperiod and temperature. In contrast, the relationship between cambial activity and climate variables in tropical regions were species- and site-specific, being mostly influenced by rainfall, relative humidity, and soil moisture (Pumijumnong & Wanyaphet, 2006; Buajan & Pumijumnong, 2012; Butz et al., 2017; Huang et al., 2018; Pumijumnong et al., 2019).

Due to the lack of clear tree-ring boundaries of most of tree species in tropical regions, investigations of tree growth and climate responses using traditional dendrochronological techniques are challenging. Recently, xylogenesis studies have been increasingly conducted in tropical areas to determine the onset and cessation of xylem formation

and its climate responses (Volland-Voigt et al., 2011; Pumijumnong & Buajan, 2013; Wang & Hamzah, 2018). However, most studies in tropical and subtropical regions are located at higher elevations with cold-dry environments, or focus on coniferous species (Pumijumnong & Wanyaphet, 2006; Huang et al., 2018), while only a few studies focus on broad-leaved tree species (Buajan & Pumijumnong, 2012; Mendivelso et al., 2016; García-Cervigón et al., 2017; Pumijumnong et al., 2019). The combination of high-resolution dendrometer and microcoring methods can provide more accurate information on the intra-annual dynamics of stem growth and xylogenesis of tropical trees (Krepkowski et al., 2011; Cocozza et al., 2016; Mendivelso et al., 2016). Yet, there is lack of information on xylem formation of tropical tree species, and the combining structural (dendrometer) and functional (microcoring) approaches may shed more light on climate impacts of intra-annual stem growth and xylem formation of tropical trees.

Toona ciliata is a native species in South and Southeast Asia, and it is also an important timber species in tropical and subtropical regions worldwide (Orwa et al., 2009). *Toona ciliata* is one of the promising deciduous tree species growing in tropical climate that form distinct annual growth rings (Heinrich & Banks, 2005). Wood anatomical structure of *T. ciliata* is characterized by semi-ring porous with distinct growth ring boundaries defined by marginal parenchyma and large early wood vessels (Islam et al., 2018). Several studies on *T. ciliata* have established chronologies to detect long-term growth trends across tropical and subtropical forests in Asia and Australia (Vlam et al., 2014; Rahman et al., 2017; Shah & Mehrotra, 2017; Zuidema et al., 2020). Tree-ring studies showed that recent warming-induced drought could be the dominant factor causing the observed growth decline of *T. ciliata* in Bangladesh and India (Rahman et al., 2017; Shah & Mehrotra, 2017). Cambial cell layers of *T. ciliata* in the tropical forest of central Thailand was highest in March and number of cambial cell layers was correlated with precipitation and water availability (Pumijumnong & Buajan, 2013). However, little is known about the seasonal dynamics of stem radial growth and xylogenesis of *T. ciliata* and their responses to environmental conditions.

In the present study, we combined high-resolution point dendrometer and microcore sampling to investigate the intra-annual stem radial growth and xylem formation of *T. ciliata* during three consecutive years (2018–2020) at two study sites with similar climate but contrasting soil water availability (here after RAIN: tropical ravine rainforest, KARST: tropical karst forest) in southwestern China. We aimed 1) to quantify intra-annual dynamics of stem radial growth and xylogenesis of *T. ciliata* and to analyze its variability between ecologically contrasting sites and among years; 2) to detect the climatic factors that limit stem radial growth and xylem formation of *T. ciliata* under contrasting soil water availability. We hypothesized that 1) Stem radial growth and xylogenesis rates of *T. ciliata* growing in the tropical karst forest are lower than that in the tropical ravine rainforest with higher soil water availability; 2) Variation in intra-annual stem radial growth and xylogenesis was mainly correlated to seasonal patterns of precipitation and soil moisture availability, with stem radial growth and xylogenesis of *T. ciliata* growing at the karst site being more limited by moisture availability than that at the tropical ravine rainforest site. This study provides the information on seasonal dynamics of *T. ciliata* growth by combining structural (dendrometer) and functional (microcoring) approaches addressed the timing, magnitude, and climate drivers in tropical forests characterized by contrasting water availability.

2. Materials and methods

2.1. Study sites, climate and species

The study was conducted in Xishuangbanna prefecture, Yunnan province, south-west China. Xishuangbanna locates at the northern edge of tropical Asia and has mountainous topography. The climate of this region is influenced by warm and wet air masses from the Indian Ocean

during summer and by continental cold and dry air masses in winter. This results in a rainy season from May to October, and a dry season from November to April (Fig. 1). The dry season is divided into a foggy and cool-dry sub-season from November to February and a hot-dry sub-season from March to April (Cao et al., 2006). In Xishuangbanna tropical botanical garden (XTBG) (21.54 °N, 101.46 °E, 580 m a.s.l.), the long-term (1959–2017) annual mean temperature is 21.9°C, annual

maximum temperature is 29.7°C, the annual mean precipitation is 1473 mm, and annual mean relative humidity is 84.9% (Fig. S1).

In this study, two study sites were selected with contrasting soil water availability. The two sites are located at 13 km distance from each other. The tropical ravine rainforest site (RAIN; 21.58 °N, 101.09 °E, 922 m a.s.l.) is a seasonal rainforest on acid soils with clay-loamy texture. The tropical karst forest site (KARST; 21.54 °N, 101.16 °E,

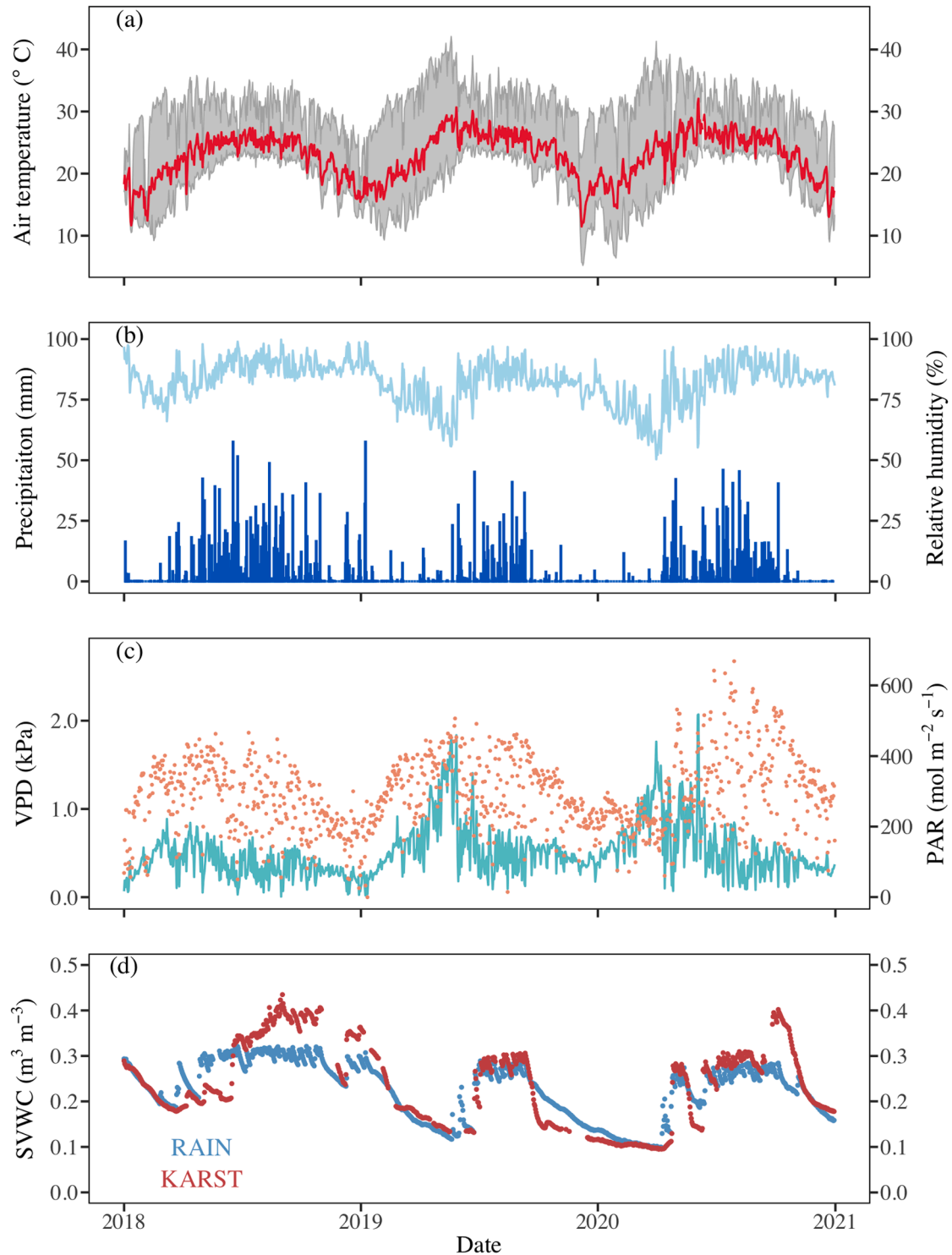


Fig. 1. Daily changes of (a) mean (red), minimum and maximum (grey shade) air temperatures, (b) precipitation (dark blue bars) and relative humidity (light blue line), (c) vapor pressure deficit (VPD, green line) and photosynthetic active radiation (PAR, brown points), and (d) soil volume water content (SVWC) at 40 cm soil depth at the ravine rainforest (RAIN, blue) and in the karst forest site (KARST, brick) in Xishuangbanna during 2018 to 2020.

602 m a.s.l.) is located on a limestone hill with shallow soils, silty-clay texture with more basic soil conditions and higher nutrient availability (Table S1). Generally, the KARST site is drier and has higher soil moisture variability than the RAIN site with higher soil water storage capacity (Fig. 1d). Compared with the karst forest (KARST), the ravine rainforest (RAIN) has a higher canopy cover and stem density (Fu et al., 2019).

In each site, five dominant *T. ciliata* trees were selected, and the height and diameter at breast height (DBH) of the trees was measured (Table 1). The mean height of the selected trees was 20.7 m and ranged from 14.7 m to 28 m, and the mean diameter at breast height was 34.5 cm and ranged from 21.5 cm to 55.7 cm. Individuals of *T. ciliata* at both study sites were leafless during late October and November for about one month, and then flushed new leaves during the dry-foggy season from December to January and showed maximum canopy cover during May to September in the rainy season. Individuals of *T. ciliata* at the karst forest site flushed leaves slightly earlier than those at the rainforest site.

2.2. Climate data

Daily climate data were obtained for the study period (2018–2020) from Xishuangbanna Station for Tropical Rain Forest Ecosystem Studies (21°55' N, 101°16' E, 560 m a.s.l.), which is ~10 km from the RAIN site and ~3 km from the KARST site. The climate variables include daily mean/minimum/maximum air temperature (Ta), precipitation (PRE), relative humidity (RH), wind speed (WS), photosynthetic active radiation (PAR). Vapor pressure deficit (VPD) was calculated from air temperature and relative humidity. Monthly means of long-term climate data (1959–2017) were also used for comparing with those of the three study years (Fig. S1). Two microclimate stations were equipped nearby each of the study sites and soil volume water content (SVWC, m³ m⁻³) at 20 and 40 cm soil depths were recorded at half-hour intervals (Fig. 1) and were averaged to daily means for further analyses.

Climate conditions differed among study years (Fig. 1), with year 2018 being wetter, while 2019 and 2020 were particularly hotter and drier than the long-term mean (1959–2017) (Fig. 1, Fig. S1). The year 2019 was the hottest and driest year during 2018–2020. The maximum temperature in 2019 was 6.6°C and 2.7°C higher than those in 2018 and 2020, respectively (Fig. 1a). Mean annual precipitation in 2019 was 44% and 69% of that in 2018 and 2020, respectively (Fig. 1b). The rainy season (the number of months with precipitation higher than 100 mm) of 2019 (from June to September) was two months shorter compared to 2018 (May to October) and three months shorter compared to 2020 (April to October) (Fig. S1). Air vapor pressure deficit (VPD) during the dry season of 2019–2020 was about twice as high as that in 2018 (Fig. 1c). Soil volumetric water content at 40 cm soil depth showed the same trend at both the ravine rainforest (RAIN) and the karst forest (KARST) sites (Fig. 1d). Due to the hot/dry conditions and the very short rainy season in 2019, the soil water contents at the two study sites were continuously decreasing from October of 2019 till April in 2020, with a deeper and faster drying trend at KARST site (Fig. 1d, Fig. S1).

Table 1

Site locations and characteristics of studying trees at the ravine rainforest (RAIN) and the karst forest (KARST) site in Xishuangbanna, southwest China.

Habitat	Site code	Latitude (°N)	Longitude (°E)	Elevation (m)	Tree ID	DBH (cm)	Height (m)	Tree age (year)
Rainforest	RAIN	21.58	101.09	922	T1	42.7	15	38
					T2	32	20.2	21
					T8	22.3	22	26
					T9	22.5	22.1	19
					T11	21.5	14.7	27
Karstforest	KARST	21.54	101.16	602	T1	52	28	33
					T2	55.7	28	86
					T4	37.4	20.7	31
					T5	31.7	17	49
					T11	27.1	19.3	35

2.3. Stem radial variations

For quantification of daily and seasonal patterns in stem radial growth, five trees at the RAIN site and four trees at the KARST site were equipped with automatic high-resolution point dendrometers with a resolution of 2 µm (DRW type, Ecomatik, Germany). To minimize the influence of water related to hygroscopic expansion and shrinkage, the outermost dead layer of the bark was removed. Stem radial changes were recorded at 10-min intervals by a data logger (DL15, HOBO, U.S.A) and regularly checked for random erroneous measurements (e.g., battery voltage discharge, physical damage by animals). Dendrometer data were recorded for three continuous years from January 2018 to December 2020.

2.4. Microcore sample collection and preparation

Wood microcores were extracted from each of the five *T. ciliata* trees at each site. Samples were taken around tree stems biweekly throughout three continuous years (2018–2020) using a Trephor microborer (Rossi et al., 2006a). At or above 1.3 m height, the outer bark was firstly removed and microcores (2 mm in diameter and 1.5 cm long) were extracted. Wood microcores with intact cambium were rotated out and immersed in Eppendorf microtubes in 50% ethanol and stored at 5°C to avoid tissue deterioration (Rossi et al., 2006b). In the laboratory, the microcore samples were dehydrated with grading ethanol and D-limonene, and successive immersion in liquid paraffin, then embedded in paraffin blocks (Rossi et al., 2006a). The sample blocks were cut in cross section with a thickness of 14–20 µm with a rotary microtome (Leica RM2245, Germany) and fixed to microscope slides. The sample slides were stained with 1% safranin for two hours and then stained with 0.5% Astra blue for one minute (Moser et al., 2010). Finally, the stained samples were mounted in EUKITT mounting medium (ORSAtec, Germany).

To investigate intra-annual xylem formation, cross-sections were observed and photographed at 100–500 × magnification with a digital camera mounted on a light microscope (DM2500, Leica). Visible and polarized light was applied to distinguish the xylem differentiation phases. In the cross sections, the cambial cells were represented by several layers of narrow thin-walled cells. The enlarging cells (vessels, fibers, and axial parenchyma) were characterized by thin primary cell walls with diameter at least twice of a cambial cell (Cufar et al., 2008). Under polarized light, enlarging cells appeared non-bright, while cells in the wall-thickening stage appeared bright and showed bi-colored (blue to red) cell walls. The mature cells showed red colored cell walls indicating complete lignification of the secondary cell walls (Fig. S2). For each section, thicknesses of the cambial zone, enlarging zone, wall thickening zone and mature zone were measured along three radial profiles using ImageJ software (ver. 1.50, <http://rsb.info.nih.gov/ij/>).

2.5. Data analysis

2.5.1. Stem radial variation

All analyses and plots were made with R statistical software (version 3.6.5, R Core Team, 2020). The raw dendrometer data of each tree (10-min resolution) were time-aligned, and erroneous shifts and jumps were detected and corrected by 'treenetproc' package (Knüsel et al., 2021) and manually corrected by 'dendRoAnalyst' package (Aryal et al., 2020). The corrected dendrometer measurements were further decomposed into an estimate of growth-induced irreversible stem increment (GRO) and an estimate of tree water deficit-induced reversible shrinkage and swelling of the stem (TWD), based on the 'zero-growth' concept which assumes no growth during periods of stem shrinkage (Zweifel et al., 2016). The accumulative growth (GRO) increases in periods when the stem radius exceeds its previous maximum ($GRO > 0$), while stem shrinkage or expansion below this maximum was defined as periods of tree water deficit (TWD). The GRO and TWD values at 10-min intervals were extracted with the R-package 'treenetproc' (Knüsel et al., 2021), and daily sums of growth (GRO rate, mm d^{-1}) and daily minimum tree water deficit (TWD, mm) were calculated for all studied trees during 2018–2020.

To investigate the seasonal dynamics of stem radial growth, a Gompertz model (Eqn 1) was fitted to the daily means of accumulative stem radius variations for each tree and for each year (Rossi et al. 2003), as:

$$Y = Y_0 + A \exp\left[-e^{(\beta - kt)}\right] \quad (1)$$

where Y represents the daily average stem radius variation, Y_0 and A are the lower and upper asymptotes, β is the x-axis placement parameter, k is the rate of change parameter, and t is day of year (DOY). Consequently, $(A - Y_0)$ corresponds to the total seasonal growth whereas $(Y_t - Y_{t-1})$ corresponds to the growth rate (mm d^{-1}). Growth phenology parameters (i.e., start and stop day, maximum growth rate and growth duration) were predicted by the Gompertz models, with the 'nsl' function in R software (R Core Team, 2020). Days of growth initiation and cessation were determined when 10% and 90% of the total annual growth were attained (Oberhuber et al., 2014).

2.5.2. Cambial activity and xylem formation

The dynamics of cambial activity and changes in the xylem differentiation phases (i.e., enlarging cells, wall-thickening cell, and mature cells) were captured by generalized additive models (GAMs) (Cuny et al., 2013) following the equation (Eqn 2):

$$y = \alpha + s(dy) + \varepsilon \quad (2)$$

where y is the vector of the biweekly thickness in different zones (cambial, enlarging, wall-thickening, mature), dy is the corresponding day of the year, s represents the cubic regression spline used for smoothing, α is the intercept, and ε is the error term. For each zone, we fitted GAMs for the mean values from five trees of each site and each year.

2.5.3. Climate-growth relationships

To investigate the influences of climate variables on stem radius increments, site-specific linear mixed-effects models were built separately, by taking the weekly sums of growth-induced stem increment (GRO rate) as dependent variable and weekly means of climate variables as fixed factors, and the individual trees nested with years (2018–2020) as random factors. We added an autoregressive term corAR1 to account for temporal autocorrelation. We calculated variance inflation factors (VIF) of the climate variables and excluded those with high collinearity according to the threshold of VIF values higher than 3.0. Firstly, we built a full model including the climate variables of air mean temperature (T_a), precipitation (PRE), relative humidity (RH), photosynthetic active radiation (PAR), wind speed (WS) and soil volume water content

(SVWC) at 40 cm soil depth. The values of GRO rate, PRE and SVWD were log-transformed to fit the normal distribution. Secondly, we performed model comparisons and selected the best model according to the lowest value of Akaike's information criterion (AIC).

To investigate the influences of climate factors on xylem formation, we built linear mixed-effects models by taking the biweekly-measured thickness of different xylem layers (log-transformed) as dependent variable and concurrent means (sums for precipitation) of climate factors as independent variable, and individual trees nested with years as random factor. All explanatory variables were scaled to their mean to improve model convergence and allow coefficient comparison. Linear mixed-effects models were performed with the R-package 'nlme' (Zuur et al., 2009).

3. Results

3.1. Seasonal variation of stem radial growth

Stem radial variation of *Toona ciliata* showed distinct seasonal patterns at different sites and years (Fig. 2, 3). In the RAIN site, the cumulative daily stem radius variation showed similar seasonal patterns but different absolute growth for different individuals and in different years. Stem radial growth started in March and ended in October (Fig. 2a), with highest growth rates occurring during May to August. In the KARST site, trees started growing at the beginning of February and ended during August or October, showing high variations among individuals and different years (Fig. 3a).

Monthly accumulated stem growth rate (GRO rate) of *T. ciliata* was higher at RAIN site than at KARST site, especially during the rainy season (Fig. 2b, Fig. 3b). The periods of high growth rates mainly concentrated during the rainy season from May to August, simultaneously with periods of low tree water deficit (TWD) (Fig. 2c, Fig. 3c). High monthly growth rates were also observed during the relatively wet months in March–April 2018 (1.28 ± 0.49 mm in RAIN and 0.75 ± 0.30 mm in KARST). High tree water deficit (TWD) was observed at RAIN site during the dry-to-wet transition and during the late growing season in 2019, and persisted until June 2020 (Fig. 2c). In contrast, high TWD in KARST site was observed in early 2019 and 2020, indicating that trees were suffering from severe water stress during these periods (Fig. 3c).

During the study period, we also observed site- and year-specific stem growth phenology (i.e., start day, stop day, and duration) (Fig. 4). Results from Gompertz models showed that *T. ciliata* trees in the ravine forest site (RAIN) generally had higher annual and maximum growth rates than those in the karst forest site (KARST), except in 2020 (Fig. 4a, b). *Toona ciliata* trees at the KARST site was characterized by an earlier start and end of growth, but by a shorter growth duration as compared with trees at the ravine rainforest site, except in 2020 (Fig. 4c, d). During the drier years 2019 and 2020, trees at KARST site stopped growing significantly earlier than trees at RAIN site ($p < 0.05$) (Fig. 4d).

3.2. Intra-annual xylem formation

Intra-annual dynamics of xylogenesis of *T. ciliata* during three consecutive years revealed similar patterns of xylogenesis phases between the ravine rainforest (RAIN) and the karst forest site (KARST) (Fig. 5, Fig. 6). Except the extreme year 2019, the thickness of the wall thickening zone of *T. ciliata* trees at RAIN site was greater than of trees at the karst forest site (KARST) (Fig. 5c, Fig. 6c). At both RAIN and KARST sites, the enlarging and wall-thickening phases captured by generalized additive models (GAMs) showed bell-shaped curves, which were skewed to the early growing season from March to June (Fig. 5b, c; Fig. 6b, c; Table S2). The cambial zone was wider and kept active for a longer period in the wet year 2018 than in the drier years 2019–2020 (Fig. 5a, Fig. 6a).

The cumulative xylem thickness of each xylogenesis phase simulated by GAMs reflected the differences of rates and durations of different

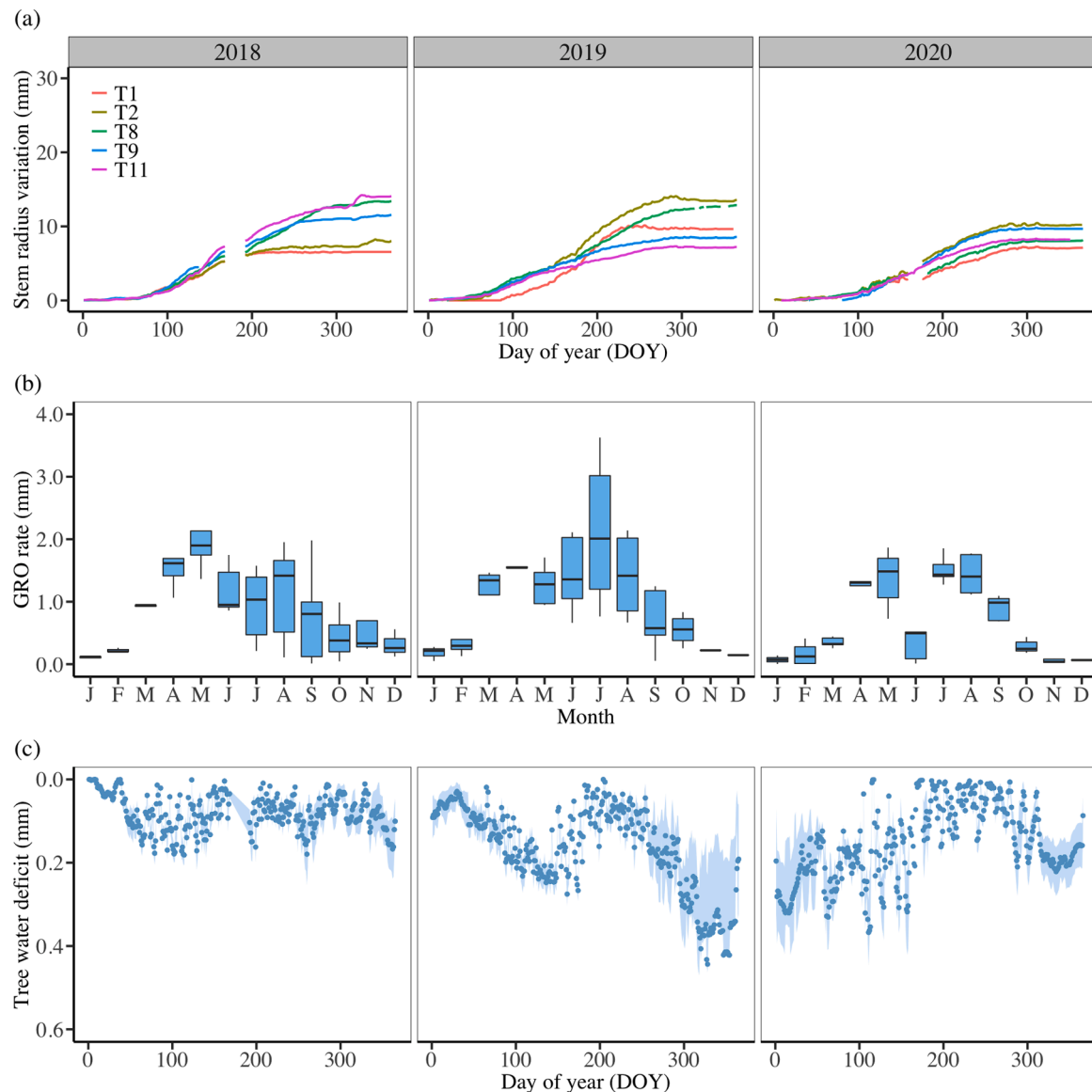


Fig. 2. (a) Cumulative daily mean stem radius variations (mm), (b) monthly boxplots of daily sums of growth-induced irreversible stem expansion (GRO rate, mm), and (c) daily minimum tree water deficit (TWD, mm) of *Toona ciliata* during 2018–2020 at the ravine rainforest (RAIN) site in Xishuangbanna. Different colors in (a) indicate different trees. Shaded area in (c) represents standard deviation.

phases among sites and years (Fig. 7, Fig. S3). *Toona ciliata* at the ravine rainforest site (RAIN) showed higher rates of xylem productivity with longer duration of each phase of xylem formation in 2018 and 2020, as compared with year 2019 (Fig. 7a, Fig. S2a). Trees at the karst forest site (KARST) showed lower rates and shorter duration of cell enlarging and cell wall thickening phases compared the rainforest site (RAIN).

Toona ciliata trees at the karst forest site (KARST) showed earlier onset and cessation of cell enlarging and wall-thickening phases than trees at the ravine rainforest site (RAIN) (Fig. 7b, Fig. S4). At the karst forest site, the onset of cell enlargement of *T. ciliata* appeared two to four weeks earlier than that at the rainforest site (Fig. S3, Fig. S4). Cell wall thickening of *T. ciliata* at the karst forest site started two to three weeks earlier than those at the rainforest site (Fig. S4). The duration for the cell enlargement at the karst forest site was one to two months shorter than that at the ravine rainforest site.

3.3. Stem growth responses to climate factors

We used linear mixed-effects models to investigate the climatic

influences on stem radius increments of *T. ciliata* over the study period (2018–2020) at two sites. Weekly sum of growth-induced irreversible stem expansion (GRO rate) was regressed with the weekly means (sums for precipitation) of multiple climate variables. The best-fitted models included positive effects of precipitation but negative effects of soil volumetric water content (SVWC) on weekly sum of GRO rate at both sites (Table 2, Fig. S5). At the ravine rainforest site (RAIN), air mean temperature also had a positive effect, while wind speed had a negative effect on weekly stem growth. At karst forest site (KARST), precipitation and relative humidity showed a positive effect, while photosynthetic active radiation showed a negative effect on stem radial growth of *T. ciliata* (Table 2, Fig. S5).

Linear mixed-effects models were built independently to investigate the effects of climate variables on the variations of the thickness of xylogenesis phases (enlarging, wall-thickening) (Fig. 8). Overall, precipitation and soil moisture availability had a positive effect for cell wall thickening of *T. ciliata* trees at both sites. Precipitation had a positive effect on the thickness of enlarging zone, but only statistically significant at the karst forest site (Fig. 8a, b). The thickness of wall-thickening zone

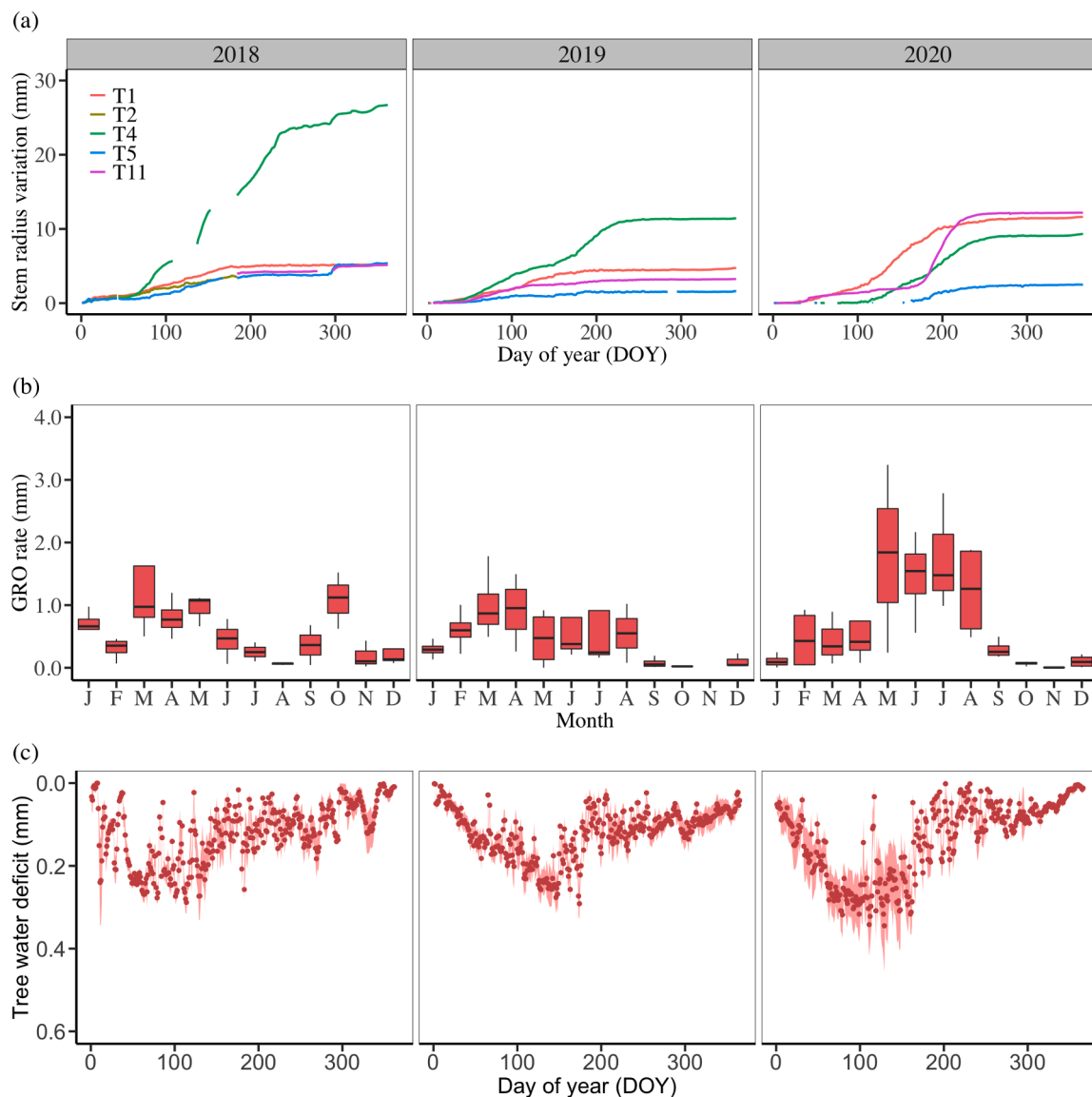


Fig. 3. (a) Cumulative daily mean stem radius variations (mm), (b) monthly boxplots of daily sums of growth-induced irreversible stem expansion (GRO rate, mm) and (c) daily tree water deficit (TWD, mm) of *Toona ciliata* during 2018–2020 at the karst forest site (KARST) in Xishuangbanna. Different colors in (a) indicate different trees. Shaded area in (c) represents standard deviation.

at the ravine rainforest site (RAIN) showed a significant positive correlation with minimum temperature, precipitation, relative humidity, and SVWC (Fig. 8a). Similarly, the thicknesses of wall-thickening zone at the karst forest site (KARST) were significantly correlated with precipitation (Fig. 8b).

4. Discussion

Our study provides the first estimates of the seasonal dynamics of stem radial growth and xylogenesis of *Toona ciliata* and their responses to environmental conditions in Asian tropical forests. The combined high-resolution point dendrometer and microcoring observations revealed distinct seasonal patterns of intra-annual growth of *T. ciliata* at different sites and years, with stem radial growth mainly occurring during March to October (Fig. 2, 3, 4). The start day of stem radial growth coincided with the occurrence of cell enlarging phase, and its end day occurred concomitantly with the cessation of cell enlarging. Individuals of *T. ciliata* at the wetter ravine rainforest site showed higher annual stem radial increment, higher growth rates, and longer durations

of xylem productivity than the drier karst forest site (Fig. 5, 6, 7). *Toona ciliata* at the karst forest showed higher resilience after the extreme drought events during late 2019 to early 2020 compared to the ravine rainforest site.

4.1. Intra-annual stem radial variations and xylem formation

The stem radial growth of *T. ciliata* mainly occurred during March to October (Fig. 2, 3). The start day of stem radial growth coincided with the occurrence of cell enlarging phase during early spring, and its end time occurred concomitantly with the cessation of cell enlarging (Fig. 4c-d, Fig. S4). Pumijumnong & Buajan (2013) found that *T. ciliata* in central Thailand had highest number of cambial cells in March. Since the monsoon season starts in May in tropical Asia, the radial growth of *T. ciliata* will be limited by the dry season moisture availability, which was also confirmed by long term tree-ring studies (Vlam et al., 2014; Rahman et al., 2017). The turgor-driven cell enlargement process might be primarily affected by water availability coupled with plant's hormones (De Micco et al., 2019), and cell wall-thickening phase was more

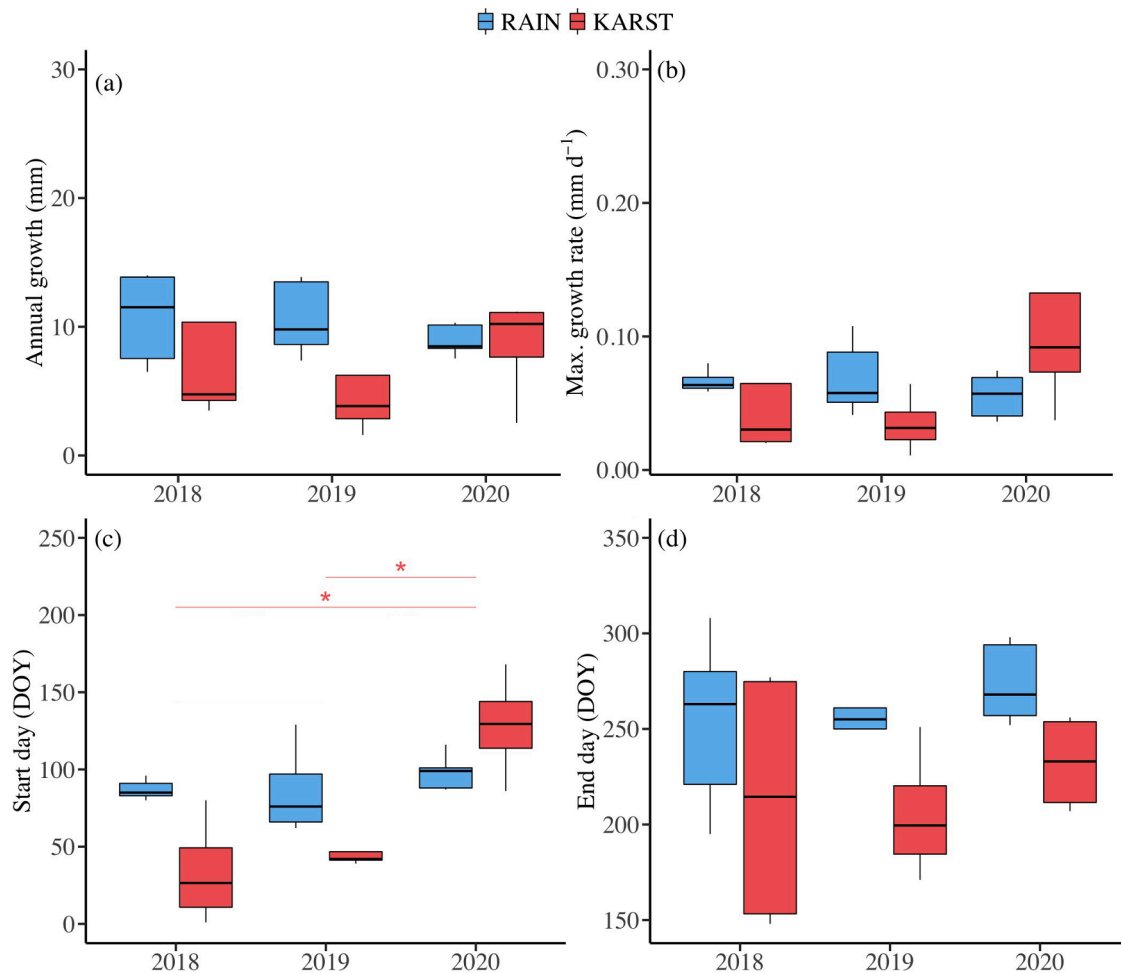


Fig. 4. Boxplots of (a) annual growth (mm), (b) maximum growth rate (mm d⁻¹), (c) start day of growth (DOY) and (d) cessation day of growth (DOY) of *Toona ciliata* for three years (2018–2020) at the ravine rainforest (RAIN, blue) and the karst forest (KARST, red) sites at Xishuangbanna. The growth phenology parameters were predicted by the Gompertz models fitted on daily mean stem radius variations. Differences between two sites were tested via paired *t*-test (black bracket) and pairwise comparisons between each site among three years (straight line), * significant difference at $P < 0.05$ level.

related to the availability of carbohydrates (i.e., photosynthesis) (Cuny et al., 2015). The occurrence of leaf flushing and radial growth of tree species from two south America tropical dry forests in wet season reflecting the influence a positive water balance and low vapor pressure deficit on the development of new leaves and xylem cells (Mendivelso et al., 2016).

In drought year 2019, the cumulative xylem thickness was reduced compared with the normal year 2018. Moreover, the cessation of cell enlargement and cell-wall thickening occurred earlier in 2019 due to low soil water availability, especially in drier site (Fig. 7, Fig. S3). Water stress triggered an earlier stop of xylem formation under a Mediterranean climate (Vieira et al., 2014). In semi-arid China, summer drought inhibited cambial activity and reduced xylogenesis with formed intra-annual density fluctuations (Gao et al. 2021). The duration of cell enlargement played an important role in determining cell size (Gao et al., 2021), whereas the cessation of xylem formation appears to be more dependent on temperature in a sub-Mediterranean ring-porous oak (Guada et al., 2020). Due to low soil water availability in the spring of year 2020, the radial growth of *T. ciliata* in both sites started during late April to early May, which was much latter compared with the year 2019. Here, we highlight that the intra-annual fluctuations in tree water deficit as a driver of annual tropical tree growth through impacts on both the rate of growth and the duration of the growth season.

4.2. Combination of dendrometer and microcoring approaches

This study combined both dendrometer and microcoring approaches to address the timing, magnitude of *T. ciliata* stem radial growth and its climate drivers in tropical forests with contrasting water availability. The annual stem radial growth detected by dendrometer method was approximate 2 mm higher than the cumulative xylem thickness that detected by microcoring method (Fig. 4, Fig. 7). Since dendrometer measurement contain signals of both xylem/phloem growth and tree water status, it's difficult to quantify the contribution of xylem and phloem to the stem variation. However, compared with the annual xylem increment, the phloem growth is much smaller (Yu et al., 2021). Diurnal fluctuations in phloem was also found to played a less important role than that of xylem for total stem radial change (Zweifel et al., 2014).

The growth cessation date detected by the dendrometer method for *T. ciliata* was one-month earlier than the cessation date of cell-wall thickening detected using the microcoring method (Fig. 4, Fig. 7). Since there is no detectable change of the stem radial in cell wall-thickening phase, the growth cessation date detected by dendrometer method would be expected earlier than that by microcoring method. The start day of radial growth in *T. ciliata* determined from the dendrometer method in 2020 was during later April to May (Fig. 4), although cell enlarging phase already started in January (Fig. S4). That's because severely water deficit in the spring of 2020 caused strong shrinkage of stem of *T. ciliata*. Mendivelso et al. (2016) also confirmed that

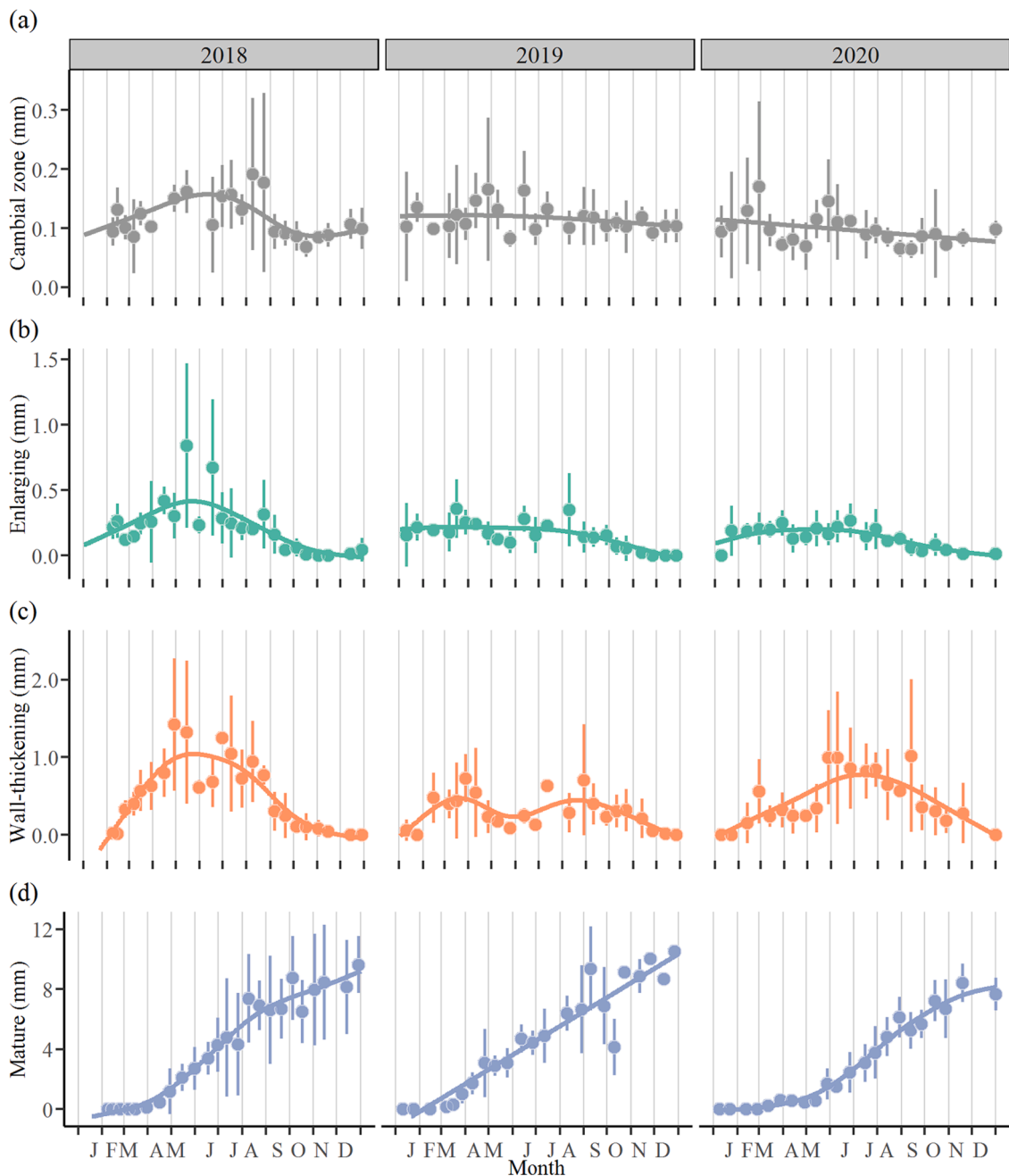


Fig. 5. Thickness of the cambial cell zone (a, mm), enlarging cell zone (b, mm), wall thickening cell zone (c, mm) and mature cell zone (d, mm) of *Toona ciliata* during 2018–2020 at the ravine rainforest site (RAIN) in Xishuangbanna. Points and vertical bars represent means and standard deviations from five trees. Lines represent the prediction of generalized additive models (GAMs) on the means.

dendrometer did not capture the actual xylem growth detected by microcore, especially in the drier forest. The high resolution dendrometer can capture the stem radial change at hourly to daily scale, however, by using xylogenesis method, we can more precisely capture the xylem growth process. Thus, both the dendrometer and xylogenesis are needed to monitor the growth dynamics of tropical tree species (Cocoza et al. 2016; Mendivelso et al. 2016).

4.3. Climate determinants of radial growth and xylem formation

Weekly accumulative stem radius increment of *T. ciliata* trees at the karst forest site was positively correlated to weekly mean relative humidity and sums of rainfall (Table 2, Fig. S5). Hu & Fan (2016) found that daily radial growth of tree species growing at a nearby karst habitat

was primarily influenced by moisture availability. Stem increments and xylem growth of trees in Ecuadorian tropical dry forest were clearly coupled with rainfall seasonality, although temperature effects were also detected (García-Cervigón et al., 2017). Previous studies revealed that inter-annual tree growth in Asian tropical regions is sensitive to moisture (Vlam et al., 2014; Rahman et al., 2019), specially, inter-annual growth of *T. ciliata* was mainly limited by moisture availability during the dry-to-wet transition season (Rahman et al., 2017, 2019). Surprisingly, weekly stem growth rates were negatively related to soil volume water content at both sites (Table 2). This negative relationship might be due to the fact that root activity would be impaired under the over-wetting soil moisture induced by heavy rainfall in the rainy season (Tei & Sugimoto, 2018).

Precipitation and soil moisture availability played a positive effect

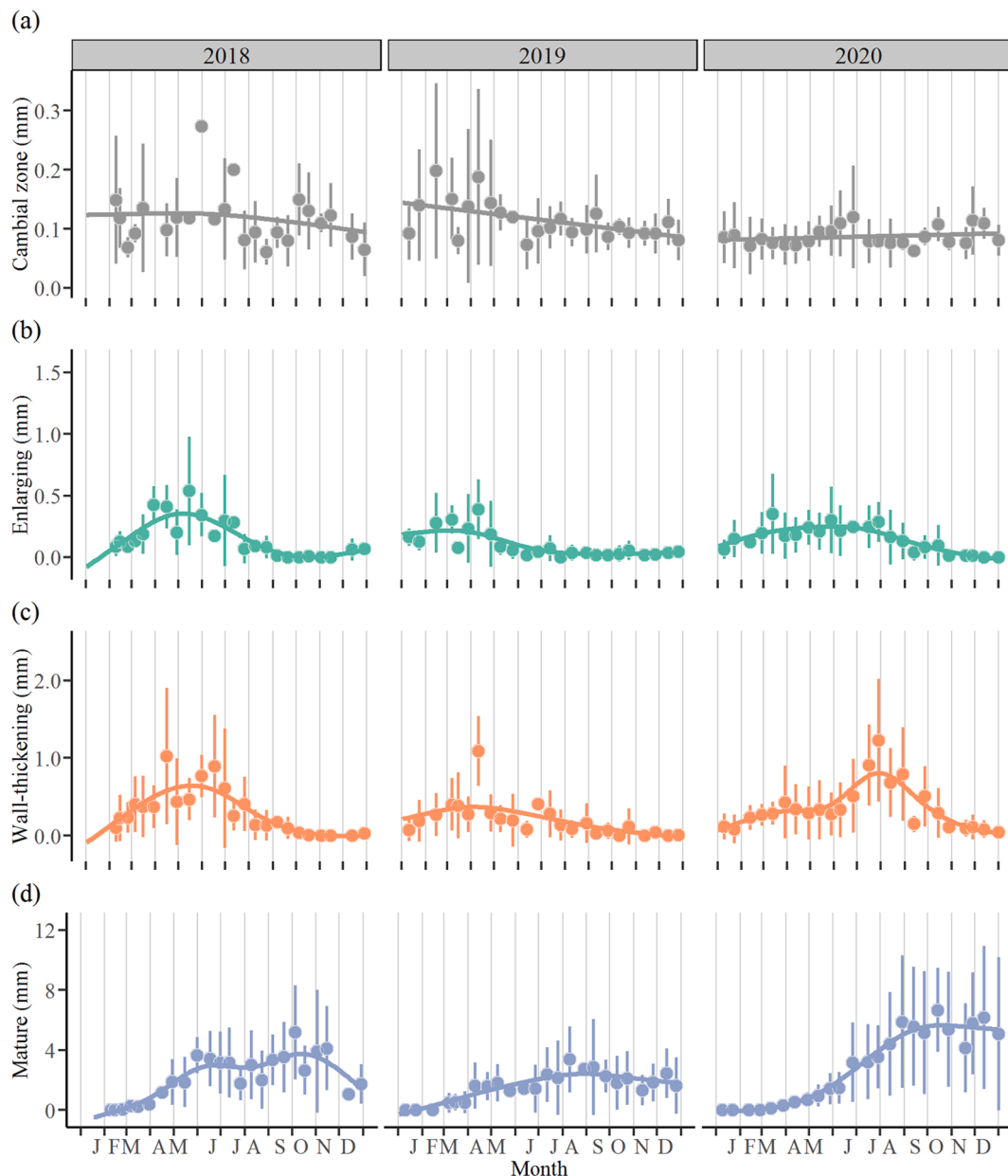


Fig. 6. Thickness of the cambial cell zone (a, mm), enlarging cell zone (b, mm), wall thickening cell zone (c, mm) and mature cell zone (d, mm) of *Toona ciliata* during 2018–2020 at the karst forest site (KARST) in Xishuangbanna. Points and vertical bars represent means and standard deviations from five trees. Lines represent the prediction of generalized additive models (GAMs) on the means.

for cell enlarging and cell wall-thickening of *T. ciliata* trees (Fig. 8). Rahman et al. (2019) found that precipitation was the dominant factor influencing the radial growth of four tropical hardwood species in Indonesia, and changes in the precipitation pattern had an apparent effect on cambial activity. Plasticity in xylem anatomical traits of two tropical species showed a significant correlation with mean accumulated precipitation during the summer season and mean temperature in December (Venegas-González et al., 2015). The studied of long-term hydraulic adjustment to global changes revealed that the xylem water transport capacity of *T. ciliata* was affected by both temperature and precipitation, but there is no significant correlations between hydraulic conductivity and radial growth (Islam et al., 2018). We found that multiple moisture related parameters were significantly and positively correlated with the cell wall thickening of *T. ciliata* in the ravine rainforest (Fig. 8). The cell wall thickening is related to the accumulation of carbohydrates of plants, thus our results indicated that the leaf photosynthetic rate of this tree species might be more sensitive to moisture

availability in the ravine rainforest than in karst forest. Our findings indicate that drought stress would advance and shorten the growing season, and thus has strong effects on growth and wood productivity of tropical trees.

4.4. Comparison between the ravine rainforest and karst habitat

Toona ciliata trees at the ravine rainforest site with higher soil water availability also showed higher annual stem increment, higher daily growth rates and xylem productivity than those of the karst forest site (Fig. 4a, b, Fig. 7). The lower radial growth in the karst forest site might be related to great tree water deficit at the end of the dry season. Soil at the karst habitat is comprised of higher proportions of clay, while the soil at the ravine rainforest is comprised by higher proportion of sand (Table S1). Although soil water content during the rainy season was similar at both sites, soil in the karst habitat became much drier during the dry season, especially in the extremely dry period from late 2019 to

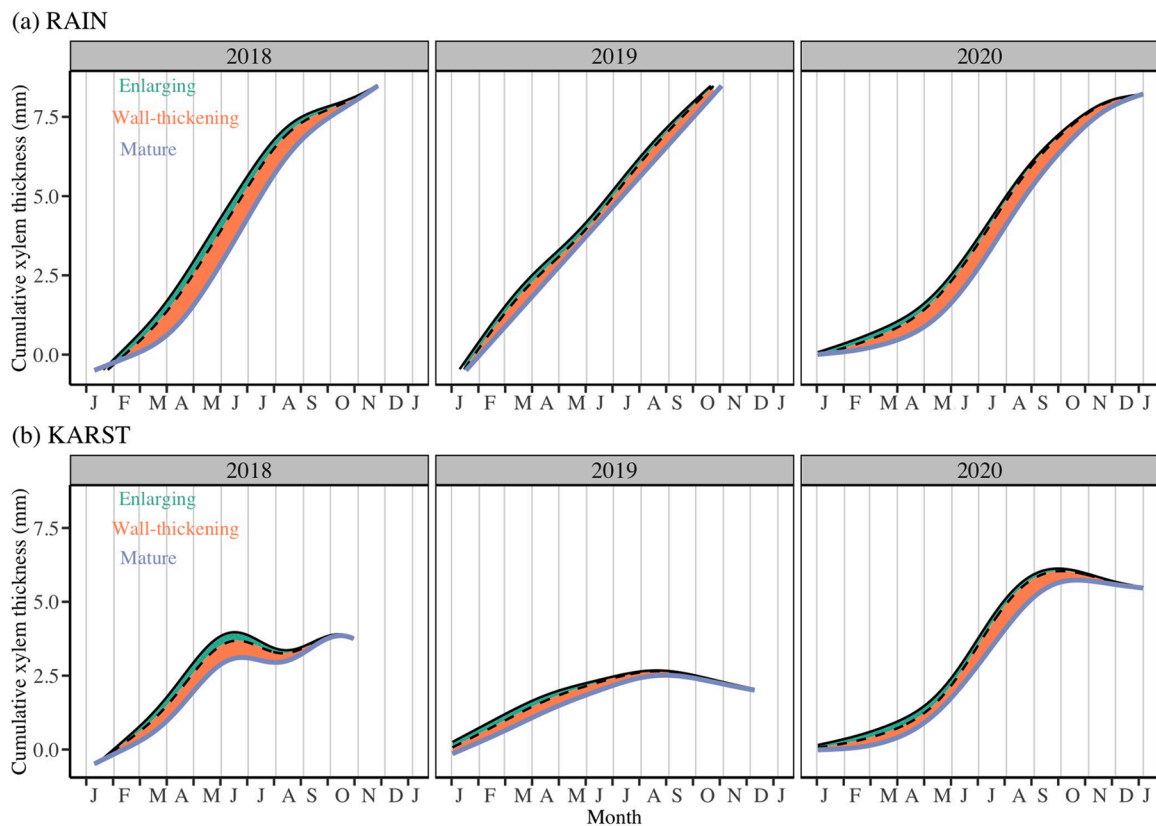


Fig. 7. Cumulative thicknesses of enlarging cell zone (green area), wall thickening cell zone (brown area) and mature cell zone (blue line) simulated by generalized additive models (GAMs) for *Toona ciliata* during 2018–2020 at the tropical ravine rainforest (a, RAIN) and the karst forest (b, KARST) sites in Xishuangbanna.

Table 2

Summary of linear mixed-effects models fitted to weekly sums of growth-induced stem increment (GRO rate) of *Toona ciliata* at the ravine rainforest (RAIN) and the karst forest (KARST) sites in southwestern China. We built models for each site with the GRO rate as dependent variable and climate variables as fixed factors and individual trees ($N=5$) nested within years ($N=3$, 2018–2020) as random factors. The climate variables of the full model are air temperature (T_a), precipitation (PRE), relative humidity (RH), photosynthetic active radiation (PAR), wind speed (WS) and soil volume water content (SVWC) at 40 cm soil depth. SE: standard error; CI: confidence interval; AIC: Akaike's information criterion; R_m^2 : marginal R^2 (variance explained by fixed factors along); R_c^2 : conditional R^2 (variance explained by both fixed and random factors).

Site	Climate variables	Estimates	SE	CI	p value	df	AIC	R_m^2	R_c^2
RAIN	Intercept	4.93	0.07	4.80 – 5.07	<0.001	471	1278	0.283	0.283
	PRE	0.42	0.06	0.31 – 0.53	<0.001				
	T_a	0.51	0.08	0.35 – 0.67	<0.001				
	WS	-0.19	0.06	-0.30 – -0.07	0.002				
	SVWC	-0.24	0.07	-0.39 – -0.10	0.001				
	Intercept	4.51	0.27	3.97 – 5.04	<0.001	352	1034	0.097	0.201
KARST	PAR	-0.14	0.07	-0.28 – 0.01	0.065				
	PRE	0.28	0.08	0.13 – 0.44	<0.001				
	RH	0.33	0.11	0.12 – 0.55	0.002				
	SVWC	-0.22	0.11	-0.43 – -0.01	0.038				

middle 2020 (Fig. 1). The soil in the karst forest is thin and has a lower water storage capacity, so plants in the karst habitat experience periodic drought.

The lower radial growth rate in the karst forest could be related to a more conservative water use strategy. Plants in the karst forest tend to have higher water use efficiency and greater xylem cavitation resistance than those in the rainforest (Zhu et al., 2017; Fu et al. 2019). However, due to the higher drought tolerance of *T. ciliata* in the karst forest, the xylem growth was able to recover faster after the drought period in 2019 (Fig. 3, Fig. 6), whereas the radial growth of *T. ciliata* in the rainforest could not recover (Fig. 2, Fig. 5). Similarly, Aguirre-Gutiérrez et al. (2019) also found that drier tropical forests have an enhanced ability to adapt ecologically to a long-term drought. Thus, our study indicates that *T. ciliata* from drier sites have higher resilience against drought and that

enhanced drought occurrence in the future might especially affect wet rainforest sites.

Our study showed that the cell differentiation of *T. ciliata* trees at the karst forest site appeared two to four weeks earlier, but the duration was one to two months shorter than that at the ravine rainforest site (Figs. S3 and S4). The earlier onset of cell enlargement of *T. ciliata* at the karst forest could be due to better light conditions at the karst forest, since the canopy at the karst forest is more open than that of the ravine rainforest. The extreme dry event may also affect the start day of growth in the drought year 2019 and the end day of growth in both years 2019 and 2020. Especially at the drier karst forest site, the start day of growth in the climatic normal year 2018 were significantly earlier than that in the dry years 2019 and 2020 (Fig. 4). Moreover, the timings and duration of growth is also affected by age (Rossi et al., 2008; Köhl et al., 2017; Zeng

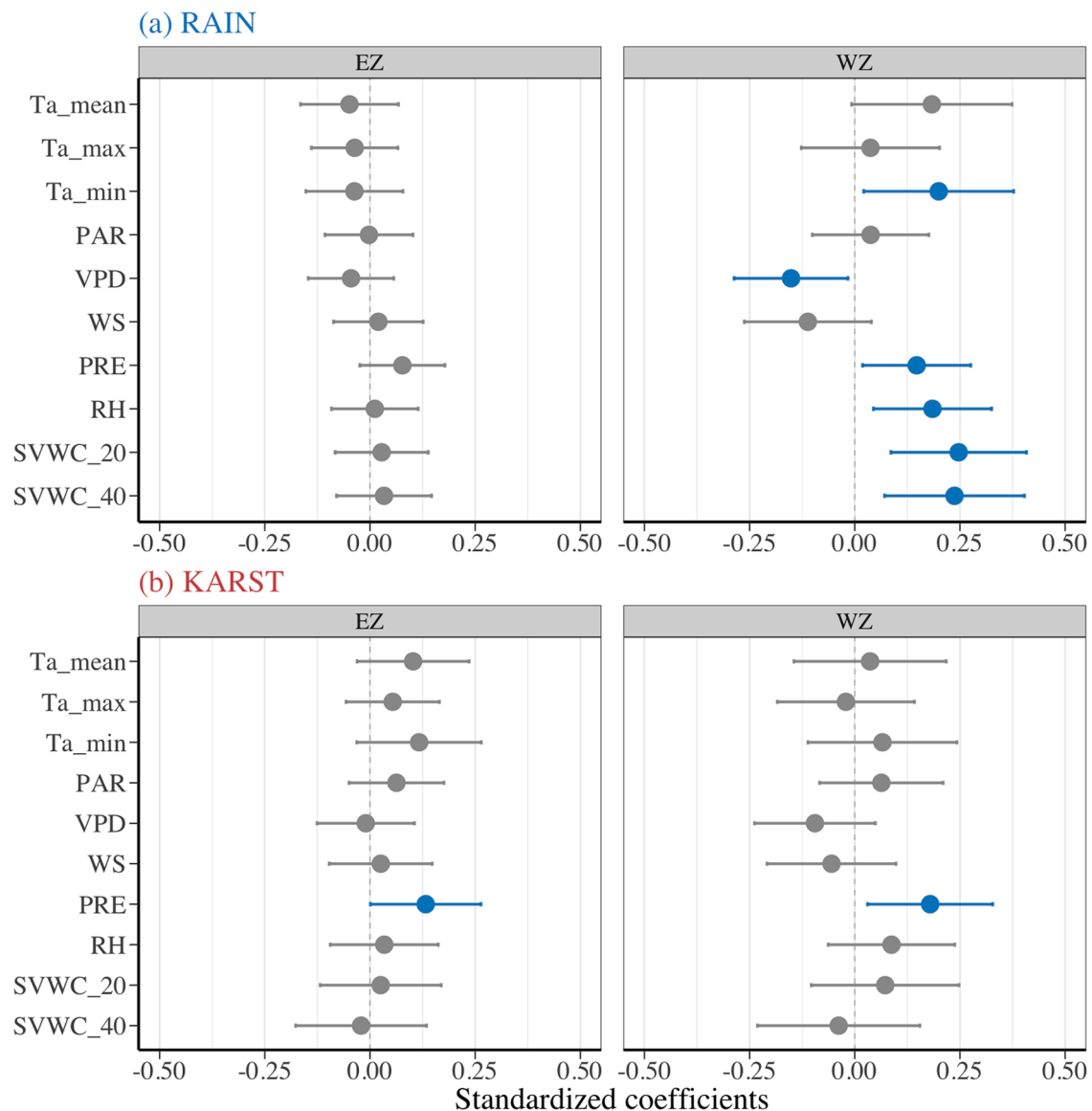


Fig. 8. Effects of climate variables on the biweekly variations of the thickness of the enlarging and wall-thickening phases of *Toona ciliata* in the ravine rainforest (a, RAIN) and the karst forest (b, KARST) sites in Xishuangbanna, south-west China. Linear mixed-effects models were built by taking the thickness of different layers (log-transformed) as dependent variable and biweekly means (sums for precipitation) of climate factors as independent variable, and individual trees as random factor. EZ, enlarging zone; WZ, wall-thickening zone. Climate variables before sampling date are T_a , mean air temperature ($^{\circ}\text{C}$); PAR, photosynthetic active radiation ($\text{mol m}^{-2} \text{s}^{-1}$); VPD, vapor pressure (k Pa); WS, wind speed (m s^{-1}); PRE, precipitation (mm); RH, relative humidity (%); SVWC_20/SVWC_40, soil volume water content ($\text{m}^3 \text{m}^{-3}$) at 20 cm/40 cm soil depth, respectively. Significant climatic variables are in blue.

et al., 2018) and size (Wang & Hamzah, 2018), which further results in differences in tree growth strategies. The differences in the age and size of the individuals of *T. ciliata* in our study may also affect the time and duration of stem radial growth and xylem formation.

Conclusions

To our knowledge, this is the first study to investigate the seasonal dynamics of radial growth and xylem formation for *T. ciliata*, a tree species with high dendrochronological potential in tropical Asia. *Toona ciliata* trees in the tropical ravine rainforest with high soil water availability had faster growth rates and xylem productivity compared to those on karst habitat with lower water availability. The combination of high resolution dendrometer and microcoring techniques over three continuous years revealed a distinct seasonal pattern of stem radial growth and xylogenesis of *T. ciliata*, with stem growth phenology (start day, end day, and duration) coincidence with xylogenesis phases. *Toona*

trees at the karst forest site showed earlier onset and cessation of cell enlarging and wall-thickening phases than those of the ravine rainforest site. Stem radius growth and xylem productivity of *T. ciliata* were mainly limited by precipitation, more so at the karst site with low soil water availability. Our study provides important insights into the seasonal growth dynamics and growth-climate relationships in tropical regions.

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.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:[10.1016/j.agrformet.2022.108906](https://doi.org/10.1016/j.agrformet.2022.108906).

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