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RELATIONSHIP OF CAMBIAL ACTIVITY AND XYLEM PRODUCTION IN TEAK (*TECTONA GRANDIS*) TO PHENOLOGY AND CLIMATIC VARIABLES IN NORTH-WESTERN THAILAND

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Seasonal cambial activity and xylem production were studied in teak trees (*Tectona grandis*) at Mae Sariang, Mae Hong Son Province, Thailand. Block samples were collected every month from October 2017 to October 2018 and from March to October 2019. Indicators of cambial activity and xylem production were correlated with climate factors. The number of cambial cell layers (CCL) was significantly and positively correlated with rainfall, relative humidity, temperature and soil moisture ($r = 0.730$, 0.515, 0.464 and 0.657, respectively). Both cambial zone width (CZW) and xylem differentiation zone width (Xydf) were significantly and positively correlated with rainfall, relative humidity and soil moisture (CZW: $r = 0.862$, 0.409 and 0.647, respectively; Xydf: $r = 0.747$, 0.436 and 0.556, respectively). Additionally, CCL was significantly and positively correlated with CZW and Xydf ($R^2 = 0.564$ and 0.740, respectively), and CZW was significantly and positively correlated with Xydf ($R^2 = 0.771$). Overall, in agreement with previous studies, the cambial activity of teak coincided with its leaf phenology; trees were active when new budding was occurring and dormant when leaves were falling. However, the cambial activity in this study started later, in accordance with the last rainfall. Indeed, rainfall in April was significantly and positively correlated with the ring-width index of teak, indicating that rainfall is the limiting factor that triggers cambial activation. The fluctuation in Asian monsoons appears to affect cambial activity, xylem productivity and ring width. This knowledge improves the understanding of the seasonal cambial activity of teak and provides useful data for teak plantation management in northwestern Thailand.

Keywords: Tropics, rainfall, xylogenesis, phenology, tree ring width

INTRODUCTION

The greatest biodiversity in the world is found in tropical rainforests, which cover 6% of earth's land surface, contain 80% of the world's biodiversity and produce 40% of earth's oxygen (Moran 1993). The tropics include the equator and parts of North America, South America, Africa, Asia and Australia which help to conserve and balance the ecosystem. Thailand is located in a tropical zone influenced by monsoons. The climate conditions in Thailand, particularly in northern Thailand, are divided into three seasons: 1) winter (November to February) which is influenced by north-eastern monsoons that bring cool and dry air from southern China to northern Thailand, 2) summer/pre-monsoon season (mid-February to May) when the weather gets warmer and 3) the rainy/wet season (mid-May to October) which is influenced by southwestern monsoons resulting in rainfall. During both the winter and summer seasons, the weather is dry. Each year, this sustained dry period results in annual ring formation in some deciduous tree species including teak (Pumijumnong 1995).

Numerous studies of tropical rainforests have focused on annual growth ring formation and cambial growth dynamics (Rao & Rajput 2001, Kempes et al. 2008, Kuang et al. 2008, Liu et al. 2009, Buajan & Pumijumnong 2012, Pumijumnong & Buajan 2013, Mendivelso et al. 2016, Rahman et al. 2019b, Kaewmano et al. 2022). Teak (*Tectona grandis*) trees measured at different sites in India during different periods of cambial activity have shown that climate conditions affect cambial activity (Rao & Dave 1981, Rao & Rajput 1999). Also, studies of teak on the Ivory Coast showed that cambial activity was related to monthly rainfall (Dié et al. 2012). Teak (*Tectona grandis*) is a plant species in the Lamiaceae family. It is naturally distributed in northern Thailand and is the dominant species in mixed deciduous forests (Kaosa-ard 1981). Teak is a hardwood and is economically significant in both the public and private sectors. The high quality of teak wood makes teak the most widely planted tree in many tropical countries, including Laos, Myanmar, Indonesia, India and countries in Africa and Latin America (Katwal 2003). Wood production is related to xylem productivity, with the amount of xylem produced differing each month. The quantity and quality of wood production also depend on the period of cambial activity. The amount of carbon accumulated in wood is related to the amount and quality of wood production (Locosselli 2018). For teak plantation management, knowledge of the factors that control teak growth, period of cambial activity and xylem production is crucial. Starting in 1994, Pumijumnong made the first studies of cambial activity in Thai teak from various sites, such as the Tak, Mae Hong Son, Lamphun and Lampang provinces. These studies noted that cambial activity started between the second week of April and the first week of May, and became inactive around the middle of October (Pumijumnong 1997). The study of cambial activity conducted in 1994 did not consider xylem differentiation zones, which can evaluate wood production. Additionally, knowledge regarding environmental effects on xylem cell differentiation of Thai teak remains lacking. Even twenty-five years later, no reports compared seasonal cambial activity and xylem production in Thai teak.

This study, therefore, investigates the ring-width chronology to monitor its response to climate factors in teak trees growing in the experimental site, and to investigate the seasonal cambial activity of teak, evaluating the relationships among cambial activity, xylem differentiation and climate factors such as rainfall, temperature and relative humidity, including soil moisture. This knowledge will improve the understanding of how seasonal cambial activity of teak changes with climate conditions and will be helpful for teak plantations in Thailand and other regions.

MATERIALS AND METHODS

Site description and climatic data

The study site is located in a teak forest plantation between 18º 10 N and 97º 55 E (altitude ~219 masl) in Mae Sariang district, Mae Hong Son Province, northwestern Thailand. The trees were planted approximately 100 years ago within an area of 150,000 m^2. The teak plantation borders a dipterocarp forest at an altitude of 390 m. The sampling period for the cambial activity study was from October 2017 to October 2019. Teak tissue samples were collected once a month, during the fourth week of each month, for the entire first year (October 2017 to October 2018), but only in the cambial activating period (March to October 2019) in the second year.

Meteorological data such as monthly rainfall, temperature and relative air humidity were obtained from the Mae Sariang meteorological station located approximately 1 km from the study site (Figure 1a, b). Total annual precipitation at the site is 1.153 mm, the annual mean temperature is 25.2 °C, and the annual mean relative humidity is 77% (60% between March and April, and 86% in August). The average maximum and minimum temperatures of the warmest and coldest months were 37.9 °C and 13.3 °C, respectively. These data are representative for the period of 1951–2019. Annually, the dry period occurs from November to March, and the wet period is from April to October. The area experiences a seasonal climate with high rainfall from April to October, mainly in August (Figure 1c). Soil moisture was detected every month using a TDR200 soil moisture meter.

Climatic conditions during the observation period

During the two years of observation and sample collection, it was noted that the rainfall in 2018 differed from 2019. The wet season in both years extended from May to October, and the dry season extended from November to April, but the total rainfall in the early rainy season was higher in 2018 than in 2019. In 2018, the maximum rainfall occurred in July, and the minimum rainfall was in February and March. In 2019, however, the rainfall peaked in August, and the minimum was in February, March and April (Figure 2). The variations in temperature and relative humidity were similar in both years. The

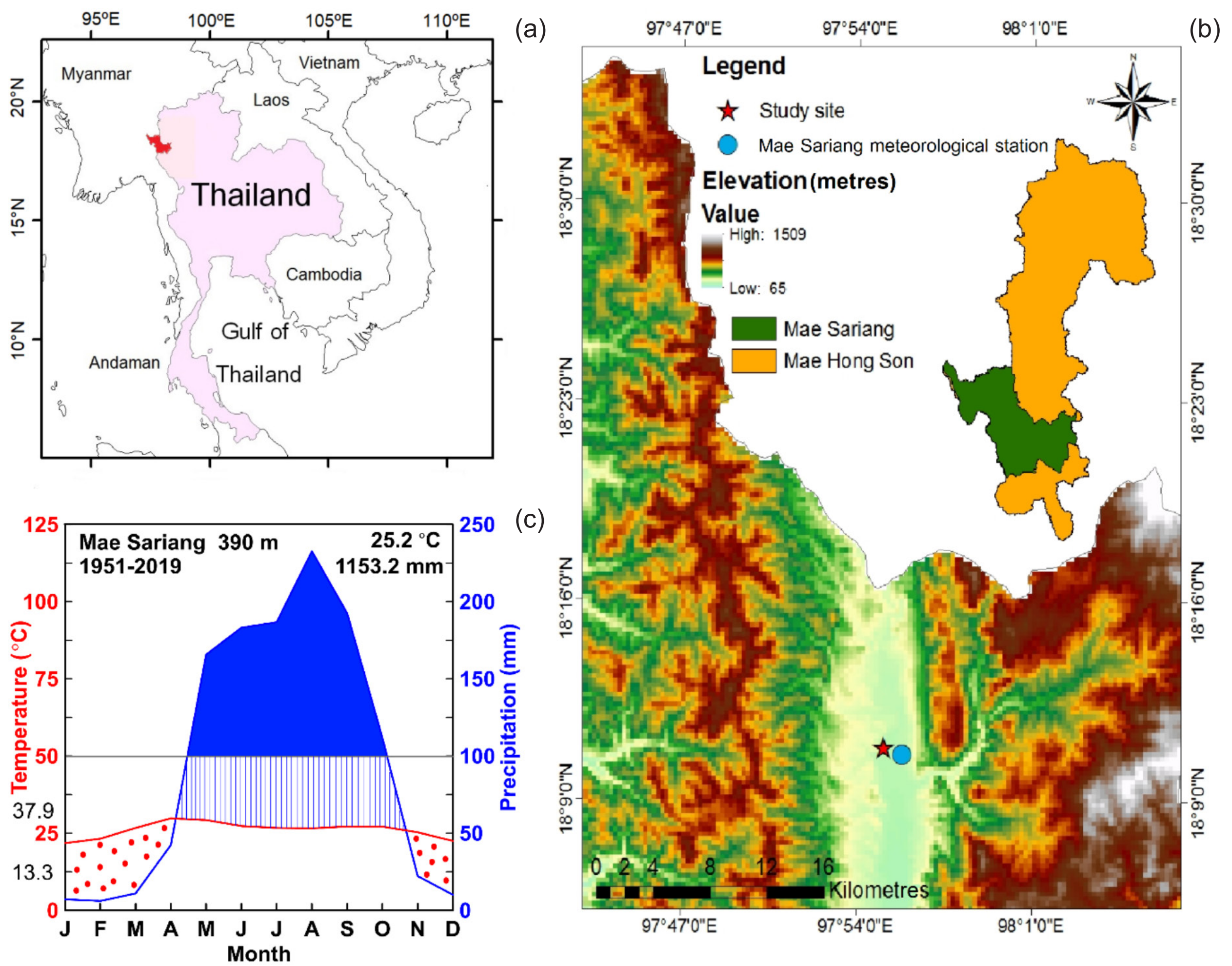

Figure 1 (a) Map of Thailand, with a red area indicating the Mae Sariang district, (b) the location of the study site and Mae Sariang meteorological station, (c) Walter and Lieth climate diagram (Walter & Lieth 1967) for the Mae Sariang meteorological station; the blue line indicates the precipitation curve, the red line indicates the temperature, the red dots indicate the dry period, blue stripes indicate the humid period and the blue area shows the super humid period; the average maximum temperature of the warmest month and the average minimum temperature of the coldest month are indicated on the left axis, the annual average temperature and annual total precipitation are shown in the upper right corner of the diagram, the climate data comprise measurements from 1951 to 2019

soil moisture was highest in July and August 2018 and lowest in April 2019. Overall, soil moisture levels were high during the wet season and low during the dry season (Figure 2).

Intra-annual sampling and phenological observations

Five teak trees with diameters of 73 – 83 cm were sampled. Each tree was approximately 100 years old (based on tree rings). Two blocks (1 cm^3) containing phloem, cambium and the outer xylem of the stem were collected from opposite sides of the trunk at the height of 1.30 m, using a cutter and chisel. The block samples were collected from the same tree every month from October 2017 to October 2018. In the second year, samples were not collected during the dormant period because the cambium was inactive, thus the samples were collected in the growing season from March to October 2019. The distance between block samples was approximately 10 cm, and they were collected in a zigzag pattern (Figure 3) to minimise the effects of the previous wounding. The collected specimens were immediately fixed in 3% glutaraldehyde. In the

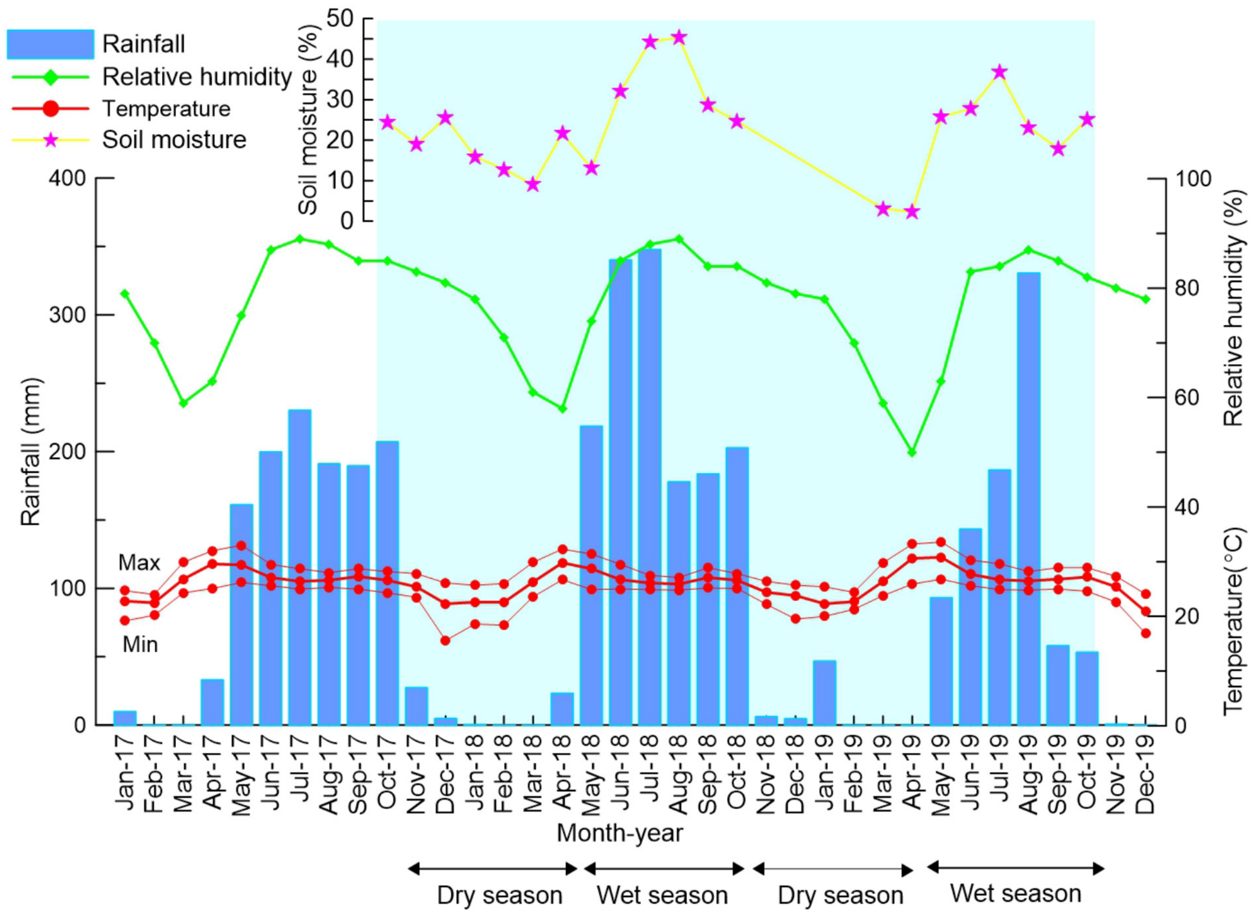

Figure 2 Soil moisture (%) observed during the study period (blue area), as well as the variation in climate data from the Mae Sariang meteorological station, including total monthly rainfall (mm), mean, maximum and minimum air temperatures (°C) and mean relative humidity (%)

laboratory, the specimens were washed in water and trimmed to 125 mm^3, then dehydrated in a graded ethanol series (10, 30, 50, 70, 90 and 99%). Polyethylene glycol 1500 was used for the embedding process, wherein specimens were embedded using stainless steel moulds and left in the freezer for at least 24 hours (Holtham & Slepecky 1995). Transverse sections were cut at a thickness of 15 µm with a rotary microtome using disposable blades. The phenology of xylogenesis was observed during the sample collection period.

Determination of cambial activity

For light microscopic observations of the cambial zone, specimen sections were stained with a 0.1% safranin O ($C_{20}H_{19}N_4$+Cl-) solution in distilled water for 5–10 min (or longer, depending upon the material) (Ma et al. 1993). After safranin O staining, sections were washed with distilled water and dehydrated in a graded ethanol series (10, 30, 50, 70, 90 and 99%) and then stained with 0.5% fast green FCF solution ($C_{37}H_{34}N_2O_{10}S_3Na_2$) in 95% ethanol for 5 min. After dehydration, the sections were passed through xylene and mounted in Permount™ mounting medium. The cambial zone width (µm), the number of cambial cell layers and xylem differentiating zone (µm) were observed under a light microscope at 40, 100, 400 and 600x magnification. The cambium zone, a thin layer of cambial cells that are rectangular during the dormant phase, varied seasonally. The number of cell layers in this time is species specific. The initial cambial cells start to divide during the trigger cycle, so the cambium zone during the active period is the zone of initial cells, including dividing cells that do not produce extension growth and secondary cell walls. In contrast, the xylem formation zone is a zone of xylem differentiation divided into expanding cells containing primary cell wall,

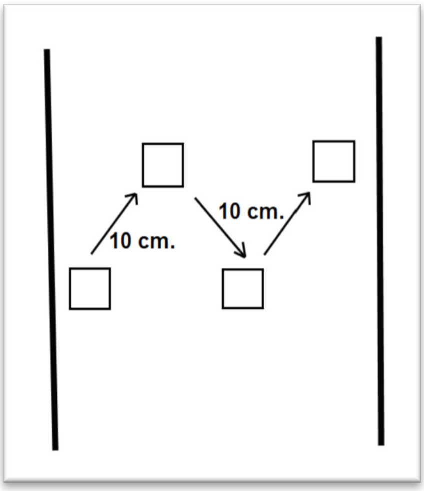

Figure 3 Cambial sampling diagram, showing the zigzag pattern of sampling used on one side of the tree

and development of secondary cell wall and its ignification (Larson 2012).

In this analysis, the cambial and xylem formation zones were determined by measuring the width of the cambial zone and the width of the first stage of xylem differentiation, which is the stage cambium cell changes to xylem cell and the primary wall is formed. Digital images were acquired using a Nikon D5100 camera connected with digiCamControl software version 2.1.0.0.

Measurements, counts and statistical analyses

The cambial zone width (CZW) and xylem differentiation zone width (Xydf) were measured, and the number of cambial cell layers (CCL) was counted. The mean and standard deviation values used to describe the range of variability were averaged from more than 20 random measurements per sample, using ImageJ software. Since samples were not collected during the dormant period of the second year, values applied to the dormancy period from November 2018 to February 2019 were the same data from November 2017 to February 2018. Pearson's correlation coefficients evaluated the correlations among the monthly average CZW, CCL, Xydf and mean monthly air temperature, mean relative humidity, total monthly rainfall and soil moisture. Correlations were calculated among the data from every tree and between both sides of each tree. One-way ANOVA was used to analyse the difference in cambial activity and Xydf among months, and multiple comparisons were performed with Tukey's posthoc test ($p < 0.05$). In the dendroclimatological study, the climate variables from the Mae Sariang meteorological station (monthly rainfall, mean, maximum and minimum temperatures, and relative humidity from 1951 to 2019) and gridded temperature/precipitation data from the Climate Research Unit (CRU TS4.03; http://cliexp.knmi.nl), including a self-calibrated Palmer drought severity index (scPDSI) that covered the study area (from 18–19 °N and 97–98 °E) with a resolution of 0.5° × 0.5°, were used for correlation analyses with the MSR index. All statistical analyses were performed using SPSS 16.0.

Terminology and definitions

The term 'cambial growth' refers to the cambial production of secondary xylem and phloem, as well as the formation, ongoing areal extension and preservation of the vascular cambium itself (Savidge 2001). A cambial cell is a part of the meristem (cambium) that generates wood (xylem) on the interior of the stem and bark (phloem) on the outside of the cambium during secondary growth of the stem of perennial woody plant species. The CCL are the layers of cambial cells that exist in both the dormant and active stages of the plant. The CZW is the width of the cambial zone, which is narrow while dormant and wide when active. Xylem differentiation zone is referred to as the cambial cell, which is differentiated to be xylem cell. It begins with a xylem precursor cell, which can differentiate into various cell types such as tracheary element, fibre and xylem axial parenchyma (Schuetz et al. 2013).

Tree-ring width sampling, measuring, cross-dating and tree-ring index development

Each of the forty teak trees that were used for dendrochronology had a straight trunk, good health and minimal traces of fire or other injuries. A total of 80 samples were collected using a 5-mm diameter increment borer. Core samples were collected in 2020 after the cambial activity investigation was completed. The core samples were dried and fixed on a wooden support and then polished using sandpaper to visualise the rings better. A digital moving stage joined with a stereomicroscope was used to measure ring widths, which were analysed using the TSAP-Win™ program (Rinn 2011). The ring-width series of each tree was checked, the actual dates were verified using the COFECHA® program (Holmes 1983), and then the ring widths of every tree were cross-dated. The ring-width index was generated from the cross-dated ring-width series using the ARSTAN program (Cook 1985, Cook & Krusic 2008). A negative exponential curve or linear regression was used to detrend the raw tree ring width series. The teak ring-width index in this study, referred to as the 'MSR index', represented the study site (Mae Sariang). The authenticity of the MSR index was qualified from the expressed population signal (EPS) and the mean interseries correlation (Rbar), which were computed over a 30-year window, with a 15-year lag period. The accepted EPS value should be greater than 0.85 (Wigley et al. 1984).

RESULTS

Teak leaf phenology

In association with data on teak phenology from a field guide to forest trees in northern Thailand (Gardner et al. 2000), the observations at Mae Sariang teak forest plantation during the sample collection period from October 2017 to 2019 showed that teak was deciduous during the dry season. Leaf fall started from mid-January to early February and lasted until late April (Table 1). Teak put new leaves in early May, which was the beginning of the wet season. The leaves matured from approximately June to October and continued to develop until the end of December. Flowering started between July and October, and the fruiting period covered two to three months, from December until January or February.

Seasonal changes in cambial zone morphology

Cambial cell layers (CCL)

The results of this study showed that the cambium was dormant from November to April, containing approximately four to five cambial cell layers. Xylem differentiating zone was not observed during the dormant period (Figure 4a). Activity in the cambium began around the beginning of May. In the cases where cambial activity was investigated at the end of April, the cambium was still dormant. In May, cambium cell division started. The CCL increased and became statistically similar to cambial activity at the end of the cambial activity period in September (Table 1). The CCL peaked in September 2018, with approximately eight to nine layers, and in July 2019, with approximately nine to ten layers (Figure 4b, c). The monthly CCL in 2018 was similar to 2019, with the highest values occurring during the wet season and the lowest during the dry season.

Cambial zone width (CZW)

The CZW was thinnest in December, and the CZW from November to February was significantly different from May to September. The CZW was thickest in July, which was the peak of the wet season (Figure 4b, c). The cambium was reactivated in May, and the CZW increased and became statistically similar to cambial activity at the end of October (Table 1). The cambial activity of each month is shown in the supplement data (Figure S1).

Seasonal changes in xylem production

Xylem differentiation zone width (Xydf)

After the formation in the cambium, the new xylem cells started to differentiate at the beginning of May in both 2018 and 2019. Differentiation was gradual, and peak xylem production covered a total period of six months (Table 1). The Xydf was widest in June and then gradually decreased until the end of October. There was no xylem differentiation zone in the

Table 1 Seasonal variation in cambial activity and xylem differentiation zone width, as well as seasonal phenological changes in teak at the Mae Sariang study site during October 2017–2019

Month-year(s) of sampling	Number of cambial cell layers	Cambial zone width (μm)	Xylem differentiation zone width (μm)	Seasonal phenological changes
Nov 17	5.74 ± 0.7^{b}	47.78 ± 3^{ab}	0	♠
Dec 17	4.98 ± 0.8^{ab}	42.74 ± 3^{a}	0	🍒 ♠
Jan 18	4.15 ± 0.4^{a}	46.06 ± 3^{a}	0	🍒
Feb 18	4.10 ± 0.3^{a}	51.10 ± 3^{ab}	0	🍒 🍂
Mar 18, 19	4.48 ± 0.2^{a}	44.78 ± 3^{a}	0	🍂
Apr 18, 19	5.06 ± 0.4^{ab}	43.96 ± 2^{a}	0	🍂
May 18, 19	7.40 ± 0.9^{c}	67.27 ± 3^{de}	191.35 ± 31^{b}	✤
Jun 18, 19	8.14 ± 0.5^{c}	72.69 ± 3^{e}	288.56 ± 70^{c}	♠
Jul 18, 19	8.26 ± 0.5^{c}	75.44 ± 4^{e}	244.01 ± 51^{bc}	❀ ♠
Aug 18, 19	8.46 ± 0.4^{c}	62.61 ± 2^{cd}	180.54 ± 33^{b}	❀ ♠
Sep 18, 19	8.02 ± 0.7^{c}	62.27 ± 7^{cd}	187.17 ± 80^{b}	❀ ♠
Oct 17, 19	5.94 ± 0.4^{b}	55.44 ± 3^{bc}	13.04 ± 13^{a}	❀ ♠
R^2	0.913	0.926	0.918	
F-ratio	45.256	49.093	49.102	
P	0.000	0.000	0.000	

Within each column, values followed by different letters are significantly different (mean ± S.D.), Tukey's HSD multiple comparisons ($p < 0.05$), ✤ budding, ♠ mature leaves, 🍂 leaf fall, ❀ flowering, 🍒 fruiting.

dry season (from November to April) when the cambium was not producing new cells (Table 1). The Xydf in June was significantly wider than that in October (Table 1), which was the end of each year's cambial activity period. The vessels first formed at the beginning of the differentiation of earlywood elements in May (Figure 4b) and continued to initiate, develop and begin lignification until the end of October. The vessels in earlywood were larger than the vessel in latewood. The xylem differentiating zone is shown in Figure 4c.

Relationship of cambial activity and xylem production with climate variables and soil moisture

A significant positive correlation was found between the current month of climate variables and the mean of CCL. However, the temperature was not significantly correlated with themean of CZW or Xydf (Table 2). The temperature of previous months was significantly and positively correlated with the mean of CCL, CZW and Xydf.

Teak ring width chronology

A total of 74 core samples from 38 trees were cross-dated, and a 111-years-long chronology of teak was generated. The chronology referred to as the 'MSR index' covered the period from 1908 to 2019 (Figure 5). The tree-ring series of the oldest tree was 113 years long, and the youngest tree contained 41 tree-rings. The EPS and Rbar ranged from 0.93–0.97 and 0.26–0.50, respectively. The EPS of the MSR index was higher than 0.85, indicating that the index is reliable (Table 3) (Wigley et al. 1984).

Climate growth response

The MSR index was significantly and positively correlated with the local climate (Mae Sariang station), including the amount of rainfall in April ($r = 0.305$, $p < 0.05$) and relative humidity in May ($r = 0.424$, $p < 0.01$). In contrast, the MSR index was significantly and negatively correlated with the mean temperature in May and September ($r = -0.382$, $p < 0.01$ and $r = -0.253$, $p < 0.05$, respectively), maximum temperature in May

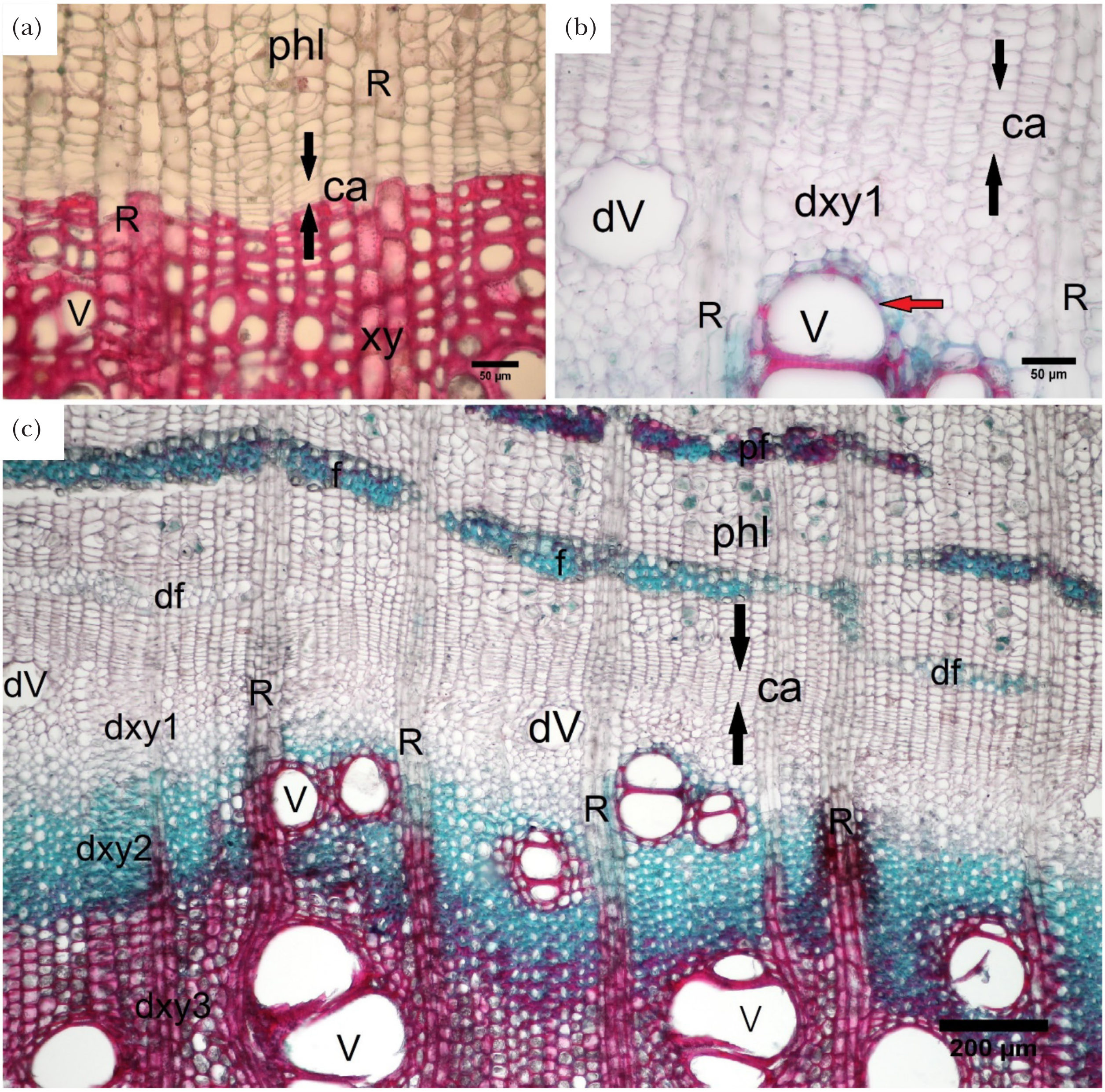

Figure 4 The seasonal cambial activity of teak in the Mae Sariang teak forest plantation; (a) cambial sample from February 2018 showing that the cambium was still dormant, (b) and (c) samples from July 2019 showing that the cambia were active and that the xylem was differentiating; the black arrows indicate the cambial zone, and the red area in (b) highlighted by the red arrow shows the vessel cell wall lignification; ca = cambium, phl = phloem, xy = xylem, V = vessel, dV = developing vessel, f = fibre, df = developing fibre, pf = fibre bands of phloem from the previous year, R = ray, dxy1 = xylem differentiation zone of the primary cell wall development and expanding cells, dxy2 = xylem differentiation zone of the secondary cell wall development and lignification, dxy3 = lignified xylem of the current year; scale bar = 50 µm in a and b, and 200 µm in c; all panels show transverse sections observed with bright-field light microscopy

Table 2 Correlation coefficients (r) of the mean number of cell layers, mean cambial zone width (µm) and mean xylem differentiating zone width (µm) of Thai teak related to climate variables and soil moisture

Climate factors	Current month				Previous month
Anatomical variables	Rainfall (mm)	Relative humidity (%)	Temperature (°C)	Soil moisture (%)	Temperature (°C)
Mean number of cambial cell layers	0.730**	0.515**	0.464**	0.657**	0.725**
Mean cambial zone width (µm)	0.862**	0.469*	0.302	0.647**	0.568**
Mean xylem differentiation zone width (µm)	0.747**	0.436*	0.380	0.592**	0.666**

**Correlation is significant at the 0.01 level, *correlation is significant at the 0.05 level

Table 3 Statistical description of the MSR index

Statistic	Statistic value
Average ring width index (mm)	0.966
Series intercorrelation	0.582
Mean sensitivity	0.343
Autocorrelation	0.737
Mean correlation among all radii	0.328
Mean correlation between trees	0.326
Standard deviation (SD)	0.206
Signal-to-noise ratio	19.350
Variance in first eigenvector	34.52%
Mean expressed population signal (EPS)	0.955
Mean interseries correlation (Rbar)	0.363

($r = -0.263$, $p < 0.05$), and relative humidity in October ($r = -0.321$, $p < 0.05$). A significant correlation was not found between the MSR index and minimum temperature. Moreover, the MSR index was significantly and positively correlated with CRU data such as rainfall in May ($r = 0.237$, $p < 0.01$) and scPDSI in March and May ($r = 0.204$, $p < 0.05$ and $r = 0.232$, $p < 0.05$, respectively). A significant negative correlation was found between the MSR index and rainfall in November ($r = -0.193$, $p < 0.05$) (Figure 6).

DISCUSSION

Cambial activity and xylem production in relation to climate factors

Teak is a ring-porous to semi-ring-porous hardwood with annual growth rings and growth ring boundaries due to one dry season per year (Pumijumnong 1995, Cardoso et al. 2015). The start of the seasonal period of cambial activity of teak (specifically Thai teak) in this study was consistent with its leaf phenology. The cambial

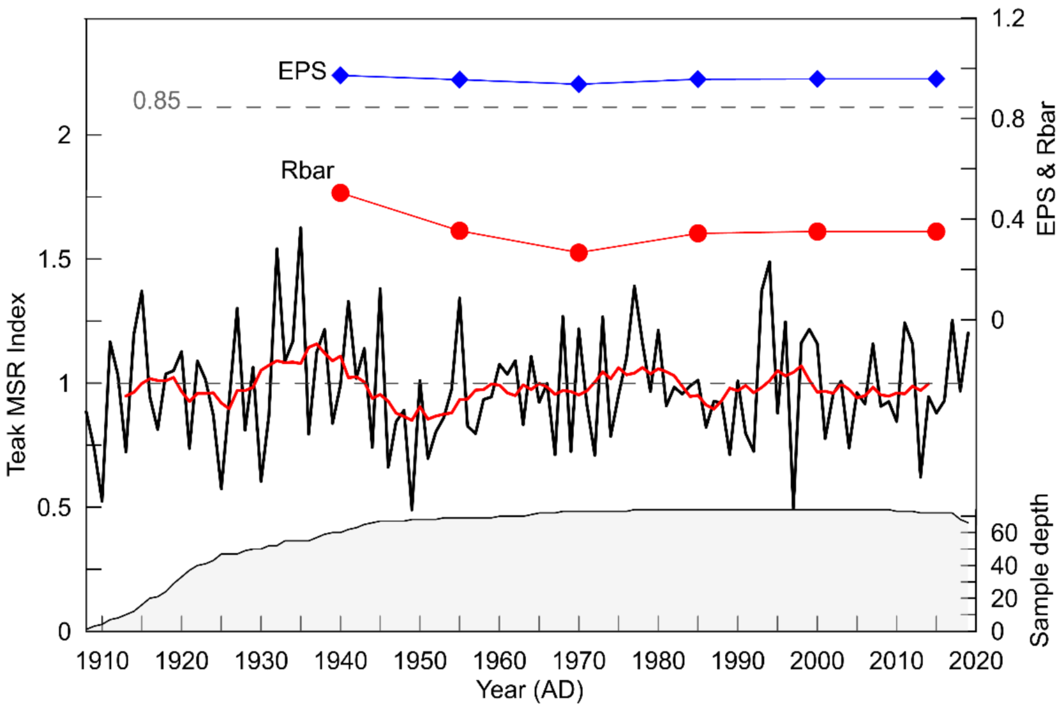

Figure 5 Residual chronology of teak MSR ring width index (black line) with an 11-year running average (red line); blue diamonds represent mean expressed population signal (EPS) values, red dots represent mean interseries correlation (Rbar) values, and the grey area shows sample depth

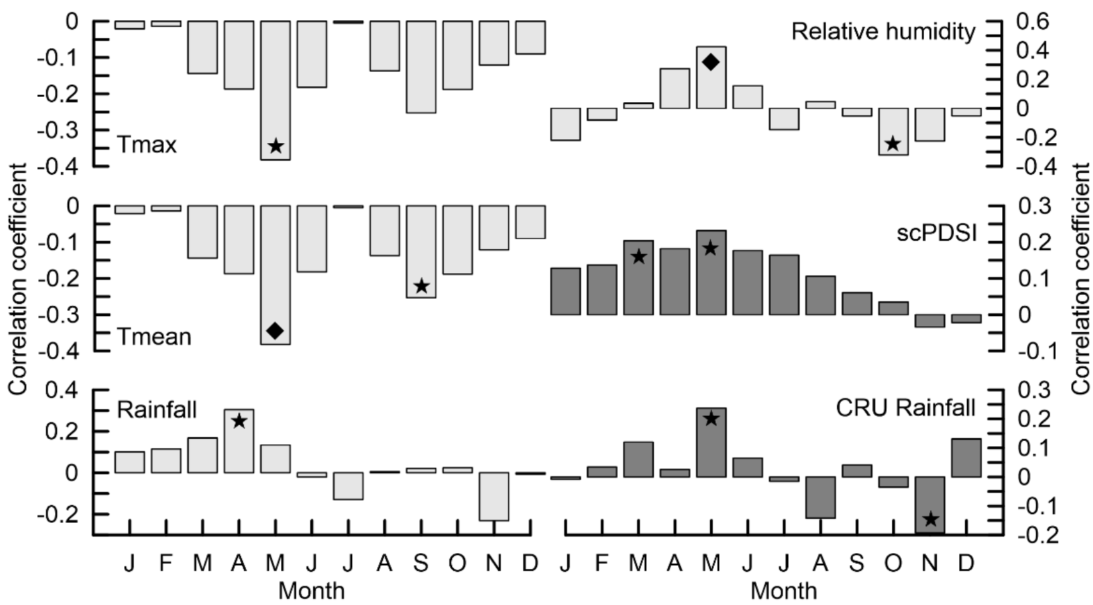

Figure 6 Correlation coefficients between the MSR index and local climate factors such as rainfall, mean temperature (Tmean), maximum temperature (Tmax) and relative humidity, and between the MSR index and climate data from the Climate Research Unit (CRU TS4.03; http://cliexp.knmi.nl), such as rainfall and self-calibrated Palmer drought severity index (scPDSI); stars indicate significance at $p < 0.05$ level, and diamonds indicate significance at $p < 0.01$ level

cells started to divide simultaneously as the start of new budding in May, and cambial dormancy began in November, even though the trees were still full of leaves. The leaves started to fall in February and were entirely shed by March or April. The leaf initiation and leaf fall of Thai teak were similar to those in Girnar Reserve forests, India (Jadeja & Nakar 2010). However, the flowering of Indian teak occurs one month later than that of Thai teak, and fruiting of Indian teak occurs one month earlier. A study of the relationship of cambial activity and phenology in teak from eastern India showed that the sprouting of new leaves and the start of cambial activity both occur in June (Rajput et al. 2005), which is consistent with teak from western India (Rao & Rajput 1999). In the current study, xylem differentiation results showed that the large earlywood vessels started forming in May, coinciding with mature leaf production. This result is consistent with the cambial activity and xylem production of teak from India (Rao & Rajput 1999), and this coinciding is also found in other tropical broadleaved species, such as *Cedrela fissilis* from São Paulo state, Brazil (Marcati et al. 2006).

Cambial activity did not differ between 2018 and 2019, with cambial activity beginning in May and ending in September in both years. Moreover, differences were found in the mean of CCL, CZW and Xydf between the wet and dry seasons in both years. A teak study on the Ivory Coast also showed variations in cambial activity between the wet and dry seasons. In that study, the cambium began to divide at the start of the rainy season, followed by xylem cell development, which continued with the cambium activity. The xylem was fully developed at the beginning of the dry season after the cambial activity stopped (Dié et al. 2012).

The active period of cambium in Thai teak is six months (May–October), alternating with a six-month-long dormancy period (November–April). In comparison, the active period of cambium in teak from western India is five months (June–October) (Rao & Rajput 1999). In southwestern India is seven months (March or April to October) (Priya & Bhat 1999), and in the central part of Java Island, Indonesia, it is approximately seven months (January–July), as shown by studies limited to one or few years (Rahman et al. 2019a). The reason of this

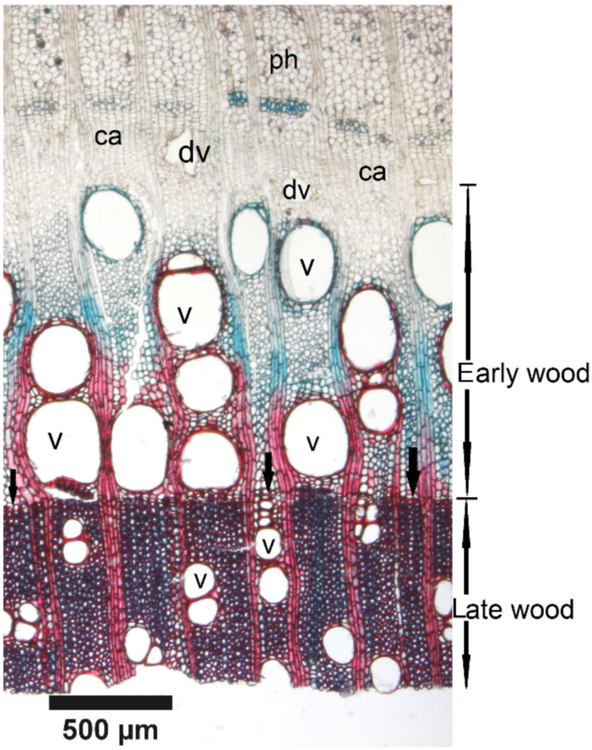

Figure 7 A cross-section showing earlywood and latewood in Thai teak; black arrows show the parenchyma band at the growth ring boundary; ca = cambium, ph = phloem, V = vessel, dV = developing vessel; scale bar = 500 µm

difference of cambial active period is the range of growing season of each site. The quantity and quality of wood production depend on the cambial activity period because it affects cellular composition of the wood. More extended periods of cambial activity produce more fibres or tracheids, affecting the thickness of the cell wall (Begum et al. 2013). Conversely, shorter periods of cambial activity produce more vessels or parenchyma, with thinner cell walls (Begum et al. 2013). The quantity and quality of wood products are consequently related to the amount of carbon accumulated in the wood (Locosselli 2018). When xylem production was investigated by measuring the Xydf, the results showed that, in Thai teak, xylem differentiation occurred throughout the cambial activity period and peaked in June in both 2018 and 2019. Xylem productivity in 2018 was slightly higher than that in 2019, consistent with the higher level of rainfall in 2018. The first cells formed at the beginning of the wet season were early wood vessel, important for water transport. The size of such vessels formed early in the wet season was larger than that of those formed later in the wet season (Figure 7). Teak forms an obvious tree ring with narrow bands of marginal parenchyma. These bands are regulated by the thick walled fibres and small vessels in the latewood.

The first study of Thai teak cambial activity in 1994 reported that cambial activity began around the second week of April to the first week of May. Teak stops growing around the middle of October (Pumijumnong 1997). The beginning of cambial reactivation in teak in 1994 was slightly earlier than the previous study, as was the start of cambial dormancy. This result may be due to the differences in interannual climate conditions during the sampling years. In 1994, rainfall started in March, whereas in 2018 and 2019, rainfall started in late April and mid-May, respectively. The current results suggest that the late arrival of rain in the early wet season, due to climate change, probably caused a delay in cambial activation and shortened the period of cambial activity, affecting the xylem productivity of the teak. Rainfall is a critical factor that stimulates cambial activity. The number of CCL, CZW and Xydf are highly and significantly correlated with rainfall compared to other factors. The results from this study were similar to the cambial activity of a teak plantation in south-eastern India, where cambial activity began in March–April, which is the pre-monsoon season, and peaked in June–July, the period with the most significant rainfall (Bhat 1998, Rajput et al. 2005). In the current study, rainfall influenced the soil moisture at the study site, showing that soil moisture also affects cambial activity. An experiment regarding soil water and cambial activity in *Cordiera concolor*, an evergreen tropical species, showed that soil water content influences cambial activity depending on the time of the year (de Lara et al. 2017). Similarly, the cambial activity of *Pinus kesiya* in northern Thailand is significantly correlated with soil moisture (Pumijumnong & Wanyaphet 2006).

Relative humidity was not a critical factor in determining the CZW and Xydf of Thai teak, as the correlation coefficient values of these factors were relatively low compared to those of soil moisture and rainfall. In contrast, when compared with relative humidity, soil moisture was highly correlated with CZW and Xydf. A study of cambial activity on Chang Island, Thailand, revealed that relative humidity was the only factor influencing the number of CCL in *Tetrameles nudiflora* (Pumijumnong et al. 2019). Relative humidity also affects the cambial activity of *T. nudiflora*, *Canarium euphyllum* and *Spondias axillaris* in central Thailand (Pumijumnong & Buajan 2013).

The temperature in the current month appears to affect only the CCL, but not the CZW or Xydf. Interestingly, however, the previous month's temperature was strongly and positively correlated with CZW and Xydf. Together, these results suggest that the current temperature stimulates cambial cell division but does not affect cambial cell enlargement. In contrast, the previous month's temperature affects cambial cell enlargement and xylem production. High temperatures may be an indirect factor affecting tree stress. Cambial activity in some tropical species has a significant negative correlation with temperature, as reported in *Macaranga gigantea* and *Endospermum diadenum* growing in the tropical rainforest of western Peninsular Malaysia (Wang & Hamzah 2019).

Climate effects on tree ring width

The amount of rainfall during the early wet season (April) and relative humidity in May affected the ring width of the teak. The amount of rainfall in April activates the cambial activity, which in turn builds the xylem which is develop to be wood in trees. The CRU T4.03 data showed that the rainfall in May was beneficial for teak ring width. Conversely, rainfall in November had a negative effect on teak ring width. The results of this study are related to those of previous studies on teak ring width from the Kong River — Mae Hong Son and Tak Provinces (Pumijumnong 2012, Lumyai & Duangsathaporn 2018, Preechamart et al. 2018). It was reported that the amount of rainfall during the rainy season affected the ring width of teak trees. In the current study, the mean and maximum temperatures in May negatively affected teak ring width, indicating that high temperature during the wet season may limit xylem production in teak trees. This negative correlation was consistent with a study of teak ring width in mature trees in two different plantation sites in the Bago Yoma Range, Myanmar and another study in the central-western region of Brazil (Hlaing et al. 2014, Ugulino et al. 2014). Teak in Nakhon Ratchasima Province, in the southern part of north-eastern Thailand, also showed a similar negative correlation with maximum and mean temperature during the rainy season (Palakit et al. 2015). Similar findings were reported in teak of India (Shah et al. 2007, Ram et al. 2008, Ram et al. 2011).

The MSR index was significantly and positively correlated with the scPDSI in March and May, indicating that drought events affect teak ring width in northwestern Thailand. Previous studies on ring width in northwestern Thailand, Vietnam and Myanmar have captured evidence of drought events, indicating that drought has effects not only in Thailand but also in other parts of Southeast Asia (Buckley et al. 2007, Sano et al. 2009, D'Arrigo et al. 2013). This relationship could reconstruct drought events in Southeast Asia (Buckley et al. 2010, Zaw et al. 2020).

Based on the current research, climate influences both cambial activity and teak ring width, clearly indicating that the monsoon season's onset affects teak's growth. In addition, high temperatures during the growing season may indirectly affect the efficiency of wood formation.

CONCLUSION

The first study was conducted to monitor teak's cambial activity and xylem production in northwestern Thailand for two growing seasons. The results showed that the critical factor for triggering cambial activity is rainfall. The most significant cambial activity occurred during the peak of the wet season in June 2018 and July 2019, whereas most xylem production occurred in June of both years. The dormant period of teak occurred during the dry season, from November to April. The number of CCL and CZW were strongly correlated with Xydf. Compared with the cambial activity of teak in 1994, the cambial activity in this study was delayed in response to climate conditions. Rainfall at the beginning of the rainy season appears to be the climate factor that stimulates cell division and teak ring formation. In comparison with those of previous reports, the findings of this study could reflect the variability of teak to the climate in northwestern Thailand and help adopt policies for teak plantation management.

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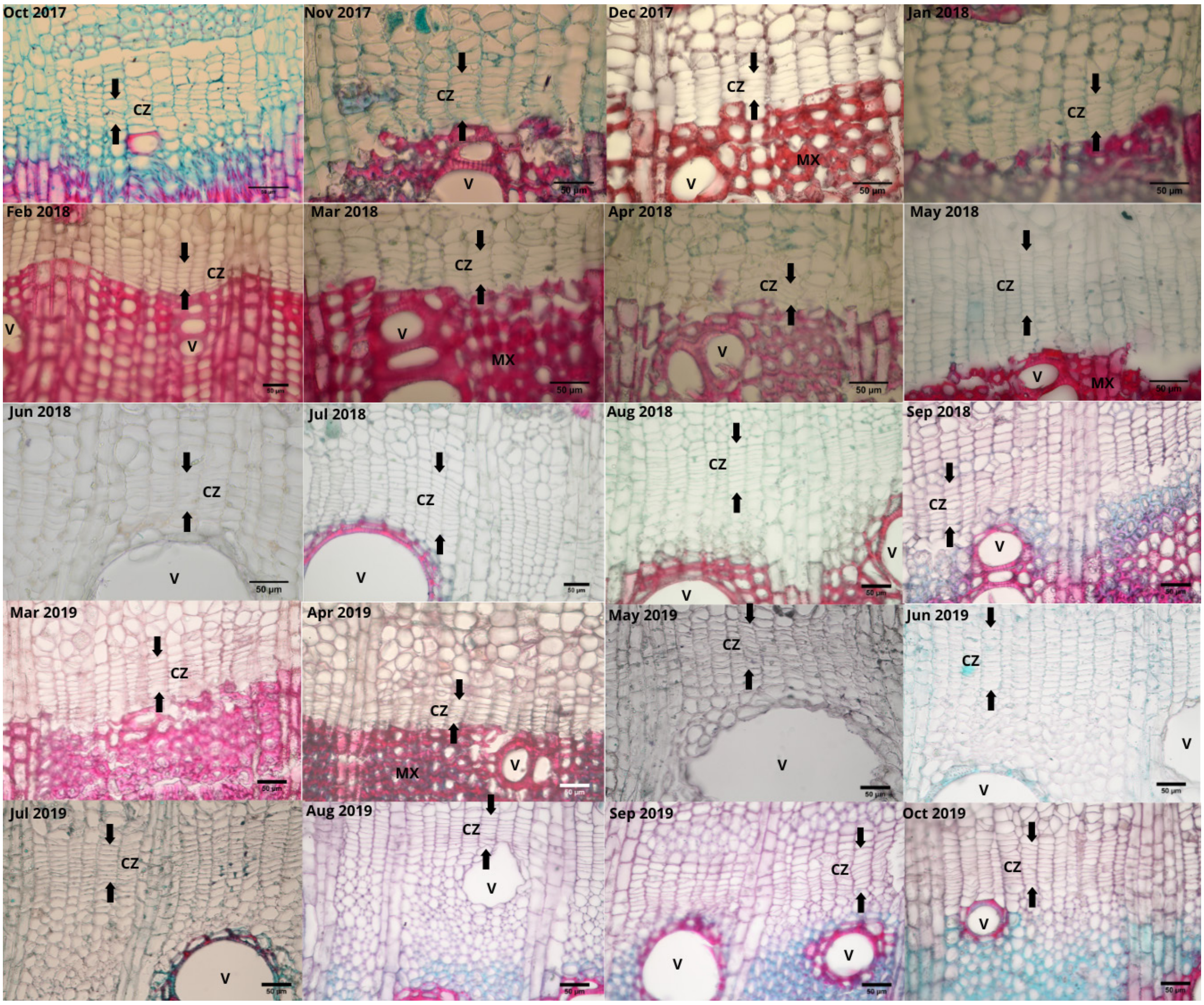

Figure S1 Cross-sectional view of cambium with adjacent xylem and phloem of *Tectona grandis* from October 2017 to October 2019; CZ = cambial zone, MX = mature xylem; V = vessel; scale bars 50 µm