



Research article

Periodic growth of *Afzelia xylocarpa* (Kurz) Craib and *Lagerstroemia duperreana* Pierre ex Gagnep. and their responses to climatic variability

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Abstract

The growth response to climatic variability was studied of *Afzelia xylocarpa* and *Lagerstroemia duperreana* growing naturally at the Sakaerat Environmental Research Station, Thailand. The monthly wood increments and leaf phenology of these two species were investigated for 1 yr. The occurrence of axial parenchyma was considered as a marker for the annual ring boundary in *A. xylocarpa*, while the variations in vessel size and fiber cell wall thickness and shape were used to identify the annual ring boundary in *L. duperreana*. The monthly wood increments and leaf flush in these trees were initiated at the onset of the rainy season or a month later. The cessation of wood increment occurred in association with leaf abscission during the dry season, from December to February. The two climatic components indicated by principal component analysis were Moisture (rainfall, relative humidity and soil moisture content) and Temperature (maximum, minimum and mean temperature); they illustrated the coupling effect of direct and indirect stimulation on tree growth. By using path analysis, the Moisture and Temperature components could be used to explain the occurrence of mature dark green leaves (MDL) 64% of the time in *A. xylocarpa*, while the moisture component alone could be used to identify 41% of the MDL occurrence in *L. duperreana*. Climatic components association with MDL could explain 45% and 67% of the formation of woody cells in these two tree species, respectively. The association of climatic components, MDL and wood increments induced 46% and 91% variation in the diameter over bark of *A. xylocarpa* and *L. duperreana*, respectively.

Introduction

Tree-ring analysis, known as dendrochronology, is generally applied to indicate long-term environmental changes in tree ring growth, especially in the temperate and boreal regions, while the studies in the tropics are still in nascent stage; numerous tropical tree species forming reliable annual rings have been verified such as *Tectona grandis* (Berlage, 1931) *Abies religiosa* (Huante et al., 1991),

Pinus kesiya and *P. merkusii* (Buckley et al., 1995) and *Taxodium mucronatum* (Stahle et al., 2000). In Thailand, only three species (*P. kesiya*, *P. merkusii*, and *T. grandis*) have been reported on and widely used in tree ring research (Buckley et al., 1995; D'Arrigo et al., 1997; Pumijumnon and Eckstein, 2011; Pumijumnon and Palakit, 2020), with reporting on other tropical tree species producing annual rings still being limited with uncertainty related to which tree species produce annual rings and the climate-related growth response.

Therefore, it is necessary to investigate the tropical tree species which can potentially produce annual rings in order to increase the scope of dendrochronological studies in the tropics. Not only should

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the wood anatomy be described precisely to indicate the annual ring boundaries and the periodic growth, but the wood increments as a function of environmental factors must be determined to further research in climate modeling using tree-ring analysis. Following the general growth model of an individual tree as described by Fritts (1976), periodic growth in terms of wood increment and leaf phenology can be used to detect and relate to climatic variability. The periodic increments in wood can be measured based on the diameter over the bark, using a dendrometer band (Palmer and Ogden, 1983; Palakit et al., 2018). This enables a continuous measurement of diameter growth and thus of the cambial activity of a tree depending on climatic events. The increments of diameter under bark can be monitored by using the Mariaux's windows technique (Mariaux, 1981) to make a reference point for measurement on the cambial zone.

Using the annual ring boundaries through tropical dendrochronological analysis, the current research aimed to investigate the periodic growth and wood anatomy of *Azizelia xylocarpa* and *Lagerstroemia duerperreana* generally distributed in the mixed deciduous and dry evergreen forests in several regions of Thailand. The periodic growth response of these two species to climatic variability was also investigated. This study can be used to tap the potential of tree-ring analysis in tropical tree species to determine climate response and to reconstruct the paleoclimate using tree species naturally distributed in several countries.

Materials and Methods

Study area

The study area was located at the Sakaerat Environmental Research Station (SERS) in northeastern Thailand (Fig. 1). This site is a dry evergreen forest, with its elevation gradually rising from 250 m above sea level (a.s.l.) at the bottom to 762 m a.s.l. at the top of the highest mountain. The slopes vary from 10% to 30% and the entire area appears to be underlain with sandstone. The majority

of the forest area is under dense dry evergreen forest, except in the north and northeast zones, where dry dipterocarp forest dominates. The climatic data for monthly rainfall, temperature—mean (Tmean), maximum (Tmax) and minimum (Tmin)—and relative humidity (RH) during the investigation periods were obtained from the meteorological station installed within the natural forest of SERS. The top five dominant tree species in this area are *Hopea ferrea*, *Shorea henryana*, *Lagerstroemia duerperreana*, *Hydnocarpus ilicifolius* and *Memecylon caeruleum*, respectively (Lamotte et al., 1998). *L. duerperreana* was selected in this study due to its occurrence of a ring-like formation in cross section, as this characteristic was not found in the other dominant tree species. Although *Azizelia xylocarpa* is not a dominant species on this site, its good ring formation as a commonly distributed species in several regions of Thailand justified its selection in the study.

Climatic data

A Walter climate diagram (Allaby, 2010) was used to provide a graphical representation of the local climatic data obtained from SERS (shown in Fig. 2). The figure illustrates the average total monthly rainfall and mean temperature data during 1969–2010 in the rainy season, from March to November, with a total rainfall and the mean temperature of 1,043.0 mm and 27.1°C, respectively. The monthly rainfall and temperature declined to 31.9 mm and 23.8°C during the dry season from December to February, while the rainy and the dry seasons, as defined by Thai Meteorological Department, lasted from mid-May to mid-October and mid-October to mid-May, respectively (Thai Meteorological Department, 2020). However, the long rainy season could be separated into two sub-periods consisting of March to July, with a lower average rainfall of 470.4 mm and August to November, with a relatively higher average rainfall of 572.5 mm. The mean temperature gradually increased to its highest value of 29.2°C at the beginning of the rainy season in April and declined to its lowest value of 21.9°C at the beginning of the dry season in December.

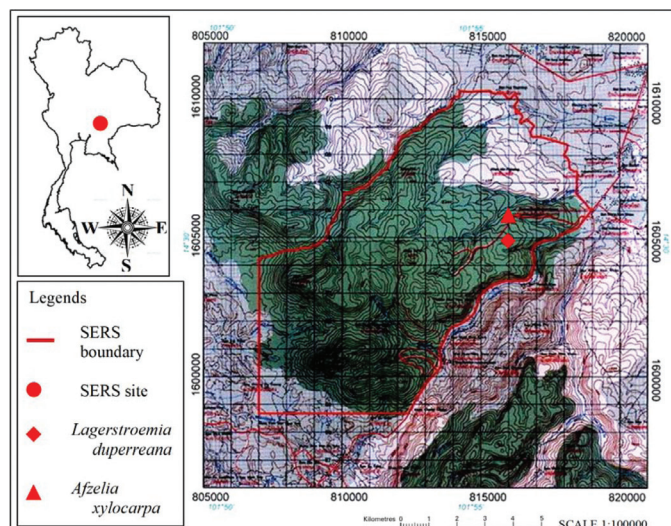


Fig. 1 Study area at Sakaerat Environmental Research Station (SERS) in northeastern Thailand

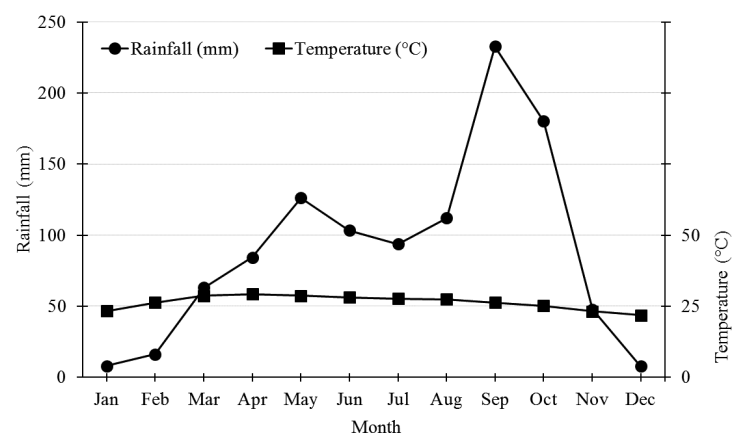


Fig. 2 Walter climate diagram for climate variables measured at Sakaerat Environmental Research Station

Method

Within the forest stand, after receiving permission to conduct the research at SERS in August 2009, six dominant trees, each with a straight trunk and symmetrical crown for each of *A. xylocarpa* and *L. duperreana* species, located on a well-drained soil, were selected to investigate the periodic growth and wood anatomy. Once a month, during September 2009–September 2010, three sampling points within the forest stand were randomly selected. At each sampling point, soil samples from depths in the range 0–30 cm, at intervals of 5 cm, were collected using a soil auger and the soil moisture content was determined using the gravimetric method (Black, 1965). In this procedure, the soil samples are measured for their weight, dried in a hot air oven at temperatures reaching 105°C until all the moisture has evaporated and then the sample weights are re-measured. The soil moisture content is then the difference between the wet and dry sample weights.

In all the six trees sampled from *A. xylocarpa* and six *L. duperreana*, leaf phenological phases of leaf flush (LF), mature with light green leaves (MLL), mature with dark green leaves (MDL) and leaf abscission (LA) were examined once a month visually using binoculars (O'Brien et al., 2008), similar to studies reporting on changes in the diameter over bark (OBD) based on a dendrometer band. This was done by installing a metal band with an accuracy of 0.1 mm on the tree to obtain a precise estimate of any increase in diameter. Once a month for 1 yr on each selected tree, the change in diameter between each month, as measured using a Vernier scale, was recorded as the monthly increment in OBD. Following O'Brien et al. (2008), the observed scores for leaf phenology were in the range 0–100% and were converted to a leaf phenological index ranging from 0 to 5. The percentage of full crown potential occupied by each category of crown cover was indicated as 0 for a bare crown, 1 for 1–20%, 2 for 21–40%, 3 for 41–60%, 4 for 61–80% and 5 for greater than 80% of the crown cover.

The periodicity in monthly wood increments and annual ring boundaries was studied using the cambial marking technique, modified from the Mariaux's windows technique. Once a month for 1 yr on one side of the tree at a height of 130 cm above the ground, cambial zones of the selected trees were marked to investigate the boundary of monthly wood increment and woody cell differentiation using a modified knife 1 mm thick and 5 mm wide (Fig. 3). An adjacent area was marked 2 cm away from the previous one. Then, 1 yr later, all the marked samples were extracted and carefully sanded on transverse surfaces using several grades of sandpaper until the marked points were visible under a stereomicroscope.

The thick wood formation between the adjacent marked points on the cambium and 12 in number for a given year, was called the monthly increment of the diameter inside (under) bark (IBD). These were measured under a stereomicroscope combined with a Velmex measuring stage having an accuracy of 0.001 mm. The accumulated monthly wood increment over a given year was termed as the annual IBD increment. Transverse sections, with a thickness in the range 10–15 µm, of the annual wood increment were also cut using a sledge microtome. These thin sections were stained with safranin and mounted on microscopic glass slides using a permount to investigate the anatomical characteristics and visible markers to identify the annual rings.

Statistical analysis

Principal component analysis (PCA) was conducted to eliminate the effect of multicollinearity in the climatic data for total monthly rainfall, temperature, relative humidity and soil moisture content. PCA was also applied to transform these climatic data into uncorrelated components (O'Brien, 2007). The hierarchical relationship between the climatic components and tree growth characteristics (leaf phenology and monthly wood increments of IBD and OBD) was examined using a multiple linear regression analysis, known as the path analysis (PA) technique, in order to exemplify both the direct and indirect effects of climatic variability on tree growth. The root mean square error of approximation (RMSEA) and the comparative fit index (CFI) were also calculated to indicate the quality of model fitting. The model was not used when the RMSEA was greater than 0.1 and the CFI lower than 0.9 (Browne and Cudeck, 1993).

Results and Discussion

Soil moisture content

Although the soil moisture content and climatic data used in the current study were collected during the periods of tree growth from 2009–2010, it could be divided into two periods covering the rainy and the dry seasons. This delineation was based on fluctuations observed in the Walter climate diagram of the actual data on local rainfall and temperature during 1969–2010, instead of the divisions generally used across the country. This was similar to the analysis done by Lamotte et al. (1998), who used the Walter climate diagram on data collected during 1982–1992 to report on the wet and the dry seasons in SERS from March to November and December to February, respectively. The soil moisture content estimated using the gravimetric method during the study period increased from the beginning of the rainy season in March–September with an average moisture content ($\pm$ SD) of $15.6 \pm 5.1\%$ and then mildly declined during October and November with an average moisture content of $12.1 \pm 3.1\%$, while the lowest moisture content ($8.8 \pm 1.3\%$) was measured during the dry period from December to February (Table 1 and Fig. 4).

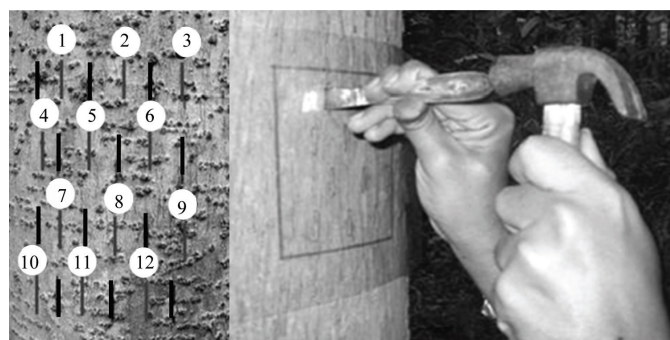
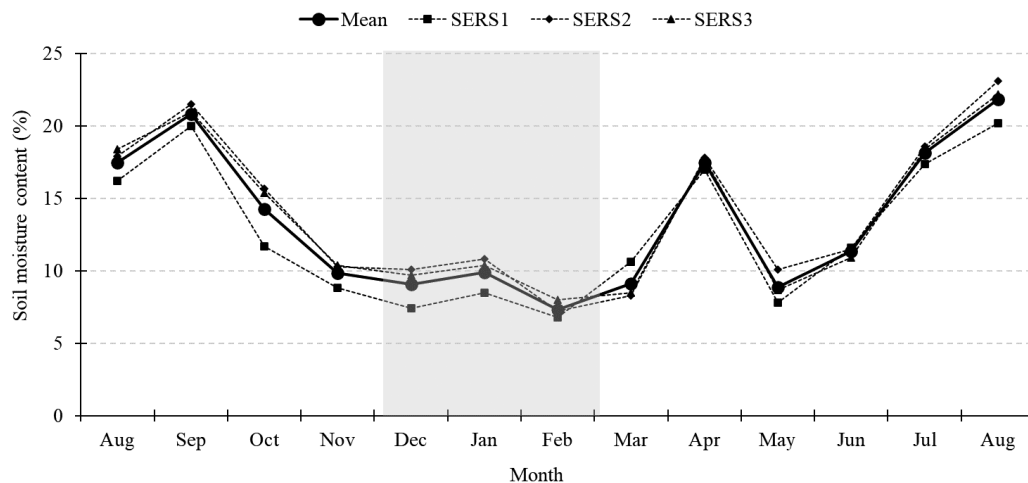


Fig. 3 Location of 12 cambial marking points, numbered once a month for 1 yr, on a sampled tree

Table 1 Soil moisture content at the Sakaerat Environmental Research Station during the study period

Month	Soil Depth (cm)						Mean±SD
	0.0–5.0	5.1–10.0	10.1–15.0	15.1–20.0	20.1–25.0	25.1–30.0	
Aug	22.6±3.2	19.1±2.1	17.5±1.6	16.1±1.4	15.3±2.0	14.5±2.0	17.5±2.0
Sep	27.3±1.7	22.4±1.4	20.7±2.1	19.1±0.7	18.2±1.1	17.2±1.0	20.8±1.3
Oct	17.2±4.0	14.4±2.9	13.8±2.2	13.4±1.3	13.1±1.2	13.6±1.7	14.3±2.2
Nov	10.1±1.3	10.0±1.1	9.7±1.0	9.8±1.0	9.6±0.4	10.0±0.8	9.9±0.9
Dec	9.5±2.2	9.3±2.2	8.9±1.5	8.9±1.2	8.8±1.1	8.8±0.9	9.0±1.5
Jan	11.9±2.0	10.9±1.6	9.6±1.1	9.3±1.0	9.0±0.9	8.7±0.9	9.9±1.3
Feb	7.3±1.1	7.0±1.2	7.5±0.8	7.5±0.4	7.3±0.5	7.5±0.3	7.3±0.7
Mar	11.1±2.2	9.6±1.0	9.0±1.1	8.7±1.3	8.3±1.3	8.3±0.9	9.2±1.3
Apr	23.1±2.7	17.5±1.1	17.6±1.0	16.9±1.0	14.7±1.3	15.1±0.9	17.5±1.4
May	8.9±2.0	9.0±1.5	8.9±1.2	8.7±0.7	8.4±0.6	9.3±1.4	8.9±1.2
Jun	14.4±1.4	11.6±0.6	10.9±0.2	10.4±0.1	10.3±0.9	10.4±1.0	11.3±0.7
Jul	22.5±1.9	18.9±0.8	17.8±0.9	17.4±0.7	16.8±0.2	15.5±1.2	18.1±0.9
Aug	32.2±4.8	23.2±2.4	19.9±0.9	19.4±0.7	18.4±1.7	18.0±1.1	21.9±2.1

**Fig. 4** Average soil moisture content during study period at Sakaerat Environmental Research Station at each sampling point (SERS1, SERS2, SERS3), where grey band indicates dry season at end and beginning of year

The monthly climatic variations in this area were affected by the north-easterly monsoon from November to March and the south-westerly monsoon from May to September, similar to other provinces in north-eastern Thailand. This finding was similar to Nawata et al. (2005), who indicated that the highest monthly rainfall over the last 20 yr (150–300 mm) occurred in September and decreased to a level comparable to the beginning of the rainy season in October. They also noted the variability in monthly rainfall during the dry season, which was less than 40 mm in November, almost undetectable in December and January and mildly increased in March. Loo et al. (2015) also reported 70% below normal levels in measured rainfall and a delayed monsoon period by 15 d in Southeast Asia.

Investigation of periodic growth

The periodic growth of *A. xylocarpa* and *L. duperreana* was divided into two parts in terms of leaf phenology and monthly wood increment. Monthly wood increment could be examined in terms of the increments in the OBD and IBD diameters. For *A. xylocarpa*, one

out of the six selected trees was not analyzed due to damage during specimen extraction from the trunk.

Leaf phenology

The phenology of LF in *A. xylocarpa* was abundant in January after a short period of being leafless in December. The MLL stage developed and emerged continuously during the months of January to August. The MDL stage was commonly observed from February to November, while yellowish leaves as an indicator of LA, rarely occurred during June to December (Fig. 5A). This was different from the leaf phenology observed for *L. duperreana*, as shown in Fig. 5B, with the timing of LF recorded in two intervals from April to May and August to November. The MLL stage development from LF was commonly found from April to November. The MDL stage first appeared in April and then was plentiful from May to November. The level of MDL abruptly dropped in December and was not found from January to March. Leaves had started to senesce, as indicated by a change in color to yellowish or brown or both in May. The level of LA was higher than for MDL in December. The bare crown in March

indicated a dormant period in *L. duperreana*. The leaf phenological scores of *A. xylocarpa* and *L. duperreana* are shown in Table 2. However, the cumulative phenological scores might be greater than the highest designated value of 5, such as the leaf phenology of *A. xylocarpa* and *L. duperreana* in November. This can be explained by the observation that most of the leaves in greater than 80% of crown cover were MDL while lower levels of LF, MLL, and LA were rarely found during this month.

In accordance with the study done by Gutierrez-Soto et al. (2008), in the current study abundant leaf crowns were produced by all tree in both species throughout the rainy season, while evergreen species such as *H. ilicifolia* and *A. odoratissima* formed their leaf canopy throughout the year (Palakit et al., 2015). Several researchers also confirmed the periods of LF and LA of tropical and deciduous tree species as being in the early part of the rainy season and throughout the dry season, respectively (Sun et al., 1996; Valdez-Hernández et al.,

2010; Palakit et al., 2019). For the tropical evergreen species, Xiao et al. (2006) suggested that leaf phenology was not determined by the fluctuations in seasonal rainfall but was probably affected by the availability of solar radiation.

Monthly wood increment

The IBD increment ($\pm$ SD) of *A. xylocarpa* was 12.14 ± 5.29 mm/yr (Fig. 6A) with a rapid increase for 5 mth during April to August (8.63 ± 3.83 mm), while the increment during the remaining 7 mth from September to March was only 3.51 ± 1.54 mm (Table 3). Although the rate of monthly IBD increments was different, the vessel diameter of *A. xylocarpa* was similar (0.098–0.11 mm) within the species throughout the year, a general characteristic of diffuse-porous species (Gizińska et al., 2015). The appearance of terminal banded parenchyma, associated with the dormancy of wood increment, indicates the termination of growing season as well as an indicator of the annual ring boundary

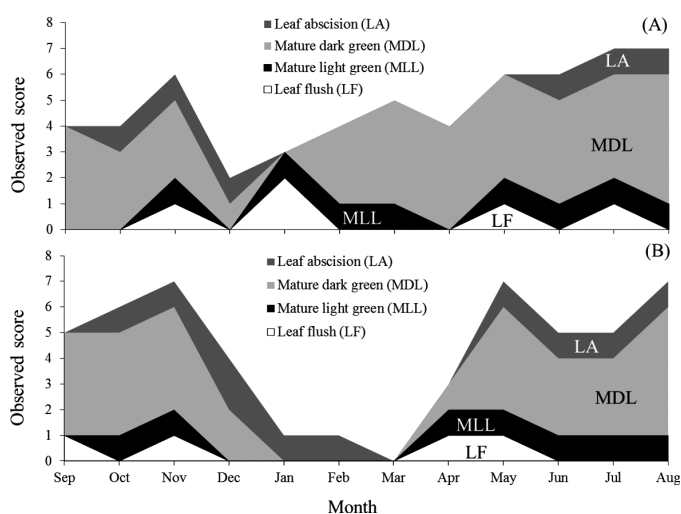


Fig. 5 Leaf phenology of species selected for study: (A) *Afzelia xylocarpa*; (B) *Lagerstroemia duperreana*

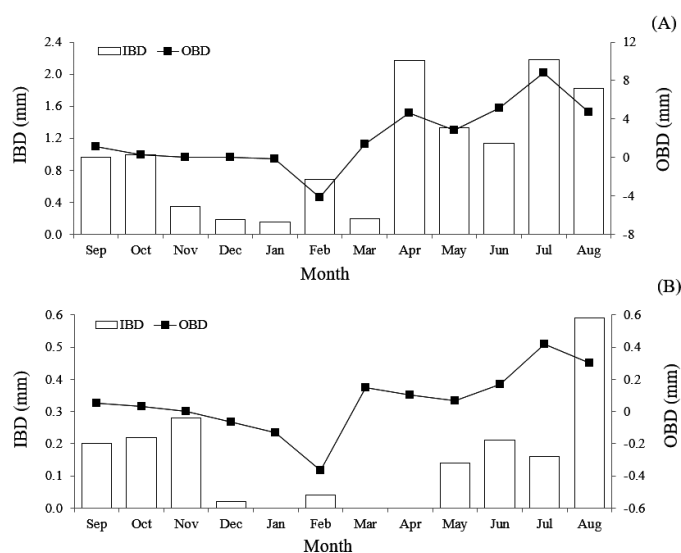


Fig. 6 Increment for diameter under (inside) bark (IBD) and cumulative diameter over bark (OBD): (A) *Afzelia xylocarpa*; (B) *Lagerstroemia duperreana*

Table 2 Leaf phenological scores of *Afzelia xylocarpa* and *Lagerstroemia duperreana*

Month	<i>Afzelia xylocarpa</i>				<i>Lagerstroemia duperreana</i>			
	LF	MLL	MDL	LA	LF	MLL	MDL	LA
Aug	0	1	4	0	1	1	5	1
Sep	0	0	4	0	1	0	4	0
Oct	0	0	3	1	0	1	4	1
Nov	1	1	3	1	1	1	4	1
Dec	0	0	1	1	0	0	2	2
Jan	2	1	0	0	0	0	0	1
Feb	0	1	3	0	0	0	0	1
Mar	0	1	4	0	0	0	0	0
Apr	0	0	4	0	1	1	1	0
May	1	1	4	0	1	1	4	1
Jun	0	1	4	1	0	1	3	1
Jul	1	1	4	1	0	1	3	1
Aug	0	1	5	1	0	1	5	1

LF = leaf flush; MLL = mature with light green leaves; MDL = mature with dark green leaves LA = leaf abscission

Crown cover scores: 0 = bare crown; 1 = 1–20%; 2 = 21–40%; 3 = 41–60%; 4 = 61–80%; 5 = >80%

Table 3 Diameter inside (under) bark (IBD) and diameter over bark (OBD) increments of five *Afzelia xylocarpa*, coded AF02 – AF06

Month	IBD (mm)						OBD (mm)					
	AF02	AF03	AF04	AF05	AF06	Mean±SD	AF02	AF03	AF04	AF05	AF06	Mean±SD
Aug	First marking as baseline measurement											
Sep	0.98	1.87	0.49	0.79	0.65	0.96±0.54	2.10	2.40	0.00	0.00	1.30	1.16±1.13
Oct	0.92	2.17	0.79	0.53	0.55	0.99±0.68	0.30	1.10	0.00	0.00	0.00	0.28±0.48
Nov	0.04	1.14	0.12	0.45	0.00	0.35±0.48	0.00	0.00	0.00	0.00	0.00	0.00±0.00
Dec	0.90	0.00	0.01	0.00	0.00	0.18±0.40	0.00	0.20	0.00	0.00	0.00	0.04±0.09
Jan	0.00	0.26	0.45	0.05	0.00	0.15±0.20	0.20	0.00	-1.10	0.00	0.00	-0.18±0.52
Feb	0.57	0.43	0.91	0.83	0.69	0.69±0.19	-2.60	-0.60	-5.30	-6.00	-6.30	-4.16±2.47
Mar	0.00	0.11	0.85	0.00	0.00	0.19±0.37	0.30	0.30	2.10	3.00	1.30	1.40±1.17
Apr	1.78	4.82	0.89	1.35	1.99	2.17±1.54	5.80	5.80	4.30	3.00	4.40	4.66±1.18
May	1.10	2.45	1.68	0.86	0.56	1.33±0.75	2.10	3.50	4.30	1.60	2.50	2.80±1.09
Jun	0.78	0.67	2.06	0.00	2.19	1.14±0.95	5.40	3.50	3.20	7.50	6.20	5.16±1.82
Jul	2.88	3.87	1.80	1.49	0.86	2.18±1.19	8.00	7.70	9.70	9.10	9.40	8.78±0.88
Aug	2.25	2.92	2.17	0.82	0.93	1.82±0.91	4.40	3.30	5.40	5.30	5.00	4.68±0.86

(Wilczek et al., 2014). An investigation of the micro-section indicated a wood porosity with single and multiple pore associations with aliform and confluent parenchyma (Fig. 7 and 9A). In accordance with the study of increments OBD, since the installation of the band dendrometers in September, the scales were not moved until January and shrinkage was observed in February during the dry period. The OBD increased rapidly from March to August with a cumulative diameter ($\pm$ SD) of 8.48 ± 6.96 mm, as shown in Table 3 and Fig. 6A.

The IBD increments in *L. duperreana* indicated a wood increment ($\pm$ SD) of 1.86 ± 0.77 mm per year. Growth dormancy was observed from December to April, with the wood diameter slightly increasing by 0.06 ± 0.16 mm, while the monthly wood increment gradually increased from May to November (Table 13 and Fig. 6B). Banded axial parenchyma-like fibers of *L. duperreana* formed during May in association with the largest vessels of approximately 0.085 mm diameter (Figs. 8C–8E and 9B), indicating the beginning of the growing season and of annual ring formation. Although wood increments at the end of the rainy season were higher than at the beginning of the season, the vessel sizes during this period gradually declined to 0.062 mm (Fig. 8F). There was only a small OBD increment ($\pm$ SD) in *L. duperreana* during September to November (0.01 ± 0.13 mm) and the OBD shrank during the dry period from December to February (-0.06 ± 0.48 mm), similar to the OBD increments estimated for *A. xylocarpa*. There was a slight increase in the dendrometer bands during March to May at the beginning of the wet season (0.03 ± 0.65 mm) and this rapidly increased from June to August (0.09 ± 0.50 mm), as shown in Table 13 and Fig. 6B.

From the observed variations in vessel size, *A. xylocarpa* and *L. duperreana* were respectively defined as a diffuse and ring porous to semi-ring porous species, similar to a previous study done by Carlquist (2001). Baas (1986) also found semi-ring porous characteristics in *Lagerstroemia* sp. Roig et al. (2005). de Pernia and Melandri (2006), Marcati et al. (2006) and Palakit et al. (2018) indicated that the occurrence of marginal parenchyma, variations in vessel size and the thick cell walls of fibers in latewood are common and detectable characteristics which can be used to identify the annual ring boundary in the tree.

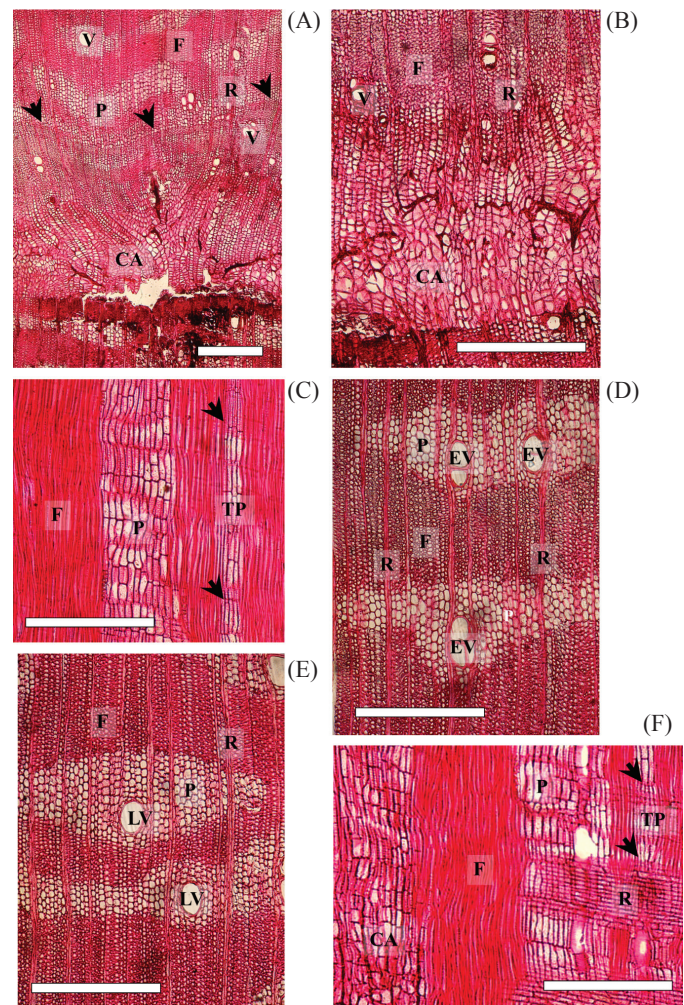
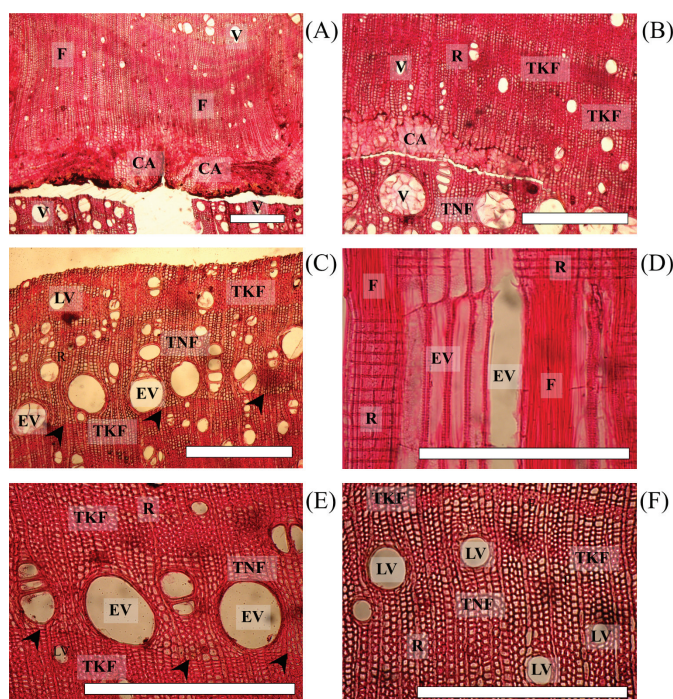
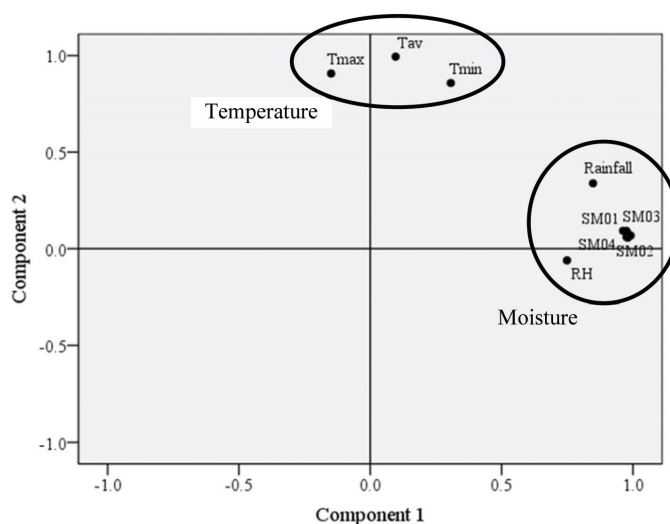


Fig. 7 Microscopic features of *Afzelia xylocarpa*: (A–B) callus cells from cambial marking; (C) terminal parenchyma on a radial section; (D) earlywood vessel with paratracheal parenchyma; (E) latewood vessel with paratracheal parenchyma; (F) latewood fiber close to marked cambial point on a radial section, where CA = callus cells; EV = earlywood vessels; F = fibers; LV = latewood vessels; P = paratracheal parenchyma; R = ray cells; TP = terminal parenchyma; V = vessels; scale bar = of 500 μ m; black arrowhead = terminal parenchyma

Table 4 Diameter inside (under) bark (IBD) and diameter over bark (OBD) increments of six *Lagerstroemia duperreana*, coded LD01 – LD06

Month	IBD (mm)							OBD (mm)						
	LD01	LD02	LD03	LD04	LD05	LD06	Mean±SD	LD01	LD02	LD03	LD04	LD05	LD06	Mean±SD
Aug	First marking as baseline measurement													
Sep	0.00	0.32	0.08	0.67	0.00	0.14	0.20±0.26	0.00	0.30	0.00	0.00	0.00	0.00	0.05±0.12
Oct	0.00	0.57	0.05	0.38	0.08	0.23	0.22±0.22	0.00	0.00	0.00	0.00	0.00	0.20	0.03±0.08
Nov	0.36	0.00	0.14	0.20	0.23	0.75	0.28±0.26	0.00	0.00	0.00	0.00	0.00	0.00	0.00±0.00
Dec	0.00	0.14	0.00	0.00	0.00	0.00	0.02±0.06	0.00	0.00	-0.30	-0.10	0.00	0.00	-0.07±0.12
Jan	0.00	0.00	0.00	0.00	0.00	0.00	0.00±0.00	0.00	0.00	-0.50	0.00	0.00	-0.30	-0.13±0.22
Feb	0.00	0.24	0.00	0.00	0.00	0.00	0.04±0.10	-1.00	-0.40	-0.50	0.00	-0.20	-0.10	-0.37±0.36
Mar	0.00	0.00	0.00	0.00	0.00	0.00	0.00±0.00	0.00	0.60	0.40	0.10	-0.10	-0.10	0.15±0.29
Apr	0.00	0.00	0.00	0.00	0.00	0.00	0.00±0.00	0.10	0.70	-0.70	0.50	0.00	0.00	0.10±0.49
May	0.00	0.00	0.26	0.25	0.21	0.13	0.14±0.12	0.00	0.20	0.10	0.00	-0.10	0.20	0.07±0.12
Jun	0.14	0.91	0.13	0.00	0.00	0.06	0.21±0.35	0.10	0.40	0.10	0.20	0.00	0.20	0.17±0.14
Jul	0.10	0.37	0.21	0.19	0.00	0.09	0.16±0.13	0.30	1.00	0.30	0.30	0.20	0.40	0.42±0.29
Aug	0.68	0.32	0.42	0.24	0.56	1.30	0.59±0.38	0.30	0.40	0.30	0.30	0.10	0.40	0.30±0.11

**Fig. 8** Microscopic features of *Lagerstroemia duperreana*: (A–B) callus cells from cambial marking; (C) total wood increment; (D) vessels in earlywood associated with thin wall fibers on a radial section; (E) vessels in earlywood associated with thin wall fibers; (F) latewood vessels, where CA = callus cells; EV = earlywood vessels; F = fibers; LV = latewood vessels; R = ray cells; TKF = bands of thick wall fibers; TNF = thin wall fibers occurring alternately along the wood increment zone; V = vessels; scale bar = of 500 µm; black arrowhead = initial parenchyma**Fig. 9** Two components of temperature and moisture using principal components analysis derived from climatic data and soil moisture content (SM) measured at the Sakaerat Environmental Research Station, where Tmax = maximum temperature, Tmin = minimum temperature, Tav = mean temperature and RH = relative humidity

The two studied species grew rapidly and maximized their wood increments during the wet period, while growth ceased during the dry period at the end and beginning of the year. Researchers have confirmed that the causes of the decline and inducement of wood increment in all broadleaved and long-leaved trees are due to drought and heavy rainfall during the dry and wet seasons, respectively (Marcati et al., 2006; Lisi et al., 2008; Palakit et al., 2015, 2018, 2019). Cufar et al. (2008) reported that during the rainy season, cambial growth is reactivated immediately after leaf unfolding and 75% of the annual ring width is formed during the first half of the season.

The OBD of the two studied deciduous species rapidly increased at the beginning of the rainy season and increment gradually decreased at the end of the season followed by a reduction in diameter during the dry season at the end and beginning of the year, similar to other deciduous species found in Thailand such as *T. grandis* and

M. azedarach (Palakit et al., 2018; 2019). The evergreen tree species growing in the study area displayed a constant OBD at the end of the wet season and during the dry season, while an abrupt shrinkage of OBD was observed in February, before the start of the wet season in March (Palakit et al., 2015). Pelissier and Pascal (2000) stated that shrinkage in OBD was affected by the amount of rainfall in terms of the soil moisture content and the water stress of the tree, also called hydrostatic stem flexibility.

Climate-periodic growth responses

To eliminate multicollinearity in the climatic data, PCA analysis was used with the criterion of eigenvalues ≥ 1 to construct two non-significantly correlated components of the climatic data. The first component, namely Moisture was composed of rainfall, RH and the soil moisture content at all sampled depths. The second component, named Temperature was composed of maximum (Tmax), minimum (Tmin), and mean temperature (Tmean). The two components shown in Fig. 10 were defined as independent factors to study the climate-growth response. It was found that they could explain 89.40% of the variance in the above climatic data.

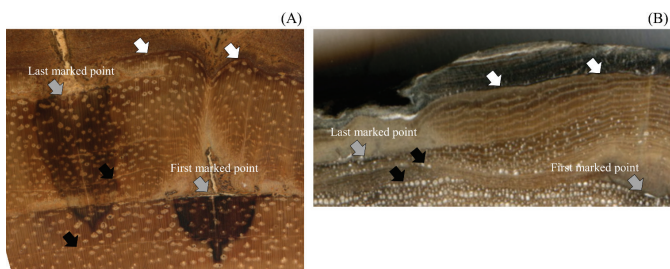


Fig. 10 Macroscopic view of annual ring formation in: (A) *Afzelia xylocarpa*; (B) *Lagerstroemia duperreana*, where black, gray and white arrows indicate annual ring boundaries, cambial marking points and transition zone of wood and bark, respectively, and the first and last marked points indicate 4 September 2009 and 3 September 2010, with wood extraction done on 3 October 2010

Then, PA was performed to determine the direct and indirect effects of the two climatic components on the growth of *A. xylocarpa* and *L. duperreana*. The climatic components of leaf phenology, IBD and increments in OBD were added to the model, with any non-significant predictors duly removed. The testing of the overall model fit indicated that the default model of *A. xylocarpa* was a good fit and could be used to explain the factors affecting tree growth ($\chi^2 = 6.632$, degrees of freedom (df) = 6, $p = 0.356$, RMSEA = 0.098, and CFI = 0.970).

In the sequential model of *A. xylocarpa* (Fig. 11), all the statistically significant ($p < 0.05$) path coefficients indicated that the Temperature and Moisture components directly affected the occurrence of MDL (correlation coefficient (r) = 0.55 and 0.58, respectively). These two climatic components affected 64% of the existing MDL. The existence of MDL also directly induced increments in IBD ($r = 0.67$), while the Temperature and Moisture components indirectly induced increments in IBD through MDL ($r = 0.37$ and 0.39, respectively). Both the direct

effects from MDL and the indirect effects from the Temperature and Moisture components induced 45% of the IBD increments. The IBD increments directly influenced the increments in OBD as detected by a dendrometer band ($r = 0.68$). The two climatic components and MDL indirectly influenced the OBD increments through increments in IBD and could explain 46% of the increment occurrences in OBD. The estimation of the total effect indicated MDL was a key factor affecting the increments in IBD ($r = 0.67$), followed by the Moisture ($r = 0.39$) and Temperature components ($r = 0.37$), respectively. The IBD increment was the main factor inducing increments in OBD ($r = 0.68$), followed by MDL ($r = 0.46$), the Moisture component ($r = 0.27$) and the Temperature component ($r = 0.25$), respectively. From the path diagram depicted in Fig. 11, a hierarchical relationship between the monthly growth of *A. xylocarpa* and several climatic data components could be used to indicate that increased available moisture from rainfall, RH, soil moisture content and temperature stimulated the abundance of MDL. The IBD increments increased rapidly when MDL was plentiful. The OBD increment was directly affected by the IBD increment associated with the indirect effect of the Moisture and Temperature components through the MDL and IBD increments.

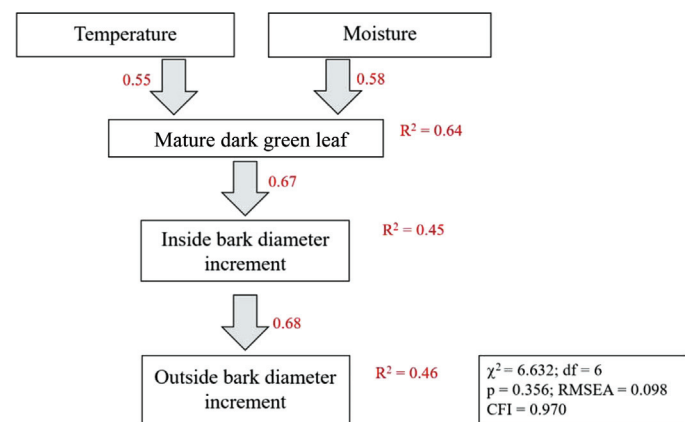


Fig. 11 Path diagram showing factors influencing monthly growth of *Afzelia xylocarpa*, where df = degrees of freedom, RMSEA = root mean square error of approximation, CFI = comparative fit index and R^2 = coefficient of determination

For *L. duperreana*, the climate-growth response model resulted in an average fit as indicated by the appropriate overall model fits ($\chi^2 = 1.238$, df = 5, $p = 0.941$, RMSEA = 0.000, and CFI = 1.000). The sequential model of the climate-growth response predicted that the Moisture component directly induced the occurrence of MDL ($r = 0.64$) and could explain 41% of such occurrences. The abundance of MDL directly generated increments in IBD ($r = 0.82$), while the Moisture component indirectly influenced the increments in IBD through the MDL ($r = 0.52$). Both MDL and the Moisture component could explain 67% of the IBD increments in *L. duperreana*, while the increments in IBD also directly influenced the increments in OBD ($r = 0.39$). Additionally, the variations in OBD increments were directly influenced by the Temperature and Moisture components

($r = -0.61$ and 0.45 , respectively) and were indirectly affected by the Moisture component through the increments in MDL and IBD ($r = 0.20$). The Moisture and Temperature components, MDL and the IBD increments induced the OBD increments and could explain 91% of the variance. From an estimation of the total effects, MDL was the most important factor inducing increment in IBD ($r = 0.82$), followed by the Moisture component ($r = 0.53$). The Moisture component was the major factor inducing OBD increments ($r = 0.66$), followed by the Temperature component ($r = -0.61$), IBD ($r = 0.39$) and MDL increments ($r = 0.32$), respectively. As shown in Fig. 12, the hierarchical climate-growth model could be used to indicate that an increase in the available moisture content stimulated the occurrence of MDL and the IBD rapidly increased when MDL was plentiful. OBD growth was induced by an increase in the Moisture component, a decrease in the Temperature component and an increase in IBD, due to an abundance of MDL and the increase in the Moisture component.

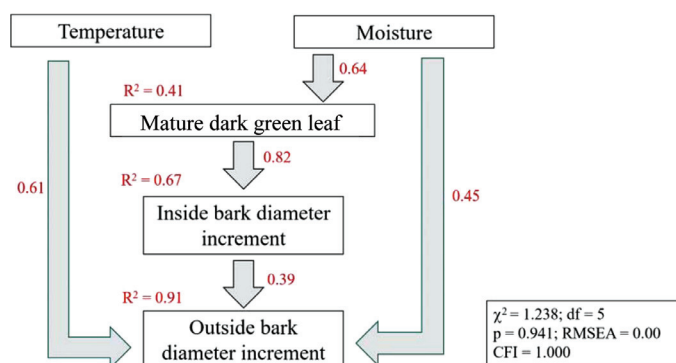


Fig. 12 Path diagram showing factors influencing monthly growth of *Lagerstroemia duerreana*, where df = degrees of freedom, RMSEA = root mean square error of approximation, CFI = comparative fit index and R^2 = coefficient of determination

The variations in the occurrence of MDL in *A. xylocarpa* and *L. duerreana* and other deciduous tree species such as *M. azedarach* and *T. grandis* is significantly related to monthly wood increments while the MDL of evergreen species did not exhibit a significant relationship with the monthly wood increments (Palakit et al., 2015, 2018, 2019). Venugopal and Liangukwang (2007) and Cufar et al. (2008) reported an increase in cambial activity and wood increment in elephant apple trees (*Dillenia indica* Linn.) and beech (*Fagus sylvatica*) after the sprouting of buds and new leaves. This was similar to the findings of O'Brien et al. (2008), who found a significant relationship between the stem increment and leaf occurrences in deciduous trees, while no significant relationship was found for the evergreen species. Luo et al. (2017) also reported a correlation between the leaf life span and photosynthetic capacity, indicating carbon assimilation and tree growth during the growing season and that the highest capacity occurred during the mature stage of leaves followed by a decline in capacity during leaf senescence.

From the climate-growth response derived from path diagrams, Borchert (1999) concluded that seasonal rainfall stimulated the development of leaf phenology, cambial activity and wood formation in deciduous trees, but that a similar process was not evident in evergreen

trees. Lisi et al. (2008) also found that the variations in wood increments in 24 tree species, located in a seasonal semi-deciduous forest of Brazil, were related to the variability in seasonal rainfall. To confirm that a significant relationship existed among climatic variables, tree phenology and tree growth, Heinrich and Banks (2006) reported longer periods of leaf abscission, shorter periods of leaf flushing, decreased vessel size and reduced wood formation in *Toona sinensis* and *T. ciliate*, when the growing conditions were constrained by minimum water and nutrient.

The OBD increments during the rainy season led to the formation of new cells, while the diameter increases and their subsequent reduction in the dormant period were probably affected by the bark water content rather than changes in wood formation (Deslauriers et al., 2003; Bräuning et al., 2008). To avoid these effects, Makinen et al. (2008) suggested the cambial marking technique to study the seasonal fluctuations in wood increments instead of using dendrometer bands. When distinct annual ring formation can be verified, tree-ring analysis can be applied to measure the annual growth and to determine the past climate-growth relationship based on the current period. In the current research, several techniques were applied to confirm the annual ring formation and climate-growth response of the species of interest. It is hypothesized that not only do *T. grandis* and *Pinus sp.* grow naturally and abundantly in north and northeastern Thailand, other species such as the mature *A. xylocarpa* and *L. duerreana* with distinct annual ring formation, also grow widely in several regions of Thailand. Future research will apply the tree-ring analysis technique used in the current study to further investigate the periodic growth patterns and the growth response to climate and environmental variability.

Conflict of Interest

The authors declare that there is no conflict of interest.

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