EVALUATION OF XYLEM MATURATION PROCESS AND EFFECTS OF RADIAL GROWTH RATE ON CELL MORPHOLOGIES IN WOOD OF BALSA (*OCHROMA PRYAMIDALE*) TREES

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Wood and Fiber Science, 54(2), 2022, pp. 149-159
https://doi.org/10.22382/wfs-2022-15

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(Received March 2022)

Abstract. The radial variations of cell morphologies (cell lengths, vessel diameter, vessel frequency, and cell wall thickness of wood fibers) were investigated for 7-yr-old *Ochroma pyramidale* trees planted in East Java, Indonesia, by developing the linear or nonlinear mixed-effects models. In addition, xylem maturation process based on the cell morphologies and effects of radial growth rate on cell morphologies were discussed. The mean values of cell morphology were as follows: vessel element length 0.59 mm, fiber length 2.16 mm, vessel diameter 221 μm, and fiber wall thickness 1.03 μm. Radial variations of cell length and vessel diameter were well explained by Michaelis–Menten equation: values increased from pith to certain position and then it became almost stable. Vessel frequency, wood fiber diameter, and wood fiber wall thickness was expressed by the formula of logarithmic formula, quadratic formula, and linear formula, respectively. Variance component ratio of category was 66.8%, 46.1%, 31.4%, 1.5%, and 33.7% for vessel element length, wood fiber length, vessel diameter, vessel frequency, and wood fiber wall thickness, respectively, whereas the model for wood fiber diameter was not converged. These results suggested that many cell morphologies were influenced by the radial growth rate. Smaller values of mean absolute error obtained in the models in relation to distance from pith were found in all cell morphologies, except for vessel frequency and wood fiber diameter. Thus, xylem maturation of this species depended on diameter growth rather than cambial age. Boundary of core wood and outer wood was 5-10 cm from pith in which increasing ratio of cell length reached <0.3%. Core wood was characterized as lower wood density and mechanical properties with shorter cell lengths and thinner wood fiber walls, whereas outer wood was characterized as higher wood density and mechanical properties with longer cell length and thicker wood fiber walls.

Keywords: Balsa, radial growth rate, radial variation, xylem maturation process.

INTRODUCTION

Balsa (*Ochroma pyramidale* [Cav.] Urban., Syn. *O. lagopus* Swartz) is a pioneer tropical fast-growing tree species in wet tropical lowlands which produces exceptionally low and wide range wood density (0.04-0.31 g/cm^3) (Easterling et al 1982; Midgley et al 2010; Rueda and Williamson 1992; Sosef et al 1998; Wiemann and Williamson 1988; Williamson and Wiemann 2010). This species is also used as plantation species in tropics (Midgley et al 2010; Pertiwi et al 2017a; Sosef et al 1998).

Xylem maturation process both in the tropical and temperate hardwood species has been evaluated by the radial variations of cell morphologies and wood properties (Bhat et al 2001; Honjo et al 2005; Kojima et al 2009a,b; Pertiwi et al 2018; Tsuchiya and Furukawa 2009a,b). The concept of "juvenile wood and mature wood" or "core wood and mature wood" is based on the radial variations of wood properties and cell morphologies in relation to xylem maturation process: juvenile wood or core wood is the wood with unstable properties, and mature wood or outer wood is the wood with stable properties (Erdene-Ochir et al 2021; Makino et al 2012; Nezu et al 2020, 2022; Wahyudi et al 2014). On the other hand, we previously reported that basic density and mechanical properties of 7-yr-old *O. pyramidale* trees planted in Indonesia were almost constant up to 8 cm from pith and then increased toward the bark (Pertiwi et al 2017a): core wood was stable but lower strength properties, and outer wood was unstable but higher strength properties. The concept of core wood and outer wood in relation to xylem maturation process in *O. pyramidale* might be different from other tropical and temperate hardwood species. Thus, detailed xylem maturation process should be clarified for this species.

Mixed-effects models are primary used to describe relationships between a response variable and some covariates in data that are grouped according to one or more classification factors (Pinheiro and Bates 2000). Examples of such grouped data include longitudinal data, repeated measures data, multilevel data, and block designs (Pinheiro and Bates 2000). By using these characteristics, radial variations of wood properties and cell morphologies in softwoods were evaluated by developing linear or nonlinear mixed-effect models models (Auty et al 2013; Dahlen et al 2018; Fujimoto and Koga 2010). Recently, we evaluated xylem maturation process of cell morphologies in a tropical tree species, *Shorea macrophylla*, planted in Malaysia by using mixed-effects models (Nezu et al 2022). In the study, the mixed-effects models with fixed-effect parameter of distance from pith and random-parameter of individual trees was used, resulting that radial variation patterns of cell morphologies could be evaluated with a consideration of variations of individuals. However, application of mixed-effect models is still limited for tropical hardwoods to evaluate the radial variations of wood properties and cell morphologies.

Evaluation of effects of radial growth rate on the wood properties is one of the interesting topics in commercial tropical fast-growing tree species (Aiso-Sanada et al 2019; Hidayati et al 2017; Ishiguri et al 2016; Kojima et al 2009a,b; Makino et al 2012; Pertiwi et al 2017a,b, 2018; Wahyudi et al 2016) because many forest managers considered that trees with fast-growing characteristics may produce wood with lower quality. We previously reported that fast-growing characteristics did not always produce the lower quality wood in several fast-growing tree species, such as *Acacia mangium, Eucalyptus camaldulensis, Gmelina arborea*, and others (Aiso-Sanada et al 2019; Hidayati et al 2017; Ishiguri et al 2016; Makino et al 2012; Pertiwi et al 2017a,b; Wahyudi et al 2016). Thus, the effect of radial growth rate on cell morphologies and wood properties should be clarified for plantation grown *O. pyramidale*.

The objectives of this study were to evaluate the xylem maturation process and effects of the radial growth rate on cell morphologies in *O. pyramidale*. Radial variations of cell morphologies were measured in 7-yr-old *O. pyramidale* trees grown in Probolinggo, East Java, Indonesia, and were evaluated by developing linear or nonlinear mixed-effect models. In addition, characteristics of core wood and outer wood in this species were also discussed.

MATERIALS AND METHODS

Samples Collection

A 10-cm thick disk strips were obtained from the disks collected at 1.2-1.3 m above the ground from the 7-yr-old balsa (*O. pyramidale* [Cav.] Urban.) at the plantation forest located in Krucil, Probolinggo, East Java, Indonesia (07°58′ S, 113°29′ E, *ca*. 1053 m in altitude). In the present study, to evaluate the effect of radial growth rate on the cell morphologies, trees were categorized into three groups based on its stem diameter (slow-, medium-, and fast-growth) as described by Pertiwi et al (2017a). The mean values and detail information on the tree growth characteristics and wood properties were reported in our previous study (Table 1, Pertiwi et al 2017a).

Cell Morphologies

Due to indistinct growth rings, the radial variation in fiber and vessel element lengths were determined at 1-cm intervals from the pith to the bark. Small pieces of wood were macerated in Schulze's solution (100 mL of 35% nitric acid with 6 g potassium chlorate). Macerated samples were washed with distilled water several times. The macerated samples were placed on glass slides, mounted with 75% glycerol, and covered with cover slips. Fiber and vessel element lengths were measured by using a profile projector (V-12B, Nikon, Tokyo, Japan) and a digital caliper (CD-30C, Mitutoyo, Kawasaki, Japan). Wood fiber and vessel element lengths were measured according to our previous paper (Pertiwi et al 2017a). A total 50 wood fibers and 30 vessel elements were measured for each position.

The radial variations of anatomical characteristics were examined by using specimens (ca. 1 cm [L] by 1 cm [R] by 1 cm [T]) collected from the pith

Table 1. Mean and standard deviation of tree characteristics and wood properties of nine selected *Ochroma pyramidale* used in the present study (Pertiwi et al 2017a).

Character	Slow growth (n = 3)	Medium growth (n = 3)	Fast growth (n = 3)	Total (n = 9)
D (cm)	22.7 ± 1.7	31.1 ± 0.2	40.8 ± 2.1	31.5 ± 8.0
TH (m)	20.0 ± 4.7	25.8 ± 4.2	26.0 ± 5.4	24.0 ± 5.1
BD (g/cm^3)	0.12 ± 0.01	0.14 ± 0.01	0.15 ± 0.02	0.14 ± 0.02
CS (MPa)	9.5 ± 1.6	9.3 ± 0.5	11.9 ± 1.5	10.3 ± 1.7

n, number of trees; D, stem diameter at 1.3 m above the ground; TH, tree height; BD, basic density; CS, compressive strength parallel to grain. Values are mean ± standard deviation.

to the bark. Transverse sections of 20-30 μm in thickness were obtained by a sliding microtome (REM 710, Yamatokoki, Saitama, Japan). The transverse sections were stained with 1% safranin, dehydrated, mounted, and covered with cover slip. The images of *O. pyramidale* wood transverse sections were captured by a digital camera (E-P3, Olympus, Tokyo, Japan) attached to a light microscope (BX51, Olympus, Tokyo, Japan). Then, the digital images were transferred to the personal computer and analyzed with ImageJ software (National Institute of Hearth, Bethesda, MD). The diameters and frequency of vessels and cell wall thickness of wood fibers were measured according to our previous report (Pertiwi et al 2017a).

Statistical Analysis

For the statistical analysis, R software version 4.0.3 (R Core Team 2020) was used. For evaluation of radial variations of cell morphologies, the following four mixed-effects models (Table 2) were developed by using the lmer function in the lme4 packages (Bates et al 2015) and the nlme function in the nlme package (Pinheiro and Bates 2000). The model with the minimum Akaike Information Criterion (AIC, Akaike 1998) was considered as the best fitted model among four models (Eqs 1-4 in Table 2).

The following intercept-only linear mixed-effects model was also developed to evaluate the effects of radial growth rate on cell morphologies:

$$y_{ij} = \mu + Category_j + e_{ij} \qquad (5)$$

where y_{ij} is the ith measured values of the jth category, μ is general mean, $Category_j$ is random effect of category, and e_{ij} is residual.

For evaluating the xylem maturation process, estimated cambial age at a certain radial position was calculated by the radius (stem diameter at 1.3 m above the ground/2) dividing by tree age (Chowdhury et al 2009b). By using the best fitted

Table 2. Model form and comparison of AIC in each model for radial variation of each cell morphology in relation to distance from pith.

Function	Eq	Model	AIC					
			VEL	WFL	VD	VF	WFD	WFWT
Linear	(1)	$y_{ij} = \beta_0 x_{ij} + \beta_1 + u_{1j} + e_{ij}$	—	—	—	—	—	**−198.70**
Logarithmic	(2)	$y_{ij} = \beta_0 \ln x_{ij} + \beta_1 + u_{1j} + e_{ij}$	−519.64	−81.03	—	**448.24**	592.34	−191.11
Quadratic	(3)	$y_{ij} = \beta_0 x_{ij}^2 + \beta_1 x_{ij} + \beta_2 + u_{2j} + e_{ij}$	−526.28	−121.07	1140.46	464.51	**564.43**	−177.13
Michaelis–Menten	(4)	$y_{ij} = \beta_0 x_{ij} / (\beta_1 + x_{ij}) + \beta_2 + u_{2j} + e_{ij}$	**−532.68**	**−156.98**	**1106.41**	488.50	—	—

Eq, equation number; AIC, Akaike information criterion; VEL, vessel element length; WFL, wood fiber length; VD, vessel diameter; VF, vessel frequency; WFD, wood fiber diameter; WFWT; wood fiber wall thickness; y_{ij}, measured value for the ith radial position from the pith of the jth individual tree; x_{ij}, the ith radial position from the pith of the jth individual tree; β_0, β_1, and β_2, fixed-effect parameters; u_{1j} and u_{2j}, random-effect parameters of β_1 and β_2 at the individual level; e_{ij}, residual. Bold indicates minimum AIC among four models in each cell morphology. Hyphen indicates that the formula was not converged.

model from Eqs (1) to (4) in each cell morphology, radial variation of the cell morphology in relation to cambial age (the *i*th estimated cambial age was used instead of the *i*th radial distance from pith in the selected equation for radial variation of cell morphologies) were also evaluated. Then, mean absolute error (MAE) was calculated for both models (explanatory variables: radial distance from pith or estimated cambial age) by the method described in our previous report (Nezu et al 2022). In addition, normality of residuals in the both models was visually confirmed by quantile–quantile (Q–Q) plot. After that, the model with minimum MAE was considered as the best model for explaining the xylem maturation process.

Boundary of core wood and outer wood was determined by increasing ratio of cell length (Honjo et al 2005). Cell lengths were estimated at 1 mm interval up to 250 mm from pith by using the selected models with only fixed-effect parameter for cell length. Increasing ratio of cell length were calculated at 1 mm interval from pith.

RESULTS

Table 3 shows statistical values of cell morphologies. Mean value of nine trees was 0.59 mm in vessel element length, 2.16 mm in wood fiber length, 221 μm in vessel diameter, two vessels/mm^2 in vessel frequency, 35.5 μm in wood fiber diameter, and 1.03 μm in wood fiber wall thickness, respectively.

Results of model selection for radial variation of cell morphologies are shown in Table 2. Michaelis–Menten equation [Eq (4)] was fitted on radial variations of cell lengths and vessel diameter (Fig 1, Tables 2 and 4). Radial variation of vessel frequency, wood fiber diameter, and wood fiber wall thickness were well explained by logarithmic formula [Eq (2)], quadratic formula [Eq (3)], and linear formula [Eq (1)], respectively (Fig 1, Tables 2 and 4).

Table 5 shows variance components obtained by Eq (5) in each cell morphology. The model of wood fiber diameter was singular fitting. The Variance component ratio of category was 66.8%, 46.1%, 31.4%, 1.5%, and 33.7% for vessel element length, wood fiber length, vessel diameter, vessel frequency, and wood fiber wall thickness, respectively.

Values of MAE in selected models for radial variations of cell morphologies in relation to distance from pith or estimated cambial age were shown in Table 6. Smaller values of MAE obtained in the models in relation to distance from pith were found in all cell morphologies, except for vessel frequency and wood fiber diameter.

Figure 2 shows increasing ratio of cell length in relation to distance from pith. The values of distance from pith in which increase ratio of cell length became <1%, 0.5%, and 0.3% were 1.4, 5.8, and 10.4 cm in wood fiber length, and 0.8, 3.1, and 5.5 cm in vessel element length, respectively.

DISCUSSION

Cell Morphologies

The fiber length of *O. pyramidale* (2.16 mm, Table 3) was longer than those in other tropical

Table 3. Mean and standard deviation of each cell morphology for nine trees.

Cell morphology	Slow growth (n = 3)	Medium growth (n = 3)	Fast growth (n = 3)	Total (n = 9)
VEL (mm)	0.57 ± 0.02	0.58 ± 0.02	0.62 ± 0.00	0.59 ± 0.03
WFL (mm)	2.06 ± 0.07	2.16 ± 0.15	2.28 ± 0.06	2.16 ± 0.13
VD (μm)	218 ± 16	209 ± 20	236 ± 3	221 ± 18
VF (No./mm^2)	3 ± 1	3 ± 1	2 ± 0	2 ± 1
WFD (μm)	35.6 ± 1.5	35.5 ± 1.4	35.4 ± 1.7	35.5 ± 1.3
WFWT (μm)	0.96 ± 0.12	1.01 ± 0.04	1.12 ± 0.09	1.03 ± 0.10

n, number of trees; VEL, vessel element length; WFL, wood fiber length; VD, vessel diameter; VF, vessel frequency; WFD, wood fiber diameter; WFWT, wood fiber wall thickness. Values are mean ± standard deviation.

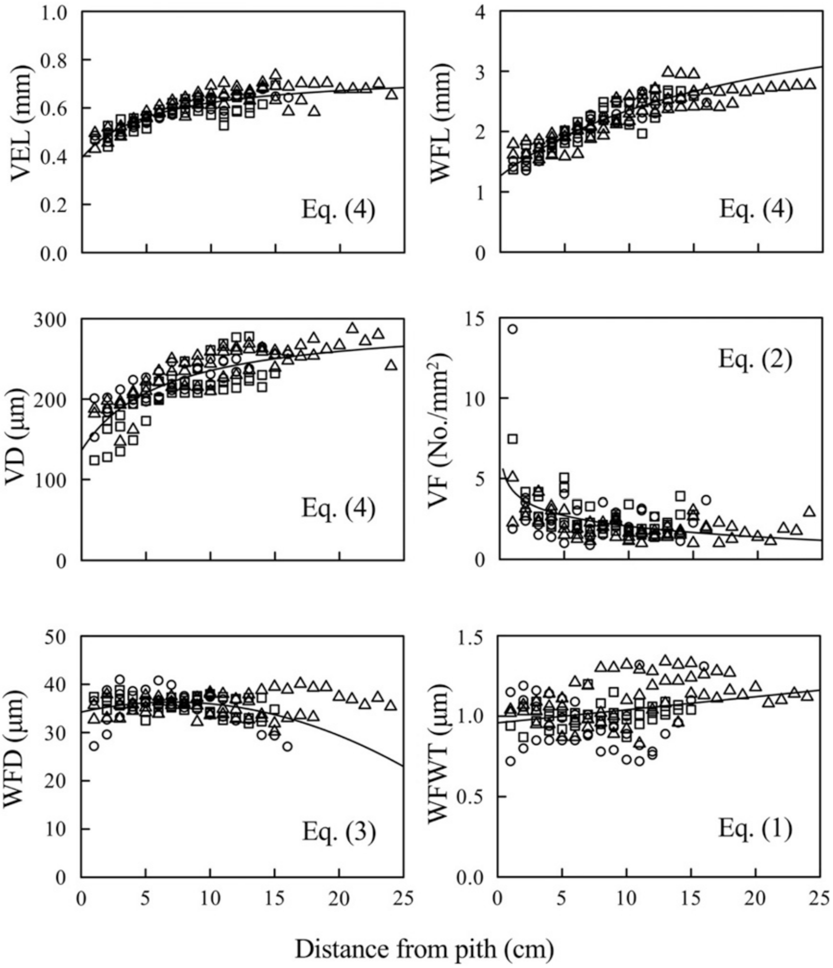

Figure 1. Radial variations of cell morphologies in relation to distance from pith. VEL, vessel element length; WFL, wood fiber length; VD, vessel diameter; VF, vessel frequency; WFD, wood fiber diameter; WFWT; wood fiber wall thickness. Eq (1), linear; Eq (2), logarithmic; Eq (3), quadratic; Eq (4), Michaelis–Menten (Table 2). Circle, triangle, and square indicate slow, medium, and fast growth, respectively. Solid line indicates regression line or curve based on the fixed parameters of the best model with smallest AIC in each cell morphology (Tables 2 and 4).

fast-growing trees, such as *A. mangium*, *A. auriculiformis*, *E. camaldulensis*, and *Falcataria moluccana* (Chowdhury et al 2009a; Honjo et al 2005; Ishiguri et al 2007; Nugroho et al 2012; Veenin et al 2005). However, the fiber length observed in the *O. pyramidale* in this study was similar to those of other species from the same family (Malvaceae), such as *Ceiba pentandra* (1.6-2.2 mm, Nordahlia et al 2016) and *Durio* spp. (1.4-2.3 mm, Ogata et al 2008). The vessel element length of *O. pyramidale* (0.59 mm, Table 3) was obviously longer than that of other tropical fast-growing tree species, such as *A. mangium* and *A. auriculiformis*, about 0.2 mm (Chowdhury et al 2009a; Honjo et al 2005) and other species in the same family such as *Heritiera* sp. (0.25 mm, Helmling et al 2018), *Abutilon stenopetalm* (0.22 mm), and *Bastardia viscosa* (0.19 mm) (Lindorf 1994). However, vessel element length of *O. pyramidale* was similar to that in *Durio* sp. (0.52 mm), which is the same family of *O. pyramidale* (Helmling et al 2018). As shown in Table 2 and Fig 1, Eq (4)

Table 4. Parameter estimates and associated standard errors (SE) and significance level of each parameter for the selected model in each cell morphology.

Cell morphology	Eq	Parameter	Estimates	SE	*t*-value	*p*-value
VEL	(4)	β_0	0.3704	0.0192	19.2660	<0.001
		β_1	7.0816	1.8745	3.7780	<0.001
		β_2	0.4066	0.0198	20.5330	<0.001
WFL	(4)	β_0	3.2383	0.3679	8.8023	<0.001
		β_1	19.6728	4.2111	4.6716	<0.001
		β_2	1.2640	0.0475	26.6338	<0.001
VD	(4)	β_0	162.49	11.91	13.64	<0.001
		β_1	6.37	1.68	3.78	<0.001
		β_2	136.18	9.16	14.86	<0.001
VF	(2)	β_0	−0.95	0.15	−6.39	<0.001
		β_1	4.26	0.31	13.57	<0.001
WFD	(3)	β_0	−0.042	0.009	−4.723	<0.001
		β_1	0.589	0.124	4.748	<0.001
		β_2	34.243	0.501	68.384	<0.001
WFWT	(1)	β_0	0.0081	0.0054	1.5020	0.247
		β_1	0.9584	0.0181	52.9810	<0.001

Eq, equation; SE, standard error; VEL, vessel element length; WFL, wood fiber length; VD, vessel diameter; VF, vessel frequency; WFD, wood fiber diameter; WFWT, wood fiber wall thickness. Eq (1), linear; Eq (2), logarithmic; Eq (3), quadratic; Eq (4), Michaelis–Menten. Equation of each cell morphology was selected as the best model in Table 2.

(Michaelis–Menten equations) was well fitted on the radial variations of cell length, suggesting that both wood fiber and vessel element lengths rapidly increased up to certain radial position from pith and then it became almost the stable. A distinct radial profile of vessel element length has been found in other tropical fast-growing tree species, such as *A. mangium* and *A. auriculiformis*: the vessel element length in these species is relatively constant from the pith toward the bark (Chowdhury et al 2009a; Honjo et al 2005). Thus, wood fiber and vessel element lengths in *O. pyramidale* showed relatively large elongation from the pith to the bark compared with those in other tropical fast-growing tree species, such as *Acacia* species.

Radial variation of vessel diameter was also well explained by Eq (4) (Michaelis–Menten equations, Table 2): vessel diameter showed rapid increase near the pith side and it gradually increased or become almost stable toward the bark side (Fig 1). The similar tendency in vessel diameter was also found in other fast-growing tree species, such as *Dysoxylum mollissimum* (Ishiguri et al 2016) and *Azadiracta excelsa* (Wahyudi et al 2016). Da Silva and Kyriakides (2007) reported

Table 5. Parameter estimates, standard errors (SE), and variance component for the models given by the Eq (5) for each cell morphology.

Cell morphology	Estimates	SE	Variance: Category	Variance: Residual	Variance component ratio of category (%)
VEL	0.590	0.015	0.00056	0.00028	66.8
WFL	2.164	0.063	0.00862	0.01005	46.1
VD	221.1	7.8	105.8	230.7	31.4
VF	2.5	0.2	0.0067	0.4478	1.5
WFWT	1.032	0.046	0.00390	0.00766	33.7

SE, standard error; VEL, vessel element length; WFL, wood fiber length; VD, vessel diameter; VF, vessel frequency; WFD, wood fiber diameter; WFWT, wood fiber wall thickness. Variance component ratio of category was calculated by dividing category variance by total variance (category + residual).

Table 6. Mean absolute error (MAE) for the developed models of radial variations for each cell morphology in relation to distance from pith or estimated cambial age.

		MAE	
Cell morphology	Eq	Distance from pith	Estimated cambial age
VEL	(4)	**0.025**	0.032
WFL	(4)	**0.139**	0.327
VD	(4)	**15.6**	18.4
VF	(2)	1.4	**1.0**
WFD	(3)	2.28	**1.90**
WFWT	(1)	**0.105**	0.109

Eq, equation listed in Table 2; VEL, vessel element length; WFL, wood fiber length; VD, vessel diameter; VF, vessel frequency; WFD, wood fiber diameter; WFWT, wood fiber wall thickness. Eq (1), linear; Eq (2), logarithmic; Eq (3), quadratic; Eq (4), Michaelis–Menten. Bold values indicate minimum MAE in each property.

that the vessel diameter in *O. pyramidale* was around 150-250 μm. In addition, the vessel diameter of *O. pyramidale* obtained in the present study was similar or slightly smaller than those of other species belonging to Malvaceae (Helmling et al 2018; Nordahlia et al 2016). Thereby, the vessel diameter values obtained in the present study were in accordance with those of the previous reports.

Da Silva and Kyriakides (2007) reported that the fiber wall thickness of *O. pyramidale* changed along with the density. As described in our previous study (Pertiwi et al 2017a), we found that the mean value of radial variation in basic density of

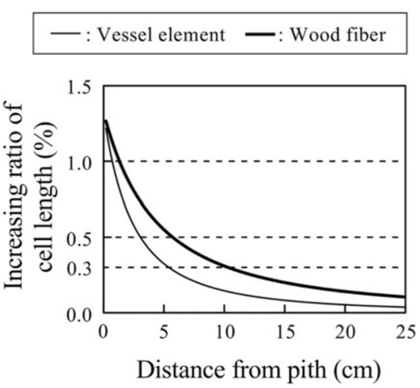

Figure 2. Radial variations of increasing ratio of cell lengths. Increasing ratio of cell lengths was determined by the best model with only fixed-effect parameters listed in Tables 2 and 4.

O. pyramidale was almost constant from pith up to 8 cm and then increased toward the bark. The mean value of fiber wall thickness slightly increased from pith to the bark, which was well explained by Eq (1) (Table 2, Fig 1). Thus, the increase of basic density in *O. pyramidale* might be correlated with increase of the wood fiber wall thickness. The wood fiber wall thickness of *O. pyramidale* wood is very small, around 1.03 μm (Table 3). Earlier study on *O. pyramidale* wood was carried out by Easterling et al (1982). They reported that the double wall thickness of *O. pyramidale* wood was 1.5 μm. In addition, Ogata et al (2008) mentioned that the wood fiber wall thickness of *O. pyramidale* is very thin, even though they did not report its real value. The wood fiber wall thickness in some species belong to Malvaceae family is around 2-5 μm, such as *Bombax ceiba*, *Bombax anceps*, *Bombax valentonit*, and *C. pentandra* (Nordahlia et al 2016). Wiemann and Williamson (1988) reported that the genetic character of pioneer tree species produces the cells as many as possible, and there is almost no time for cell wall thickening during early-stage growth. Thus, characteristics of *O. pyramidale* as pioneer tree species in tropics might be lead that the *O. pyramidale* wood possess the thinnest cell wall in early-stage growth among these Malvaceae family.

Effects of Radial Growth Rate on Cell Morphologies

Singular fitting on the model means that variances of one or more linear combinations of effects are (close to) zero (Bates et al 2015). The effect of the radial growth rate on wood fiber diameter was minimal in *O. pyramidale* because the developed model [Eq (5)] was singular fitting in wood fiber diameter. On the other hand, higher values of variance component ratio of growth category indicate that the measured properties may be affected by radial growth rate, suggesting that growth category influenced on the many cell morphologies in *O. pyramidale* (Table 5). However, fast-growth trees could be characterized by longer cell length, larger vessel diameter, and thicker cell wall of wood fiber (Table 3). In addition, the highest mean values of basic density and compressive strength were found in fast-growth trees among three growth categories (Table 1, Pertiwi et al 2017a). These characteristics in cell morphologies might not have negative impact for utilization of wood from this species as solid wood. It is concluded that the faster growth characteristics of this species did not always produce the lower quality of wood. Similar results were obtained in other tropical fast-growing tree species (Aiso-Sanada et al 2019; Hidayati et al 2017; Ishiguri et al 2016; Kojima et al 2009a,b; Makino et al 2012; Pertiwi et al 2017a,b; Wahyudi et al 2016). The characteristics of trees in fast-growth category in this study might be closely related with radial variations of cell morphologies (Fig 1): wood after about 10 cm from pith was longer cell lengths and thicker cell wall of wood fibers.

Xylem Maturation Process

Smaller values of MAE obtained in the models in relation to distance from pith were observed in all cell morphologies, except for vessel frequency and wood fiber diameter (Table 6), suggesting that radial variation of almost all cell morphologies in this species can be well-explained as function of distance from pith. It is thus concluded that the xylem maturation in *O. pyramidale* trees depends on the diameter growth rather than cambial age. Xylem maturation depending on diameter growth were also recognized in the many tropical fast-growing trees (Hidayati et al 2017; Honjo et al 2005; Ishiguri et al 2016; Kojima et al 2009a,b; Pertiwi et al 2018). Thus, characteristics of xylem maturation depending on diameter growth might be one of the characteristics in tropical fast-growing trees.

We previously reported that radial variations of basic density and mechanical properties of this species were almost constant up to 8 cm from pith and then sharply increased toward the bark (Pertiwi et al 2017a). As shown in Fig 2, the distance from pith in which increase ratio of cell length became <0.3% were 10.4 cm in wood fiber length, and 5.5 cm in vessel element length, respectively. Although the distance from pith showing increase ratio <0.3% was differed between wood fiber length and vessel element length, the boundary between core wood and outer wood judging from increase ratio of 0.3% was almost similar to the boundary determined by the radial variations of basic density and mechanical properties reported in a previous report (Pertiwi et al 2017a). Thus, it is considered that xylem maturation starts after 5-10 cm from pith (estimated age = 1.7-3.3 yr for 5 cm, and 3.4-6.5 cm for 10 cm) in this species.

Core wood (or sometimes referred as juvenile wood) in tropical hardwoods is characterized by lower wood density and strength properties with larger variations of cell morphologies and wood properties. On the other hand, higher wood density and strength properties with smaller variations of cell morphologies and wood properties are found in outer wood (or sometimes referred as mature wood) in hardwood species in tropics (Makino et al 2012; Wahyudi et al 2014). We previously reported that the value around pith area and near bark side was about 0.1 and 0.2 g/cm^3 in basic density, 10 and 20 MPa in compressive strength parallel to grain, 3 and 10 GPa in modulus of elasticity, and 15 and 40 MPa in modulus of rupture, respectively (Pertiwi et al 2017a). From the results obtained in the previous study and the present study, core wood (up to 5-10 cm from pith) and outer wood (after 5-10 cm from pith) can be characterized as follows: 1) core wood is lower basic density and mechanical properties with shorter cell length and thinner wood fiber wall but variations of basic density and mechanical properties are small, 2) outer wood is higher basic density and mechanical properties with longer cell length and thicker wood fiber wall but variations of basic density and mechanical properties are large. Thus, *O. pyramidale* trees might have different strategies of xylem maturation compared with other tropical fast-growing tree species. Further research is needed to clarify the relationships between xylem maturation process and tree survival strategies in pioneer species (eg sensitivity to light) in *O. pyramidale* as well as other tropical fast-growing tree species.

CONCLUSION

In the present study, the radial variations of anatomical characteristics were investigated for 7-yr-old

O. pyramidale trees with different radial growth rate by using linear or nonlinear mixed-effect models for clarifying xylem maturation process and effects of radial growth rate on the anatomical characteristics in this species. Results of model selection for radial variations of cell morphologies revealed that almost all cell morphologies, except for wood fiber diameter and wood fiber wall thickness, increased or decreased up to certain radial position from pith and then became almost stable. Variance component ratio of growth category showed relatively higher values in all cell morphologies except for vessel frequency and wood fiber diameter, suggesting that cell morphologies of this species were influenced by the radial growth rate. However, these characteristics in cell morphologies might not have negative impact for utilization of wood from this species as solid wood. It is concluded that the faster growth characteristics of this species did not always produce the lower quality of wood. Smaller values of MAE obtained in the models in relation to distance from pith were found in all cell morphologies, except for vessel frequency and wood fiber diameter. Thus, xylem maturation of this species mainly depended on diameter growth rather than cambial age. Boundary of core wood and outer wood was 5-10 cm from pith in which increasing ratio of cell length reached $<0.3\%$. Core wood was characterized as lower wood density and mechanical properties with shorter cell lengths and thinner wood fiber walls, whereas outer wood was characterized as higher wood density and mechanical properties with longer cell length and thicker wood fiber walls. In conclusion, radial growth promotion by intensive silvicultural treatments for plantation of this species will not always result in producing lower quality of wood.

ACKNOWLEDGMENTS

The authors express their sincere thanks to Mr. Setiyo Budi Nugroho, Parta Wood, Surabaya, Indonesia, for providing us wood materials, and to Mr. Soekmana Wedatama and Mr. Dany Mahardhika for helping us in the field experiments.

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