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Relationship between the xylem maturation process based on radial variations in wood properties and radial growth increments of stems in a fast-growing tree species, *Liriodendron tulipifera*

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Abstract

Promoting wood utilization from fast-growing tree species is one solution to address supply and demand issues relating to wood resources while sequestering carbon dioxide in large quantities. Information on the quality of wood from fast-growing tree species and its relationship with changes in stem size is essential for promoting the establishment of plantations and wood utilization of fast-growing tree species. To explore the relationship between the xylem maturation process and radial growth increments of stems in fast-growing tree species, we examined radial variations in annual ring widths and wood properties in *Liriodendron tulipifera* in Japan. The cambial ages at which current annual increment and mean annual increment values were greatest were 4.9 years and 7.4 years, respectively. Based on radial variations evaluated by mixed-effects modeling of wood properties, all properties increased or decreased near the pith before becoming stable towards the cambium. Changing ratios of multiple wood properties at 1-year intervals became stable after a cambial age of 9 years. These results point to an ecological strategy in *L. tulipifera*, in which there is a tradeoff between radial growth increments and wood properties. As part of this strategy, in response to competition among individual trees within a stand, the tree produces a large volume of xylem with lower physical and mechanical properties, allowing it to increase its volume faster than that of the surrounding trees. Subsequently, it produces xylem that is more stable, with greater physical and mechanical properties. This wood forms at a slower growth rate compared to the xylem that forms at the time of initial tree growth. Based on the ecological strategy adopted by *L. tulipifera*, wood that forms before a cambial age of 9 years can be used for utility applications, and wood that forms after a cambial age of 9 years can be used for structural applications.

Keywords: Annual ring width, Anatomical characteristics, Physical and mechanical properties, Core wood, Outer wood

Introduction

To fill the gap in the supply and demand for wood resources, one solution is to promote the utilization of wood from fast-growing tree species. In addition to resolving supply issues, the use of wood from fast-growing tree plantations can reduce atmospheric carbon dioxide, as the trees can act a massive carbon sink. Information on the quality of wood from fast-growing

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tree species is essential for promoting the establishment of plantations and wood utilization of fast-growing tree species.

In many cases, wood that forms in the region near the pith exhibits relatively unstable properties, whereas wood located outside of this zone has stable properties [1, 2]. The former is referred to as 'core wood' or 'juvenile wood' and the latter as 'outer wood' or 'mature wood' [1, 2]. The boundary between the core and outer wood is the position, where xylem maturation commences. In fast-growing tree species, xylem maturation is commonly estimated by radial variations using a single trait of the anatomical characteristics [2–9]. However, radial variation patterns can vary among species [4–6, 9, 10]. At the species level, physical and mechanical properties, as well as anatomical characteristics also can vary [4, 6, 9, 10]. For example, Ohbayashi and Shiokura [5] found that anatomical characteristics changed considerably near the pith, and then became stable in three tropical fast-growing tree species, *Anthocephalus chinensis* and *Gmelina arborea* in the Philippines and *Eucalyptus saligna* in Brazil. They also revealed that the oven-dry density increased slightly from the pith toward the cambium. Thus, the positions, where these properties become stable differed between anatomical characteristics and oven-dry density in these species. In a study on *Populus simonii* × *beijingensis* grown in China, cambial age showing a stable value of vessel lumen diameter in radial variation was earlier than that of wood fiber length and vessel element length [9]. Thus, to shed light on the boundary between the core and outer wood exactly, studies need to focus on radial variations in multiple traits in fast-growing tree species. We recently estimated the boundary position in tropical fast-growing tree species (*Acacia mangium*, *Maesopsis eminii*, and *Melia azedarach*) in Indonesia based on radial variations in anatomical characteristics and physical and mechanical properties [10]. Although the boundary positions differed, depending on which properties, it was possible to estimate the boundary using multiple wood properties, combined with mixed-effects modeling and an exponential function with convergence. To our knowledge, this method of determining boundary positions has not been applied in fast-growing tree species in temperate zones. The xylem maturation process in fast-growing tree species in temperate zone needs to be elucidated to promote the utilization of wood from these trees.

Radial growth increments can be represented by a sigmoid model, such as the Gomperz function [11]. Based on the sigmoid model, the current annual increment (CAI), which is the difference in radial growth at the beginning and end of the year, can be estimated. In addition to the CAI, the mean annual increment (MAI) can be calculated by dividing the growth values through time by the number of years. Both the CAI and MAI are used in silviculture. For example, thinning and harvesting are conducted at times of maximum CAI and MAI values, respectively. Numerous studies have investigated the relationship between the xylem maturation process and radial growth increments of stems expressed as CAI and MAI in many fast-growing tree species [3, 5, 7, 9, 12, 13]. In previous research, we estimated this relationship in various fast-growing tree species in tropical and boreal zones [14, 15]. In *Eucalyptus camaldulensis* in Thailand (tropical zone), after 5 years, the basic density and compressive strength values of the wood were stable, and the radial growth increments of stems reached maximum values [14]. However, based on an analysis of fiber increments in *Betula platyphylla* in Mongolia (boreal zone), xylem maturation began before the age of 10 years compared to the age showing maximum radial growth increments [15]. Thus, the relationship between the xylem maturation process and radial growth increments of stems might differ among properties, tree growth conditions, and others. To our knowledge, no studies on the xylem maturation process have focused on multiple properties of wood and radial growth increments of stems in fast-growing tree species in a temperate zone. The relationship between the xylem maturation process and radial growth rate should be elucidated in temperate fast-growing tree species belonging to genus *Populus*, *Eucalyptus*, *Liriodendron*, and *Paulownia*.

Liriodendron tulipifera L. is considered to be among the fastest growing tree species in the temperate zone. Although its wood is used for furniture and structural timber in North America [16], this species is used mainly in roadside and garden plantings in Japan. Recently, the establishment of plantations of fast-growing tree species with short rotations has been considered for improving the profitability of the forestry and wood industry in Japan. At present, the Japanese forestry and wood industry sectors, thus, focus on the fast-growing tree species, including *L. tulipifera*. Several trail examinations of *L. tulipifera* grown in Japan for furniture and structural lumber are desirable [17, 18]. Previously, we evaluated the quality of dimension lumber (2 by 4 lumber, 38 × 89 mm in cross section) from this species and found that its bending properties were similar to those of *Cryptomeria japonica*, which is the main species used for structural lumber in Japan [18]. However, the xylem maturation process in *L. tulipifera* and its relationship to radial growth increments are unknown.

In the present study, we investigated radial growth increments and radial variations in anatomical characteristics and physical and mechanical properties in *L. tulipifera* in Japan. We evaluated radial variations in wood properties using linear or nonlinear mixed-effects models. In addition, we estimated the cambial age at which xylem maturation began based on selected models of radial variations in multiple wood properties. Furthermore, we elucidated the relationship between the xylem maturation process and radial growth increments. We suggest appropriate utilization of *L. tulipifera* wood based on the ecological strategy of this species.

Materials and methods

Materials

Nine trees were obtained from the nursery of Utsunomiya University, Japan (36°32'N and 139°54'E). The nine trees were regenerated through coppicing stem after cutting the stems once. The trees were planted at 1 – 2 m intervals. The genetic source was unknown. The stem diameter was measured at 1.3 m above the ground using a diameter tape. After felling the trees, tree height was measured using a tape measure. The mean stem diameter and tree height values were 16.9 cm and 12.2 m, respectively (Table 1) [18]. The number of annual rings at 1.3 m above the ground ranged from 9 to 14 (Table 1), suggesting that the tree age was around 10 years or more [18].

A disc with 2 cm in width was taken at 1.3 m above the ground from each tree for measurements of annual ring width and anatomical characteristics. In addition, logs with 50 cm long were obtained from 0.8 to 1.3 m above the ground for use in bending and compressive tests.

Table 1 Statistical values of growth characteristics and wood properties of sampled trees

Property	Mean	SD	Minimum	Maximum
Stem diameter (cm)	16.9	4.6	11.7	26.4
Tree height (m)	12.2	3.6	6.8	16.3
Number of annual rings	11	2	9	14
Wood fiber length (mm)	1.42	0.05	1.35	1.51
Vessel element length (mm)	0.71	0.05	0.62	0.77
Vessel frequency (No./mm^2)	101	13	89	133
Vessel diameter (μm)	75.3	3.7	69.6	79.3
Wood fiber diameter (μm)	28.1	3.2	24.7	35.0
Wood fiber wall thickness (μm)	2.62	0.90	1.80	4.81
Air-dry density (g/cm^3)	0.43	0.05	0.37	0.50
MOE (GPa)	6.22	0.43	5.40	6.89
MOR (MPa)	60.0	6.2	52.2	72.0
Compressive strength (MPa)	30.4	2.3	27.3	34.7

Number of trees = 9. SD, standard deviation; MOE, modulus of elasticity; MOR, modulus of rupture. The stem diameter and number of annual rings were measured at 1.3 m above the ground [18]. Each statistical value in each wood property was calculated using the mean value of each tree obtained by averaging the value at each radial position within a tree

Measurements

Bark to bark radial strips with the pith (5 cm in a tangential direction and 1 cm in a longitudinal direction) were prepared from the discs. The transverse surface of the radial strip was sanded, and a transverse image of the strip was obtained using an image scanner (GT-9300; Epson, Suwa, Japan) with 800 dpi. Annual ring width was measured from pith to bark in two directions using ImageJ software (National Institute of Health, Bethesda, Maryland, USA). Annual ring width at each cambial age was determined by averaging annual ring width values obtained from two directions in a strip.

Small stick samples (10 [L] × 1 [R] × 1 [T] mm) and small block samples (10 [L] × 10 [R] × 5 [T] mm) were collected from the radial strips at 1 cm intervals from the pith to the cambium. The stick samples were macerated with Schultze's solution (100 mL of 35% nitric acid containing 6 g of potassium chloride). The macerated samples were placed on a slide glass and mounted with a coverslip and 75% glycerol. The lengths of 50 wood fibers and 30 vessel elements were then measured using a profile projector (V-12B; Nikon, Tokyo, Japan) and a digital caliper (CD-30C; Mitutoyo, Kawasaki, Japan). Transverse sections with 20 μm thickness were prepared from the block samples using a sliding microtome (REM-710; Yamato Kohki, Saitama, Japan). The sections were stained with 1% safranin, dehydrated with graded ethanol, and finally immersed in xylene. The sections were placed on glass slides and mounted using Bioleit (Oken Shoji, Tokyo, Japan) and coverslips. Digital images in each radial position were obtained using a microscope (BX-51; Olympus, Tokyo, Japan) equipped with a digital camera (DS-2210; Sato Shouji Inc., Kawasaki, Japan). Using the cross-sectional images at each radial position, vessel frequency, vessel diameter, wood fiber diameter, and wood fiber wall thickness were determined using ImageJ software. The number of vessels in the digital images was counted, while the vessel frequency was calculated by dividing the number of vessels by the area of each transverse sectional image. The diameters of wood fibers and wood fiber lumina were determined by averaging the major and minor radii, respectively. Each entire wood fiber wall region was regarded as a trapezoid, and the wood fiber wall thickness was calculated using the method described by Yoshinaga et al. [19]. In each radial position, 30 vessels and 50 wood fibers were measured.

Pith-to-bark radial boards with pith (2 cm width and 50 cm thickness) were collected from the logs. After air-drying in a laboratory at 20 ℃ and 65% relative humidity, the boards were planed so that they were 1 cm width. Finally, bending strength specimens (160 [L] × 10 [R] × 10 [T] mm) and compressive strength specimens (20 [L] × 10 [R] × 10 [T] mm) were successively prepared from the pith toward the bark of the boards. The static bending test was conducted using a universal testing machine (MSC-5/200-2; Tokyo Testing Machine, Tokyo, Japan). A load was applied to the center of the specimens on the radial surface with a 140 mm span and 4 mm/min load speed. The load and deflection were recorded using a personal computer. The modulus of elasticity (MOE) and modulus of rupture (MOR) were calculated using the following formulae:

$$\mathrm{MOE(GPa)} = \frac{\Delta P l^3}{4 \Delta Y b h^3} \times 10^{-3} \quad (1)$$

$$\mathrm{MOR\ (MPa)} = \frac{3Pl}{2bh^2} \quad (2)$$

where ΔP (N) is the difference in the load between 10 and 40% values of the maximum load, l (mm) is the length of the span, ΔY (mm) is deflection due to ΔP, b (mm) and h (mm) are the width and height of the specimen, and P (N) is the maximum load. After the static bending test, a block (10 [L] × 10 [R] × 10 [T] mm) without any visual defects was prepared from each specimen for measuring the moisture content and air-dry density. A compressive test was conducted using a universal testing machine with a load speed of 0.5 mm/min.

Compressive strength parallel to grain was calculated using the following formula:

$$\text{Compressive strength (MPa)} = \frac{P}{A} \quad (3)$$

where P (N) is the maximum load and A (mm^2) is the cross-sectional area of the specimen. In the test, the mean ± standard deviation of the moisture content of the bending test specimens and compressive test specimens was 13.3 ± 0.3% and 10.9 ± 0.2%, respectively.

Statistical analysis

Statistical analysis was conducted using R (Version 4.0.2, [20]). To evaluate radial growth increments and radial variations in wood properties, linear or nonlinear mixed-effects models were developed using the lmer package [21] or nlme package [22].

The estimated stem diameter (without bark) in relation to cambial age was regarded as twice the value of the cumulative annual ring width at 1.3 m above the ground in each tree. To evaluate radial growth increments, radial variations in estimated stem diameters at 1.3 m above the ground in relation to cambial age were determined using nonlinear mixed-effects models based on the Gompertz function (Table 2). In each model, individual tree was the random effect (Table 2). Among the three models, the most parsimonious model was selected based on the Akaike information criterion (AIC) [23]. In addition, the statistical significance of each fixed-effect parameter was evaluated in the selected model using the lmerTest package [21]. Based on the selected model, the CAI and MAI were calculated using the following formulae:

$$\mathrm{CAI(cm/y)} = a_0 a_2 \exp\left(-e^{a_1 - a_2 \mathrm{CA}}\right) \times e^{a_1 - a_2 \mathrm{CA}} \quad (4)$$

$$\mathrm{MAI(cm/y)} = \frac{a_0 \exp(-e^{a_1 - a_2 \mathrm{CA}})}{\mathrm{CA}} \quad (5)$$

where a_0, a_1, and a_2 are the parameters obtained from the selected radial growth model, and CA is the cambial age. The equation of CAI is the first derivative equation of the radial growth model in Table 2. Based on Eqs. 4 and 5, the cambial ages at which CAI and MAI values were greatest were calculated. In addition, the ratio of the variance component of individual trees and residual to the total variance was calculated [24].

To evaluate radial variations in wood properties, linear or nonlinear mixed-effects models were developed based on linear (Models b-1 and b-2), logarithmic (Models c-1 and c-2), or quadratic functions (Models d-1 to d-3), with cambial age as the explanatory variable, wood properties as the response variable, and individual tree as the random effect (Table 3). Among the developed models, the model with the lowest AIC value was considered the most parsimonious model. In the selected model, the significance of the fixed-effect parameters and the ratios of

Table 2 Developed models for stem diameter in relation to cambial age and obtained AIC values in each model

Model	Equation	Random effects	AIC
a-1	$D_{ij} = (a_0 + Tree_{0j})\exp(-e^{a_1 - a_2 CA_{ij}}) + e_{ij}$	Asymptotic value	**236.15**
a-2	$D_{ij} = a_0\exp(-e^{a_1 + Tree_{1j} - a_2 CA_{ij}}) + e_{ij}$	Start position of the curve	–
a-3	$D_{ij} = a_0\exp\left(-e^{a_1 - (a_2 + Tree_{2j}) CA_{ij}}\right) + e_{ij}$	Slope	293.66

D_{ij}, estimated stem diameter at 1.3 m above the ground at the *i*th cambial age of the *j*th individual tree; CA_{ij}, *i*th cambial age of the *j*th individual tree; a_0, a_1, and a_2, fixed-effect parameters; $Tree_{0j}$, $Tree_{1j}$, and $Tree_{2j}$, random-effect parameters at the *j*th individual tree level; e_{ij}, residuals; –, the model failed to converge. The bold value represents the minimum AIC value

Table 3 Developed model for the radial variation of wood properties and AIC values of each model

Model	Equation	Random effects	AIC									
			Wood fiber length	Vessel element length	Vessel frequency	Vessel diameter	Wood fiber diameter	Wood fiber wall thickness	Air-dry density	MOE	MOR	Compressive strength
b-1	$WP_{ij} = (b_0 + Tree_{0j})CA_{ij} + b_1 + e_{ij}$	Slope	−42.601	−202.72	590.04	407.34	292.43	119.05	−181.55	129.18	367.59	283.83
b-2	$WP_{ij} = b_0CA_{ij} + b_1 + Tree_{1j} + e_{ij}$	*y*-intercept	−39.643	−194.19	589.34	411.29	251.08	85.408	−198.38	132.31	360.97	278.70
c-1	$WP_{ij} = (c_0 + Tree_{0j})\ln(CA_{ij}) + c_1 + e_{ij}$	Slope	**−55.725**	**−213.43**	562.33	388.96	–	–	−193.37	**122.75**	359.30	278.85
c-2	$WP_{ij} = c_0\ln(CA_{ij}) + c_1 + Tree_{1j} + e_{ij}$	*y* value at 1st annual ring from pith	−54.718	–	**559.09**	**388.93**	**244.59**	**67.019**	**−199.62**	126.48	**356.64**	**275.82**
d-1	$WP_{ij} = (d_0 + Tree_{0j})CA_{ij}^2 + d_1CA_{ij} + d_2 + e_{ij}$	Opening quadratic parabolas	−42.334	–	573.03	403.80	330.40	165.56	−152.97	131.17	374.51	290.87
d-2	$WP_{ij} = d_0CA_{ij}^2 + (d_1 + Tree_{1j})CA_{ij} + d_2 + e_{ij}$	Slope of the tangent line at the *y*-intercept	−42.471	−195.05	571.63	402.35	299.73	128.39	−167.53	132.70	369.72	289.05
d-3	$WP_{ij} = d_0CA_{ij}^2 + d_1CA_{ij} + (d_2 + Tree_{2j}) + e_{ij}$	*y*-intercept	−41.656	–	566.65	402.12	254.35	–	−183.35	137.92	–	284.33

MOE, modulus of elasticity; MOR, modulus of rupture; WP_{ij}, wood properties at the *i*th cambial age of the *j*th individual tree; CA_{ij}, *i*th cambial age of the *j*th individual tree; b_0, b_1, c_0, c_1, d_0, d_1, and d_2, fixed-effect parameters; $Tree_{0j}$, $Tree_{1j}$, and $Tree_{2j}$, random-effect parameters at the *j*th individual tree level; e_{ij}, residuals; –, the model failed to converge. The bold value represents the minimum AIC value in each wood property the variance components of the random-effect parameters to the total variance were calculated [24].

The cambial age at which xylem maturation commenced was determined according to the modified method of Ngadianto et al. [10]. In the present study, the explanatory variable was considered cambial age instead of distance from pith in Ngadianto et al. [10]. Each wood property was estimated at 1-year intervals in the selected model containing only the fixed-effect parameters. The changing ratio of various wood properties at 1-year intervals were calculated as absolute values. An exponential model with a plateau was fitted to the data for changing the ratio of each wood property using the following formula:

$$\mathrm{CR}_1 = a_1 {b_1}^{\mathrm{CA}_1} + c_1 \quad (6)$$

where CR_1 is the changing ratio of each wood property, CA_1 is the cambial age, and a_1, b_1, and c_1 are fixed-effect parameters. c_1 is the plateau value in Eq. (6). An exponential model was then fitted to the data for the changing ratio using the following formula:

$$\mathrm{CR}_2 = a_2 {b_2}^{\mathrm{CA}_2} \quad (7)$$

where CR_2 is the changing ratio of each wood property, CA_2 is the cambial age, and a_2 and b_2 are fixed-effect parameters. When CR_2 in Eq. (7) equaled c_1 in Eq. (6), CA_2 was regarded as the cambial age at which xylem maturation commenced.

Results

In the radial growth model, the minimum AIC value was obtained in Model a-1 (Table 2). The p-values of the fixed-effect parameters in the model were all below 0.05 (Table 4). Therefore, the model based on Model a-1 was regarded as the optimum model for explaining radial growth. In addition, high variance component in individual tree (99.1%) in the model (Table 4) suggested that asymptote values of stem diameter differed at the individual tree level. Figure 1 shows the regression curves for the estimated stem diameter, CAI, and MAI in relation to cambial age based on the selected model with only fixed-effect parameters. The estimated stem diameter increased from the pith toward the bark, whereas radial growth increments decreased with an increase in cambial age. The cambial age at which CAI and MAI values were greatest were 4.9 and 7.4 years, respectively (Fig. 1).

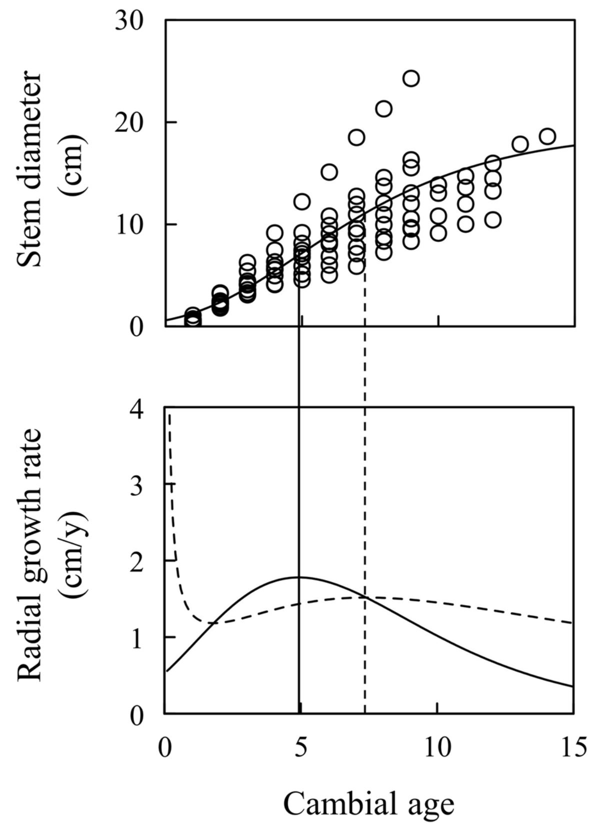

Fig. 1 Changes in estimated stem diameter and radial growth rate in relation to cambial age. Note: Circles and solid line in the upper figure represent original values of estimated stem diameter at 1.3 m above the ground and regression curve based on the fixed-effect parameters of the selected model (Table 4). Solid and dashed lines in the lower figure indicate CAI and MAI based on the selected model (Model a-1 in Table 2) with only fixed-effect parameters. Solid and dashed lines in the vertical direction of both figures indicate cambial age showing maximum CAI (4.9 years) and MAI (7.4 years)

Table 4 Estimated values of the fixed and random effects of the selected models for stem diameter in relation to cambial age

Fixed-effect parameters					Random-effect parameters			
Parameter	Estimates	SE	*t*-value	*p*-value	Parameter	SD	Variance component	Variance component ratio (%)
a_0	19.186	2.166	8.86	< 0.001	$Tree_{0j}$	6.219	38.673	99.1
a_1	1.242	0.031	40.15	< 0.001	e_{ij}	0.588	0.346	0.9
a_2	0.252	0.012	21.04	< 0.001				

Fixed- and random-effects parameters were estimated by the selected model (Model a-1 in Table 2). SE, standard error; SD, standard deviation

At the cambial age with maximum CAI and MAI values, the estimated stem diameter values were 7 and 11 cm, respectively, regardless of individual trees.

Mean values of wood properties in the nine trees are shown in Table 1. Among seven developed radial variation models, Model c-1 or c-2 was selected for all wood properties (Table 3). The p-values of the fixed-effect parameters (c_0 and c_1) in each wood property were below 0.05 (Table 5), suggesting that the model based on the logarithmic function was the optimum model for explaining radial variations in these wood properties. Minimum AIC values were obtained in the Model c-1 with the random slope of individual trees in wood fiber length, vessel element length, and MOE, whereas the Model c-2 with the random intercept of the individual tree showed minimum AIC values in vessel frequency, vessel diameter, wood fiber diameter, wood fiber wall thickness, air-dry density, MOR, and compressive strength (Table 3). Figure 2 shows the regression curves for radial variation of all wood properties based on only the fixed-effect parameters of the selected model. All wood properties increased or decreased near the pith and then became stable toward the cambium. Based on the selected models, the highest variance component value for an individual tree was obtained for wood fiber wall thickness (90.8%), followed by wood fiber diameter (88.0%), air-dry density (71.3%), MOR (39.8%), vessel element length (38.5%), vessel diameter (27.7%), vessel frequency (27.6%), compressive strength (26.9%), MOE (11.2%), and wood fiber length (2.6%) (Table 5).

The changing ratio of each wood property at 1-year intervals and the regression curve based on the exponential function of all wood properties in relation to cambial age are shown in Fig. 3. As shown by the results, the changing ratio became stable after a cambial age of 9 years (estimated stem diameter = approximately 14 cm) (Table 6).

Discussion

When calculating cambial ages at which CAI and MAI values are maximum based on the Gompertz function, the parameters a_1 and a_2 are used [9]. If a model including random effects in a_1 or a_2 was selected, CAI and MAI are affected by random effects. In the present study, the model with a random effect of individual trees on the parameter of a_1 or a_2 was not selected in the radial growth model, indicating that genetic factors seem to

Table 5 Estimated values of the fixed and random effects of the selected models for radial variations of wood properties

Property	Model	Fixed-effect parameters					Random-effect parameters			
		Parameter	Estimates	SE	*t*-value	*p*-value	Parameter	SD	Variance component	Variance component ratio (%)
Wood fiber length	c-1	c_0	0.2991	0.0326	9.162	< 0.001	$Tree_{0j}$	0.0220	0.0005	2.6
		c_1	0.9300	0.0543	17.117	< 0.001	e_{ij}	0.1354	0.0183	97.4
Vessel element length	c-1	c_0	0.0545	0.0125	4.370	< 0.001	$Tree_{0j}$	0.0273	0.0007	38.5
		c_1	0.6226	0.0143	43.576	< 0.001	e_{ij}	0.0345	0.0012	61.5
Vessel frequency	c-2	c_0	− 41.55	3.73	− 11.143	< 0.001	$Tree_{1j}$	9.66	93.25	27.6
		c_1	167.70	7.14	23.496	< 0.001	e_{ij}	15.63	244.28	72.4
Vessel diameter	c-2	c_0	15.469	0.987	15.676	< 0.001	$Tree_{1j}$	2.561	6.561	27.7
		c_1	50.300	1.889	26.622	< 0.001	e_{ij}	4.135	17.100	72.3
Wood fiber diameter	c-2	c_0	0.767	0.275	2.786	0.007	$Tree_{1j}$	3.076	9.461	88.0
		c_1	26.807	1.127	23.785	< 0.001	e_{ij}	1.135	1.287	12.0
Wood fiber wall thickness	c-2	c_0	0.8169	0.0675	12.094	< 0.001	$Tree_{1j}$	0.875	0.765	90.8
		c_1	1.2988	0.3133	4.145	< 0.001	e_{ij}	0.278	0.077	9.2
Air-dry density	c-2	c_0	0.0479	0.0075	6.345	< 0.001	$Tree_{1j}$	0.0395	0.0016	71.3
		c_1	0.3562	0.0176	20.258	< 0.001	e_{ij}	0.0250	0.0006	28.7
MOE	c-1	c_0	0.9634	0.2047	4.707	< 0.001	$Tree_{0j}$	0.2247	0.0505	11.2
		c_1	4.7813	0.2927	16.333	< 0.001	e_{ij}	0.6344	0.4025	88.9
MOR	c-2	c_0	9.038	1.718	5.262	< 0.001	$Tree_{1j}$	4.680	21.907	39.8
		c_1	46.800	3.087	15.161	< 0.001	e_{ij}	5.756	33.135	60.2
Compressive strength	c-2	c_0	2.140	0.810	2.642	0.011	$Tree_{1j}$	1.659	2.753	26.9
		c_1	27.247	1.375	19.819	< 0.001	e_{ij}	2.735	7.481	73.1

MOE, modulus of elasticity; MOR, modulus of rupture; SE, standard error; SD, standard deviation. Fixed- and random-effects parameters were estimated by the selected model (Table 3)

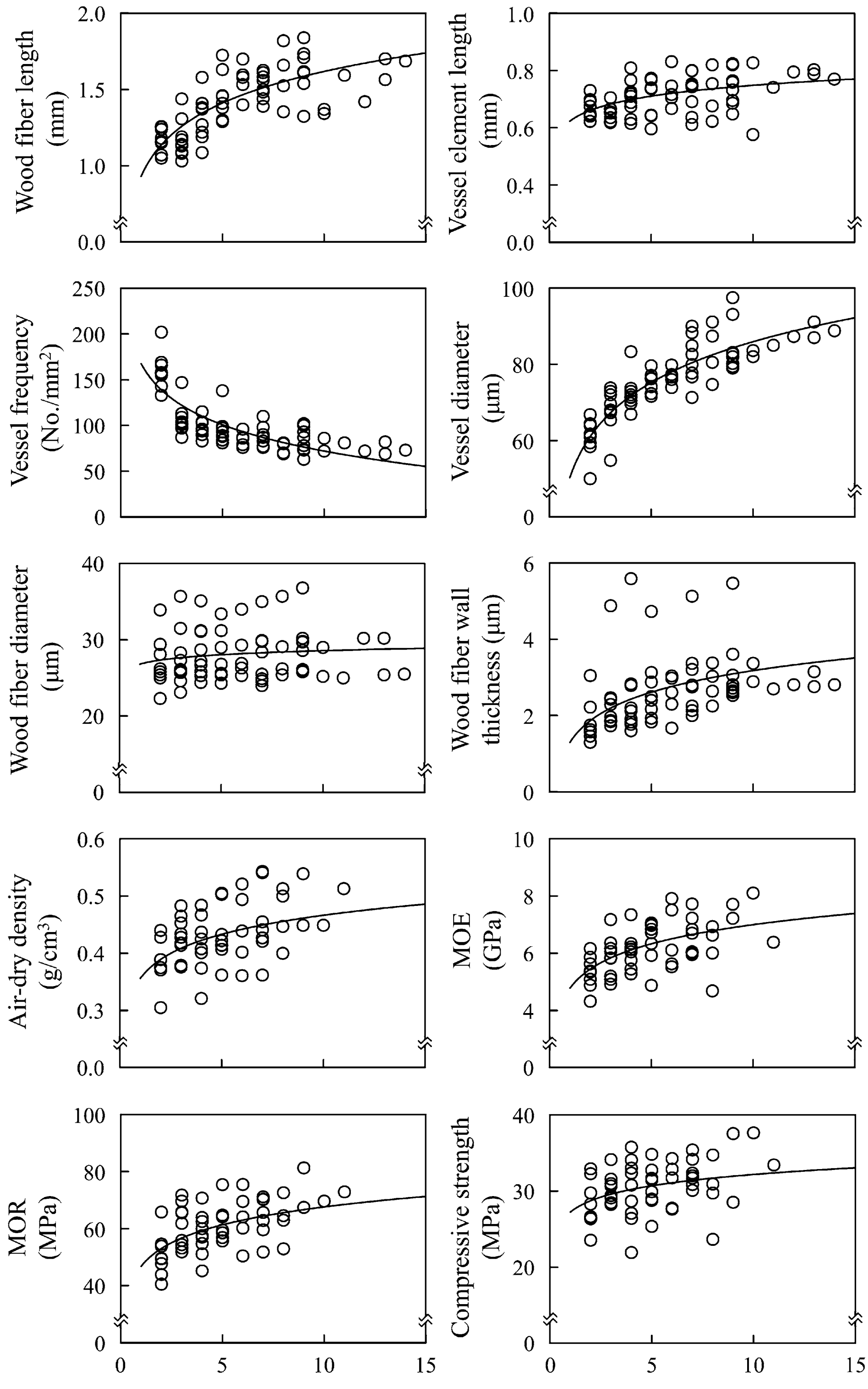

Fig. 2 Radial variations of wood properties. Note: Circles and solid curves represent the original values of each wood property and regression curve based on the fixed-effect parameters of the selected model (Table 5). MOE, modulus of elasticity; MOR, modulus of rupture

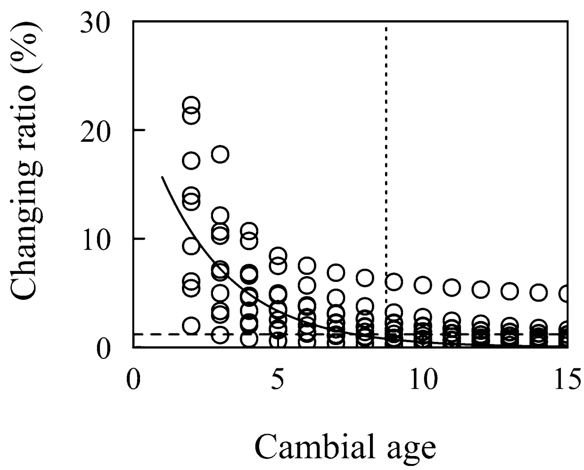

Fig. 3 Radial variation of the changing ratio of various wood properties at 1-year intervals in relation to cambial age. Circles represent estimated values of changing ratio at 1-year intervals based on the fixed-effect parameter in the selected model for each wood property. Solid line shows regression curve of changing ratio of 10 wood properties $\left(CR_2 = 28.251 \times 0.696^{CA_2}\right)$. Dashed line represents asymptote value ($c_1 = 1.1917$). The dotted line represents the estimated cambial age starting xylem maturation (interception point between CR_2 and c_1).

affect radial growth increment but not cambial age showing maximum radial growth increment of stems.

A number of studies have examined radial variations and mean values of several wood properties in *L. tulipifera* in the United States [16, 25, 27] and Japan [17, 18, 28, 29]. Furukawa et al. [28] found that wood fiber length increased from the pith, while vessel element length slightly increased from the pith in *L. tulipifera* in Japan. In a study of *L. tulipifera* in North Carolina, United States, at the age of approximately 50 years, wood fiber length increased from the pith (1.0 mm) toward the bark (1.9 mm) [25]. In another study of *L. tulipifera* in the United States, Shupe et al. [26] reported that basic density at 1 m above the ground increased toward the bark (0.4 g/cm^3 near the pith and 0.5 g/cm^3 in outermost) at the age of 40 years. The radial variation patterns of cell length and air-dry density obtained in the present study (Fig. 2) were similar to those found in previous studies [26, 28].

Itoh [29] reported that the vessel diameter of *L. tulipifera* in Japan ranged from 50 to 70 µm. In a study on *L. tulipifera* in the eastern United States, Uzcategui et al. [27] reported the following range of minimum to maximum values for the mechanical properties: 0.36 – 0.60 g/cm^3 for air-dry density, 7.07 – 11.5 GPa for MOE, 54.5 – 108.6 MPa for MOR, and 30.4 – 56.3 MPa for compressive strength. Similarly, another study on the mechanical properties of *L. tulipifera* in the United States reported values of 10.90 GPa for MOE, 70.0 MPa for MOR, and 38.2 MPa for compressive strength under 12% moisture contents [16]. The mean values for vessel diameter, air-dried density, MOR, and CS of the nine trees in the present study were within the range reported in the literature, whereas the value for MOE was relatively lower.

The selected model for explaining radial variations in cell length and MOE included the variables of individual tree as the random slope (Model c-1, Table 3). Thus, the rate of change in the aforementioned properties from the pith toward the cambium might differ among individual trees. On the other hand, the model with a *y*-value at the first annual ring from the pith of the individual tree was selected in vessel frequency, vessel diameter, wood

Table 6 Relationships between radial growth increment and xylem maturation process in fast-growing tree species

Species	Location	Climates	Cambial age showing peak value of CAI	Cambial age showing peak value of MAI	Cambial age where wood properties became stable (Wood properties used as the indicator)	Reference
L. tulipifera	Japan	Temperate	4.9	7.4	9 (multiple wood properties)	In this study
Populus simonii × beijingensis	China	Dry	5.7	8.8	9.8 (wood fiber length) 10.2 (vessel element length) 7.2 (vessel lumen diameter)	Tsuchiya and Furukawa [9]
E. camaldulensis	Thailand	Tropical	4.0	–	5.5 (basic density and compressive strength)	Nezu et al. [14]
B. platyphylla	Mongolia	Subarctic	28.8	–	15 – 17 (wood fiber length)	Erdene-ochir et al. [15]

Climate classification is based on Köppen climate classification fiber diameter, wood fiber wall thickness, air-dry density, MOR, and compressive strength. This finding indicated that these wood properties depend on the values at the first annual ring, which differed among individual trees, and that the radial variation pattern itself is not affected by differences among individual trees. Based on these results, we conclude that the effect of the individual tree on radial variation patterns might differ among properties in *L. tulipifera*. Thus, the cambial age at which xylem maturation commences in this species can be determined using multiple wood properties, regardless of differences in individual trees.

The relationship between radial growth increments and the xylem maturation process based on radial variation patterns of single or several wood properties has been reported for several fast-growing tree species in dry [9], tropical [14], and subarctic climates [15] (Table 6). In these studies, wood properties became stable below the age of 10 years at the time of peak CAI and MAI values in *L. tulipifera* in Japan (Fig. 1), *Populus* × *beijingensis* in China [9], and *E. camaldulensis* in Thailand [14], suggesting that xylem maturation occurs in accordance with a decrease in the radial growth rate in these species. Wireman and Williamson [30] showed that the radial increase in basic density was associated with a shift in the allocation of resources from growth with the production of low-specific gravity wood to greater structural reinforcement of the trunk (production of denser wood) in three tropical pioneer species (*Hampea appendiculata*, *Heliocarpus appendiculatus*, and *Ochroma pyramidale*) in Costa Rica. Larjavaara and Muller-Landan [31] hypothesized that a large stem of low-density wood could have greater strength at a lower construction cost than a thinner stem of high-density wood. Therefore, several fast-growing tree species, including *L. tulipifera*, in tropical and temperate zones appear to produce a large volume of xylem with lower physical and mechanical properties to increase their volume faster than that of surrounding trees due to competition among individual trees within a stand. After reaching a certain stem diameter, xylem with stable wood properties forms at a slower growth rate. The trade-off between radial growth increments and wood properties with an increase in cambial age might occur due to ecological strategy in fast-growing tree species. Rungwattana and Hietz [13] stated that stem diameter is an essential parameter to include in studies on the functional ecology of wood for understanding the different ecological strategies of tree species. However, as stem diameter is a one-dimensional trait that serves as an index of tree size, changes in tree height and/or volume should also be considered.

Wood properties vary from the pith toward the bark in *L. tulipifera* due to the ecological strategy of this species. Based on the radial variation models of multiple wood properties, we estimated cambial age at the time of xylem maturation commencement. Our results suggest that *L. tulipifera* wood can be divided into unstable and stable, with unstable wood having lower physical and mechanical properties and stable wood having greater physical and mechanical properties. In general, the latter type of wood is suited to structural applications. Thus, *L. tulipifera* wood that forms after the commencement of xylem maturation (i.e., cambial age of 9 years) can be utilized for structural applications, whereas wood that forms before this cambial age can be utilized for utility applications. Exploring the relationship between the xylem maturation process and radial growth increments of stems in other fast-growing tree species in relation to the ecological strategy of the species can promote wood utilization.

Conclusions

To elucidate the relationship between the xylem maturation process based on multiple properties and radial growth increments of stems in a fast-growing tree species, radial variations in annual ring width and anatomical, physical, and mechanical properties were determined in *L. tulipifera*. The maximum current annual increment and mean annual increment found after 4.9 and 7.4 years, respectively, and changes in the ratios of multiple wood properties became stable after a cambial age of 9 years, suggesting that xylem maturation in *L. tulipifera* occurs just after a decrease in radial growth increments of the stems. Based on our findings, *L. tulipifera* appears to adopt an ecological strategy, whereby it produces a large volume of xylem with lower physical and mechanical properties in the initial stages of growth, followed by the production of xylem with stable wood properties. Based on the ecological strategy adopted by *L. tulipifera*, wood that forms before a cambial age of 9 years can be used for utility applications, whereas wood that forms after 9 years is more stable, with greater physical and mechanical properties, and can be used for structural applications. Understanding the relationship between radial growth increments and wood properties in relation to ecological strategies may promote wood utilization of fast-growing tree species.

Abbreviations

MOE: Modulus of elasticity; MOR: Modulus of rupture; AIC: Akaike information criterion; CAI: Current annual increment; MAI: Mean annual increment.

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Author contributions
IN and FI designed the research layout, collected and analyzed data, and drafted the manuscript. All authors discussed the results and conclusions and contributed to writing the final manuscript.

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The data sets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing interests
The authors declare that they have no competing interests.

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