EVALUATION OF RELATIONSHIPS BETWEEN CAMBIAL AGE-RELATED CHANGES IN RADIAL GROWTH INCREMENTS OF STEMS AND WOOD PROPERTIES IN *PAULOWNIA TOMENTOSA* TREES GROWN IN FUKUSHIMA, JAPAN

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Abstract. Information on the relationship between cambial age-related changes in stem size and wood properties is essential for promoting plantation forestry and utilization of fast-growing tree species. In this study, cambial age-related changes in radial growth increments of stems and wood properties were preliminarily examined using mixed-effects modeling of ~25-yr-old *Paulownia tomentosa* trees planted in Fukushima, Japan. A Gompertz model was well-fitted to cambial age-related changes in stem diameter. The cambial ages showing the maximum current annual increment and mean annual increment estimated by the radial growth model were 5.4 and 7.3 yr, respectively. Although radial growth decreased after a certain cambial age, the mean annual increment value was still more than 2 cm per year until 25 yr. Most anatomical characteristics increased from the pith and stabilized toward the cambium. On the other hand, physical and mechanical properties were stable from the pith toward the cambium: the fixed-effect parameter estimates in the selected *y*-intercept model were 0.29 $g\cdot cm^{-3}$ for air-dry density, 4.02 GPa for MOE, and 40.3 MPa for MOR. Thus, a large volume of xylem with low and stable physical and mechanical properties values was produced for more than 20 yr, suggesting that the rotation age of plantations of this species can be determined from the viewpoint of wood quantity. In addition, the wood can be used where low density, but stable properties is an advantage at any age in this species.

Keywords: Anatomical characteristics, physical properties, mechanical properties, mixed-effects modeling, *Paulownia tomentosa*.

INTRODUCTION

Woody biomass production from fast-growing plantations is desirable to meet the increasing demands for wood resources. Because fast-growing trees can store massive carbon from the atmosphere in a short time, planting these trees also has merit for solving environmental issues. Therefore, promoting the establishment of plantations and wood utilization of fast-growing tree species is important not only to sustainable wood resources but also to minimize global warming by sequestering atmospheric carbon dioxide. At present, among several fast-growing tree species

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including *Melia azedarach* L., *Cunninghamia lanceolata* (Lamb.) Hook., *Liriodendron tulipifera* L., and *Eucalyptus* spp. have been considered as candidates for plantations in Japan (Hirohashi et al 2012; Yokoo et al 2021; Nezu et al 2022; Ido et al 2023).

The relationships between radial growth increments of the stem and anatomical characteristics have been examined in several broad-leaved tree species concerning trade-offs between quantity and quality of wood (Tsuchiya and Furukawa 2008, 2009a, 2009b, 2009c). Generally, the growth stages of trees can be divided into young, middle, and old based on the cambial age-related changes in radial growth increments of the stem (Fig 1, Kataoka 1992; Salas-Eljatib et al 2021). The young stage occurs from the beginning of the radial stem increments to the age t_1 at the point of the maximum current annual increment (CAI). The middle stage is from age t_1 to age t_2 at the point of the mean annual increment (MAI). The old stage is over age t_2. Age t_1 corresponds to the inflection point of the S-shaped growth curve of the radial stem increment, and age t_2 is when CAI equals MAI (Kataoka 1992). To estimate the cambial age at the maximum point of CAI and MAI, the regression model based on the Gompertz growth function is fitted to the stem diameter or cumulative ring width over time in several broad-leaved tree species (Tsuchiya and Furukawa 2008, 2009a, 2009b, 2009c). On the other hand, a nonlinear regression model based on a quadratic function with a plateau was applied to describe cambial age-related changes in anatomical characteristics (Tsuchiya and Furukawa 2008, 2009a, 2009b, 2009c). The maturation age of each anatomical characteristic was regarded as the cambial age reaching a plateau value in the regression model. As a result, the maturation age of anatomical characteristics, such as wood fiber length and vessel lumen diameter, is similar at ages t_1 or t_2 in broad-leaved tree species (Tsuchiya and Furukawa 2009a). Tsuchiya and Furukawa (2009b) also investigated the relationships between the maturation ages of the wood fiber length, vessel element length, and vessel lumen diameter and the boundary age between the stages

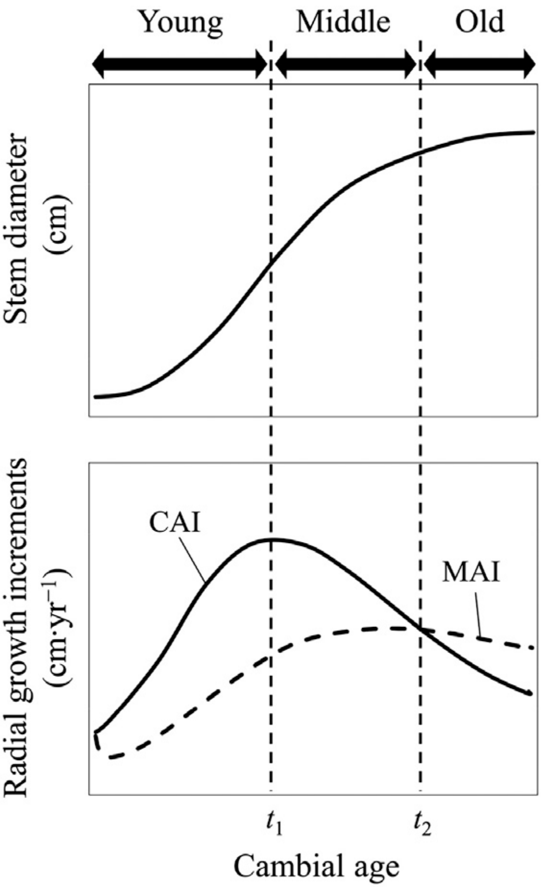

Figure 1. Schematic of the developmental stage of radial growth increment (modified from Kataoka 1992; Salas-Eljatib et al 2021): Upper graph, S-shaped growth curve fitted to the radial growth; lower graph, curves of the current annual increment (CAI) and mean annual increment (MAI); t_1, age showing maximum CAI; t_2, age showing maximum MAI.

of diameter growth in *Populus simonii* and *Populus* × *beijingensis* planted in China. In addition, the relationship between the maturation age of vessel lumen diameter and radial growth was also elucidated in 30 different broad-leaved tree species grown in Japan (Tsuchiya and Furukawa 2009c). The 30 species were classified into three types: 1) maturation age similar to age t_1 rather than age t_2 (13 species), 2) maturation age similar to age t_2 rather than age t_1 (15 species), and 3) no relationships between cambial age-related changes in vessel lumen diameter and radial growth (two species). Studies of several broad-leaved tree species (Tsuchiya and Furukawa 2008, 2009a, 2009b, 2009c) suggest that there is a trade-off between radial growth increments of the stem and anatomical characteristics: the wood with mature anatomical characteristics might be formed after radial growth rate slows. Suppose this trade-off is adapted for the fast-growing tree species used for plantation development. In that case, the balance between the quantity and quality of wood obtained from the fast-growing tree plantations may be controlled by some silvicultural treatments. In addition, to utilize the wood obtained from the fast-growing tree plantations for value-added products, such as solid wood, the trade-off concepts should be evaluated for the other qualities of wood, such as density and strength properties.

Recently, the relationships between radial growth increments of stems and multiple wood properties were clarified in a fast-growing tree species, *L. tulipifera* planted in Japan using mixed-effect modeling of cambial age-related changes in these properties (Nezu et al 2022). The maximum CAI and MAI determined by stem diameter were found at 4.9 and 7.4 yr, respectively. In addition, all measured wood properties changed near the pith before becoming stable toward the cambium (Nezu et al 2022). The changing ratio of multiple wood properties at 1-yr intervals became stable after a cambial age of 9 yr (Nezu et al 2022). These results suggest a trade-off between radial growth increments of stems and wood properties in *L. tulipifera*: the tree produces a large volume of wood with lower wood properties, and the wood with greater and more stable properties forms as growth slows compared with the initial growth. The trade-offs in this species suggest that wood that forms before a cambial age of nine can be used for utility applications and wood thereafter can be used for structural applications (Nezu et al 2022). Thus, wood utilization based on this trade-off concept should be evaluated for other fast-growing tree species.

Trees in the genus *Paulownia* are native to East Asia, where they are particularly widespread in South Korea, China, and Japan (Young and Lundgren 2023). They also have been introduced to many other areas globally, including the United States and Europe in the mid-19th century (Young and Lundgren 2023). *Paulownia tomentosa* (Thunb.) Steud. has historically been planted for furniture and musical instruments in Japan (Kumakura 1957; Nagata et al 2013). For example, a tree of this species was planted at the birth of a daughter and harvested for making chests of drawers when she married in Japan (Kumakura 1957; Nagata et al 2013). This old custom indicates not only the cultural importance of *Paulownia* in Japan but also the fast-growth characteristics that produced enough wood to make chests of drawers. The Japanese Forestry Agency, Ministry of Agriculture, Forestry, and Fishery considers the wood of *P. tomentosa* a ‘special forest products’: wood from this species has not been recognized as wood produced from forestry species in Japan. Recently, the declining number of traditional provenances of *P. tomentosa* has been a serious problem in Japan. Focusing on the fast-growth characteristics of *P. tomentosa* might allow this species to be used as a plantation tree species to produce wood for construction and interior uses as well as biomass for fuel helping to achieve both sustainable wood production and the traditional uses of *Paulownia*.

Many researchers have reported MAIs of stems and wood properties of *P. tomentosa* (Kitamura and Imata 1955; Kitamura 1956; Wood Mechanics of Wood Technology Division 1957; Takashima et al 1959; Olson and Carpenter 1985; Nasir and Mahmood 2000; Koman et al 2017; Tomczak et al 2023). Kitamura and Imata (1955) reported that MAI, air-dry density, MOE, MOR, and compressive strength were 1.9 $cm \cdot yr^{-1}$, 0.253 $g \cdot cm^{-3}$, 5.18 GPa (52,900 $kg \cdot cm^{-2}$), 36.3 MPa (370 $kg \cdot cm^{-2}$), and 20.4 MPa (208 $kg \cdot cm^{-2}$) in three trees of 6-yr-old *P. tomentosa* planted in Niigata, Japan. In 7- and 12-yr-old *P. tomentosa* trees grown in the United States, MAI, basic density, and wood fiber length were 1.85 $cm \cdot yr^{-1}$, 0.274 $g \cdot cm^{-3}$, and 0.81 mm, respectively (Olson and Carpenter 1985). Koman et al (2017) reported that air-dry density, MOE, MOR, and compressive strength were 0.30 $g \cdot cm^{-3}$, 3.49 GPa, 41.5 MPa, and 22.1 MPa in *P. tomentosa* at the age of less than 10 planted in Hungary. They also reported cambial age-related changes in wood properties in young (less than ca. 10 yr) *P. tomentosa* trees (Kitamura and Imata 1955; Olson and Carpenter 1985; Koman et al 2017). However, the cambial age-related changes in radial growth increments of stems and wood properties estimated using the modeling approaches, and their relationship have not been elucidated yet in *P. tomentosa.*

In the present study, radial growth increments of stems and wood properties (anatomical characteristics, and physical and mechanical properties) were measured in *P. tomentosa* planted in Fukushima, Japan. The objectives of this study were 1) to evaluate the cambial age-related changes in these properties using linear or nonlinear mixed-effects modeling and 2) to clarify whether the trade-off between radial growth increments of the stems and wood properties in *L. tulipifera* is adapted in *P. tomentosa*.

MATERIALS AND METHODS

Materials

Four trees of *P. tomentosa* (Thunb.) Steud. were used in the present study. The trees were grown in Kaneyama, Fukushima, Japan (37°21′62″N, 139°26′84″E, and 412 m above sea level), which is a traditional *Paulownia* wood production site. Seed origin and age were unknown. The annual ring number at 0.4 m above the ground was 24 or 25 (Table 1). Disks (about 30 cm long) were collected from 0.1 to 0.4 m above the ground in each tree. Bark-to-bark radial strips with pith (about 5 cm in width) were collected from a random position (without any eccentric growth) on each disk. The radial strips were cut again into two strips (1 cm thickness in the longitudinal direction) for measuring annual ring width and anatomical characteristics with the remaining (∼) 16 cm section used for preparing specimens for static bending properties and compressive strength parallel to the grain.

Annual Ring Width and Anatomical Characteristics

The radial strips were sanded, and then transverse images of the strips were obtained by an 800 dpi image scanner (GT-9300; Epson, Nagano, Japan) ($0.032\ mm \cdot pixel^{-1}$). Annual ring width was measured from the pith to the bark side using ImageJ (National Institute of Health, Bethesda, MD). The cumulative ring width was calculated using the annual ring width.

Table 1. Anatomical, physical, and mechanical properties of four *P. tomentosa* trees.

	Tree no.						
Property	1	2	3	4	Mean	SD	CV (%)
Number of annual rings	24	25	25	24	25	1	4.0
Annual ring width (mm)	8.15	9.79	9.77	10.06	9.44	0.87	9.2
Stem diameter (cm)	39.1	49.0	48.9	48.3	46.3	4.8	10.4
Wood fiber length (mm)	1.01	1.05	0.97	1.01	1.01	0.03	3.0
Vessel element length (mm)	0.81	0.85	0.77	0.80	0.81	0.04	4.9
Vessel frequency ($No \cdot mm^{-2}$)	7.3	6.1	6.4	5.8	6.4	0.6	9.4
Vessel diameter (μm)	128	134	132	143	134	6	4.5
Wood fiber diameter (μm)	26.5	28.2	26.4	28.6	27.4	1.1	4.0
Wood fiber wall thickness (μm)	1.7	1.5	1.5	1.5	1.6	0.1	6.3
Air-dry density ($g \cdot cm^{-3}$)	0.32	0.28	0.27	0.29	0.29	0.02	6.9
MOE (GPa)	4.42	3.81	3.93	3.96	4.03	0.27	6.7
MOR (MPa)	44.1	40.4	39.7	37.1	40.3	2.9	7.2
Compressive strength parallel to grain (MPa)	14.3	14.6	17.1	15.6	15.4	1.2	7.8

SD, standard deviation; CV, coefficient of variation; MOE, modulus of elasticity; MOR, modulus of rupture. Number of annual rings, annual ring width, and stem diameter were measured at 0.4 m above the ground. To calculate each statistical value in a wood property, the individual mean was obtained by averaging the value at each cambial age within an individual.

To determine the anatomical characteristics, transverse sections (20 μm in thickness and 10 mm in tangential direction) were successively obtained at 5-cm intervals from pith to bark by a core microtome (WSL, Birmensdorf, Switzerland). The sections were stained with safranin, dehydrated through an ethanol series, dipped into xylene, and then put on slide glasses and mounted with a few drops of 75% glycerol and a coverslip. Transverse images were taken by a digital camera (CD-30C; Mitutoyo, Kanagawa, Japan) and a microscope (V-12B; Nikon, Tokyo, Japan). Photomicrographs of transverse images at the cambial ages of 2 and 24 in tree no. 2 are shown in Fig 2. The xylem of this species consisted of vessels, wood fibers, axial parenchyma, and ray parenchyma (Fig 2). The wood is semi-ring-porous (Fig 2). In this study, the anatomical characteristics (vessel frequency, vessel diameter, wood fiber diameter, and wood fiber wall thickness) were determined in every annual ring by ImageJ. Small wood specimens (1 [R] × 1 [T] × 10 [L] mm) were collected from each annual ring from the pith in the strips. Sticks from the innermost and outermost positions within an annual ring were macerated with Schultze's solution (100 mL of 35% nitric acid containing 6 g of potassium chloride). The macerated vessel elements in the pore zone and wood fiber in the outer pore zone were projected on a profile projector (V-12B; Nikon, Tokyo, Japan), and then cell length was measured by a digital caliper (CD-30C; Mitutoyo). A total of 30 vessels and 50 wood fibers were measured in each annual ring.

Physical and Mechanical Properties

Bending and compression tests were conducted according to the method described in Nezu et al (2022), which was partially modified from JIS Z 2101:2009 (Japanese Industrial Standards 2009). Bending (10 [R] × 10 [T] × 160 [L] mm) and compression test specimens (10 [R] × 10 [T] × 20 [L] mm) were successively collected from pith

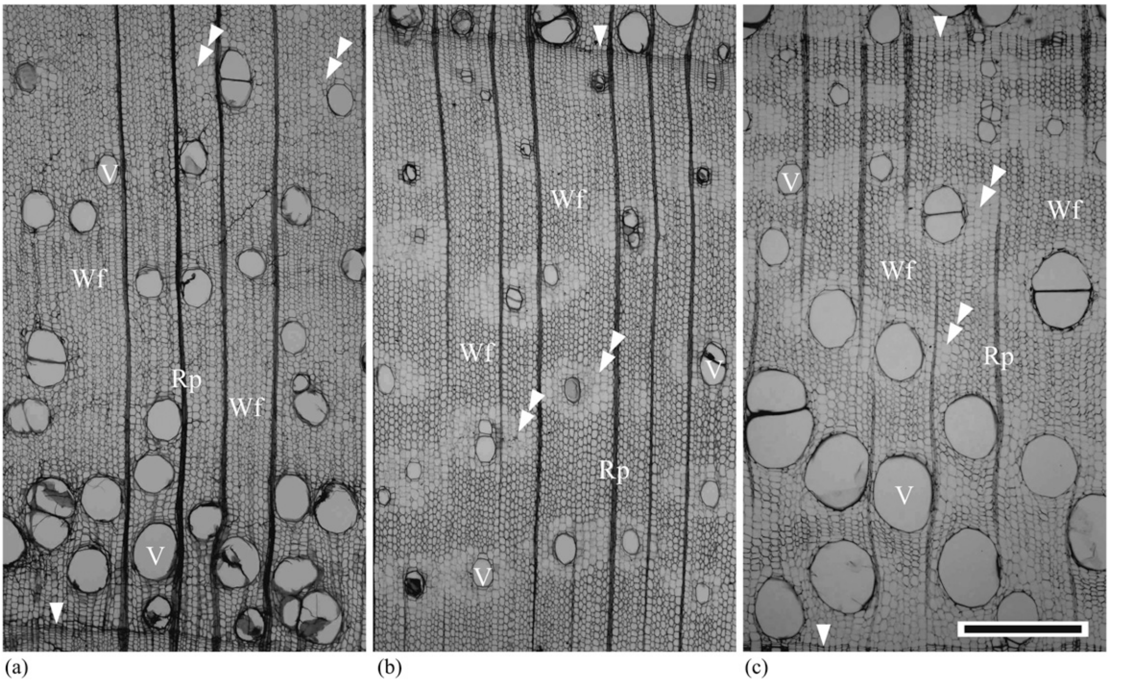

Figure 2. Photomicrographs of transverse sections: (a) the pore zone at the cambial age of two; (b) the outer-pore zone at the cambial age of two; (c) the cambial age of 24. V, vessel; Wf, wood fiber; Rp, ray parenchyma; arrowhead, annual ring boundary; double arrowheads, axial parenchyma; bar, 500 μm.

to bark from the strip. The specimens were conditioned to constant weight at 24°C and 65% RH for around 2 wk. The static bending test was conducted on a universal testing machine (MSC-5/200-2; Tokyo Testing Machine, Tokyo, Japan). The load was applied at the center of the radial section of the specimen with 140 mm of span at 2 mm/min. After the bending test, a block (10 [R] × 10 [T] × 10 [L] mm) without any visual defects, such as knots or cracks, was cut from each specimen and oven-dried to determine MC and air-dry density. The compression test was also conducted by the same testing machine with a 0.3 mm/min load speed. The average MC was 9.1 ± 1.7% in the static bending test and 9.6 ± 1.7% in the compression tests, respectively. The MOE, MOR, and compressive strength parallel to the grain were calculated using load–deflection data (Nezu et al 2022).

Statistical Analysis

Statistical analysis was conducted using R (Version 4.2.2) (R Core Team 2022). Cambial age-related changes in stem diameter and wood properties were evaluated using regression models developed based on the linear mixed-effect model using the packages "lmer" and "lmerTest" (Bates et al 2015) or nonlinear mixed-effects models using the package "nlme" (Pinheiro and Bates 2000).

The stem diameter (excluding bark) in relation to cambial age was regarded as twice the value of the cumulative ring width at 0.4 m above the ground in each individual tree. The regression model of cambial age-related change in stem diameter was developed based on the Gompertz function (Table 2). In each model, stem diameter was the response variable, cambial age was the explanatory variable, and the individual tree was the random effect. The best of the three models was selected based on the Akaike information criterion (AIC) (Akaike 1998). Based on the selected model, the CAI and MAI were calculated by Eqs 1 and 2:

$$\mathrm{CAI}\ \left(\mathrm{cm}\cdot\mathrm{yr}^{-1}\right) = \alpha_0\alpha_2 e^{\alpha_1-\alpha_2\mathrm{CA}} e^{-e^{\alpha_1-\alpha_2\mathrm{CA}}} \quad (1)$$

$$\mathrm{MAI}\ \left(\mathrm{cm}\cdot\mathrm{yr}^{-1}\right) = \frac{\alpha_0 e^{-e^{\alpha_1-\alpha_2\mathrm{CA}}}}{\mathrm{CA}} \quad (2)$$

where α_0, α_1, and α_2 are parameters obtained from the selected model for radial growth model, and CA is cambial age. The cambial age showing maximum CAI and MAI was calculated.

The cambial age-related changes in wood properties were evaluated using regression models based on only *y*-intercept (Eq 1), linear (Eqs 2 and 3), logarithmic (Eqs 4 and 5), or quadratic functions (Eqs 6-8) with the explanatory variable of cambial age, response variable of each wood property, and random effect of the individual tree (Table 3). The model with the lowest AIC value was considered the best model. In the selected model for cambial age-related changes in stem diameter and wood properties, the ratio of the variance component of random-effect parameters to the total variance was calculated (Nakagawa and Schielzeth 2010).

The relationships between cambial age-related changes in radial growth increments of stems and wood properties between *P. tomentosa* and another fast-growing tree species *L. tulipifera*

Table 2. Comparison of AIC values among three models for cambial age-related change in stem diameter.

Eq	Formula	Explanation about random-effect parameter	AIC
I	$D_{ij} = (\alpha_0 + \mathrm{Tree}_{0j}) e^{-e^{\alpha_1-\alpha_2\mathrm{CA}_{ij}}} + \varepsilon_{ij}$	Asymptotic value	**365.53**
II	$D_{ij} = \alpha_0 e^{-e^{\alpha_1+\mathrm{Tree}_{1j}-\alpha_2\mathrm{CA}_{ij}}} + \varepsilon_{ij}$	Start position of the curve	477.62
III	$D_{ij} = \alpha_0 e^{-e^{\alpha_1-(\alpha_2+\mathrm{Tree}_{2j})\mathrm{CA}_{ij}}} + \varepsilon_{ij}$	Slope	416.35

D_{ij}, stem diameter at 0.4 m above the ground at the *i*th cambial age of the *j*th individual tree; CA_{ij}, the *i*th cambial age of the *j*th individual tree; α_0, α_1, and α_2, fixed-effect parameters; Tree_{0j}, Tree_{1j}, and Tree_{2j}, random-effect parameters at the *j*th individual tree level; ε_{ij}, residuals. The bold value represents the minimum AIC value among the developed models.

Table 3. Comparison of AIC values among eight models in each wood property.

Eq	Formula	Explanation about random-effect parameter	Wood fiber length	Vessel element length	Vessel frequency	Vessel diameter	Wood fiber diameter	Wood fiber wall thickness	Air-dry density	MOE	MOR	Compressive strength
1	$WP_{ij} = \beta_0 + Tree_{0j} + \varepsilon_{ij}$	*y*-Intercept	−192.00	−434.80	363.94	748.21	328.07	−4.978	**−258.04**	**135.03**	**393.27**	288.63
2	$WP_{ij} = (\beta_0 + Tree_{0j})CA_{ij} + \beta_1 + \varepsilon_{ij}$	Slope	−240.87	−441.43	**335.90**	702.80	338.60	−35.102	—	—	—	—
3	$WP_{ij} = \beta_0 CA_{ij} + \beta_1 + Tree_{1j} + \varepsilon_{ij}$	*y*-Intercept	−247.01	−442.62	339.56	697.85	315.94	−36.642	—	—	—	**287.60**
4	$WP_{ij} = (\beta_0 + Tree_{0j})\ln(CA_{ij}) + \beta_1 + \varepsilon_{ij}$	Slope	−261.36	−446.53	—	696.70	**315.41**	−77.056	—	—	—	—
5	$WP_{ij} = \beta_0 \ln(CA_{ij}) + \beta_1 + Tree_{1j} + \varepsilon_{ij}$	*y*-Value at 1st annual ring from the pith	**−263.82**	**−447.27**	338.56	**694.83**	—	**−77.955**	—	—	—	—
6	$WP_{ij} = (\beta_0 + Tree_{0j})CA_{ij}^2 + \beta_1 CA_{ij} + \beta_2 + \varepsilon_{ij}$	Opening quadratic parabolas	—	−421.71	—	—	348.45	−54.392	—	—	—	—
7	$WP_{ij} = \beta_0 CA_{ij}^2 + (\beta_1 + Tree_{1j})CA_{ij} + \beta_2 + \varepsilon_{ij}$	Slope of the tangent line at the *y*-intercept	−236.21	−421.67	—	—	341.92	−63.422	—	—	—	—
8	$WP_{ij} = \beta_0 CA_{ij}^2 + \beta_1 CA_{ij} + \beta_2 + Tree_{2j} + \varepsilon_{ij}$	*y*-Intercept	—	−422.77	—	—	—	−72.292	—	—	—	—

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}, the *i*th cambial age of the *j*th individual tree; β_0, β_1, and β_2, fixed-effect parameters; $Tree_{0j}$, $Tree_{1j}$, and $Tree_{2j}$, random-effect parameters at the *j*th individual tree level; ε_{ij}, residuals; —, the model failed to converge or the model with *p*-values of the fixed-effect parameters more than 0.05. The bold value represents the minimum AIC value among the developed models.

were examined for physical and mechanical properties estimated at 1-yr intervals based on the optimum radial variation models with only fixed-effect parameters (Nezu et al 2022). The specific MOE and MOR were calculated by dividing the estimated MOE and MOR by air-dry density from the pith toward the cambium at 1-yr intervals.

RESULTS

The mean stem diameter of sample trees was 46.3 cm with about 25 annual rings (Table 1). Table 2 shows the comparison of AIC values in the models for cambial age-related change in stem diameter. The model with random effects of the individual tree on asymptote value (Eq I) was optimum among the three models. Figure 3 shows the regression curves of cambial age-related changes in stem diameter, CAI, and MAI based on the selected model (Table 2) with only fixed-effect parameters (Table 4). CAI increased until the cambial age of 5.4 yr, and MAI increased with increasing cambial age until 7.3 yr (Fig 3) then both indicators decreased toward the cambium. The stem diameters were around 17 and 23 cm at the cambial age showing maximum CAI and MAI values, respectively. Values were more than 2 cm·yr^{-1} until 25 yr (Fig 3), especially for MAI.

Individual mean anatomical, physical, and mechanical properties from pith to cambium were 1.01 mm in wood fiber length, 0.81 mm in vessel element length, 6.4 No·mm^{-2} in vessel frequency, 134 μm in vessel diameter, 27.4 μm in wood fiber diameter, 1.6 μm in wood fiber wall thickness, 0.29 g·cm^{-3} in air-dry density, 4.03 GPa in MOE, 40.3 MPa in MOR, and 15.4 MPa in compressive strength parallel to the grain, respectively (Table 1). Among the eight developed models for radial variation of wood properties, the logarithmic model (Eq 4 or 5) was well-fitted for all anatomical characteristics except for vessel frequency (Table 3). The *y*-intercept model (Eq 1) was an optimum model for explaining the radial variation of physical and mechanical properties except for compressive strength (Table 3). The linear model (Eq 2 or 3) fitted well for vessel frequency and compressive

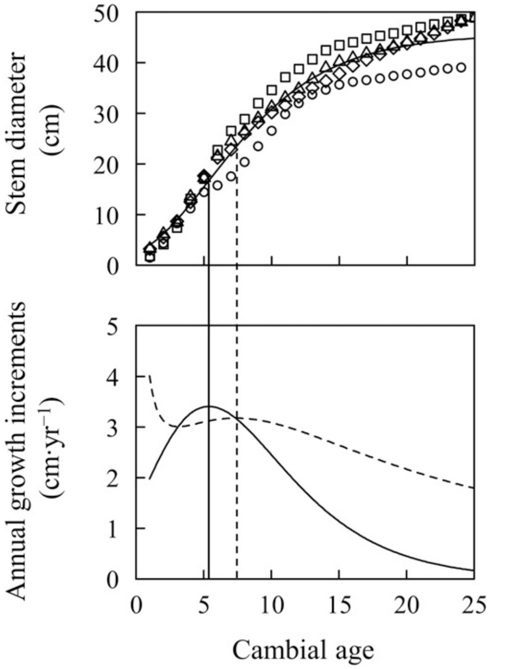

Figure 3. Cambial age-related changes in stem diameter and annual increment: Circles, squares, triangles, and diamonds represent measured values of the stem diameter in each individual tree. The solid curve in the upper figure represents the regression curve based on the selected model with only the fixed-effect parameters (Tables 2 and 4). Solid and dashed curves in the lower figure indicate CAI and MAI based on the selected model (Model I in Table 2) with only fixed-effect parameters. Solid and dashed lines in the vertical direction indicate cambial age showing maximum CAI (5.4 yr) and MAI (7.3 yr).

strength (Table 3). The selected model included a random intercept of individual trees for almost all wood properties, whereas the model with the random slope was selected for vessel frequency and wood fiber diameter. Based on the model selection, radial variations of measured anatomical characteristics and wood properties are shown in Fig 4 with regression lines or curves of only fixed-effect parameters (Table 4). For the selected models about cambial age-related changes in stem diameter and wood properties, the highest variance component ratio for individual trees was obtained for stem diameter (88.6%), followed by air-dry density (84.1%), MOE (49.1%), wood fiber wall thickness (30.7%), wood fiber length (26.6%), MOR

Table 4. Estimated values of the fixed-effect parameters of the selected models in each property in relation to cambial age.

Property	Eq	Parameter	Estimates	SE	*t*-value	*p*-value
Stem diameter	I	α_0	45.686	1.828	24.988	<0.001
		α_1	1.092	0.031	35.695	<0.001
		α_2	0.203	0.005	36.992	<0.001
Wood fiber length	5	β_0	0.0814	0.0070	11.615	<0.001
		β_1	0.8215	0.0220	37.295	<0.001
Vessel element length	5	β_0	0.0133	0.0025	5.308	<0.001
		β_1	0.1717	0.0062	27.511	<0.001
Vessel frequency	2	β_0	0.16	0.04	4.389	0.003
		β_1	4.39	0.34	12.744	<0.001
Vessel diameter	5	β_0	16.45	1.95	8.421	<0.001
		β_1	95.73	5.28	18.123	<0.001
Wood fiber diameter	4	β_0	1.110	0.245	4.532	<0.001
		β_1	24.855	0.474	52.457	<0.001
Wood fiber wall thickness	5	β_0	0.235	0.020	11.583	<0.001
		β_1	1.022	0.067	15.321	<0.001
Air-dry density	1	β_0	0.2930	0.0130	22.500	<0.001
MOE	1	β_0	4.0150	0.1873	21.430	<0.001
MOR	1	β_0	40.250	1.444	27.870	<0.001
Compressive strength	3	β_0	0.133	0.048	2.769	0.007
		β_1	14.002	0.723	19.357	<0.001

SE, standard error; MOE, modulus of elasticity; MOR, modulus of rupture. Fixed-effect parameters were estimated by the selected model (Tables 2 and 3).

(20.3%), compressive strength (15.2%), vessel diameter (12.3%), wood fiber diameter (4.9%), vessel element length (2.7%), and vessel frequency (0.1%) (Table 5).

Figure 5 shows the cambial age-related changes in MOE, MOR, AD, specific MOE, and specific MOR based on the selected radial variation model with only fixed-effect parameters listed in Table 4 for *P. tomentosa* and a reference for *L. tulipifera* (Nezu et al 2022). The air-dry density, MOE, and MOR in *P. tomentosa* were lower from the pith to the cambium and almost half of the values in the outermost compared with *L. tulipifera*. On the other hand, the specific MOE and MOR values were almost the same between these species over the time.

DISCUSSION

Cambial Age-Related Changes in Wood Properties

The mean values of wood properties in the present study (Table 1) were within the range of those in the previous studies (Kitamura and Imata 1955; Olson and Carpenter 1985; Tomczak et al 2023), although the tree age and sampling place differed among studies.

Several studies have examined radial variations of anatomical characteristics and wood properties at young ages (less than ca. 10 yr) of *P. tomentosa* planted in several countries (Kitamura and Imata 1955; Olson and Carpenter 1985; Tomczak et al 2023). Kitamura and Imata (1955) investigated air-dry density, MOE, MOR, and compressive strength of heartwood and sapwood in 6-yr-old plantation trees of *P. tomentosa* grown in Niigata, Japan. MOE and MOR did not differ between heartwood and sapwood, although heartwood had lower air-dry density and higher compressive strength than sapwood. Wood fiber length increased from the pith toward the cambium, reaching a length of 0.85-0.90 mm at 8 yr, and then decreased until 12 yr at 0.1 m above the ground in *P. tomentosa* naturally grown in southern Kentucky, United States (Olson and Carpenter 1985). Tomczak et al (2023) reported that wood fiber length, vessel element length, and vessel

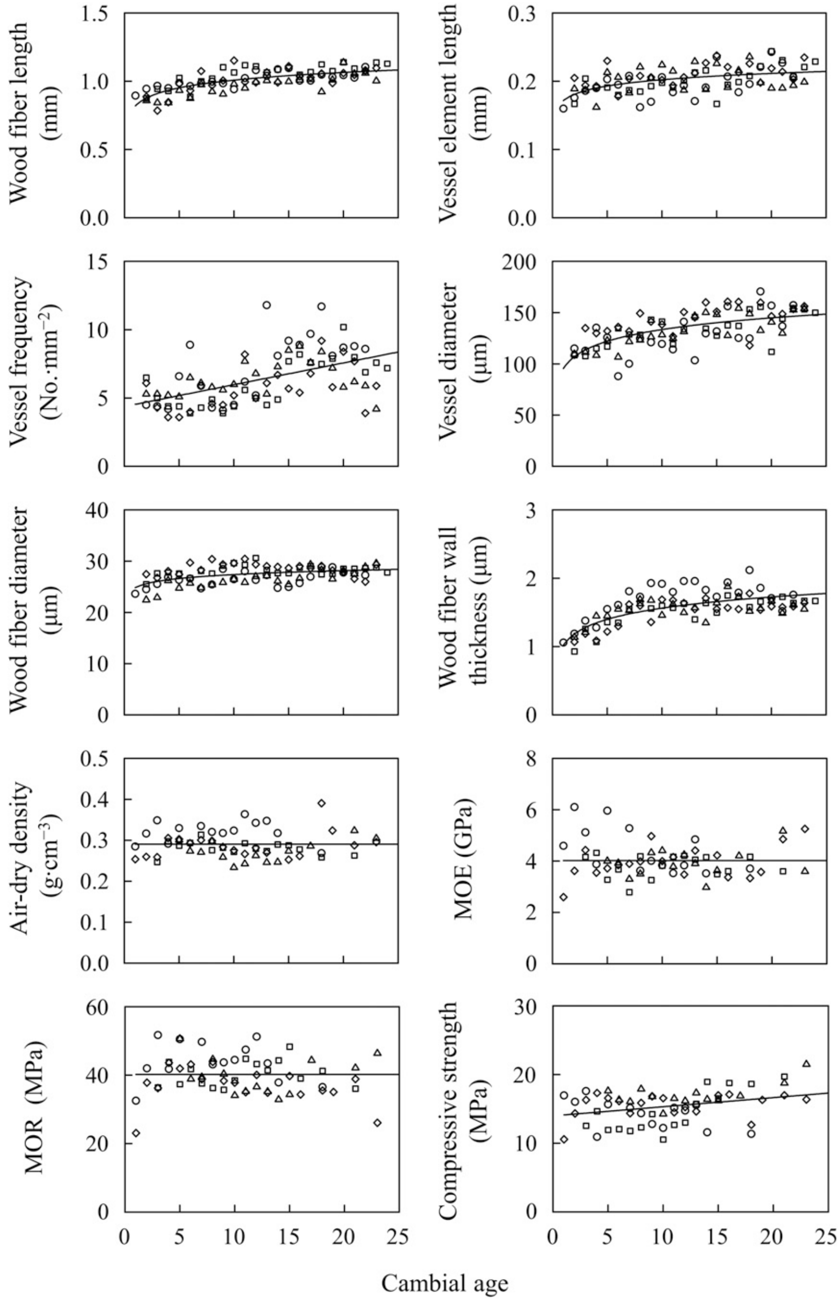

Figure 4. Cambial age-related changes in anatomical, physical, and mechanical properties: MOE, modulus of elasticity; MOR, modulus of rupture. Circles, squares, triangles, and diamonds represent measured values of each wood property. The solid line or curve represents the regression line or curve based on the fixed-effect parameters in the selected model (Tables 3 and 4).

Table 5. Variance component ratios of individual trees of the selected models in each property.

Property	V_{Tree}	V_E	V_{Tree} (%)
Stem diameter	12.888	1.662	88.6
Wood fiber length	0.7875×10^{-3}	0.2169×10^{-2}	26.6
Vessel element length	0.7826×10^{-5}	0.2794×10^{-4}	2.7
Vessel frequency	0.29×10^{-2}	2.14	0.1
Vessel diameter	20.83	149.13	12.3
Wood fiber diameter	0.087	1.699	4.9
Wood fiber wall thickness	0.811×10^{-2}	0.183×10^{-1}	30.7
Air-dry density	0.6704×10^{-3}	0.1269×10^{-3}	84.1
MOE	0.1319	0.1365	49.1
MOR	6.660	26.150	20.3
Compressive strength	0.795	4.429	15.2

V_{Tree}, variance component of individual tree; V_E, residual variance; V_{Tree} (%), variance component ratio of the individual tree to the total variance. MOE, modulus of elasticity; MOR, modulus of rupture. Fixed-effect parameters were estimated by the selected model (Tables 2 and 3).

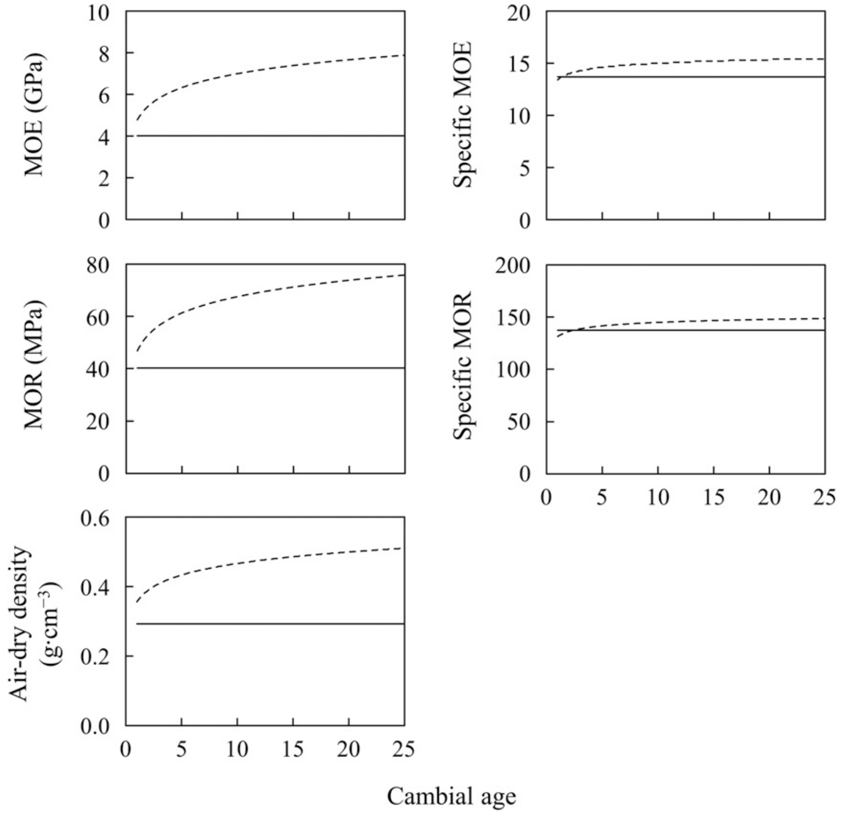

Figure 5. Cambial age-related changes in estimated physical and mechanical properties in *P. tomentosa* and *L. tulipifera*: MOE, modulus of elasticity; MOR, modulus of rupture; solid line, *P. tomentosa*; dotted curve, *L. tulipifera*. The MOE, MOR, and AD were estimated by the selected model with only fixed-effect parameters (Table 4 in this study for *P. tomentosa* and Nezu et al (2022) for *L. tulipifera*). Specific MOE and MOR were calculated by dividing MOE and MOR by estimated air-dry density.

diameter increased from the 1st to 4th annual rings in 4-yr-old *P. tomentosa* planted in Poland. In the present study, the model selected showed that all anatomical characteristics, except for vessel frequency, increased near the pith and then became stable toward the cambium (Fig 4). Vessel frequency and compressive strength gradually increased from the pith toward the cambium, while air-dry density, MOE, and MOR did not change with increased cambial age. The radial variation patterns of anatomical characteristics, MOE, and MOR in aged trees in the present study were similar to those previously found in younger trees (Kitamura and Imata 1955; Olson and Carpenter 1985; Tomczak et al 2023). On the other hand, radial trends in air-dry density and compressive strength differed between the present study and those by Kitamura and Imata (1955). However, the ratios of mean values in heartwood to sapwood for air-dry density and compressive strength were 1.00:0.96 (0.259 and 0.249 $g \cdot cm^{-3}$ in heartwood and sapwood) and 1.00:1.05 (19.6 and 18.6 MPa [200 and 190 $kg \cdot cm^{-2}$] in heartwood and sapwood), respectively, in the previous study (Kitamura and Imata 1955). The results suggest that there might be small differences in air-dry density and compressive strength among different radial positions. The result is similar to that of the present study (Fig 4). In summary, the xylem with uniform density and strength properties might be formed over the time in this species.

The selected model for explaining cambial age-related changes in wood properties included a random intercept of individual trees for almost all wood properties (Table 3). In addition, high variance component ratios (around 50% and more) of individual trees were found with air-dry density and MOE (Table 5). These findings suggest that although the patterns in all wood properties over the time were among individual trees, density and MOE might differed at the individual tree levels in *P. tomentosa*.

Ishiguri et al (2024) found that the MOR of 2 × 4 *P. tomentosa* lumber (38 × 89 mm × 1820 mm) from Tochigi, Japan with a 5% lower tolerance limit with a 75% confidence level was 12.1 MPa. MOR values of 2 × 4 lumber for construction, standard, and utility grades in the Notification of Ministry of Land, Infrastructure, Transport and Tourism No. 910 were 14.8, 8.2, and 3.9 MPa, respectively, in JS-II (*Cryptomeria japonica*), which is the most common plantation species in Japan (Japan 2 × 4 Lumber JAS Council 2023). Thus, the MOR values for *P. tomentosa* reported by Ishiguri et al (2024) exceeded values for utility grade but were lower than those for construction grade in JS-II. Since the MOR was stable from the pith to the cambium (Fig 4), wood for utility applications might be obtained at any radial positions in the stem.

Specific MOE and MOR values from pith toward the cambium were almost the same between *P. tomentosa* and *L. tulipifera* (Fig 5) suggesting a common ratio of xylem strength values to unit xylem volume among fast-growing tree species. To clarify this hypothesis, exploring cambial age-related changes should be conducted for other fast-growing tree species.

Relationships between Cambial Age-Related Changes in Radial Growth Increments of Stems and Wood Properties

We previously examined the relationships between the cambial age-related changes in radial growth increments of stems and wood properties in fast-growing tree species, *L. tulipifera* has grown in Japan (Nezu et al 2022). As a result, xylem maturation started at 9 yr after reaching the maximum CAI and MAI at 4.9 and 7.4 yr, respectively: a trade-off between radial growth rate and wood properties existed in *L. tulipifera* (Nezu et al 2022). Cambial ages showing the maximum CAI and MAI in *P. tomentosa* were similar to those in *L. tulipifera* (Nezu et al 2022)(Fig 3). To compare the volume at the same age between these two species, stem diameter at 15 yr (the maximum age of sampled trees for *L. tulipifera* in the previous study [Nezu et al 2022]) was estimated by substituting 15 for the explanatory variables in the best model with only the fixed-effect parameters for cambial age-related changes in stem diameter in each species. The estimated values of stem diameter at 15 yr were around 40 cm in

P. tomentosa and 20 cm in *L. tulipifera*, respectively. Therefore, the time to maximum CAI and MAI were almost the same between these species, but the stem diameter of *P. tomentosa* might be twice that of *L. tulipifera*.

Based on the radial variation modeling for each wood property, radial variations for anatomical characteristics, except for vessel frequency, were similar for both species (Fig 3, Nezu et al 2022), with each characteristic increasing from the pith outward and then stabilizing. On the other hand, the radial variations of air-dry density, MOE, and MOR in *P. tomentosa* (Fig 5) were stable from the pith toward the cambium, while they increased and then became stable in *L. tulipifera*. In addition, these properties in *P. tomentosa* were lower than those in *L. tulipifera*. Larjavaara and Muller-Landau (2010) stated that wood density generally mediates a trade-off between strength and economy of construction, with higher wood density providing higher strength but at a higher cost. They also hypothesized that a large trunk of low-density wood could achieve greater strength at a lower construction cost than a thin trunk of high-density wood. The trade-off supposed by Larjavaara and Muller-Landau (2010) might be related to the ability of *P. tomentosa* consistently form xylem with lower wood density, MOE, and MOR to achieve a faster radial growth compared with *L. tulipifera*.

CONCLUSIONS

In this study, cambial age-related change in stem diameter was well-fitted to the model with the Gompertz function. CAI and MAI reached their maximum at 5.4 and 7.3 yr, respectively. Based on the model selection for cambial age-related changes in wood properties, most anatomical characteristics increased from the pith and stabilized toward the cambium. On the other hand, air-dry density, MOE, and MOR did not change with increase in cambial age. The estimated fixed-effect parameters in the selected model were 0.29 $g \cdot cm^{-3}$ for air-dry density, 4.03 GPa for MOE, and 40.3 MPa for MOR, respectively. These results suggest that xylem with low but stable values of air-dry density, MOE, and MOR is formed for more than 20 yr in *P. tomentosa*. On these findings, in contrast to *L. tulipifera*, there might not be a trade-off between quantity and quality of wood for *P. tomentosa*: xylem with low and stable physical and mechanical properties is produced to keep a faster radial growth rate. Thus, the physical and mechanical properties of this species might be uniform regardless of whether the tree is in the young, middle, or old stages. Therefore, the rotation age of plantations of this species can be decided from the viewpoint of the quantity of wood. In addition, the wood obtained from the plantation can be used for the same final products (ie utility applications) at any growth stage. Based on the results of the present study, plantation forestry and wood utilization using fast-growing tree species are recommended based on the relationships between cambial age-related changes in quantity and quality of wood at the species level.

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