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Relationship between the radial variation of ray characteristics and the stages of radial stem increment in *Zelkova serrata*

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Abstract We used ten discs from two *Zelkova serrata* trees – five discs from each tree at sampling heights of 1, 4, 7, 10, and 13 m above the ground – and investigated the radial variation in ray characteristics, i.e., ray area (cross-sectional area of rays on a tangential section), ray density (number of rays/mm^2 on a tangential section), and ray proportion (the percentage of the area occupied by rays on a tangential section) and analyzed the pattern of variation with respect to the three stages (early, middle, and late) of radial stem increment as estimated using the Gompertz growth function. A juvenile–mature pattern of variation was observed in ray area and ray density. Ray area increased in the inner part of stem and fluctuated around a certain value in the outer part of the stem, and ray density decreased in the inner part of stem and tended to be constant in the outer part of the stem. The maturation age of ray density was similar to the age at the boundary between the early and the middle stages of radial stem increment, but ray area and ray proportion did not relate to the stages of radial stem increment.

Key words Ray proportion · Ray area · Ray density · Radial stem increment · Maturation · Juvenile wood

Introduction

Wood near the pith derived from young cambium is called juvenile wood, whereas the wood formed in the outer region is called mature wood. The quality of juvenile wood is often inferior to that of mature wood, and the extent of juvenile wood varies within and between individuals. This variability results in variation in the quality of logs. Therefore, for effective utilization of wood it is important to know the extent of juvenile wood present within a trunk.

The demarcation between juvenile (core) wood and mature (outer) wood has often been made on the basis of the radial variation in the size of axial (tracheary) elements which generally show a juvenile–mature pattern of variation. In hardwoods, vessel element length, wood fiber length, and vessel diameter have often been used as demarcation indicators of juvenile wood.[1–12]

The volume increment of the stem can be divided into young, thrifty, and late stages. The young stage comprises the period from the start of growth to the age at which the current volume increment reaches its maximum, while the late stage occurs beyond the age at which the mean volume increment reaches its maximum. The thrifty stage lies between these two stages.[13] The current volume increment is the amount of wood volume formed during a certain year, and the function of current volume increment is calculated using the first derivative of the volume increment function. The mean volume increment is the wood volume per year which was formed up to a certain year; the function of the mean volume increment is calculated by the volume increment function divided by the age.[14]

We applied this concept to the radial stem increment (cumulative ring width with ring number from the pith). That is, we divided the radial stem increment into early, middle, and late stages. The early stage comprises the period from the start of growth to the age at which current annual increment (CAI) reaches its maximum, while the late stage occurs beyond the age at which mean annual increment (MAI) reaches its maximum. The middle stage lies between these two stages. We found that the radial variation in the size of axial elements (vessel element length, vessel diameter, and wood fiber length) is related to the stages of radial stem increment in some hardwoods,[15–18] i.e., the size of the axial elements increased rapidly in the early stage and increased slowly or remained more or less constant in the late stage, and the maturation ages (the age at the stabilization point of a characteristic value) were often similar to

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either the age at the boundary between the early and the middle stages or the middle and the late stages. This result indicated that the region of juvenile wood might correspond to the wood formed in the early stage, while the region of mature wood might correspond to the wood formed in the late stage. However, we found this relationship in some axial (tracheary) elements and have not yet confirmed the relationship in radial elements.

Larson[19] showed that radial elements (rays) occupy a relatively larger area of wood (average value of about 16%) in hardwoods than they do in softwoods (average value of about 7%). Kawamura measured the radial shrinkage and Young's modules of individual multiseriate rays which were cut from untreated wood, and concluded that rays strongly influence the radial shrinkage of wood.[20,21] Rahman et al. measured ray characteristics (size, number of rays per mm^2 and proportion on the tangential section) and radial compression strength in teak wood, and suggested that the radial variation in the ray characteristics showed a specific pattern that depends on species; in addition, they found that the ray proportion had an important influence on the radial compression strength of wood.[22] Therefore, it is important in hardwoods to investigate the radial variation of ray characteristics.

Zelkova serrata is one of the most important hardwood trees in Japan. The wood of this tree is used extensively for construction (it is famous as the source of timber used in shrine and temple construction), ship building, furniture, lacquerware, plywood, and wood carvings. However, there are few studies on the radial variation of ray characteristics in this species. In this study, we investigated the relationship between the radial variations of ray characteristics (ray proportion, ray area, and ray density) and the stages of radial stem increment in *Z. serrata*.

Materials and methods

Samples

We used ten discs from two *Zelkova serrata* trees (designated tree A and tree B) that were grown in Tottori Prefecture, Japan (Table 1). The height of tree A was 20.3 m and that of tree B was 20.6 m. Five discs from each tree were obtained from different stem heights (1, 4, 7, 10, and 13 m above the ground). The trees were felled in December 1997. A radial strip oriented from the pith to the bark was obtained from each disc. Each radial strip was divided into a few small blocks (T × L × R: 15–25 × 15–25 × 5–25 mm^3). The blocks were not embedded in resin. A transverse microtome section was obtained from each block for measuring the annual ring width. The transverse sections (20-μm thick) were stained with safranin, dehydrated in an ethanol series, and mounted in Bioleit (Oken, Tokyo, Japan). Tangential microtome sections were obtained from the second ring (from the pith) outward, and at intervals of two or three rings, for measuring the ray proportion, ray area, and ray density. The tangential microtome sections (20-μm thick) were also stained with safranin, dehydrated in an ethanol series, and mounted in Bioleit.

Table 1. Summary of the samples

Tree	Sampling height (m)	Number of rings	Radius (mm)
A	1	44	134
	4	35	92
	7	32	99
	10	28	79
	13	22	64
B	1	54	163
	4	38	117
	7	33	86
	10	28	73
	13	23	59

Measurements

The annual ring width was measured four times from the transverse permanent slides with a projecting microscope at 20× magnification, after which the mean values were calculated and the radial stem increment (cumulative ring width with ring number from the pith) was obtained.

For measuring the ray area (cross-sectional area of a ray on a tangential section), ray density (number of rays per mm^2 on a tangential section), and ray proportion (the percentage of the area occupied by rays on a tangential section) tangential microtome sections were projected onto the screen of a projecting microscope at 100× magnification. Then, the outlines of the rays were drawn using a pen on tracing paper. Images were scanned at 200 dpi and then input and recorded on a computer. Ray area was measured for 60–327 rays (mean 127 rays) in each annual ring. Ray density was measured in four parts of each annual ring. The ray proportion was measured in four parts of each annual ring. The mean values of the ray area, ray density, and ray proportion were also calculated.

Statistical analysis

Nonlinear segmented regression analysis of a quadratic model with a plateau[4] was used for estimating the maturation age. The model was fitted using the nonlinear regression procedure in SPSS Regression Models 12.0.

To estimate the ages at the boundary between the early and the middle stages (age t_1) and between the middle and the late stages (age t_2) of radial stem increment, we used the nonlinear regression procedure in SPSS Regression Models 12.0 for fitting the Gompertz growth function to the relation between the cumulative ring width (dependent variable) and the ring number from the pith (independent variable). The Gompertz growth function is defined as follows:[23]

$$y = Ae^{-e^{p-qt}} \qquad (1)$$

where y is the cumulative ring width and t is the ring number from the pith. A, p, and q are the parameters determined by the nonlinear regression analysis.

For CAI the equation was solved using the first derivative, defined as

$$y' = Aqe^{p-qt}e^{-e^{p-qt}} \tag{2}$$

Age t_1 corresponds to the age at which CAI is at its maximum, and it was obtained by dividing p by q.

MAI was estimated using the following function:

$$\frac{y}{t} = \frac{Ae^{-e^{p-qt}}}{t} \tag{3}$$

Age t_2 is obtained when CAI (Eq. 2) equals MAI (Eq. 3), i.e., $tqe^{p-qt} = 1$. Age t_2 was estimated by using Excel's solver tool after parameter p and q were determined. A representation of how to determine the stages of radial stem increment is shown in Fig. 1.

Results and discussion

Radial stem increment

The radial stem increment (cumulative ring width with ring number from the pith) showed a sigmoid curve (Fig. 2). The Gompertz growth function fitted very well to the radial stem increment; the coefficient of determination ranged from 0.993 to 0.999. The age at the boundary between the early and the middle stages (age t_1) ranged from 8.8 years to 31.6 years, and the age at the boundary between the middle and the late stages (age t_2) ranged from 13.5 years to 49.9 years. This means that the period of the stages of the radial stem increment varied widely among the samples. The maximum values of age t_1 and age t_2 were observed in the samples which were obtained at a stem height of 1 m in both trees A and B (Table 2).

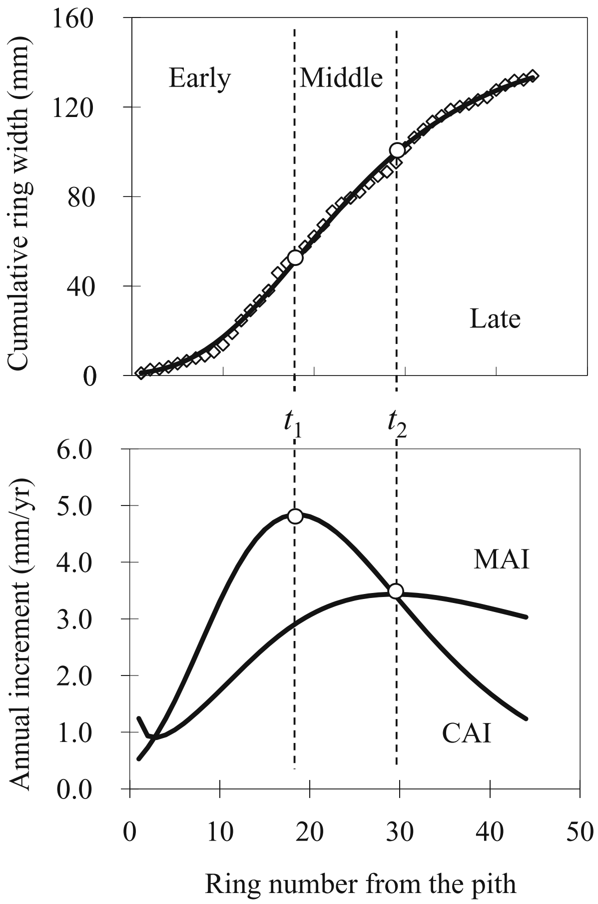


Fig. 1. Stages of the radial stem increment (cumulative ring width with ring number from the pith). *Upper*: the Gompertz growth curve fitted to the radial stem increment. *Lower*: curves of current annual increment (*CAI*) and mean annual increment (*MAI*). t_1 is the age at which CAI reaches a maximum and t_2 is the age at which MAI reaches a maximum. $0 \le t < t_1$ represents the early stage; $t_1 \le t \le t_2$ represents the middle stage; and $t_2 < t$ represents the late stage

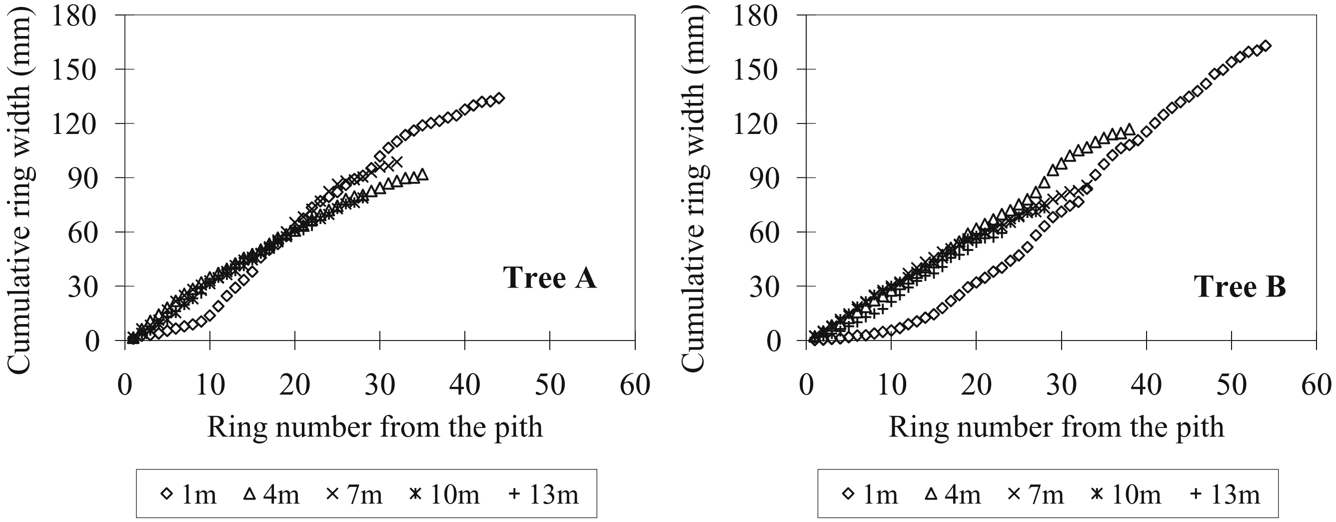


Fig. 2. Radial stem increment (cumulative ring width with ring number from the pith) in trees A and B

Table 2. Estimated ages at boundary between the early and middle stages (age t_1) and the middle and late stages (age t_2) of the radial stem increment, and maturation ages of ray area and ray density estimated using nonlinear segmented regression analysis[4]

Tree	Sampling height (m)	Age t_1 (year)	Age t_2 (year)	Maturation age (year)	
				Ray area	Ray density
A	1	18.6	29.4	29.1	21.9
	4	12.1		24.2	12.3
	7	15.5	21.9	15.8	13.3
	10	11.6	17.2	26.3	10.7
	13	8.8	13.5	36.4	10.9
B	1	31.6	49.9	35.8	45.5
	4	20.1	29.8	37.2	19.4
	7	12.2	16.8	27.4	22.8
	10	11.1	15.0	17.7	13.4
	13	12.1	18.9	11.4	12.4

The age t_2 in the sample obtained at a stem height of 4 m in tree A could not be estimated

Radial pattern of variation in ray characteristics

The radial pattern of variation in ray proportion differed within a tree (Fig. 3). In the sample at 1 m stem height, there was an increasing trend in the inner part of the stem and variation in the outer part of the stem. On the other hand, in the other samples, the ray proportion fluctuated around a certain value or slightly decreased from the pith to the bark. The quadratic with a plateau model was a bad fitted to the radial variation of ray proportion in many samples and the model sometimes could not be fitted. We considered that the quadratic with a plateau model was not applicable to the radial variation of ray proportion in this study. Therefore, the maturation age in terms of ray proportion was not estimated.

The pattern of variation in ray density was similar among all the samples. It showed a decreasing trend up to a certain

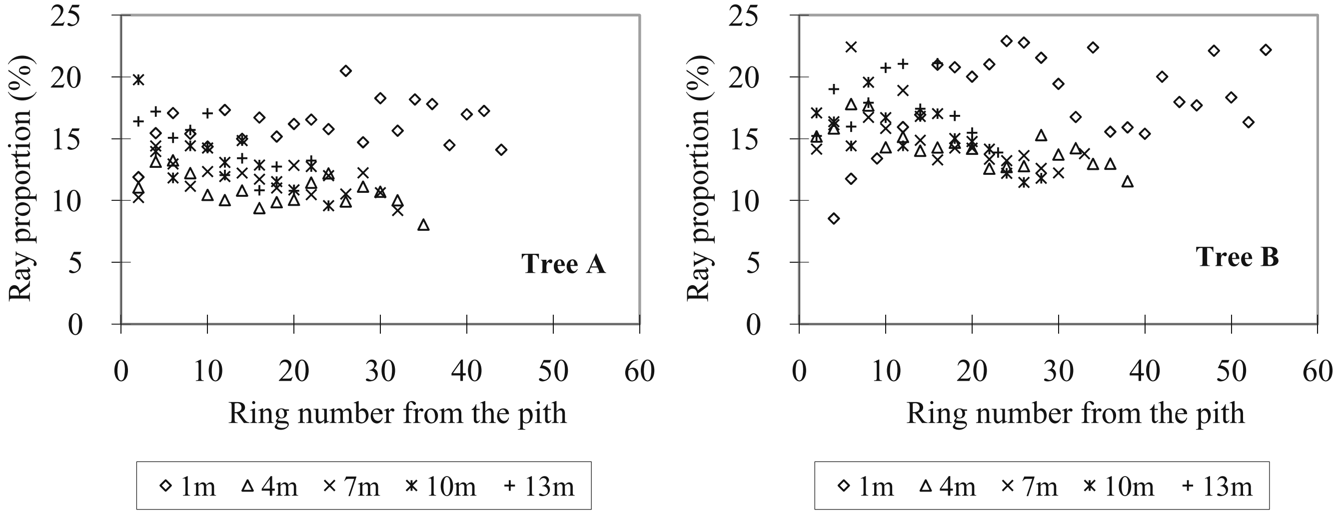


Fig. 3. Radial variation of ray proportion (the area occupied by rays on a tangential section) at different heights from the stem base for trees A and B

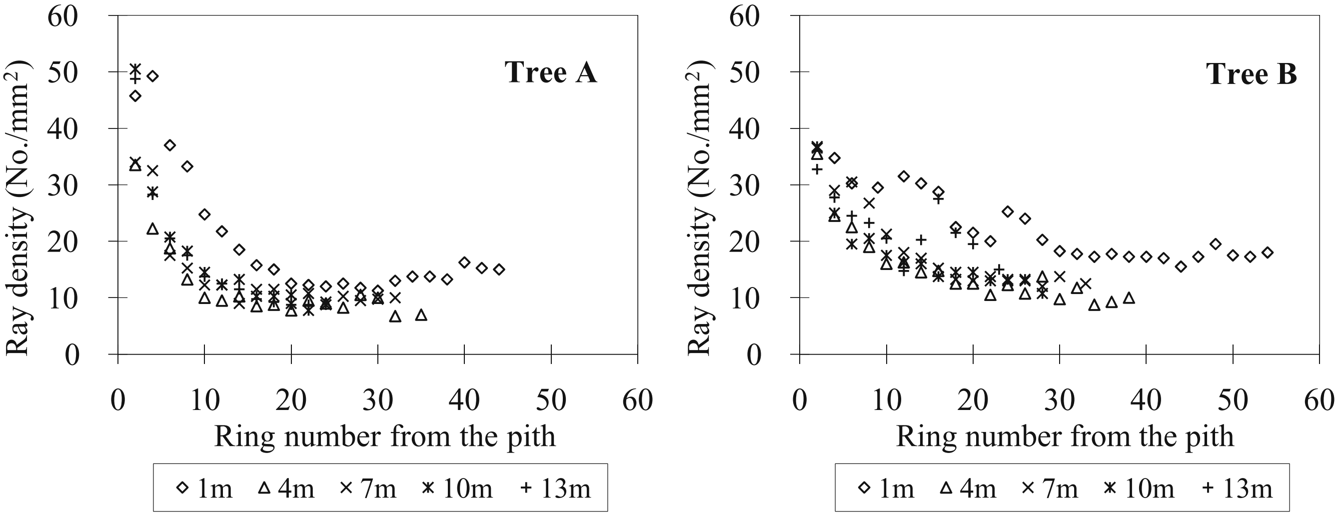


Fig. 4. Radial variation of ray density (number of rays/mm^2) at different heights for trees A and B

ring number from the pith; thereafter, it tended to be more or less constant (Fig. 4). Similar patterns have been reported in other hardwood species[24,25] and softwood species.[26,27] The maturation age in terms of ray density ranged from 10.7 years to 45.5 years (Table 2) and was similar to age t_1. The mean difference between the maturation age of ray density and age t_1 was 3.6 years, and the two ages were correlated significantly at the 1% level (Fig. 5). Age t_1 means the point at which the radial stem increment changes from acceleration to deceleration. It was considered that the variation of ray density was related to the acceleration of the radial stem increment.

The ray area showed an increasing trend with the ring number from the pith in the inner part of stem and fluctuated around a certain value in the outer part (Fig. 6). An increasing trend in ray area was observed, by which uniseriate rays changed to multiseriate rays and the area of multiseriate rays was enlarged (Fig. 7). Barghoorn[28] classified the ontogenetic development of rays into three types in hardwood species: species with both multiseriate and uniseriate rays in the outer part of the stem but only uniseriate rays near the pith (type A), species with only multiseriate rays in the outer part but both uniseriate and multiseriate rays near the pith (type B), and species with only multiseriate rays in the outer part but only uniseriate rays near the pith (type C). *Z. serrata* was classified as type B. A similar pattern of development in ray area was reported in *Ulmus fulva*, of the same family, Ulmaceae.[29] The quadratic with a plateau model fitted well to almost all the samples; the coefficient of determination (R^2) exceeded 0.805, except for the sample obtained at the height of 13 m from tree B ($R^2 = 0.583$). The

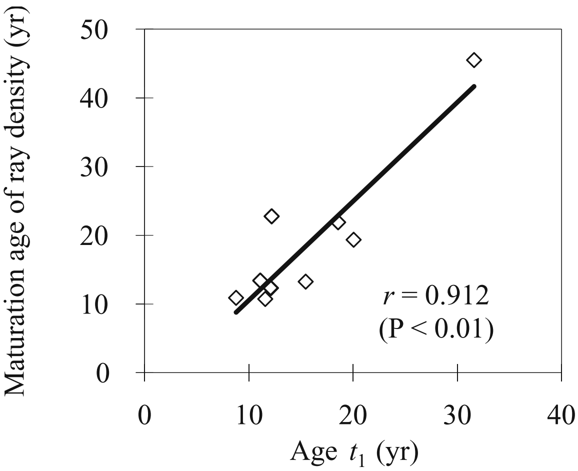


Fig. 5. Correlation between the maturation age of ray density and age t_1

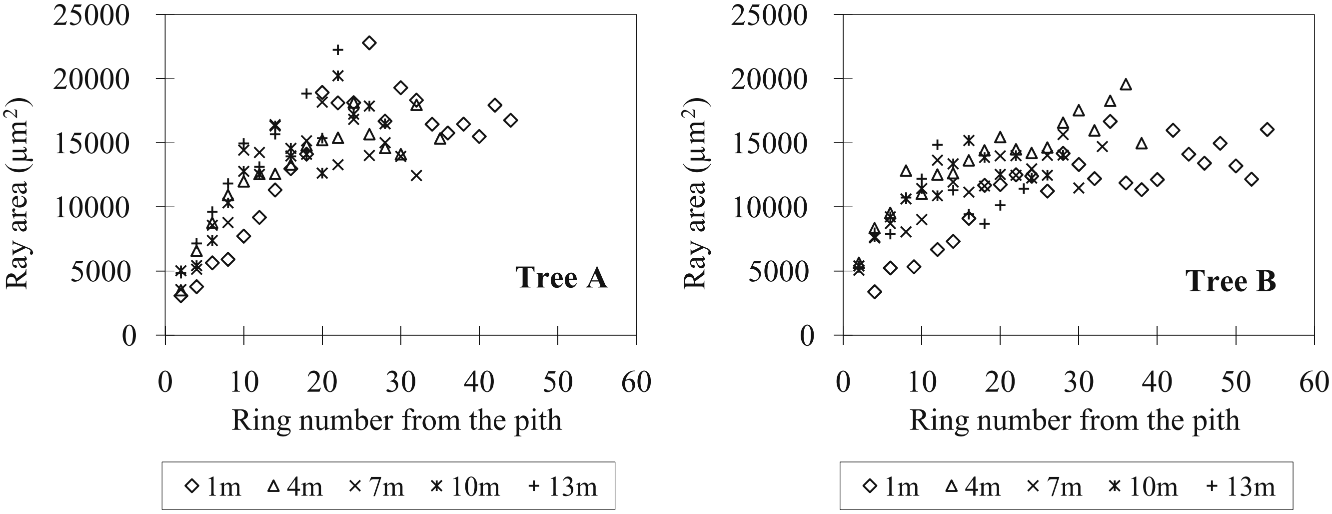
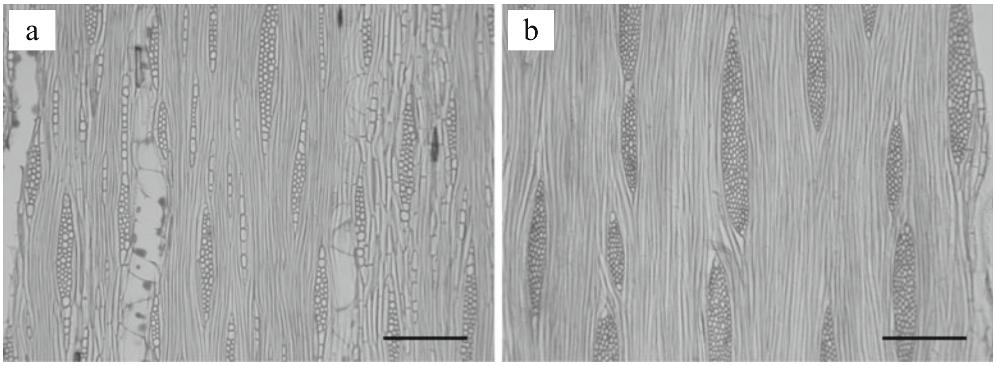


Fig. 6. Radial variation of ray area at different heights from the stem base for trees A and B

Fig. 7. Rays on tangential section of 2nd ring from the pith (**a**) and 44th ring from the pith (**b**). *Bars* 200 μm



estimated maturation age (age at the stabilization point of the ray area) ranged from 11.4 years to 37.2 years (Table 2) and did not correlated significantly with either age t_1 or age t_2. We considered that the variation of ray area did not relate to the stages of radial stem increment, but the stabilization point of ray area in terms of distance from the pith exceeded 5.2 cm in all samples, except for the sample obtained at a height of 13 m from tree B in which the quadratic with a plateau model fitted badly. This result indicated that ray area tended to increase in the wood within a 5 cm radius of the stem. The wood formed within a 5 cm radius in the trunk is defined as juvenile wood by Fukazawa and Ohtani.[30] It can be said that the ray area tended to increase in the juvenile wood, and it was considered that the radial variation of ray area might be related to the distance from the pith.

The variation of ray proportion depends on the variation of ray area and ray density. If the rate of increase in ray area and the rate of decrease in ray density are balanced, or both the variations in ray area and ray density have stabilized, the ray proportion becomes stable. However the results of this study showed that the ray proportion did not tend to stabilize in *Z. serrata*. It was considered that the fluctuation of ray proportion in the early stage was due to the imbalance between the rate of increase in ray area and the rate of decrease in ray density, but in the middle and the old stages, the fluctuation of ray proportion was due to the variation of ray area because ray density tended to be stable in those stages. Therefore, it was considered that the stabilization point of ray proportion depends on the maturation age of the ray area.

Conclusions

In *Zelkova serrata*, the relationships between the ray characteristics (ray area, ray density, and ray proportion) and the stage of radial stem increment is as follows:

1. No specific variation was found in the radial variation of ray proportion, and the radial variation of ray proportion did not relate to the stage of the radial stem increment.
2. Ray density decreased in the early stage and tended to be constant in the middle and the late stages; the maturation age of ray density was similar to the age at the boundary between the early and the middle stages (age t_1) of the radial stem increment. The maturation age of ray density can be estimated from the radial stem increment.
3. Ray area tended to increase from the pith outward up to a certain ring number from the pith and then tended to stabilize, but the variation did not relate to the stage of the radial stem increment. An increasing tendency was observed within 5 cm from the pith in almost all samples. It was considered that the radial variation of ray area might be related to the distance from the pith rather than the acceleration of radial stem increment.

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