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SUMMARY
In *Quercus serrata*, radial variations of wood fibre length, earlywood vessel element length, and earlywood vessel lumen diameter were investigated and maturation ages of them were estimated using nonlinear segmented regression analysis as proposed by Peszlen (1994). In addition, the age at the maximum point of current annual increment and mean annual increment were estimated by using the Gompertz growth function fitted to the variation of cumulative ring width with ring number from the pith. In the same radial strip, the maturation ages both of wood fibre length and the earlywood vessel element length were similar, and those were close to the ages at the maximum point of current annual increment, whereas the maturation age of earlywood vessel lumen diameter was generally greater, close to the age at the maximum point of mean annual increment. These results indicate that earlywood vessel lumen diameter is the best indicator of the three anatomical properties tested and that a relationship exists between the maturation ages of the size of axial elements and radial stem increment.

Key words: Juvenile wood, mature wood, cell size, vessel elements, wood fibres, radial variation, stem increment.

INTRODUCTION
Wood is often divided into two zones, juvenile wood and mature wood. Juvenile wood is formed by young cambium in which anatomical structure, such as cell length and cell width, changes rapidly with cambial age, while mature wood is formed after length of fusiform cambial cells become more or less constant or increase much more slowly with cambial age (Funada 2003). In softwoods, age demarcation between juvenile wood and mature wood has been made based on the radial variation of tracheid length (Shiokura 1982; Yang *et al.* 1986; Lee & Wang 1996), because tracheids are a dominant component of softwoods, and they are approximately the same length as the fusiform cambial cells from which they are derived (Bailey 1920). On the other hand, in hardwoods, vessel elements in diffuse-porous wood and earlywood vessel elements in ring-porous wood are approximately the same length as the fusiform cambial cells from which they are derived (Bailey 1920; Kitin *et al.* 1999), and wood fibres constitute the dominant component. The age demarcation between juvenile wood and mature wood has been based on the radial variations of various anatomical properties (Bhat *et al.* 2001); espe-
cially wood fibre length, vessel element length, and vessel lumen diameter have frequently been accepted as the anatomical properties for age demarcation between juvenile and mature wood (Furukawa & Hashizume 1987; Furukawa et al. 1989; Helińska-Raczkowska & Fabisiak 1991, 1999; Helińska-Raczkowska 1994; Peszlen 1994; Lei et al. 1996; Gartner et al. 1997; Furukawa et al. 2000; Huang & Furukawa 2000; Bhat et al. 2001). However, in *Castanea crenata* the maturation age of wood fibre length (WFL) and earlywood vessel lumen diameter (EVLD) sometimes differed widely in the same radial strip, and were related to the developmental stage of radial stem increment, i.e., WFL increased during the young stage of radial stem increment while EVLD increased during the young and middle stage of radial stem increment. The developmental stage of radial stem increment was estimated by the Gompertz growth function (Tsuchiya & Furukawa 2008). This indicates the likelihood of a relationship between the age demarcation between juvenile wood and mature wood based on the size of axial elements and the developmental stage of radial stem increment.

*Quercus serrata* is one of the most common deciduous hardwood trees found in the secondary forests of Japan, and has ring-porous wood with distinct annual ring boundaries and its radial variation of wood fibre length and vessel element length shows a juvenile-mature pattern (Furukawa et al. 1983).

The objectives of this study were to estimate the maturation ages of WFL, EVLD, and earlywood vessel element length (EVEL), to investigate the relationship between the age demarcation between juvenile wood and mature wood and the developmental stage of radial stem increment.

**MATERIALS AND METHODS**

**Samples**

We used 12 disks from 4 *Quercus serrata* trees that were grown at the Tottori University Forest in Hiruzen, Tottori Prefecture, Japan. From Trees A and B, 5 disks each were obtained from different stem heights (1.3, 3.8, 6.3, 8.8, and 11.3 m from the stem base) to investigate the height effect on the maturation age of each anatomical property and a radial strip oriented from the pith to the bark was obtained from the northern aspect of each disk. The samples obtained from 1.3, 3.8, 6.3, 8.8, 11.3 m stem heights were named A-1, A-2, A-3, A-4, A-5 in Tree A and B-1, B-2, B-3, B-4, B-5 in Tree B, respectively. From trees C and D, 1 disk each was obtained from breast height (1.3 m from the stem base) and 2 radial strips oriented from the pith to the bark were obtained from the northern and southern aspects of each disk to investigate the directional effect on the maturation age of each anatomical property. The samples obtained from the northern and southern aspects were named C-1, C-2 in Tree C and D-1, D-2 in Tree D. Each radial strip was divided into a few small blocks. Trees A and B were felled in September 2003, and trees C and D in October 2004.

**Measurements**

For measuring EVLD and the annual ring width, a transverse microtome section (20 μm thickness) was obtained from the surface of each block, stained with safranin, dehydrated in an ethanol series, and mounted in Bioleit. Microphotographs of the sec-
tions were taken using a digital camera (CAMEDIA C5050ZOOM, Olympus) attached to an optical microscope. Moreover, we measured cross-sectional areas of all vessel lumens in the first row of earlywood of each annual ring except the first annual ring and the outermost annual ring by using image analyzing software (Win Roof version 5.02, Mitani), and calculated diameter from the areas as if all vessels were circular in transverse section. The mean EVLD in each annual ring was determined. The width of

Figure 1. Schematic drawing of the developmental stage of radial stem increment. Upper graph: growth curve of cumulative ring width with ring number from the pith. Lower graph: curves of current annual increment (CAI) and mean annual increment (MAI) with ring number from the pith. $t_1$ = age at the point of maximum CAI; $t_2$ = age at the point of maximum MAI. $0 < t < t_1$ = the young stage; $t_1 < t < t_2$ = the middle stage; $t_2 < t$ = the old stage.
each annual ring excluding the outermost one was measured 4 times using the transverse section with a projecting microscope at a magnification of ×20, and mean values were calculated.

Match-sized wood chips were cut from the center and earlywood portion of each annual ring in order to measure WFL and EVEL, respectively. These chips were macerated in Jeffrey’s solution (a mixture of equal volumes of 5% nitric acid and 5% chromic acid) at 40 °C for 24–48 h. The macerated elements were washed with distilled water, and temporary slides were prepared. In each growth ring, the tip-to-tip lengths of 50 wood fibres and 30 vessel elements were measured using a projecting microscope at a magnification of ×100. The mean WFL and EVEL values were determined.

**Statistical analysis**

For estimating the difference in the maturation age of WFL, EVLD and EVEL, nonlinear regression analysis of a quadratic model with a plateau was used to describe the relation between the measured properties as dependent variables and the ring number from the pith as the independent variable (Peszlen 1994). The model was fitted using the nonlinear regression procedure in SPSS Regression Model 12.0.

The developmental stage of radial stem increment is divided into 3 stages, young, middle, and old. A schematic drawing of the developmental stages of radial stem increment is shown in Figure 1. The young stage is from the beginning of the radial stem increment to the age \( t_1 \) at the point of maximum current annual increment (CAI). The middle stage is from age \( t_1 \) to the age \( t_2 \) at the point of 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). The annual increment was estimated by the Gompertz growth function which was fitted to the relation between the cumulative annual ring width as the dependent variable and the ring number from the pith as the independent variable by using the nonlinear regression procedure in SPSS Regression Models 12.0. The Gompertz growth function is defined by Liao et al. (2003) as:

\[
y = A \exp(-e^{a-bt})
\]  
\[
y = \frac{A \exp(-e^{a-bt})}{t}
\]

\( y \): cumulative annual ring width (radius) at age \( t \)
\( t \): cambial age (ring number from the pith)
\( A, a, \) and \( b \): parameters determined by the nonlinear regression analysis

The function of CAI is calculated using the first derivative, which is defined as:

\[
y' = Ab \exp(-e^{a-bt})e^{a-bt} = ybe^{a-bt}
\]  
\[
y' = \frac{A \exp(-e^{a-bt})}{t}t
\]  
\[
y' = \frac{A \exp(-e^{a-bt})}{t}
\]

The age at the point of maximum CAI corresponds to the inflection point of the growth curve. If the second derivative of the Gompertz growth function equals zero, CAI attains the maximum value. Therefore, age \( t_1 \) is obtained when \( t_1 = a/b \).

The function of MAI is calculated by the Gompertz growth function divided by \( t \), defined as:

\[
y = \frac{A \exp(-e^{a-bt})}{t}
\]  
\[
y = \frac{A \exp(-e^{a-bt})}{t}
\]  
\[
y = \frac{A \exp(-e^{a-bt})}{t}
\]

\( y \): cumulative annual ring width (radius) at age \( t \)
\( t \): cambial age (ring number from the pith)
\( A, a, \) and \( b \): parameters determined by the nonlinear regression analysis
Age $t_2$ is obtained when CAI (equation 2) equals MAI (equation 3); $t_{bea-bt} = 1$. Age $t_2$ was estimated by using Microsoft Excel’s solver tool after parameters $a$ and $b$ were determined.

RESULTS AND DISCUSSION

Radial variation in size of axial elements

The radial variations of WFL, EVLD, and EVEL are shown in Figures 2–4. WFL and VLD increased rapidly in the inner part of the stem, and these values increased slightly or were constant in the outer part of the stem (Fig. 2 & 3). In the inner part of the stem, the variation with ring number from the pith of WFL and EVLD was similar to a quadratic curve, and in the outer part of the stem, they showed a more or less flat line. The quadratic function with a plateau model fitted well. The coefficient of determination of the model in each sample ranged from 0.779 to 0.951 for WFL and from 0.647 to 0.967 for EVLD. On the other hand, EVEL increased slightly with ring number from the pith, especially in the samples obtained from 11.3 m stem heights: sample no. A-5 and B-5 (Fig. 4). The coefficient of determination of the model in each sample ranged from 0.384 to 0.798. The period of increase in the inner part of xylem was sometimes prolonged for EVLD, when compared to the other parameters, as reported previously in Castanea crenata (Tsuchiya & Furukawa 2008).

In all the parameters, the plateau value estimated using the model was generally low in the higher stem heights with respect to all the anatomical properties. The ratio of the maximum value to the minimum value of different stem heights was relatively high for WFL (89.7% in Tree A and 84.3% in Tree B) in comparison to the values of EVLD (75.5% in Tree A and 79.7% in Tree B) and EVEL (77.8% in Tree A and 79.7% in Tree B). This result indicated that the height effect on the plateau value of vessels was strong (EVLD and EVEL). Aloni and Zimmermann (1983) suggested that high auxin levels near the young leaves induce narrow vessels while low auxin levels far from the young leaves induce wide vessels. The wood at 11.3 m stem height may be formed under relatively high auxin levels because elongation of shoots would be slow in the high part of the tree and the distance from the young leaves to the cambium is generally short.

The plateau value in the opposite side samples at the same stem height in Tree C and Tree D was approximately the same, and the ratio of the minimum value to the maximum value for WFL, EVLD, and EVEL in Tree C and Tree D was 96.6% and 95.0%, 93.4% and 99.7%, and 97.7% and 99.7%, respectively. This indicated that the direction effect on the plateau value of all of the three anatomical properties was weak.

Maturation age of each anatomical property

The maturation ages of WFL, EVLD, and EVEL ranged from 8–27 years, 11–38 years, and 9–26 years, respectively, in all samples. They differed widely not only within a tree at the different stem heights but also among trees at the same stem heights. However, it was similar between the northern and the southern aspects at the same stem height, except for the maturation age of EVEL in Tree D. The maturation ages at the upper stem height were generally lower than those at the lower stem height in all
three anatomical properties. This means that the maturation age is not determined only by cambial age, and that maturation ages for individual species should not be fixed in different stem heights.

In the same radial strip, the maturation ages of WFL and EVEL were similar, whereas that of EVLD was generally greater. The mean difference between the maturation age

Figure 2. Radial variation of wood fibre length (WFL) with ring number from the pith.
of WFL and EVEL was 3.6 years: WFL and EVLD, 8.0 years: and EVEL and EVLD, 8.3 years. This result disagreed with previous reports in poplar, for which the maturation age of WFL, VEL, VLD were approximately the same (Furukawa et al. 2000; Huang & Furukawa 2000).

Figure 3. Radial variation of earlywood vessel element length (EVEL) with ring number from the pith.

![Figure 3](image_url)
Juvenile wood is defined by its rapid change in cell size: therefore, the wood up to the period of the highest maturation ages of the 3 anatomical properties was regarded as juvenile wood. The maturation age of EVLD was generally the highest in the same radial strip among the other anatomical properties: therefore, juvenile wood was often

Figure 4. Radial variation of earlywood vessel lumen diameter (EVLD) with ring number from the pith.
determined on the maturation age of EVLD. On the one hand, mature wood is defined as that in which the vessel element length tends to be constant: however, in this study, the other properties—generally EVLD—sometimes continued to change even after EVEL became constant. Therefore, mature wood was also defined mainly on the basis of EVLD. We considered that among the three factors, EVLD was the best demarcation indicator for *Quercus serrata*.

**Radial stem increment**

The Gompertz growth function fitted very well to the radial variation of cumulative ring width. The coefficient of determination ranged from 0.979 to 0.999. The age at the point of maximum CAI (age $t_1$) ranged from 9–22 years, and that at the point of maximum MAI (age $t_2$) ranged from 11–34 years. These ages differed widely in stem heights within the same tree; they were relatively low at the upper stem height compared to the lower stem height. However, they were similar between the northern and the southern aspect. The period from the beginning of growth to age $t_1$ was referred to as the young growth stage, that from age $t_1$ to $t_2$ to middle growth stage, and that from $t_2$ up to the end of growth to old growth stage (Kataoka 1992). That is, the young growth stage was generally longer at the lower stem heights compared to that at the upper stem heights, and this result seemed to coincide with the tendency demonstrated by the maturation age of WFL, EVLD, and EVEL at different stem heights. On comparing the radial trend of anatomical properties during each growth stage, an increasing trend was observed during the young growth stage: only EVLD showed an increasing trend during the middle growth stage, and all properties tended to be constant during the old growth stage.

![Figure 5](image_url)

Figure 5. The relationship between the maturation ages of the three anatomical properties and age $t_1$ or age $t_2$. $t_{wfl} =$ the maturation age of wood fibre length (WFL); $t_{evel} =$ the maturation age of earlywood vessel element length (EVEL); $t_{evld} =$ the maturation age of earlywood vessel lumen diameter (EVLD).
growth stage. This trend was also observed for WFL and EVLD in *Castanea crenata* (Tsuchiya & Furukawa 2008).

The maturation age of WFL and EVEL was similar to age $t_1$, and that of EVLD was similar to age $t_2$ (Fig. 5). The mean difference between the maturation age of WFL and age $t_1$ was 3.2 years; it was 3.5 years between the maturation age of EVEL and age $t_1$, and 4.4 years between the maturation age of EVLD and age $t_2$. These results indicated that the ontogenetic development in size of axial elements related to the ontogenetic development of radial stem increment. The schematic drawing of the result is shown in Figure 6. The estimation of the maturation age of each anatomical property is very time-consuming, whereas measuring annual ring width is very easy especially in ring-
porous woods. The result of this study indicates the possibility of calculating the age demarcation between juvenile wood and mature wood with the developmental stage of radial stem increment.

CONCLUSION

A juvenile-mature pattern was generally observed in the radial variations of all anatomical properties in this study, but EVEL sometimes showed an indistinct juvenile-mature pattern. The period of rapid change in the inner part of xylem was sometimes prolonged for EVLD in comparison to the other parameters.

Maturation ages of WFL and EVEL were similar, whereas that of EVLD was generally greater in the same radial strip. On the basis of the definition of juvenile and mature wood in the three anatomical properties, it was considered that EVLD was the best demarcation indicator for *Quercus serrata*.

Maturation ages of WFL and EVEL were often similar to the age at the point of maximum CAI (age $t_1$), whereas that of EVLD was often similar to the age at the point of maximum MAI (age $t_2$). This indicates the relationship between the maturation in the size of axial elements and the developmental stage of radial stem increment.

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