

Original article

Variation of vessel lumen diameter in radial direction as an indication of the juvenile wood growth in oak (*Quercus petraea* Liebl)

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Summary — Radial variations of vessel lumen diameters and number of vessels per unit area were investigated in sessile oak wood from 3 trees in the same stand. With increasing growth-ring age, the lumen diameters of earlywood and latewood vessels and the number of earlywood vessels per unit area increased, especially in the core zone of stem cross-section; the number of earlywood vessels per unit area decreased. Results of measurements of the variation in conductive elements in oak wood suggest that the juvenile (core) wood of the oak trees may contain approximately 30 growth rings. For the same annual rings from the pith, a very significant tree effect appeared for the vessel characteristics measured.

Quercus petraea / vessel / diameter / number per unit area

Résumé — La variation radiale du diamètre du lumen des vaisseaux du bois, un indice de la durée de la période de croissance juvénile chez le chêne (*Quercus petraea* Liebl). On a examiné l'évolution du diamètre des lumens des vaisseaux et de leur nombre par unité de surface depuis la moelle jusqu'à l'écorce sur 3 chênes sessiles provenant d'un même peuplement. Lorsque l'âge du cerne compté depuis la moelle augmente, le diamètre des lumens des vaisseaux du bois de printemps augmente et leur nombre par unité de surface diminue. Dans le bois d'été, le diamètre des lumens et leur nombre par unité de surface augmentent lorsque l'âge augmente. Cet effet de l'âge du cerne est très sensible au voisinage de la moelle. Les résultats de l'étude des variations des éléments conducteurs en fonction de l'âge depuis la moelle montrent que la zone de bois juvénile chez le chêne concerne à peu près les 30 premiers cernes depuis la moelle. Pour le même âge depuis la moelle, un effet individuel (effet arbre) très significatif apparaît pour les caractéristiques des vaisseaux prises en considération dans l'étude.

Quercus petraea / vaisseaux / diamètre / nombre par unité de surface

INTRODUCTION

This paper is a continuation of studies on the variation in the structures and properties of oak wood (Maeglin, 1976; Petrić and Šćukanec, 1980; Nepveu, 1984a, 1984b, 1990; Gasson, 1985; Helińska-Raczkowska, 1990; Helińska-Raczkowska and Fabisiak, 1991). An improved understanding of the laws governing changes in structural features of wood in the function of wood cross-section radii, as well as the relationship between these changes and conditions of tree growth in a stand, is very important from the wood-application and silviculture-practice points of view. It should be noted that only quantitative assessments of the influence of different factors on wood formation will provide the information needed in silviculture practice so as to produce trees of a desired quality (Trotter, 1986; Wagenführ *et al.*, 1989). In previous studies, juvenile wood produced by juvenile (immature) cambium was investigated, but little attention has been paid to the hardwoods (Nepveu, 1981; Zobel and van Buijtenen, 1989). In particular, a lack of reliable criteria for distinguishing the juvenile and mature wood in one tree appears to be very inconvenient. Therefore, in this study lumen diameters of earlywood and latewood vessels and the

number of vessels per unit area in oak trees of even-aged stands with different growth characteristics were measured to fill the information gap.

MATERIALS AND METHODS

The experimental site was located in a 78-year-old (according to the management plan) even-aged oak stand (*Quercus petraea* Liebl) in the western part of Poland (52°33'N and 16°50'E) on the site of the experimental forests of the Agricultural University in Poznań. With reference to the measured diameters of trees, one experimental tree was selected from each of the dominant, intermediate, and suppressed classes (table I). Discs for experiments were taken at a height corresponding to the 1/4 height of the tree measured from the butt-end (table II). Strips were cut along the northern radius of each disc (20 mm in width along the tangential direction and 20 mm in height along the fibres). For the investigation, the following annual rings, counted from the pith, were selected: 3, 6, 9, 12, 15, and further out towards the bark, every fifth ring. Permanent slides of growth-ring transection were taken from each of these rings for measurements.

The lumen diameter of earlywood and latewood vessels was measured on samples to include all the growth rings under study. Measurements were made using the system described before (Helińska-Raczkowska, 1990). For each of the annual rings studied, 15 measurements of earlywood and latewood vessel

Table I. Characteristics of the oak trees studied.

<i>Tree characteristics</i>	<i>Tree growth conditions</i>		
	<i>Dominant</i>	<i>Intermediate</i>	<i>Suppressed</i>
Tree age * (years)	76	74	70
Diameter outside bark (cm)	36	23.5	18
Tree height (m)	23	22	16.5
Crown height (m)	12	13	13
Crown index **	0.5	0.6	0.8

* Number of growth rings on butt-end cross-section; ** ratio of crown length to tree height.

Table II. Characteristics of the oak tree discs studied from 1/4 tree height.

<i>Tree growth conditions</i>	<i>Distance from butt-end (m)</i>	<i>Diameter of disc (cm)</i>	<i>Number of growth rings (nb)</i>
Dominant	5.5	27	65
Intermediate	5.5	19	62
Suppressed	4	12	63

lumen diameter (inner diameter) were made. The maximal tangential inner diameter of the first row earlywood vessels in the growth ring and latewood vessels located near the border of growth rings were measured. On the cross-section, the number of earlywood and latewood vessels per unit area, *i.e.* their number per 1 mm² of the transection of earlywood and latewood part of the annual ring, was also determined. However, the number of latewood vessels per unit area was determined at the border of the annual ring.

RESULTS AND DISCUSSION

Statistical analysis of the measurements indicated that the mean coefficient of variation for earlywood vessel lumen diameter is 17 (8...32)%, while for latewood it is 18 (10...29)%. Histograms of the diameters and a comparison of the arithmetical means and modal values suggest that the distribution of vessel lumen diameters is close to normal.

Radial variation of earlywood vessel lumen diameter and the number of earlywood vessels per unit area is shown in figure 1. It follows from these data that the increment of earlywood vessel lumen diameter increases continuously with the increase of cambial age of growth rings up to about 30 yr. The vessel lumen diameter remained more or less constant with any further increase of the cambial age of growth rings. Increase in the earlywood vessel lumen diameter in the outerwood was significant compared with that in the pith area; on aver-

age it reached 90%. As the age of growth rings increased, the number of earlywood vessels per unit area decreased (fig 1), the variation of this characteristic being the greatest in the area from pith to about the 30th growth ring. There was a negative correlation between earlywood vessel lumen diameter and their number per unit area (fig 2), which means the greater the earlywood vessel lumen diameters, the lower the number of the earlywood vessels per unit area. For example, for the vessel lumen diameter of 300 µm, their number per unit area was 5/mm², while for the diameter of 120 µm, the number of the vessels per unit area increased to 25/mm². Such a relationship between the diameter of vessel lumen and their number per unit area can be explained by functional reasons (Bamber and Curtin, 1974; Baas, 1982; Ziemermann, 1983; Carlquist, 1988). It is also worth mentioning that the diameter of earlywood vessel lumen was negatively correlated with the width of annual rings for a given tree, *i.e.* the narrower the annual rings, the greater the diameter of earlywood vessel lumen (fig 3, for example, for a dominant tree). For latewood vessels, with increasing age of growth rings, an increase in the lumen diameter and in the number of vessels per unit area was observed (table III). However, an increase in the diameter of latewood vessel lumina in the outerwood zone, in comparison with the vessel in the corewood zone was significantly smaller than for earlywood vessels, and on average it amounted to 30%. On the other hand, the number of

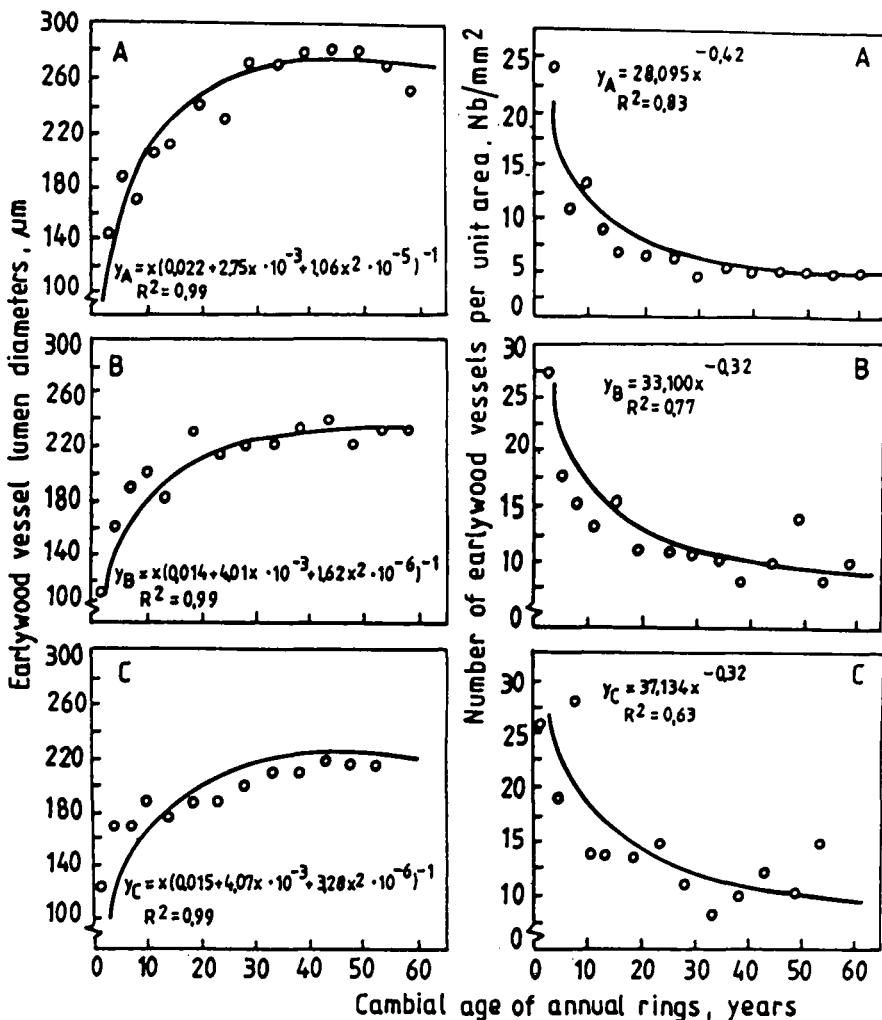


Fig 1. Relationship between the earlywood vessel lumen diameters (left) number of earlywood vessels per unit area (right) and the age of growth rings of the 3 oak trees belonging to dominant (A), intermediate (B), and suppressed (C) trees. Each social status is represented by only one tree, and so no valid conclusion can be inferred about the effect of the social status on vessel characteristics. The equations of the curves are as follows: A (left) $y_A = x(0.022 + 2.75x \cdot 10^{-3} + 1.06x^2 \cdot 10^{-5})^{-1}$, $R^2 = 0.99$; (right) $y_A = 28.095x^{-0.42}$, $R^2 = 0.83$; B (left) $y_B = x(0.014 + 4.01x \cdot 10^{-3} + 1.62x^2 \cdot 10^{-6})^{-1}$, $R^2 = 0.99$; (right) $y_B = 33.100x^{-0.32}$, $R^2 = 0.77$; C (left) $y_C = x(0.015 + 4.07x \cdot 10^{-3} + 3.28x^2 \cdot 10^{-6})^{-1}$, $R^2 = 0.99$; (right) $y_C = 37.134x^{-0.32}$, $R^2 = 0.63$.

latewood vessels per unit area tended to increase with the increasing age of the growth ring, even reaching 300% in the outerwood zone in comparison with the corewood zone.

Radial variation of the number of earlywood and latewood vessels per unit area varied (fig 4). The number of earlywood vessels per unit area decreased as the age of growth rings increased, while that of late-

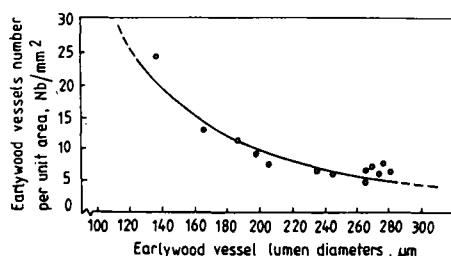


Fig. 2. Relationship between number of earlywood vessels per unit area and lumen diameters in the dominant oak tree. The equation of the curve is $y = 178142x^{-1.85}$, $R^2 = 0.90$.

wood vessels increased. It should be also noted that high variability exists between individual trees for the number of earlywood and latewood vessels per unit area. The same is true for the diameter of earlywood vessel lumina, which varies from 310 μm in

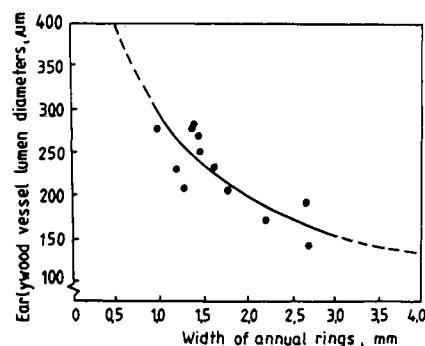


Fig. 3. Ring widths and the earlywood lumen diameters in the dominant oak tree. The equation of the curve is $y = 293.22x^{-0.57}$, $R^2 = 0.65$.

the dominant tree to 220 μm in the suppressed tree. Diameters of latewood vessel lumina, on the other hand, exhibit an inter-tree variability but this is lower than for the other above-mentioned characteristics.

Table III. Parameters of the regression equation given by formula $y = x(a + bx + cx^2)^{-1}$ for the relationship between the lumen diameters of latewood vessels (y , μm), vessel number per unit area (y , No./mm²) and the age of growth rings of oak trees (x , yr).

Tree growth conditions	Regression equation parameters			R^2
	a	b	c	
Dominant tree	0.095	0.027	1.051×10^{-4}	0.99
	0.063	2.615×10^{-3}	1.530×10^{-5}	0.96
Intermediate tree	-7.431×10^{-3}	0.052	-2.179×10^{-4}	0.99
	0.080	2.495×10^{-3}	4.520×10^{-5}	0.93
Suppressed tree	0.484	8.511×10^{-3}	4.524×10^{-4}	0.88
	0.034	7.559×10^{-3}	2.335×10^{-5}	0.87

Above line: latewood vessel lumen diameter; below line: vessel number per unit area.

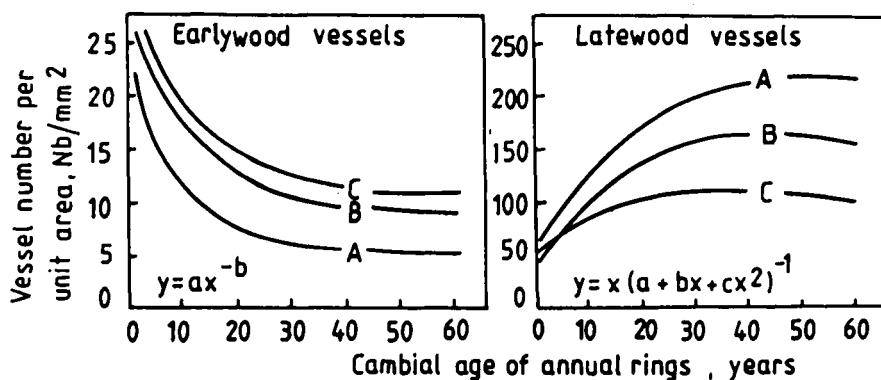


Fig 4. Between-tree variability in an even-aged stand on number per unit area of the earlywood (left) and latewood (right) vessels; A: dominant; B: intermediate; C: suppressed tree. Each social status is represented by only one tree and so no valid conclusion can be inferred about the effect of the social status on vessel characteristics. The equations of the curves are as follows: earlywood: $y = ax^{-b}$; latewood $y = x(a + bx + cx^2)^{-1}$.

The absolute values of the vessel lumen diameter measured were similar to those reported in the literature (Wagenführ and Scheiber, 1974; Wagenführ, 1984; Wagenführ *et al.*, 1989). As regards the number of latewood vessels per unit area in the mature wood, the values obtained are closest to those collected by Vichrov (1954).

The curves of radial variation of earlywood vessel lumen diameter or number per unit area of vessels may be used as an indicator of the border between the juvenile (corewood) and the mature wood (outerwood). The zone of juvenile wood may be assumed to comprise growth rings from pith to those that have either a constant diameter of earlywood vessel lumen or a constant number per unit area. In other words, the number of years taken to reach a more or less constant earlywood lumen diameter or its number per unit area may be used as a junction between the juvenile and the mature wood in oak. Due to the value of the determination coefficient R^2 , the diameter of the vessel lumen is preferable as the indicator. In the case considered here, the transition period of juvenile wood into mature wood

would be about 30 yr on visual estimation. The same limit can be (visually) accepted for the 3 trees considered here. It is worth mentioning that the juvenile period of oak development, determined on the basis of changes in earlywood vessel lumen diameter, overlaps the zone of juvenile wood determined on the basis of radial variation in fibre length (Helińska-Raczkowska and Fabisiak, 1991). Moreover, it should be noted that the juvenile period of oak development, determined on the basis of radial variation in wood anatomical elements, corresponds to the juvenile period of tree development established on the basis of the number of years a tree needs to achieve reproduction capabilities, which for *Q robur* usually takes from 25 to 30 yr (Wareing and Philips, 1985).

Juvenile oak wood was characterized by wider growth rings than mature wood, a higher percentage of latewood, and a higher wood density (dry weight, green volume basis) by about 100 kg/m³. Average density differentiation of examined oak wood is given in table IV. However, an attempt to use these parameters to differ-

Table IV. Average density differentiation of examined oak wood.

Tree growth conditions	Basic density (kg/m ³)		Difference
	Corewood (< 30th ring)	Outerwood (> 30th ring)	
Dominant tree	590	490	100
Intermediate tree	620	550	70
Suppressed tree	600	500	100

entiate between juvenile and mature wood failed.

Generally, the results of our studies are in agreement with the basic laws of ecological and functional anatomy, by which we mean the broadly understood influence of climatic, biotic, and edaphic factors on the variations in wood structure. According to these laws, deteriorated conditions of tree growth may result in a decrease in the diameter of earlywood vessels and increase their number per unit area (Carlquist, 1988; Van den Over *et al.*, 1981; Baas, 1982). The comparison between the 3 trees taken into consideration here (1 dominant, 1 intermediate, 1 suppressed tree) seems to be in accordance with these bibliographic results but our sampling is not complete enough to confirm this point seriously. However knowledge of the laws mentioned above with reference to hardwoods is limited (Denne and Dood, 1981), which has also been evidenced in this paper. Due to the scarcity of experimental material, this study should be considered as an introductory. It seems necessary therefore to extend these studies to other species from the *Quercus* genus and to other genera from the group of ring-porous wood (*e.g.*, *Fraxinus*, *Ulmus* and *Robinia*).

CONCLUSIONS

Radial variation of the diameter of earlywood vessels in oak and their number per unit area

is generally related to the age from the pith in the juvenile wood (corewood). With increasing age of growth rings, the diameter of earlywood and latewood vessel lumina and the number of latewood vessels per unit area increases, while the number of earlywood vessels per unit area decreases. The zone of juvenile wood determined from the curves of radial variation in earlywood vessel lumen diameter consists of approximately 30 growth rings. For the same age from the pith, a very significant tree effect appears for the diameter of vessel lumen and the number of vessels per unit area.

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