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Radial evolution of vascular elements in the oak *Quercus ilex* L. wood

M. Berrichi[1], K. Benabdelli[2], A. Haddad[3]

[1]*Department of Forest Resources, Faculty of Nature and Life and Earth Sciences and the Universe, University of Tlemcen, Tlemcen, Algeria*

[2]*Department of Biology, Faculty of Nature and Life Sciences, University of Mascara, Mascara, Algeria*

[3]*Department of Agronomic Sciences, Faculty of Nature and Life Sciences, University of Mostaganem, Mostaganem, Algeria*

ABSTRACT: In order to describe and measure the evolution of vascular elements in time, we examined two groups of samples of the green oak (*Quercus ilex* Linnaeus) wood. These groups are on the same radial plane and come from two trees growing under identical conditions and with different ages. The first group is located in the internal zone between the 15th and 19th growth ring and the second group is situated in the external area before the sapwood. The analysis of results shows the outside zone with isolated, numerous and large vessels compared to the internal zone. The results also explain how the vascular elements develop in advanced age.

Keywords: vessel diameter; number of vessels; early wood; latewood; evolution

The wood mass of oak has four types of cells: conducting vessels, fibres for support, ray parenchyma and axial parenchyma (Campredon 1980; Prat 2004; Benoit 2011).

The vessels are the conduction system of sap, they have a disposition and varied dimensions (Zimmermann 1983; Huber 1993; Gartner 1995). The vessels communicate with each other by perforations.

The vessels are grouped in rows at the beginning of the ring in the initial wood (Sachsse 1984; Collardet, Besset 1992; Benoit 2011). Their tangential diameter is up to 400 µm (Grosser 1977; Fengel, Wegener 1989) or even 500 µm (Jacquiot et al. 1973; Cloutier 2002). Small vessels have a specific provision due to their location and organization (Bakour 2003). Granier et al. (1996) showed that small latewood vessels could operate many years; the loss of conductivity is generally accompanied by the gradual blockage of vessels by tyloses (Bowes, Mauseth 2008).

The vessel diameter, length and the density of vessels are linked to the species (Polge, Keller 1973; Kanowski et al. 1991; Benoit 2011). Nevertheless, soil heterogeneity, light, temperature and humidity of the air around the shaft, the internal structure of the trunk, the asymmetry of the crown, root architecture and age can strongly influence the conductive elements (Carlquist 1988; Lafont et al. 1988; Trouy 2015).

The objective of this study is to describe and quantify the development of these elements with age in the radial direction from the pith of *Quercus ilex* Linnaeus in the far west of Algeria (Terni forest).

We chose to measure simple morphological criteria of the vessels: average diameter, number per unit of area and length. Fletcher (1975), Gasson (1987), and Guilley and Nepveu (2003) estimated that these parameters have an important role in the ecophysiological functioning of trees.

Before focusing on the evolution of vascular elements in oak wood, a number of additional factors could explain the change in the size of these elements:

(*i*) The environment: Prat (2004) and Barij (2006) showed that the xylem structure is strongly dependent on the local environment of a tree. The results of Kramer (1964), Aussenac (1993), Corcuera et al. (2004), and Eckstein (2004) showed that the availability of water, temperature and light affect the dimensions, the number of cells and the changes in the average diameter of vessels. Flechter (1975) showed that wet years produce small-sized vessels. Huber (1993) noted no relationship between vessel area and annual growth layer in the adult wood of *Quercus robur* Linnaeus and *Quercus petraea* (Mattuschka) Lieblein. In addition, the same author showed a small but significant correlation that exists between the individual surface of the pore and one of the studied climate data (maximum temperatures of autumn months outstripping the vessel formation). The authors cited by Hroš and Vavrčík (2014) argue that the vessel size is mainly controlled by water availability at the time of vessel formation and by temperature in the Mediterranean. The vessel size should decrease when water availability is low;

(*ii*) The leaf area index: Huber (1993) showed that in *Q. robur* and *Q. petraea* in the year following the removal of leaves on young trees, vessels have small areas. Granier et al. (1999) and Infante et al. (2001) stated that a high leaf area index affects the flow of the sap;

(*iii*) Age of the tree: Gasson (1987) and Barij (2006) demonstrated that the vessel size increases with age. Lafont et al. (1988) mentioned that evolution is marked by an increase in vessel diameter. In the case of *Q. petraea*, Helinska-Raczkowska (1994) noted wider and fewer vessels for springwood in the external zone, and numerous and larger vessels in the external area of late wood. Detienne (1988) and Normand (1998) noted for the vessels of hardwood in general a growth in number and an increase in pore diameter. Kolář et al. (2012) reported that the surface area of the largest early wood vessel increased with age in the direction from pith outwards, in the case of *Q. robur* and *Q. petraea* like in subfossil oaks found in the area of Moravia (Czech Republic).

In this study, we attempt to describe, quantify and verify hypotheses collected in this retrospective bibliography and try to apply them to the wood of *Q. ilex* located within the limits of the steppe and forest areas.

METHODS

Presentation of the study area. The *Q. ilex*, object of this study, was taken from the forest of Terni – Tlemcen, in the extreme west of Algeria (Fig. 1).

The main characteristics of the study area are as follows: (*i*) average altitude: 1,200 m, (*ii*) average annual precipitation (1960–2014): 565 mm, (*iii*) average maximum temperature (July): 29.08°C, (*iv*) average minimum temperature (January): 2.11°C, (*v*) bioclimatic floor: sub-humid to cool winters, (*vi*) the seasonal rainfall regime (1960–2014): spring – winter – autumn – summer.

In the Mediterranean context this *Q. ilex* is one of the most dominant species in forests (Barbero et al. 1992; Dahmani 1997; Berrichi et al. 2010). In Algeria, the green oak extends throughout the north and covers 700,000 ha (21% of Algeria's forest area) from the coastline to the Saharan Atlas and from the Moroccan border to the Tunisian border (Letreuch 1995). The area that it occupies in the Mountains of Tlemcen would be 82,000 ha, i.e. 41.1% of the total forest area (Berrichi 1993).

Wood sampling. Microscopic cuts were made in accordance with a protocol of sampling small blocks for analysis, in relation with the agreed tar-

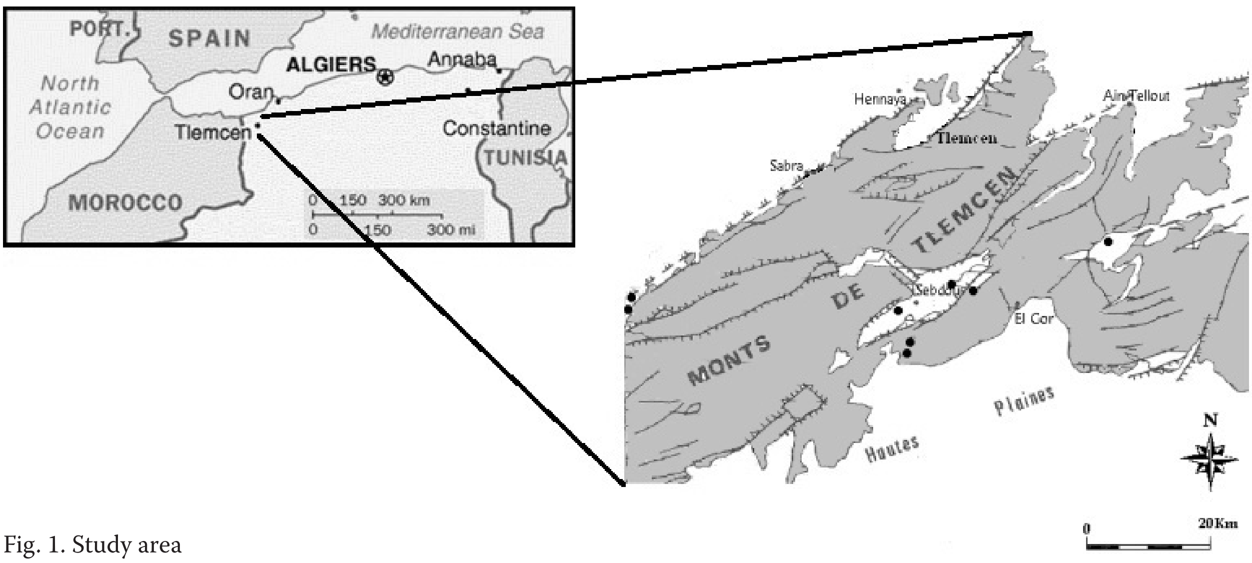

Fig. 1. Study area

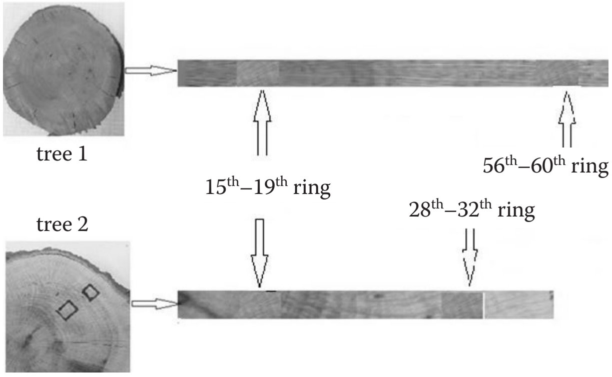

Fig. 2. Scheme of the experimental blocks

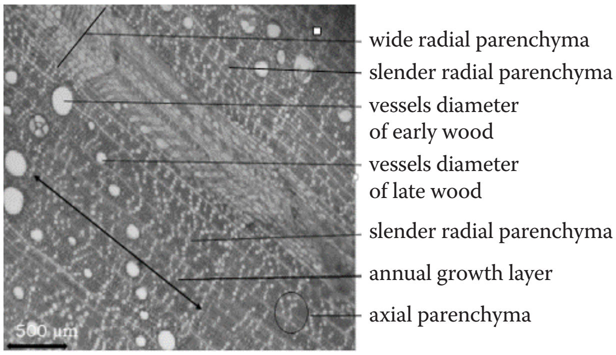

Fig. 3. Transversal plane of *Quercus ilex* Linnaeus

get. After verification of the central position of the pith in the radial direction and east exposure, we identified the internal zone and the external zone, which corresponds to the wood transition between sapwood and heartwood (Fig. 2). The selection of the external zone is explained by the arrival at the final structure of some characters proposed by Normand (1998) for some hardwood species. The characteristics of the two trees of *Q. ilex* are presented in Table 1.

Model of the vessel wood analysis. The model of the wood analysis (Table 2) is a vessel model designed and inspired by Venet (1974), Detienne (1988), and Normand (1998). In this model, we were interested only in vessels with regard to description and quantification. From each zone of the two trees, we realized 60 measurements of vessel diameter in early wood, 60 measurements of vessel diameter in latewood and 50 measurements of the number of vessels per mm^2.

Table 1. Characteristics of trees and wood samples

	Tree 1	Tree 2
Age of the tree	86	51
Height (m)	7.35	6.20
Circumference at 1.30 m (cm)	82.3	65.5
Internal zone	15^{th}–19^{th} ring	15^{th}–19^{th} ring
External zone	56^{th}–60^{th} ring	28^{th}–32^{th} ring

RESULTS

Descriptive characterization

A transversal plane (Fig. 3) shows the descriptive characters of *Q. ilex*.

The image of the pores given by the transversal plane of the two samples differs from one area to another. The pores are grouped into a radial line in the internal zone and are completely isolated in the external zone (Fig. 4). The pores of the two areas are relatively stretched in radial direction.

Quantitative characterization

The histograms (Fig. 5) show the characteristics of the *Q. ilex* vessel elements.

The histograms (Fig. 5) of measured characteristics and Table 2 of the vessel wood analysis show the different classes of each character and give an idea of differences between the internal zone and external zone of vessels in *Q. ilex*.

The principal changes related to vascular elements as they pass from the internal area to the external area are as follows:

(*i*) In vessel diameter of early wood (Fig. 5a): the diameter of the early wood vessels is "average" (65% in internal zone and 50.8% in external zone) and

Table 2. Model of the vessel wood analysis (Venet 1974; Detienne 1988; Normand 1998)

Vessel diameter		Vessel length		*N* per mm^2	
Class (µm)	qualification	class (µm)	qualification	class	qualification
< 50	very thin	< 350	short	< 2	very rare
50–100	thin	350–800	average	2–6	rare
100–200	average	> 800	long	6–20	average
200–300	wide			> 20	many
> 300	very wide				

N – number of vessels

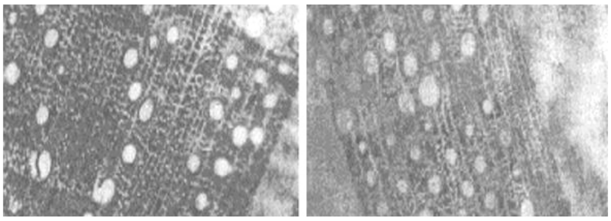

Fig. 4. Variation in the disposition of the pores of *Quercus ilex* Linnaeus in internal (a) and external (b) area

"thin" (23.3% in internal zone and 22.5% in external zone). A higher proportion of large vessels is present in the external zone (20.8% against 8.3%);

(*ii*) In vessel diameter of latewood (Fig. 5b): the diameter of latewood vessels is "thin" in the two zones (67.5% in internal zone and 49.2% in external zone). A higher proportion of average vessels is present in the external zone (35.8% against 17.5%);

(*iii*) In vessel density per mm^2 (Fig. 5c): the number of vessels per mm^2 is sometimes average (54% in internal zone and 77% in external zone) and sometimes high (46% in internal zone and 36% in external zone);

(*iv*) In vessel length (Fig. 5d): the vessel length is mainly average (56% in internal zone and 68% in external zone) and short (38% in internal zone and 18% in external zone). The external zone contains more long vessels (14% against 6%).

The results lead to information on the concept of the evolution of vessels from the internal to the external zone (Table 3).

Based on the results of Table 3 and the histograms of Fig. 5, we conclude about the vessels of *Q. ilex*:

(*i*) About vessel diameter of early wood: the diameter is "average" and the largest vessels are present in the external zone;

(*ii*) About vessel diameter of latewood: the latewood pores are "fine" and the largest vessels are also present in the external zone;

(*iii*) About vessel density: the number of vessels per area is "average" and the largest vessels are also present in the external zone;

(*iv*) About vessel length: the vessel length is "average" and in the external zone there are longer vessels.

The general qualification of vascular elements of *Quercus ilex* L. is "average". Indeed, in the Mediterranean area, green oak rarely exceeds 7 meters in height. In this regard, Carlquist (1988) noted that dwarfing of a plant may result in a diminution of vessel element length and diameter.

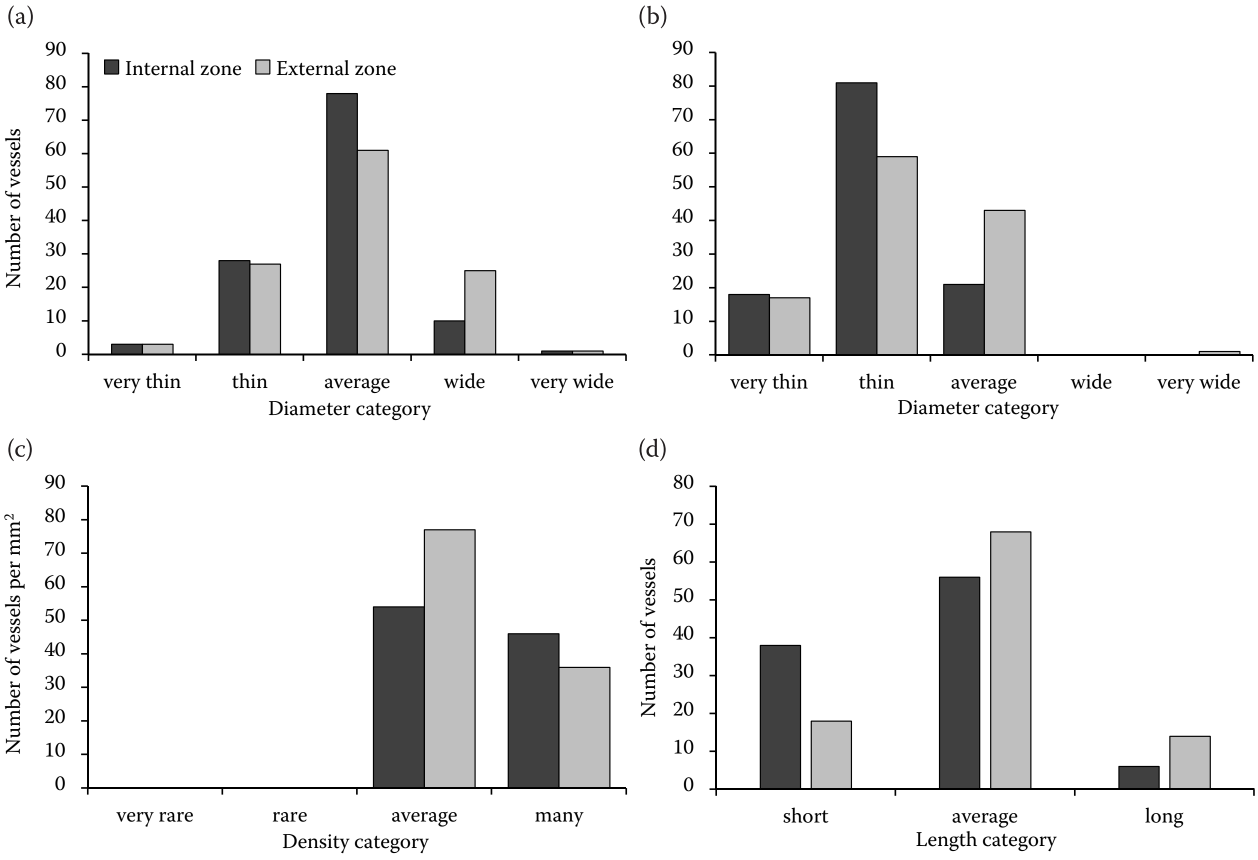

Fig. 5. Histograms of wood characteristics of the vessels: diameter in early wood (a), diameter in latewood (b), density (c), length (d)

Table 3. Variability of the vascular elements of *Quercus ilex* Linnaeus

	Average		SD		*CV* (%)		*F*-value (5%)		
	INZ	EXZ	INZ	EXZ	INZ	EXZ	observed	theoretical	difference
EW (μm)	123.85	171.70	39.15	46.94	33.57	29.22	6.51	1.96	S
LW (μm)	70.41	86.57	20.93	24.53	30.28	29.90	3.43	1.96	S
VD (*N* per mm^2)	16.97	21.42	4.62	6.04	27.08	27.34	3.68	1.96	S
L (μm)	459.00	476.00	310.0	268.0	58.95	49.70	1.47	1.96	NS

EW – vessel diameter in early wood, LW – vessel diameter in latewood, VD – vessel density, *N* – number of vessels, L – vessel length, INZ – internal zone, EXZ – external zone, SD – standard deviation, *CV* – coefficient of variation, S – significant difference, NS – non-significant difference

DISCUSSION

The study of the radial evolution of vascular elements of *Q. ilex* shows:

(1) As descriptive result: the pores are grouped into a radial line in the internal area and completely isolated in the external area. The change in the arrangement of pores is the first descriptive result;

(2) As quantification result: the external zone compared to the internal zone shows these effects for each parameter:

(*i*) For the importance of the vessel lumen and vessel number in the external zone and in the internal zone according to Hacke et al. (2001), Meinzer (2003), Bucci et al. (2004), and Perré et al. (2012) suitable indicators are water storage capacity and conducting efficiency of water in the stem of *Q. ilex*. The surface of the lumen is 0.12 mm^2 in the internal zone, and 0.28 mm^2 in the external zone. Is this increase in the vessel surface a consequence of the effect of age or the effects of climate conditions? The only assumptions that we have are the aging of the cambium (age) and the annual rainfall, 664 mm of rain during the period of wood formation of the internal zone against 588 mm for the external zone. For the flow of sap, the vessel volume in the external zone is 0.13 mm^3·mm^{-3}, while in the internal zone this volume is only 0.05 mm^3·mm^{-3}. The variation of density is dependent on the vessel volume (Natterer et al. 2004). In the heartwood, this volume is the first indication of wood density (Berrichi 2015);

(*ii*) The diameter of early wood and latewood vessels is large in the external zone. This situation causes a decrease of the fibre proportion and consequently a decrease in the wood density of the external zone. Wood strength is highly dependent on the xylem structure, any increase in the diameter of the vessels would imply a low proportion of fibres, and consequently a lower density compared to wood containing small vessels (Gartner 1995; Mattheck, Kubler 1995). Guilley (2000) mentioning research works on the wood of *Q. petraea*, *Q. robur*, and *Quercus garryana* Douglas ex Hooker showed that aging cambium leads to a reduction in the proportion of fibres.

CONCLUSIONS

With aging, the wood vessels of *Q. ilex* when we approach the outside of the trunk, acquire the following types of adjustments: the vessels are isolated and become larger and numerous. This radial evolution of the vascular elements causes a reduction in the space occupied by the fibrous tissues, wood rays and axial parenchyma.

Taking into account the cell thickness of fibres that is in our case significantly thicker in the internal zone by 7.12 μm compared to 6.27 μm in the external zone (Berrichi 2015), we can conclude that wood density decreases with distance from the pith. Polge and Keller (1973), Klumpers (1994), Guilley (2000), Natterer et al. (2004), and Perré et al. (2012) showed that density decreases when the cambium is aging.

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Corresponding author:

Mohammed Berrichi, Ph.D., University of Tlemcen, Faculty of Nature and Life and Earth Sciences and the Universe, Department of Forest Resources, Abi Ayed Abdelkrim Street 22, 13000 Tlemcen, Algeria; e-mail: berrichi_mohamed@yahoo.fr