Earlywood vessel features in *Quercus faginea*: relationship between ring width and wood density at two sites in Portugal

Vicelina B Sousa(1), José Luís Louzada(2), Helena Pereira(3)

Wood anatomy holds relevant information for tree development and timber quality (e.g., wood density), which is important for the sustainability of the species. *Quercus faginea* Lam. (Portuguese or Lusitanian oak) is an autochthonous Mediterranean oak species characterized by a shrinking natural distribution area and use abandonment. We studied the variation of several wood properties and their relationships with the aim of determining and possibly increasing the wood economic value of this species. The anatomical features of earlywood vessels (area, number, frequency and proportion) were investigated in twenty *Q. faginea* trees sampled at two locations within the natural distribution of the species in Portugal. Moreover, we analyzed the variation of vessel features from pith to bark, the radial growth and the wood density to search for patterns and relationships among the analyzed parameters. Mean earlywood vessel area increased with cambial age up to 60-70 years and then leveled off. An inverse pattern was found for the number of vessels per ring beyond that age. Similar radial patterns of all vessel features were found at both sites, and no significant differences in earlywood vessel area were found between sites. The within-tree development of earlywood vessels was age-related, though not influenced by growth. Earlywood vessel features explained the variation of wood density, i.e., wood density of *Q. faginea* was strongly negatively correlated with both mean vessel area and proportion.

Keywords: *Quercus faginea*, Earlywood Vessels, Wood Density, Ring Width, Variation

Introduction

Vessel size and distribution throughout a growth ring deeply affect tree physiology and wood utilization. Vessels are the main cell types of the vascular transport system of plants and their importance is higher when the species are under threat of, for example, drought. In fact, the conductive area of vessels seems related to the conductive efficiency and tracks intra-seasonal information (Carlquist 2001, Fonti et al. 2009, 2010). Wood characteristics such as texture (i.e., the wood appearance due to cell morphology and density) are affected by vessel characteristics, thereby the quality of wood products is also vessel related (Zobel & Van Buijtenen 1989, Stanzl-Tschegg 2011). The measurement of vessel features such as area and diameter used to be a very time-consuming task. However, the current use of microscopy coupled with image analysis makes data acquisition and processing more efficient (Gussow 1985, Sass & Eckstein 1994, Fonti et al. 2002, Leal et al. 2007). Recently, the number of studies focusing on the variation of vessel features (e.g., with age, growth and site) and their relation to other wood characteristics (e.g., density) has increased, although data is still scanty and results are often species-specific. The main tendencies in studies on vessel diameter variation have been recently discussed by Anfodillo et al. (2013), with special attention to the relationship between axial conduit widening and tree height. Vessels are key contributors to wood density, that is inversely proportional to their size and number (Savidge 2003). In oaks, vessel proportion (i.e., the percentage of xylem cross-section occupied by vessels) is one of the major anatomical factors affecting latewood density (Rao et al. 1997) and specific gravity (Zhang & Zhong 1992). For instance, in *Quercus suber* vessel size and number were found to contribute significantly to mean ring wood density (Leal et al. 2011).

Contrasting results have been reported so far regarding the variation of vessels with age and tree growth. In *Quercus alba* the percentage of earlywood vessel area was influenced by the radial position, but not by the ring width (Phelps & Workman 1994). Earlywood vessel area was larger in fast-growing than in slow-growing *Juniperus nigra* trees, but no correlation was found between the earlywood vessel area and ring width (Phelps & Workman 1994). Denne et al. (1999) reported that the total vessel proportion decreased significantly as the ring width increase in *Nothofagus nervosa*, a diffuse porous hardwood species. In *Q. suber*, the vessel size increased from pith outwards, explaining 32% of the total variation in wood ring density (Leal et al. 2007, Leal et al. 2011). In *Q. rubra*, vessel percentage was also found to be correlated with specific gravity, independently of soil types (Hamilton & Knauss 1986). As for ring porous species, it is generally accepted that latewood wood is responsible for the variation in wood ring density, while earlywood width is relatively constant (Chauhan et al. 2006). *Quercus faginea* Lam. is a ring porous oak natural occurring mainly in Portugal and Spain. It was more abundant in the XV-XVI centuries when it was used as a valued timber species, while nowadays it is mostly considered for conservation purposes (Capel & Catry 2007, Carvalho 1997). Recent studies have shown that vessels represent about 15-17% of the xylem tissue in *Q. faginea*, with higher values near the bark, and earlywood vessel diameters also increased radially from pith to bark (Sousa et al. 2014). In this species wood density components (ringwood, earlywood and latewood density) decreased radially and were influenced by tree growth factors (Knapić et al. 2011).

In this work, the distribution pattern of earlywood vessels within the ring and its relationship with the cambial age have been investigated, as well as the relation between vessel parameters and wood density components. To address the above goals, early-
wood vessel features (area, number, frequency and proportion) were analyzed in relation to ring width and wood density in *Quercus faginea* trees grown in two sites located in the natural range of the species in Portugal. Sampling included 10 trees with 40 years of age on average and 10 trees with a mean age of 125 years.

**Material and methods**

Twenty *Q. faginea* trees were selected in naturally-regenerated, unmanaged forests in Portugal, near Macedo de Cavaleiros (site 1 - 41° 30′ N, 7° 01′ W) and Vimeiro (site 2 - 39° 29′ N, 9° 01′ W). The climate is Mediterranean tempered by oceanic influence. The mean annual temperature is 12 and 15 °C, and the mean annual rainfall 700 and 890 mm at site 1 and 2, respectively. Mean diameter at 1.30 m above the ground was 21 and 37 cm, and mean tree height was 11 and 15 m at site 1 and 2, respectively. For each sampled tree, a wood disc was excised at 1.3 m above the ground level. The wood was analyzed within a radial strip from pith to bark taken in the same compass direction.

Wood density was determined by X-ray microdensitometry and the first results were reported in Knapić et al. (2011). The data on mean ring density, earlywood density, late-wood density, heterogeneity index, latewood percentage and ring width were comprehensively analyzed and related with vessel features. The transverse surface of the wood was clear both in very narrow growth regions characterizing the latewood.

Ten dominant or co-dominant trees with no visible signs of decay were harvested at each site. Sampled trees were on average 40 and 125 years-old at the time of sampling in site 1 and 2, respectively. Mean diameter at 1.30 m above the ground was 21 and 37 cm, and mean tree height was 11 and 15 m at site 1 and 2, respectively. For each sampled tree, a wood disc was excised at 1.3 m above the ground level. The wood was analyzed within a radial strip from pith to bark taken in the same compass direction.

Mean vessel area (or lumen area of earlywood vessels), vessel proportion (percentage of cross sectional area occupied by the earlywood vessels per growth ring), vessel number (total of earlywood vessels counted by ring) and vessel frequency (number of earlywood vessels per mm²) were determined for each annual ring, totaling about 1650 rings. Measurements were carried out within a frame window of approximately 2.3 mm of tangential width, while the radial dimension varied with each earlywood width, from the inner to the outermost ring. For the determination of vessel frequency and proportion, the total window measurement frame area excluding rays was used.

Terminology follows the IAWA list of microscopic features for hardwood identification (IAWA Committee 1999).

Statistical analysis were performed (α = 0.05) using the software package SPSS® ver. 19 (IBM, NY, USA) to analyze the cambial age (i.e., ring number), tree and site effects on earlywood vessel features (mean area, number, density and proportion). Pearson’s correlations among ring width and ring density components were determined, and regression curves estimated.

**Results**

**Variation of earlywood vessel features**

The ring porous nature of the *Q. faginea* wood was clear both in very narrow growth rings (e.g., at the outermost rings of the older trees) and within the inner growth rings (Fig. 1a, Fig. 1b). For a detailed description of the wood anatomy of the species, see Sousa et al. (2014).

The frequency distribution of vessel area was skewed to the left at both sampling sites, even though more pronounced at site 1 (Fig. 2a, Fig. 2b). Analyzing the above distribution by age intervals, we observed that small vessels with area ≤ 0.020 mm² are more frequent in the initial years, while above 60 years the distribution is no longer skewed (Fig 2c, Fig 2d).

Tab. 1 summarize the observed vessel features at each sampling site. Overall, mean

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For more information, refer to the supplementary materials or the original publication for detailed analysis and data presentation. The described methodology and results provide insights into the growth patterns and anatomical features of *Quercus faginea* in the specified regions of Portugal, highlighting the importance of environmental factors on wood density and vessel characteristics.
Earlywood vessel features in *Quercus faginea*

Vessel area, vessel frequency and vessel proportion were relatively higher at site 2 as compared with site 1, while vessel number was lower.

Radial variation of earlywood vessel area showed a large increase in the initial years up to the 60/70th rings, with a slight decrease onwards (Fig. 3a). At site 2 the maximum earlywood vessel area reached 0.038 mm², decreasing to 0.032 mm² (ca. 200 µm tangential diameter) near the bark. The increment of vessel area over the same cambial age period was higher at site 1. Regression analysis indicated that a second degree polynomial model best predicted the mean vessel area as a function of cambial age ($R^2=0.96$, p < 0.001 and $R^2=0.92$, p < 0.001 at site 1 and 2, respectively - Fig. 3a).

**Tab. 1** - Mean value, coefficient of variation (in brackets) and range (lower row) of earlywood vessel area (MVA, mm²), vessel number (NV), vessel frequency (VF, n mm⁻²) and vessel proportion (VP, %) by tree at site 1 (mean of 30 rings by tree) and site 2 (mean of 100 rings by tree).

<table>
<thead>
<tr>
<th>Site</th>
<th>MVA</th>
<th>NV</th>
<th>VF</th>
<th>VP</th>
</tr>
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<tbody>
<tr>
<td>1</td>
<td>0.020 (78)</td>
<td>18.0 (59)</td>
<td>3.1 (52)</td>
<td>6.0 (67)</td>
</tr>
<tr>
<td></td>
<td>0.013-0.034</td>
<td>7.0-19.0</td>
<td>2.0-4.6</td>
<td>1.1-8.0</td>
</tr>
<tr>
<td>2</td>
<td>0.026 (78)</td>
<td>8.1 (45)</td>
<td>4.2 (77)</td>
<td>9.9 (74)</td>
</tr>
<tr>
<td></td>
<td>0.018-0.030</td>
<td>6.2-10.1</td>
<td>2.1-8.0</td>
<td>5.3-15.9</td>
</tr>
</tbody>
</table>

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The average vessel number decreased at both sites from pith to bark, though the decrease was more pronounced at site 1 (Fig. 3b). For predicting vessel number based on cambial age, both second degree polynomial and linear regression proved to fit well (R² = 0.72, p < 0.001 and R² = 0.60, p < 0.001 at site 1 and 2, respectively). The relationship between the number of vessels and the mean vessel area per ring fitted both linear and second degree polynomial curves well (R² = 0.74, p < 0.001) at site 1 (Fig. 4a), while a poorer fitting (though still significant at p < 0.001) was observed analyzing both sites and site 2 separately (Fig. 4b, Fig. 4c). Indeed, medium to strong negative correlations were found between the number of vessels and mean vessel area (Pearson’s r = -0.162 at both sites; r = -0.461 at site 1; r = -0.216 at site 2 - Tab. 2, Tab. 3, Tab. 4). Although some year-to-year fluctuations occurred, no specific trends of variation of vessel frequency with age was observed (Fig. 5).

Vessel proportion showed an increase with age from the pith up to the 70th ring, with a maximum of 18.4% and then a slight decrease towards the bark (Fig. 6). This radial pattern was similar to that observed for the mean vessel area (Fig. 3a).

The proportion of vessels was related to ring width, i.e., the highest proportion was found in the narrowest rings and vice versa. Strong correlations were found between ring width and the number of vessels per ring (0.462 < r < 0.541), vessel frequency (-0.331 < r < -0.411) and vessel proportion (-0.425 < r < -0.541). The average vessel number decreased at both sites from pith to bark, though the decrease was more pronounced at site 1 (Fig. 3b). For predicting vessel number based on cambial age, both second degree polynomial and linear regression proved to fit well (R² = 0.72, p < 0.001 and R² = 0.60, p < 0.001 at site 1 and 2, respectively). The relationship between the number of vessels and the mean vessel area per ring fitted both linear and second degree polynomial curves well (R² = 0.74, p < 0.001) at site 1 (Fig. 4a), while a poorer fitting (though still significant at p < 0.001) was observed analyzing both sites and site 2 separately (Fig. 4b, Fig. 4c). Indeed, medium to strong negative correlations were found between the number of vessels and mean vessel area (Pearson’s r = -0.162 at both sites; r = -0.461 at site 1; r = -0.216 at site 2 - Tab. 2, Tab. 3, Tab. 4). Although some year-to-year fluctuations occurred, no specific trends of variation of vessel frequency with age was observed (Fig. 5).

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<table>
<thead>
<tr>
<th>Variable</th>
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<th>VD</th>
<th>VP</th>
<th>MD</th>
<th>EWD</th>
<th>LWD</th>
<th>LWP</th>
<th>RW</th>
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<td>-0.225**</td>
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<td>-0.39**</td>
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<td>-1</td>
<td>1</td>
<td>-0.331</td>
<td>-0.425**</td>
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<tr>
<td>RW</td>
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<td>-1</td>
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<td>-0.331</td>
<td>-0.425**</td>
<td></td>
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</table>

Tab. 3 - Correlation coefficients between vessel variables, wood density and ring width within the first 100 rings common to all trees at site 2. Mean values by tree and ring (n=898, 100 rings × 10 trees excluding rings without vessels). (**) p<0.01 (2-tailed). Labels as in Tab. 2.
The best-fitted models for the prediction of earlywood vessel features based on ring width are presented in Fig. 7. Regardless of site, wider rings showed the higher number of vessels and the lower mean vessel area, vessel frequency and proportion.

**Influence of earlywood vessel features on wood density**

Considering the common period of 30 rings in the trees of the two sites, the mean wood density and the earlywood density were inversely correlated with the mean vessel area (r = -0.449, p < 0.01), as well as the mean wood density with the vessel proportion per ring (r = -0.367, p < 0.01). The number of vessels was negatively correlated with wood density (r = -0.166, p < 0.01) and earlywood density (r = -0.228, p < 0.01). The correlation of vessel frequency with wood density was not significant (Tab. 4).

Overall, the wood density components (mean density, earlywood and latewood density) were inversely correlated with mean vessel area (-0.287, P < 0.01 < r < -0.449, P < 0.01) and vessel proportion (-0.254, P < 0.01 < r < -0.455, P < 0.01 - Tab. 2, Tab. 3, Tab. 4). The correlations between the wood density components and the number of vessels and vessel frequency were positive and weak within each site.

**Discussion**

In this study, the overall frequency distribution of vessel was left-skewed, as previously reported for *Q. faginea* (Villar-Salvador et al. 1997, Corcuera et al. 2004a, Alla & Camarero 2012), *Q. robur* and *Q. ilex* (García-González & Eckstein 2003, Campeelo et al. 2010, Corcuera et al. 2004b). The vessel distribution seems age-related, and the

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**Tab. 4 - Correlation coefficients between vessel variables, wood density and ring width within the common years period (the first 30 rings) at both sites. Mean values by tree and ring (n=589, 30 rings × 20 trees excluding rings without vessels). (**): p<0.01 (2-tailed). Labels as in Tab. 2.**

<table>
<thead>
<tr>
<th>Variable</th>
<th>NV</th>
<th>MVA</th>
<th>VD</th>
<th>VP</th>
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<th>EWD</th>
<th>LWD</th>
<th>LWP</th>
<th>RW</th>
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<td>-0.455**</td>
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<td>0.061</td>
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<td>-0.061</td>
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<td>EWD</td>
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<td>0.084</td>
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<tr>
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<td>0.061</td>
<td>1</td>
<td>0.061</td>
<td>0.377**</td>
</tr>
</tbody>
</table>

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r < -0.557 - Tab. 2, Tab. 3, Tab. 4).
large number of small vessels in the initial years seem to be responsible of the above distortion.

The mean area of earlywood vessels observed in this study is consistent with the range of values (0.020-0.034 mm$^2$) reported by Alla & Camarero (2012) for *Q. faginea*. The area of vessels observed for this species was larger or similar as compared with other co-occurring evergreen oak species such as *Q. coccifera*, *Q. ilex* and *Q. suber*, but smaller than the vessel size reported for *Q.
Earlywood vessel features in Quercus faginea

Correlates with mean vessel area (portion and frequency, although positively

The decrease of ring width with age


Denné MP, Cahalan CM, Aebisher DP (1999). In-


