

Bark anatomy and cell size variation in *Quercus faginea*

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Abstract: The bark structure of *Quercus faginea* Lam. in trees 30–60 years old grown in Portugal is described. The rhytidome consists of 3–5 sequential periderms alternating with secondary phloem. The phellem is composed of 2–5 layers of cells with thin suberised walls and narrow (1–3 seriate) tangential band of lignified thick-walled cells. The phellogen is thin (2–3 seriate). Secondary phloem is formed by a few tangential bands of fibres alternating with bands of sieve elements and axial parenchyma. Formation of conspicuous sclereids and the dilatation growth (proliferation and enlargement of parenchyma cells) affect the bark structure. Fused phloem rays give rise to broad rays. Crystals and druses were mostly seen in dilated axial parenchyma cells. Bark thickness, sieve tube element length, and secondary phloem fibre wall thickness decreased with tree height. The sieve tube width did not follow any regular trend. In general, the fibre length had a small increase toward breast height, followed by a decrease towards the top. Fibre width decreased with height in most of the cases, but in some trees a slight increase was noticed at the top.

Key words: *Quercus*, bark, anatomy, fibre, sieve tube elements

1. Introduction

The Portuguese oak (*Quercus faginea* Lam.) is a species native to the western Iberian Peninsula and the North African countries of Morocco, Tunisia, and Algeria. The species grows well in the temperature range of 15–25 °C in the summer and from –4 to 8 °C in the winter, with annual precipitation between 350 and 2000 mm (Oliveira et al., 2001). It is a medium-sized deciduous or semievergreen tree growing to a height of 20 m and a diameter of 80 cm.

In Portugal, *Quercus faginea* coexists with other oak species such as *Quercus ilex* L., *Quercus suber* L., *Quercus pyrenaica* Willd., and *Quercus robur* L. The distribution has become fragmented in the last centuries (Fabião & Silva, 1996), and there are concerns on future area reduction with warming and reduced rainfall trends, since drought is the main limiting factor of sub-Mediterranean oaks (Cotillas et al., 2009), specifically for *Q. faginea* (Corcuera et al., 2004; Montserrat-Marti, 2009).

Studies on bark anatomy are scarce when compared to previous studies on wood. However, knowledge on bark structure and its variation within and between individuals of a species, as well as age-related trends, are important to assess bark's diagnostic value and to determine its potential uses (Roth, 1981). In this area, literature is also scarce (i.e.

Trockenbrodt, 1994; Quilhó et al., 2000; Jorge et al., 2000; Babu et al., 2010; Arihan & Güvenç, 2011; Tavares et al., 2011).

Only very limited information was published on the bark of the *Quercus* L. species. Bark anatomy of white and northern red oak was first described by Chang (1954). Whitmore (1962) compared the bark structure and surface pattern of mature trees of *Q. robur*, Howard (1977) observed the bark structure of 11 *Quercus* species, Trockenbrodt (1991, 1994, 1995) studied the qualitative and quantitative anatomy of *Q. robur* bark, and Sen et al. (2011a, 2011b) described in detail the bark of *Q. cerris* L. var. *cerris*. One exception is the research effort and detailed knowledge gathered on *Q. suber* bark, which is due to the economic importance of its cork component, as reviewed by Pereira (2007).

The present study investigated the bark structure as well as between- and within-tree size variation of the sieve tube elements and secondary phloem fibres in *Q. faginea*. The results are the first to be published on the bark of this species, thereby also adding new information on the structural characteristics of *Quercus* spp. barks. We also think that this knowledge, besides being necessary to assess potential bark uses, has a role in the research on the sustainability of *Q. faginea* in its indigenous regions.

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2. Materials and methods

The anatomical studies were made from the bark of 10 randomly selected *Quercus faginea* Lam. trees, growing in pure stands in north-eastern Portugal, in the district of Bragança (41°30'41"N, 7°01'06"W; altitude 554 m, 600–800 mm annual rainfall, and 12–14 °C mean temperature). Tree characteristics are shown in Table 1. The soils are mainly Orthic Dystric Leptosols on shale or granite rocks and Orthic Eutric Leptosols on basic rocks. The pH varies from acid to neutral, and the hard rock is found within 50 cm of the surface.

Cross-sectional 5-cm-thick discs were cut from each tree along the stem at different height levels, and 2 cross-diameters were measured for bark thickness determination.

For qualitative anatomical characterisation, bark samples were collected at breast height (bh), i.e. at 1.30 m above ground. The samples were impregnated with DP1500 polyethylene glycol, and transverse and longitudinal microscopic sections of approximately 17 µm thickness were prepared with a Leica SM 2400 microtome using Tesafilm 106/4106 adhesive (Quilhó et al., 1999). The sections were stained with a double staining of chrysoidine/astra blue. Sudan 4 was also used for selective staining of suberin. The stained sections were mounted on Kaiser glycerine, and after 24 h drying, the lamellas were submerged into xylol for 30 min to remove the Tesafilm, were dehydrated on 96% and 100% alcohol, and were mounted on Eukitt.

For quantitative studies, specimens were taken from bark samples collected at 3 tree height levels (base, bh, and 75% of total height), and samples were taken sequentially from the cambium towards the periphery. Specimens were macerated in a 1:1 solution of 30% H₂O₂ and CH₃COOH at 60 °C for 48 h and then stained with astra blue. Length, width, and cell wall thickness of 40 fibres and 40 sieve tube elements were measured on each specimen using a microscope and a semiautomatic image analyser. The number of measurements was previously calculated to give an accuracy of 95% at the 0.05 probability level. The

Table 1. Characteristics of the *Quercus faginea* trees (mean and standard deviation, min. and max. of 10 trees).

	Mean ± std. dev.	Min.–Max.
Tree age (years)	40.4 ± 7.50	34–60
Total tree height (m)	10.5 ± 0.67	10–12
Height of living crown (m)	8.3 ± 1.34	6–11
Stem height (m)	2.2 ± 1.02	1–4
Diameter at bh (cm)	20.9 ± 4.20	16–29
Bark thickness at bh (cm)	1.0 ± 0.29	1–1

tangential diameter of parenchyma cells, sclereids, and cluster of sclereids were also measured to estimate their range of values.

A light microscope Leica DM LA with camera Nikon Microphot-FXA was used for light microscopic observations.

Mean values for the tree were calculated as the arithmetic mean of the 3 height levels in each tree. Analysis of variance (ANOVA) was applied to determine if the differences of sieve tube elements and bark fibre size within and between trees were statistically significant at a 0.05 confidence level. Statistical calculations were carried out with IBM SPSS Statistics v.19 software.

The descriptive terminology for bark structure follows Trockenbrodt (1990), Junikka (1994), and Richter et al. (1996).

3. Results and discussion

The bark of the *Quercus faginea* trees showed a scaly surface of grey-brown colour, with short but deep longitudinal furrows (Figure 1). The visual appearance was similar to other *Quercus* spp. (Whitmore, 1962; Howard, 1977). The bark thickness ranged between 0.5 cm and 1.4 cm at bh (Table 1), corresponding to 10% of the total tree radius. Table 2 presents the data for each tree showing that bark thickness tends to increase with age, i.e. higher values occur in the base of the tree, agreeing with observations in other taxa (Trockenbrodt, 1994; Quilhó et al., 2000). There was a significant difference between the bark thickness of each tree at the 3 height levels, indicative of a significant axial variation of bark thickness in the tree.

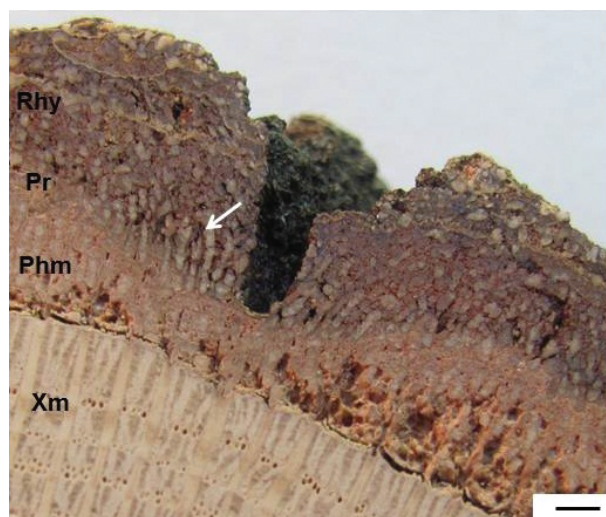


Figure 1. Transverse section of *Quercus faginea* bark. Phm: secondary phloem; Pr: periderm, Rhy: rhytidome; arrow: clusters of sclereids; Xm: xylem. Scale bar = 2 mm.

Table 2. Mean bark thickness of 10 *Quercus faginea* trees at 3 height levels (base, bh, and top).

	Bark thickness (cm)									
	1	2	3	4	5	6	7	8	9	10
Top	0.43	0.35	0.15	0.50	0.23	0.50	0.40	0.43	0.33	0.43
bh	1.18	1.03	0.50	0.75	0.63	1.20	1.23	1.38	0.85	1.00
Base	1.88	1.00	0.68	1.18	0.85	3.83	1.28	2.08	2.13	1.88

3.1. Bark structure

The bark structure of *Q. faginea* was identical in the 10 trees. It was possible to distinguish macroscopically in the bark cross-section the phloem, the periderm, and the rhytidome. Abundant clusters of sclereids were observed across the whole section of the bark and constituted a conspicuous feature as shown in Figure 1. In general the *Q. faginea* bark showed many similarities with those described for other *Quercus* species (Whitmore, 1962; Howard, 1977; Sen et al., 2011a).

The rhytidome was persistent and represented a substantial proportion of the bark (Figure 1). It consists of 3–5 sequential periderms alternating with the layers of dilated secondary phloem (Figure 2). In contrast to other oak species (Whitmore, 1962), no shedding of the outermost periderms was observed in *Q. faginea*.

The periderm appeared undulated, and its phellem curved slightly, forming discontinuous arching layers in cross-section (Figure 2). Sometimes the irregular course of

the periderm was a consequence of the presence in its path of sclereid clusters and fused rays (Figure 2). *Q. faginea* did not produce extensive phellem or cork layers, as is the case in the discontinuous phellem of *Q. cerris* (Sen et al., 2011a, 2011b) or in the continuous phellem of *Q. suber* (Pereira et al., 1992; Graça & Pereira, 2004).

Each phellem layer comprises 2–5 layers of isodiametric or sometimes radially flattened cells arranged into more or less a distinct radial pattern with evenly thin, suberised walls and a narrow (1–3 seriate) band of radially flattened cells with evenly thick and pitted lignified walls (Figure 3). On the inside, these lignified cells are also accompanied by 1–3 layers of thin-walled phellem cells, which are, however, somewhat crushed; their radial pattern is distorted due to the compressive strain against this more rigid layer. This band of sclerified cells in the phellem was also observed in *Q. cerris* (Sen et al., 2011b) but was not reported in the phellem layer of *Q. suber* (Pereira, 2007).

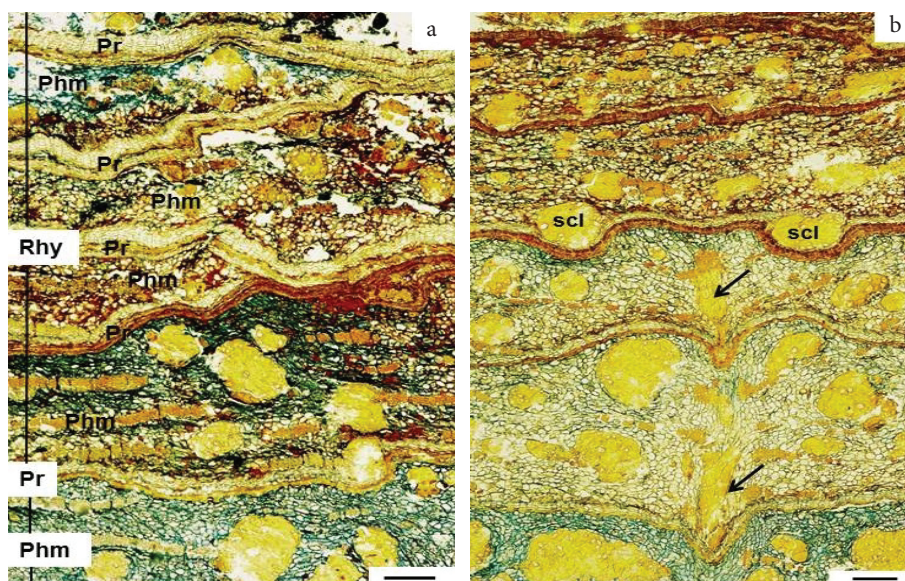


Figure 2. Transverse section of *Quercus faginea* bark. a- Phm: secondary phloem; Pr: periderm; Rhy: rhytidome. b- The irregular course of the periderm is due to the formation of clusters of sclereids (scl) and fused rays (arrow). Scale bars = 125 µm.

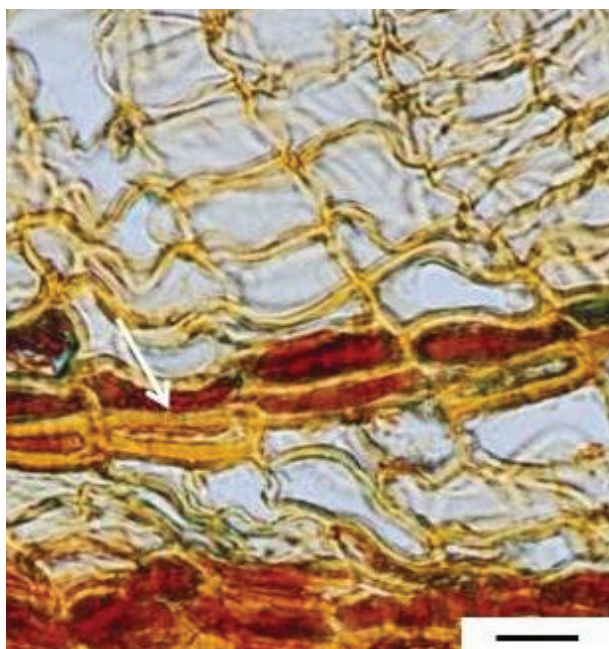


Figure 3. Phellem layer of *Quercus faginea* (transverse section) with suberised phellem cells with tangential and radial walls uniformly thickened, aligned radially, and phellem cells with thickened sclerified walls (arrow) filled with dark compounds. Scale bar = 25 µm.

The phelloderm was poorly developed, composed of 2–3 thin-walled cells in radial rows and resembling the adjacent parenchyma cells, except for their radial alignment. Dark

stained material was observed in the cells of phellem and phelloderm. The phellogen with rectangular and thin-walled cells was difficult to distinguish in cross-section.

The secondary phloem of *Quercus faginea* (Figure 4) is nonlayered, and growth rings were not observed, in contrast to *Q. robur* (Trockenbrodt, 1991), *Q. cerris* var. *austriaca* (Babos, 1979a), and *Q. cerris* var. *cerris* (Sen et al., 2011a).

The noncollapsed phloem in *Q. faginea* is a narrow layer. A thin layer of noncollapsed phloem was also described by Sen et al. (2011a) in another *Quercus* species and by Roth (1981) and Cufar et al. (2011) in another genus. In the transverse section the initial portion of secondary phloem was characterised by the occurrence of multiseriate tangential bands of axial parenchyma cells and sieve tube elements alternating with tangential rows of fibres (3–5 cells wide). These rows are crossed by secondary phloem rays (Figures 4).

When the secondary phloem ceases its conducting function, the cells collapse and the tangential fibre bands are interrupted by small groups of sclereids, forming clusters (Figure 4). The size of the clusters is variable (132–312–675 µm; values are given as ranges with means), and their quantity increases throughout the collapsed secondary phloem towards the periderm, giving rise to an altered structure of the secondary phloem accompanied by a slight distortion of the secondary phloem rays (Figure 4) and some dilatation of the axial parenchyma cells. These features represent the adjustment of the secondary phloem to tree growth (Quilhó, 1999).

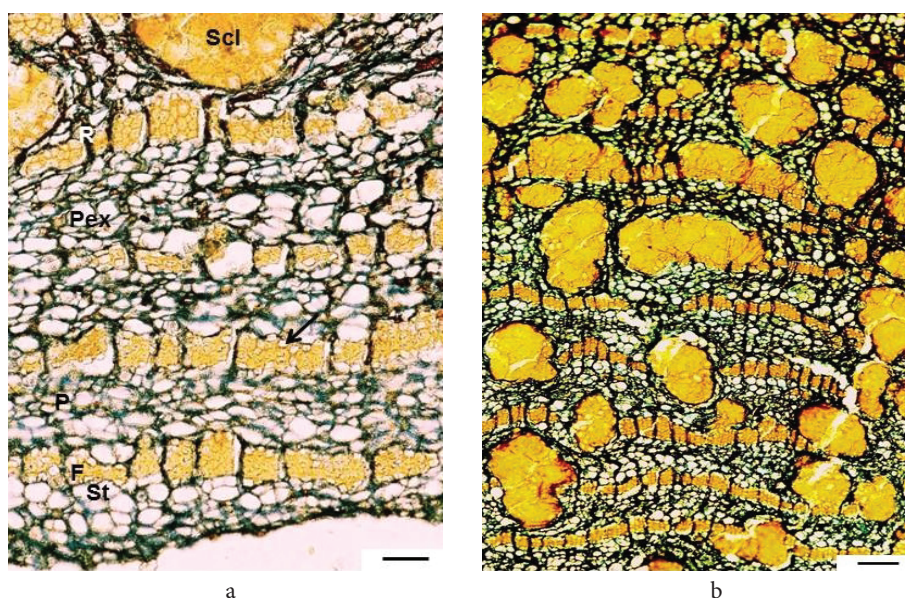


Figure 4. Transverse section of the secondary phloem of *Quercus faginea*. a- near the vascular cambium and outward; St: sieve tubes; F: fibres bordered by crystalliferous axial parenchyma (arrow); P: axial parenchyma; R: ray; Pex: expanded parenchyma cells; Scl: clusters of sclereids. b- Collapsed secondary phloem. Clusters of sclereids increased significantly throughout the collapsed secondary phloem towards the periderm. Scale bars: a = 50 µm; b = 125 µm.

The sieve tube elements had a round to an irregular shape in transverse section, about 22–38–58 μm in diameter and 206–311–338 μm in length with unligified thin walls and with companion cells, which are recognised either in transverse or longitudinal sections (Figure 5). The sieve elements were solitary or in groups of 2 or 3 with a tangential arrangement; the sieve plates were inclined, compound, with 3–8 sieve areas in a scalariform pattern with numerous sieve pores (Figure 5) and lateral sieve areas. Similar observations were made by Chang (1954) for white and northern red oaks.

The axial parenchyma of the secondary phloem appears in strands of 3–6 cells and has round to rectangular thin-walled cells of irregular size in transverse view (Figure 4). It was located between the tangential bands of fibres and interspersed with sieve elements that were sometimes difficult to distinguish from the axial parenchyma cells. Strands of crystal-bearing axial parenchyma of approximately equal length (6 to >10 cells) were found along the margins of the fibre band (Figures 6 and 7), as it occurs also in other *Quercus* species (Howard, 1977; Trockenbrodt, 1991; Quilhó et al., 2003; Sen et al., 2011a). Druses and prismatic crystals occurred profusely in the axial

chambered parenchyma cells (Figure 7). Although crystals occur in the noncollapsed phloem, Evert and Eichhorn (2006) mentioned their accumulation in cells bordering those undergoing sclerification in the collapsed phloem.

The axial parenchyma cells proliferated and enlarged (22 to 56 μm) in the outer portion of the phloem forming the dilatation tissue (Figure 8). The development of this tissue due to the increase of stem diameter is in agreement with observations of Trockenbrodt (1991) in *Q. robur* and Sen et al. (2011a) in *Q. cerris* var *cerris* and was also described by Evert and Eichhorn (2006) in another genus.

Secondary phloem fibres were arranged parallel to the vascular cambium in continuous tangential bands, about 2 to 4 cells wide, sometimes interrupted by groups of sclereids (Figure 4). The fibres were 0.799–0.878–1.016 mm long and 19–20–22 μm wide; the fibres were slender with narrow lumens and with tapered overlapping end, although sometimes bifurcated (Figure 9), caused by the adjustment to adjacent cells during elongation and intrusion, as stated by Iqbal and Ghouse (1983). They were usually thick walled (7.93–8.84–9.66 μm) and lignified.

Secondary phloem rays are the outward continuation of the wood rays and occurred in 2 sizes: narrow uniseriate rays (uniseriate, 3 to 10 cells high) and broad rays (multiseriate, up to 20 cells wide and >100 cells high) (Figure 6). Both were frequently homocellular with short procumbent cells (Figure 7) as in the bark of other *Quercus* species (Howard, 1977; Sen et al., 2011a). The narrow rays followed a straight to undulated direction in the beginning of the noncollapsed secondary phloem, but towards the periphery they showed a moderate dilatation due to the tangential stretching and anticlinal cell divisions. In the outer phloem close to the periderm, the ray dilatation tissue could be confused with the axial parenchyma.

Sclerification of radial parenchyma cells occurred early in the noncollapsed phloem near the cambium, mostly in fused broad rays. This is in agreement with the findings of Evert and Eichhorn (2006), who reported the differentiation of sclereids in oaks first in the rays and later in dilatation tissue, in clusters of variable size; the radial parenchyma cells sclerification was also reported in *Quercus* spp. (Howard, 1977; Babos, 1979a; Trockenbrodt, 1991; Graça & Pereira, 2004; Sen et al., 2011a). Figures 2 and 6 show sclerified broad rays in the rhytidome and in a portion of the noncollapsed phloem, respectively.

Sclereids were abundant and formed a high proportion of *Q. faginea* bark, as in other oaks (Howard, 1977). In general they were isodiametric (31–126 μm , in tangential size), although they may attain various shapes, and had thick and polylamellate walls transversed by minute pit channels when seen in transverse section (Figure 8) or in dissociated cells (Figure 9). Sclereids originated from axial parenchyma cells and lacked the typical intrusive

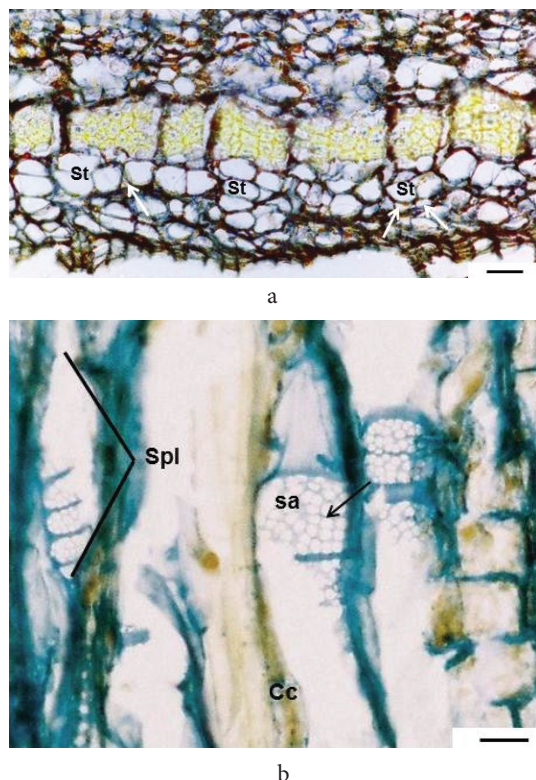


Figure 5. Sieve tubes of *Quercus faginea*. a- Sieve tubes (St) and companion cells (arrow) in noncollapsed secondary phloem in transverse section. b- Sieve plate (Spl) with sieve areas (sa), sieve pores (arrow), and companion cells (Cc) in a longitudinal view. Scale bars: a = 12.5 μm ; b = 25 μm .

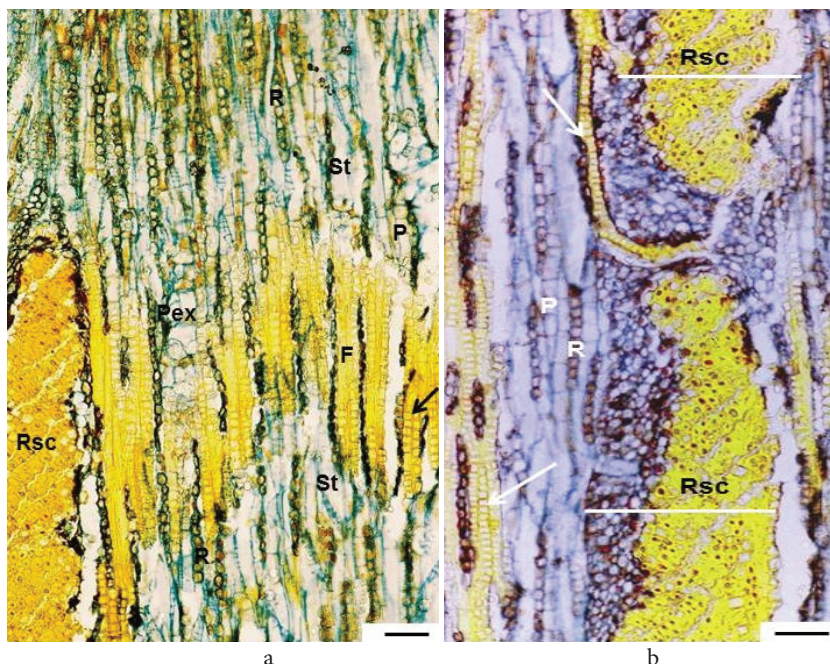


Figure 6. Tangential section of noncollapsed secondary phloem in *Quercus faginea*. a- St: sieve tubes; F: fibres bordered by crystalliferous axial parenchyma (arrow); P: axial parenchyma; R: uniseriate ray; Rsc: multiseriate ray with all cells sclerified; Pex: expanded parenchyma cells. b- Fused ray (⌋) partially sclerified (Rsc), radial parenchyma cells became highly sclerified; crystalliferous parenchyma cells (white arrow). Scale bars = 50 µm.

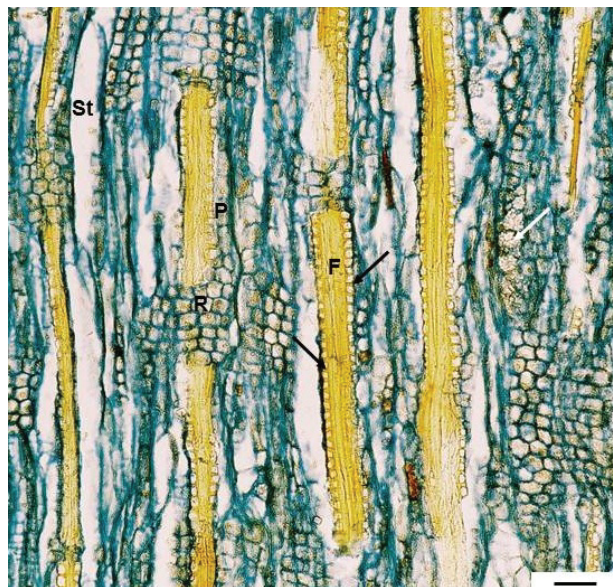


Figure 7. Radial section of noncollapsed secondary phloem in *Quercus faginea*. St: sieve tubes; F: fibres bordered by crystalliferous axial parenchyma (black arrow); P: axial parenchyma; R: rays homocellular with frequently short procumbent cells; and druses (white arrow). Scale bar = 50 µm.

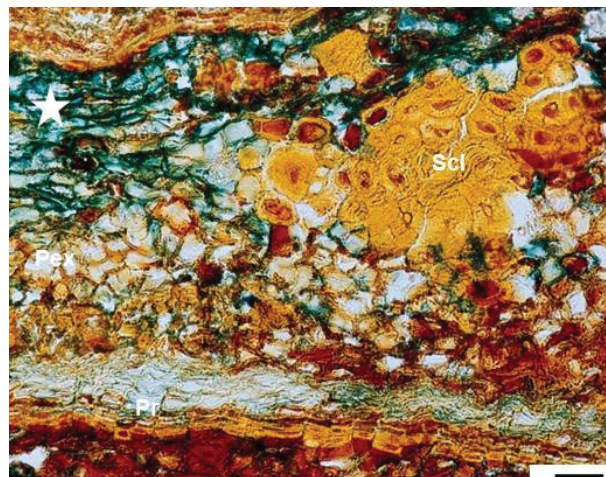


Figure 8. Dilatation tissue in the rhytidome of *Quercus faginea*: proliferation of parenchyma cells (star), expanded axial parenchyma cells (Pex), and sclereids (Scl) isolated by the periderm (Pr), in transverse view. Scale bar = 50 µm.

growth of the phloem fibres, in accordance with Evert and Eichhorn (2006). The “expanded parenchyma cells” (Quilhó et al., 1999) or cells of intermediate type (Richter et al., 1996) undergo gradual changes in shape, form, and cell wall thickness (Figures 4 and 6). Finally those cells develop into sclereids by the progressive sclerification of



Figure 9. Maceration of *Quercus faginea* bark; sclereids with crystals (white arrows) and (F) fibres sometimes are bifurcated (black arrow). Scale bar = 50 µm.

their walls. Sclereids frequently included large prismatic crystals (Figure 9) and dark compounds.

Sclereids occurred mostly in groups that might fuse, giving rise to prominent clusters that sometimes attained large tangential or radial diameters. In the transverse section, the clustered sclereids (Figure 4) showed a tangential or radial arrangement: they were adjacent to the fibre groups or formed radial bands near or within the broad rays, as in other *Quercus* species (Trockenbrodt, 1991; Sen et al., 2011a). The highest proportion of sclereids was observed in the outer and dilated portion of the phloem near the periderm, although sclerified cells also differentiated near the vascular cambium. The increase of sclereids with growth is according to observations of Trockenbrodt (1991, 1994) in *Q. robur*. The occurrence of sclereids is of practical relevance since they can limit the use of bark (Hoffmann & Ouellet, 2005).

3.2. Size variation of sieve tube elements and secondary phloem fibres

Table 3 summarises the sieve tube element and secondary phloem fibre dimensions and their range of variation in each tree height level.

The tree mean and range of values for length and width of sieve tube elements were 299–311–431 µm and 37–38–40 µm, respectively. Sieve tube elements of *Q. faginea* fit into the length categories I (>400 µm) and II (250–400 µm) as defined by Richter et al. (1996). The average values of sieve tube elements sizes fit into the range of values reported by Trockenbrodt (1994) in some individual trees of the genus *Quercus*. The analysis of variance for the length and width of sieve tube elements showed that the height level was highly significant ($P < 0.001$) to explain their variation. A decrease of sieve tube element length with tree height was

observed in all the trees (Figure 10). This trend of variation could reflect the increase of the cambial initials with age, causing a corresponding increase of the length of sieve tube elements. In contrast, the sieve tube width did not follow any regular trend within the tree (Figure 10), although sieve tube elements tend to be larger in the upper part of the stem (Table 3). Similar patterns of axial variation of length and width of sieve tube elements were reported by Iqbal and Ghouse (1983), Trockenbrodt (1994), and Quilhó et al. (2000) in some individuals in various species such as *Q. robur*, *Populus tremula* L., *Prosopis spicigera* (L.) Druce, and *Eucalyptus globulus* Labill.

The between-tree variability of secondary phloem fibre length, width, and wall thickness was highly significant ($P < 0.001$). No correlations were found between fibre size and tree diameter.

The average secondary phloem fibre length of 0.88 mm fits in the range reported by Trockenbrodt (1994) for *Q. robur* (0.72 mm to 0.91 mm in 12- to 33-year-old trees) and by Sen et al. (2012) for *Q. cerris* var. *cerris* (0.73 mm to 1.68 mm in 70- to 80-year-old trees). The secondary phloem fibre width and wall thickness were on average 20 µm and 9 µm, respectively. Babos (1979b) reported the average secondary phloem fibre diameter in *Q. cerris* bark as 15.1 µm.

It is frequently reported that secondary phloem fibres are longer than wood fibres (Parameswaran & Liese, 1974; Jorge et al., 2000). In this study, the secondary phloem fibres of *Q. faginea* were shorter than the wood fibres (0.88 mm

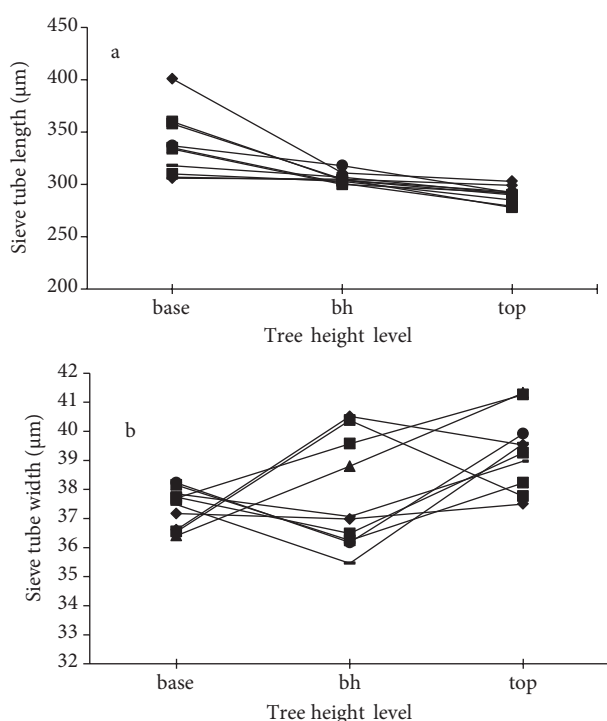


Figure 10. Axial variation of sieve tube elements in 10 *Quercus faginea* trees: a- length, b- width.

Table 3. Sieve tube elements and fibre dimensions in secondary phloem of *Quercus faginea* (mean, standard deviation, and min. and max. of 10 trees at each tree height level).

	Sieve tube element		Fibre		
	Length (µm)	Width (µm)	Length (mm)	Width (µm)	Wall thickness (µm)
Top	290.2 ± 7.87 (207–385)	39.3 ± 1.30 (22–61)	0.82 ± 0.046 (0.43–1.29)	20.2 ± 0.80 (14–30)	8.6 ± 0.41 (5–13)
bh	305.8 ± 5.26 (200–450)	37.8 ± 1.87 (22–61)	0.92 ± 0.116 (0.60–1.75)	20.0 ± 3.12 (10–31)	8.9 ± 1.49 (4–14)
Base	336.6 ± 29.86 (188–431)	37.4 ± 0.67 (23–52)	0.90 ± 0.054 (0.46–1.42)	20.6 ± 0.93 (13–29)	9.1 ± 0.39 (5–13)

vs. 1.13 mm long), although the maximum value of fibre length was found in the bark (Table 3) since the wood fibre length ranged 0.8 to 1.4 mm, as determined by Sousa et al. (2009) in the same trees. There was a significant difference ($P < 0.001$) between wood and bark fibre length at bh. The secondary phloem fibre width and wall thickness values are close to those reported for the wood of the same trees of 15–23 µm and 5–8 µm, respectively (Sousa et al., 2009).

There was not a linear relationship between length, width, and fibre wall thickness and tree age at bh, although the oldest tree (60 years old) had the widest and thickest fibres (22 µm and 9.7 µm, respectively).

There was a highly significant ($P < 0.001$) axial variation of secondary phloem fibre length with a small increase from the base to bh, followed by a decrease towards the top in the majority of individuals (Figure 11). This is in accordance with the dimensions of the cambial fusiform initials that generally increase from stem base to a certain tree height and then decrease towards the uppermost part of the tree (Larson, 1963; Ridoutt & Sands, 1994). This pattern of variation was found in *Acacia nilotica* (L.) Willd. ex Delile and *P. spicigera* (Iqbal & Ghouse, 1983), but the inverse was shown by Trockenbrodt (1994) in *Q. robur* with longer fibres in the top of the tree. Fibre length depends also on the degree of intrusive growth (Ghouse & Siddiqui, 1976; Khan & Siddiqui, 2007; Lev-Yadun, 2010) and on maturation and outlines of surrounding cells (Jura-Morawiec, 2008), which can justify the different patterns of axial variation described for other genera, i.e. *Eucalyptus* (Quilhó et al., 2000) and *Acacia* (Tavares et al., 2011). As Bailey and Tupper (1918) showed, the vessel element length is approximately equal to the length of fusiform cambial initials. Sousa et al. (2009) determined the length of vessel elements in wood at bh to be 214–459–696 µm in the same trees. The comparison of the mean length of secondary phloem fibres at bh (Table 3) with the mean length of vessel elements at the same height level allows us

to estimate that the secondary phloem fibres grow about 1.9 times the size of the fusiform cambial initials.

In general, secondary phloem fibre width and cell wall thickness decreased only slightly from the base to the top (Figure 11). However, regarding the width of fibres, this trend of axial variation was not recognised in all the trees, and a slight increase was also noticed at the top. In the tree the variations of fibre width ($P < 0.05$) and cell wall thickness ($P < 0.01$) were of small magnitude. There are no comparable studies concerning the axial variation of the secondary phloem fibre width and wall thickness for *Quercus*, but the same pattern of variation was also described for *E. globulus* (Quilhó et al., 2000) and is sustained by the studies of Ridoutt and Sands (1994).

Width and fibre wall thickness could be affected by alterations of hormonal content, i.e. a longitudinal decreasing auxin concentration is responsible for fibre enlargement (Lev-Yadun & Aloni, 1991). However, information is still scarce on hormone interaction during cambial development and on genetic regulation of secondary vascular growth and cell differentiation (Elo et al., 2009; Lev-Yadun, 2010; Spicer & Groover, 2010).

4. Conclusions

The bark anatomy of *Quercus faginea* was characterised for the first time. The rhytidome of *Q. faginea* includes successive periderms with a substantial amount of secondary phloemic tissue and abundant compact nodules of sclereids and sclerified broad rays. *Q. faginea* does not produce an extensive phellem or cork layers, and the phelloderm is poorly developed.

The sequence of tissues in the secondary phloem, the type of sieve tube elements, sieve plates, fibres, axial and radial parenchyma, formation of sclereids, and type of crystals were similar to those of other *Quercus* spp.

Q. faginea bark thickness, sieve tube element length, and phloem secondary fibre cell wall thickness decreased

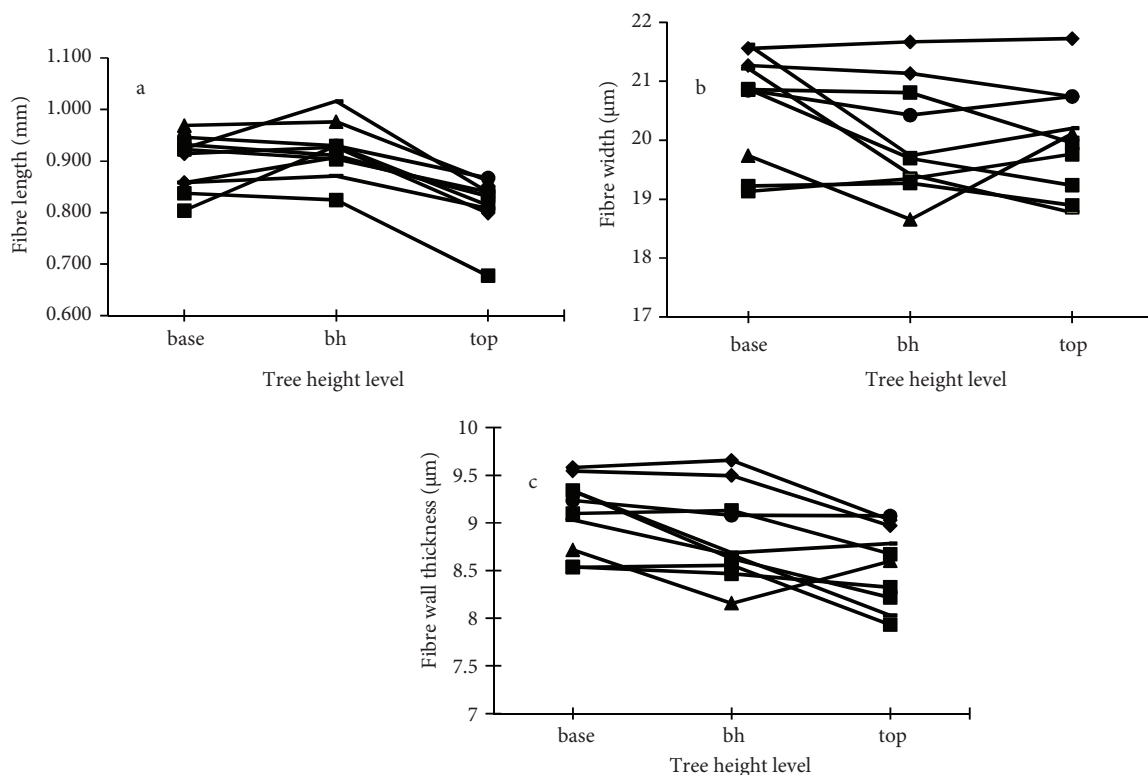


Figure 11. Axial variation of secondary phloem fibres in 10 *Quercus faginea* trees: a- length, b- width, c- wall thickness.

with tree height; in contrast, the sieve tube element width did not follow any regular trend within the tree. The secondary phloem fibre length had a small increase from the base to bh, followed by a decrease towards the top in the majority of individuals. Fibre width decreased within the tree for most trees, but in some a slight increase was observed at the top.

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