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Differences in bark anatomy between stem and branches of *Olea europaea* L.

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Summary – In addition to morphological characteristics, bark anatomy can provide a more detailed picture of the function of different bark tissues. In the current study, we examined and compared the bark anatomy of the stem and branches of 20-year-old *Olea europaea* L. We hypothesised that there are differences in bark anatomical traits between stem and branches, which reflect their functional differences in a tree. We found that the widths of bark, phloem + cortex, and periderm significantly differed in the stem and branches; all tissues were wider in the stem. The size and area of the sieve tubes and the proportion of sclerenchyma in the oldest part of the phloem + cortex differed in the stem and the branches. At the same time, numerous similarities in the stem and branch bark anatomy were observed: (1) annual phloem increments could not be determined in the youngest phloem adjacent to the cambium; (2) a distinction between non-conducting and conducting phloem was not possible because the collapse of sieve tubes in non-conducting phloem was not prominent enough to be determined visually; (3) dilatation of rays and axial parenchyma was locally clearly visible; (4) the proportion of phloem and cortex changed with distance from the cambium; secondary phloem constituted the entire bark tissue adjacent to the cambium, while cortex prevailed next to the periderm and (5) phelloderm width did not change with bark age. Differences in the bark structure of the stem and branches of olive trees imply functional differences between these two tree parts and point to different ecological contexts. Moreover, branch bark trait values cannot be used to extrapolate to the main stem bark (or vice versa). Differences support previous studies that have reported that different tree parts are exposed to different microenvironments.

Keywords – conducting phloem, cortex, increment, non-conducting phloem, phelloderm, periderm, sclerenchyma, sieve tubes.

Introduction

Olea europaea L. is one of the oldest cultivated plants and for centuries has been of great economic importance in the Mediterranean basin for its crop and wood production (Kyriakis & Fasseas 2010). Although the classification of the genus *Olea* has not yet been precisely defined, recent literature divides it into three subgenera: *Tetrapilus*, *Paniculatae* and *Olea* (cultivated olive and wild relatives) (Rugini *et al.* 2011). The subgenus *Olea* is divided into two sections: *Ligustroides* (about 10 species) and *Olea* (one species: *europaea*). *O. europaea* is the Mediterranean olive tree, the only species cultivated for oil production and consumption. There are more than 1000 cultivars, although many of them are merely different landraces derived from the same original genetic stock or differently named varieties derived from the same original genetic stock. The cultivated olive is thus not considered a species, but rather a group of forms originating from mutations and natural hybridizations (Rugini *et al.* 2011).

Olive trees can live 1000 years or longer, but the exact age is often difficult to determine due to tree trunk morphology, which limits the use of standardized dendrochronological methods (Arnan *et al.* 2012). Generally, the

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Oleaceae family consists of many genera with a great diversity of wood structure, among which the wood anatomy of *O. europaea* has been summarized (Baas *et al.* 1988) and later also compared between stem and twigs (De Micco *et al.* 2008). With a few exceptions (Filippou *et al.* 2007; Kyriakis & Fasseas 2010), the bark anatomy of olive trees is less well known. A recent study showed that xylem transport efficiency and certain bark traits are related in the branches of different Cupressaceae species, indicating that coordination between wood and bark tissues exists and affects tree functioning, also in response to various stress events (e.g., drought) (Jupa *et al.* 2024).

Bark has a complex anatomical structure, which is reflected in many vital functions that bark tissues perform simultaneously (i.e., functional coupling) for woody plants (Rosell 2019). The functions of the inner bark are: (1) photosynthate translocation (sieve elements), (2) storage of non-structural carbohydrates, water and other compounds (parenchyma), (3) wound closure (meristematic cells and parenchyma) and (4) in some cases also photosynthesis (chlorophyllous cells in the cortex) (Wittmann & Pfanz 2014; Cernusak & Cheesman 2015; Rosell 2019). The outer bark (rhytidome) is mainly involved in the protection of inner tissues from various external hazards (Pfanz 2008; Romero *et al.* 2009; Rosell *et al.* 2014; Pausas 2015; Shtein *et al.* 2023; Hoffmann *et al.* 2024). All bark provides mechanical support (sclerenchyma) (Niklas 1999). Besides a marked heterogeneity of bark across woody plants, morphological differences also exist between different tree parts, i.e., stem, branches and roots, which are subject to different microenvironments and might reflect their functional and ecological differences (Rosell *et al.* 2015). Although some bark traits are age-related (e.g. the bark thickness), thicker (outer) bark in the stems could reflect the need for higher protection from fires, herbivores, pathogens, and other hazards, as damage to the stem would result in greater growth reduction (greater risk for tree mortality) than damage to the branches (Butler *et al.* 2012; Pausas 2015; Rosell *et al.* 2015). Thicker bark is also associated with faster wound closure (parenchyma, cork cambium), greater mechanical support (sclerenchyma in the entire bark), and greater water and non-structural carbohydrate storage (parenchyma in the inner bark) (Niklas 1999; Rosell *et al.* 2014). By contrast, bark photosynthesis is limited by the thickness of the outer bark, which acts as a light barrier (Pfanz *et al.* 2002; Saveyn *et al.* 2010). Consequently, it can be assumed that bark photosynthesis is more common in branches with generally thinner outer bark compared to stems. Due to its presumably greater metabolic activity, the photosynthetic bark (branches) could require a higher water content (inner bark) than non-photosynthetic bark (stems) (Rosell *et al.* 2015).

In addition to macroscopic characteristics of bark tissues (e.g., thickness, density) in different tree parts, a more detailed examination of bark traits at the cellular level would provide further information on functional trade-offs among different cell types/tissues. For example, it has already been shown that the phloem conduit diameters differ in different tree parts due to axial widening; the sieve tubes are wider in the stem than in the branches (Petit & Crivellaro 2014; Jyske & Hölttä 2015; Gričar *et al.* 2017). By optimising the diameter of the sieve tubes, the mass flow of sugar solutions through the phloem transportation system minimizes the influence of the path length on the hydrodynamic resistance (Petit & Crivellaro 2014). In the current study, we examined and compared the bark anatomy of the stem and branches of *O. europaea*. We hypothesised that there are differences in bark anatomical traits between stem and branches, which reflect their functional differences in a tree.

Material and methods

Study site description

The study was conducted in an olive grove in Dekani (45°32′48.95″N, 13°48′52.54″E, 76 m asl), which is located 6.5 km from the port of Koper in the Littoral region of southwestern Slovenia. The climate at the site is sub-Mediterranean, with an average annual temperature for the period 1975–2017 of 13.3°C, an average January temperature of 4.8°C, and an average July temperature of 23.2°C. The average annual precipitation for this period is 974 mm, which is fairly evenly distributed throughout the year but can vary greatly from year to year. The wettest month is October, with 116 mm average precipitation, while the driest month is January, with 62 mm average precipitation.

Climate data were obtained from the nearest meteorological station, in Portorož (45°30′59.88″N, 13°34′47.89″E, 31 m asl), 20 km from the study area, reference period 1975–2017 (ARSO Slovenian Environmental Agency). The soil type is clay loam with a mean depth of 0.74 m.

The olive grove is about 25 years old and located in a typical olive-growing area on a south-east facing slope. The olive trees are planted on terraces and are spaced 5 m × 6 m apart, with an overall plantation density of 300 trees per hectare. The olive grove has a sunny and airy position and is covered with natural greenery (Noč *et al.* 2024). The grove is planted with the Istrska Belica (*Olea europaea* L., cv. 'Istrska belica'), a local Istrian variety. This olive variety is the most widespread variety in the northern part of the Adriatic region and is intensively propagated in Slovenian Istria and in the Friuli-Venezia Giulia region in Italy (Bandelj *et al.* 2004; Baruca Arbeiter *et al.* 2014). Due to its long history in this area, it is better adapted to the local winter conditions and low temperatures compared to other varieties but it is more sensitive to fruit-fly infection and peacock-eye disease, which affects the quality of the olive oil (Valenčič *et al.* 2020). Compared to other varieties, this variety bears later; at technological maturity, the fruits are green to reddish in colour, while the oil content is above average. The olive oil has a high phenol content, which gives the oil a special flavour characterized by bitterness and pungency (Noč *et al.* 2024).

Sampling and section preparation

Sampling was performed at the end of September 2016 when the radial growth of *Olea europaea* was completed. Ten trees around 20 years old, similar in their diameter at breast height (14 ± 1.5 cm) and height (5–7 m), were selected for the study. The samples were taken from two tree parts: (1) from the stem, 1.3–1.5 m above the ground, and (2) from a branch, around 3 m from the apex. The sampled branches, with diameters at the sampling locations of around 5 cm, were located approximately 2 m above the ground. A Trephor tool (Rossi *et al.* 2006) was used to extract microcores of 2.4 mm in diameter from trees. The microcores contained bark, cambium and outer xylem. Immediately after removal from the trees, the microcores were fixed in FAA (formaldehyde/50% ethanol/acetic acid solution) and, after 1 week, immersed in a series of ethanol solutions of increasing concentration (70, 90%, and 95%) until pure, water-free alcohol was reached. The samples were then embedded in paraffin blocks from which 8–12-μm-thick permanent cross-sections were cut using a Leica RM 2245 rotary microtome (Leica Microsystems, Wetzlar, Germany) and stained with a safranin (Merck, Darmstadt, Germany) (0.04%) and Astra Blue (Sigma-Aldrich, St. Louis, MO, USA) (0.15%) water mixture (for details, see Prislan *et al.* (2022). Cross-sections were mounted in Euparal (Waldeck, Münster, Germany) and were observed under an Olympus BX51 light microscope (Olympus, Tokyo, Japan) using transmission light mode. Histometric analyses were performed at 4×, 10×, and 20× magnifications with the Nikon NIS-Elements Basic Research version 2.3 image analysis system (Tokyo, Japan).

Histometric and statistical analyses

On the cross-sections, we observed and compared the anatomical structure of bark tissues in the stems and branches of olive trees. Specifically, we measured the following parameters in bark (Fig. 1):

(1) Widths of (i) the entire bark, (ii) phloem and cortex, and (iii) periderm along three radial files in each histological section. Since the phloem and cortex could not be demarcated in a radial direction, measurements were made for both tissues together (i.e., phloem + cortex). Proportions of phloem + cortex and periderm to the total bark width were then calculated.
(2) Diameters (radial and tangential) and areas of 10 randomly selected sieve tubes in the youngest phloem adjacent to the cambium. To do this, we defined a rectangular area in the youngest phloem adjacent to the cambium in the image analysis system. In this area, the first 10 random points that fell on the sieve tubes marked the cells that we measured.

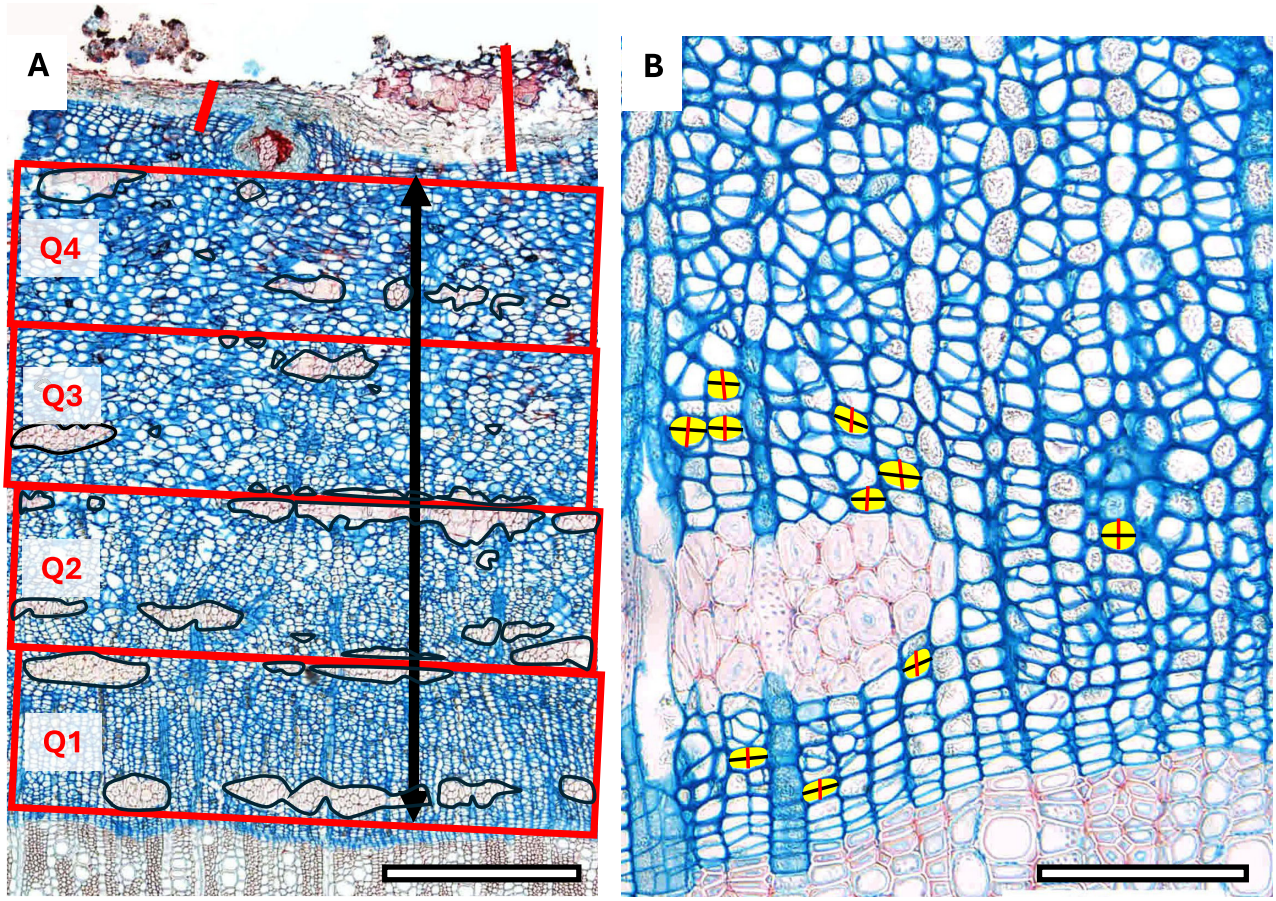

Fig. 1. Illustration of performed measurements in the phloem of *Olea europaea*. (A) Width of periderm (red line), width of phloem + cortex (black arrow), division of phloem + cortex into quarters (red frames), sclerenchyma (black borders). Quarter 1 was located next to the cambium and quarter 4 next to the periderm. Q, quarter. Scale bar = 500 µm; (B) Sieve tubes in the youngest phloem: areas (yellow areas); radial dimensions (red lines) and tangential dimensions (black lines). Scale bar = 100 µm.

(3) % of the sclerenchyma area in the bark divided into quarters according to the distance from the cambium. Quarter 1 was located next to the cambium and quarter 4 next to the periderm.

The terminology for bark anatomy follows Trockenbrodt (1990) and Angyalossy *et al.* (2016). The bark of olive trees includes sclerenchyma, i.e. cells that are variable in form and size, and have more or less thick, often lignified, secondary walls. Sclerenchyma provides mechanical support and includes olive tree fibres and sclereids. Phloem fibres are elongated, tapering sclerenchyma cells with lignified secondary walls and rare pits. They develop from the vascular cambium and undergo intrusive growth during development. Sclereids are highly variable in form and size but are not much elongated. They have thick, often polylamellate, lignified secondary walls with many pits. Sclereids develop mainly in the nonconducting phloem, cortex, and periderm by modification of parenchyma cells (Angyalossy *et al.* 2016). In this article, we did not distinguish between sclereids and phloem fibres, but we considered them as sclerenchyma in the analysis. The walls of sclerenchyma were stained red and exhibited birefringence in polarised light.

The average values of tissue width, sieve tube dimensions, and% of sclerenchyma per bark quarter were calculated from replicated measurements performed within each microscopic sample. Averages of traits measured (n = 10) were

then subjected to linear mixed models to test the differences between stem and branches. Three was used as a random (blocking) factor in the models. Separate models were derived for each level of tissue type, sieve tube dimension, and bark quarter. Normality and homogeneity of variance were assessed graphically. All tests were performed at a 0.05 significance level within the R environment (R Core Team 2024). The main packages used were lme4 (Bates *et al.* 2015) for modelling and ggplot2 (Wickham 2016) for graphing.

Results

Annual phloem increments could not be determined in the stem and branches of olive trees, even in the youngest phloem adjacent to the cambium. There were no morphological differences in early and late phloem sieve tubes, which would allow a distinction between phloem increments (Fig. 2). In addition, a distinction between nonconducting and conducting phloem was not feasible because a collapse of sieve tubes in the nonconducting phloem, a typical secondary change associated with the cessation of their conducting function, was not clearly expressed on the cross-sections. Dilatation of rays and axial parenchyma was locally nicely visible in the nonconducting phloem (Fig. 5a). In all samples, the cortex was still preserved and alternating radial bands of cortex and phloem were apparent in the older part of the phloem (Fig. 2b, c). The proportion of phloem and cortex changed with distance from the cambium; while the secondary phloem constituted the entire bark tissue adjacent to the cambium, the cortex prevailed next to the periderm.

Visual inspection of the samples revealed that the bark was wider (in absolute values) in the stem than in the branches (Fig. 2). Indeed, we found statistically significant differences in the absolute values of widths of all measured bark parameters, i.e., entire bark ($F = 127.4$; $P = 0.000^{***}$), phloem + cortex ($F = 123.9$; $P = 0.000^{***}$) and periderm ($F = 17.05$; $P = 0.000^{***}$), in the stem and branches of olive trees (Fig. 3). The absolute width of bark was approximately 61% wider in the stem compared to the branches (mean values stem = 5.0 mm; branch = 1.9 mm). The periderm represented 6% and 10% of the bark in the stem and branches, respectively.

The sizes and area of the sieve tubes significantly differed between the stem and branches (Fig. 4). Both radial and tangential diameters of the conduits were larger in the stem than in the branches, i.e., 20% ($F = 17.31$; $P = 0.000^{***}$) and 23% ($F = 28.81$; $P = 0.000^{***}$), respectively. This resulted in 36% larger sieve tube areas in the stem compared to the branches ($F = 43.34$; $P = 0.000^{***}$).

In an analysis of the proportion of sclerenchyma in the bark tissues, i.e., in the phloem and cortex, we divided the phloem tissue into quarters to check how the sclerenchyma proportion changed with age and tree part (stem *versus* branches) (Fig. 5). Sclerenchyma in olive trees included fibres and sclereids (Fig. 2b,c, 5). As already mentioned, we did not distinguish between them although the two types of sclerenchyma differ in their ontogeny, but both provide mechanical support. Sclereids are highly variable in shape and size, so the distinction between these two cell types on cross-sections may not always be reliable. Therefore, we did not examine the potential changes in their morphology or distribution. Unlike in the stems, a sclerenchyma ring composed of groups of sclereids and fibres in the cortex was clearly visible in the branches (Figs 2b,c and 5b).

In the stem and branches, the proportion of sclerenchyma did not on average compose more than 20% of the phloem and cortex tissues (Fig. 6). The highest differences in the proportion of sclerenchyma between the stem and branches were detected in the oldest, fourth quarter ($F = 74.37$; $P = 0.000^{***}$). Statistically significant differences were also found in the third quarter ($F = 4.685$; $P = 0.045^{*}$), while in the first and second quarters, the proportion of sclerenchyma did not differ between the stem and branches ($F = 0.964$; $P = 0.34$ and $F = 0.615$; $P = 0.444$, respectively). In the fourth quarter, the average value of the sclerenchyma proportion was higher in the branches, whereas in the third quarter, it was higher in the stem. Comparing the proportions of sclerenchyma among the quarters in the stem, we detected the highest and comparable values of sclerenchyma proportion in the first two quarters (mean values Q1 = 17.5%; Q2 = 18.2%). The proportion of sclerenchyma then decreased over the distance

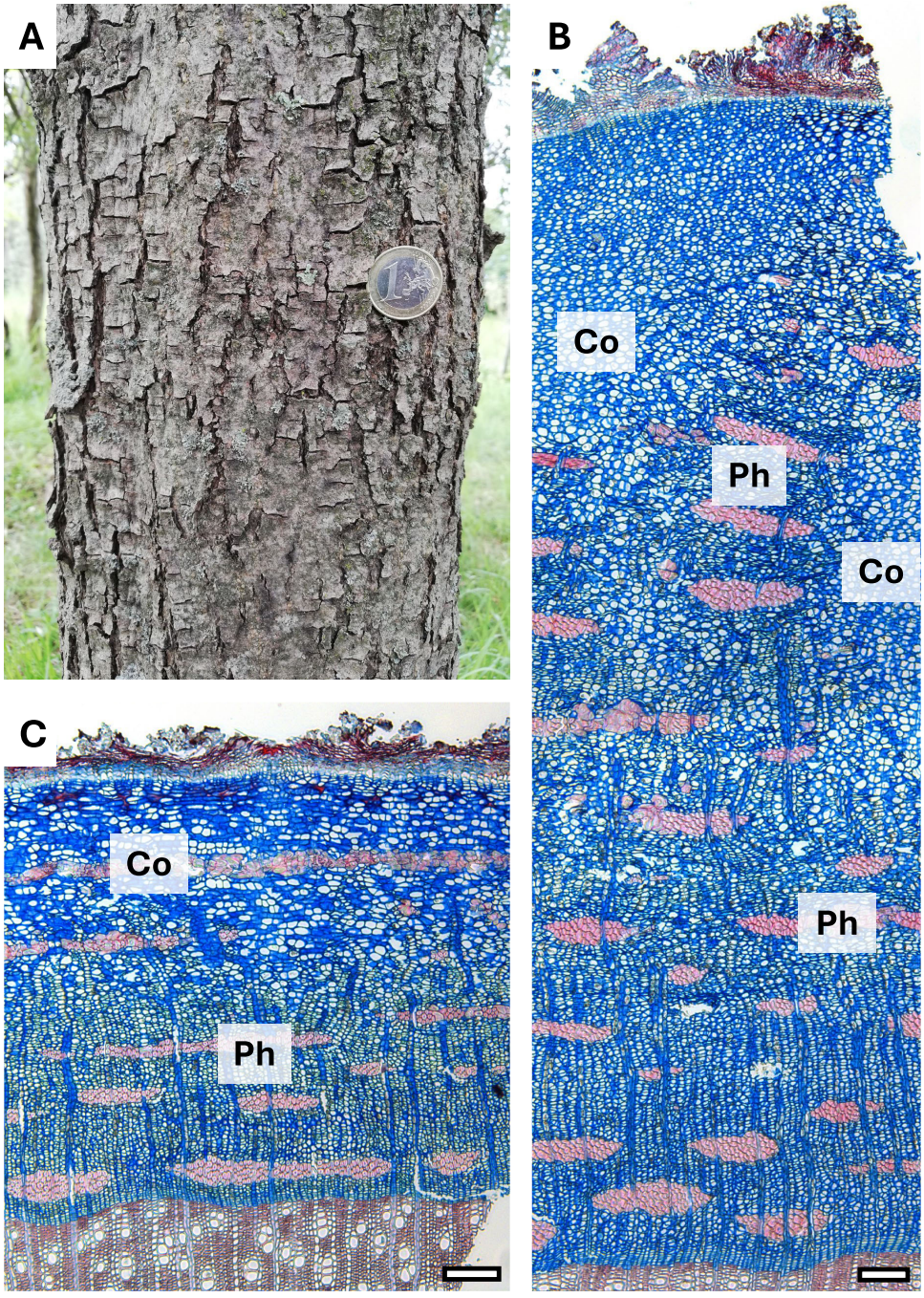

Fig. 2. (A) Macroscopic structure of bark of *Olea europaea*. (B) Microscopic structure of olive bark in the stem. (C) Microscopic structure of olive bark in the branch. Co, cortex; Ph, phloem. Scale bars = 200 µm.

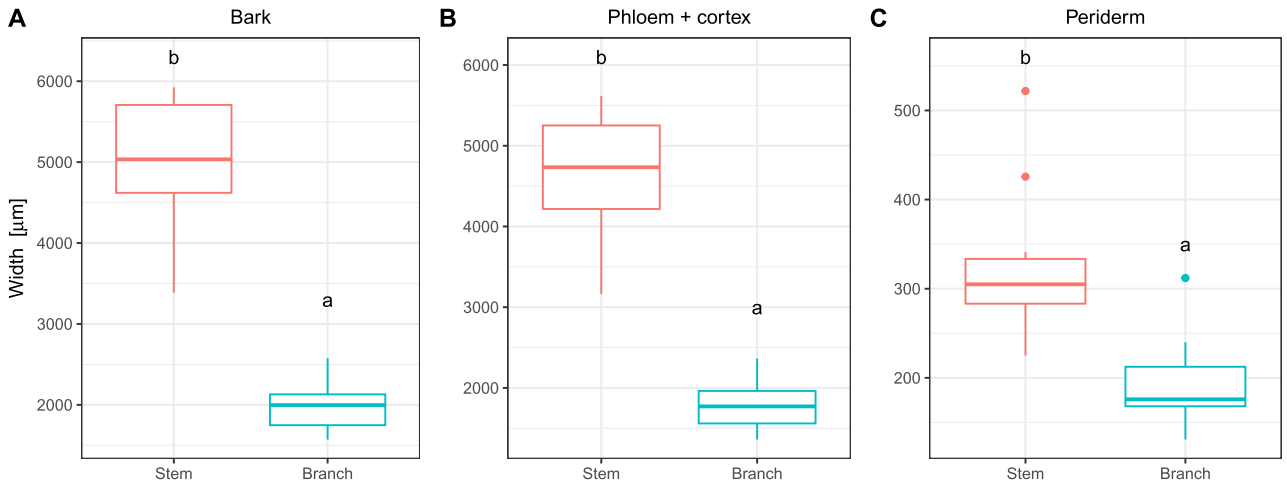

Fig. 3. Boxplot for the widths of bark (A), phloem + cortex (B) and periderm (C) for stem and branches in olive trees (n = 10). The letters above boxplots denote the statistical significance of the difference between groups at a 0.05 significance level.

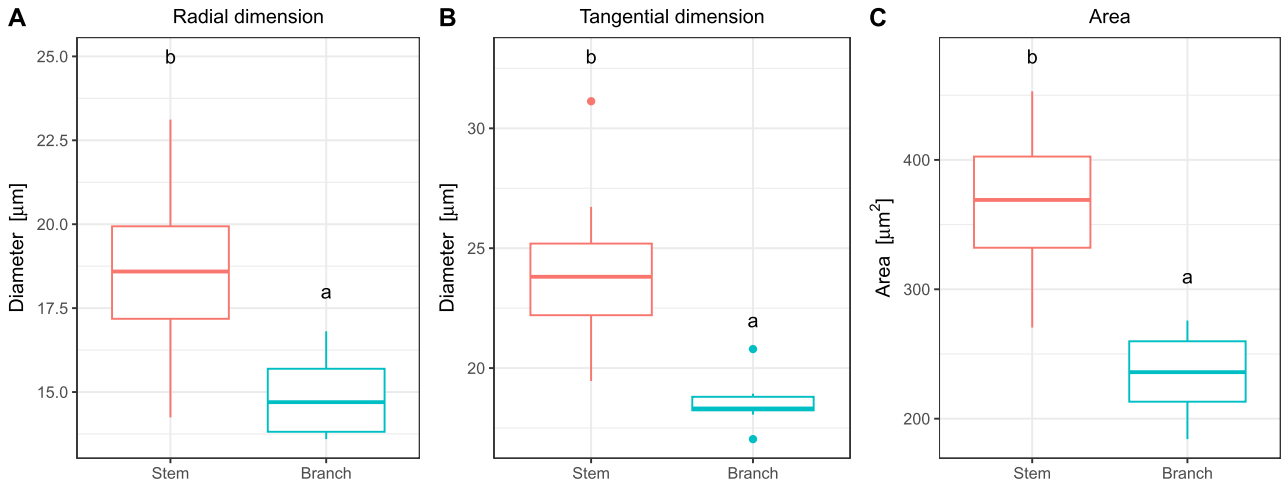

Fig. 4. Boxplots for radial (A) and tangential (B) diameters and area (C) of sieve tubes for stem and branches in olive trees (n = 10). The letters above boxplots denote the statistical significance of the difference between groups at a 0.05 significance level.

from the cambium towards the periderm and reached its lowest mean value in the fourth quarter (Q4 = 6.3%). In the branches, the lowest mean value of the sclerenchyma proportion was noted in the third quarter (Q3 = 8.8%), while the mean values in the first, second, and fourth quarters were comparable (Q1 = 19.2%; Q2 = 16.5%; Q4 = 18.3%) (Fig. 6).

Periderm was generally wider in the stem than in the branches (Fig. 3c), which was expressed in the width of the phellem, while the phelloderm width was comparable in the two tree parts. In cross-section, the phelloderm and phellogen cells were difficult to distinguish in the periderm (Fig. 7). A layer of phellogen was located between the phelloderm inwards and phellem cells outwards. The phelloderm and phellogen cells had thin-walled cells in radial rows, which morphologically resembled the adjacent parenchyma cells, except for their radial alignment. The narrow phelloderm was composed of 2–3 cell layers of rectangular to round cells. Phellem cells were difficult to count due to age-related changes, which altered the cell morphology and disrupted their radial arrangement. Different types of cells were present in the phellem: thin-walled and wide-lumened cells were adjacent to the phellogen and thin-walled

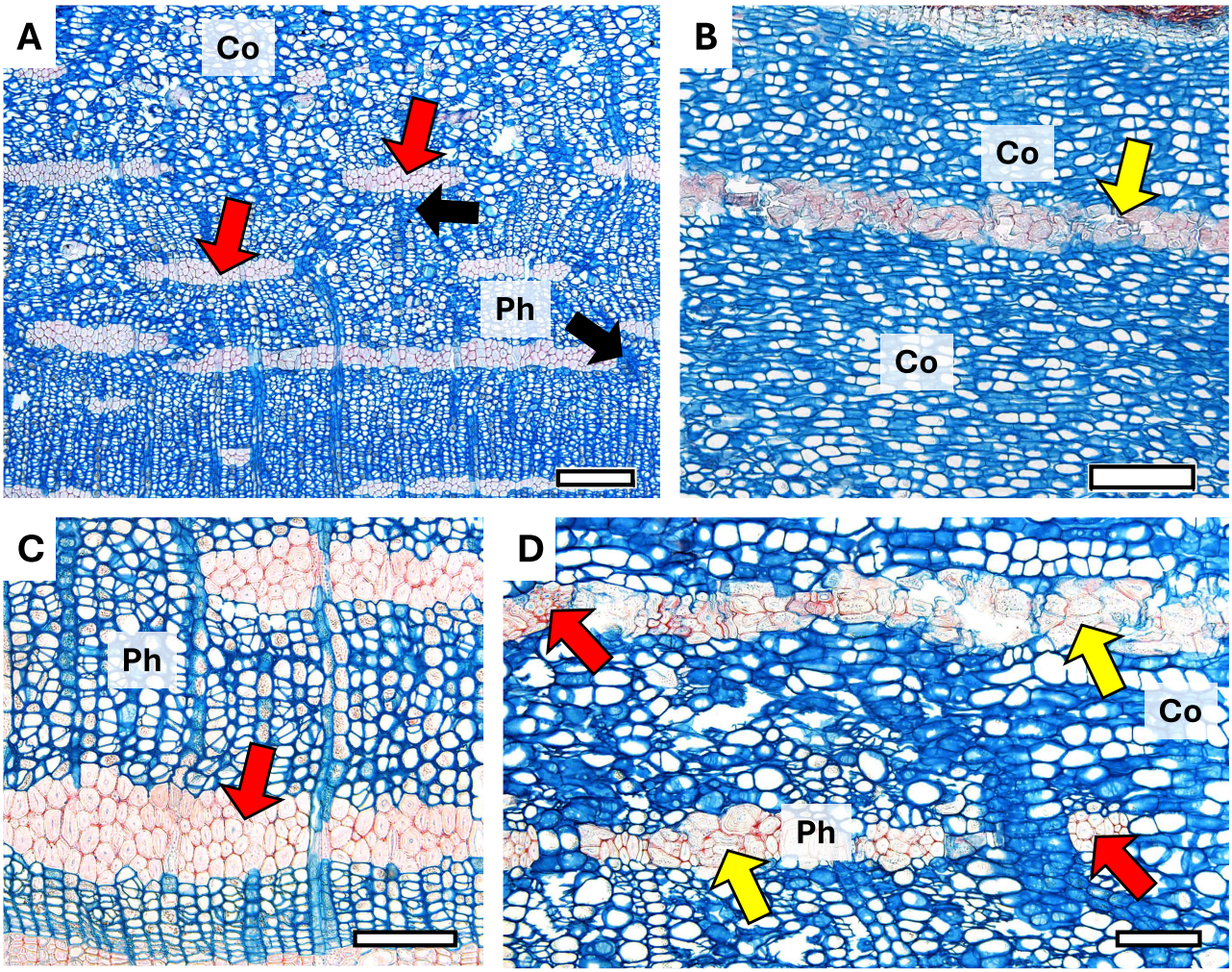

Fig. 5. Anatomy of phloem and cortex of *Olea europaea*: (a) Phloem fibres (red arrows) and dilatation of rays (black arrows). (b) Sclereids (yellow arrow) in cortex. (c) Phloem fibres in phloem (red arrows) and (d) phloem fibres (red arrows) and sclereids (yellow arrows) in phloem and cortex. Co, cortex; Ph, phloem. Scale bars = 200 µm (a, b) 100 µm (c, d).

and narrow-lumened were in older (outer) cells. Moreover, outer phellem cells were brownish coloured indicating the presence of different (phenolic) compounds. Lenticels were observed in some samples in the periderm in stem and branches (Fig. 7c,d). At these locations, the number of phelloderm cells increased markedly, i.e., from 2–3 layers to 4–6 layers and even 10 or more layers. Since the sampled olive trees were only around 20 years old, a rhytidome had not yet formed in the stems.

Discussion

The absolute widths of bark, both of the phloem + cortex and the periderm, the size and area of the sieve tubes, and the proportion of sclerenchyma in the oldest part of the phloem + cortex significantly differed between the stem and branches of olive trees. In addition to these differences, numerous similarities in the stem and branch bark anatomy of this species were noticed: (1) annual phloem increments could not be determined in the youngest phloem

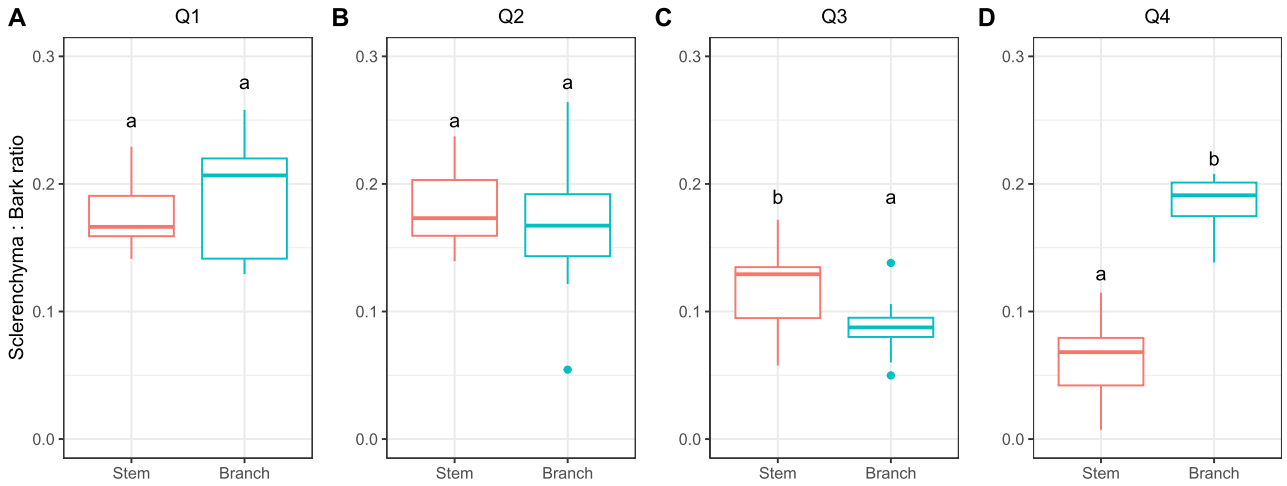

Fig. 6. Boxplots for sclerenchyma: Bark ratio in 1–4 quarters (Q) of phloem + cortex width for stem and branches in olive trees (n = 10). The letters above boxplots denote the statistical significance of the difference between groups at a 0.05 significance level.

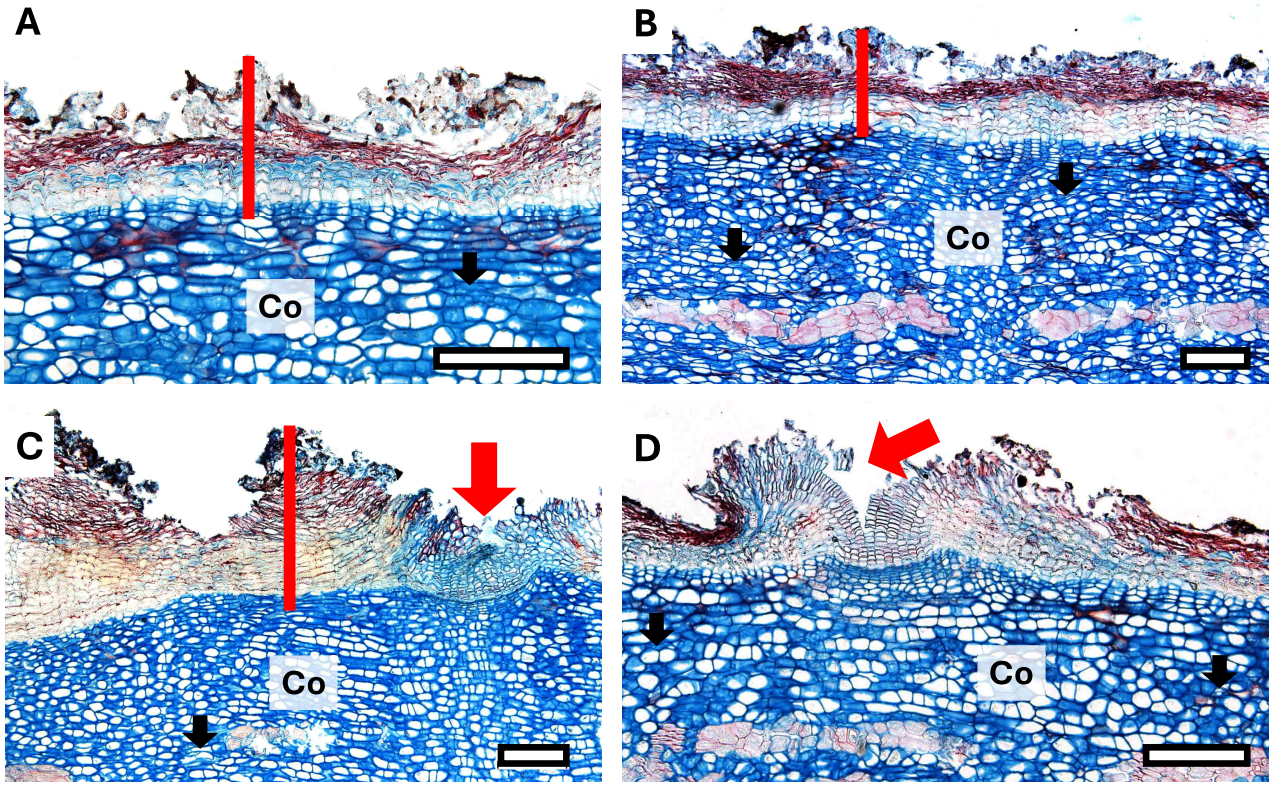

Fig. 7. Anatomy of periderm (red lines), lenticels (red arrows), and tubular-like structures (red arrows) in branches (a, d) and stem (b, c) of *Olea europaea*. Co, cortex. Scale bars = 200 µm.

adjacent to the cambium; (2) a distinction between non-conducting and conducting phloem was not possible because the collapse of sieve tubes in the non-conducting phloem was not prominent enough to be determined visually; (3) dilatation of rays and axial parenchyma was locally clearly visible; (4) the proportion of phloem and cortex changed with the distance from the cambium; secondary phloem constituted the entire bark tissue adjacent to the cambium, while cortex prevailed next to the periderm and (5) the phelloderm width did not change with bark age.

Bark thickness

In numerous angiosperm species, it has already been established that the thickness of the bark is closely related to the tree stem diameter (tree age) (Rosell *et al.* 2017). It is generally thinner in the branches, especially the outer bark (Poorter *et al.* 2014; Rosell *et al.* 2015; Rosell 2016). We also found that the bark of olive trees was wider in the stem than in the branches, i.e., about 5 mm and 2 mm, respectively. A simple calculation of the proportion of the thickness of bark and phloem + cortex in relation to the diameter (bark + xylem) of a stem or branch showed that the proportions of bark and phloem + cortex in the stem were about 9% and 6% lower than in the branches of olive trees, respectively, which is in line with previous findings (Hölttä *et al.* 2013). Despite species-specific differences in bark width and structure, uniform axial scaling patterns of xylem and bark tissues is probably associated with different functional requirements in different tree parts (Jyske & Hölttä 2015). Jupa *et al.* (2024) recently suggested that the relationships between hydraulic traits (xylem and phloem) and bark structure in Cupressaceae tree species result from their functional adaptation to the given environmental conditions. In addition to the impact of environmental factors on bark traits, their variation may also result from trade-offs and coordination between the multiple functions of bark. Furthermore, bark traits covary with wood and leaf traits as part of the main dimensions of plant variation (Rosell *et al.* 2017).

Structure of the youngest phloem

There was no typical structure of early and late phloem in olive trees, with sieve tubes differing in their morphological characteristics, which is commonly found in trees from temperate and cold climates (Gričar *et al.* 2016). We were therefore unable to determine the youngest phloem increment of 2016. In this sense, the phloem structure in olive trees resembles the structure of pine species (*Pinus halepensis* and *Pinus pinea*) from the Mediterranean region (Balzano *et al.* 2020), with which growth-ring boundaries between the phloem increments could not be demarcated. However, in these pines, a seasonal trend in the size of sieve cells was noted and was positively related to water availability (Balzano *et al.* 2020), supporting the fact that cell enlargement depends on turgor pressure in the cell (Hölttä *et al.* 2010). The absence of any intra-annual variations in the size of sieve tubes adjacent to the cambium in the stem and branches of our sampled olive trees could be explained by the fact that the site is well supplied with precipitation (around 1000 mm per year), which is fairly evenly distributed throughout the year. The completely different structure of the conducting phloem in trees from different locations shows that environmental factors also affect the formation of phloem cells and reflects the adaptation of radial growth of trees to local environmental conditions (Gričar *et al.* 2016, 2024).

In environments with mild winter temperatures and a sufficient water supply, a lack of true dormancy in trees is possible (Nanayakkara *et al.* 2019). In the case of *Pinus halepensis* and *Pinus radiata*, it has been found that the cambium in the stem does not exhibit true winter dormancy and that the production of new cells and cell differentiation on the phloem side may occur throughout the year if the conditions permit (Barnett 1971; Prislan *et al.* 2016; Nanayakkara *et al.* 2019). Whether this is also the case with olive trees is difficult to conclude without detailed observations of the seasonal changes in cambial and phloem cells at the ultrastructural level. For that, proper sample preparation and examination at higher resolutions with more sophisticated equipment (e.g., SEM, TEM) is required. However, in our samples taken at the end of September, cambial cell productivity on the phloem side was not detected and the cambium appeared to be dormant, as concluded from thicker cambial cell walls and

narrow cambium composed of only 4–5 cell layers. In support of our assumptions, previous studies have shown (López-Bernal *et al.* 2020) that an absence of true dormancy in the cambium of olive trees is highly unlikely because reproductive budburst does not proceed satisfactorily unless sufficient chilling occurs during the winter. This is why olive trees do not perform well in warm equatorial regions (Miyasaka & Hamasaki 2016). The survival of olive trees is also limited by low temperatures, so regions with a temperature drop below –12°C are not suitable for olive plantations, which are consequently restricted to between latitudes 30° and 45°. However, winter chilling is required only for the reproductive development of olive trees, while vegetative growth may proceed satisfactorily throughout the whole season without any winter chilling in the case of favourable environmental conditions, which has been confirmed in natural conditions and greenhouse experiments (López-Bernal *et al.* 2020). Nevertheless, Hartmann & Porlingis (1957) found that the growth of olive trees in the winter period was negligible, which could be related to a slight vegetative rest period triggered by the short photoperiod. These observations were only performed at a cellular level, without special attention to the phloem part. The state of the cambium and radial growth (including cell differentiation) of olive trees in the winter period therefore remains open for future studies.

Sieve tube characteristics

We found that the diameters of sieve tubes were about 36% larger in the stem than in the branches, which is congruent with the conduit tapering along the stem axis (Petit & Crivellaro 2014; Jyske & Hölttä 2015). Larger sieve tube dimensions in the stem indicate differences in their efficiency in different tree parts of olive trees. A more detailed analysis of all cell types and their proportion, including quantitative data of all functional sieve tubes (i.e., number and size) in conducting phloem would be needed fully to estimate its conducting efficiency. However, we could not detect a collapse of sieve tubes in olive trees in the cross-sections, which is an indicator of the completion of their conducting function. A demarcation between conducting and non-conducting phloem was not therefore possible. The end of the conducting function of sieve tubes is accompanied by the presence of a definitive callose in the sieve areas, autolysis of the contents of the cell, and, finally, destruction of the cell (Esau 1969; Trockenbrodt 1990). These processes can be observed after appropriate tissue preparation on longitudinal sections (Angyalossy *et al.* 2016; Prislan *et al.* 2018). In addition to sieve tube size, their fine structure, such as the distribution and anatomy of the sieve plates and sieve plate pores, may impact greatly on the potential conducting efficiency of sieve tubes (Mullendore *et al.* 2010; Liesche *et al.* 2017). Nothing is known about differences in the fine structure of conduits in different tree parts or within/between years but such knowledge would improve our understanding of the role of the ultrastructural characteristics of sieve tubes on their potential transport capacity.

Cortex and older phloem

Since outer bark (rhytidome) had not yet formed in the stems of our sampled olive trees, the cortex was still preserved in the form of alternating radial bands with phloem. The cortex represents primary ground tissue in woody plants and is located between the vascular system and the dermal tissue and can be detected in younger bark. Unlike phloem, the cortex does not contain rays, and it is commonly modified by dilatation and sclerification processes (Angyalossy *et al.* 2016). In olive trees, the cortex is composed of parenchymatous cells (involved in storage, wound closure, and differentiation into sclereids) and sclerenchyma (mechanical support). According to Kyriakis & Fasseas (2010) chloroplasts (photosynthesis) are often present in the cortex of olive trees. We found that the proportion of phloem and cortex changed with distance from the cambium; the share of secondary phloem decreased with bark age. In contrast, the cortex occupied older tissue adjacent to the periderm. As already mentioned, a collapse of sieve tubes was not clearly expressed in the nonconducting phloem but a dilatation of rays and axial parenchyma, to keep up with the increasing diameter of the stem, branches, and roots, was apparent.

While the conductive capacity of the sieve tubes is limited only to one or two growing seasons and is lost in the nonconducting phloem, the parenchyma cells remain functional as storage tissue for several years (Spicer 2014). It

depends on the tree species and the tree age, but the nonconducting phloem generally represents a large part of the living bark tissue, therefore the amount of parenchyma there is not negligible (Gričar *et al.* 2018). In addition to the storage and transport of non-structural carbohydrates, nutrients and water, the bark parenchyma (axial and radial) is involved in the wood closure in case of mechanical injury and defence in case of pathogen attack (Spicer 2014); however, the function of parenchyma cells may also depend on their location in the tree (root, stem, xylem, bark) (Richardson *et al.* 2015). Moreover, in the nonconducting phloem and cortex, parenchyma cells undergo age-related changes such as inflation and sclerification; the degree of these changes determines a trade-off between storage and mechanical functions in the bark.

Sclerenchyma (fibres and sclereids) primarily provide mechanical support (Angyalossy *et al.* 2016). In addition to the fibres formed in the secondary phloem, sclerenchyma was also formed in the cortex. Since sclereids generally vary greatly in shape and size and in some cases resemble phloem fibres in cross-sections, no age-related trend in their characteristics could be established. The formation of a sclerenchyma ring composed of groups of sclereids in the cortex presumably coincides with the development of the first periderm (Kyriakis & Fasseas 2010). We found a significant difference in the proportion of sclerenchyma between the stem and branches in the oldest bark, i.e., in the fourth quarter, while the difference was less significant in the third quarter and was not significant in the first two quarters. A more or less continuous sclerenchyma ring consisting of groups of sclereids and fibres was clearly visible in the cortex of the branches. In contrast, individual areas of groups of sclereids were present in the stem. At this stage, it can only be speculated that this is related to the greater thickness of the stem bark compared to the branches, resulting in greater absolute values of sclerenchyma. As reported by Kyriakis & Fasseas (2010), periderms with lenticels develop simultaneously with a sclerenchyma ring in the cortex. The ring is tangentially oriented and composed of groups of sclereids and presumably separates photosynthate from storage in the cortex. Although Kyriakis & Fasseas (2010) reported this ring in the stem, we observed it only in branches, while in the stems, the cortex adjacent to the periderm contained the smallest proportion of sclerenchyma compared to the other three quarters of bark tissues. The discrepancies between their findings and ours could be attributed to the difference in the age of the sampled trees.

Kyriakis & Fasseas (2010) recently reported a new cell type, i.e., tubules, which ramify the photosynthetic cortex of the stems and branches in olive trees. The function of this network of tubules is not yet known. Tubules form an anastomosing network of groups of elongated parallel cells, 20–30 μm in diameter, which appear irregularly polygonal in cross-section. In contrast to other cells in the cortex, these cells have no intercellular spaces. The network is evenly distributed within the cortex, irrespective of the orientation of the stem and branch (Kyriakis & Fasseas 2010). We also observed cell structures in the cortex that fit the description of tubules described by the authors (Fig. 7). However, we did not perform more detailed analyses on the potential differences in their quantity or distribution between the stem and the branches because it was difficult to reliably distinguish them from the parenchymal cells in cross-sections. Our distinction between these two cell types was mainly based on the cell wall thickness (they are thinner in tubules) while the colour of the walls of tubules and parenchyma did not differ.

Periderm characteristics and its effect on the photosynthetic activity of bark

An outer dead bark had not yet formed in our sampled olive trees; however, the width of the periderm was greater in the stem than in the branches. The wider periderm in the stem was probably related to the fact that the bark on the stem is older than in the branches. In particular, the width of the phellem differed, while the phelloderm was comparable in the two tree parts. A higher number of phellem cells in the stem indicates greater protection against external influences. The first phellogen (cork cambium) in the periderm is active as long as the bark remains smooth, i.e., until the beginning of the formation of successive layers of periderm, which leads to the formation of the rhytidome (Trockenbrodt 1990). The surface of the bark in olive tree stems starts to change from smooth to partially smooth and partially rough when the trees are about 30 years old (Filippou *et al.* 2007). This change is

associated with the cessation of photosynthetic activity in the rough part of the bark, in which no photosynthetic tissue is present. According to Filippou *et al.* (2007), the proportion of each type of bark (smooth *versus* rough) appeared to be independent of the tree age, and smooth, photosynthetically active bark is widespread. However, light transmission through the phellem is age-dependent and decreases rapidly in stems older than five years. This is explained by the gradual replacement of the epidermis by the periderm and the increasing number of phellem cells. The photosynthetic cortex is shed with rhytidome formation (Filippou *et al.* 2007). We can conclude from this that photosynthetic activity is higher in the branches than in the stem, although this was not the subject of our research. Photosynthetic bark, which is commonly present in numerous tree species, has been found to contribute up to 11% of the carbon in branch wood of evergreen eucalyptus (Cernusak & Hutley 2010). In the case of water stress, it can represent as much as 50% of plant carbon gain (Franco-Vizcaíno *et al.* 1990). Carbon assimilation of woody tissue thus plays a significant role in the whole-tree carbon budget (Saveyn *et al.* 2010). However, there are differences between bark photosynthesis in stems and twigs/branches, which is generally limited by outer bark thickness, which acts as a light barrier (Pfanz 2008). Consequently, photosynthesis is more common in twigs/branches with a thinner outer bark than in main stems. The probability of photosynthetic activity is just 50% if the outer bark is about 1 mm thick, while practically no bark is photosynthetic in the case of more than 4 mm thick outer bark (Rosell *et al.* 2015). Finally, bark photosynthetic activity also varies among tree species (Pfanz *et al.* 2002).

Olive tree bark is known to be photosynthetically active (Filippou *et al.* 2007). Although photosynthetic activity is concentrated in the spring, and restricted to favourable environmental conditions, i.e., water availability (Bustan *et al.* 2011), olive trees are evergreen species, so the photosynthetic activity of olive leaves does not stop during winter and the produced assimilates are stored in the parenchyma (López-Bernal *et al.* 2020). The duration of the winter dormant period is thus likely to influence carbon partitioning among different tree organs and, probably, tree productivity (López-Bernal *et al.* 2020). In Mediterranean conifers and in evergreen broadleaved trees, it has been reported that leaf photosynthesis is slightly reduced but not suppressed during mild winters (Troeng & Linder 1982; Awada *et al.* 2003; Miyazawa & Kikuzawa 2005). Photosynthates produced in the autumn and winter periods can therefore be used for the differentiation of xylem and/or phloem cells (Barnett 1971).

A limited part of the periderm, in which the phellogen is more active than elsewhere, produces a tissue that, in contrast to the phellem, has a relatively open arrangement of cells, which are called lenticels. They are common components of the periderm of stems and roots (Angyalossy *et al.* 2016). Lenticels are isolated regions (pores) in the periderm of woody plants that enable gas exchange between the atmosphere and tree tissues in the otherwise impervious outer protective layers of the periderm (Rosner & Morris 2022). Recent studies have shown that lenticels may play a role in recovery from drought stress, in defence against insects and fungal/bacterial pathogens, in wound healing, and in keeping stems upright; however, the structure-function relationships of lenticels remain poorly understood (Rosner & Morris 2022).

Conclusions

In addition to morphological characteristics, bark anatomy provides an even more detailed picture of the function of different bark tissues in olive trees. The separation of the bark tissue into phloem + cortex and periderm parts, the observation of secondary changes during the transition from the conducting to the nonconducting phloem, the analysis of the sieve tube characteristics in the conducting phloem, and the presence and distribution of sclerenchyma in different quarters of the phloem + cortex tissues revealed the complexity of the bark structure and the associated processes, which are still far from being understood. We found notable differences in the bark structure of the stem and branches of olive trees, which suggest that functional disparities between stem and branch bark exist. The branch bark trait values cannot be used to extrapolate to the main stem bark (or vice versa) but they support previous studies that different tree parts are exposed to different microenvironments, which is reflected in

the bark functional traits (Rosell *et al.* 2015). According to Rosell *et al.* (2014), the differences in cell morphological characteristics and the relative amount of different cell types and tissues in the bark probably reflect trade-offs among the bark functions. Since recent work by Jupa *et al.* (2024) showed that there is a relationship between xylem and bark traits in Cupressaceae tree species, which affects tree functioning, future studies should examine whether this is also the case in other tree species. The authors observed that water transport efficiency and embolism resistance in xylem are related to thicker layers of living phloem (transport and storage) and dead bark tissues (insulation properties), respectively (Jupa *et al.* 2024). Due to the strong hydraulic connection between the xylem and phloem vascular systems through rays, Pfautsch *et al.* (2015) already proposed considering them as a single, highly segregated system. In the current paper on olive trees, we did not compare the characteristics of xylem and bark tissues/cells; however, a similar trend, was observed for all measured bark parameters (i.e., the narrower thickness of bark tissues and smaller phloem conduits), was found also in the xylem; the width of the xylem increments of 2016 and the vessel size were smaller in the branches than in the stem of olive trees (Gričar & Eler in revision). Regarding conduit characteristics in xylem and phloem, the tapering of conduits along the stem axis has been confirmed in numerous angiosperm and gymnosperm tree species (Anfodillo *et al.* 2012; Petit & Crivellaro 2014; Jyske & Hölttä 2015; Gričar *et al.* 2017), which seems to be a key feature of long-distance transport architectures of xylem and phloem (Petit & Crivellaro 2014). The size of the conduits, which varies within the tree, contributes greatly to their conduction efficiency. However, for a comparison of the consistency of xylem and bark traits in different tree parts, the characteristics of the entire xylem portion and not just the youngest xylem increment would have to be included. This is because in contrast to the ring-porous tree species, the diffuse-porous tree species usually do not form heartwood, consequently, vessels perform a conducting function over several years or even decades. This must be taken into account when evaluating the efficiency of the conduction system in the xylem in relation to the bark traits in the diffuse-porous tree species (Schume *et al.* 2004; Jupa *et al.* 2016).

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