

Structure and identification of root bark of *Quercus robur* L.

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Abstract. The root bark structure of *Quercus robur* L. was analysed at different stages of root development and compared to the structure of stem bark. Root bark thickness varied considerably between different roots. Sclereid quantity decreased with increasing distance from the stem, which means it increased with age. Visible growth increments diminished with increasing distance from the stem. In lateral roots crystal quantity decreased with increasing distance from the stem. In lateral roots secondary phloem fibre length, sieve tube member length, and sieve tube diameter showed no regular trend. There were only a few basic structural differences between root and stem bark. The zone of cell differentiation (cell expansion, lignification) was wider in root bark; sieve tube collapse was delayed. In lateral root bark fewer sclereids were formed. The first-formed periderm often originated from deeper cell layers. Thus, primary elements were lacking after periderm formation. In root bark the phellem cell walls were of equal thickness. Thus, phellem lacked visible growth increments. Root bark phellem cells were slightly larger. The root phelloderm was more distinct. The secondary phloem fibres were slightly shorter than those in stem bark. Sieve tube members of stem and root bark were of similar length and diameter. The qualitative bark anatomical characters of oak root bark are suitable for root identifications. Due to minor structural differences between root and stem bark the characters must be used with care.

Key words: Bark structure – Bark anatomy – Root bark – Identification – *Quercus robur* L.

Introduction

Tree roots frequently damage buildings and other structures, for example the sewerage system. For legal reasons

and to prevent further damage, it is often necessary to identify the trees that caused the damage. In most cases, this identification is carried out on the basis of the structure of root wood. Sometimes, however, an identification based exclusively on wood is not successful. The root wood may differ too much from the stem wood usually used as reference material. Furthermore, enough wood for a complete record of the wood anatomical characters might not be available. In this case, it is appropriate to include the structure of bark in the identification process. There are relatively few results on the use of stem bark structure for diagnostic purposes. However, these results show that bark anatomical characters may have a high diagnostic value (e.g. Parameswaran and Liese 1968; van Wyk 1985; Archer and van Wyk 1993). Yet, the variability of stem bark structure in relation to bark age has to be considered (Trockenbrodt 1991). So far, the anatomy of root bark has been described by only a few authors and it is rarely used for identification purposes (e.g. Gasson 1979; Cutler et al. 1987). Mostly these descriptions are restricted to very young bark. There are no studies on the structure of mature root bark and its variability during root development. For this reason, the bark structure of taproot and lateral roots of *Quercus robur* L. was analysed at different stages of root development and compared to the structure of stem bark. The reported details on the structure of stem bark were obtained from earlier observations (Trockenbrodt 1991, 1994, 1995) and from other authors (e.g. Holdheide 1951).

Materials and methods

In bark, especially root bark, precise selection of samples of known history (e.g. year of tissue formation) is not feasible. Thus, the samples were taken at different distances from the stem. The distances were chosen as regularly as possible. Furthermore, the diameter decrease of the roots and the intactness of the root bark tissue were taken into account. The samples do not correspond to regular age intervals, because in most cases, it was impossible to determine the sample age by xylem growth rings.

In two planes, at 10 cm and 50 cm depth, lateral roots branched horizontally off the taproot of the 37-year-old oak tree analysed.

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Samples were removed from the taproot and from two opposite lateral roots of each plane. Samples included bark, cambial zone, and a narrow portion of xylem. They were immediately fixed in FAA (formalin-acetic acid-alcohol). In case of a distinct eccentricity of the lateral roots, samples were taken from both the upper and the lower sides of the root.

The taproot bark was analysed at ground level and at five distances from the ground level (20, 30, 40, 50, 70 cm). The corresponding bark thickness was 14.1, 8.0, 6.7, 4.9, 3.9, 3.6 mm. From lateral root A1, samples were taken at a distance of 10, 25, 40, 65, 90, and 110 cm from the taproot. The corresponding bark thickness was 1.1, 1.3, 1.3, 1.3, 0.9, and 0.9 mm for the upper side of the root, and 2.1, 1.3, 1.5, 1.1, 0.9, and 0.9 mm for the lower side. A2 samples were taken at a distance of 20, 50, 70, and 90 cm. The bark thickness, showing no distinct eccentricity, was 0.9, 0.7, 0.7, and 0.6 mm. From B1 and B2, samples were only taken at a distance of 15 cm. The bark thickness of the upper and lower side of the roots was 3.3 and 2.7 mm in B1 and 1.8 and 2.3 mm in B2.

In order to stabilise the bark tissue, the FAA was replaced by PEG (Polyethyleneglycol 1500). Sections were prepared with a sliding microtome. The thickness of the transverse, tangential and radial sections was 10–20 μm . The tangential sections were prepared from the non-collapsed phloem in the vicinity of the vascular cambium. After staining the tissue with Astra blue and Acridin red - Cryosidin, the sections were embedded in glycerine. Macerations were prepared with Jeffrey's solution (cf. Gerlach 1969).

The following bark anatomical characters were analysed: bark thickness; tissue arrangement; presence, type, and location of crystals; structure of the periderm; quantitative tissue proportions; length of the secondary phloem fibres; and length and diameter of the sieve tube members.

Tissue proportions were measured in a square area (length of a side = bark thickness) of the transverse section. The quantity of sieve tubes and the entire phloem parenchyma was determined in combination as conduction and storage tissue, because in transverse sections it was difficult to distinguish between sieve tubes and axial phloem parenchyma cells and between axial phloem parenchyma and phloem rays in the dilatation tissue. Bark fibres and sclereids were analysed separately and in combination as sclerenchymatic tissue. The area of the periderm was determined, including sequent periderms of a rhytidome if present.

The length of secondary phloem fibres was determined in macerates of a 500 μm wide part of the bark adjacent to the vascular cambium. The length was calculated from 100 measurements per macerate. In order to avoid any influence of the sieve tube collapse and changes of cell dimensions during tissue dilatation, the length and the diameter of the sieve tube members were determined in the non-collapsed phloem. The values were calculated from 50 measurements per sample. All measurements were made with a semi-automatic image analyser. The data were processed by commercial computer programs. The bark anatomical terminology follows Trockenbrodt (1990).

Results and discussion

Bark thickness

The bark thickness of the taproot decreased from 14.1 mm at ground level to 3.6 mm at 70 cm depth. The bark thickness of the lateral root A1 varied between 0.6 and 2.1 mm, that of A2 between 0.6 and 0.9 mm. It decreased gradually with increasing distance from the taproot. The lateral roots B1 and B2 showed slightly thicker barks (1.8–3.3 mm) than those of A1 and A2.

Root bark is generally thought of as being less thick than stem bark of the same age. However, only Eremin and Maksimov (1973) and Eremin and Sivak (1977) report

corresponding measurements in some conifer barks. In oak, the exact age of the bark samples could not be determined because often distinct growth rings were not found in the xylem or phloem of the roots.

Tissue arrangement

The general structure of the taproot bark at ground level and at 20, 30 or 40 cm depth was overall similar to that of mature, thick stem bark. However, some differences were evident (Fig. 1). In oak broad phloem rays develop when cambial initials between several uniseriate rays are eliminated. Due to a high number of these fusing rays, the course of the cambial zone was irregular in root bark. Fused rays protruded deeply into the xylem. The zone of cell differentiation was widened. The tangential bands of secondary phloem fibres were widely spaced. Growth increments were hardly visible. The sieve tubes started to collapse at a relatively long distance from the cambium. Sclerification of the tissue was more distinct than in stem bark. Numerous large, round or oval sclereid groups were formed in the secondary phloem. Form and shape of the sclereids were similar to those in stem bark. In the area of the fusing rays, sclereid groups were often wedge-shaped. Some of these sclereids were elongated radially. The rhytidome was distinct, but diminished in width with increasing distance from ground level. Primary bark elements were missing. Most of the uniseriate phloem rays did not show any dilatation. Dilatation was mainly restricted to axial phloem parenchyma cells.

The structure of bark samples taken at a distance of 50 and 70 cm from ground level exhibited some differences from those taken at a distance of 20, 30 and 40 cm (Fig. 2). In spite of being fairly thick, the bark samples contained only a few sclereids. These sclereids were often relatively thin-walled and isodiametric. Although no rhytidome was formed, primary bark elements were not observed. The sample from 50 cm depth still showed tangentially arranged groups of secondary phloem fibres. At 70 cm depth, the formation of secondary phloem fibres was reduced. Often, only a few small groups or even solitary fibres were




Fig. 1. *Quercus robur*; taproot bark – 20 cm distance from ground level; transverse section; scale bar = 1 mm; large arrows – sequent periderm, small arrows – secondary phloem fibres, asterisks – sclereids, rh – rhytidome

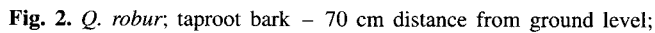


Fig. 2. *Q. robur*; taproot bark – 70 cm distance from ground level; transverse section; scale bar = 500 μm ; black arrows – secondary phloem fibres, white arrows – sclereids

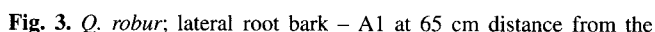


Fig. 3. *Q. robur*; lateral root bark – A1 at 65 cm distance from the taproot; transverse section; scale bar = 500 μm ; arrows – fused phloem rays with sclereids

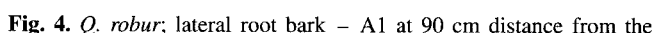


Fig. 4. *Q. robur*; lateral root bark – A1 at 90 cm distance from the taproot; transverse section; scale bar = 200 μm ; arrows – primary phloem fibres, asterisks – sclereids

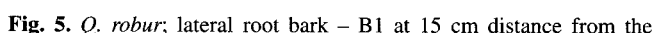
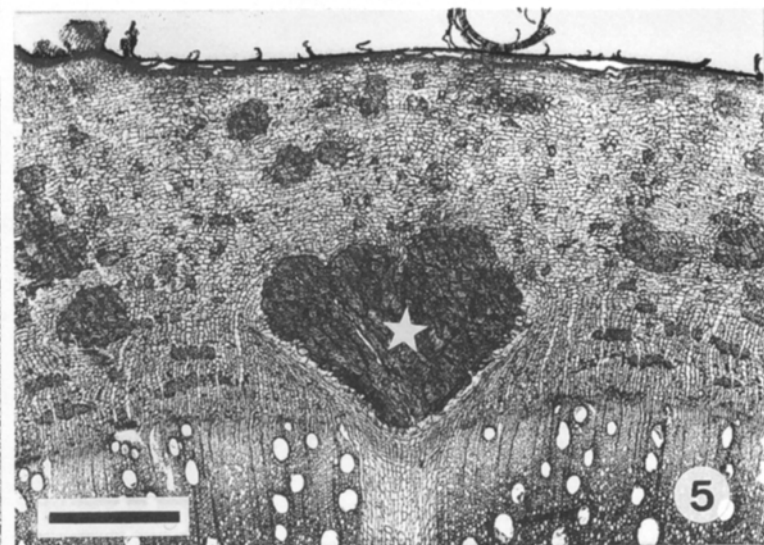
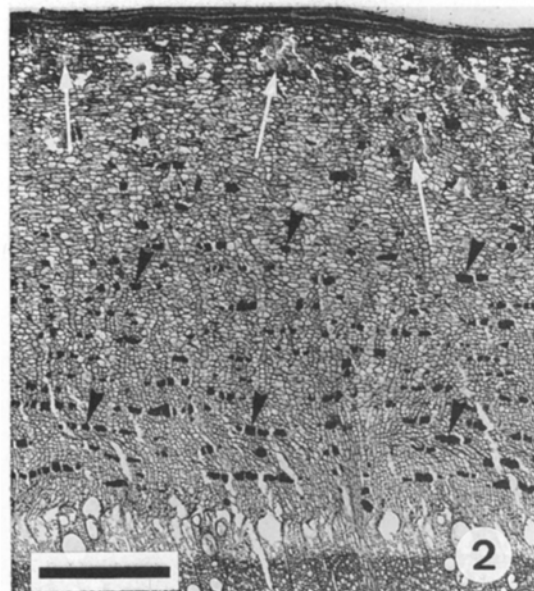
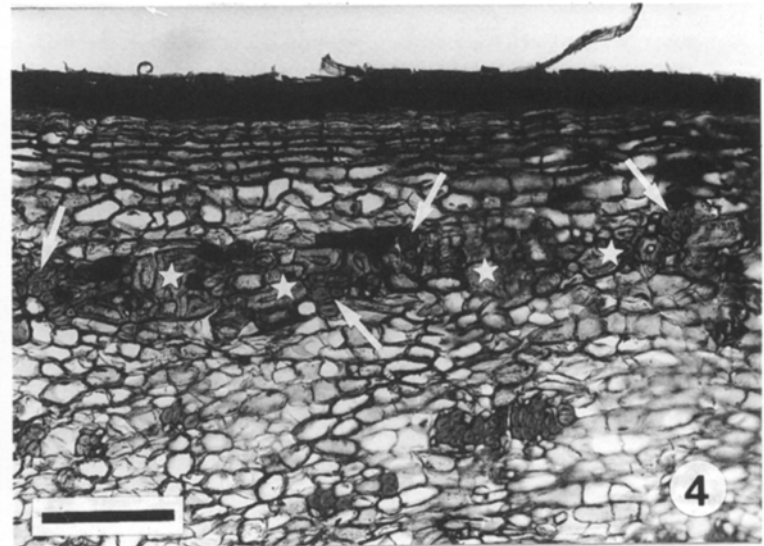
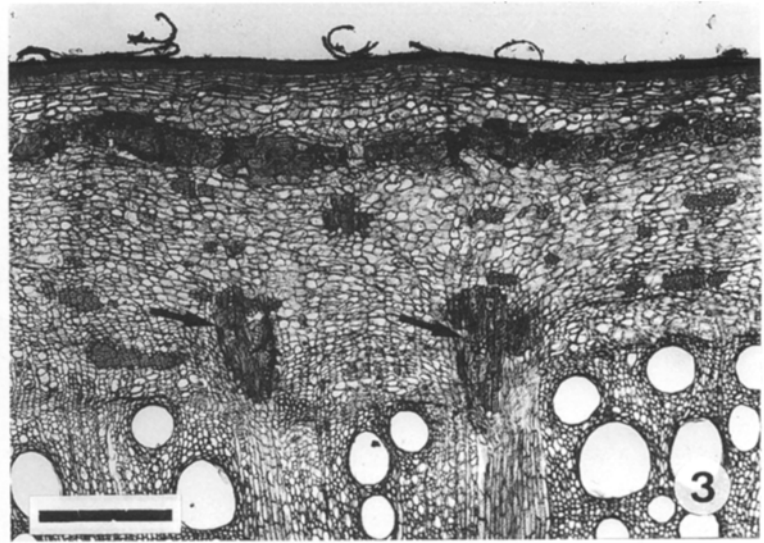
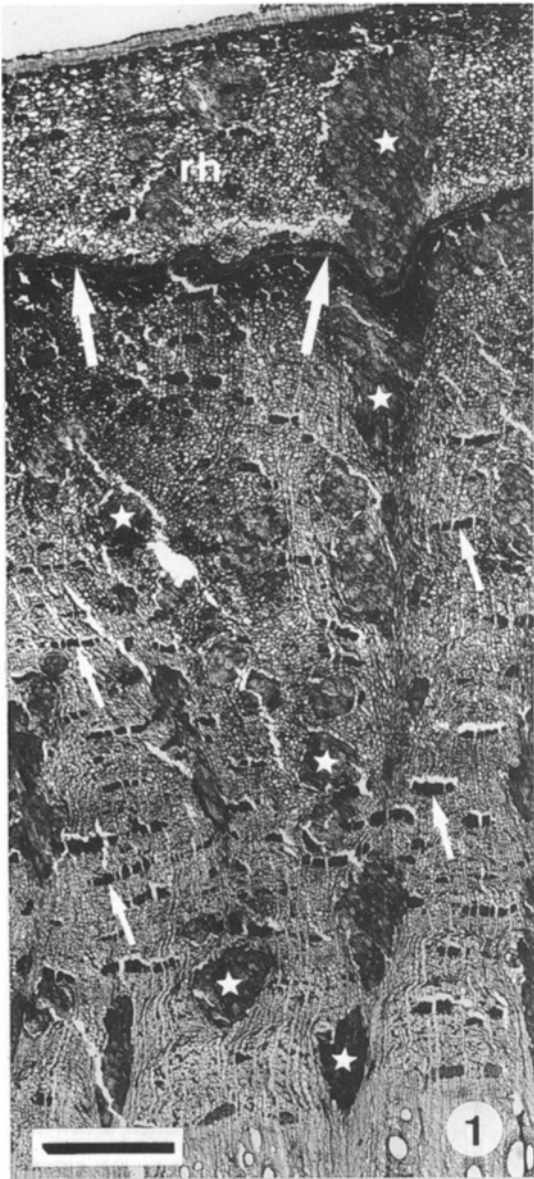


Fig. 5. *Q. robur*; lateral root bark – B1 at 15 cm distance from the taproot; transverse section; scale bar = 1 mm; asterisk – wedge-shaped sclereid group in the area of fused phloem rays



present. Due to a diffuse dilatation, the tissue arrangement was obscured. The number and distinctness of the fused rays had decreased.

Lateral root A1 also exhibited the general structure of oak bark. The bark thickness differed only slightly between all samples. Although the bark was relatively thin, broad fused phloem rays were present. The rays often protruded deeply into the xylem (Fig. 3). Often, sclereid groups were formed by these fused rays and the cells between fusing rays. Apart from these groups no sclereids were present in the secondary phloem. Primary phloem fibres were present. In contrast to those in stem bark they did not form compact groups. Rather they were solitary or formed relatively small, isolated groups (Fig. 4). As in stem bark, the primary phloem fibres were partly connected by narrow, tangentially arranged sclereid groups. However, this band of fibres and sclereids was discontinuous. Unlike that of stem bark, the cortex of the lateral root was not very wide.

Bark samples of lateral root A2 differed only slightly from each other. Compared to A1, the primary phloem fibres were less connected by sclereids. They were located in isolated, tangentially arranged small groups separated by wide gaps. In the secondary phloem only the sample nearest the taproot showed some sclereid groups similar to those in stem bark. Fused rays were missing.

Round and irregular-shaped groups of sclereids were present in the secondary phloem of the bark of lateral roots B1 and B2. Large, wedge-shaped sclereid groups were formed in the area of the distinctly fused rays (Fig. 5). Elements of primary origin, i.e. primary phloem fibres, connecting sclereids and cortex were missing.

Up to now the variability of root bark structure with age or distance from the stem/taproot has not been analysed. According to the present study, there is a decreasing amount of sclereids with increasing distance from the stem, i.e. an increase of sclereids with increasing root bark age. In all roots the regular arrangement of bark tissue and the visibility of growth increments in bark diminish with increasing distance from the stem. Often, growth ring boundaries in secondary phloem are visible because sieve tubes of the late phloem are smaller than those of the early phloem. Sometimes the sieve tubes collapse after 1 year, thus delimiting the recent growth increment. In root bark, however, the differences in sieve tube size between early and late phloem diminish with increasing distance from the stem, and the sieve tube collapse is delayed. The phenomenon of diminishing growth rings in roots is well known for xylem (e.g. Kny 1908; Liese 1926; Riedel 1937). Exposed roots develop stem-like xylem, i.e. distinct growth rings (e.g. Wieler 1891; Kny 1908). Exogenous factors (light, temperature) as well as hormonal modifications along the stem axis (cf. Aloni 1987) seem to be responsible for the formation of these structures.

Only a few authors have recorded structural differences between root and stem bark. Fewer sclereids in root bark were observed by Casparis (1918) for some Simaroubaceae, by MacDaniels (1918) for *Populus deltoides*, by Blunden et al. (1974) for four species of *Goniothalamus*, and by Datta and Datta (1976) for two species of *Plumeria*.

In lateral roots of oak fewer secondary phloem fibres and/or narrow phloem fibre bands were observed. Esau

(1969) also reported fewer phloem fibres in roots. A decrease in the quantity of primary phloem fibres from stem to roots was also described for some other plants (e.g. Aloni and Gad 1982) and explained by a decreasing hormonal stimulus in basipetal direction (cf. Aloni 1987).

In root bark samples in which elements of primary origin are no longer present, the phloem rays run through the tissue up to the periderm. In these samples no rhytidome was formed. This specific condition is caused by the manner of formation of the first-formed periderm. In stem bark, the first-formed periderm originates from a subepidermal cell layer (Douliot 1889; Esau 1969). Generally, in root bark the first-formed periderm originates from deeper cell layers, mostly at the boundary between the cortex and the secondary phloem (Douliot 1889; Haberlandt 1918; Esau 1977). In the present study, some root bark samples showed elements of primary origin and/or a narrow cortex. This indicates that the origin of the first-formed periderm may vary between subepidermal cell layers and deeper cell layers.

The brief description of young oak root bark made by Cutler et al. (1987) in their "Root identification manual of trees and shrubs" corresponds to the observations of young root bark in the present study.

Crystals

Solitary calcium oxalate crystals were present in thick-walled, lignified cells of parenchyma strands. The length of these strands was similar to that of the secondary phloem fibres. The strands correspond to the "chambered crystaliferous fibres" ("Kristallkammerfasern") of the old literature. However, the strands are of parenchymatic origin (Esau 1969). In root bark of oak they were located at the inner and outer border of the groups of secondary phloem fibres. Additionally, some sclereids contained similar crystals. Crystal quantity varied between the samples. Druses were located in phloem parenchyma cells. Close to the vascular cambium these cells were thin-walled and chambered. There were no differences between stem bark and root bark with regard to presence and arrangement of solitary crystals (Fig. 6). Druses were frequently present in the taproot, above the lateral roots B and in A1. Here, the quantity of crystals decreased with increasing distance from the stem. Beneath the lateral roots B and in A2, however, druses were scarce.

The presence of crystals in young root bark of oak described by Cutler et al. (1987) corresponds to the observations made for young bark in the present study. Further observations on root bark crystals are lacking.

Periderm

The taproot samples taken close to ground level exhibited a distinct rhytidome. No rhytidome was formed at a distance of 50 cm and 70 cm from the ground level. Here, the phellem cells of the first-formed periderm appeared to be slightly larger than those in the stem bark. Generally, the

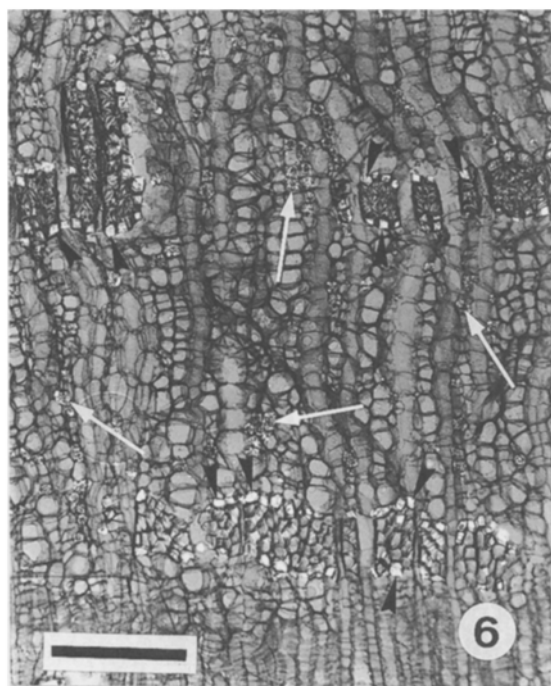


Fig. 6. *Q. robur*; lateral root bark – A1 at 25 cm distance from the taproot; transverse section; polarisation microscopy; scale bar = 200 μm ; arrowheads – solitary crystals in the cell strands adjacent to the secondary phloem fibres, arrows – druses in axial phloem parenchyma cells

samples showed fewer rows of phellem cells than stem bark.

No rhytidome was formed in the lateral roots. The lateral roots, too, showed a narrow phellem with relatively large cells (Fig. 7). The cell wall thickness was similar in all root phellem cells. Thus, in contrast to stem bark, root bark phellem did not show any growth increments.

In root bark, the phelloderm appeared to be more distinct than in stem bark. The root bark samples did not differ. Root bark periderm has otherwise not been described.

Quantitative tissue proportions

The variability of tissue proportions within the taproot bark and the lateral root bark is illustrated in Figs. 8–10. Lateral root A1 showed a distinct eccentricity. Therefore, the tissue proportions were separately analysed for the upper and the lower side of the root. Both sides showed a similar development, although the absolute values differed. Figures 8–10 indicate that a quantitative analysis of tissue proportions, as performed here, is not suitable for an exact description of bark structure in roots. Only a few trends were observed. In the taproot, the quantity of sclereids distinctly increased with increasing bark thickness, i.e. many sclereids were formed in the taproot bark above the lateral roots B1 and B2. Beneath these lateral roots, relatively few sclereids were present in taproot bark. In lateral roots A1 and A2, the proportion of sclereids decreased with increasing distance from the taproot (decreasing bark thickness) and increased again in the

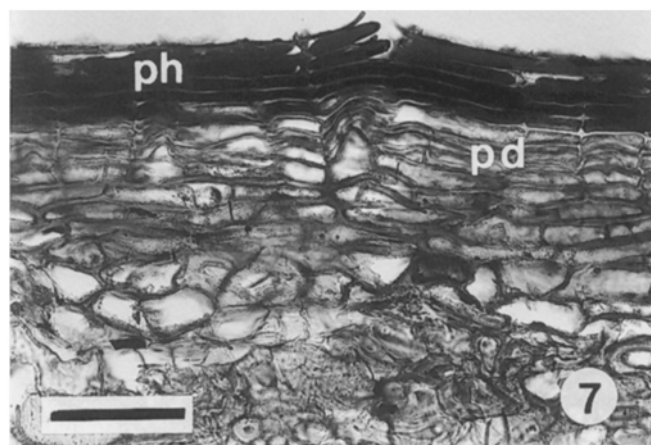


Fig. 7. *Q. robur*; lateral root bark – A1 at 40 cm distance from the taproot; transverse section; scale bar = 100 μm ; first-formed periderm, ph – phellem, pd – phelloderm

most distant sample. This increase is caused by the presence of sclereids connecting the primary phloem fibres. Thus, it is possible to state a general increase of sclereids in the secondary phloem with increasing bark thickness or bark age as it is known from stem bark (Trockenbrodt 1994). Compared to stem bark, slightly less sclerenchymatic tissue was observed in the bark of lateral roots. Similar observations were made by MacDaniels (1918) for *Populus deltoides* and *Ulmus americana*. According to Casparis (1918), the relatively small amount of sclereids in root bark is caused by the higher pressure of the soil. A decrease of sclerenchymatic tissue in root bark corresponds to the well-known decrease of supporting tissue in the xylem of roots (e.g. Wieler 1891; Riedel 1937). An interpretation of structural differences between stem bark and root bark, which are based on physiological or mechanical necessities, has to be considered speculative as long as our knowledge about the functional anatomy of bark tissue remains so meagre.

Length of secondary phloem fibres

In the taproot, the length of the secondary phloem fibres varied between 490 and 1370 μm (average: 890 μm). There was a distinct decrease of fibre length from the ground level to a depth of 30 cm. Between 30 and 50 cm depth there was a distinct increase, followed by a slight decrease at 70 cm depth. No regular trend was observed.

In A1, fibre length varied slightly between the upper and the lower side of the root with no regular trend. Considering the average values from upper and lower sides, there was a decrease of fibre length from approximately 980 μm to 880 μm with increasing distance from the taproot (Fig. 11). The average length of all taproot samples was 950 μm . In A2, the phloem fibre length varied with no regular trend. The average was 870 μm . The average phloem fibre lengths of B1 and B2 were 890 μm and 870 μm .

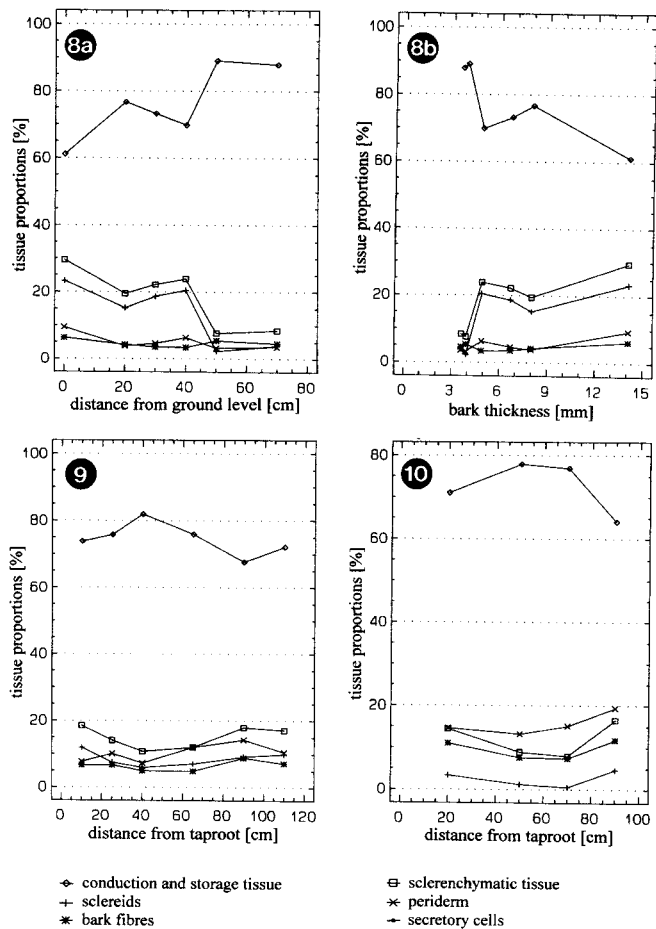


Fig. 8a,b. *Q. robur*; taproot bark; tissue proportions in relation to the distance from the stem (a) and in relation to bark thickness (b)

Fig. 9. *Q. robur*; lateral root bark (A1); tissue proportions in relation to the distance from the taproot (average from upper and lower side of the root)

Fig. 10. *Q. robur*; lateral root bark (A2); tissue proportions in relation to the distance from the taproot

The length of phloem fibres in roots had not been investigated earlier. The decrease of phloem fibre length with increasing distance from the taproot in lateral root A1 corresponds to the well known increase of the length of cambial initials with age of the stem. According to some authors (e.g. Vurdu and Bensend 1979; Rusch 1973), wood fibres of some trees are longer in roots than in the stem. However, the phloem fibres in lateral root bark of oak are always shorter than in stem bark (910 μm).

Length and diameter of sieve tube members

In the present study, the sieve tube member lengths showed no regular trend. Within the taproot and the lateral roots the length varied between 300 and 540 μm . In the taproot, the tangential diameter of the sieve tubes varied between 25 and 30 μm ; there was no regular trend. In A1, there was a slight increase in diameter from 32 to 37 μm with increas-

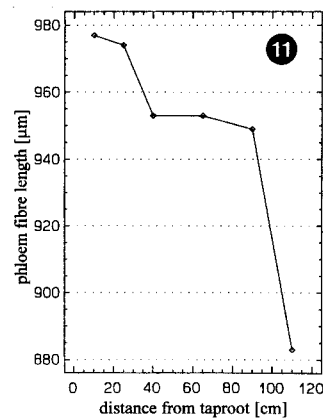


Fig. 11. *Q. robur*; lateral root bark (A1); length of secondary phloem fibres in relation to the distance from the taproot

ing distance from the taproot. In A2, B1, and B2, the sieve tube diameters were constant (A2: 25 μm ; B1: 32 μm ; B2: 34 μm).

The length of sieve tube members is influenced by the length of the cambial initials and, in some cases, by anticlinal divisions of the phloem mother cells (secondary partitioning) and/or by intrusive growth of sieve tube members (Esau and Cheadle 1955; Cheadle and Esau 1958). The increase of the length of cambial initials with age in the stem results in a corresponding increase of sieve tube member length. A decrease of sieve tube member length by anticlinal divisions was rarely observed in *Quercus* (Esau and Cheadle 1955). There was no evidence for such divisions in the present study. Sieve tube member length showed no regular trend in the roots investigated. Similar studies from other authors do not exist. Sieve tube members in both stem and root bark showed a similar length. The average length (490 μm) corresponds to stem values reported by Huber (1939), Chang (1954), and Trockenbrodt (1994).

Sieve tube diameter in root bark varied considerably. It did not show any regular trend. The average diameter in root and stem bark was 25–35 μm .

Identification of oak root bark

Only a few studies include information on the diagnostic value of root bark. According to von Alten (1908), the presence of sclereids and secretory cells in the cortex as well as the presence, shape, and arrangement of sclereids, secretory cells, and crystals in the secondary phloem are important for identifying root barks. Gasson (1979) uses the shape and arrangement of sclerenchymatic cells of barks to identify roots of different genera of the Caprifoliaceae. The “Root identification manual of trees and shrubs” by Cutler et al. (1987) is useful for the identification of relatively young bark. The present study of root and stem bark of oak reveals that most of the diagnostic qualitative bark anatomical characters of stem bark are also present in root bark. However, some differences are evident. In the root, sieve tube collapse is delayed, the growth increments diminish

with increasing distance from the stem, and the first-formed periderm often originates in deeper tissue zones, consequently elements of primary origin are often missing. With regard to quantitative bark anatomical characters, there are more differences between root and stem bark. Generally, the quantity of sclerenchymatic tissue (sclereids, fibres) is lower in root bark. Secondary phloem fibres are shorter in root bark and phellem cells are larger. Thus, the first impression of bark of different roots may be quite different. Nevertheless, the similarities and differences between oak root and stem bark observed in the present study reveal that the qualitative bark anatomical characters of oak are suitable for diagnostic purposes, if they are applied carefully.

Acknowledgements. I thank R.F. Evert and R. Aloni for critically reading and improving the manuscript.

References

- Aloni R (1987) Differentiation of vascular tissues. *Annu Rev Plant Physiol* 38: 179–204
- Aloni R, Gad AE (1982) Anatomy of the primary phloem fiber system in *Pisum sativum*. *Am J Bot* 69: 979–984
- Alten H von (1908) Beiträge zur vergleichenden Anatomie der Wurzeln, nebst Bemerkungen über Wurzelthyllen, Heterorhizie, Lenticellen. Dissertation, University of Göttingen
- Archer RH, Wyk AE van (1993) Bark structure and intergeneric relationships of some African Cassinoideae (Celastraceae). *IAWA J* 14: 35–53
- Blunden G, Aye Kyi, Jewers K (1974) The comparative stem and root anatomy of *Goniothalamus andersonii*, *G. macrophyllus*, *G. malayanus* and *G. velutinus* (Annonaceae) from the peat swamps of Sarawak. *Bot J Linn Soc* 68: 209–225
- Casparis P (1918) Beiträge zur Anatomie der Simarubaceenrinden. Dissertation, University of Basel
- Chang YP (1954) Anatomy of common North American pulpwood barks. TAPPI Monographs Series No 14
- Cheadle VI, Esau K (1958) Secondary phloem of Calycanthaceae. *Univ Calif Publ Bot* 29: 60–67
- Cutler DF, Rudall PJ, Gasson PE, Gale RMO (1987) Root identification manual of trees and shrubs. Chapman and Hall, London
- Datta SK, Datta PC (1976) Bark drugs of *Plumeria*. *Q J Crude Drug Res* 14: 129–142
- Douliot H (1889) Recherches sur le péricarde. *Ann Sci Nat Bot* 10: 325–395
- Eremin VM, Maksimov VM (1973) Differences in the anatomical structure of root bark and stem bark of Scots Pine (in Russian). *Lesnoi Zhurnal (Voronezh)* 16: 5–9
- Eremin VM, Sivak SV (1977) Differences of root bark and stem bark in some conifers (in Russian). *Lesnoi Zhurnal (Voronezh)* 20: 5–9
- Esau K (1969) The phloem. *Handbuch der Pflanzenanatomie*, vol 5/2. Gebrüder Borntraeger, Berlin
- Esau K (1977) Anatomy of seed plants. 2nd edn. Wiley, New York
- Esau K, Cheadle VI (1955) Significance of cell divisions in differentiating secondary phloem. *Acta Bot Neerl* 4: 346–357
- Gasson PE (1979) The identification of eight woody genera of the Caprifoliaceae by selected features of their root anatomy. *Bot J Linn Soc* 78: 267–284
- Gerlach D (1969) Botanische Mikrotechnik. Thieme, Stuttgart
- Haberlandt G (1918) Physiologische Pflanzenanatomie. 5th edn. W Engelmann, Leipzig
- Holdheide W (1951) Anatomie mitteleuropäischer Gehölzrinden. In: Freund H (ed) *Handbuch der Mikroskopie in der Technik*, vol V/1. Umschau, Frankfurt/Main, pp 193–367
- Huber B (1939) Das Siebröhrensystem unserer Bäume und seine jahreszeitlichen Veränderungen. *Jahrb Wiss Bot* 88: 176–242
- Kny L (1908) Ueber das Dickenwachstum des Holzkörpers der Wurzeln in seiner Beziehung zur Lotlinie. *Ber Dtsch Bot Ges* 26: 19–50
- Liese J (1926) Beiträge zur Kenntnis des Wurzelsystems der Kiefer (*Pinus sylvestris*). Habilitationsschrift Forstliche Hochschule Eberswalde. Springer, Berlin Heidelberg New York
- MacDaniels LH (1918) The histology of the phloem in certain woody angiosperms. *Am J Bot* 5: 347–378
- Parameswaran N, Liese W (1968) Beitrag zur Rindenanatomie der Gattung Entandophragma. *Flora (Jena) Abt B* 158: 22–40
- Riedel H (1937) Bau und Leistungen des Wurzelholzes. Dissertation Technische Hochschule Dresden. Gebrüder Borntraeger, Leipzig
- Rusch J (1973) Vergleichende anatomische Untersuchungen des Holzes von Wurzel und Stamm bei verschiedenen Laubbaumarten. Dissertation, University of Freiburg
- Trockenbrodt M (1990) Survey and discussion of the terminology used in bark anatomy. *IAWA Bull ns* 11: 141–166
- Trockenbrodt M (1991) Qualitative structural changes during bark development in *Quercus robur*, *Ulmus glabra*, *Populus tremula* and *Betula pendula*. *IAWA Bull ns* 12: 5–22
- Trockenbrodt M (1994) Quantitative changes of some anatomical characters during bark development in *Quercus robur*, *Ulmus glabra*, *Populus tremula* and *Betula pendula*. *IAWA J* 15: 387–398
- Trockenbrodt M (1995) Calcium oxalate crystals in the bark of *Quercus robur*, *Ulmus glabra*, *Populus tremula* and *Betula pendula*. *Ann Bot* 73 (in press)
- Vurdu H, Bensed DW (1979) Specific gravity and fiber length in European Black Alder roots, branches, and stems. *Wood Sci* 12: 103–105
- Wieler A (1891) Ueber die Beziehung zwischen Wurzel- und Stammholz. *Tharandter Forstl Jahrb* 41: 143–171
- Wyk AE van (1985) The genus *Eugenia* (Myrtaceae) in southern Africa: structure and taxonomic value of the bark. *S Afr J Bot* 51: 157–180