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QUALITATIVE STRUCTURAL CHANGES DURING BARK DEVELOPMENT IN QUERCUS ROBUR, ULMUS GLABRA, POPULUS TREMULA AND BETULA PENDULA*

by

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Summary

The development of bark structure of *Quercus robur* L., *Ulmus glabra* Huds., *Populus tremula* L. and *Betula pendula* Roth is being described. Profound structural changes can be observed during the first years after secondary growth has started. In all four species the epidermis is replaced by a periderm, the cortex shows intensive dilatation growth, and the groups of primary bark fibres are pushed apart. The collapse of sieve tube members starts with the second year. With proceeding secondary growth, the specific formation of sclerenchymatic tissue, especially sclereids, and the dilatation growth are processes which strongly affect the bark structure of *Quercus robur*, *Populus tremula* and *Betula pendula*. In addition, wide, fused phloem rays develop in *Quercus robur*. The structure of *Ulmus glabra* bark is affected by the formation of phloem fibre-/sclereid-like cells and mucilage cells and by dilatation growth. The histological pattern of *Ulmus glabra* bark stabilises to a great extent after the first few years, the other barks investigated show further developmental processes over many years. In all species the formation of a rhytidome is the last distinct modification of bark structure.

Key words: Quercus robur L., *Ulmus glabra* Huds., *Populus tremula* L., *Betula pendula* Roth, bark anatomy, bark development.

Introduction

In spite of its wealth of features and peculiarities bark anatomy is seldom used for plant taxonomical considerations (e.g. Zahur 1959; Richter 1981; van Wyk 1985; Trockenbrodt & Parameswaran 1986). Obtaining bark samples authenticated by herbarium vouchers is laborious if not impossible because barks rarely are a part of botanical collections. Moreover, bark tissue often is an extremely heterogeneous material, and commonly applied techniques for sample preparation are inadequate. However, the main reason for today's limited use of bark anatomy for taxonomical work is a lack of knowledge about the structure of bark and its development. Contrary to wood, bark structure changes continuously with age. Information about the variability of bark structure, especially within one individual during its growth, is essential for an estimation of the diagnostic value of bark anatomical features. Up to now only a few investigations have dealt with the developmental anatomy of bark. Some of these are on pharmacognostic aspects of certain barks (Speyer 1907; Birnstiel 1922; Hasler 1936), and some information can be found in more general literature on the anatomy of bark (e.g. Hanstein 1853; Möller 1882; Thorenaar 1926; Chang 1954; Reinders & Reinders-Gouwentak 1961; Esau 1969). The variability of certain bark features within one individual tree was analysed by Raskatov and Kosichenko (1968), Kosichenko (1969),

* Dedicated to Prof. Dr. Walter Liese on the occasion of his 65th birthday.

Nicholls & Phillips (1970), Liese and Parameswaran (1972), Parameswaran and Liese (1974), Ghouse and Siddiqui (1976a, b), Ghouse and Yunus (1976), Ghouse and Hashmi (1977), Ghouse and Iqbal (1977, 1981), Yunus *et al.* (1977), Aday (1978), Ezell and Stewart (1978), Ghouse *et al.* (1982), Iqbal and Ghouse (1983) and Röckle (1986). Most of these papers are restricted to short descriptions of cell length variability.

The intention of this paper is to contribute to the broadening of our knowledge about structural changes of bark tissue during its development. First, qualitative changes of the basic bark structure are described. Quantitative changes and the diagnostic value of single bark anatomical features will be discussed in subsequent papers.

Material and Methods

Tree species suitable for the investigation had to fulfill certain requirements:

- sufficient preservation of bark with age, i.e. no early formation of rhytidome combined with the loss of bark tissue;
- typical representatives of different structural wood and bark types;
- sufficiently complex structure, i.e. a high number of possibly varying features.

Accordingly, the ring-porous hardwood species *Quercus robur* L. and *Ulmus glabra* Huds. as well as the diffuse-porous hardwood species *Populus tremula* L. and *Betula pendula* Roth were chosen. Initially, five individuals of *Quercus robur* were analysed. The investigation revealed no tree-to-tree differences in their basic bark structure and development. One individual of *Ulmus glabra* and *Populus tremula* and two of *Betula pendula* were examined. For details about the age and height of the selected trees see Table 1.

A sample selection following biological and mathematical rules (cf. Kučera & Bariska 1982) is not practicable for working on bark, because all structural information is stored in a very small area, and tertiary tissue changes impede the removal of exactly defined samples. Thus, the samples were taken at regular distances along the stem, regular age intervals (determined from xylem growth rings), regular stem diameter intervals, and according to the intactness of the tissue. *Quercus robur* bark was sampled at 5–9 height levels which correspond to a bark age of 1–33 years, bark thickness of 0.2–9.5 mm and stem diameter of 0.4–16.5 cm. *Ulmus glabra* bark samples were taken from 12 height levels representing bark age of 1–24 years, bark thickness of 0.7–10.7 mm and stem diameter of 0.4–25.0 cm. *Populus tremula* bark samples derived from 9 height levels which correspond to a bark age of 1–11 years, bark thickness of 0.6–4.7 mm and stem diameter of 1.0–14.0 cm. *Betula pendula* bark was sampled at 12–13 height levels with a corresponding age of 1–16 years, bark thickness of 0.4–12.0 mm and stem diameter of 0.3–24.0 cm. Sections from all levels were prepared and analysed with a light microscope and a semi-automatic image analyser.

Table 1. Age and height of the investigated trees.

		Age (years)	Height (m)
Oak	I	37	14.5
Oak	II	30	11.8
Oak	III	14	6.8
Oak	IV	14	4.8
Oak	V	15	2.1
Elm	I	24	16.0
Poplar	I	12	14.5
Birch	I	10	5.0
Birch	II	16	10.0

The samples included bark, cambial zone, and mostly a narrow zone of adhering xylem. They were fixed in formalin-acetic acid-alcohol, penetrated with polyethylene glycol 1500, and sectioned on a sliding microtome, often with the help of adhesive tape. The sections were double-stained with astra blue and acridine red-crysoidin. Additional samples were embedded in glycol-methacrylate (cf. Ruetze & Schmitt 1986). Macerations were prepared with Jeffrey's solution (cf. Gerlach 1969).

The terminology follows Trockenbrodt (1990).

Results

Quercus robur L.

All five oak trees analysed reveal a similar development of bark structure. Differences are more of a quantitative nature than deviations from a basic pattern. Therefore the bark development of oaks I–V is described together.

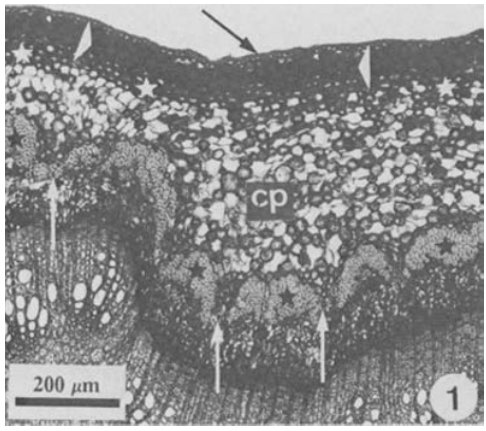
The youngest samples represent the shoot shortly after secondary growth has started (Fig. 1). The course of the vascular cambium is still irregular. Groups of primary bark fibres are arranged parallel to the vascular cambium. The individual groups are linked by slightly enlarged sclereids. Inside the primary bark fibre groups, primary phloem elements are located followed by the first secondary phloem elements. The phloem rays are exclusively uniseriate. The cortex outside the band of primary bark fibres consists of an inner zone of isodiametric cortex parenchyma cells, slightly enlarged due to dilatation growth, and a narrow outer zone of small cortex collenchyma cells. The outermost layer of the shoot is the intact epidermis. Immediately beneath the epidermis the formation of the periderm has started.

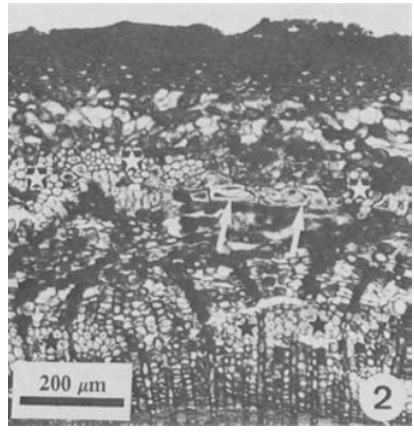
Caused by the progressing secondary growth, bark structure already changes within the first year (Fig. 2). The epidermis is ruptured, and remnants adhere to the intensively developing periderm. The cortex collenchyma primarily expands through anticlinal cell division. The parenchyma cells of the cortex undergo intensive dilatation growth. They are partly enlarged and stretched tangentially or divided anticlinally. The groups of primary bark fibres are pushed apart and most of the gaps are filled with developing sclereids. These are enlarged only slightly. Their shape varies. They often stretch tangentially, rarely radially, or they are isodiametric. The primary phloem is collapsed or it dilates. First groups of secondary phloem fibres show thick-walled, lignified, chambered, crystal containing cells of approximately equal length at their inner and outer sides. In the secondary phloem a few isodiametric sclereids are formed. The course of the vascular cambium is still irregular.

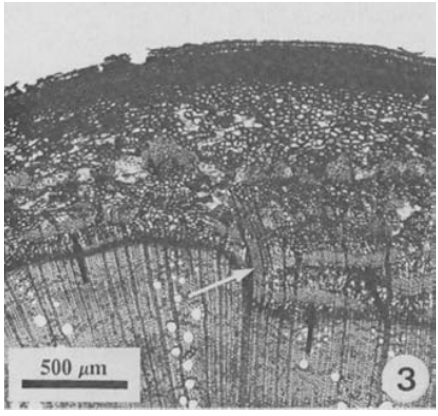
With secondary growth proceeding (Fig. 3) additional tangential bands of secondary phloem fibre groups of up to 8 cells in depth have developed. They also are accompanied by chambered crystalliferous cells. Uniseriate phloem rays traverse the fibre groups. The first broad phloem rays develop when the cambial initials between 3–5 uniseriate rays are eliminated. This fusion is strongest where the cambium bends distinctly. Some fibre groups with a radial width of 15–20 cells can be found close to the broad rays. The rays are subject to slight dilatation, i.e. the cells enlarge slightly and round off, but they do not divide.

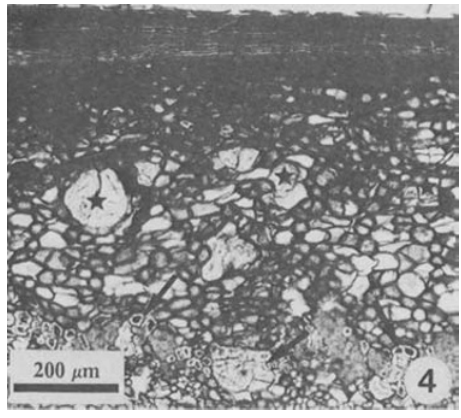
The cortex sclereids of older bark develop solitarily or in spherical groups (Fig. 4). The sclereid groups between the groups of primary bark fibres enlarge. The formation of sclereids in the secondary phloem increases, especially between adjacent phloem fibre groups. The transformation of phloem parenchyma cells into sclereids is often initiated by one cell, and it proceeds centrifugally (Figs. 5 & 6). In transverse sections the sclereid groups often appear spherical or stretched tangentially (Fig. 6), in radial sections also spherical but stretched axially. Solitary sclereids are common, too. The sclereids' forms and dimensions vary a lot. As a rule, sclereids in the secondary phloem are larger than the ones in the cortex and in the band of primary bark fibres and sclereids.

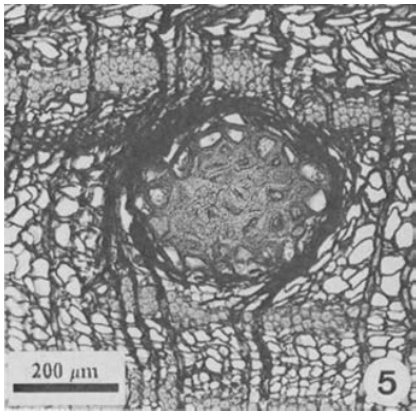
After several years, bark shows growth ring patterns (Fig. 6). At the beginning of the growth period only non-lignified cells, predominantly sieve tube members are formed, followed by tangential secondary phloem fibre bands (groups) of different tangential length (0.1–several mm). Subsequently a zone of non-lignified cells is formed, sometimes followed by a second band of secondary phloem fibres. At the end of the growth period a narrow layer (1–3 cells) of axial phloem parenchyma cells is formed. However, this sequence is not obligatory, it might be incomplete. It also can be disturbed by a collapse of sieve tube members, sclerification, and beginning dilatation growth. The zigzag course of the vascular cambium is restricted to the area of fused rays. The fu-

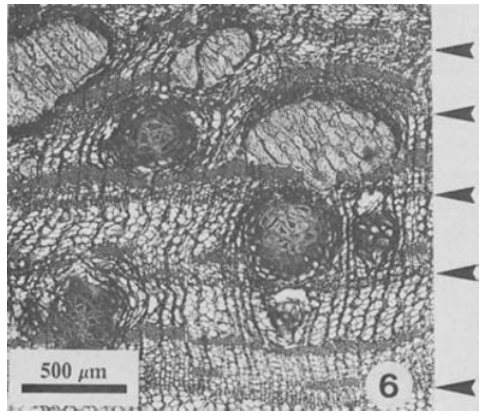












sion of phloem rays proceeds (15–25 cells), they often protrude into the xylem (Fig. 7). Within the outer secondary phloem the uniseriate phloem rays become indistinguishable from the surrounding tissue due to the dilatation of both the rays and the surrounding tissue.

With increasing secondary growth the distance between groups of primary bark fibres strongly increases and often they are difficult to localise. The band of primary bark fibres and sclereids now mainly comprises sclereid groups of irregular width, and it is often interrupted by gaps. Dilatation growth and sclerification increase resulting in an irregular, less organised outer secondary phloem and cortex. The groups of sclereids partly fuse longitudinally.

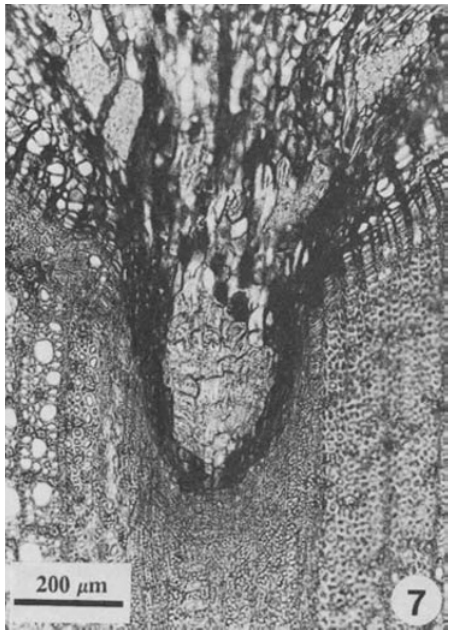
During the formation of a rhytidome parts of the first formed periderm, cortex, and phloem are isolated from the tissue by sequent periderms (Fig. 8). If these parts adhere to the last formed periderm, even primary elements of the bark may remain in the outer rhytidome (Fig. 8). More often, the isolated parts are shed, leaving a bark which exclusively consists of living secondary phloem and the last formed periderm. Therefore it contains a few sclereids, and it appears well organised because the tissue modified by sclerification and dilatation growth is partly shed.

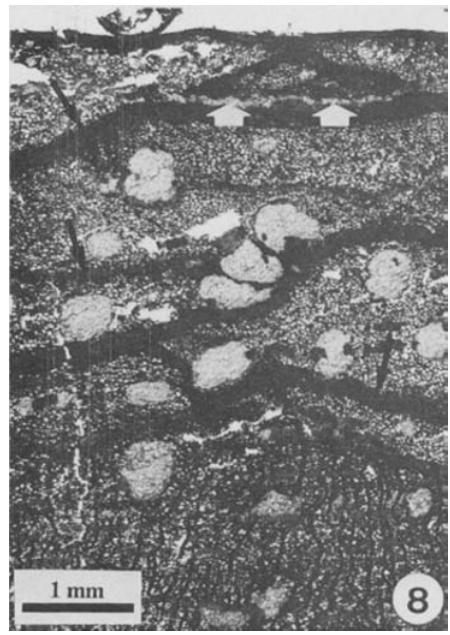
Ulmus glabra Huds.

The youngest sample (Fig. 9) shows an almost circular course of the vascular cambium. Outwards up to three tangential layers of axial phloem parenchyma strands are formed, each of them 1–3 cells wide. The cells contain organic material. The layers alternate with two layers of sieve tube members, companion cells and crystal containing phloem parenchyma cells. A distinct pattern in the radial sequence of these layers has not developed yet. The layers of predominantly sieve tube members are up to 8 cells deep; 1–3 seriate phloem rays run through the secondary phloem. Outside the outermost tangential phloem parenchyma layer, elements of the primary phloem can be found (Fig. 10), some are partly or totally collapsed. Groups of primary bark fibres are located outside the primary phloem. These groups are separated but appear as a continuous tangential band. The cortex consists of a zone of round, slightly enlarged cortex parenchyma cells with many intercellular spaces and scattered secretory cells (mucilage cells) and a narrow zone of cortex collenchyma cells. Immediately beneath the epidermis the periderm is formed.

With proceeding secondary growth a stratification of the secondary phloem becomes more evident (Fig. 11). The epidermis is ruptured within the first year, the periderm becomes a noticeable part of the bark. The cortex collenchyma cells expand vigorously and divide anticlinally. The cortex parenchyma cells enlarge, stretch tangentially and divide anticlinally; intercellular spaces develop. Due to dilatation growth, the groups of primary bark fibres are pushed apart. The primary phloem elements and the outermost sieve

Figs. 1–6. *Quercus robur* L. Transverse section. – 1: Bark in the first year of development shortly after secondary growth had started (black asterisks = primary bark fibre groups, white asterisks = cortex collenchyma, black arrow = epidermis, white arrows = sclereids, white arrowheads = periderm, cp = cortex parenchyma). – 2: Bark in the first year of development after proceeding secondary growth (black asterisks = secondary phloem fibre groups, white asterisks = primary bark fibre groups, white arrows = sclereids). – 3: Few years old bark (black arrows = secondary phloem fibre groups, white arrow = wider secondary phloem fibre group in the proximity of fused uniseriate phloem rays). - 4: Several years old bark (asterisks = sclereids in the cortex, arrows = sclereids between primary bark fibre groups). – 5: Centrifugally oriented differentiation of a sclereid group. – 6: Bark with distinct growth rings (arrowheads) and sclereid groups in the secondary phloem (partly in the stage of differentiation).





Figs. 7 & 8. *Quercus robur* L. Transverse section. – 7: Multiseriate phloem ray protruding into the xylem. – 8: Old bark with distinct rhytidome (black arrows = sequent periderms, white arrows = remnants of the ring formed by primary bark fibres and sclereids).

tube members of the secondary phloem are collapsed. An entirely different type of cells is formed resembling phloem fibres in shape (Figs. 12 & 13) and sclereids because they develop from axial phloem parenchyma strands (Figs. 13 & 14). A classification as either sclereids or phloem fibres appears to be impossible (cf. Trockenbrodt 1990). Close to the vascular cambium, the two newly formed tissue zones consist mainly of sieve tube members. They do not contain any of the cells mentioned before. Secretory cells are only located in the cortex. Due to the straight course of the phloem rays and the stratification of the secondary phloem, the bark presents a regular geometrical pattern (Fig. 11).

Each following year 3 or 4 tissue zones are formed consisting mainly of sieve tube members. They are separated by tangential

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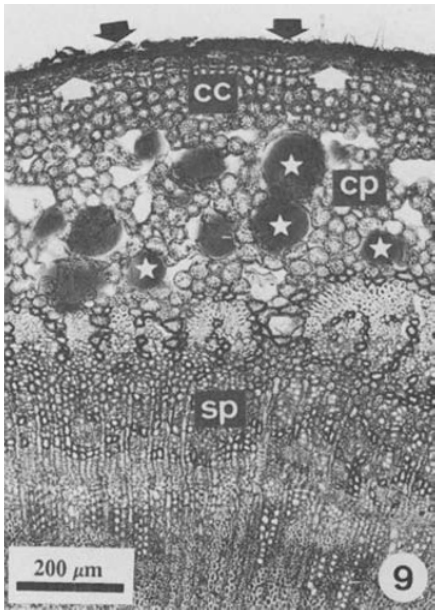
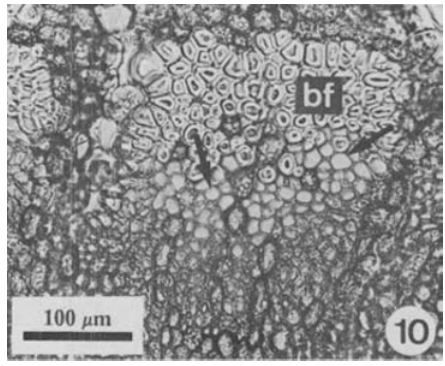
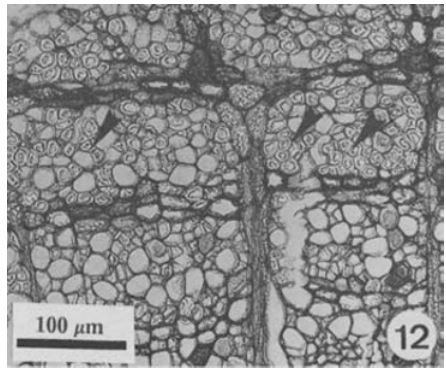
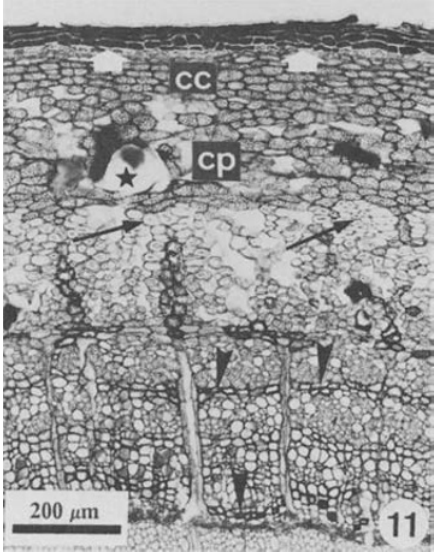
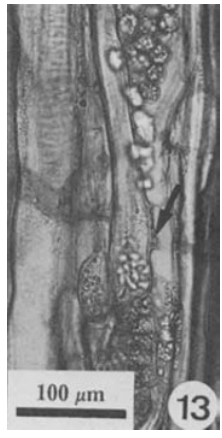
Figs. 9–14. *Ulmus glabra* Huds. Transverse section. – 9: Bark in the first year of development shortly after secondary growth had started (black arrows = epidermis, white arrows = periderm, white asterisks = secretory cells (mucilage cells) of the cortex, cc = cortex collenchyma, cp = cortex parenchyma, sp = secondary phloem). – 10: Bark in the first year of development shortly after secondary growth had started (bf = primary bark fibres, arrows = elements of the primary phloem). – 11: Bark in the first year of development after proceeding secondary growth (white arrows = periderm, black arrows = primary bark fibre groups, black arrowheads = axial phloem



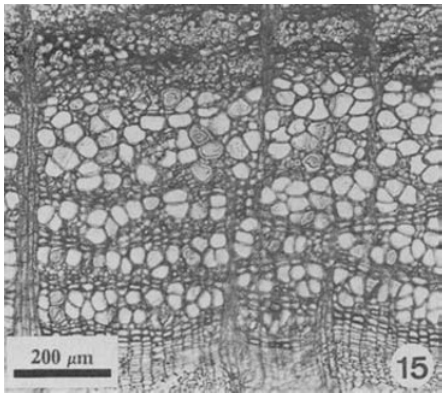


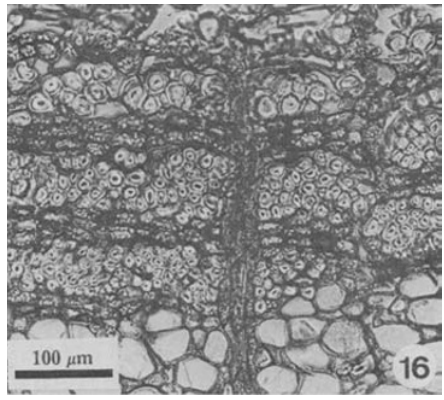


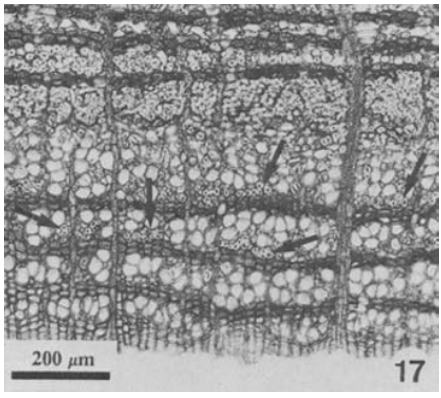


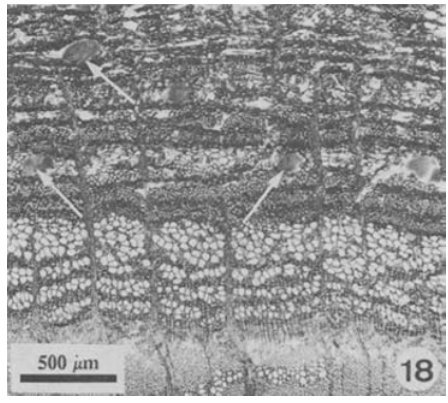


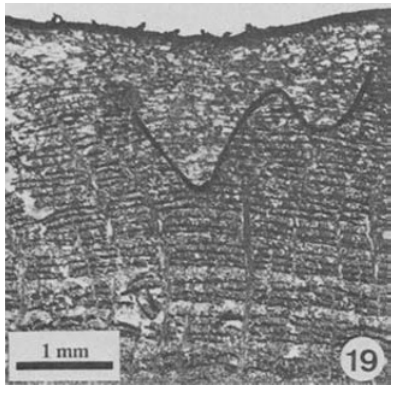
parenchyma cells with phenolic content, black asterisk = secretory cell (mucilage cell) in the cortex, cc = cortex collenchyma, cp = cortex parenchyma). – 12: Bark in the first year of development after proceeding secondary growth (arrowheads = sclerenchyma cells resembling phloem fibres). – 13: Development of phloem fibre-/sclereid-like cells from axial phloem parenchyma strands (arrow = former connection to a neighbouring cell). – 14: Development of phloem fibre-/sclereid-like cells from axial phloem parenchyma strands (arrow = slightly elongated cells with blunt ends).

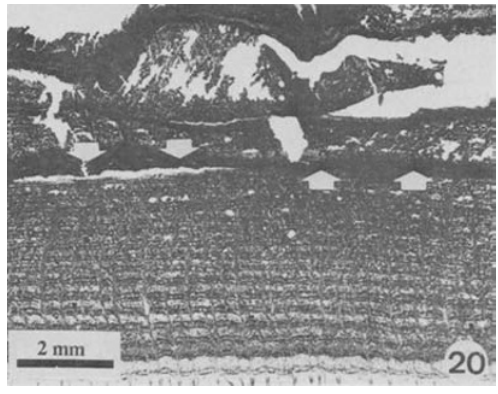












Figs. 15–20. *Ulmus glabra* Huds. Transverse section. – 15: Last formed growth ring of the bark (early phloem sieve tubes with larger diameter than late phloem sieve tubes, sclerenchymatic cells absent in this growth ring). – 16: Tangential agglomerates of the phloem fibre-/sclereid-like cells. – 17: Phloem fibre-/sclereid-like cells (arrows) in the last formed growth ring. – 18: Secretory (mucilage) cells (arrows) in early phloem. – 19: Dilatation restricted to wedge-shaped areas beneath the periderm (outlines of dilated area redrawn). – 20: Bark after the formation of a rhytidome. Secondary phloem up to the last formed sequent periderm (arrows) appears homogeneous.

layers (2–4 cells wide) of axial phloem parenchyma strands. The width of the zones as well as cell dimensions decrease from early to late phloem (Fig. 15). The tissue is characterised by a collapse of sieve tube members, the formation of phloem fibre-/sclereid-like cells, the formation of secretory cells, and dilatation growth. Most of the sieve tube members collapse during the second year. Those of the late phloem collapse completely, whereas some of the early phloem remain intact for some years. When the sieve tube members collapse, phloem fibre-/sclereid-like cells develop and protrude into the space formerly occupied by the sieve tube members. These cells appear as tangential agglomerates in transverse sections (Fig. 16). But they are not as closely connected to each other as the secondary phloem fibres (e.g. in oak bark), because they develop from axial phloem parenchyma strands (Figs. 13 & 14). They always occupy less space than non-collapsed sieve tube members. Thus the growth rings become compressed. The time when cells start to develop varies within the tree. In younger samples first developmental stages may be present in the periphery of the current growth ring (Fig. 17). In old samples the phloem fibre-/sclereid-like cells develop in the preceding year's growth ring (Fig. 18).

With increasing secondary growth more secretory cells are formed (Fig. 18), yet they are absent close to the cambium. Dilatation growth is mainly restricted to wedge-shaped zones at the periphery of the bark (Fig. 19). Here the cells are tangentially stretched, some divide anticlinally. In adjacent bark areas tangential growth stress is compensated by a radial compression of the tissue, tangential expansion of cells and the formation of intercellular spaces. Due to a constant repetition of these processes, even older samples appear to be relatively homogeneous. When a rhytidome is formed in older bark, this homogeneity is intensified by the separation of tissue modified by dilatation growth (Fig. 20).

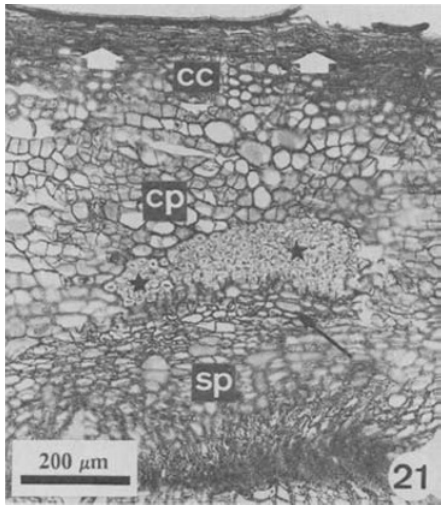
Populus tremula L.

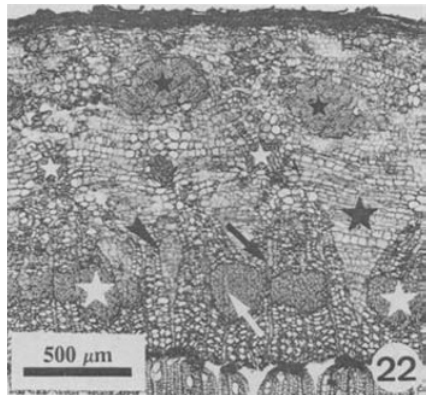
The youngest sample represents the bark shortly after secondary growth has started (Fig. 21). The course of the vascular cambium is circular. The secondary phloem consists of sieve tube members, companion cells, axial phloem parenchyma cells and uniseriate phloem rays. Outside the secondary phloem primary phloem elements and primary bark fibres are located. The areas of primary phloem are strongly pushed apart by dilatation growth. In the secondary phloem only phloem rays dilate. In the cortex all cells are affected, they are conspicuously enlarged and rounded off. Tangential rows of closely related cells reveal that anticlinal divisions of cortex parenchyma cells are frequent. The outer cortex consists of tangentially stretched collenchyma cells and a few slightly enlarged sclereids. The outermost layer of the shoot is the newly formed periderm with adhering remnants of the epidermis.

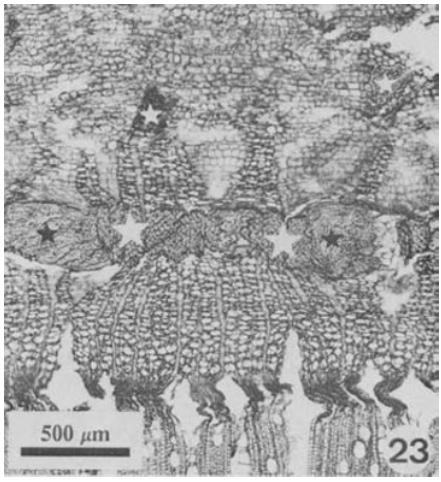
Groups of secondary phloem fibres up to 15 cell wide develop within the first year (Fig. 22). Some of these groups are very close to each other, resembling a nearly continuous tangential band. They are accompanied by thick-walled, lignified, chambered crystalliferous cells. Phloem rays run through the fibre groups and undergo sclerification when in direct contact with the secondary phloem fibres. Numerous small groups of sclereids are scattered immediately beneath the periderm. Some groups of sclereids develop in the cortex. Most sclereids are rounded irregularly or isodiametric. Some sclereids develop between the groups of secondary phloem fibres, the first formed always in contact with the fibre groups. Dilatation growth proceeds; some phloem rays exhibit a funnel-shaped dilatation growth, others only partly dilate, and some rays remain unchanged (Fig. 22).

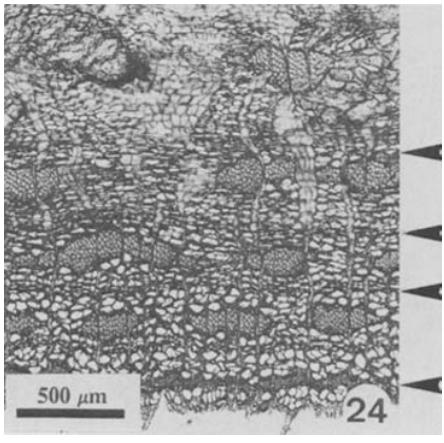
With increasing secondary growth the oldest groups of secondary phloem fibres are connected by sclereid groups (Fig. 23). These sclereids develop from axial phloem parenchyma cells and dilated phloem rays. Thus, in transverse sections some sclereids appear more or less isodiametric and some tangentially extended. In radial sections most sclereids are round, and sclereid groups are often axially elongated.

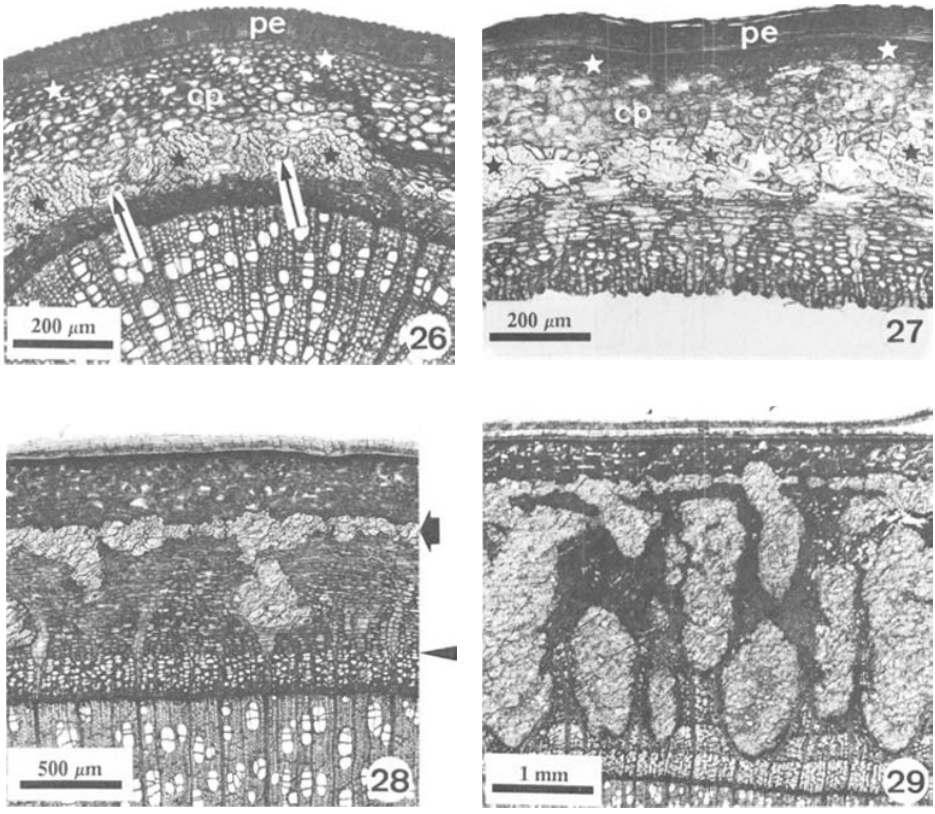
Even young bark exhibits growth rings (Fig. 24). They result from a sequential development of different cell types during one











Figs. 26–29. *Betula pendula* Roth. Transverse section. – 26: Bark in the first year of development shortly after secondary growth had started (white asterisks = cortex collenchyma, black asterisks = primary bark fibre groups, arrows = sclereids, pe = periderm, cp = cortex parenchyma). – 27: Bark in the first year of development after proceeding secondary growth (small white asterisks = cortex collenchyma, large white asterisks = sclereids, black asterisks = primary bark fibre groups, pe = periderm, cp = cortex parenchyma). – 28: Three year old bark (arrowhead = growth ring boundary, arrow = continuous band of sclereids and primary bark fibres). – 29: Several year old bark. Extensive sclerification.

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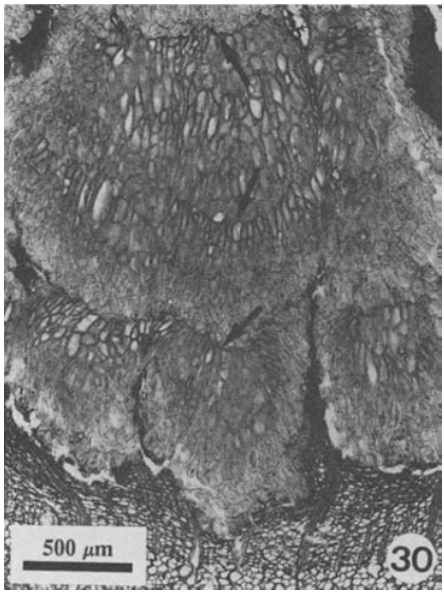
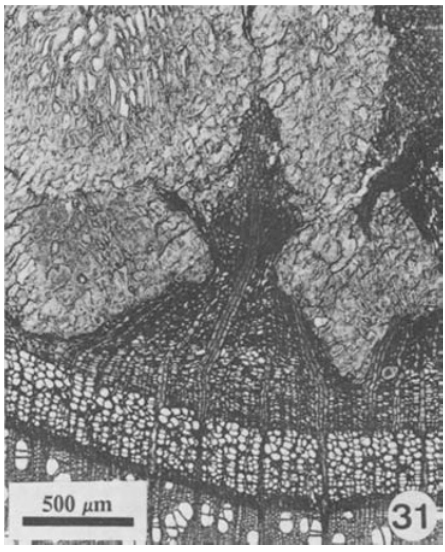
Figs. 21–25. *Populus tremula* L. Transverse section. – 21: Bark in the first year of development shortly after secondary growth had started (white arrows = periderm, black arrow = primary phloem elements, asterisks = primary bark fibre group, cc = cortex collenchyma, cp = cortex parenchyma, sp = secondary phloem). – 22: Bark in the first year of development after proceeding secondary growth (small black asterisks = sclereids in the cortex, large black asterisk = funnel-shaped phloem ray dilatation, small white asterisks = primary bark fibre groups, large white asterisks = secondary phloem fibre groups, black arrow = unchanged phloem ray, white arrow = sclerified phloem ray traversing a group of secondary phloem fibres, black arrowhead = phloem ray dilatation restricted to a certain area). – 23: Secondary phloem fibre groups (large white asterisks) connected by sclereid groups (black asterisks). Small white asterisks = primary bark fibre groups. – 24: Growth rings (arrowheads = growth ring boundaries) in several years old bark. – 25: Old bark after formation of a rhytidome.





Figs. 30–32. *Betula pendula* Roth. Transverse section. – 30: Growth rhythm in sclereid groups (arrows = sclereid group boundaries). Radially elongated sclereids. – 31: Few growth rings visible in the not sclerified secondary phloem between the sclereid groups. – 32: Old bark with extensive formation of a rhytidome (arrows = last formed sequent periderm).

growth period accompanied by the collapse of sieve tube members. At the beginning of a growth period a zone of predominantly sieve tube members is formed followed by tangentially arranged groups of secondary phloem fibres. The size of these groups varies a lot, but their radial width (3–15 cells) tends to decrease with age. A second zone of sieve tube members, companion cells, and axial phloem parenchyma cells develops. At the end of the growth period a narrow layer of 1–3 axial phloem parenchyma cells is formed. The sieve tube members usually start collapsing in the last year's phloem but intact ones may still be present in older parts of the phloem. The growth ring pattern is significantly disturbed by increasing sclerification and dilatation growth. Groups of sclereids develop in the entire secondary phloem except the current growth ring. They fuse and form large, irregularly shaped groups. Frequently sclereid groups start developing close to secondary phloem fibres. Their development is similar to the one in oak bark. The patterns of dilatation growth are maintained with increasing age. Cortex cells enlarge and divide, axial phloem parenchyma cells round off and enlarge only slightly. The phloem ray dilatation is funnel-shaped in the outer secondary phloem. It is restricted to parts of the ray in the inner secondary phloem. Primary elements of the bark are still present but more and more segregated.

In old bark a rhytidome is formed but the numerous sequent periderms lie very close to each other separating only small parts of the tissue (Fig. 25).

Betula pendula Roth

Because both sample trees do not differ very much with regard to their basic bark structure their development is described together.

The youngest sample shows the shoot a short time after secondary growth has started (Fig. 26). From the vascular cambium a narrow zone of secondary phloem is formed consisting of sieve tube members, companion cells, axial phloem parenchyma cells and 1–3 seriate phloem rays. The primary phloem elements between the secondary phloem and groups of primary bark fibres are completely collapsed. The fibre groups are pushed apart due to the dilatation of phloem rays and especially of the cortex parenchyma cells. The latter enlarge, round off and divide anticlinally, the cortex collenchyma cells expand tangentially or divide anticlinally. Some slightly enlarged sclereids develop between the groups of primary bark fibres. The outermost layer of the shoot is a distinct periderm with adhering remnants of the epidermis.

Sclerification and dilatation growth proceeds (Fig. 27) in the first year. Funnel-shaped phloem ray dilatation occurs. The distance between groups of primary bark fibres increases and the gaps are partly filled with sclereid groups. Together they form an irregular tangential band. Sclereids also develop in the cortex.

With increasing secondary growth the bark exhibits growth rings (Fig. 28). In every growth period a zone consisting of sieve tube members, companion cells, axial phloem parenchyma cells and phloem rays is formed. The diameter of the sieve tube members decreases from the beginning to the end of the growth period. At the end of the growth period a layer of 1–4 axial phloem parenchyma cells is formed. Secondary phloem fibres are absent. The collapse of sieve tube members starts in the preceding year's secondary phloem, but it remains incomplete for several years. The latest growth ring is free of sclereids. Funnel-shaped phloem ray dilatation starts in the last year's secondary phloem and is restricted to multiseriate rays. Cells of the uniseriate rays enlarge slightly but they do not divide. The band of sclereids and primary bark fibres is nearly continuous (Fig. 28). Beneath this band sclereid groups have developed and have partly fused with the band.

The influence of sclerification on bark structure increases with growth. Huge, mostly radially oriented groups of sclereids develop (Fig. 29). Sclerification proceeds from initial cells outwards. When an older sclereid group is reached, both groups fuse. Thus large sclereid groups exhibit growth rhythms. Sclereids not fully differentiated may lie be-

side completely developed ones, or the inner sclereids of an old group are smaller than the outer ones of a young group (Fig. 30). But these growth rhythms do not correspond to the annual ring pattern of the secondary phloem. The axial dimension of the sclereid groups often exceeds several millimetres. In addition, the groups enlarge tangentially and therefore compress the remaining secondary phloem. Rarely more than 3 or 4 growth rings are discernible (Fig. 31). The individual sclereids vary a lot in form and shape, but they often are radially extended (Fig. 31). Remnants of the former continuous band of sclereids and primary bark fibres are still visible. Because of the intensive sclerification dilatation growth is restricted to the cortex cells and a slight tangential enlargement of phloem ray cells outside the latest growth ring.

In older bark a massive rhytidome is formed. Large parts of the bark are isolated by sequent periderms, but adhere to the remaining bark (Fig. 32).

Discussion

Literature data on the bark of the investigated tree species often correspond to one of the developmental stages described above, but sometimes they deviate.

According to Hanstein (1853), isolated groups of primary bark fibres are arranged in a circle in the bark of *Quercus robur*. A few sclereids lie between the groups. Groups of sclereids are scattered in the tissue. The amount of sclereids increases with growth. Möller (1882) observed the same arrangement of primary bark fibres. He mentions that the sclereid groups of the secondary phloem are relatively small. Both authors investigated young bark. Speyer (1907) describes the structure of young and old bark of *Quercus robur*. The first does not show a continuous sclereid-fibre ring, whereas the old bark does. The bark of *Quercus robur* examined by Holdheide (1951) does not show any such ring-like structure but his description corresponds to the older sample of the present study. He observed growth layers, broad phloem rays protruding into the xylem, and an intensive dilatation growth close to these rays. According to Holdheide (1951), the 'splitting' of the broad phloem rays is caused by dilatation growth or "during the formation of the rays." In the present investigation the study of the phloem ray formation revealed that the broad rays develop by fusion of narrow phloem rays. The fusion is caused by the elimination of cambium initials as it was described for wood rays by Braun (1955). Reinders and Reinders-Gouwentak (1961) describe 1, 2, 5, and 42 year old bark samples of *Quercus robur* and *Q. petraea*. According to these authors the two species show no differences in their basic bark structure. This is supported by observations by Holdheide (1951). During the first year the groups of primary bark fibres are connected to a circle by sclereids. Already in the 5 year old sample the ring consists mainly of sclereids. Remnants of this ring are present in rhytidome parts of the 42 year old bark. The intensity of sclerification and dilatation varies considerably between the developmental stages. The stages correspond to those described above.

The primary elements of the bark are dealt with in the papers of Möller (1882), Speyer (1907), and Reinders & Reinders-Gouwentak (1961); Holdheide (1951) does not mention them at all.

Descriptions of other *Quercus* species often differ from those on *Quercus robur*, see Howard (1977) and Nanko & Côté (1980) on several oak species from North America, Babos (1979) on *Quercus cerris* Loud. and Röckle (1986) on *Quercus rubra* L. Part of these deviations might be due to genetic differences between species or species groups; Chang (1954) proposed this for the oak subgenera *Erythrobalanus* and *Lepidobalanus*, but the characteristics he classifies as general differences (e.g. the arrangement of sclerenchyma) were not confirmed by Howard (1977). Möller (1882) and Röckle (1986) differently describe the presence of a sclereid-fibre-ring and the degree of sclerification in bark samples of *Quercus rubra*. These differences might be caused by a different developmental stage of the samples.

Developmental studies of elm bark are not available. The description of mature bark of *Ulmus glabra* by Holdheide (1951) corresponds to the older, thicker bark samples described above.

Hanstein (1853), Möller (1882), Chang (1954), and Nanko & Côté (1980) describe bark of different developmental stages of *Ulmus laevis, U. campestris* and *U. americana*. Hanstein (1853) observes primary bark fibres forming a continuous ring whereas Möller (1882) reports isolated groups. The authors do not mention any dilatation growth for elm, only Holdheide (1951) finds wedge-shaped dilatation areas in older bark of *Ulmus glabra*. The analysis of *Ulmus americana* and *U. alata* by Nanko and Côté (1980) is very similar to the one of *Ulmus glabra* by Holdheide (1951).

Literature data on the presence of mucilage cells in *Ulmus* bark differ to a great extent. According to Möller (1882), Solereder (1899), and Metcalfe & Chalk (1950) mucilage cells are often present in the bark of the Ulmaceae, but individuals without these cells may be found. Möller (1882) describes mucilage cells in the bark of *Ulmus procera* and *U. rubra,* Melchior (1927) in *Ulmus laevis, U. glabra* and *U. rubra,* Holdheide (1951) in *Ulmus glabra* and *U. minor,* and Chang (1954) in *Ulmus americana* and *U. rubra*. Möller (1882) does not mention any mucilage cells in his descriptions of the bark of *Ulmus laevis*. Neither do Nanko and Côté (1980) for *Ulmus alata* and *U. americana*. In addition, Metcalfe and Chalk (1950) report of groups of mucilage cells which coalesce to cavities in the cortex of the genus *Ulmus*. Such cavities were not observed in the investigated bark samples of *Ulmus glabra*.

Compared to the descriptions of oak bark those of elm bark show more similarities because in elm bark enlarged sclereids are not formed, only slight dilatation growth occurs and the main changes of the tissue take place within the first few years.

Developmental studies of poplar bark were conducted by Kosichenko (1969), Rees & Shiue (1957/58), and Bosshard & Stahel (1969). According to Kosichenko (1969), elliptic groups of secondary phloem fibres are formed in *Populus tremula* during the first 10 years. These groups are located at considerable tangential distance. After the 10th year the fibre groups become narrower and connect to tangential bands. Therefore age and dilatation growth seem to cause the large tangential distance between the secondary phloem fibre groups in the young bark of the investigated poplar tree. Most observations of Kosichenko (1969) stand in accordance with the bark description above. However, his conclusion that tissue starts changing earlier in young bark than in older bark is untenable. The fact that in young bark of the higher stem phloem ray dilatation starts closer to the cambium than in older bark of the stem base should not be related to time but to a response to an increase of girth which is considerably stronger in a young tree. Moreover, the present study does not reveal an earlier sclerification with increasing height.

The observations for the development of bark of *Populus tremuloides* described by Rees and Shiue (1957/58) corresponds with ours. According to Bosshard and Stahel (1969), sclerification is a modification of the bark of *Populus robusta,* especially in a juvenile stage of development. The forms of sclerification observed during the present investigation are similar to those found by Bosshard and Stahel (1969) but, in contrast, the sclerification is more intensive in the older bark than in the juvenile stage.

Other papers on the anatomy of poplar bark are those of Möller (1882) on *Populus alba, P. nigra, P. pyramidalis* and *P. tremula,* Perrédès (1903) on 11 different poplars, Holdheide (1951) on *Populus nigra* and Chang (1954) on *Populus tremuloides*. In most of these studies only one developmental stage is described, mostly that of thin, young bark (Möller 1882; Perrédès 1903). Especially Perrédès (1903) mainly analyses cortex, primary bark fibres and young secondary phloem. He finds only funnel-shaped phloem ray dilatation. But, dilatation growth restricted to small parts is not clearly visible before an age of approximately 10 years. Perrédès (1903) mentions 'older' barks with 5 layers of secondary phloem fibres, so his bark is still quite young. Holdheide (1951) and Chang (1954) analyse old secondary phloem without further information on primary elements of the bark.

The anatomical structure of the bark of different birch species is subject of only a few investigations. There are no develop-

mental studies. The description of primary elements of *Betula pendula* bark by Möller (1982) corresponds to that given above, his information on how sclereid groups are arranged in the secondary phloem reveals that his samples were young. The observations of Holdheide (1951) show many similarities with those of the older samples of the present investigation. He describes the same mechanism of sclereid group development. The study by Bhat (1982) on *Betula pendula* and *B. pubescens* is not sufficiently informative with regard to basic bark structure. Only he observes secondary phloem fibres in birch bark. All the other authors never observed any secondary phloem fibres. Only these three papers deal with *Betula pendula* bark. In all the other papers different species are analysed.

According to Chang (1954), the sclereid group formation in *Betula alleghaniensis* and *B. papyrifera* is similar to the centrifugal one observed in *Quercus robur* and *Populus tremula*. In general, the sclerification appears to be less intensive than in the *Betula pendula* trees of the present investigation. While Chang's (1954) description of the young bark agrees with the above observations, that of the older bark reveals large differences. These may be due to the selection of different species or to differences in age or the samples' thickness.

The variety of developmental processes in bark and the variability of bark characters within and between species were studied in relation to bark age, bark thickness, stem height, and stem diameter. It is impossible to determine the degree of influence of each separate factor. These quantifiable factors only affect but do not determine the physiological causes of variation. Every variation depends on the different supply with carbohydrates, phytohormones, water and nutrients, which is caused by a varying metabolism. The metabolism changes with a number of abiotic and biotic factors like temperature, light intensity, precipitation, etc. There is not much information available on the relations between these factors and the structure with regard to tree bark or phloem. This, and the small number of individuals investigated, do not allow to consider the details of bark development observed in the present investigation to be generally valid. It is unknown whether the structural variability observed here reflects only a part of the variation possible in bark structure. Additional studies on the variability and development of bark structure are urgently needed.

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