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QUANTITATIVE CHANGES OF SOME ANATOMICAL CHARACTERS DURING BARK DEVELOPMENT IN QUERCUS ROBUR, ULMUS GLABRA, POPULUS TREMULA AND BETULA PENDULA

by

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Summary

Quantitative changes of certain anatomical characters during bark development of *Quercus robur* L., *Ulmus glabra* Huds., *Populus tremula* L. and *Betula pendula* Roth were analysed.

Generally, bark thickness increases continuously with age. The time of rhytidome formation varies considerably between species and individuals and does not show a regular relation to bark thickness or stem diameter. The quantity of sclereids increases with age in most trees. The development of conduction and storage tissue varies considerably, although in most trees its quantity remains more or less constant after a certain age. In elm the quantity of secretory cells decreases with age. Oak shows an increase of phloem ray height with age and an increase of phloem ray width of some rays due to fusion of uniseriate rays. In elm uniseriate phloem rays are more frequent in young bark. The length of secondary phloem fibres significantly increases in oak and poplar. The sieve tube members do not exhibit a regular developmental trend with regard to cell length, although they tend to be slightly longer in old bark. The tangential diameter of sieve tubes considerably increases up to a certain age in most trees.

It is impossible to determine precisely the time range of those changes; they vary between species and individuals. However, some changes are restricted to the transition from primary to secondary growth, others seem to stabilise after approximately 10 years and some last longer.

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

Introduction

We know enough details about the anatomical structure and the development of wood to use wood anatomy as a tool for taxonomic studies. The few studies using the anatomy of bark for such a purpose (e.g. Archer & Van Wyk 1993; Trockenbrodt & Parameswaran 1986) are based on the rather limited knowledge of bark. But detailed information about the possible variation of bark anatomical characters is an indispensable prerequisite if bark structure is to be successfully applied in plant systematics. Therefore, a study on the structural development of the bark of some European hardwoods was conducted. The qualitative changes during its development were described earlier (Trockenbrodt 1991). The present paper deals with the quantitative changes of some bark anatomical characters.

Material and Methods

Individuals of *Quercus robur* L., *Ulmus glabra* Huds., *Populus tremula* L. and *Betula pendula* Roth were analysed. For details regarding the age and the height of the trees see Trockenbrodt (1991).

Bark samples were taken at regular distances along the stem, regular age intervals (determined from xylem growth rings), and regular stem diameter intervals. Furthermore,

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the tissue had to be without any visible damage. For sample preparation methods and more details regarding age, location and thickness of the samples as well as the corresponding stem diameters see Trockenbrodt (1991).

The bark anatomical characters studied were:

— bark thickness
— time of rhytidome formation
— tissue proportions
— height and width of phloem rays
— phloem fibre length
— length and diameter of sieve tube members

Within few individuals (oak, poplar) some characters (bark thickness, time of rhytidome formation, phloem fibre length) were analysed with regard to differences between the south and north side of the stem.

The analysis of certain bark anatomical parameters is problematic because all anatomical information is stored in a comparatively small area. In addition, tertiary tissue changes are common during bark development (cf. Trockenbrodt 1991). Because of the sieve tube collapse it was impossible to determine the sieve tube quantity within the entire bark. In the non-collapsed part it often was extremely difficult to distinguish between sieve tubes and axial phloem parenchyma cells. In addition, tissue dilatation makes it impossible to distinguish between axial phloem parenchyma and phloem rays. As a consequence, sieve tubes were quantified along with the entire phloem parenchyma as conduction and storage tissue. The quantities of bark fibres – i.e. primary and secondary phloem fibres – and sclereids were analysed separately and combined as sclerenchymatic tissue. In oak and poplar primary and secondary phloem fibres as well as sclereids are present, in birch primary phloem fibres and sclereids only. In addition to primary phloem fibres, elm exhibits sclerenchymatic cells which – like sclereids – develop from phloem parenchyma cells but resemble secondary phloem fibres in shape (cf. Trockenbrodt 1991). Therefore, only the quantity of sclerenchymatic tissue was determined. Also, in all species the area of the periderm was determined including the sequent periderms of a rhytidome, if present. In elm bark secretory cells were determined separately. Tissue proportions were measured in a square area of the transverse section with sides as long as the width of the entire bark.

To determine the length of the secondary phloem fibres a 500 µm wide part of the bark adjacent to the vascular cambium was macerated. Because of the small annual radial growth of bark, secondary phloem fibres of more than one growth period had to be analysed together. Their length was calculated from 100 measurements per sample.

Because of the sieve tube collapse and the changes of cell dimensions during tissue dilatation the length and the diameter of the sieve tube members were determined in the non-collapsed phloem. Sieve tube collapse effects the radial cell diameter first. Therefore, the tangential cell diameter was determined. The values are based on 50 measurements per sample.

The height and especially the width of the phloem rays are effected by tertiary tissue changes. For this reason the phloem ray dimensions were analysed close to the vascular cambium.

For measurements a semi-automatic image analyser was used. The data were processed by commercial statistic and drawing computer programs.

Bark anatomical terms are used as suggested by Trockenbrodt (1990).

Results

Bark thickness

In all individuals bark thickness increases more or less continuously with age (Fig. 1). There are no significant differences between the north and the south side of the trees. In oak I–IV bark of the same age shows a similar thickness; the corresponding values of oak V are smaller. In birch I and birch II barks of the same age differ in thickness.

Time of rhytidome formation

The younger individuals of oak do not show any rhytidome. In one individual rhytidome formation starts at the age of 9 at the north side of the tree and at the age of 19 on the south side. In another one the formation starts at the age of 26 at the north side and at

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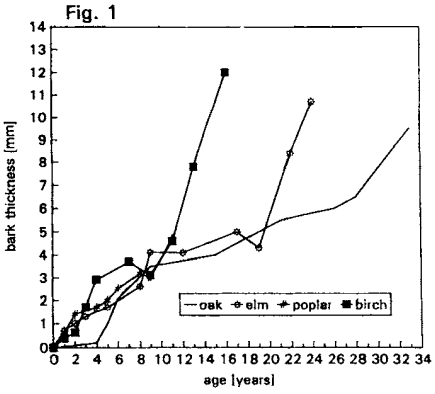

Fig. 1. Bark thickness of oak I, elm, poplar and birch I in relation to bark age.

the age of 21 at the south side. In general, a regular development of rhytidome was not observed. In elm rhytidome formation starts at the age of 17, in poplar at the age of 8 on both sides of the tree. One individual of birch exhibits rhytidome formation at the age of 8, the other one at the age of 13.

Tissue proportions

The determination of absolute values was of secondary importance. Diagrams, in particular, are suitable to illustrate how tissue proportions tend to develop. Absolute values are not included here; they may be deduced from the diagrams. Because all samples of one individual were included into a diagram some age groups may be represented more than one time (e.g. Fig. 3).

Tissue proportions were related to age, height, bark thickness and stem diameter. The resulting diagrams showed such a high degree of correspondence that only those related to age are presented.

The results of the quantitative analysis of tissue proportions differ considerably between the species and between the individuals. No general and exact relationships between tissue proportions and age, height, bark thickness or stem diameter were observed. This high variability is illustrated in Figures 2–5. Only some trends of development can be described for certain individuals or species.

The quantity of sclereids increases considerably during the first 8 years in oak I, 4 years in oak III, 6 years in poplar, 8 years in birch and then remains more or less constant. In oak II it increases only slightly and in oak IV and V it is more or less constant. There are no sclereids in elm.

The development of conduction and storage tissue varies even more between individuals. Its quantity remains more or less constant after some years in oak I–IV and birch I & II and during a long period in elm. However, oak I–III exhibit a considerable increase and birch a decrease before this constant level is reached. In poplar there is a constant quantity for 6 years and then it decreases continuously.

The quantity of bark fibres and sclerenchymatic tissue decreases during the first 1–3 years in oak I and II, and elm.

In elm the area occupied by secretory cells decreases with age. Only the sample taken at the stem base exhibits an increase.

Height and width of phloem rays

In oak phloem rays are of two distinct sizes, uniseriate ones and very broad multiseriate (10–20) ones. Phloem ray height was analysed in 4–28 year old samples; the analysis was restricted to uniseriate phloem rays. Ray height varies between 1 and 24, rarely 40 cells. After approximately 10 years most phloem rays are 6–15 cells high, in younger bark 4–12 cells.

Measurements in 3–22 year old samples of elm reveal no significant differences between age groups, but phloem rays tend to be smaller in young bark. Phloem rays are 1–30 cells high, very rarely up to 100 cells.

In the 2–11 year old samples of poplar phloem rays are 1–28, mostly 5–13 cells high. There are no significant differences between age groups.

There are also no significant differences between the bark samples of birch. Phloem rays are 1–28 cells high, most of them 4–13 cells.

In oak there are no broad phloem rays for the first two years. Those rays start to develop at the age of 3. They only form a distinct character in older bark. There are no further differences.

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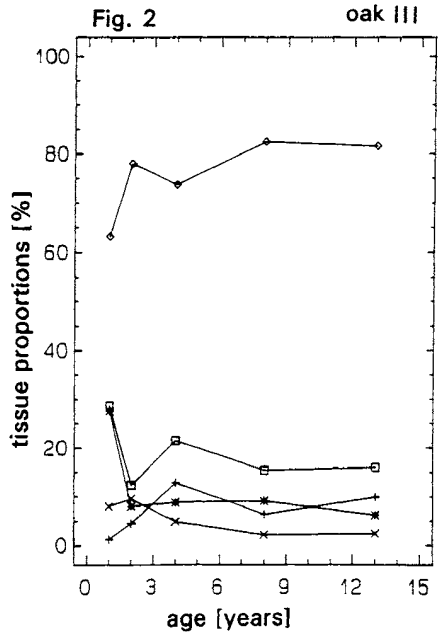

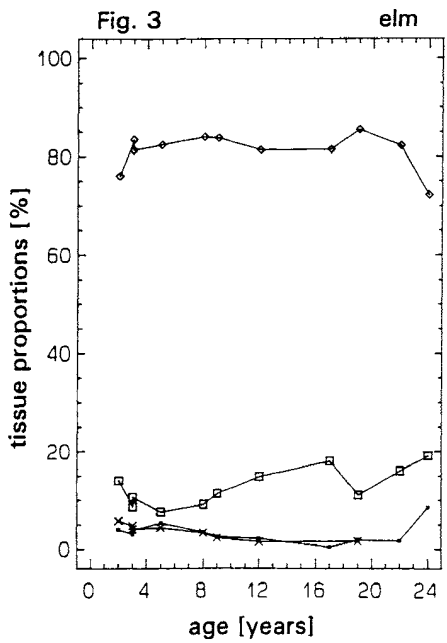

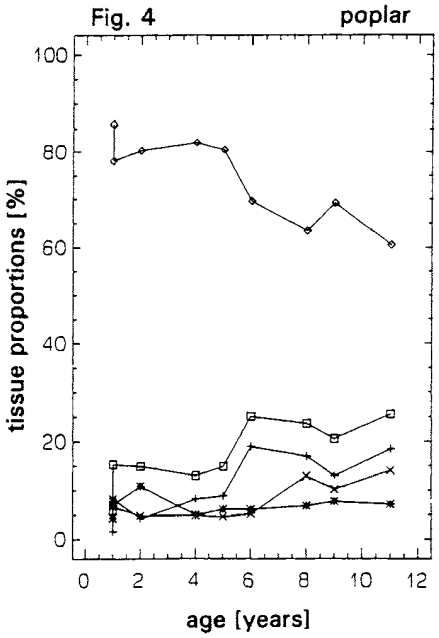

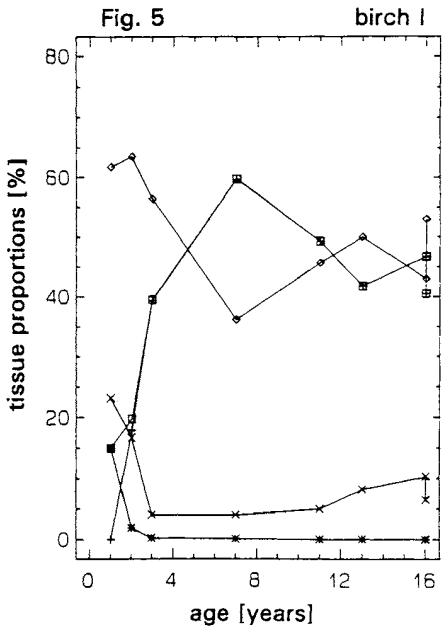

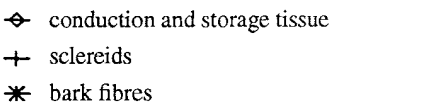

Figs. 2–5. Bark tissue proportions in relation to bark age. – 2: Oak III. – 3: Elm. – 4: Poplar. – 5: Birch I.

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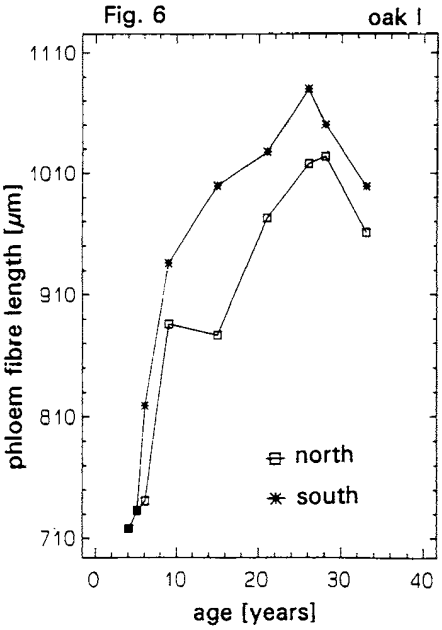

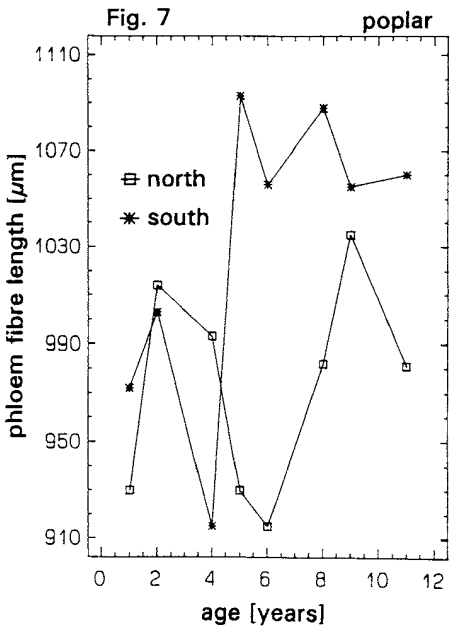

Figs. 6 & 7. Secondary phloem fibre length in relation to bark age. – 6: Oak I. – 7: Poplar.

In elm phloem rays are 1- to 7-seriate. In older bark 4- to 6-seriate rays are numerous; their number decreases in younger bark, but differences are not significant.

Poplar phloem rays are exclusively uniseriate.

Birch phloem rays are 1- to 3-seriate. There are no differences between age groups.

Phloem fibre length

In oak I (Fig. 6) secondary phloem fibre length increases continuously with age and decreases again in the oldest samples. The north and south side of the stem show a similar development from 720/720 µm (4 years) to 1020/1080 µm (28/26 years) and back to 960/1000 µm (33 years). Up to the age of 9 the increase is distinct, later moderate. In view of the high variability of secondary phloem fibre length (540–1470 µm) the differences between north and south are not significant. The average length is 910 µm. Oak II–IV do not reveal differences between the north and south side of the stem. In oak II secondary phloem fibre length increases from 690 µm (2 years) to 890 µm (9 years) to 980 µm (26 years); it ranges from 520 µm to 1360 µm, the average is 890 µm. In oak III length increases from 660 µm (2 years) to 910 µm (13 years); the range is 430–1260 µm, the average 820 µm. The secondary phloem fibre length of oak IV increases from 610 µm (2 years) to 800 µm (12 years); the range is 440–1090 µm, the average 720 µm. In oak V the secondary phloem fibres of the south side tend to be shorter than those of the north side but differences are not significant. In general, the length increases from 690 µm (3 years) to 800 µm (13 years), the range is 430–1240 µm, the average 750 µm.

Secondary phloem fibre length of poplar varies between the north and the south side of the stem and between age groups (Fig. 7). It ranges from 590 to 1460 µm; the average is 1000 µm. Higher values were observed in older samples.

There are no secondary phloem fibres in the bark of elm and birch.

Length and diameter of sieve tube members

There are no significant differences between the north and south side of the stem.

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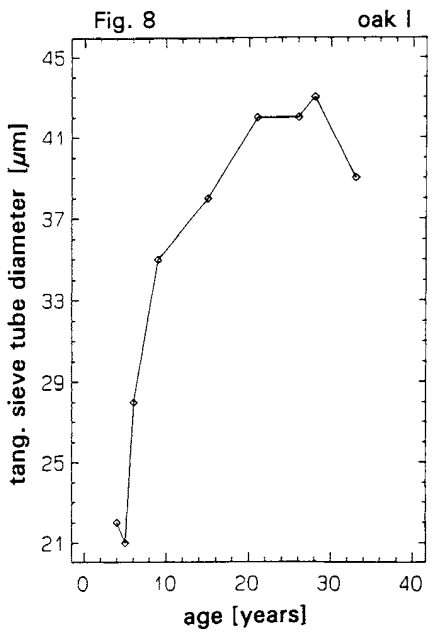

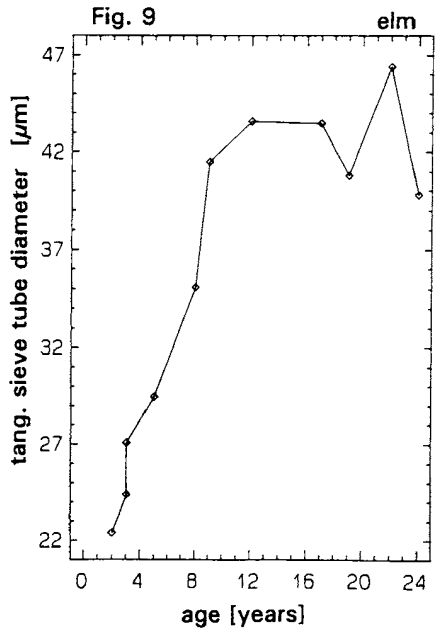

Figs. 8 & 9. Tangential sieve tube diameter in relation to bark age. – 8: Oak I. – 9: Elm.

Regular developmental changes of sieve tube member length were not observed. In oak I sieve tube members of the young bark (up to 4 years) are somewhat shorter (230–310 µm) than those of older bark samples (300–540 µm). A few sieve tube members reach a length of 580–620 µm. Sieve tube members of oak II–V are 300–540 µm long. In elm the length ranges from 80 µm to 250 µm. In young bark there tend to be more shorter sieve tube members. In young bark of poplar (up to 5 years) sieve tube members are 160–310 µm long; in older bark a few sieve tube members reach a maximum of 660 µm. In birch all samples show a length of 470–780 µm.

In oak I the diameter of sieve tubes increases considerably from 22 µm in 4 year old bark to 43 µm in 28 year old bark and then decreases again to 39 µm in 33 year old bark (Fig. 8); the average is 34 µm. The values for oak II are 28 µm (1 year), 42 µm (22 years), 38 µm (26 years) and 35 µm (average). In oak III the diameter continuously increases from 21 to 34 µm (average 29 µm). Oak IV and V exhibit smaller sieve tubes with a diameter of 25–28 µm and 18–19 µm respectively. Also in elm the diameter increases with age from 22 µm (2 years) to 44 µm (12 years) and then varies around this value (Fig. 9). The average is 36 µm. In poplar the diameter increases from 34 µm (1 year) to 48 (5 years) and then varies around this value. The average is 43 µm. Birch does not show a distinct trend of diameter development, although young bark exhibits the smallest values. The average is 25 µm.

Discussion

Bark thickness

Generally bark thickness increases continuously with age. The comparison of several individuals of one species (e.g. oak I and oak V, birch I and birch II) reveals that bark thickness may differ at the same age, as bark thickness is influenced by other factors than age. Although high variability of bark thickness within one species has repeatedly been described (e.g., Hale 1955; Wiedemann 1932), little is known about its cause. The differences between samples of the same age of oak I and oak V may be caused by different site conditions. Compared to the domi-

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nating oak I the suppressed growing oak V exhibits considerably thinner bark. Investigations on phloem growth processes and growth differences between xylem and phloem in stressed trees would presumably shed light on this question.

The observed differences between the north and the south side of the trees do not follow any regular pattern. According to Schanze (1920, cited by Huber 1935) and Röckle (1986), however, bark of the south side of a tree is always thicker, possibly because of an increased rhytidome formation (see below).

Time of rhytidome formation

The age where rhytidome formation starts varies considerably between the individuals of oak and birch. According to Babos (1979), rhytidome formation starts at the age of 30 in *Quercus cerris*. Hartig (1851) reported rhytidome formation of oak between the age of 25 and 35. De Bary (1877) observed rhytidome formation in *Ulmus effusa* at the age of 3–4, in *Betula alba* at the age of 5–6 and in *Populus sp.* at varying ages. Lindquist (1946) also reported rhytidome formation in some *Betula* species before the age of 10, in other *Betula* species at varying age. Glitzenstein and Harcombe (1979) suspect that rhytidome formation is an adaptation to site conditions, because in dry habitats *Quercus falcata* exhibits earlier rhytidome formation. De Zeeuw (1941) emphasised that in some trees intense exposure to light leads to an early formation of rhytidome. According to Schanze (1920, cited by Huber 1935) and Huber (1935), rhytidome formation is more distinct on the south side of a tree due to a higher exposure to sunlight. Furthermore, sequent periderm formation, i.e. rhytidome formation is known to be induced by wounding (e.g. Küster 1925). Lev-Yadun and Aloni (1990) propose that the hormones, auxin and ethylene, are the major factors controlling periderm/rhytidome formation and the effects of light exposure, wounding and other factors are caused by the relative level of these two hormones.

In the present study no regular pattern was observed with regard to rhytidome formation. Further investigations on endogenous and exogenous influences on rhytidome formation are necessary.

Tissue proportions

There are extremely few studies on the variability of bark tissue proportions. Observations of *Quercus rubra* by Röckle (1986) are difficult to compare with the present study, because his work does not include detailed information on age, bark thickness and stem diameter. However, *Quercus rubra* exhibits a similar trend of sclereid development.

A decrease of secretory cell quantity with age in elm was also reported by Flückiger (1883). The observed increase at the stem base presumably represents the transition to root bark which generally shows more secretory cells.

The quantitative analysis of tissue proportions turned out to be unsuitable for a precise description of bark development. The variability was much too high. Only basic trends could be observed for some species. There is a considerable decrease in quantity of bark fibres during the first few years followed by a substantial increase of sclereids. The quantity of bark fibres decreases because the primary phloem fibres occupy a comparatively large area of the young bark. It is not possible to describe exact time limits for these changes. They vary between individuals and species, although some (e.g. the decrease of bark fibres) are restricted to the transition from primary to secondary growth whereas others (e.g. increase of sclereids) may stabilise after approximately 10 years or continue for a longer time.

Height and width of phloem rays

Only in oak the analysis of phloem ray height reveals significant differences between age groups. Up to the age of 9 years the average height is smaller than in older bark where the rays are 6–15 cells high. According to Braun (1955), most xylem rays of *Quercus robur* are 5–15 cells high. A comparison with his results seems to be appropriate because phloem rays derive from the same cambium initials as xylem rays and the measurements were made close to the vascular cambium where no dilatation had taken place. Braun's observations were made along the radius of a stem disk without consideration of the tree height. Such analysis is not suitable for tree bark. Braun (1955) observed an

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increase of ray height with age caused by cell division and fusion of rays. This trend, which is partly reduced by the splitting of some rays is confirmed partly by the measurements in bark.

DeSmidt (1922) described xylem rays of *Ulmus fulva* and their distribution. He analysed uniseriate and multiseriate rays separately. The uniseriate ones are 2–8 cells high, the multiseriate ones 4–100 and more cells. The height of the uniseriate ones increases with age. In the present study uniseriate and multiseriate phloem rays were analysed together because of a gradual transition between the two forms, e.g. high uniseriate rays with very small 2- to 3-seriate portions. An increase with age was not observed. The height range is similar to that observed by DeSmidt (1922).

The present study does not reveal an increase of poplar phloem ray height with age as observed for poplar xylem rays by Braun (1955), but the range of height is similar (5–13–15). Kosicenko (1969) reported a phloem ray height of 230 µm, 218 µm and 228 µm for 3, 10 and 24 year old *Populus tremula* bark and no increase with age.

Likewise birch does not show a regular development of phloem ray height.

It is well known (e.g. Braun 1955) that the broad rays in the xylem of oak develop when uniseriate rays fuse. However, in his developmental study Braun (1955) did not mention the time of the first fusion. In the present study first fusions occur at the age of 3.

Young elm bark exhibits more uniseriate and less multiseriate phloem rays than old bark. This trend is supported by DeSmidt (1922) who observed a higher number of uniseriate xylem rays in the crown of *Ulmus fulva*.

There are no differences between age groups in poplar and birch.

Phloem fibre length

The length of the secondary phloem fibres in relation to age and stem height is the only bark anatomical parameter investigated by several other authors. Those studying length changes with regard to stem height are not that numerous. The length of secondary phloem fibres of *Quercus rubra* increases for more than 30 years, then remains constant for a certain period of time and then decreases again (Röckle 1986). An increase from 4 to 10 year old oak bark was observed by Voillot (1985). According to Parameswaran and Liese (1974), there is a moderate decrease of the length of secondary phloem fibres in *Shorea negrosensis* from the upper part of the stem towards the middle part followed by an increase towards the older stem base region. In contrast, Iqbal and Ghouse (1983) observed an increase from the upper stem part to the middle part followed by a decrease downwards the stem in *Acacia nilotica* and *Prosopis spicigera*. Only *Acacia nilotica* shows longer fibres again in the oldest sample at the stem base. According to Ezell and Stewart (1978), the length increases continuously with age in *Liquidambar styraciflua*. No significant changes in length were reported by Nicholls and Phillips (1970) for *Eucalyptus viminalis* and by Aday (1978) for *Albizia falcataria*.

For the majority of age related studies of secondary phloem fibre length samples were taken at one height but in different distances from the vascular cambium. Röckle (1986) reported a decrease in length with increasing distance from the cambium, i.e. an increase with age, in *Quercus rubra*. A similar but less regular trend was observed by Liese and Parameswaran (1972) in four tropical hardwoods. However, in another study (Parameswaran & Liese 1974) three species with storied structure – *Mansonia altissima, Pterocarpus marsupium, Triplochiton scleroxylon* – exhibit an increase of secondary phloem fibre length towards the vascular cambium. Two of the three non-storied species investigated (*Shorea squamata, Mangifera altissima*) show a similar development. In contrast, *Pentacme contorta* has shorter fibres near the cambium. Varying developmental trends were observed in several tropical hardwoods by Ghouse and Siddiqui (1976a, b), Ghouse and Yunus (1976), Ghouse and Hashmi (1977), Yunus et al. (1977), Ghouse and Iqbal (1977) and Iqbal and Ghouse (1983). In the majority of the species the fibre length increases from the bark periphery towards the vascular cambium, but this trend is often indistinct. In some spe-

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cies the maximum length was found in the middle of the bark; rarely species exhibit their longest phloem fibres at the bark periphery. *Acacia nilotica* was included in two studies and the trends observed are contradictory (Ghouse & Iqbal 1977; Iqbal & Ghouse 1983). According to Nicholls and Phillips (1970), phloem fibre length of *Eucalyptus viminalis* does not vary at all. In *Albizia falcataria* and *Bombax ceiba* Aday (1978) and Ghouse et al. (1982) observed an increase with age for individuals of different age groups.

In the present study secondary phloem fibre length was measured close to the vascular cambium at varying stem heights. Like *Quercus rubra* (Röckle 1986) the oaks exhibit an increase downward the tree, in oak I up to an age of 26, but a constant period as observed in *Quercus rubra* after 30 years is not present. Both species, however, show again shorter fibres close to the stem base. An increase in fibre length in the uppermost part of the tree, as reported by Parameswaran and Liese (1974) for *Shorea negrosensis*, was only observed in oak V. Because young bark of the uppermost part of the tree is very thin, primary phloem fibres might have been measured together with secondary phloem fibres. This may explain the increase because primary phloem fibres are much longer than secondary phloem fibres (Esau 1969). This is supported by measurements in oak IV where primary phloem fibres are much longer than secondary phloem fibres (1829 µm/770 µm).

According to Parameswaran and Liese (1974), an increase in length of cambial initials is responsible for the increase of length of secondary phloem fibres in the upper part of the tree. However, it is known from numerous studies on the development of the length of xylem cells and cambial initials (cf. Larson 1963) that the length of cambial initials generally increases from the stem base to a certain tree height and then decreases towards the uppermost part of the tree. The results of the present study and those of Röckle (1986) and Iqbal and Ghouse (1983) roughly correspond to this development. Across the radius cambial initial length increases with age (cf. Larson 1963). According to Liese and Parameswaran (1972), Ghouse and Siddiqui (1976a, b), Ghouse and Yunus (1976), Ghouse and Hashmi (1977) and Ghouse and Iqbal (1977), this is the cause for the observed increase of secondary phloem fibre length from the periphery towards the vascular cambium. Varying apical intrusive growth of the phloem fibres as reported by Ghouse and Iqbal (1979) and Siddiqui et al. (1976) may obscure the age trend and may be responsible for irregular development and the few conflicting observations.

Samples of similar age show a similar phloem fibre length in oak I–III; fibres are shorter in oak IV and oak V. The average length in oak I and oak II corresponds to observations of other authors (e.g. Wiese 1977) for *Quercus robur* (approx. 1000 µm). Oak III–V show shorter fibres. This may be explained by the youth of oak III (cf. Voillot 1985) and the influence of site conditions in oak IV and oak V which grew suppressed by neighbouring trees.

There are no regular differences between the north and the south side of the trees with regard to phloem fibre length development. Similar observations were made by Parameswaran and Liese (1974) and Röckle (1986).

Length and diameter of sieve tube members

The present study does not reveal regular developmental trends for the length of sieve tube members, although sieve tube members tend to be shorter in younger bark of some individuals. An increase in length with age was observed by Röckle (1986) in *Quercus rubra* and by Iqbal and Ghouse (1983) in *Acacia nilotica* and *Prosopis spicigera*. According to Raskatov and Kosicenko (1968), *Populus tremula* shows an increase within the first ten years. Parameswaran and Liese (1974) analysed the sieve tube member length of several tropical species in relation to age represented by the distance from the vascular cambium. In species without storied structure (*Mangifera altissima, Pentacme contorta, Shorea negrosensis, Shorea squamata*) sieve tube members at the periphery are shorter than those close to the cambium. But compared to secondary phloem fibres this trend is less distinct. In species with storied structure

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(*Mansonia altissima, Pterocarpus marsupium, Triplochiton scleroxylon*) sieve tube member length is more or less constant along the radius. An increase towards the cambium was observed by Liese and Parameswaran (1972) in *Dialyanthera otoba, Gambeya gigantea, Isoberlinia doka* and *Shorea negrosensis*. To a lesser degree this trend is present in *Bauhinia variegata* and *Terminalia arjuna* (Yunus et al. 1977) and in several species of *Acacia* and *Prosopis* (Ghouse & Iqbal 1977). No regular development was observed in *Melia azedarach* and an opposite development in *Azadirachta indica* (Yunus et al. 1977). Schulz and Behnke (1987), analysing branches of varying age, found an increase in length of sieve tube members with age in *Fagus sylvatica*. Already MacDaniels (1918) observed a similar development in several hardwoods (e.g. *Populus deltoides, Ulmus americana*).

According to Esau and Cheadle (1955), length of the sieve tube members is determined by the length of the cambium initials and, possibly, by anticlinal divisions of the phloem mother cells (secondary partitioning) and by apical intrusive growth. The increase of the length of cambial initials with age causes a corresponding increase of the length of sieve tube members. The constant length of cambial initials of species with storied structure (cf. Hejnowicz & Hejnowicz 1959) explains the constant length of sieve tube members in those species studied by Parameswaran and Liese (1974).

A shortening of sieve tube members by secondary partitioning was frequently observed (Esau & Cheadle 1955; Zahur 1959), but rarely found in birch, poplar and oak (Esau & Cheadle 1955) and never in *Populus deltoides* (Isebrands & Larson 1973). In the present study no evidence was found for secondary partitioning.

With regard to the diameter of sieve tubes Raskatov and Kosicenko (1968) reported an increase for the first 10 years followed by a more or less constant period in *Populus tremula*. Some *Acacia* and *Prosopis* species do not show any regular relation between sieve tube diameter and distance from the vascular cambium, but there is a slight increase from the upper part of the stem downwards followed by a constant period (Ghouse & Iqbal 1977; Iqbal & Ghouse 1983). MacDaniels (1918) observed an increase with age in some hardwoods (e.g. *Populus deltoides, Ulmus americana*). An increase was also reported for *Populus* × *euramericana* cv. *Robusta* by Stahel (1968) and for branches of *Fagus sylvatica* by Schulz and Behnke (1987).

In the present study the majority of individuals show an increase of the sieve tube diameter with age. This development was not present in birch, although the smallest diameter was found in young bark, too. The length of the period of increase varies between trees and could not be determined in some individuals because apparently it had not ended at the time of sampling.

The average values of sieve tube diameter fit into the range of values reported by most other authors (e.g. Huber 1939; Raskatov & Kosicenko 1968; Kosicenko 1969). In poplar a slightly smaller diameter was observed by Perrédès (1903) and Rees and Shiue (1957/58).

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