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Ontogenesis and structure of periderm in *Acer negundo* L. and x *Fatshedera lizei* Guillaum

MARZENA WACOWSKA

Department of Plant Anatomy and Cytology, Warsaw University, Krakowskie Przedmieście 26/28, 00-927 Warszawa, Poland

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Abstract

The ontogenesis and structure of the periderm were investigated in two dicotyledonous plants: *Acer negundo* L. and x *Fatshedera lizei* Guillaum. In *Fatshedera lizei* periderm is produced by the monolayer of phellogen proper, whereas in *Acer negundo* sometimes cells in the immediate neighbourhood of phellogen proper, particularly the phelloderm participate in the formation of periderm. In *Acer negundo* at the boundary with the next annual phellem increment typical phelloid cells are present. Their thick walls contain pectins, cellulose and lignin, but do not contain suberin. The presence of phelloid was not detected in *Fatshedera lizei*. The walls of the phellem cells with horseshoe shaped thickenings of the inner tangential walls contain, beside pectins, cellulose and lignin, also a thin suberin layer directly on the primary walls. Thus, they are specifically shaped thickwalled cork cells. It is suggested to refer to the suberin layer jointly with the thick cellulose-lignin layer of the walls of thickwalled cork cells by the term "secondary wall". The term "tertiary wall (lamella)" is reserved for thin wall strata of the type of "membranogenic stratum" and "warty stratum". In *Acer negundo* the structure of the suberin layers in the thick cell walls of cork proper is complex.

Key words: cell wall, cork cells, periderm, phelloid

INTRODUCTION

The terminology concerning periderm has not changed since the review paper by Mühldorf (1926) appeared. The periderm consists of: phellogen, cork (phellem) deposited outside by phellogen and the parenchymatic phelloderm forming inwards. Wacowska and Tarkowska (1983) proposed new terms for the particular stages of periderm development, initiated in the subepiderm. Cells capable of division formed after the first division of subepiderm are named primary phellogen. The name phellogen proper was given to the

single cell layer lying immediately outside the phelloderm. Phellogen zone refers to the periderm layer of several-cell thickness, preserving meristematic properties.

Phellem of some gymnospermous and dicotyledonous plants contains, beside cells with suberised walls (cork proper), also cells of different chemism and wall thickness, but having a common trait, that is a lack of suberin in the cell walls. Cells of this kind occurring singly or in continuous layers are called phelloid. The latter may be thinwalled (*Betula alba*), thickwalled (*Liriodendron tulipifera*), with horseshoe-shaped thickenings in the walls (*Viburnum opulus*), with purely cellulose walls or saturated to various degrees with lignin.

Attempts have been undertaken to elucidate the role of phelloid: the thickwalled type is supposed to be an additional mechanical protection for the underlying tissues, whereas the thinwalled type may participate in the cracking and desquamation of older parts of the bark. The role of the single phelloid cells in the phellem remains obscure.

Cork proper may be composed of thickwalled cork cells with a cellulose layer on the suberin wall and cells of thinwalled cork without it. The cellulose layer may undergo lignification. It may be so thin that it is undetectable in the light microscope, or my be absent. The investigations of Wattendorff (1973b) in the electron microscope demonstrated a complete lack of this deposit in *Larix* and *Picea*.

The delicately lamellated suberin layer of thick- and thinwalled cork is generally considered as a secondary wall, whereas the cellulose layer as a tertiary wall (lamella) (Mader 1954, Sitte 1966, Wattendorff 1973a, b, Frey-Wyssling 1976, Schmidt and Schönherr 1982, Vogt et al. 1983).

The role of cork in the plant is well known so is its origin and development. In the pertinent literature, however, exhaustive data are lacking on its ontogenesis, structure, role and factors inducing phelloid cell differentiation. The present study is a continuation of the foregoing investigations concerning phelloid of *Viburnum opulus* (Wacowska and Tarkowska 1983). The investigations have been extended to comparative studies on the development and structure of the periderm in two selected dicotyledonous plant species and an attempt is made to establish the terminology concerning thickwalled cork cell walls.

MATERIAL AND METHODS

The periderm of stems of two species was investigated: *Acer negundo* L. (*Aceraceae*) and x *Fatshedera lizei* Guillaum (*Araliaceae*) — an intergeneric hybrid of *Fatsia japonica* Decne. et Planch. and *Hedera helix* L.

The observations were made in the light microscope (LM) and partly in the electron microscope (EM). For LM examination fresh material fixed in chromacetoformalin (CrAF 0.5:1:20%) or in 70 per cent ethyl alcohol was used for preparing free-hand or microtome sections. The microtome sections were stained with iron haematoxylin after Heidenhain (Gerlach 1972) and fuchsin O with picric acid (Braune et al. 1975).

The chemism of the periderm cell walls was tested by routine specific staining and microreactions and with polarised light.

Material from *Acer negundo* stems for EM examination was fixed in glutaraldehyde after Karnovsky (1965) at pH 7.2 and postfixed in 2 per cent OsO_4 and embedded in Epon 812. Ultrathin sections were cut with an LKB ultramicrotome, contrasted by Reynolds' method (1963) and inspected in a Tesla BS 500 electron microscope.

RESULTS

Acer negundo L.

Young annual *A. negundo* stems are covered with epiderm with a thick underlying cuticle. In the first year periderm is initiated only under the lenticels and forms arches under them. In the subsequent years successive arched annual cork increments appear immediately under the previous year's cork (Fig. 1). On the edges of the cork arches periderm is initiated in the subepiderm. In the 4th-6th year of stem development the peridem arches expanding to the sides coalesce forming a continuous ring around the stem. The annual cork increments are distinctly circumscribed (Figs. 1 and 4).

The periderm is formed of radial rows of overlying phellem cells, phellogen and phelloderm (Figs. 2 and 3). Each row of phellem formed in the course of one vegetation season is usually built of 3-4 cells of various structure and wall chemism. Towards the end of the year there remain, in the mature periderm at the border of phellem and cortical parenchyma, with similar frequency, either two cells of parenchymatous character, that is phellogen proper cell and phelloderm cell (Fig. 2) or only a phelloderm cell (Fig. 3). This is the result of the fact that in the last phellogen proper division in the given season either a phellem cell and phellogen proper cell may arise or two phellem cells.

Two ways of development of the periderm can be distinguished in dependence on the site of its initiation (Fig. 18). Figure 18, part A shows periderm initiation in the subepiderm. The first periclinal division leads to the formation of phelloderm inwards and of primary phellogen towards the periphery. The majority of the observed divisions marked on the

diagram as II occur in the primary phellogen and lead to formation of phellogen proper. Only few divisions were noted in cells considered as phelloderm. Subsequent divisions occur only in phellogen proper. Figure 18, part B illustrates periderm formation under the last year's cork layer. The starting point of this process may be the above mentioned two or only one cell of parenchymatous character neighbouring the cortex parenchyma and capable of divisiom. When there are two cells, it is possible as early as after the first division to distinguish phellogen proper and phelloderm, if there is only one cell these tissues can be recognised only after the second division.

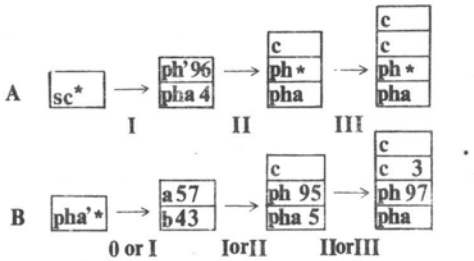
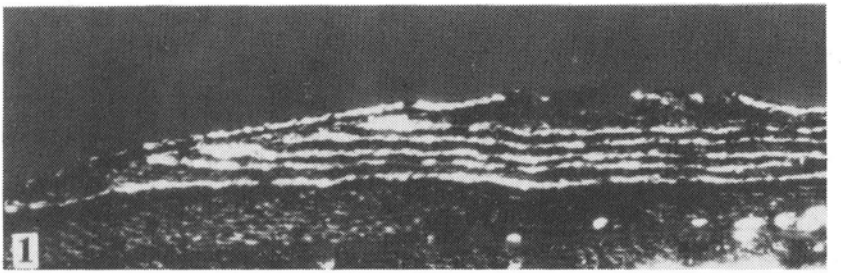


Fig. 18. Two variants (A and B) of periderm development in *Acer negundo*. A — immediately under epiderm, B — under last year's phellem, I-III — successive cell divisions, arabic numerals — — approximate percentage of observed divisions in particular cells at the given stage of periderm development, * — 100% of divisions at given stage of periderm development, sc — subepidermal cell, ph' — primary phellogen cell, ph — phellogen proper cell, pha' — dividing phelloderm cell originating from foregoing year, pha — newly formed phelloderm cell, c — cork cell, a and b — cells of unidentified type, explanation in text

The division leading to unequivocal distinction of phellogen proper and phelloderm occurs with a similar frequency in both of the overlying cells (see Fig. 18B, cells a and b), hence it is difficult to identify the type of these cells. The upper cell (Fig. 18B, a) may be a phellogen proper cell remaining from the previous year, a newly formed primary phellogen cell of even a cork cell. The second cell (Fig. 18B, b) may be a last year's or newly formed phelloderm cell or a cell of newly formed primary phellogen. The subsequent divisions occur almost exclusively in the phellogen proper, only sporadically in cells of its immediate neighbourhood.

Figs. 1-6. Cross sections through periderm of *Acer negundo* stems aged several years Fig. 1. Arched annual cork increments under lenticel Polarised light. x 25. Figs. 2 and 3. Row of overlying periderm cells at border with cortex parenchyma. A — thinwalled cork cells, B — thickwalled cork cells, arrowhead — phelloid cell, ph — phellogen proper, pha — phelloderm. Fig. 2. Fuchsion O with picric acid. Fig. 3 — iron haematoxylin. Figs. 2 and 3 — x 1000. Fig. 4. Successive annual cork increments. Polarised light. x 100. Figs. 5 and 6. Thickwalled cork cells of type B. Variously shaped pits with a lamellated cellulose-lignin layer. Iron haematoxylin. x 1200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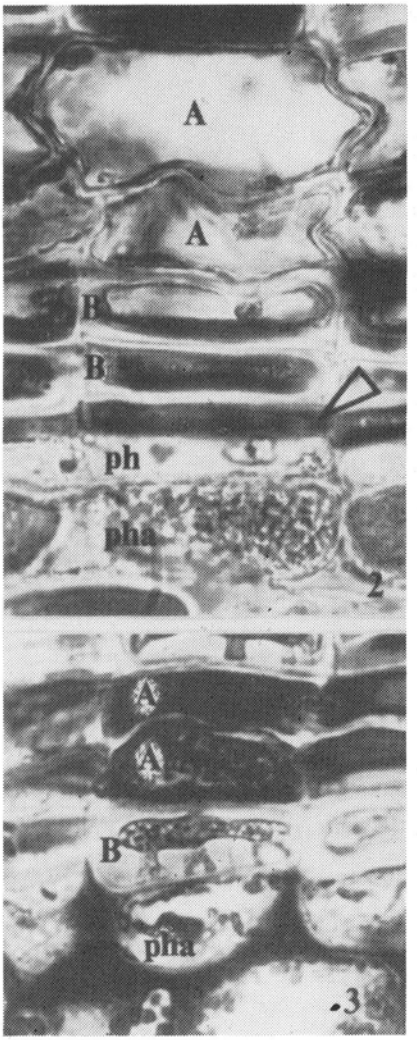
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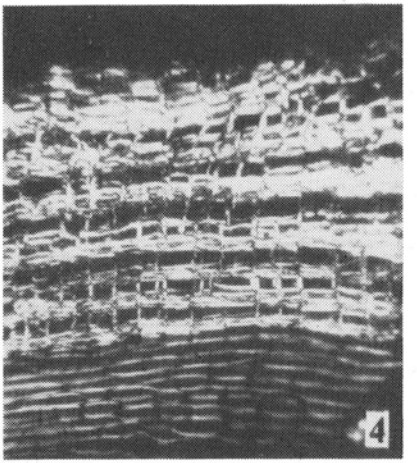
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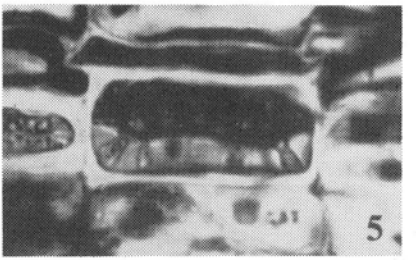
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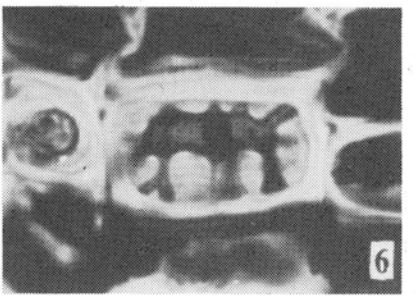
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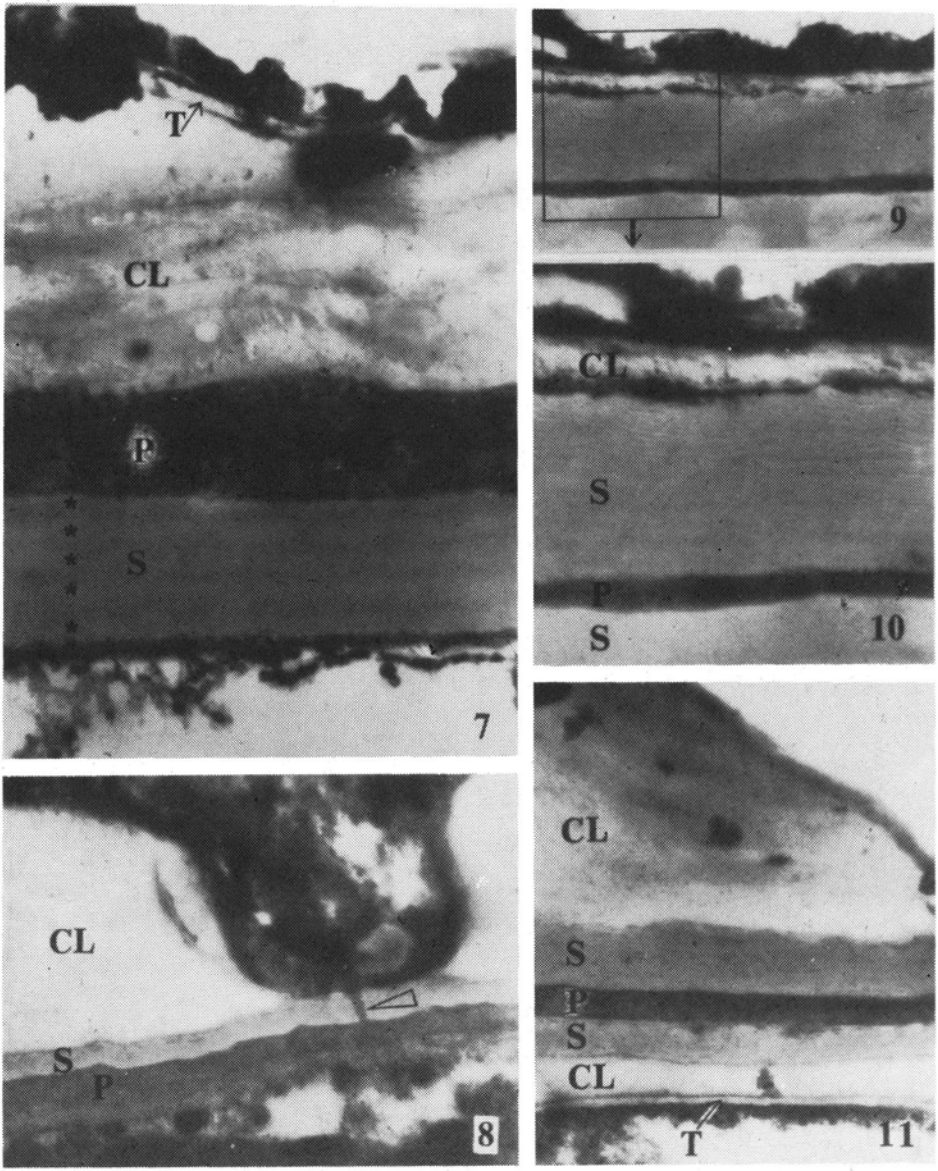
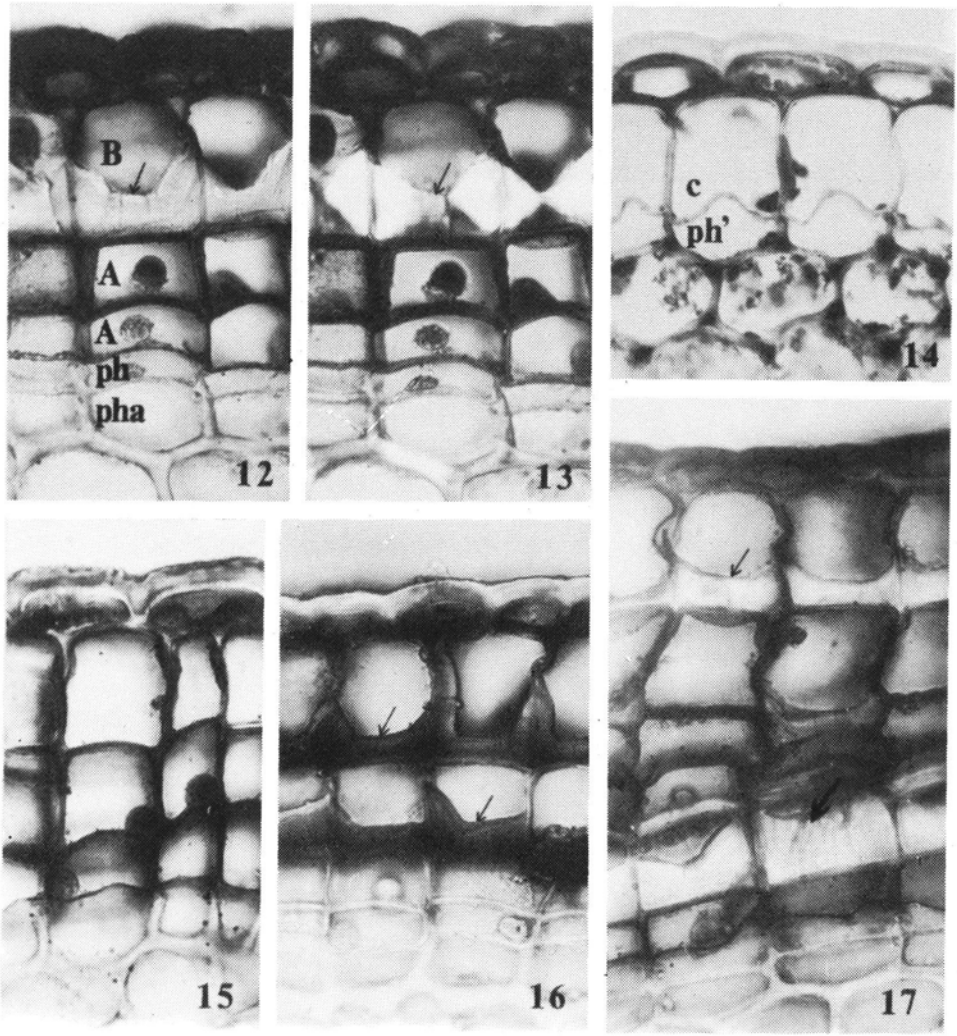


Figs. 7-11. Ultrastructure of cell walls of *Acer negundo* phellem: P — middle lamella and two primary walls bordering on it, S — suberin layer, CL — cellulose-lignin layer, T — tertiary wall

Fig. 7. Boundary between phelloid cell (above) and thinwalled cork cell (below). Asterisks — thick strata in suberin layer. Fig. 8. Boundary between thickwalled cork cell (above) and phellogen (below). Simple pit with plasmodesm (arrowhead) passing through suberin layer. Figs. 9 and 10. Fragment of thickwalled cork cell wall. Thin cellulose-lignin layer on suberin wall. Fig. 10. (enlarged fragment of Fig. 9) — in suberin layer alternating electron clear and dark thin lamellae are visible, the younger markedly thicker than the older ones. Fig. 11. Boundary between two thickwalled cork cells. Very thick cellulose-lignin layer in upper cell wall. Rather thin cellulose-lignin layer in lower cell wall, tertiary wall is visible. Figs. 7-9 and 11 — x 30 000, Fig. 10 — x 60 000



Figs. 12-16. Cross sections through periderm of annual *Fatshedera lizei* stems
Fig. 12. Subepidermal cork cells with horseshoe-shaped wall thickenings. A — thinwalled cork cell, B — thickwalled cork cell, ph — phellogen proper, pha — phelloderm. Sudan Black B. Fig. 13. The same fragment in polarised light. Fig. 14. First stage of periderm development. Stage of two overlying cells. c — cork cell, ph' — primary phellogen cell. Iron haematoxylin. Fig. 15. Cork cells without horseshoe thickenings seen in Figs. 12 and 13. Sudan Black B. Fig. 16. Two cork cell layers with horseshoe-shaped wall thickenings. Floroglucin HCl Fig. 17. Periderm of two-year-old stem. Horseshoe thickening of cork walls from first year (thin arrow) and second year (thick arrow). Sudan Black B. Figs. 12-17 — x 550

Three types of phellem cells have been distinguished in *Acer negundo* in dependence on the structure and chemical composition and lumen size of these cells.

Type A. Cells with a broad lumen, thin suberised cell walls (Figs. 2 and 3, A). In the middle lamella and primary wall pectins were found. It was observed in the EM that in the suberin layer of these cells strata of 80-230 nm can be distinguished, most frequently of 150-170 nm (Fig. 7, asterisks) which consist on the average of 30-40 thin typical suberin lamellae. The thickness of the latter alternating electron dense and electron clear lamellae varies from 4.8 to 5.4 nm.

Type B. Cells tangentially more flattened than in type A. The thick cell wall is built of a suberin layer and a cellulose-lignin one deposited inwards with a small pectin content. Pectins are present in larger quantities in the middle lamella and primary wall. Both layers, the suberin one and cellulose-lignin one, may be of various thickness (Figs. 8-11). In the suberin layer, like in type A cells, alternating electron clear and dense lamellae of 4.8-7.8 nm thickness were revealed in the EM, the younger, that is proximal ones distinctly thicker than the older ones (Fig. 10). The strata formed of thin lamellae were noted only in thick suberin layers. The thickness of these strata, however, is less than in type A cells, amounting on the average to 40-50 nm and comprising only several lamellae.

The cellulose layer saturated to various extents with lignin may cover only the surface of the inner tangential wall (Fig. 5), or even only its fragment, or else it may be very thick and occupy a large part of the cell lumen (Figs. 3, B and 6). After staining as well as in polarised light the parallel lamellation of this layer is usually visible. At the bottom of the numerous, frequently branched pits (Figs. 3, B; 5 and 6) there appear plasmodesms penetrating through the suberin layer (Fig. 8, arrowhead). In some cells at the border of the thick cellulose-lignin layer and protoplasts there is an additional thin layer on the wall, detectable only in the EM (Fig. 11, T). It would seem that it may be a tertiary wall. This layer was not noticeable in the LM after all the stainings and microreactions, hence its chemism could not be determined.

Type C. Cells tangentially strongly flattened with an exceptionally narrow lumen (Fig. 2, arrowhead). Thick cellulose cell walls with traces of pectin substances strongly saturated with lignin. Lignins and pectins were most aboundant in the middle lamella and primary wall, especially in the periaxial part of the cells. Numerous simple pits in the walls. At the border of the protoplast, like in cells of type B, an additional tertiary layer in the wall was found as earlier suggested (Fig. 7, T). Staining and microreaction as well as observation in the EM prove that in the walls of type C cells there is no suberin. Thus, these cells may be considered as phelloid.

It was also ascertained that the middle lamella and the two primary walls adjacent to it at the border of the phelloid cell and the immediately underlying thinwalled cork cell of the next year are exceptionally thick as compared with the same structures occurring at the border of cells in other parts of the phellem (cf. Fig. 7 and Figs. 8, 9 and 11, B).

The row of overlying phellem cells formed in one year comprises: in the direction towards the stem centre: one or two, seldom three thinwalled cells of type A, one or two, sometimes three thickwalled type B cells, one, if any, phelloid cell of type C.

The distribution of the substances composing the cell walls of the three distinguished phellem cell types in *Acer negundo* is shown in Fig. 19.

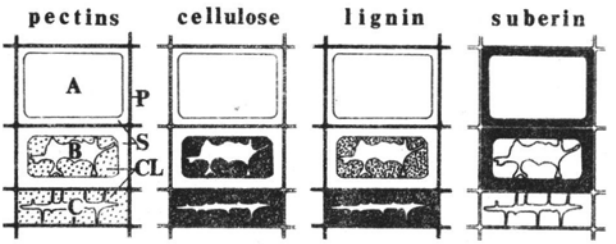


Fig. 19. Chemism of cell walls of the types of phellem cells in *Acer negundo*. Particular wall layers variously shaded in dependence on intensity of staining obtained: A — thinwalled cork cell, B — thickwalled cork cell, C — phelloid cell, P — middle lamella and two primary walls bordering on it, CL — cellulose-lignin layer, S — suberin layer

x *Fatshedera lizei* Guillaum

It is an ornamental house plant, therefore, it is difficult to estimate the age of the stems by examining the structure of the wood. In an annual stem the periderm is initiated in the subepiderm on the whole stem periphery (Fig. 14). One-year periderm consists of radial rows of 4-5 overlying cells (Figs. 12, 13 and 16), two of which of parenchymatous character are phellogen and phelloderm, and two or three consist of cork cells of different structure and wall chemism. In the following years the number of parenchymatous cells in the radial row does not change, but the cork cell number gradually increases.

The initial stages of periderm development are shown in the diagram (Fig. 20). The first division in the subepidermal cells leads to the formation under the epiderm of phellem cells and primary phellogen at the border of the cortex parenchyma. The second division in the primary phellogen leads to the formation of phelloderm and phellogen proper, in which all the subsequent cells divisions occur, notwithstanding the periderm age.

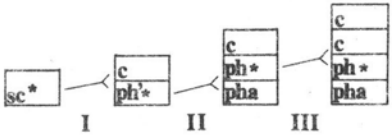


Fig. 20. *Fatshedera lizei* periderm development: I-III — three successive cell divisions, * — 100% of divisions at given stage of periderm development, sc — subepidermal cell, ph' — primary phellogen cell, ph — phellogen proper cell, pha — phelloderm cell, c — cork cell

In the *Fatshedera lizei* periderm two types of mature cork cells were distinguished in the LM.

Type A. Cells with broad lumen usually slightly flattened tangentially, cell walls thin, suberised (Fig. 12, A). Pectins were found in the middle lamella and primary wall.

Type B. Usually cells larger than in type A. A characteristic feature of the walls of these cells is the occurrence on a thin suberin stratum of a lamellated cellulose layer highly saturated with lignin and with traces of pectin substances. Pectins are present in larger quantities in the middle lamella and primary wall. The thick cellulose-lignin layer occupies the surface of the inner tangential wall and a part of the radial ones, hence its shape resembles more or less a horseshoe (Figs. 12, 13, 16 and 17, arrows). It contains some few simple pits.

The distribution of the substances composing the walls of both types of phellem cells in *Fatshedera lizei* is shown in Fig. 21.

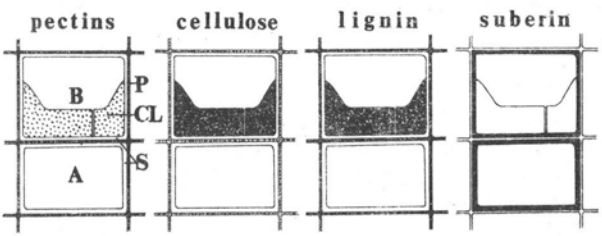


Fig. 21. Chemism of cell walls in two types of phellem cells of *Fatshedera lizei*. Particular wall layers shaded to various extent in dependence on intensity of staining obtained. A — thinwalled cork cell, B — thickwalled cork cell, P — middle lamella and two primary walls bordering on it, CL — cellulose-lignin layer, S — suberin layer

The cork cell arising as the result of division of the subepidermal cell, bordering on the epiderm has in the mature stage usually a horseshoe-shaped thickening on the inner tangential wall (Figs. 12 and 13, arrows). It is not, however, always formed (Fig. 15). In the first year, in the radial

row of peridermal cells there may arise one (Figs. 12 and 13) or two (Fig. 16) cells with such thickenings. The remaining cork cells formed in the same year have thin walls and do not exhibit the characteristic thickenings. On the basis of the periderm structure only the age of annual and two-year-old stems can be determined (Fig. 17). In the following years only cells with horseshoe-like thickenings are formed, so that the boundaries between the annual cork increments disappear.

Phelloid cells were not found in the periderm of *Fatshedera lizei*.

DISCUSSION

Two taxonomical distant, but not random, dicotyledonous plant species were chosen for the investigations. Preliminary observations demonstrated both in *Acer negundo* and in *Fatshedera lizei* a differentiated phellem structure comprising cells differing in shape and wall structure. Noteworthy are cells which in their shape and wall thickness resemble phelloid.

LM investigations of the chemical composition of the cell walls and observations of their structure in the EM showed that in *A. negundo* only in 20-30 per cent of the radial phellem cell walls constituting the successive annual increment there appear phelloid cells. They are always present at the border of the next annual cork increment as the last youngest cells. The greatly thickened sclerenchymatous phelloid walls contain pectin substances, cellulose and lignin, but no suberin. In each of the radial rows of phellem cells formed in the same vegetation season, a smooth transition was noted from thinwalled cork cells via thickwalled cork cells to phelloid cells if the latter are present. Phelloid cells of *Acer negundo* are innermost cells of the annual phellem increment of the same year and do not form continuous layers. Therefore, the specific protective function ascribed to them in this tree species seems doubtful. This role is much better fulfilled by the thickwalled cork cells.

Preliminary LM observation demonstrated that in the phellem of *Fatshedera lizei* there are cells in which the inner tangential walls and parts of the radial ones are greatly thickened and have a horseshoe-like shape. Phelloid cells with similary shaped walls have been found in the periderm of *Viburnum opulus* (Wacowska and Tarkowska 1983). Moreover, the structure of the entire periderm, especially in annual stems, greatly resembles the same tissue in *Viburnum opulus*. Detailed study of the chemism of the cell walls demonstrated, however, that in *Fatshedera lizei* the horseshoe shaped thickenings containing pectins, cellulose and lignin are deposited in a thin suberin layer. Suberin was not found, however, in cells with similar wall thickenings in *Viburnum opulus*. If we assume that the term phelloid refers to the phellem cells the walls of which do not contain suberin, then the cells with horseshoe-shaped wall thickenings in *Fatshedera*

lizei cannot be considered as phelloid. In the latter species they are thickwalled cork cells with characteristically shaped walls. It results there from that the appearance of the cells, their shape and wall thickness may be misleading. Identification of phelloid as a distinct type of cells within the phellem requires analysis of the chemical composition of the cell walls.

Investigations on the ontogenesis of the periderm demonstrated that in the case of *Fatshedera lizei* the phellem cells, apart from those lying immediately under the epiderm originate exclusively from division of the phellogen proper monolayer, notwithstanding the age of the periderm. In *Acer negundo* the situation is more complicated. Beside phellogen proper, the phelloderm cells possess meristematic properties. This appears especially at the beginning of formation of the successive annual cork increments. Few divisions were noted also in the cells lying immediately outside the phellogen proper. The greater part of the divisions observed in the course of periderm formation occurs in the phellogen proper. Therefore, in *Acer negundo*, like in *Fatshedera lizei* there is no typical phellogen zone, such as has been described in *Viburnum opulus*. Thus, in various plants the periderm is produced either by the phellogen proper monolayer or the phellogen zone of several-cell thickness.

In the course of investigation of the complex structure of thickwalled cork cell walls the problem of terminology referring to the particular layers of these walls arose. The investigators mentioned in the Introduction described the suberin layer bordering on the primary wall as secondary wall, whereas the overlying cellulose layer is referred to as tertiary wall or tertiary lamella. According to Frey-Wyssling (1976) the tertiary wall ("T-wall") is very thin. Often two strata can be distinguished in it: "the membranogenic stratum" with a high matrix content and parallelly arranged cellulose fibrils and the "warty stratum" occurring in the form of minute mulls and warts. The appearance of the thick and pitted cellulose--lignin layers in the phellem cell walls of *Acer negundo* and *Fatshedera lizei* does not agree with the description of the tertiary wall given by Frey--Wyssling. Moreover, the distinct lamellation of these layers is a characteristic trait of thick secondary walls. Clowes and Juniper (1968) claim that the term "tertiary wall" suggests marked differences between this type of wall and primary and secondary walls. Therefore, the present author proposes to describe as secondary wall of thickwalled cork cells both layers, that is the suberin one and the overlying cellulose one saturated or not with lignin.

In the EM, at the border of the walls and protoplast of phelloid cells and some thickwalled cork cells a thin layer was found in the

wall, of unknown chemical composition. The present author suggests to consider it as a tertiary wall of "membranogenic stratum" type.

Thus, the term "tertiary wall (lamella)" would be reserved for very thin layers of the type of "membranogenic stratum" and would also comprise the characteristic warty and trabeculate formations appearing commonly both in gymno- and angiosperms in the tracheids, vessels and fibres (Wardrop and Davies 1962, Ledbetter 1963, Wardrop et al. 1963, Schmid and Machado 1964) and even in phloem companion cells (Wark 1965).

In observations of the phellem wall cells ultrastructure in *Acer negundo* the presence of two kinds of subunits was noted in the suberin layers of thin- and thickwalled cork walls. The first kind are typical for common suberin walls with alternating electron clear and dark lamellae of 4.8-7.8 nm thickness. Schmidt and Schönherr (1982) determined analogous lamellae in the walls of cork cells of potato tubers as 5-10 nm thick. Ryser et al. (1983) measured accurately the thickness of such lamellae in the cellulose--suberin walls in green cotton fibres and report their thickness as 4.2 ± 0.4 nm. Suberin lamellae, notwithstanding the examined plant have in various plant species a similar thickness. The second kind of subunits are "superlamellae" — strata 40-230 nm thick built of several to several score thin lamellae independently of the cell type. They can be distinguished only in thick suberin layers. The authors of the above quoted papers disregarded them.

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Ontogeneza i struktura perydermy u Acer negudo L. i x Fatshedera lizei Guillaum

Streszczenie

Badano ontogenezę i strukturę perydermy dwu wybranych gatunków roślin dwuliściennych: *Acer negundo* L. i x *Fatshedera lizei* Guillaum. U *Fatshedera lizei* peryderma wytwarzana jest przez jednowarstwowy fellogen właściwy, natomiast u *Acer negundo* w budowie perydermy uczestniczą niekiedy komórki bezpośrednio sąsiadujące z fellogenem właściwym, a zwłaszcza felloderma. U *Acer negundo*, na granicy z następnym rocznym przyrostem fellemu, występują typowe komórki felloidu. Ich grube ściany zawierają pektyny, celulozę i ligninę, ale ale nie zawierają suberyny. U *Fatsedera lizei* nie stwierdzono obecności felloidu. Ściany komórek fellemu z podkowiastymi zgrubieniami wewnętrznych ścian stycznych, poza pektynami, celulozą i ligniną, zawierają także cienki pokład suberynowy odkładany bezpośrednio na ścianach pierwotnych. Są to więc specyficznie ukształtowane komórki korka grubościennego. Autorka proponuje, aby pokład suberynowy łącznie z grubym pokładem celulozowo-ligninowym ścian komórkowych korka grubościennego określić wspólnie terminem "ściana wtórna". Nazwa "ściana (lamella) trzeciorzędowa" zostaje zachowana dla cienkich pokładów ściennych typu "membranogenic stratum" i "warty stratum". U *Acer negundo* stwierdzono złożoną strukturę pokładów suberynowych w grubych ścianach komórkowych korka właściwego.