THE INTRUSIVE GROWTH OF INITIAL CELLS IN RE-ARANGEMENT OF CELLS IN CAMBIUM OF *TILIA CORDATA* MILL.

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ABSTRACT

In the cambium of linden producing wood with short period of grain inclination change (2-4 years), the intensive reorientation of cells takes place. This is possible mainly through an intrusive growth of cell ends from one radial file entering space between tangential walls of neighboring file and through unequal periclinal divisions that occur in the „initial surface". The intrusive growth is located on the longitudinal edge of a fusiform cell close to the end, and causes deviation of cell ends in a neighbouring file from the initial surface. Unequal periclinal division divides a cell with a deviated end into two derivatives, unequal in size. The one of them, which inherits the deviated end, leaves the initial surface becoming a xylem or phloem mother cell. This means that the old end is eliminated. The intensity of intrusive growth and unequal periclinal divisions is decisive for the velocity of cambial cell reorientation. The oriented intrusive growth occurs only in the initial cells. For that reason, changes in cell-ends position do not occur within one packet of cells but are distinct between neighbouring packets.

KEY WORDS: cambium, intrusive growth, unequal periclinal division, initial surface

INTRODUCTION

During seasonal activity of cambium as the result of continuous periclinal divisions, packets of cells are visible on the cross section of phloem and xylem increment. Examining cell packets, the occurrence of anticlinal divisions and radial dimension of cells in the rays, makes possible the positive identification of an initial cell (Sanio 1873, Mischke 1890, Bannan 1950, 1968, Wilson et al. 1966, Mahmood 1968, 1971, 1990, Murmanis 1970, 1977, Timell 1980, Włoch and Zagórska- Marek 1982, Włoch 1988). Locating the cell allows us to distinguish the situation in which after periclinal division the mother cell is deposited on the side of wood, from the one resulting in mother cell deposition on the side of bark.

The number of cells making one packet is different on the side of wood from that on the side of bark. In the first case the packets usually consist of four cells, whereas in the second one, of two (Mahmood 1968, 1990, Timell 1980, Włoch and Zagórska-Marek 1982, Włoch 1988). At the location of the initial cell, there is a packet of four cells, the so-called "Sanio's four" consisting of the initial cell, a mother, and two daughter cells. Sometimes, in absence of the division in the initial cell, in its derivative or both, the packet consists of only three or even two cells (Murmanis 1970, 1977, Timell 1980, Włoch and Zagórska-Marek 1982).

Cell arrangement in non-storied cambium changes in result of such cellular events like: oriented intrusive growth of cell ends, oriented anticlinal divisions (Hejnowicz 1975) and imperfect periclinal divisions (Savidge and Farrar 1984). In storied cambium anticlinal divisions are less important for the intensity of cell reorientation than in non-storied cambium (Zagórska-Marek 1984). The mechanism of reorientation depends mainly on intrusive growth and elimination of parts of the neighboring initial cells as a result of unequal periclinal divisions (Hejnowicz and Zagórska-Marek 1974, Włoch 1976, 1981).

The intensity of cell re-arrangement in storied cambium depends on growth activity of the initial cells (Zagórska-Marek 1975, 1984, Włoch and Zagórska-Marek 1982, Włoch 1987, Włoch and Bilczewska 1987, Włoch and Wawrzyniak 1990). Till now, the activity was defined on the basis of:

1. the presence of furcated cell ends (Zagórska-Marek 1975), (furcation of the cell end represents the intermediate stage between two succesive positions of the end on the border between adjacent storeys)
2. the extent of cell-end dislocation along the storey border measured in a number of passed by cell ends from the adjacent storey.

The state of ends of rebuilding cells, contacting on the border between storeys (defined on the base of the placement of growing end) changes in subsequent, adjacent layers of cambium discontinuously. The investigation of cambium of linden reveals that the state of cell ends within one packet is the same and changes progressively in subsequently deposited packets. The given state is transferred to the mother cell which usually transfers it to the four-cell packet of xylem or two-cell packet of phloem. The most advanced re-arrangment occurs in the packets which contain initial cell, in other words in the "Sanio's four" (Włoch 1988), (Fig. 1). If the position of cell ends within the "Sanio's four" is the same, then it would be impossible to point out the locality of the initial cell. However, in most cases the state of cell ends in the "Sanio's four" is not the same and the initial cell is the one with most advanced rebuilding. This means that the oriented intrusive

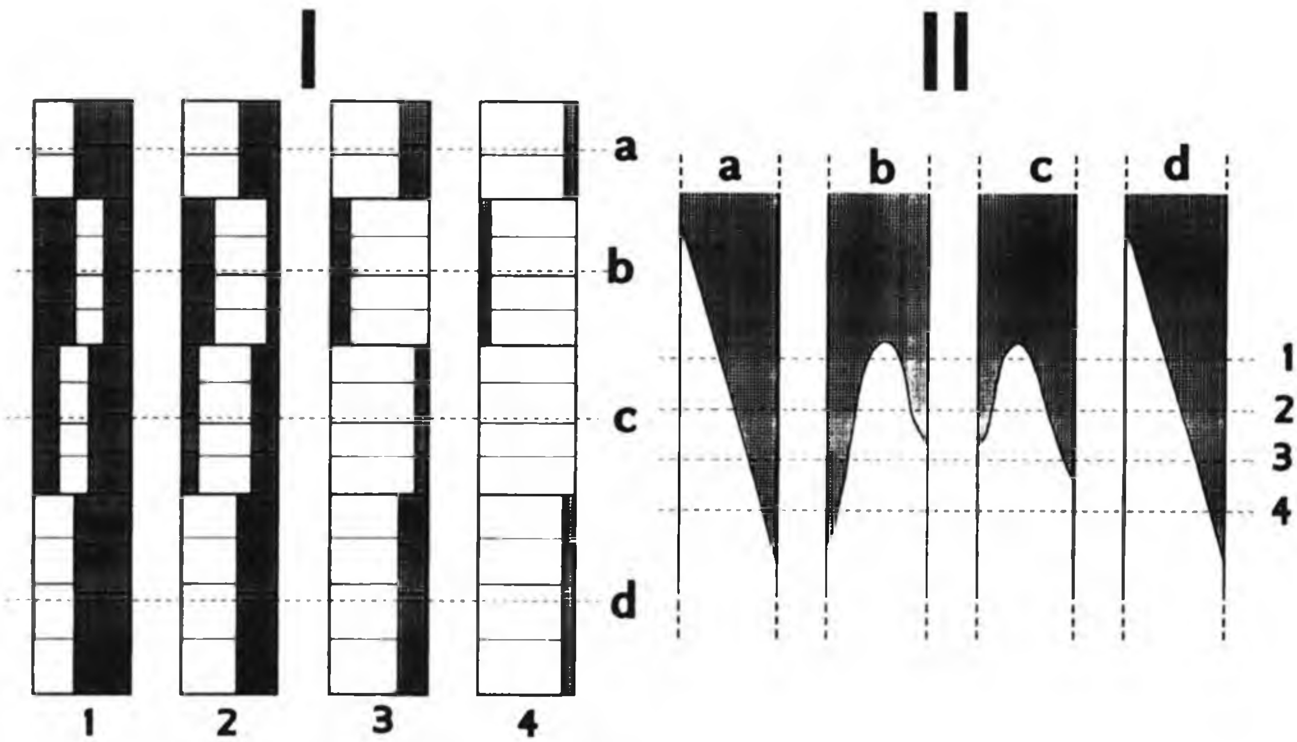

Fig. 1. The scheme illustrating the re-arrangement of cell ends in two neighboring radial files. Column I – series of transverse sections, column II – series of tangential sections. The basal end of the cell from the upper file is furcated. Its rebuilding took place in configuration Z (view from the bark side). 1, 2, 3, 4 – selected succeeding transverse sections; a, b, c, d – selected succeeding tangential sections passing through the middles of cell packets. First packet on the top consists of two cells determined for phloem, the second packet consisting of four cells contains initial cell; the following third and fourth packet, consisting of four cells, are determined for xylem. To simplify the scheme inclined tangential walls and deviation of cell ends from the initial surface are omitted

growth and unequal periclinal divisions occur only in the initial cells.

The analysis of the arrangement of growing ends reveals that the initial cells in cambial zone are located nearer to phloem, and that their radial dimension is relatively big (Wloch and Zagórska-Marek 1982, Włoch 1988).

The intrusive growth is located both on radial and longitudinal edge of the initial cell (Włoch 1981), (Fig. 2). The intrusive growth on the longitudinal edge, occurring between the tangential walls of neighboring cells, leads to the overlapping of parts of two neighboring initial cells from one radial file.

The fragment of the cell, which is most deviated from the layer of initial cells, is eliminated. It proceeds as follows: the plain of a new periclinal division does not pass across the deviated part of a cell, so newly formed daughter cells are unequal in size, the smaller cell becomes the initial cell (Hejnowicz 1961, 1974, Catesson 1974). The described mechanism is the most important way of re-arrangement of storied cambium.

In normally growing cambium the configuration of cellular events (and in consequence wood grain) depends on the behavior of initial cells. In a given period of time and in a given location cambial cell re-arrangement proceeds in one, defined direction. Such areas, where the cellular events occur in one configuration are defined as domains (Hejnowicz 1964, Bannan 1966).

The aim of this work is to indicate the contribution of oriented intrusive growth and unequal periclinal divisions in cell reorientation in the storied cambium in its normal growing conditions.

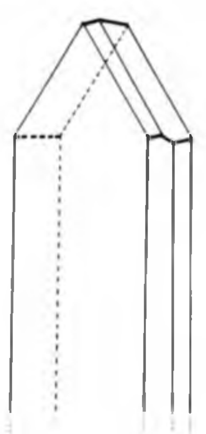

Fig. 2. The end of cambium cell with various edges. Radial edges are marked with a bold line, longitudinal ones with a thin line. The radial edges are either apical or lateral.

MATERIAL AND METHODS

Cambium of the 100 year old linden was sampled from the trunk at the height of 1 m above the ground level, at the time of its highest seasonal activity (Włoch and Zagórska-Marek 1982). Samples were fixed in glutaraldehyde fixative, dehydrated in alcohol series and embedded in the epon resin (Włoch 1981). Then they were sectioned with ultramicrotome. Longitudinal and transverse sections 3 μm thick were stained with PAS method and toluidine blue. Series of sections were analyzed microscopically. Fragments of cambium where the cell re-arrangement was visible were photographed. On the basis of serial photographs of transverse sections, the tangential reconstruction was made (Hejnowicz 1961, Włoch 1981).

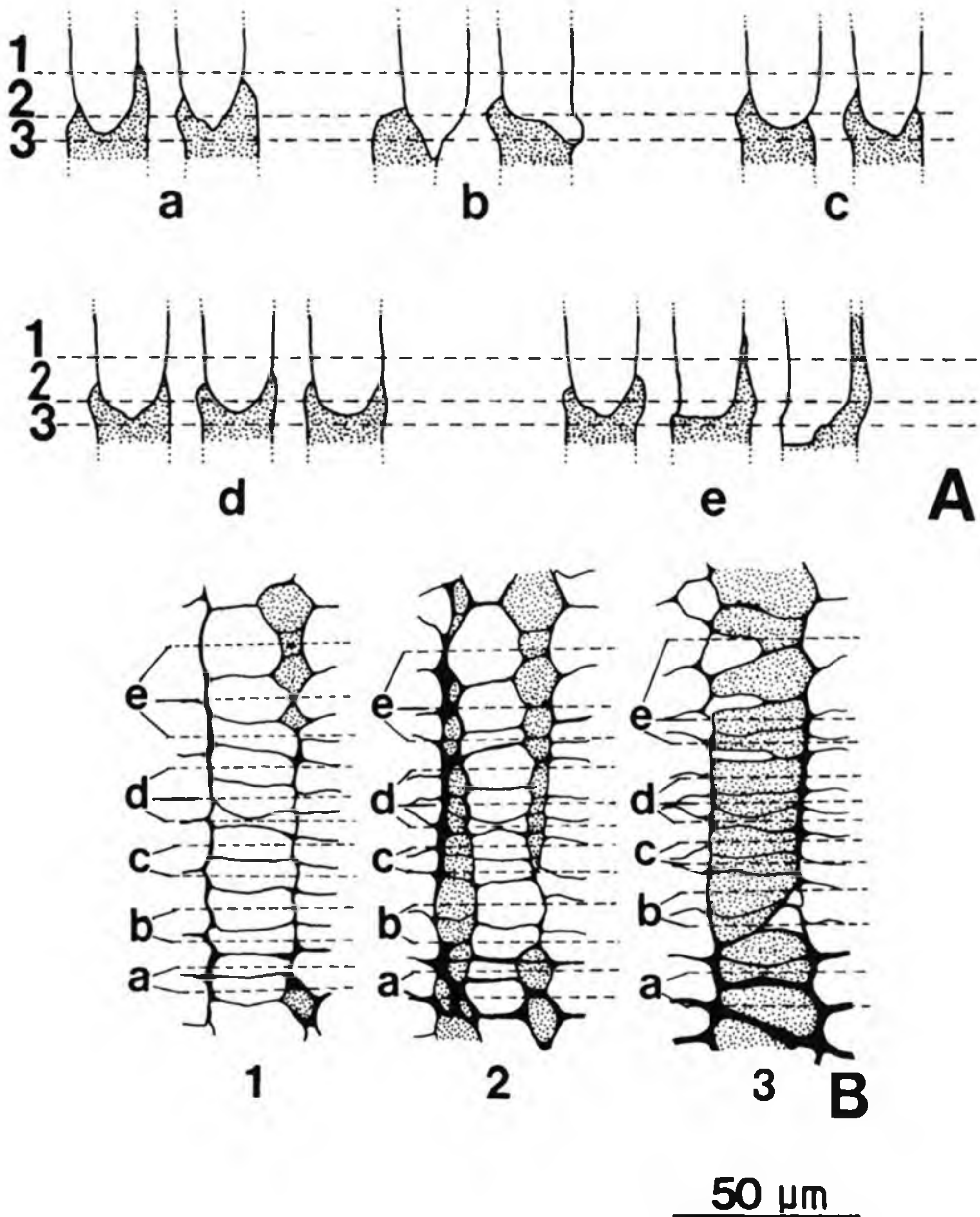

Fig. 3. The scheme illustrating re-arrangement of neighboring ends of initial cells in two radial files on the border between storeys.
A – Adjacent reconstruction of location of the cell ends within cell packets **a** – **e** prepared on the basis of series of transverse sections. Dashed line indicates three levels of transverse sections which are shown in Fig. 3B.
B – Transverse sections corresponding to the successive levels 1, 2, 3, shown in Fig. 3A. Packets containing 3 or 2 cells are marked with letters of the alphabet (**a** – **e**). Dashed lines – cells within selected packets (only dotted area).

Selected photographs of transverse sections were overlapped in order to show the state of cell ends that were rebuilding (active) in comparison with the state of cell ends which were not changing (inactive) in neighboring files.

RESULTS

In the cambium of linden during its highest seasonal activity, the packets of cells are best visible. The packet containing the initial cell usually consists of four cells (Sanio's four), sometimes it contains only 3 or even 2 cells. Nevertheless the initial cell can be always easily identified.

When in the reconstruction the position of an apical end of the initial cell in one radial file is examined in relation to the basal end of the cell from the upper storey the process of rebuilding becomes clear, Fig. 3. The end becomes furcated, whereas the basal end of the cell in the upper layer is not furcated, Fig. 3A. In the packet **a** shown in Fig. 3B the cells are determined for the bark side. The packet **b** is made of the initial cell and its closest derivative. In the neighbourhood of the latter packet changing status of the basal end of a cell from the upper storey is most distinct. The end grows between tangential walls of the lower storey, so that the "old" end of the lower initial cell is eliminated (lack of furcation). Two-cell packets **b** and **c**, and the three-celled packet **d**, distinguished by analysis of the state of cell ends, give the evidence that the periclinal divisions leading to the formation of four-cell packets didn't take place. In Fig. 3 only a part of the packet **e** is visible.

In order to explain the change of cell-end state, two transverse serial sections (marked in the Fig. 3B with numbers 2 and 3) were overlapped (Fig. 4). The vertical distance between these two sections was 12 μm. The vertical view of overlapped transverse sections shows that the cell walls in other files in both sections almost cover each other. It means that the re-arrangement of the cells takes place only in one radial file. At the site of the change the new walls of periclinal divisions do not twist (thin arrow). The change of the state of the initial cell end is a result of intrusive growth on the longitudinal edge between tangential walls of cells of the neighbouring file. It causes a deviation of these walls, so they locally become inclined (wide arrow). Therefore the deviation of the tangential walls does not result from twisting of the plain of division. Inclined tangential walls are observed on the borders of packets. This confirms that the intrusive growth on the longitudinal edges takes place exclusively in the initial cells. This kind of growth results in overlapping of the ends of two initial cells and causes local disturbances of radial growth in the layer of the initial cells. Overlapping of the ends is transitional, and the end of one initial cell, the more deviated one, is eliminated after unequal periclinal division.

Cell-end furcation does not always mean the active cell re-arrangement. On the other side, during the process of cell re-arrangement mutual changes in cell end positions in subsequently formed packets are not always associated with the presence of furcated ends. This happens when the re-arrangement starts with the intrusive growth of the initial cells between the tangential walls of neighboring file, instead of the radial ones. Periclinal division that follows these events saves the position of deviated end. The situation when the intrusive growth which splits the tangential walls influences cell arrangement but does not result in furcation of cell ends, is shown in Fig. 5 and 6.

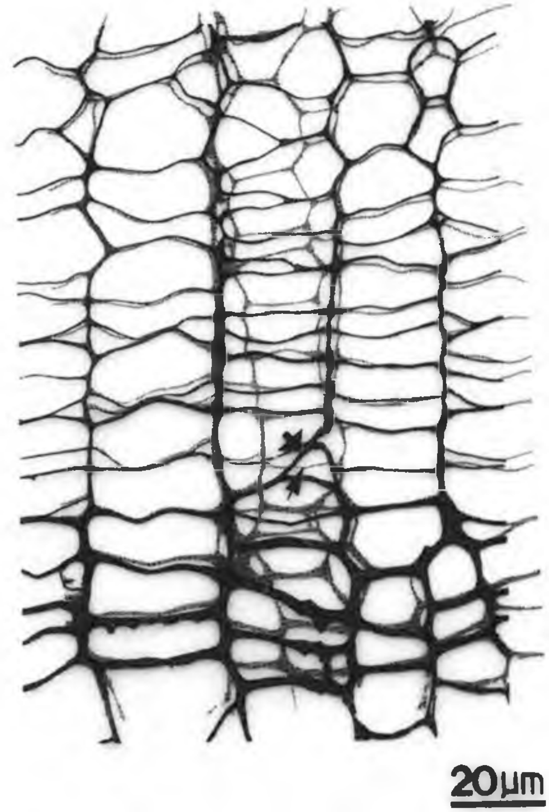

Fig. 4. Overlapped photographs of two transverse sections distant 12 μm one from another. The upper section is lighter. The wide arrow indicates inclinally deviated tangential walls of cells from the lower storey. The thin arrow indicates the partition wall of the new unequal periclinal division in the upper storey.

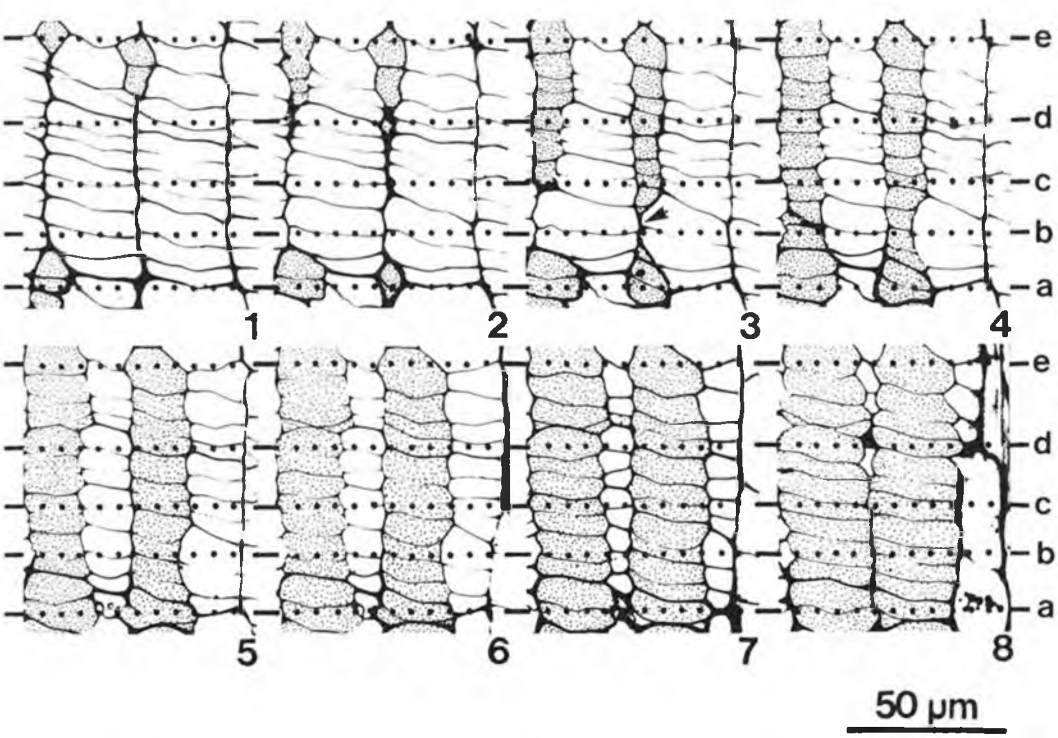

Fig. 5. Photographs of a series of transverse sections.Two files are shown with cambial cells where the process of re-arrangement occurs. The sections are 3 μm thick – the series is made from every fourth section.The dotted line indicates cells (**a** – **e**) which are shown in Fig. 6. in the longitudinal view. The dotted line (**d**) indicates the place where the initial surface occurs. The cells indicated with the arrow exhibit the most advanced re-arrangement of ends. Re-arrangement takes place in configuration Z. Apical ends of cells from the lower file are filled with a dotted pattern.

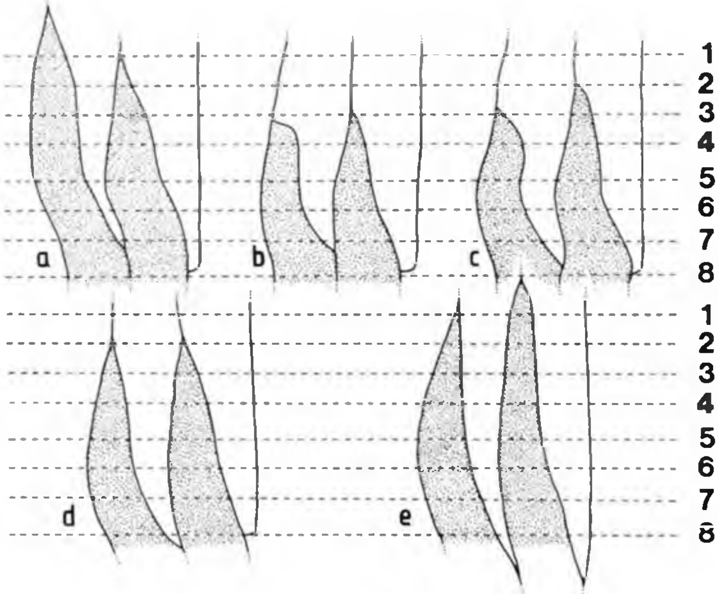

Fig. 6. Picture illustrating cell ends re-arrangement of two contacting cells from two selected files on the border between storeys in the longitudinal reconstruction. Dashed lines (1 – 8) indicate the levels on which the photographs shown in Fig. 5. were taken. Drawings are shown in five different planes (**a** – **e**).

From photographs of a series of transverse sections (shown in Fig. 5) three were chosen. The photograph of the uppermost section (1) overlapps the photograph of the middle section (2), (Fig. 7A), and the middle one overlapps the lowest one (3), (Fig. 7B). Section 1 is 25 µm away from section 2, which is 18 µm away from section 3. At the location where the intrusive growth of the initial cell separates the tangential walls of the neighboring files (wide arrow), one may see the deviation of tangential walls of the adjacent cells in the same radial file (Fig. 7A, thin arrow).

The possible changes in mutual position of cell ends of two initial cells during cell re-arrangement from the configuration Z to the configuration S (arrows), are shown schematically in Fig. 8. The intrusive growth may separate radial walls, which results in cell-end furcation, or the tangential walls, which results in a change of cell end position without furcation. There

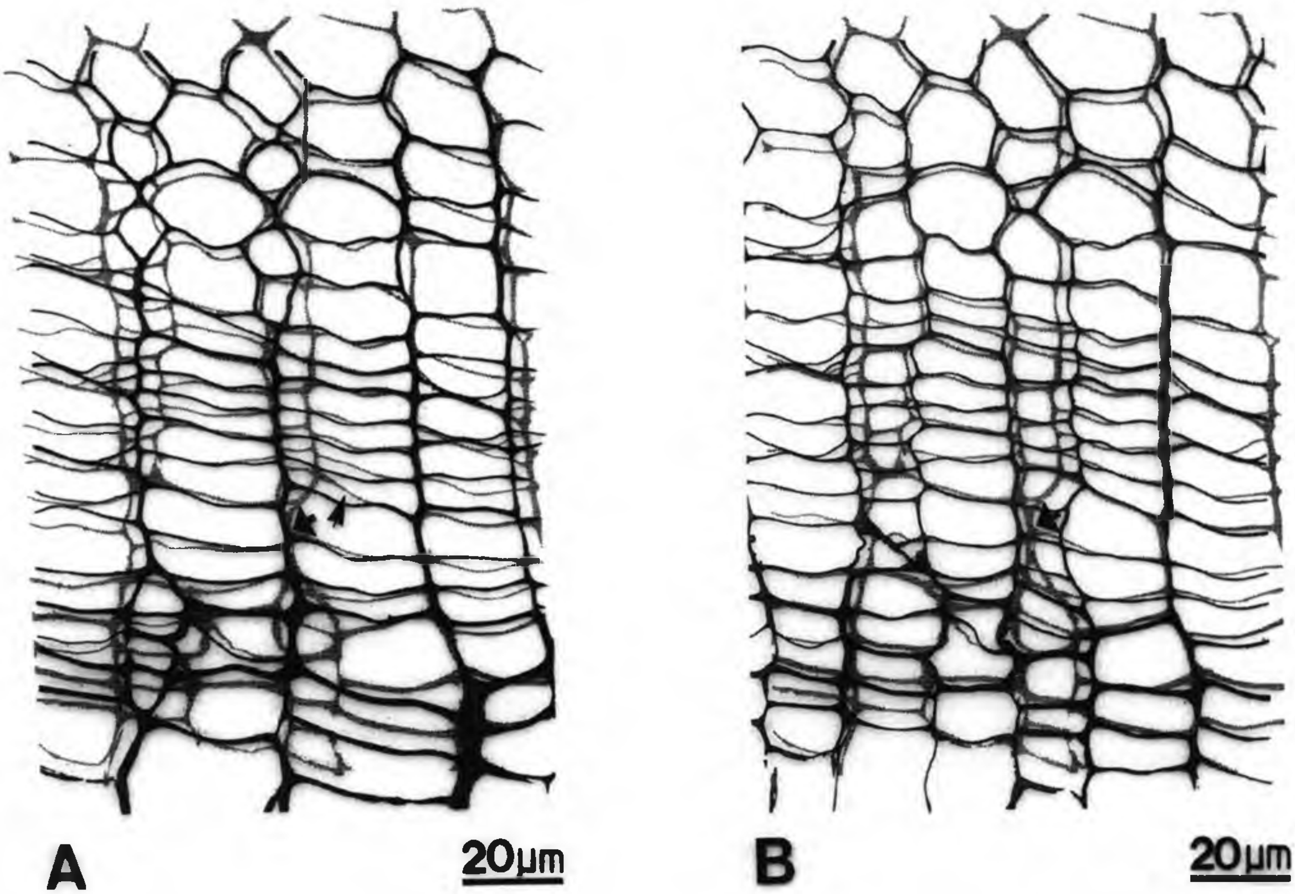

Fig. 7A and B. Overlapped pairs of photographs of transverse sections; the distance between sections in each pair of photographs is as follows: pair A – 25 µm, pair B – 18 µm.
The wide arrow indicates the largest scope of end state. The deviation of tangential wall is indicated with the thin arrow.

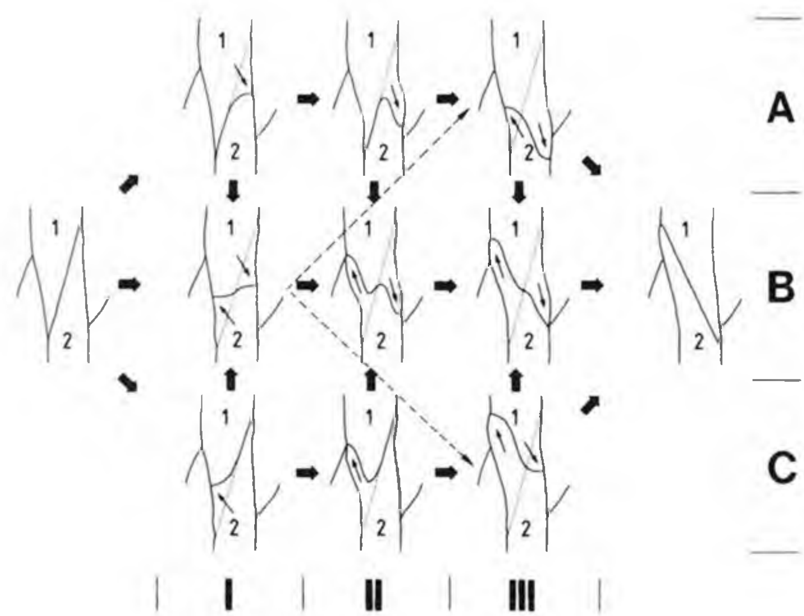

Fig. 8. The scheme illustrating possible changes of cell ends position of fusiform cells from the neighboring storeys on the border beween storeys (ends grow simultaneously or at different times). The rebuilding occurs in configuration S. Upper series (A) – represents the situation when the basal end is active, lower file (C) – when the apical end is active; middle series (B) – when both apical and basal neighboring ends are active (simultaneous activity of contacting ends was not observed); I, II, III – different stages of re-arrangement advancement. Wide arrows – direction of rebuilding, dashed arrows – cell re-arrangement without the stage of cell end furcation, small arrows – direction of intrusive growth.

are shown three different situations illustrating growth of initial cell ends (A-C) in three stages of the possibility (I–III). In the stage I, as a consequence of intrusive growth which separates the tangential walls, the change of cell end position takes place and the furcation does not occur. In the second stage the intrusive growth separating radial walls leads to the cell-end furcation. The most advanced change of the cell end position in the stage III, is a consequence of coupling of both types of intrusive growth. This direction of rebuilding is marked with short, wide arrows, whereas cell re-arrangement occuring without the stage of cell end furcation is marked with dashed arrows. In the normal growing cambium both ways of cell re-arrangement may exist.

DISCUSSION

Cambium is a special and very difficult to define tissue (Schmid 1976). Murmanis (1977), while investigating the packets of cells in active and resting cambium of *Quercus rubra* L. by electron microscope, she could not distinguish initial cells, and for that reason she concluded that each cell from the packet "Sanio's four" could undertake the function of an initial cell in future. Puławska (1973), while searching the presence of periclinal divisions in neighboring files concluded, that the sequence of divisions during formation of four-cell packets is optional. According to Catesson (1980) it is likely that under the influence of a local tension the status of an initial cell may be shifted to any other cell from the packet. We applied a developmental criterion, because it is very difficult to distinguish an initial cell using the anatomical methods (Murmanis 1977, Timell 1980, Catesson 1984). Savidge and Farrar (1984) on the basis of their observation of the natural spiral grain development in *Picea glauca* (Moench.) Voss. and during the extorted re-arrangement in the bridges of cambium in *Pinus concorta* Dougl. ssp. latifolia concluded, that the status of the initial cell or mother cell does not exist and one should rather refer to the regulatory factor controlling the behaviour of undifferentiated cells in each radial file. According to Warren-Wilson (1978), the sum of the respective concentration of auxin and saccharosis could be this factor. Either in storied or nonstoried cambium the cell re-arrangement occurs. This process, sometimes becoming very dynamic, is connected with the change of the cell inclination in the tangential direction, to the trunk axis. The re-arrangement is also connected with the cyclic change of the cells' length (Krawczyszyn and Romberger 1979).

It has been observed that the rebuilding in the storied cambium happens mainly due to the intrusive oriented growth between the tangential walls. It leads to the local overlap of the initial cell ends and to their deflection from each other. The periclinal divisions that occur in such situations are unequal, because the deflected cell ends are out of the division plain. The plains of the unequal periclinal divisions are undistinguishable from other periclinal division plains occuring in the whole cambial zone (Bannan 1955, Wilson et al. 1966, Schmid 1976, Catesson 1984). As the result of unequal periclinal divisions two derivative cells of different sizes are formed. These divisions lead to the partial elimination of the old (deflected) initial cell ends (Hejnowicz 1961, Hejnowicz and Zagórska-Marek 1974).

Savidge and Farrar (1984) while studying the intensive cell re-arrangement in non-storied cambium introduced a term „imperfect periclinal divisions". It seems to be similar to the term „unequal periclinal divisions", but the one used by Savidge and Farrar was not precisely defined.

Our observations of transverse sections reveal that in storeyed cambium of linden, with intensive cell re-arrangement, the tangential walls between subsequent packets are sometimes inclined. However, these are not the twisted tangential walls, but they are formed in the process of deflection of already existing walls under the influence of intrusive oriented growth between the tangential walls of neighboring cells.

The oblique periclinal walls which are visible between the packets and a different range of the ends of fusiform cells in succesive cell packets, confirm the rebuilding of the whole cell arrangement as the result of changes in initial cells. Gradual changes occuring in the initial cells are recorded in the formed mother cell and, after its division, in the derivative cells.

A furcation of the end of the fusiform cell was often described as a medial stage in a cell re-arrangement in cambium. In the case of the intrusive oriented growth between tangential walls, the process of rebuilding is carried on without the furcation of the ends.

Considering the mechanisms described in this paper, which take part in the rebuilding of the cell arrangement, and the opinions of many authors, we have decided to introduce a term "initial surface" instead of the initial layer of cells. The term "initial surface" is used here in the physiological sense (probably it is a place of a special concentration of morphogenes) and in the geometrical sense, according to the anatomical slides, analysis.

CONCLUSIONS

1. The rebuilding of cell arrangement depends mainly on the oriented intrusive growth of the initial cell ends between tangential walls of cells in the neighboring file. The ends of initial cells overlap, what is the reason of their local deflection. The periclinal division does not occur in the deflected end and that is why two cells of different size are formed. Consequently, there occurs the elimination of the deflected end of one initial cell.
2. The intrusive oriented growth between the tangential walls has an influence on the intensive cell re-arrangement, but does not lead to an increase of cambium surface.
3. The intrusive oriented growth does not result in the furcation of the cell ends.
4. The twisted periclinal walls are observed between the cell packets and a different range of the cell ends in the successive packets. This suggests that the intrusive oriented growth between tangential walls refers only to cells of the initial surface.

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LITERATURE CITED

BANNAN M. W., 1950. The frequency of anticlinal divisions in fusiform cambial cells of *Chamaecyparis*. Amer. J. Bot. 37: 511-519.

BANNAN M. W., 1955. The vascular cambium and radial growth in *Thuja occidentalis* L. Can. J. Bot. 33: 113-138.

BANNAN M. W., 1966. Spiral grain and anticlinal divisions in the cambium of conifers. Can J. Bot. 44: 1515-1538.

BANNAN M. W., 1968. Anticlinal divisions and the organization of the conifer cambium. Bot. Gaz. 129: 107-113.

CATESSON A. M., 1974. Cambial cells. In: Dynamic aspects of plant ultrastructure. Ed. A. W. Robards, London. Mc Graw Hill: 358-390.

CATESSON A. M., 1980. The vascular cambium. In: Control of shoot growth in trees. Ed. C. H. A. Little, Proc. IUFRO Workshop, Fredericton, Canada; 12-40.

CATESSON A. M., 1984. Cambial dynamics. Ann. Sc. Nat. 6: 23- 44.

HEJNOWICZ Z., 1961. Anticlinal divisions, intrusive growth and loss of fusiform initials in nonstoried cambium. Acta Soc. Bot. Pol. 30: 729-758.

HEJNOWICZ Z., 1964. Orientation of the partition in pseudotransverse division in cambia of some conifers. Can. J. Bot., 42: 1685-1691.

HEJNOWICZ Z., 1974. Pulsation of domain length as support for the hypothesis of morphogenetic waves in the cambium. Acta Soc. Bot. Pol. 43: 261-271.

HEJNOWICZ Z., 1975. A model of morphogenetic map and clock. J. Theor. Biol. 54: 345-362.

HEJNOWICZ Z., ZAGÓRSKA-MAREK B., 1974. Mechanism of changes in grain inclination in wood produced by storied cambium. Acta Soc. Bot. Pol. 43: 381-398.

KRAWCZYSZYN J., ROMBERGER J. A., 1979. Cyclical cell length changes in wood in relation to storied structure and interlocted grain. Can. J. Bot. 57: 787-794.

MAHMOOD A., 1968. Cell grouping and primary wall generations in the cambial zone, xylem and phloem in *Pinus*. Aust. J. Bot., 16: 177-195.

MAHMOOD A., 1971. Numbers of initial-cell divisions as a measure of activity in the yearly cambial growth pattern in *Pinus*. Pak. J. For. 21: 27-42.

MAHMOOD A., 1990. The parental cell walls, pp. 113-126, in. The vascular cambium. Ed. M. Iqbal, Research Studies Press Ltd., J. Wiley and Sons Inc. N.Y. Chichester, Toronto, Brisbane, Singapore.

MISCHKE K., 1890. Beobachtungen über das Dickenwachstum der Coniferen. Kgl. Bayr. Bot. Ges. zu Regensburg. Bd. VI : 1-32.

MURMANIS L., 1970. Locating the Initial in the Vascular Cambium of *Pinus strobus* L. by Elektron Microscopy. Wood Sci. and Technol. 4: 1-14.

MURMANIS L., 1977. Development of vascular cambium into secondary tissue in *Quercus rubra* L. Ann. Bot., 41: 617-620.

PUŁAWSKA Z., 1973. The parenchymo-vascular cambium and its derivative tissues in stems and roots of *Bougainvillaea glabra* CHOISY (*Nyctaginaceae*). Acta Soc. Bot. Pol. 42: 41-61.

SANIO K., 1873. Anatomie der gemainen Kiefer (*Pinus sylvestris* L.). Jahrb. Wiss. Bot. 9: 50-126.

SAVIDGE R. A., FARRAR J. L., 1984. Cellular adjustment in the vascular cambium leading to spiral grain formation in conifers. Can. J. Bot. 62: 2872-2879.

SCHMID R., 1976. The elusive cambium – another terminological contribution. IAWA Bull 4: 51-59.

TIMELL T. E., 1980. Organization and Ultrastructure of the Dormant Cambial Zone in Compression Wood of *Picea abies*. Wood Sci. and Technol. 14: 161-179.

WARREN-WILSON J., 1978. The position of regenerating cambia: auxin/sucrose ratio and the gradient induction hypothesis. Proc. R. Soc. Lond. B. 203: 153-176.

WILSON B. F., WODZICKI T. J., ZAHNER R., 1966. Differentiation of cambial derivatives: proposed terminology. Forest Sci. 12: 438-440.

WŁOCH W., 1976. Cell events in cambium, connected with the formation and existence of a whirled cell arrangement. Acta Soc. Bot. Pol. 45: 313-326.

WŁOCH W., 1981. Nonparallelism of cambium cells in neighbouring rows. Acta Soc. Bot. Pol. 50: 625-636.

WŁOCH W., 1987. Transition areas in the domain patterns of storied cambium of *Tilia cordata* Mill. Acta Soc. Bot. Pol. 4: 645-665.

WŁOCH W., 1988. Chiralne zdarzenia komórkowe i wzór domenowy w kambium lipy (*Tilia cordata* Mill.). Prace naukowe Uniwersytetu Śląskiego w Katowicach.

WŁOCH W., BILCZEWSKA E., 1987. Fibrillation of events in the cambial domains of *Tilia cordata* Mill. Acta Soc. Bot. Pol. 56: 19-35.

WŁOCH W., WAWRZYNIAK S.,1990. The configuration of events and cell growth activity in the storied cambium of the linden (*Tilia cordata* Mill.). Acta Soc. Bot. Pol.1-4: 25-43.

WŁOCH W., ZAGÓRSKA-MAREK B., 1982. Reconstruction of storied cambium in the linden. Acta Soc. Bot. Pol. 51: 215-228.

ZAGÓRSKA-MAREK B., 1975. Growth activity of fusiform initials in storied cambium. Acta Soc. Bot. Pol. 44: 537-552.

ZAGÓRSKA-MAREK B., 1984. Pseudotransverse divisions and intrusive elongation of fusiform initials in the storied cambium of *Tilia*. Can. J. Bot. 62: 20-27.

WZROST INTRUZYWNY KOMÓREK INICJALNYCH W PRZEBUDOWIE UKŁADU KOMÓREK W KAMBIUM *TILIA CORDATA* MILL.

STRESZCZENIE

W kambium lipy produkującej drewno o krótkim około 2-4 letnim okresie zmiany nachylenia włóknistości zachodzi intensywna zmiana nachylenia komórek. Zmiana ta jest wynikiem ukierunkowanego wzrostu intruzywnego końców komórek inicjalnych między ściany peryklinalne sąsiednich komórek i występowania nierównych podziałów peryklinalnych na powierzchni inicjalnej. Taki wzrost intruzywny jest zlokalizowany na krawędzi stycznej komórki wrzecionowatej i powoduje odchylenie końców komórkowych rzędu sąsiedniego od powierzchni inicjalnej. Nierówne podziały peryklinalne dzielą komórki mające odchylone końce na dwie nierówne komórki potomne. Komórka potomna większa o odchylony koniec wychodzi z powierzchni inicjalnej i tym samym „stary koniec" zostaje wyeliminowany. Intensywność ukierunkowanego wzrostu intruzywnego i nierównych podziałów peryklinalnych decyduje o szybkości przebudowy komórek w kambium. Ukierunkowany wzrost intruzywny nie zachodzi poza komórkami inicjalnymi i dlatego nie obserwuje się zmiany położenia końców w obrębie poszczególnych kompleksów komórkowych. Zmiana ta jest natomiast wyraźna pomiędzy kompleksami.

SŁOWA KLUCZOWE: kambium, wzrost intruzywny, nierówny podział peryklinalny, powierzchnia inicjalna.