Title: Mechanism of changes in grain inclination in wood produced by storeyed cambium

Author: Zygmunt Hejnowicz, Beata Zagórska-Marek

Citation style: Hejnowicz Zygmunt, Zagórska-Marek Beata. (1974). Mechanism of changes in grain inclination in wood produced by storeyed cambium. "Acta Societatis Botanicorum Poloniae" (Vol. 43, no. 3 (1974) s. 381-398), DOI: 10.5586/asbp.1974.036

UNIWERSYTET ŚLĄSKI
W KATOWICACH

Biblioteka
Uniwersytetu Śląskiego

Ministerstwo Nauki
i Szkolnictwa Wyższego

Mechanism of changes in grain inclination in wood produced by storeyed cambium

Z. HEJNOWICZ, B. ZAGÓRSKA-MAREK

Botanical Institute, Wrocław University, Poland

Abstract

The changes in cell orientation in the cambium of *Entandrophragma* producing wood with interlocked type of grain, and in the cambium of *Tilia* in a spirally girdled stem are traced through serial tangential sections of wood. In *Entandrophragma* the changes result from the intrusive growth of a fusiform cell whih repeatedly produces a new pointed tip from one side of the existing tip which disappears. This causes a sort of creeping of cell ends of one storey past those of the adjoining storey. The oppositely directed ends of the cells belonging to one storey creep in opposite directions so that the position of the cell centres remains constant and only the angle between the cells and the stem axis changes. The stratification of short rays in *Entandrophragma* represents an adaptation to the changes in cell orientation involved in the formation of interlocked grain. The mechanism of changes in grain inclination in *Tilia* is intermediate between that based on the creeping of cell ends and that based on pseudotransverse division and intrusive elongation which is known in non-storeyed cambia.

INTRODUCTION

Grain pattern is defined as that formed by the general orientation of the longitudinal axes of wood cells. It may be parallel to the stem axis or inclined either to the right (Z) or to the left (S). At a particular site in the stem (along the radius) the inclination of grain may change cyclically from one to the other alternative type in successive groups of annual rings. This cyclic change may be accompanied by a different course of grain on the surface of any particular ring. When the course is helical along the whole trunk or its long segment, slanting either eight or left, the grain is said to be of interlocked type. When the course is serpentine the grain is of wavy type.

Changes in the inclination of wood cells reflect corresponding changes in the alignment of cells in the cambium (with the exception of the cases in which they are due to asymmetrical torsion of the stem, Hejnowicz 1973b). The anatomical basis

of these changes in the cambium has been discussed in a number of papers of which the latests are those by K r a w c z y s z y n (1972), H e j n o w i c z and R o m b e r g e r (1973). H e j n o w i c z (1974). All those papers, however, dealt with non-storeyed cambia. They revealed that in non-storeyed cambium the changes in cell orientation are based on anticlinal pseudotransverse division and intrusive growth (overlapping of oppositely directed tips and splitting of rays). The orientation of these events which may be either to the right (Z) or to the left (S) is non-random. It is controlled by the domain pattern, i.e. the pattern of delineable areas in which alternative orientational tendencies prevail. The domain pattern migrates in respect to the cells within it, what causes reversals of domain type at each particular site in the cambium. The domain pattern is not directly visible, however, if the frequency of anticlinal division and the rate of intrusive growth are high, the domain pattern produces a wavy or serpentine pattern of cell arrangement in the cambium, and thereby in the wood. The radial split face of such a wood shows grain undulations which run at some angle in respect to the rays. The length of the undulation measured parallel to the annual ring is related to the domain length, while the angle is related to the migration rate of the domain pattern. The longer the domains the faster their migration and the longer and steeper the undulations of grain.

In storeyed cambium the anticlinal divisions are of radial type and intrusive growth occurs to a limited extent. Yet some trees characterized by cambium of this type have interlocked or wavy grain in the wood. It is also known that adaptive changes in the orientation of cambial cells may occur in storeyed cambium (N e e f 1914).

MATERIALS AND METHODS

The changes in the cambium were followed through serial tangential sections of wood. Two species provided the wood for studies: *Entandrophragma cylindrica* — a tropical tree (Sapele Mahogany), and *Tilia parvifolia*. Sapele wood was collected at the sawmill at Dobroszyce, Poland, in the form of quarter-sawn boards 3 m long. Blocks having tangential faces 4×12 mm and radial length of 40 mm were prepared and tangential sections were cut from them with a sliding microtome. The sections were 32 μm thick. The longest series encompassed 20 mm of the wood radially. To remove the dark substance from the parenchyma the sections were attached in groups of eigth to a slide, and fastened by means of two elastic bands to prevent falling off. They were immersed in Javelle water for half an hour, then washed for 12 hours and transferred through ethyl alcohol to xylene. The sections were mounted in Canada balsam. Those which included axial parenchyma were chosen for photography. The image of the parenchyma enlarged 238 times was microscopically projected on photographic paper. The series of photographic images were the direct object of our study.

The samples of *Tilia* wood were derived from fast growing sprouts about 10 years old, which one year earlier, in early spring, had been treated by cutting spiral grooves about 5 mm wide into the bark up to the wood to produce a spiral angle of 30°

(approximately 40 cm interval between successive loops). Blocks appropriate for microtome sectioning were prepared, each containing the annual ring formed after the treatment and also a few inner rings of wood. Series of tangential sections and photographic images were prepared in the same way as in the case of Sapele wood.

<center>RESULTS</center>

Entandrophragma cylindrica

In general Sapele Mahogany is characterized by interlocked grain. This is indicated by the ribbon figure on the radial sawn surface, i.e. the figure formed by dark and light bands due to differences in the reflection of light from differently cut xylem elements on this surface. When a narrow piece was sawn transversaly off the end of a radial board and split radially down by means of a long knife applied to the upper transverse surface, the fracture on the upper surface was straight but that on the lower surface sinuous, (Fig. 1).

In some boards the ribbon figure was not disturbed by any additional bands and was parallel to the annual rings (Fig. 2 A). This parallelism indicates that the grain was of uniform inclination on the ring surfaces in the logs 3 m long which provided the boards, i.e. the grain was of interlocked type. In some boards the bands were not strictly parallel to the rings but intersected them at a narrow angle, running centrifugally upward (Fig. 2 B). This means that the grain course on the ring surface was serpentine and the areas of Z and S inclination on each surface were displaced upward as compared with the same areas on the surface of the previous ring. In some other boards the ribbon figure was interrupted by additional bands which ran at a small angle to the rays (Fig. 2 C), producing a figure which may be called mottled according to the description of Panshin and de Zeeuw (1970). The bands of ribbon figure not parallel to the annual rings indicate that the change of grain orientation in *Entadrophragma* is related to the migrating domain patterns, similarly as in trees with non-storeyed cambium (Krawczyszyn 1972).

The samples for sectioning were collected from boards with ribbon figure almost undisturbed by any additional bands. If we denote the mean radial span of one cycle in the sinuous fracture on the radial split face as D, and the maximal angle by which the grain changes its orientation as A, the board from which the main series derived was characterized by D = 36 mm and A = 40° (Fig. 1).

The cambium of *Entadrophragma cylindrica* is storeyed what can be recognized in the axial parenchyma. The latter is of strand type, i.e. it is formed by transverse divisions of fusiform cells with each strand of approximately the same shape as the original fusiform initial in the cambium. The strands are arranged in long but low storeys (Fig. 5 A). Also the rays in Sapele wood are stratified. The rays are multiseriate but only one storey in height and in general they do not extend beyond the storey. The axial strand parenchyma is mostly terminal, four or more cells wide. Within annual rings additional bands of parenchyma may occur. In the main series
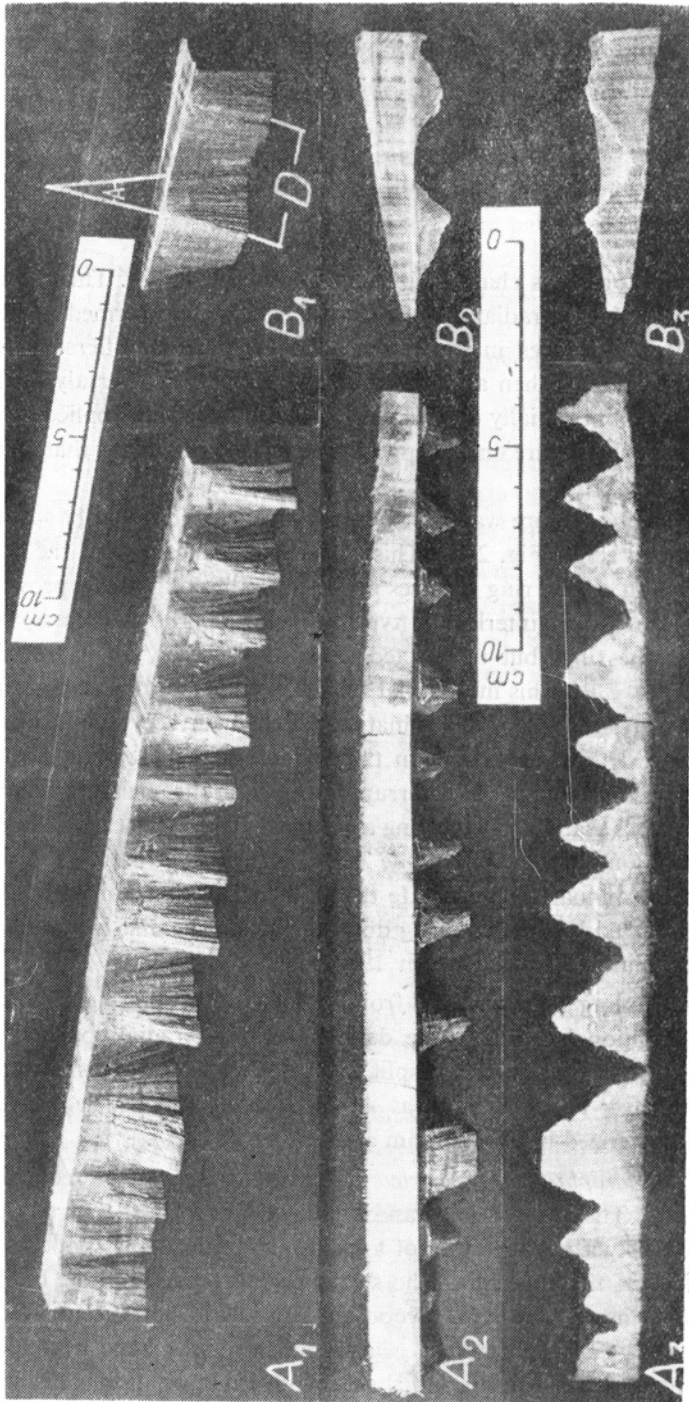
Fig. 1. *Entadrophragma cylindrica*. Different views of 25 mm broad piece of wood (stick) sawn transversaly off the radial board and split radially.

A — 1 piece sawn from the board

with ribbon figure, *B* — a piece which provided the main series of sections

1 — facial view of the radial split surface, *2* — upper transverse surface to which edge of the long knife was applied, *3* — lower transverse surface showing the sinuous fracture. A is the amplitude of interlocked grain, A is the radial span of one cycle of interlocked grain, A is the amplitude of the change in grian inclination

D is the radial span of one cycle of interlocked grain, A is the amplitude of the change in grian inclination

the mean radial distance between the sections containing the parenchyma appropriate for studies (including terminal layers and intraring bands), and the mean width of annual rings, were 0.9 mm and 2.1 mm, respectively.
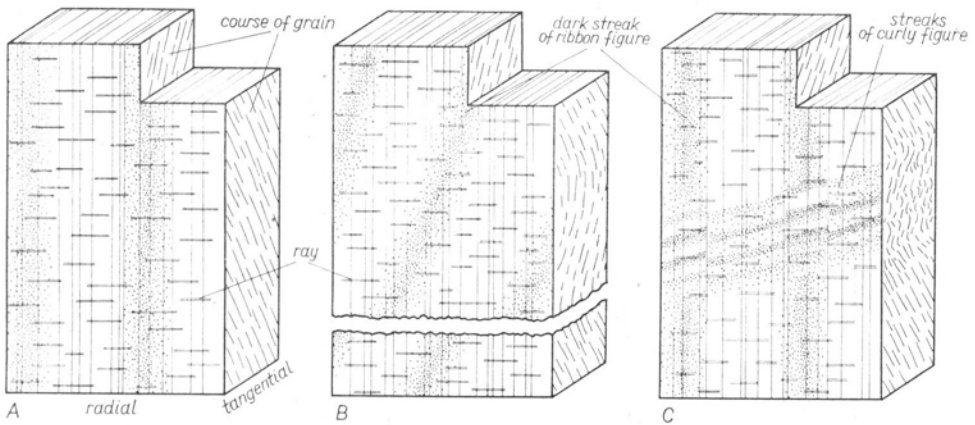

Fig. 2. Schematical illustration of the types of grain in *Entadrophragma* wood, as seen on radial and tangential faces. Stippled and unstippled streaks on the radial surface correspond to the zones of different grain orientation.

A — interlocked grain with the streaks parallel to annual rings. In such a case the orientation of cambial cells is the same throughout a large cambium area. *B* — similar as in A but the streaks form a small angle with annual rings. In this case there were areas in the cambium differing in the orientation of cells and the borders between these areas migrated along the stem. *C* — locally curly pattern of grain superimposed on the interlocked pattern. The streaks of the curly pattern form a small angle with the rays.

The series of tangential sections comprising the parenchyma made possible tracing of the cambial events during the formation of the interlocked grain. The representative sections from the main series are illustrated in Fig. 3. The most significant event was the change of contacts between the ends of the fusiform initials belonging to two storeys. The ends of one storey creeped past the ends of the adjoining one. The direction of creeping was the same for the ends similarly directed in all storeys (either upper of lower ones) during a certain period, and thereafter it was reversed, for instance in the case of upper ends in the series shown in Fig. 3 the direction was to the left within the radial distance from 0.0 to 3.7 mm, next to 23.7 mm it was to the right and then again to the left. The directions of displacement of the opposite ends of cells belonging to one storey obviously were reverse so that the relative position of the centers of cells and rays remained generally constant and only the inclination of the cell and ray axes changed. The displacement of cell ends resulting in changing of the inclination of cells is shown in Fig. 4 schematically.

During the period of change of grain orientation in one direction ($\frac{1}{2}$ D according to the previous notation, Fig. 1) the cell ends of one storey creeped past 9 ends of the next in the main series which is illustrated in Fig. 3. Since the mean cell length (storey height) is 0.506 mm and the mean cell width is 0.035 mm, the displacement for 9 cells is equivalent to the change in grain orientation for 34.6°. This agrees with the

0,5 mm

+13°   23,7   +7°   25,9   −2,5°   28,4
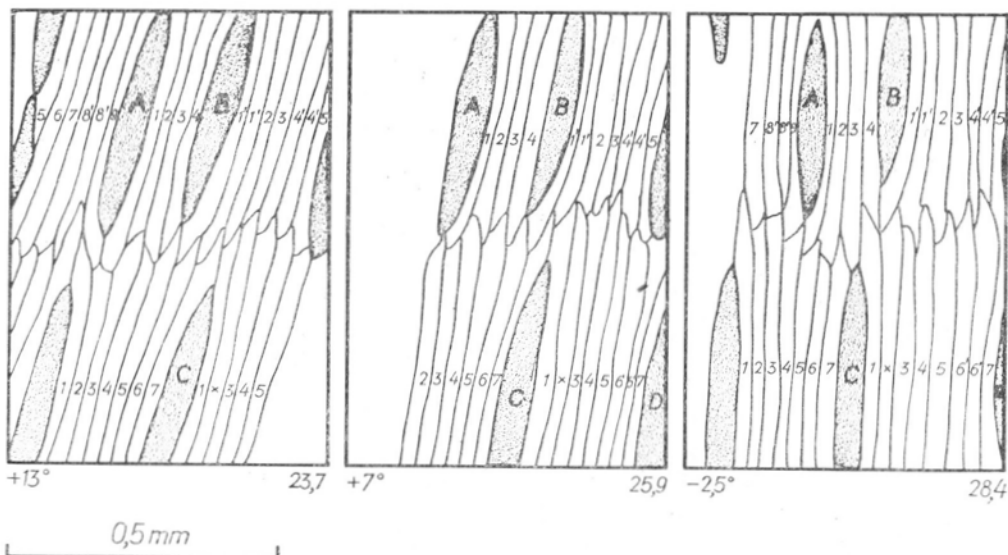
0,5 mm
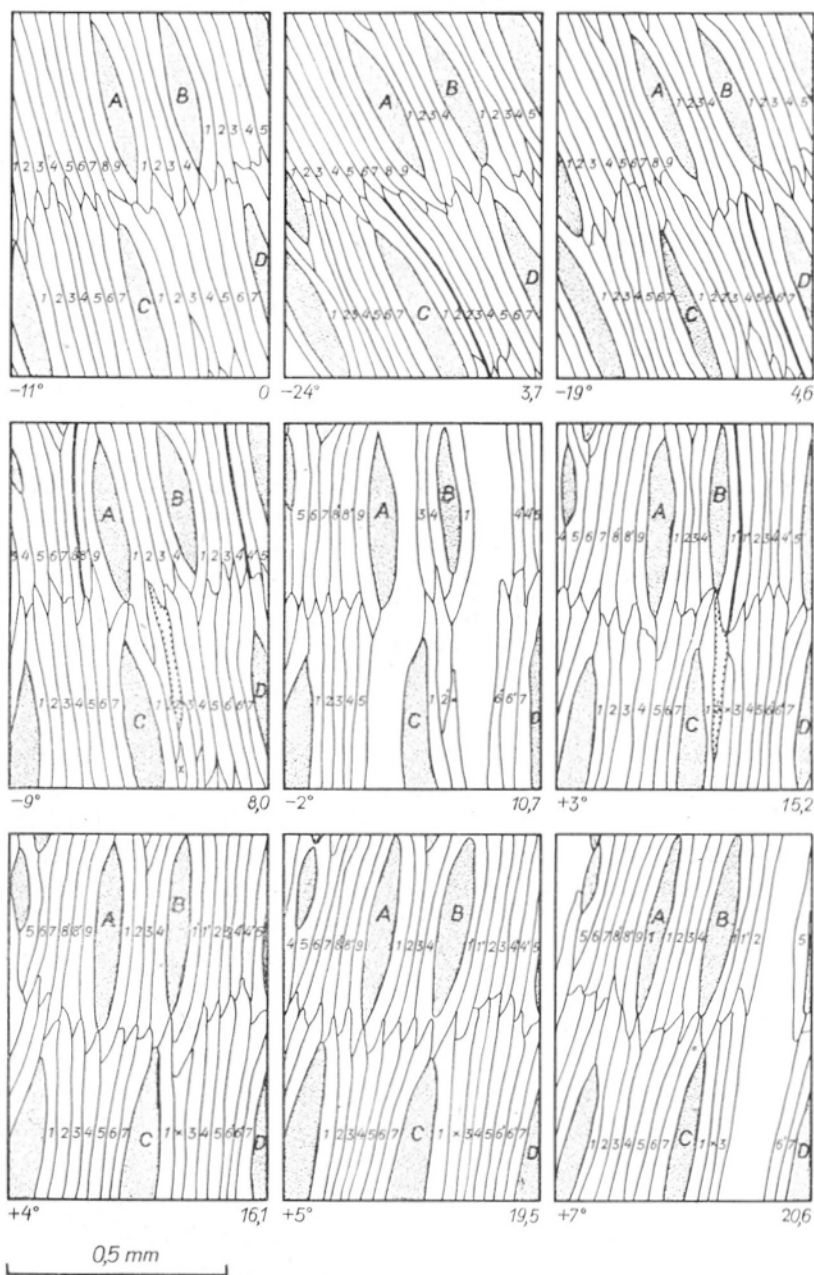
Fig. 3 *Entandrophragma*. Outlines of fusiform strands of parenchyma cells (representing the fusiform initials in the cambium) and wood rays in representative sections from the main series studied.

The cells are numbered to facilitate their tracing. Where a longitudinal division occurred in the fusiform initial the newly formed partition is shown by a heavy line. The two daughter cells received the same number as their mother cell to which an apostrophe is added. The rays are stippled. The cell which is to be lost is indicated by a dotted contour on the section where it was last visible. The empty areas are those in which the strands of parenchyma cells could not be identified. The number in the right corner indicates the relative position of the section in respect to the first one in the series (in mm). The mean angle between the cell axis and stem axis (the latter is parallel to loong side) is given in the left corner. The inclination to the right is assumed as positive

amplitude in the change of grain inclination (A — according to the notation in Fig. 1) observed in the wood sample from which the series was derived.

Let us consider some details of the creeping of cell ends. Where the inclination of cells changed to the right two ends which originally overlapped in S-fashion
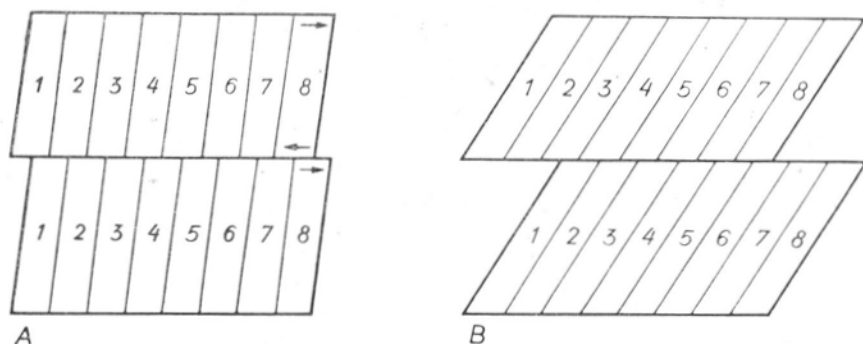

Fig. 4 Scheme of mutual displacement of cell ends resulting in constant position of cell centres and change in the orientation of the cell axis

A — initial state, B — after displacement by 2 cells
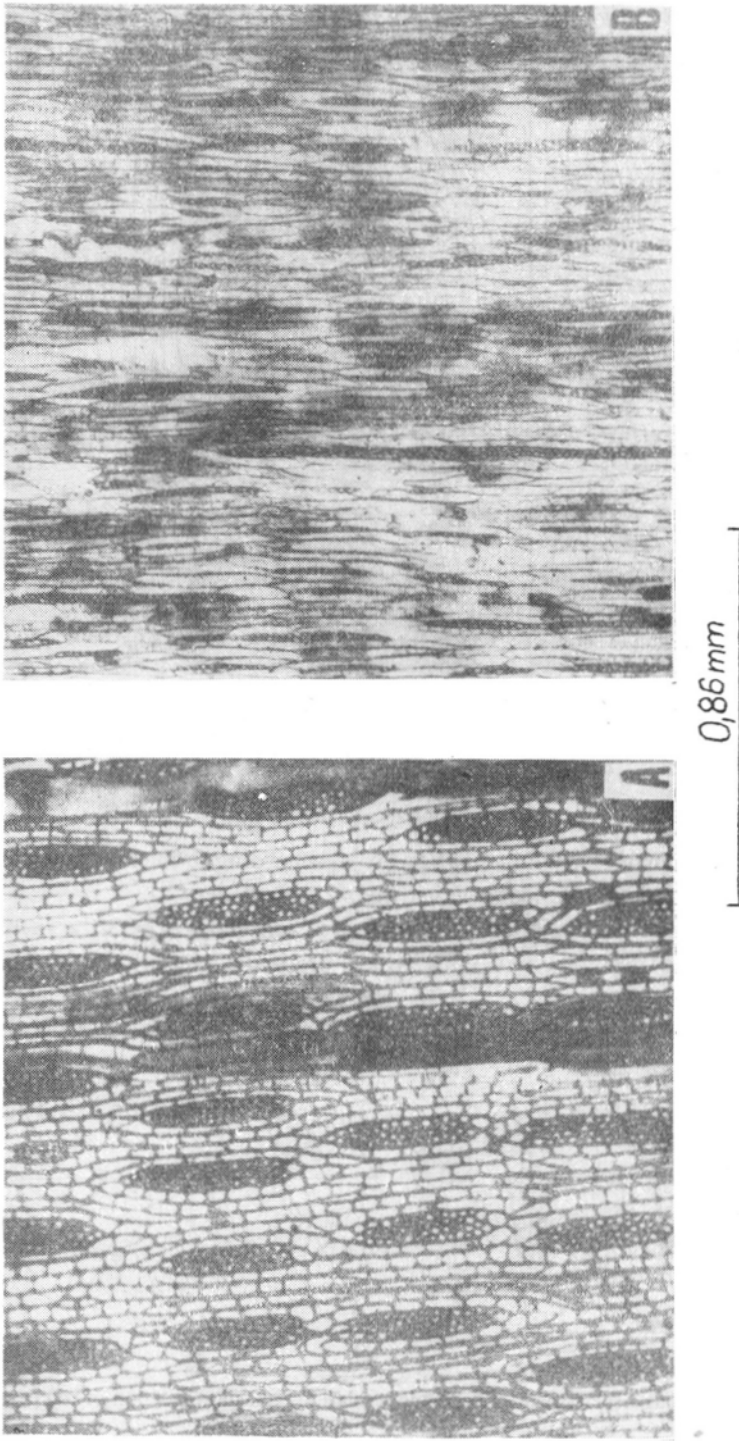
7

0,86mm

Fig. 5. A — *Entadrophragma*. Tangential section comprising strand parenchyma. B — *Tilia*. Tangential section through the poorly differentiated wood formed after spiral incision of the stem.

changed the overlap from S to Z, and those which overlapped in Z-fashion lost their contact because the lower left neighbour or the upper right neighbour or both intruded between their ends (Fig. 6), During this readjustment some ends became forked owing to the formation of a new pointed tip on one side of the existing one. After the formation of the new tip the previous one disappeared (Fig. 3 and Fig. 7 B) The forks were observed both at the upper and the lower end, however, in a given fusiform initial and a particular phase of its development the fork occurred mostly at one end.
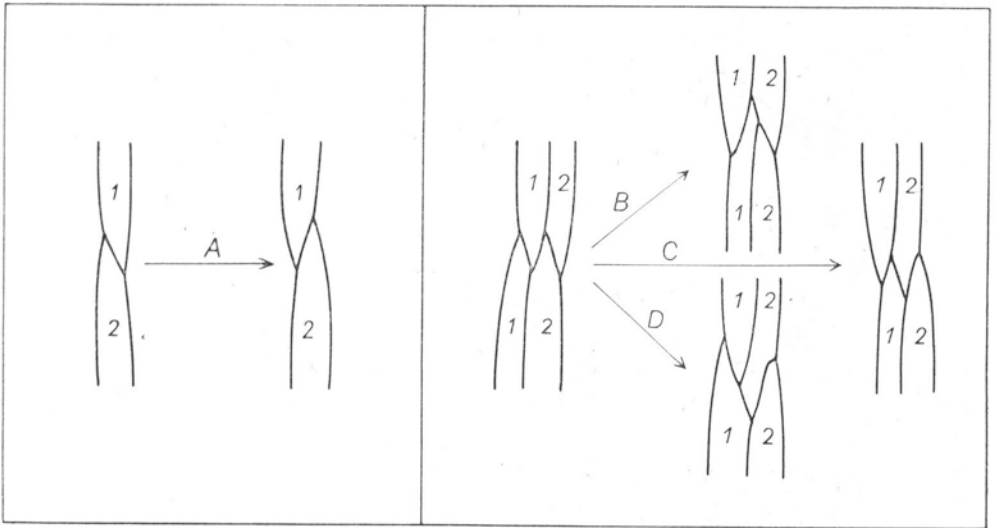

Fig. 6 Scheme of changes in mutual position of cell ends when the inclination changes to the right. A — change of overlap from S to Z. B-D — separation of two ends which initially overlapped in Z-fashion

The readjustment of cell ends by forking represents a case when a new pointed tip is formed before the old one disappears. However, in some cell ends the pointed tip was first withdrawn from among a pair of oppositely directed ends and then a new tip formed on the appropriate side of this pair (Fig. 7 A). Thus, the sequence of the two events — formation of new tip and disappearance of the previous one — varied at different ends.

Changing of the inclination of rays was passive; the ray adjusted its orientation to that of the fusiform initials. Some superposed rays the ends of which lay on the contact line between the storeys were temporarily united.

Tilia parvifolia

This species is characterized by storeyed cambium, however, the rays are non--stratified in contrast to those of *Entandrophragma*. Most rays are several storeys high. In spirally girdled stems the orientation of the grain in newly formed wood readjusted gradually to the girdle. Just above the groove it became parallel to the
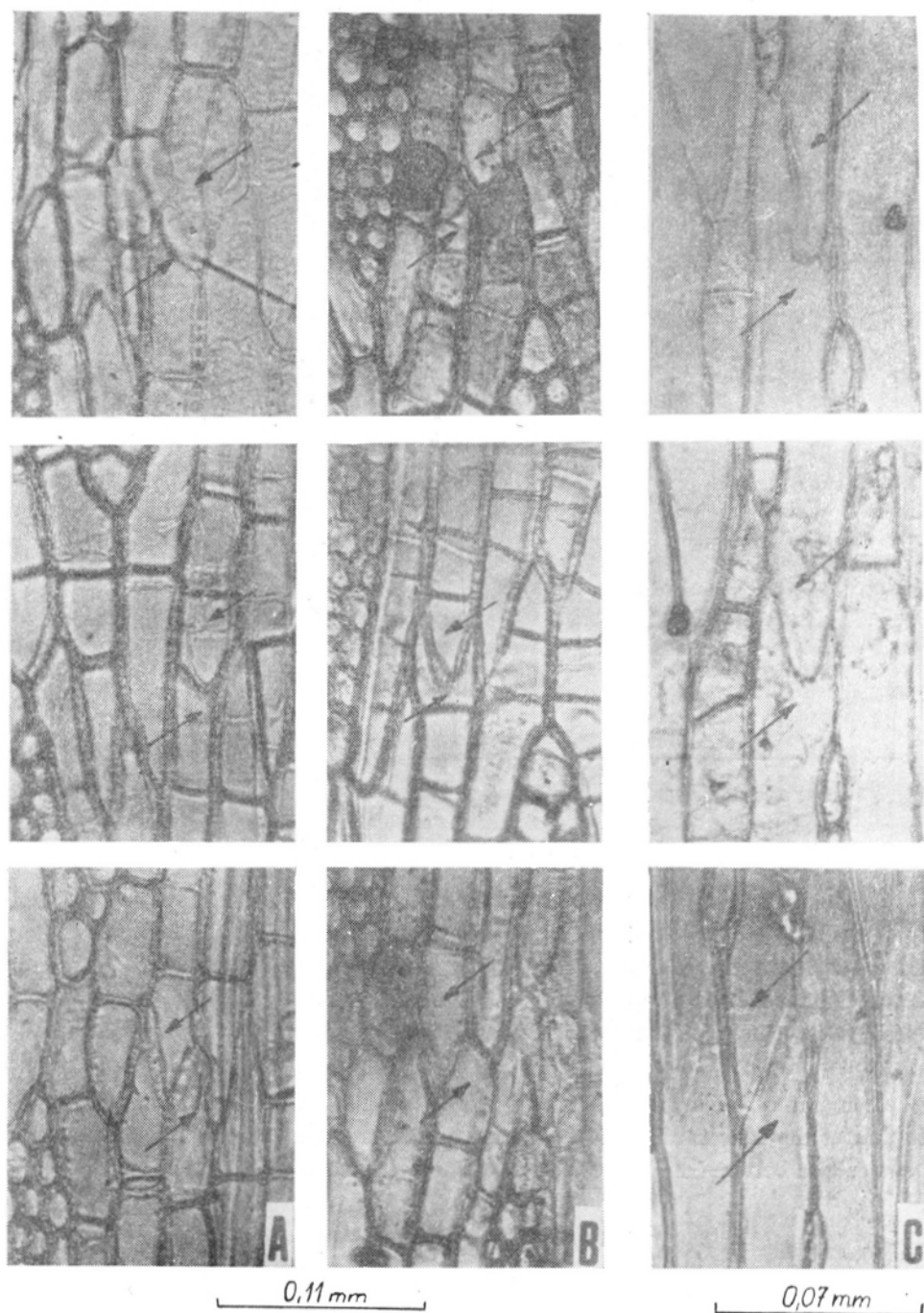
0,11 mm   0,07 mm

Fig. 7 Series of 3 photographs each from successive sections (vertically) illustrating the change of
mutual position of two oppositely directed cell ends (arrows).

A and B — *Entandrophragma*, without forking of the end and with forking, respectively. C — *Tilia*, with forking

latter already 4 weeks after the treatment in spring, however, the longer the distance from the girdle the lower the rate of orientation change.

The wood formed in girdled stems was less differentiated than that in untreated stems, especially the extent to which intrusive growth occurred during fibre differentiation was lower so that the cambial cell pattern in wood was preserved well enough to read out the cambium history (Fig. 5 B). As the grain became readjusted to the spiral girdle the differentiation of wood gradually reappeared. Nevertheless, we could trace the changes throughout several months after the treatment. In the proximity of the girdle the readjustment of cambial cells involved numerous transverse divisions of fusiform initials which brought about considerable shortening of the initials and loss of storeyed structure. This was followed by oriented intrusive growth which changed cell orientation and increased their length. Such a readjustment of the cambial structure has already been described in *Tilia* by Neef (1914). Further away fom the girdle the way of changing the orientation of cells was intermediate between that in *Entandrophragma* and that in non-storeyed cambia.

Fig. 8 illustrates the changes which occurred during the reorientation of the cambial cells 2 cm above the girdle. As seen, the long rays underwent splitting by intrusively growing fusiform initials. Some fusiform initials divided pseudotransversely. The extent of intrusive growth in fusiform initials during the reorientation of cells was evidently high at some ends, especially in those which were splitting the long rays and were formed by pseudotransverse divisions. However, other ends behaved similarly as in *Entadrophragma*, being involved in the creeping past the ends of the adjoining storey. Some ends became then temporarily forked (Fig. 7 C). Owing to the extensive intrusive elongation and the pseudotransverse divisions the storeyed pattern was partly lost during the change of cell orientation.

DISCUSSION

The displacement of cell ends belonging to one storey in respect to oppositely directed ends of the adjoining storey involved events of two types: the formation of a new pointed tip and disappearance of previous tip. Both seem to be based on intrusive growth so it is worthwhile to consider this type of growth.

Intrusive growth occurs when a cell grows by means of localized extension which separates the primary walls of neighbouring cells without severance of the contacts between the growing cell and its neighbours beyond the site of the extension. Some gliding of the cell wall past another may occur only within this site. How large is this extension site? Studies on the cambium of *Larix* (Hejnowicz 1963) indicated that intrusive growth was strictly limited to the edge of the growing cell end, at least in the case of ends originating from transverse divisions which had been induced by wounding the stem. In such a case narrow processes were formed at the radial edges of the transverse walls (Fig. 9) so there is no doubt that, at least at the beginning of formation of the process, the intrusive growth was limited to the very edge. Extrapolating this observation we may expect that also at the pointed end the intrusive
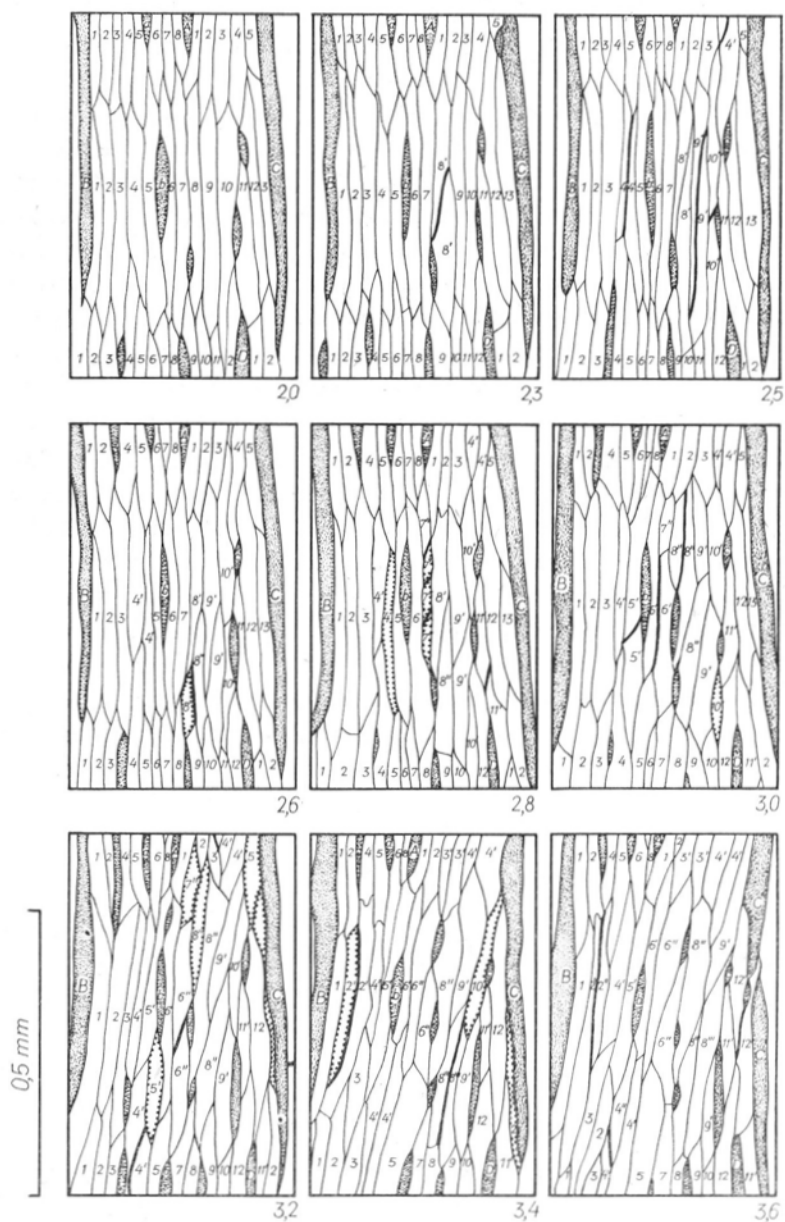
Fig. 8 *Tilia parvifolia*. Outlines of fiber-tracheids at the same site in a series of tangential sections of the wood formed in spirally girdled stem.

The spiral girdle was of Z-type. The cells are numbered to facilitate their tracing. Where a longitudinal division occurred in the fusiform initial the newly formed partition is shown by a heavy line. The two daughter cells received the same number as their mother cell to which an apostrophe was added. The rays are stippled. The cell which is to be lost is indicated by a dotted contour on the section where it was last visible. The nembers in the right corner indicate the relative position of the section in respect to the inner border of the annual ring formed after the treatment

growth is limited to its very edge. Since the extension is to separate the walls of neighbouring cells, the localization at the cell edge, i.e. at the line where three cells meet, is appropriate. Probably every edge is potentially a site of intrusive growth.
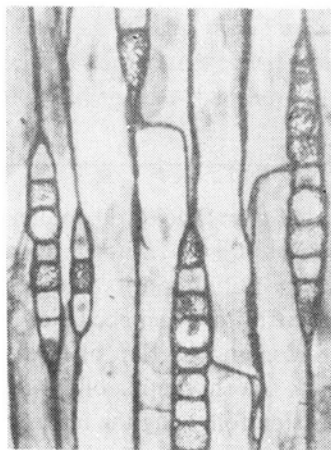

Fig. 9. *Larix europea*. Intrusive growth in fusiform initials at edges of obtuse cell end (from studies of wounded cambium, Hejnowicz 1963)

Some intrusive growth occurs in storeyed cambium even if there is no change in cell orientation. This is the kind of growth which follows radial division. Beijer (1927) studied the readjustment which occurred at cell ends after radial division in storeyed cambium and concluded that the pointed ends were restored to both daughter cells by slight intrusive growth (Fig. 10). Additional intrusive growth would be necessary to form a new tip as a step towards displacing the end in one storey past oppositely directed ends of the next storey, as has been described in the present paper.
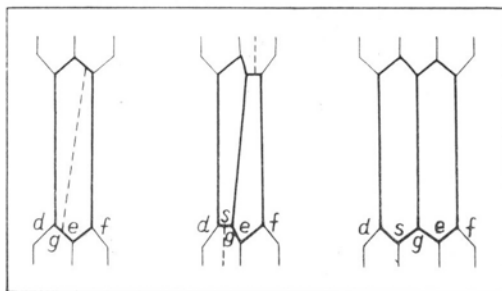

Fig. 10 Scheme of readjustement at cell ends after radial division in fusiform initials in storeyed cambium (after Beijer 1927, Fig. 12, II)

In general there are three edges at one end of a fusiform cell in storeyed cambium (Fig. 11 A). The actual pointed end should be considered as the result of previous intrusive growth at the middle edge. If in further development the intrusive growth starts at one of the side edges, the end becomes forked (Fig. 11 B). Forking of the cell end evidently is the result of intrusive growth at the radial edge where previously no extension was localized.

The mechanism of disappearance of a previous tip involves also intrusive growth, however, in this case the extension is localized on the tangential edge instead of the
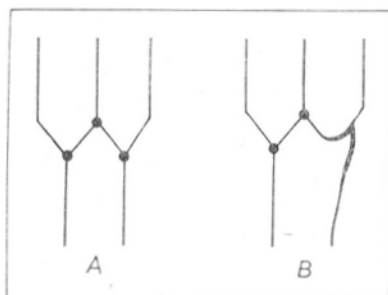
Fig. 11. Three radial edges at the end of a fusiform cell viewed on tangential section before (A) and after (B) intrusive growth started at the right edge

radial one. Studies on conifer cambium (Hejnowicz, 1961 and others unpublished) indicate that a fusiform initial may intrude between the tangential walls of the fusiform initial and its daughter cell belonging to the neighbouring radial tier. Such an intrusion often occurs at the place where two radial tiers overlap. It brings about a change in overlap orientation as illustrated in Fig. 12. At the transitional stage there is a shortening of the fusiform initial in the tier B owing to unequal tangential division following the intrusion. It looks so as if a part of the initial in B were disappearing. Probably on this basis the disappearance of the tips in the storeyed cambium occurs when the cell ends of one storey creep past ends of the adjoining one.
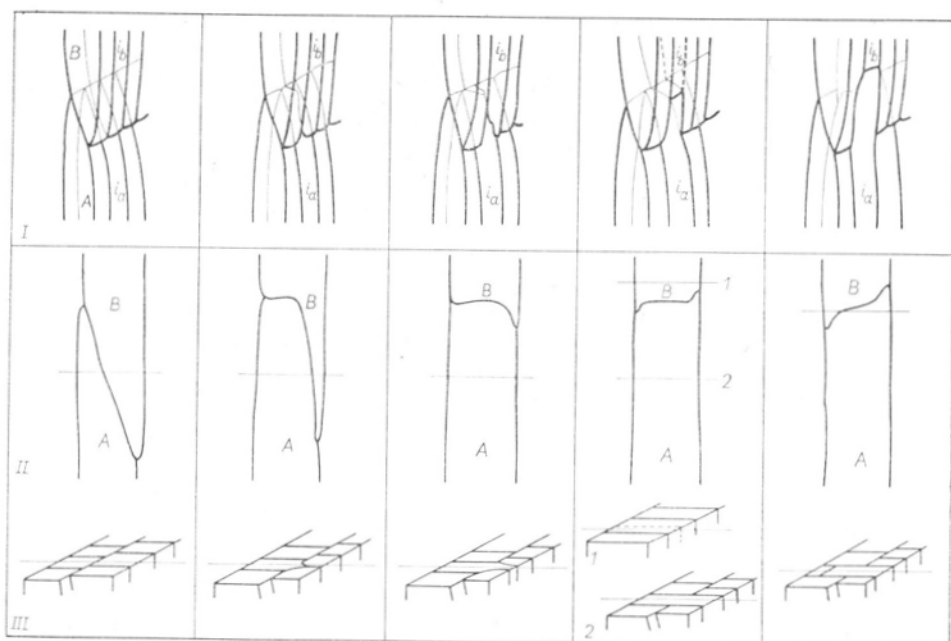

Fig. 12. Schematic illustration of change in the overlap of two fusiform initials belonging to tiers A and B

Initially the overlap is of S type and it changes owing to the intrusion of i_a between the end of i_b and its derivative. This intrusion proceeds between tangential walls. Unequal division (dashed line) in i_b produces a shortened initial in row B. Further intrusive growth in i_a and i_b between radial walls establishes the overlap of Z type. I — schematic three dimensional view of 5 successive developmental stages. II and III — the same as in I but referring to tangential section in the plane of the fusiform initials and to the transverse section, respectively. The transverse line in II shows the level of the transverse plane to which the drawing in III corresponds. The line in III indicates the longitudinal plane of the drawings in II

In non-storeyed cambium the system which orients the intrusive growth (over-lapping of oppositely directed tips and splitting of rays) operates on the basis of the domain pattern (Hejnowicz 1971, Krawczyszyn 1972; Hejnowicz and Rom-berger 1973).

Where two tips oppositely directed come into contact, or the tip of a fusiform cell comes into contact with two cells of a ray, a pair of 3-contact edges is formed (Fig. 13), though the 3-contact edges on a tip may be located so near that they appa-
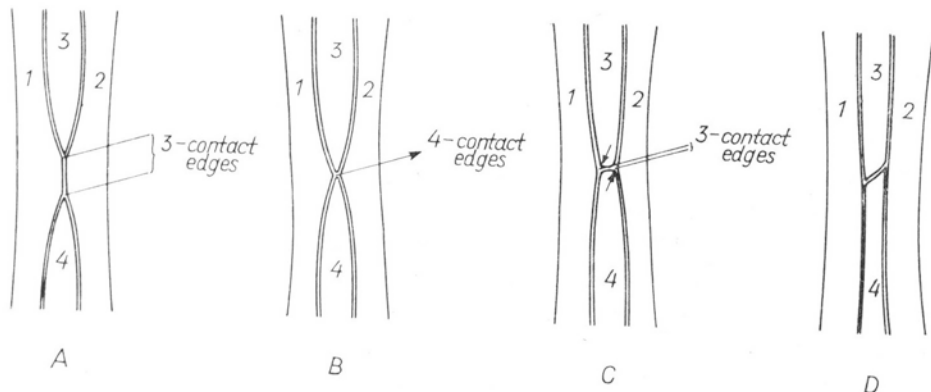

Fig. 13. Diagram showing the overlapping of intrusively growing tips.

A — two oppositely directed tips, *B* — the tips come into contact, *C* — a pair of edges of threefold contact at each tip. The right edge, as seen from cell center, is indicated by an arrow at each end. *D* — overlap of Z type resulting from intru-sive growth at the right edge.

rently form one 4-contact edge. In each pair the proper edge is chosen for intrusive growth according to the existing domain. There is no doubt that also in *Entan-drophragma* the edge for intrusive growth is determined on the basis of the migrating domain pattern in the cambium. This follows from the fact that, at least in some trees, the bands of the ribbon figure on the radial sawn surface cross annual rings, this indicating a fast migration of domains of considerable length. From previous studies it can be seen that in different species the domain length L varies from a few to several hundred millimeters and the velocity of domain migration V varies from a fraction to tens of millimeters per year. There is a general rule that the longer the domain the faster its migration, so that the period of duration T of one domain at a particular site is roughly constant and lasts about 10 years (Hejnowicz 1973, 1974). Two or more domain patterns characterized by different L and V but the same T may be superposed in the same cambium. The case of Sapele Mahogany with the bands in ribbon figure parallel to annual rings should be considered as corresponding to very long and very fast domains. It was mentioned that in some radial boards beside the bands of the ribbon figure there were additional bands which ran at a small angle to the rays (mottled figure). This figure should be inter-preted as due to two superposed domain patterns: one with high values of L and V, and the other with low values. The radial span of one cycle in the change of orien-tation of grain in *Entendrophragma* (radial distance between the crests of two successi-

ve undulations) is comparable with that in other interlocked or wavy woods and speaks in favour of a general constancy of duration of one domain at a particular site in the cambium.

The discussion indicates that the two types of cambia — storeyed and non-storeyed — are similar as regards the mechanism of changes in the orientation of cells. In both an important role is played by oriented intrusive growth. However, in non--storeyed cambium the growth is long- lasting at a particular edge at the cell and so that the end elongates up to the time when the whole cell disappears as an initial, while in the storeyed cambium such as that in *Entandrophragma* the intrusive growth constantly changes the edge occurring at one untill a pointed tip is formed there, and at the same time previous tip disappears.

In non-storeyed cambium the fast change in cell orientation is possible only when the frequency of pseudotransverse divisions and the rate of intrusive growth are high. These must be compensated by an adequately high rate of loss of cells from the cambium (Hejnowicz 1968). In the case of storeyed cambium there is no special need for loss of cells, however, previously formed tips must disappear to make the creeping of cell ends possible.

Rays in storeyed cambium may extend through several storeys (long rays) or may be only one-storey or less in height (short rays). If there are only short rays in the cambium they are stratified in common storeys with the fusiform initials. The cambium is then stratified not only in respect to the fusiform initials but also to the rays. Where rays are long they must be split when the cambium changes the orientation of its cells, as in *Tilia*. However, where rays are short and stratified the orientation may change without splitting of rays. It seems that a stratified arrangement of rays in storeyed cambium should be considered as an adaptation to the changes in cell orientation which are a requisite of interlocked grain in wood.

REFERENCES

Beijer J. J., 1927, Die Vermehrung der radialen Reihen im Cambium, Rec. trav. Bot. Neerl. 24: 631—786.

Hejnowicz, Z. 1961, Anticlinal division, intrusive growth, and loss of fusiform initials in non-storied cambium, Acta Soc. Bot. Pol. 30: 729—748.

Hejnowicz, Z., 1963, Intrusive growth, transverse and pseudotransverse divisions in fusiform initials of wounded cambium of *Larix europaea*, (summary in English), Acta. Soc. Bot. Pol. 32: 493—503.

Hejnowicz Z., 1968. The structural mechanism involved in the changes of grain in timber, Acta Soc. Bot. Pol. 37: 347—365.

Hejnowicz Z., 1971, Upward movement of the domain pattern in the cambium producing wavy grain in *Picea excelsa*, Acta Soc. Bot. Pol. 40: 499—512.

Hejnowicz Z., 1973. Morphogenetic waves in cambia of trees. Plant Science Letters 1:359—366.

Hejnowicz Z., 1973b. Domain pattern and spiral grain, IUFRO, Meeting of Division II, South Africa.

Hejnowicz Z., 1974. Pulsations of domain length as support for the hypothesis of morphogenetic waves in the cambium, Acta Soc. Bot. Pol. 43:

Hejnowicz Z., and J. A. Romberger, 1973. Migrating cambial domains and the origin of wavy grain in xylem of broadleaved trees, Amer. J. Bot. 60: 209—222.

Krawczyszyn J., 1972. Movement of the cambial domain pattern and the mechanism of formation of interlocked grain in *Platanus*, Acta. Soc. Bot. Pol. 41: 443—461.

Neef F., 1914. Uber Zellumlagerung. Ein Beitrag zur experimentellen Anatomie, Zeitschr. f. Bot. 6: 463—547.

Panshin A. J. and de Zeeuw C., 1970. Textbook of Wood Technology. Third Ed. vol. 1. McGraw-Hill Book Comp. New York

Author's address:
Prof. dr Zygmunt Hejnowicz
Institute of Molecular Biology
Silesian University;
Jagiellońska Str. 28,
40-032 Katowice; Poland
Mgr Beata Zagórska-Marek
Botanical Institute, Wrocław University,
Kanonia 6/8 Str.; 50-328 Wrocław, Poland

Mechanizm zmiany w nachyleniu włóknistości drewna produkowanego przez kambium piętrowe

Streszczenie

Badania przeprowadzono na przykładzie *Entandrophragma cylindrica* oraz *Tilia parviflora*. Obydwa gatunki posiadają kambium typu piętrowego, różnią się jednak wysokością i ułożeniem promieni drzewnych. W przypadku *Entandrophragma* wszystkie promienie są krótkie i leżą w obrębie pięter komórek wrzecionowatych tworząc regularne poprzeczne szeregi. U *Tilia* wysokość wielu promieni jest kilka razy większa niż wysokość piętra komórek wrzecionowatych. U *Entandrophragma* orientacja komórek w kambium zmienia się cyklicznie: od silnie nachylonej w jednym kierunku (na lewo albo na prawo) do nachylonej równie silnie w przeciwnym kierunku. Wynikiem tego jest zapleciona włóknistość drewna. W przypadku *Tilia* zmiana orientacji komórek w kambium była wymuszona przez spiralne nacięcie kambium w pniu.

Badania podstawowe przeprowadzono na seriach mikrotomowych przekrojów stycznych drewna, wykorzystując do odtworzenia historii kambium pokłady miękiszu drzewnego — w przypadku *Entandrophragma*, zaś włókna niewydłużone na skutek nacięcia kambium — w przypadku *Tilia*.

Stwierdzono, że zmiana orientacji komórek inicjalnych w kambium *Entandrophragma* polegała na stałym jednokierunkowym przemieszczaniu się końców komórek należących do jednego piętra względem końców komórek piętra przyległego. Kierunek przesuwania się górnych i dolnych końców komórek każdego piętra był przeciwny, dzięki czemu położenie środków komórek, a także środków krótkich promieni nie zmieniło się. Zmianie natomiast ulegała orientacja osi komórek i promieni. Szczegółowe zbadanie wzajemnego przesuwania się końców komórkowych wykazało, że zasadniczą rolę w tym procesie odgrywa wzrost intruzywny. Występujące licznie widełkowate zakończenia inicjałów wrzecionowatych reprezentowały stan pośredni pomiędzy dwoma kolejnymi położeniami danego końca względem końców komórek przyległego piętra. Rozwidlenie końca było spowodowane tym, że wzrost intruzywny na nowej krawędzi promienistej końca komórki rozpoczynał się zanim pierwotny koniec został wycofany. Niekiedy obserwowano odmienną kolejność tych zdarzeń: najpierw ulegał zanikowi koniec pierwotny a dopiero potem, na odpowiedniej krawędzi, rozpoczynał się wzrost intruzywny prowadzący do wytworzenia nowego zaostrzonego

końca. Wybór krawędzi promienistej, prawej lub lewej, następował zgodnie z wymogami aktualnie panującego kierunku zmiany orientacji. U *Entandrophragma* wybór ten był określony typem aktualnie panującej domeny. W naciętym kambium *Tilia* sposób zmiany orientacji komórek był pośredni między tym, jaki występuje u *Entandrophragma* a tym, jaki jest znany dla kambium niepiętrowego. Oprócz wzajemnego przesuwania się końców komórkowych występowały liczne, odpowiednio zorientowane, skośne podziały antyklinalne. Niektóre komórki inicjalne ulegały znacznemu wydłużeniu. Długie promienie występujące u *Tilia* były najpierw rozszczepiane przez rosnące intruzywnie końce komórek, a powstałe w ten sposób fragmenty ulegały pochyleniu zachowując stałe położenie swych środków. Udział skośnych podziałów antyklinalnych, oraz wzrostu intruzywnego wydłużającego komórki, w mechaniźmie zmiany orientacji komórek kambium *Tilia*, powodował częściową utratę piętrowości przez to kambium. Piętrowe ułożenie promieni, jakie występuje u *Entandrophragma*, można uważać za przystosowanie kambium piętrowego do zmiany orientacji swych komórek podczas produkowania przezeń drewna z włóknistością zaplecioną.