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Transition areas in the domain patterns of storeyed cambium of *Tilia cordata* Mill.

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Abstract

The occurrence of interlocked grain, generated by storeyed cambium, was observed in the wood of linden. The inclination of the grain changed periodically every two to four years. In general, the direction of the change of grain was compatible with the occurrence of configuration *Z* or *S* of cellular events. If, in the cambium during the generation of a growth ring, the domain border did not pass the examined area, the events were of one configuration type only, otherwise, there were two types of events aggregated into microareas. The microareas were the result of unsynchronous activities of groups of cambium cells. A growth ring area through which a domain border passed during the year under consideration was called the transition area.

Key words: storyed cambium, interlocked grain, microareas, transition area

INTRODUCTION

The basic mechanism of reconstruction of the arrangement of cells in storeyed cambium of linden is the change of contacts of the ends of initial cells on the cambium borders, resulting from directional intrusive growth on the lateral subapical edges of fusiform cells. A new end is thus formed. The initial cell temporarily has two ends. A few appropriately oriented periclinal divisions completely eliminate the old end. The wall of the periclinal division twists at the end of the cell in such a way, so that the old end is found at the distal side in respect to the initial layer, and in this way gradually undergoes elimination in the initial cell. During this time the new end grows intrusively until a new contact is formed (Hejnowicz and Zagórska-Marek 1974, Włoch and Zagórska-Marek 1982). Anticlinal pseudotransverse divisions can also have an effect on the reconstruction of the arrangement of cells (Zagórska-Marek 1984), however, they occur with a low frequency in the linden. Not all ends of initial cells are active in reconstruction at the same time; the activity of groups of cells is asynchronous. Changes in activity depend more on the fact that active cell ends lose their activity and other, previously inactive ends acquire it, rather than on the movement of activity to the ends of neighboring cells. This type of change in activity in specific periods of activity of cambium has been called fibrillation by us (Włoch and Bilczewska 1987).

Two types of rays are usually found in linden cambium: low, single-rowed, which fits within the area of a given storey of fusiform cells, and high, multi-rowed, whose height exceeds that of the storeys of fusiform cells (Włoch 1985). The high rays become split at the borders of fusiform cell storeys due to the changes in the contacts of initial cell ends, but the branches formed as the result of such splitting can reunite if they come into contact again. The low rays bend along with the fusiform cells and do not undergo events. Those which reach the border of a storey can unite and become high, multi-rowed rays. The examination of the direction of uniting and splitting of rays makes it possible to trace the direction of reconstruction of cell arrangement over relatively large regions.

In linden cambium, as in other trees, there are areas where a specified configuration of events dominates (to the right — *Z*, or to the left — *S*), that is, where domains exist (Włoch 1985). However, the size of these areas-domains has not been determined, and so the domain pattern is unknown. In the case of a sufficiently high frequency of events, the shifting domain pattern is evidenced by the wavy grain of wood (Hejnowicz 1973, 1975). We have observed such a grain pattern in the linden (Włoch and Zagórska-Marek 1982, Zagórska-Marek 1984, Włoch 1985, Włoch and Bilczewska 1987). On this basis, we can suppose that there is a migrating domain pattern in the storeyed cambium of linden. The samples of wood taken for the study of the configuration of cellular events were significantly smaller than the length of the grain wave, and due to that, it had not been possible to check if this supposition was true.

In the case of linden, the change of configuration in a small area of cambium can take place with a much higher frequency (Włoch and Bilczewska 1987) than in trees having non-storeyed cambium (Hejnowicz 1971, Krawczyszyn 1972, Hejnowicz and Romberger 1973, Pyszyński 1977). In linden, the duration (inverse of frequency) of a configuration of events lasted about 2 years, in trees with non-storeyed cambium it lasted

10-20 years. The question arises about the nature of the relationship between the frequent change of configuration of events and the wavy grain of linden wood.

MATERIAL AND METHODS

EXAMINATION OF WOOD GRAIN

The trunk of a 36 year-old linden with grain undulation visible on the surface of the wood, was chosen for study. A board 10 cm thick and 1 meter long was cut at about the breast height diameter. The board was halved along the pith. One half was cut into transverse sticks, 5 cm thick. A knife blade was applied to the upper surface of the stick, along its radius and hit with a hammer to split the stick. At all points of the stick, the splitting occurred along the grain. The split sticks were then arranged in their original orientation and sequence (Fig. 1). On the lower edge of the split in each stick, changes in the inclination of the grain were visible along the ray. The limits of the growth rings and the cycle of changes in the orientation of the grain were marked on the lower surface of the split sticks (Fig. 2).

EXAMINATION OF CELLULAR EVENTS IN THE CAMBIUM

A sample of wood study was taken from the upper part of the board for further. The sample encompassed the entire radial dimension and 1.3 cm × 0.5 cm of the tangent dimension. Tangent sections, about 30 μm thick, were cut from the sample at the growth ring borders containing terminal parenchyma of the wood. A map of events in the rays was drawn on the basis of comparison of the studied rays in the terminal parenchyma of 25 successive growth rings of the wood, from the 11th to 36th (last) ring.

The sections containing fragments of terminal parenchyma with a well-preserved arrangement of cambial cells were photographed. The same fragment of the tangent surface, 1 mm × 0.5 mm, was selected from successive photographs encompassing growth rings 11 to 19. The arrangement of cells was traced, and the changes in the position of cells' ends between the neighboring storeys of fusiform cells were analyzed. In this way, a map of events in fusiform cells was drawn.

RESULTS

ANALYSIS OF WOOD GRAIN

We observed periodical changes in the inclination of the wood grain in the successive, tangent layers, which caused interlocking of the grain. In a given area of a certain layer, all of the cells were inclined in one direction. In the next layer (centrifugally), the inclination of the layer

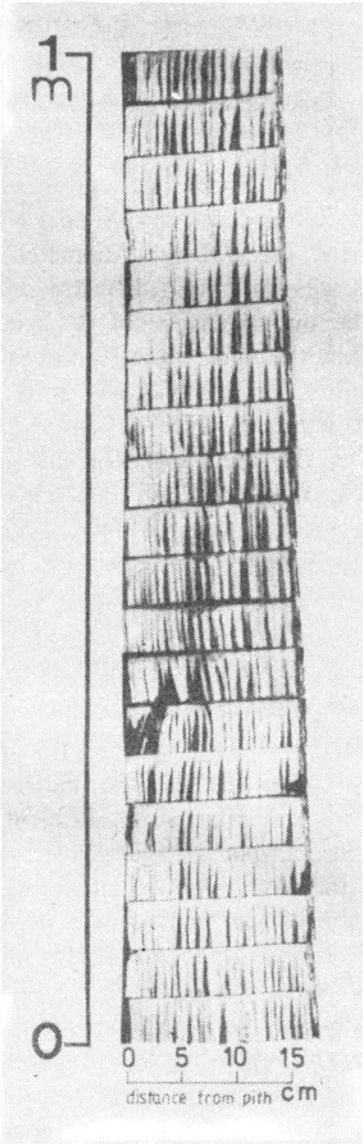

Fig. 1. The surface of a radial split (from the pith to cambium) of a board cut from the trunk of a 36-year-old linden. The board was cut into 5 cm high sticks and split. The split sticks were then arranged in their original orientation and sequence

changed. When it attained its maximal inclination, it began to change in the opposite direction, and the cycle was started over. The light and dark strands visible on the radial surface of the board (Fig. 1), corresponded to areas of different inclination of the grain. These strands, however, were not arranged exactly parallel to the growth rings, but formed a small angle with them. If we were to reconstruct the time-course of changes in the arrangement of cells in the cambium, we would obtain a grain wave with a long wave length and low amplitude, rising quickly up the trunk.

Analysis of wood grain can be conducted on the basis of the outline of the edges of sticks split along the radius. As mentioned above, the light and dark strands on the radial surface are connected with the waviness of the lower edge of the sticks. This waviness is the result of cyclic changes in the inclination of the grain (Fig. 2). The edge of the split stick is made up by sections inclined once to one side, then to the other. On Fig. 2 the sections are marked with circles which correspond with the layers whose grain changed from *Z* to *S* inclination, centrifugally, that is, the inclination changed to the left (*S*). This does not mean that the inclination of the grain is *S*, it can be *Z*, but changing so as to decrease the degree of inclination to *Z*. The lines representing the lower edges of each split stick were retraced and complied in their original arrangement, but in a more condensed form, shortening the longitudinal dimension by several fold. The borders of the growth rings were drawn on such a drawing with a thinner line (Fig. 3), and the parts corresponding to the layers of changes of inclination in the *S* direction were dotted. It can be seen that they form stripes. In this way a picture has been obtained, which along with the undotted stripes (changes in inclination towards *Z*), form a pattern similar to the pattern of light and dark strands on the radial surface of the wood. The exact marking of the growth rings on Fig. 3 makes it possible to

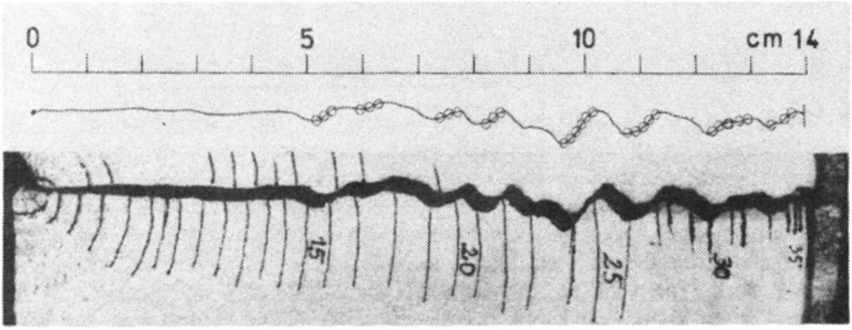

Fig. 2. The lower transverse surface of a split stick. The outline of the wavy edge is visible. The sections on the edge marked with circles correspond to the inclination of the grain in the *S* direction. Annual rings are marked

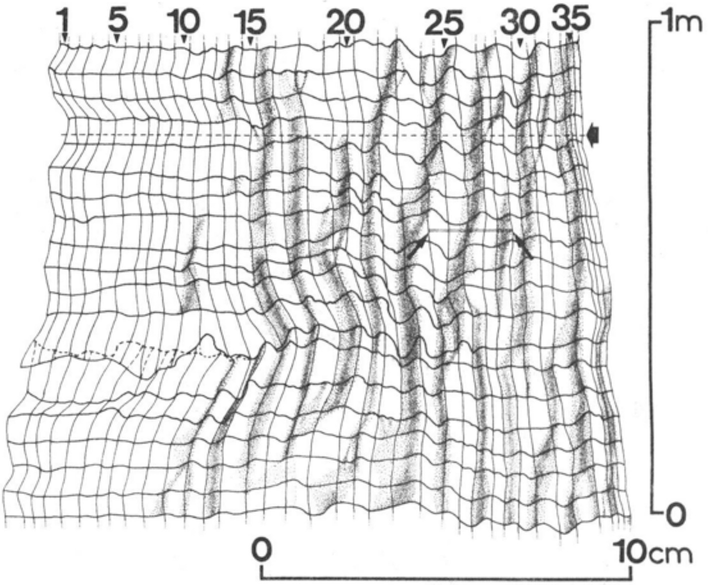

Fig. 3. A diagram of the radial split of a segment of the trunk, obtained by putting together the edge lines of consecutive split sticks. The places where the inclination of the grain changes in the *S* direction are shaded. The thinner vertical lines mark the borders of annual rings. The numbers in the upper part of the figure denote the successive growth rings. The broken line marks the point from which a sample was taken for analysis of events, an arrow shows the same place from the side of the cambium. The rectangle marked with arrows shows the area on the basis of which the diagram presented in Fig. 8. was drawn. The vertical scale presents the dimension along the vertical axis, the horizontal scale — the radial dimension

determine the wave length and cycle of changes in the orientation of the grain. The wave length is the distance between the points of intersection of two successive stripes of the same kind, with the border of the annual ring. The duration of the cycle of orientation change of grain corresponds to the number of growth rings between two intersection points of a ray with two successive stripes of the same type. It can be seen that the wave length varies from about 40 cm to over 100 cm. The length of the grain wave corresponds to the height of a pair of domains; the height of one domain is then from about 20 cm to 50 cm. The cycle of reorientation of grain is only 2-4 years long. It results from this that the rate of migration of the wave of grain orientation along the axis of the trunk is about 10-50 cm per year.

ANALYSIS OF CELLULAR EVENTS

Wood rays

The configuration of events dealing with rays are studied on the basis of comparison of two successive maps of events in the terminal parenchyma

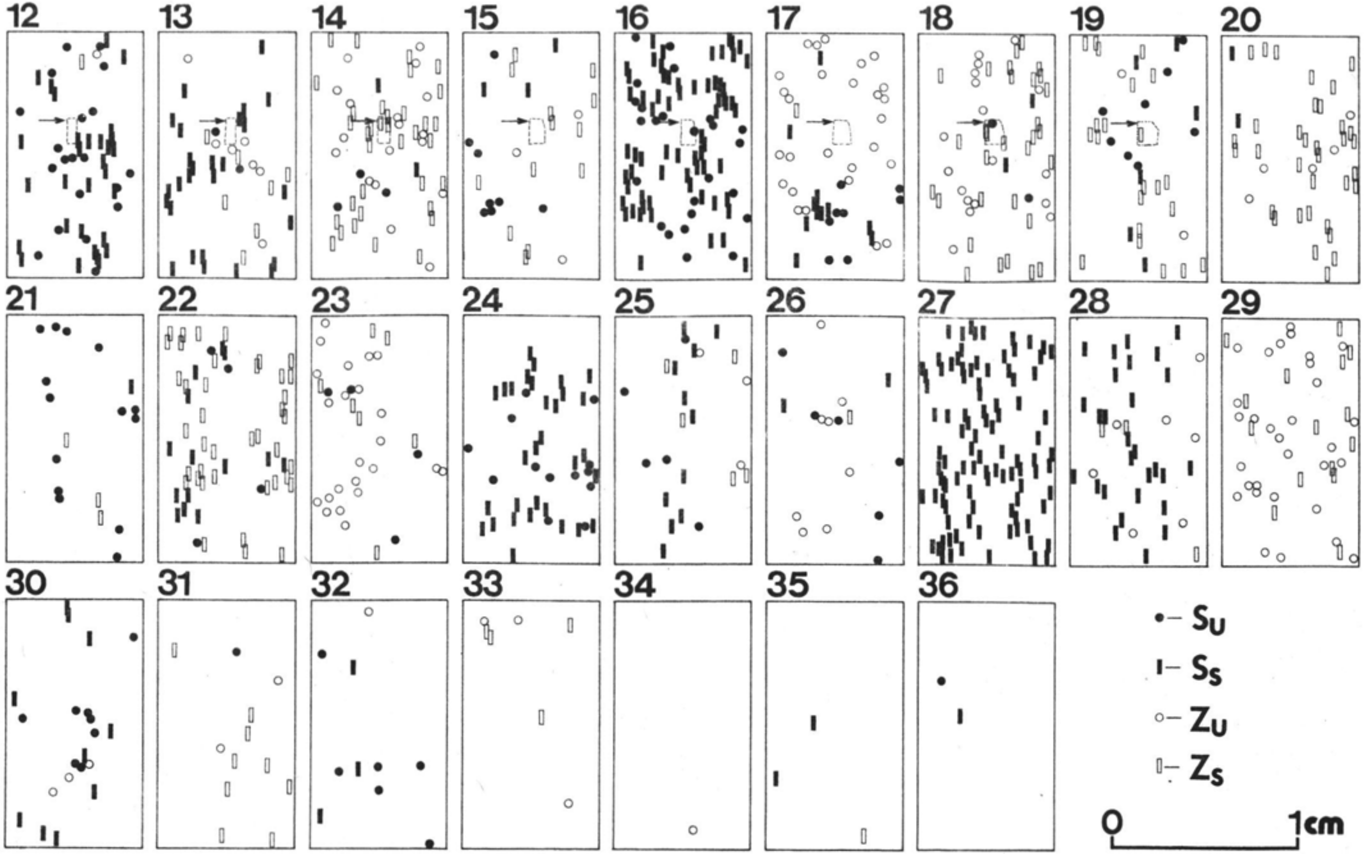

Fig. 4. Maps showing the uniting and spliting of rays in 25 successive growth rings of a 36-year-old linden trunk. The numbers in the upper left corner of a map denote the number of the successive ring. The places where the changes in the position of the ends of fusiform cells were studied, shown on Fig. 6, are circled by a broken line (maps 11-19). Rectangles and circles denote ray splitting and uniting, respectively. Full symbols indicate *S* events, open symbols — *Z* events

on the border of annual rings. An area 1.3 cm high and 0.5 cm wide was examined. The sample was removed from a place where the change in the orientation of the grain was most clearly visible (Fig. 3). It encompassed 25 rings. The place from where the sample was taken is marked on Fig. 3 by a broken line and arrow from the cambium side. The maps showing the uniting and splitting of the rays in this sample in the successive 25 annual rings (from 11 to 36) are shown on Fig. 4. Events are marked on it using four different types of symbols. They describe both the type and kind of event. "Type" denotes the configuration of the event; to the right (*Z*) — an open mark, to the left (*S*) — a full mark. "Kind" denotes the anatomical type of event; uniting — a circle, splitting of the ray — a square. When taking into consideration all of the marks at the same time, high variation in the density of events on successive maps becomes noticeable. For example, high density of events is seen on maps 14, 16-18, 22 and 27, while a low density is visible on maps 26 and 30-36. It is interesting to note that a low density of events on one map is accompanied by a high density on the succeeding one. This means that a low intensity of events one year precedes a high intensity the following year, which is exceptionally clearly seen on maps 15 and 16, 21 and 22, 26 and 27. Non-uniform distribution of events can sometimes be noticed on a single map. There can be more events in one region of a map than in another, as seen on maps 13, 19, 22 and 23.

During the analysis of the kind of events on successive maps, it can be seen that after a period in which splitting dominates, uniting of rays prevails. On maps 12, 13 and 14, a more or less equal number of both kinds of events is seen. Then, on maps 15 and 16, there is a predominance of splitting, followed by a dominance of uniting of rays on map 17. Sequentially we see: on maps 18, 19 and 20 a predominance of splitting, on map 21, of uniting, on map 22 — of splitting and again on map 23 — of uniting. On maps 24 and 25 we see mainly splitting, on map 26, mainly uniting. Map 27 is exclusively splitting, which also prevails on map 28, while on map 29 there is again a prevalence of uniting. There is a low number of events on the subsequent maps 30-36, although there too, such an alternation of event kinds can also be noticed.

Frequent changes in the configuration of events can be observed. On maps 12 and 13, the *S* type events prevail. On maps 14 and 15 we see mainly the *Z* type events. Map 16 is exclusively of *S* type events. On maps 17-20 the predominance of Z type events is visible, on map 21 — type *S*, on maps 22 and 23, again of type *Z*, 24 and 25 — *S*, 26 — *Z*, 27 and 28 — *S*, 29 — *Z*, 30 — *S*, 31 — *Z*, 32 — *S*, 33 — *Z*. On maps 34-36, due to the very low number of events, it is not possible do determine if there is a predominance of one type of event over the other. It is interesting that on maps 16. 24 and 27 we see only *S* type events, while on map 29 only *Z* type. on maps 12 and 21, *S* type events strongly dominate, on maps 14, 18, 20, 23 and 31, *Z* type events prevail. On the remaining maps, one type of events is seen to dominate over the other to a greater of lesser extent.

Let us now compare the results of the analysis of the events in the rays and changes in the grain. Concurrently with the changes in the configuration of events between successive annual rings, a change in the inclination of the wood grain took place. The question arises about the relationship between the value of the changes in the angle of the grain to the frequency of a specific type of event (that is, the number of events on the studied surface per year). It should be remembered that the maps represent the sum of events which we record only once per year in the terminal parenchyma. This corresponds to a layer of wood of a thickness equal to the length of the ray segment between two successive borders of annual growth. On Fig. 3, it corresponds to the sections on the broken line between the vertical lines. Visual comparison of darkened and light areas in these sections with the maps shows that the darkened regions correspond to the maps with a predominance of *S* type events (compare rings 16, 21, 24 and 27 along the broken line with the maps with the same numbers) and conversely, the light areas correspond to the maps with a predominance of *Z* type

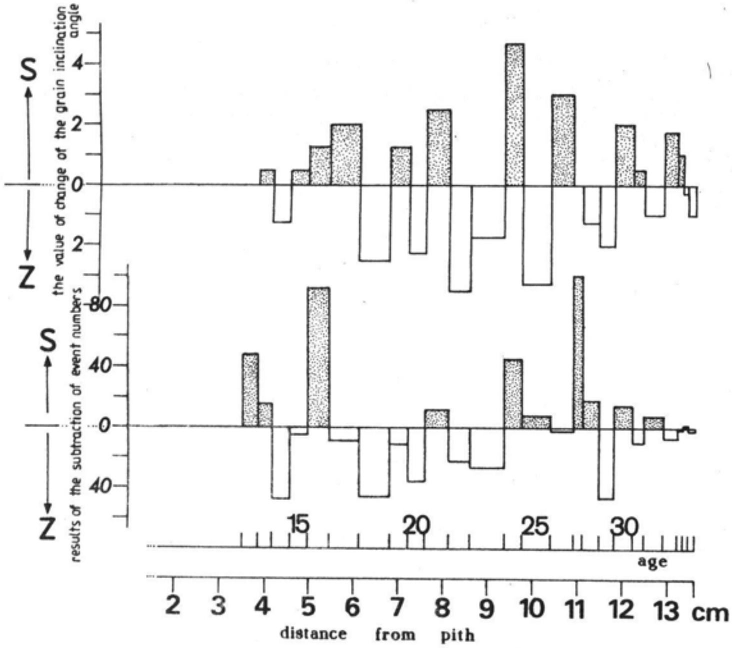

Fig. 5. A diagram comparing the value of the change in the angle of inclination of grain in successive rings (upper diagram) with the difference between the number of *Z* and *S* events (lower diagram)

events (compare rings 20 and 29 with maps the same numbers). For more precise, quantitative comparison, a diagram is presented on Fig. 5 which compares the size of the change in the angle of inclination of the grain in successive annual rings with the result of the subtraction of the number of *Z* and *S* events, that is, only the number of events by which one type of event exceeded that of the other is presented on the diagram. It is interesting that both graphs correspond with each other, that is, the change in the type of dominating event corresponds to the change in the direction of inclination, as well as generally, a high predominance of events corresponds to a large change in the inclination. The agreement of both graphs on the diagram is especially well visible in rings 13-24.

On Fig. 3 we see that in some of the rings on the broken lines, light and dark areas also occur simultaneously (rings 17, 19, 22 and 25). This means that during the formation of these rings, a domain border moved through the studied area. Therefore, on the map of events we can expect the occurrence of both types of events. For maps 17, 19 and 22 this expectation is fully fulfilled. What is interesting is that on successive maps of these locations, events of opposite configurations do not form a random mixture, as could be expected, but separate into irregular microareas. This is especially well visible on maps 13, 15, 17, 19, 22 and 25. This phenomenon should be analyzed in detail based on the analysis of events on the ends, of fusiform cells.

Ends of fusiform cells

Fragments of the sections on which the uniting and splitting of rays was studied and on which the terminal parenchyma was best visible, were chosen and their cellular arrangement was traced. From previous studies it is known that the cellular arrangement in the terminal parenchyma is the same as in the cambium cells which produced it. The arrangement of cells in the cambium was reconstructed for 9 consecutive growth rings (from 11 to 19) on the basis of a series of such drawings. The size of the areas studied in such a way was considerably smaller than the maps on which rays were studied, and encompassed about 1 mm × 0.5 mm of the terminal parenchyma area (Fig. 6). On Fig. 4, these areas are marked with a broken line. On the basis of the arrangement of the cells in the successive fragments of the parenchyma, the direction of migration of the ends of the initial cells during their 9-year period of activity was traced back. The mutual transpositioning of opposite ends of cells belonging to neighboring storeys (the upper ends of the cells of one storey change their position in respect to the lower ends of the cells of a higher storey) led to changes in the inclination of the axis of initial cells. Changes in inclination were cylic; the axes of initial cells were tilted in one direction, then after some time, assumed

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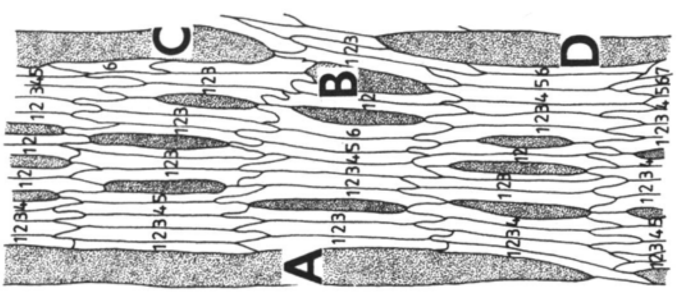
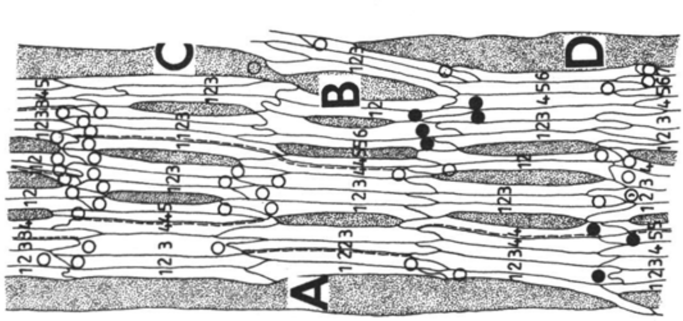
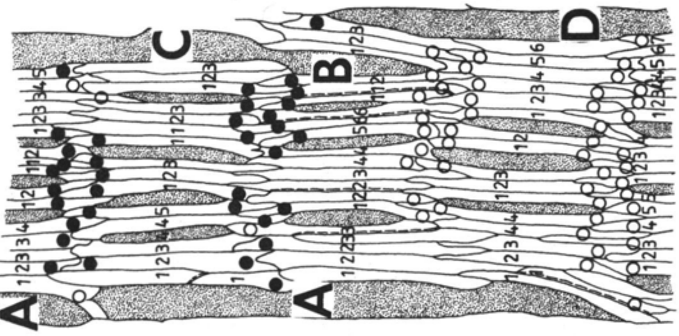


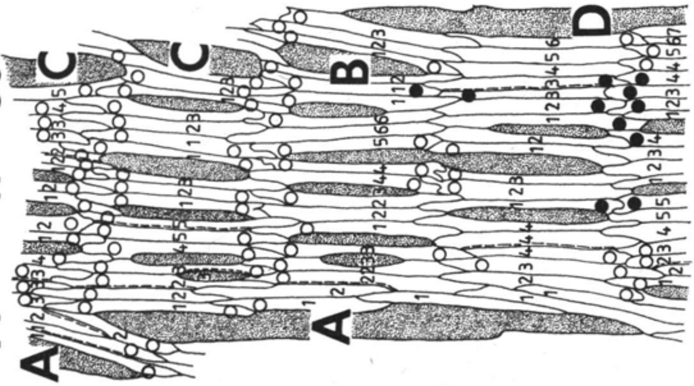
12 ● – 8 ○ – 40



13 ● – 35 ○ – 50



14 ● – 11 ○ – 80



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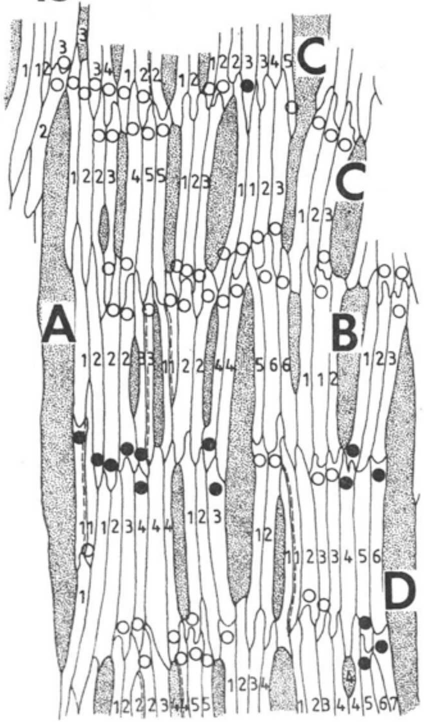

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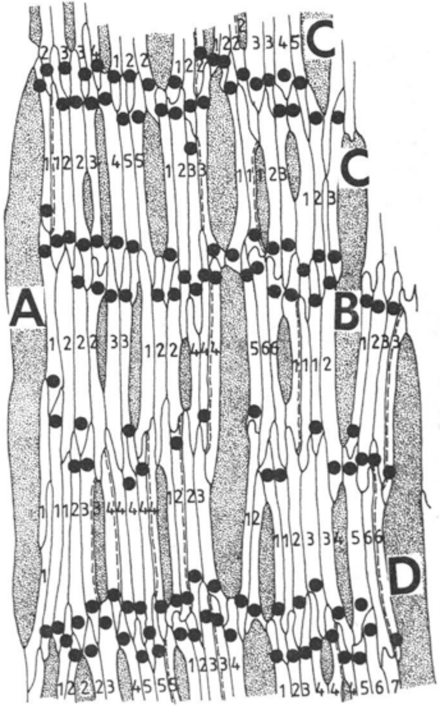

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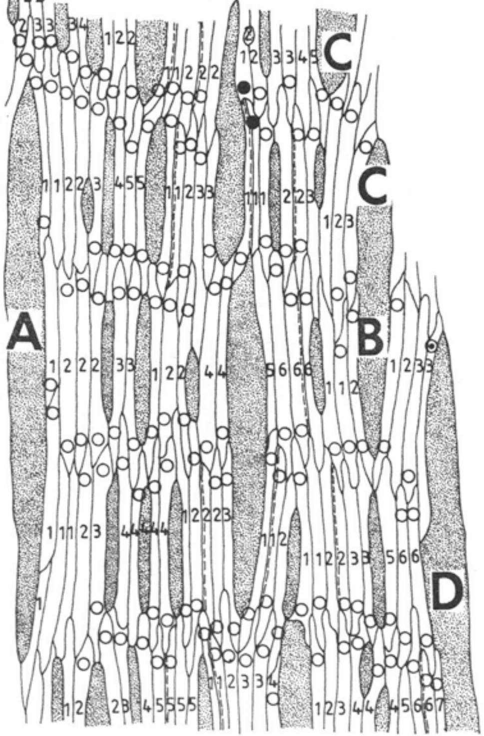

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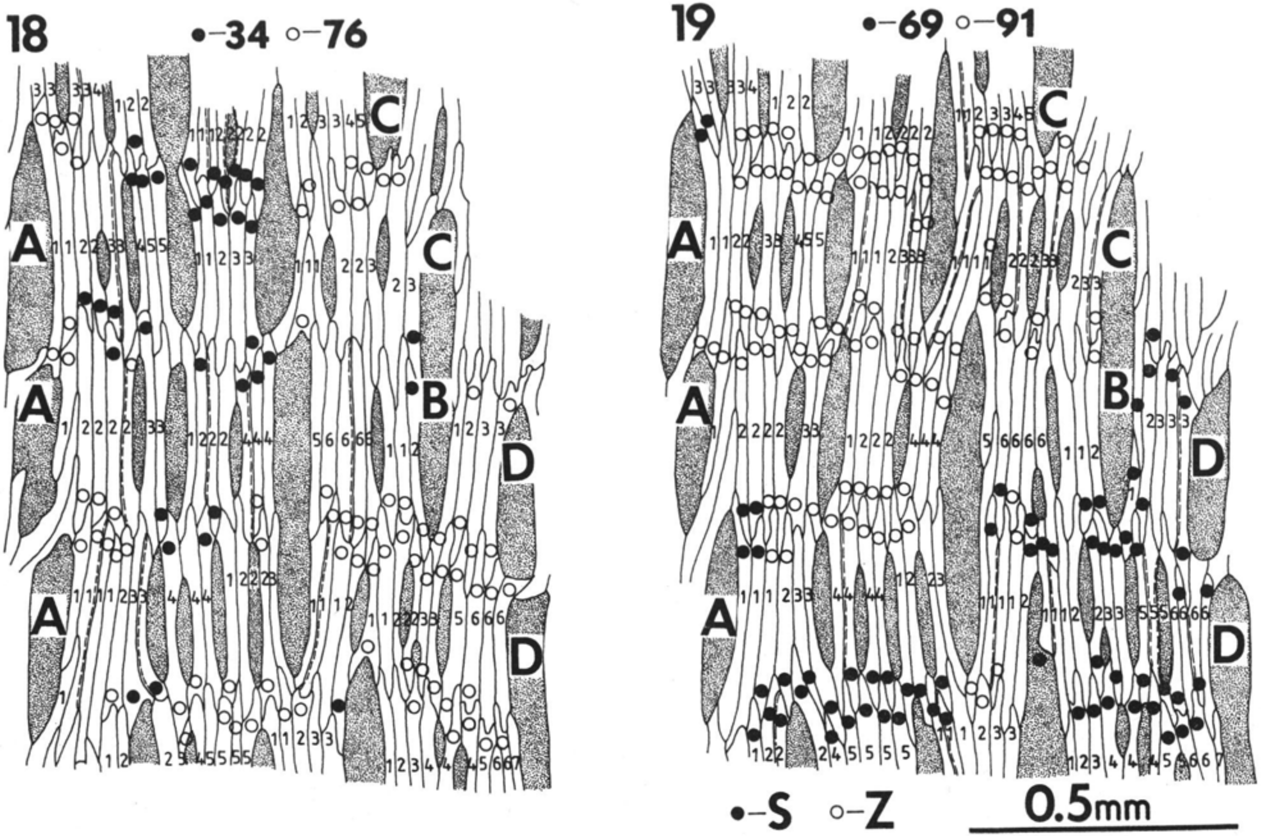

Fig. 6. A series of 9 drawings of successive terminal parenchyma layers of wood on the borders of rings 11-19. The surfaces are marked on Fig. 4. The cell ends which underwent transposition are marked with a circle. Full circles — movement to the left, that is to *S*, open circles — movement to the right, to *Z*. The rays are dotted. Larger rays are denoted by letters in a way showing their uniting and splitting. The numbers in the upper left corner denote the number of the annual ring. The numbers in the upper right corner denote the number of active ends in both types of configurations. Anticlinal divisions are marked with solid and broken lines. Radial files of fusiform cells are numbered

an inclination in the opposite direction. The ends which migrated through the studied area are marked with a circle. Those whose migration led to an inclination to the left (*S*) are marked with a dark circle, those causing inclination of cells to the right (*Z*) are marked with an open circle. Upon observation of the distribution of the symbols standing for configuration, it becomes evident that there is no randomness in it; events of opposite configurations do not mix with each other, but form separate, larger or smaller microareas. As mentioned above, microareas are also found on maps on which the plotted events deal with rays. The drawings presented on Fig. 6 were copied leaving out the outline of the cells (Fig. 7). The places where the movement of cell ends leading to inclination of cells to the left (*S*) were shaded. In this way, a mozaic representation of microareas of a given configuration was obtained. The microareas changed according to the principle of "fibrillation", that is, groups of cell ends changed their configuration in an unsynchronized manner. In many places, the changes occurred year by year, in others, a given configuration lasted 2 or even 3 years.

Taking into account the fact that the velocity of migration of the wave of orientation of grain, and due to this, the rate of migration of domain borders equals 10-50 cm per year, and that the height of the studied area was 1 mm, it is obvious that we could not register the movement of the domain borders in the tiny studied area, but only the appearance of one, and disappearance of another type of configuration of events. How can the domain borders which so rapidly migrate, and in this way the changes in configuration of events, be reconciled with the existence of microareas (groups of cell ends) with an opposite configuration of events? It should be underscored that the method used in this study gives the sum of events which occurred in the given area over the period of one year.

It is known from previous studies on storeyed cambium that initial cells are active over a certain period, then they become inactive. In addition, the changes in activity are not synchronous. If that is so, and if the groups of active cells alternate with groups of inactive cells, then the method of registration used here must give a pattern of microareas such as that shown on the model (Fig. 8). For simplicity, a synchronous change of activity was accepted. The cycle of changes in the configuration of events on the model is the same as that found on the long rectangle shown on Fig. 3 by two arrows. The configuration of events changed approximately every year. It can be seen that depending on the growth ring in which the maps of events are analyzed, one configuration of events occurred over the entire area in a given year, or microareas with opposite types of events alternating yearly were found. In the sample studied in this investigation, the cycle of configuration changes was often longer than two years, and approached four years. The height of domains also changed often from 20 to 50 cm. It should be expected that

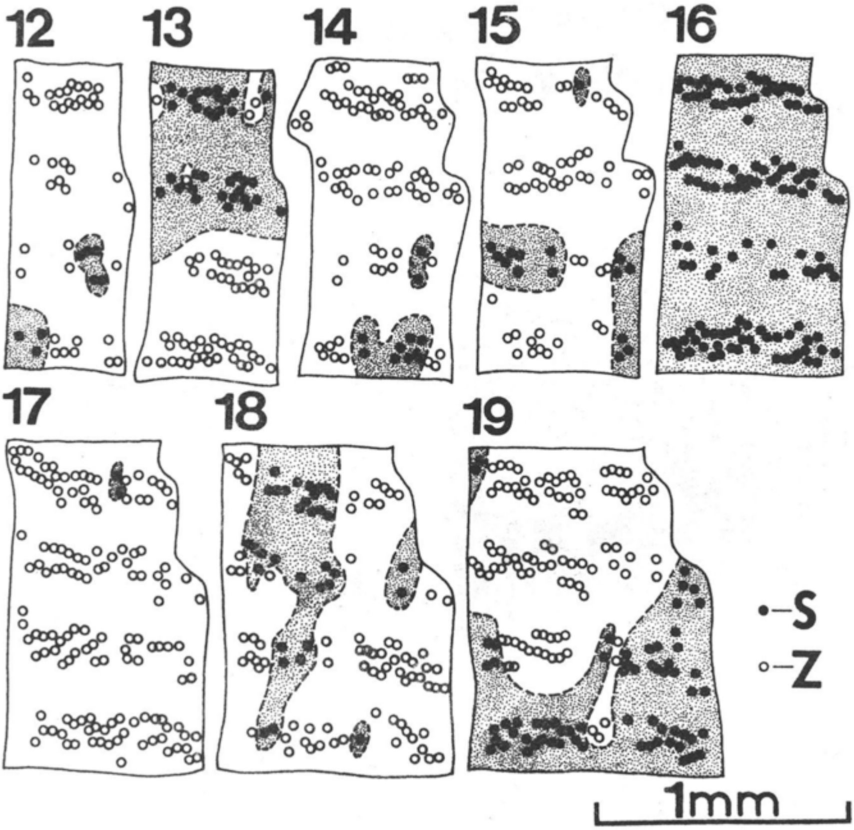

Fig. 7. A diagram, made on the basis of Fig. 6, in which the outline of the cells has been omitted. Cell ends which had undergone transposition, are marked with a circle. Full circles — movement to the left, that is to *S*, open circles — movement to the right, that is to *Z*. The microareas in which cell ends moved to the left (*S*) are dotted. Numbers in the upper left corner denote the annual ring number

variation in the length of activity periods of cell groups also had place. A consequence of such variability is the unsynchronized occurrence of one type of events in successive growth rings, with the occurrence of once greater, once smaller microareas of opposite configurations (Figs. 4 and 7).

In analyzing a random growth ring on a 1 m section along the trunk axis (as shown on Fig. 3), we can assume, as described above, the darkened area to be an *S* domain, the light area to be a *Z* domain. It can be seen that in some of the growth rings, there are areas through which the domain border did not pass, and areas through which it did. In the latter, one part of the ring is shaded and another part is not. In those places through which the domian border did not pass, only one type of events is registered as the sum of events in the terminal parenchyma during a one year period of activity of the cambium. In the opposite case, there will be events in two configuration types with one of the two dominating, depending on during what period of cambial

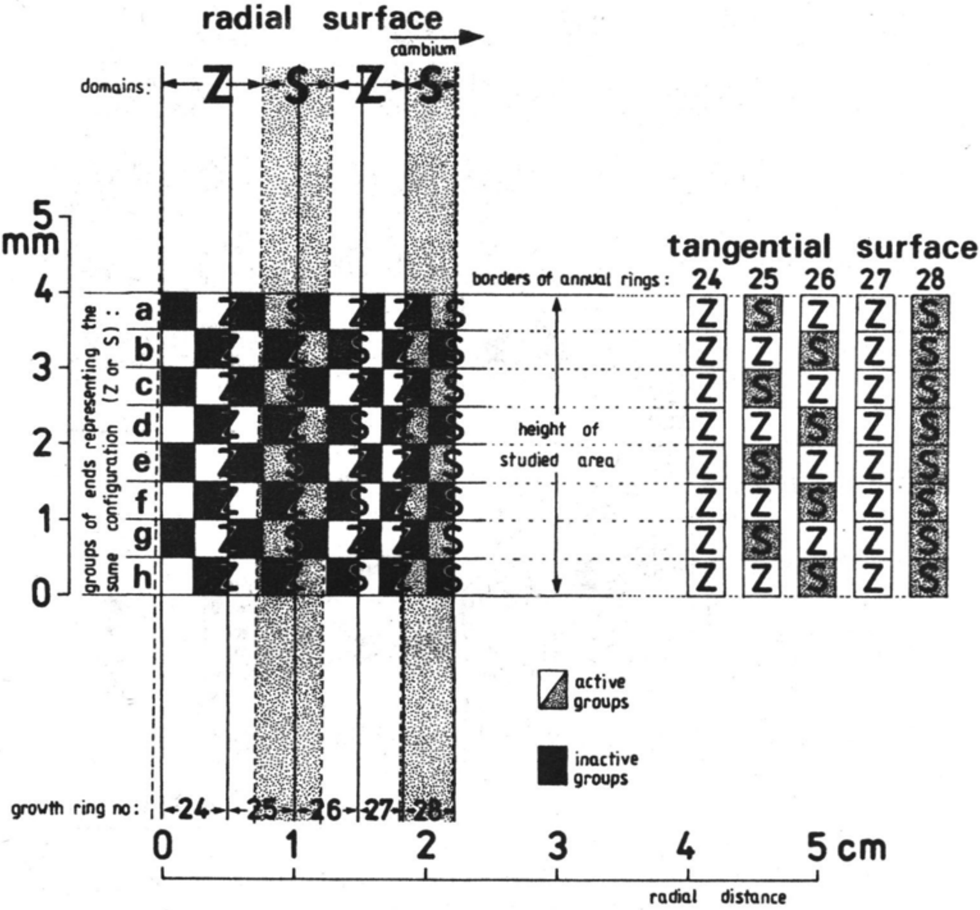

Fig. 8. A diagram illustrating the way in which the microareas in the successive annual rings change their configuration, giving the effect of fibrillation. The diagram was made on the basis of changes in the inclination of the grain for growth rings 24 to 28 in the place marked on Fig. 3 by a rectangle and two arrows. Continuous vertical lines indicate the growth ring borders, broken lines — domain borders. Eight groups of cell ends were discerned in the studied material and labeled from "a" to "h". It was assumed that the initial cells are either active or inactive in reconstruction during the season (black and white fields). Activity occurs in turn in groups. Microareas here are the points of intersection of growth ring borders with the individual groups of cell ends. The microareas seen in the tangent plane are shown on the side. The *S* or *Z* configuration of events is the sum of the events which occurred in the given microarea during the period of one year. For example, the microarea at the place of intersection of group "a" with the border of ring 24 is in *Z* configuration, the microarea at the point of intersection of group "c" with the border of ring 25 is in *S* configuration, etc. The individual microareas on the border of ring 24 have the same configuration of events (*Z*) of all groups from "a" to "h", on the border of ring 25, configurations *Z* and *S* occur alternately in the individual groups. On the next, 26th border, the situation is reversed, and *Z* configurations are substituted by *S* configurations. In those places where the border domains passed at about the middle of the annual

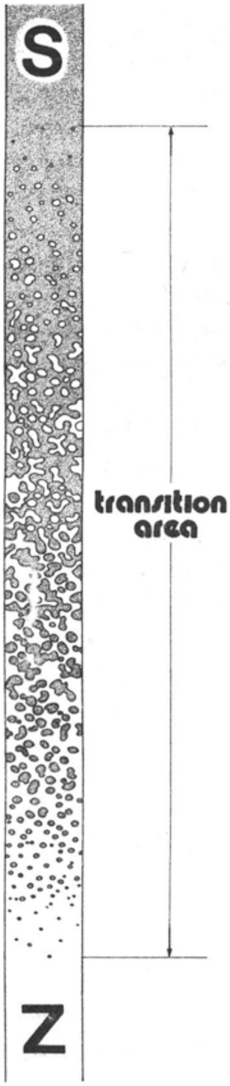

Fig. 9. A diagram in the tangent plane showing the occurrence of the transition area between domains *Z* and *S* as the result of the sum of two types of events occurring during one year on the growth ring border. The microareas where *S* configuration events occur are shaded. The microareas where *Z* configuration events occur are unshaded

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growth, microareas with both types of configurations were formed alternately along the trunk axis. In those places where the domain borders on the studied area did not pass through the growth ring, there is only one type of configuration which changes with the change in domain type activity the domain border passed. It results from this that between an area of one type of configuration of events and an area of the opposite type a transition area will be formed over a large area of the annual ring, due to the summing of events occurring during one year. This will be an area whose height will be determined by the length of the segment between the points of intersection of domain borders with one, successive border of annual growth. On a certain area of terminal parenchyma, events of a given configuration in groups of cell ends will begin to gradually disappear, and simultaneously events of the opposite configuration will start to appear in groups of cell ends, until a complete change of configuration is attained. The expected appearance of an entire transition area in the domain pattern of linden cambium is presented on a diagram in Fig. 9. The ratio of the size of the area encompassed by transition regions observed in the terminal parenchyma to the size of the areas in which only one configuration of events is found, has a decisive role in determining the duration of one type of configuration and the rate of migration of domain borders. With the two year cycle of configuration changes and the high rate of migration of domain borders in the terminal parenchyma of linden, we may not be able at all to register greater areas in which only one type of event occurred, as would result from the large height of domains, but only greater and smaller microareas characteristic for the transition area.

DISCUSSION

Domain patterns can differ in the height of domains as well as in respect to the rate of pattern migration. With a high frequency of events, they are reflected in the grain of the wood. Studying the wood grain makes it possible to draw conclusions about the height of domains and rate of migration of patterns on the surface of the cambium. The grain wave length, and therefore the height of a pair of domains, ranges from a few millimeters to several meters (Hejnowicz and Romberger 1979). The greatest known grain wave length in *Entandrophragma* exceeds one meter. In *Platanus*, the height of domains is 8-28 cm (Krawczyszyn 1972), in *Aesculus*, 25 cm (Pyszyński 1977). The smallest known domian height of cambium producing wavy grained wood, *Fraxinus* and *Acer*, is only a few millimeters (Hejnowicz and Romberger 1973). There is a relationship between the rate of domain pattern migration and domain height: the higher the domain, the faster the migration of a given pattern, that is, the longer the grain wave, the faster it travels. In the cases described until now, this relationship corresponded to a low variability of the grain period *T*, that is the cycle of changes in orientation of the grain in the radial direction. The period *T*, which is the quotient of length by velocity $T=\frac{\lambda}{V}$, is the least variable parameter of waves (Hejnowicz 1973, 1975). In the case of the linden described in this study, the domains are relatively large, but they move faster than in the species described previously, because the period is shorter; *T*, in the linden under study, is 2-4 years. The relationship of the configuration of events to the changes in inclination of the grain indicates that we are dealing with frequent changes in the domain type, every 1-2 years. In the previous paper (Włoch and Zagórska-Marek 1982), we described the translocation of active ends of cambial fusiform cells and the direction of translocation of the ends. It was shown that in a 35 μm thick layer of cambium, which corresponds to 7-8 cells in a radial row, changes in the configuration of events occur simultaneously over the whole studied area (2 mm in height). Not all of the initial cells which formed this small layer of cambium were active during this period of reconstruction, groups of active and inactive cells were formed. While following the active ends in this sample from the side of the phloem, we noticed that the events were in configuration *Z* and as we approached the layer of initial cells, the configuration began to change to *S*. By compiling the events which occurred over the entire studied layer of cambial cells, we obtained a picture of the distribution of cell activity during this time. It was observed that groups of active cells were formed, each with a specified configuration of events, positioned alternatingly with inactive groups; active groups in configuration *Z* were formed earlier than in *S*. Most likely, rapid translocation of domain borders occurred and simultaneously a periodic lack of synchrony of activity of groups of initial cells took place.

The perfect object for studying the activity of groups of cells in successive unicellular layers turned out to be the terminal parenchyma in the wood of *Entandrophragma* (Hejnowicz and Zagórska-Marek 1974, Zagórska-Marek 1975). It forms a small multicellular layer up to 500 μm thick, sufficient however, to observe active groups. Generally, *Entandrophragma* is characterized by the occurrence of interlocked grain. Grain stripes form a small angle with growth rings. By following the successive layers of terminal parenchyma over a small area, changes in the orientation of grain every few years over the whole studied area were observed. Because the cycle of changes in the orientation of grain encompasses a significantly thicker layer of wood than that studied, so signs of migration of domain borders were not found in the studied material — all of the active groups were in one configuration of events in a given layer of parenchyma. In studying a small fragment of the surface of terminal parenchyma in the linden, that is in spaces of one year, with its frequent changes in orientation of the grain, the probability of finding a migrating domain border is very high. The domain borders migrate so quickly, however, that on the studied area we get the impression of simultaneous changes in configuration of events over the entire studied area. We see then, that active groups of one type of configuration suddenly disappear, passing unsynchronously into inactive groups, while in other places, in the place of previously inactive groups, active groups with an opposite configuration of events appear. This phenomenon was previously described by us as fibrillation of activity of fusiform cell ends (Włoch and Bilczewska 1987). When studying the restructuring of the cell arrangement in sufficiently large periods of time when the intensity of restructuring is high, as for instance in *Entandrophragma* between successive layers of terminal parenchyma, we observe that the ends of all of the cells changed their position, that is as if all of them were active at the same time. This probably is due to the fact that the period of activity of the indivivual groups of cells is shorter than the period between the formation of parenchyma layers. The sum of events between the successive layers of terminal parenchyma in *Entandrophragma* gives the impression that all of the cells were restructured, that is, that all of the cells are active (Hejnowicz and Zagórska-Marek 1974). A similar picture of the sum of events was obtained by us in this study in the case of intensive restructuring in the terminal parenchyma of linden. The probability of finding a migrating domain border here is, however, much higher due to the relatively small *T*, and we obtain in the sum of events of a one year period, both types of events. In spite of the fact that in the presented example most of the cells on the studied surface were active in restucturing during the one year cycle, and no isolated active areas were found, we are of the opinion that the occurrence of active and inactive areas over a given period of time is a general rule for storeyed cambium. Activity does not depend on the type of configuration, but it is, however, lower in transition areas, that is near domain borders, both in storeyed cambium (Zagórska-Marek 1984), and unstoreyed cambium (Hejnowicz 1968, 1971, Krawczyszyn 1972, Pyszyński 1977). In this study, in the transition area, due to the lower frequency of events, groups of active and inactive cells were seen more clearly (Fig. 6, rings 12-15) than in the area corresponding to the central part of the domain (Fig. 6, rings 16-17). The precondition for isolating active groups is the occurrence of inactive groups, and these occur when there is a low frequency of events.

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Strefy przejściowe we wzorze domenowym kambium piętrowego Tilia cordata Mill.

Streszczenie

W drewnie z pnia 36 letniej lipy, utworzonym przez kambium piętrowe, zaobserwowano występowanie włóknistości zaplecionej o niezwykle krótkim cyklu zmiany orientacji włóknistości, bo zaledwie 2-4 letnim. Na powierzchni kambium włóknistość jest falista, gdzie długość fali jest zmienna od około 40 do ponad 100 cm. Oznacza to, że szybkość przemieszczania się fali orientacji włóknistości, i w związku z tym szybkość przemieszczania się granicy domen, wynosi 10-50 cm na rok. Wycięto małą próbkę obejmującą cały wymiar promieniowy, w której na obszarze 1,3 cm wysokości i 0,5 cm szerokości badano konfigurację zdarzeń komórkowych i sporządzono mapy zdarzeń dla 25 kolejnych przyrostów rocznych. Zdarzenia odczytywano w cyklu rocznym przez porównywanie kolejnych warstw miękiszu terminalnego. Zaobserwowano, że na ogół istnieje zgodność między wielkością zmiany kąta nachylenia włóknistości i różnicą liczb zdarzeń *Z*-owych i *S*-owych na kolejnych mapach Każda mapa jest sumą zdarzeń jakie wystąpiły w kambium w jednym roku. Jeżeli w tym okresie granica domen na badanym obszarze nie przemieściła się, zdarzenia są tylko jednego typu, w przeciwnym wypadku są to zdarzenia jednego i drugiego typu tworzące wyraźne mikroobszary. Mikroobszary są rezultatem niesynchronicznej aktywności grup końców komórkowych komórek wrzecionowatych. Obszar przyrostu rocznego, w którym przemieszczała się granica domen, charakteryzujący się występowaniem mikroobszarów nazwano strefą przejściową między jednym i drugim typem domeny.