

Movement of the cambial domain pattern and mechanism of formation of interlocked grain in *Platanus*

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(Received: October 4, 1971.)

Abstract:

The orientation of splitting and uniting of rays, which served as an indicator of the orientation of morphogenic events occurring in cambium, was determined on series of veneers covering large tangential faces of *Platanus* trunks. It has been shown that cambium consists of orientational domains of Z- and S-type. They are perpendicular to, or slightly inclined with respect to, the trunk axis. Axial dimensions of domains are 8—28 cm. They move upward along the trunk, at a rate 6,5—12 mm per radial mm of xylem produced. Migration domain patterns are responsible for the formation of the interlocked grain.

INTRODUCTION

The cambium of a tree, being a long-lived meristematic tissue, is capable of extensive changes in cell arrangement. This includes changes in orientation with respect to the bole axis. This readjustment is related to oblique anticlinal divisions, intrusive growth, and elimination of fusiform initials from the cambium (Newmann 1955; Bannan 1966; Hejnowicz 1968; Harris 1969; Krawczy szyn 1971; Hejnowicz and Romberger 1972). Intrusive growth, which is localised in the tips of fusiform cells in a very small area of the wall, brings about formation of new contacts between cells. When tips of two cells growing intrusively in opposite directions meet, they overlap either to the right or left. Another effect of intrusive growth is splitting of rays, and thus formation of new strands of fusiform initials inclined to the right or to the left. Initial cell decline and elimination compensates for the additional cells formed as a result of anticlinal divisions

and for increased length of cells due to intrusive growth. Cell decline and elimination acts selectively (Bannan and Bayly 1956).

The above-mentioned events occur in two alternative forms: the right (Z) and the left (S). One form predominates in initials occupying a certain local area of the cambium. Such an area of cells is called a domain and is either of the Z or S type. Within a domain Z type anticlinal divisions are accompanied by Z type overlapping of tips of intrusively growing fusiform cells and Z type splitting and uniting of rays. The S type events occur in a similar manner (Hejnowicz and Krawczyzsyn 1969; Krawczyzsyn 1971; Hejnowicz and Romberger 1972). Thus, the type of domain may be determined on the basis of the orientation of splitting and uniting of rays.

The type of domain in a given part of the cambium does not remain constant but changes in time. This is due to the migration of domains in respect to the cells along the trunk (Krawczyzsyn 1971; Hejnowicz 1971; Hejnowicz and Romberger 1972). Oriented cellular events (if they occur frequently enough) elicit changes in the orientation of cambium cells (Bannan 1966; Hejnowicz 1968; Hejnowicz and Romberger 1972). These changes induce changes in the orientation of the grain in wood.

Wood with interlocked grain is one of the more important types of wood in which continuous changes of grain orientation occur. In this type of grain the inclination of wood elements changes from right to left and *vice versa* in groups of successive growth rings many times during the life of the tree. Interlocked grain occurs in many Indian and tropical timbers (Martley 1920; Panshin 1933; Limaye 1954) and in *Platanus* (Brown et al. 1949). The author has advanced an hypothesis that the domain structure of the cambium is the basis for development of interlocked grain (Krawczyzsyn 1971). The present work develops this hypothesis.

MATERIALS AND METHODS

The investigations were performed on a trunk segment of *Platanus acerifolia* Willd. The segment included 162 annual rings; its diameter was 90 cm and length was 85 cm. The segment was cut from the bole of a tree that had been growing in Wrocław, its base being four meters above the base of the tree. Part of the segment was cut using a machine for making veneers. A series of veneers 85 cm long, approximately 30 cm wide and 0.8 mm thick were obtained. They were approximately tangential to the annual rings. Annual rings were identified on the veneers; with suitable lighting boundaries between them were visible as thin bands of lighter tissue. Outer surfaces of the veneers were scraped off with a razor blade and a rectangular grid 3.5×2.5 cm was placed on them so

that its localization with respect to particular rays was the same on all veneers. Small knots were used as the orientation points. Each rectangle of the grid was photographed from a distance about 20 cm using an Exacta camera. The photographs were magnified 15 times. Veneer surfaces were moistened with water shortly before photographing them in order to obtain better contrast between the rays and the remaining wood material. Series of the photographs representing the surfaces of successive annual rings served as the material for determining the domain pattern. Every ray in the photograph of the outer surface of an annual ring (N) was identified with respect to the rays in the corresponding photograph of the outer surface of the previous ring (N-1). If a ray splitting or uniting event had occurred a mark indicating the orientation (Z or S) was made on the photograph N. Two different sites: I — 14×5 cm, and II — 38.5×2.5 cm of the investigated segment were studied.

Supplementary analyses were performed on tangential microtomic sections. For this purpose blocks of wood were boiled in water and cut into sections 35μ thick by means of a sliding microtome. They were attached to slides with Haupt's adhesive, dried and deaerated in boiling absolute alcohol, transferred to xylene, and embedded in Canada balsam.

RESULTS

1. Grain pattern

An area of wood surface from which the bark was removed is shown in Fig. 1A. A serpentine check running parallel to the grain is visible. It was formed during the drying of the wood. Grain direction was marked with white lines on some larger tangential wood surfaces, revealing roughly parallel serpentine curves (Fig. 1B). Successive segments of these curves are alternately inclined to the right (Z) and left (S) from the vertical about eight times in an axial distance of 75 cm. These data indicate that *Platanus* has a wavy grain, and that the areas with Z grain inclination alternate with these of S type along the trunk, Fig. 1C. Their dimensions in the direction of the bole axis vary from 4 to 15 cm. Some areas are inclined, others perpendicular to the bole axis. The maximum deviation of the grain with respect to the bole axis varies from 3° to 20° in different areas. These areas presumably extend farther across the trunk than the area of wood studied.

When a block of *Platanus* wood is split radially with a chisel, the upper edge of the block where the tool was applied will be cut straight, but the corresponding edge on the opposite end of the block will be

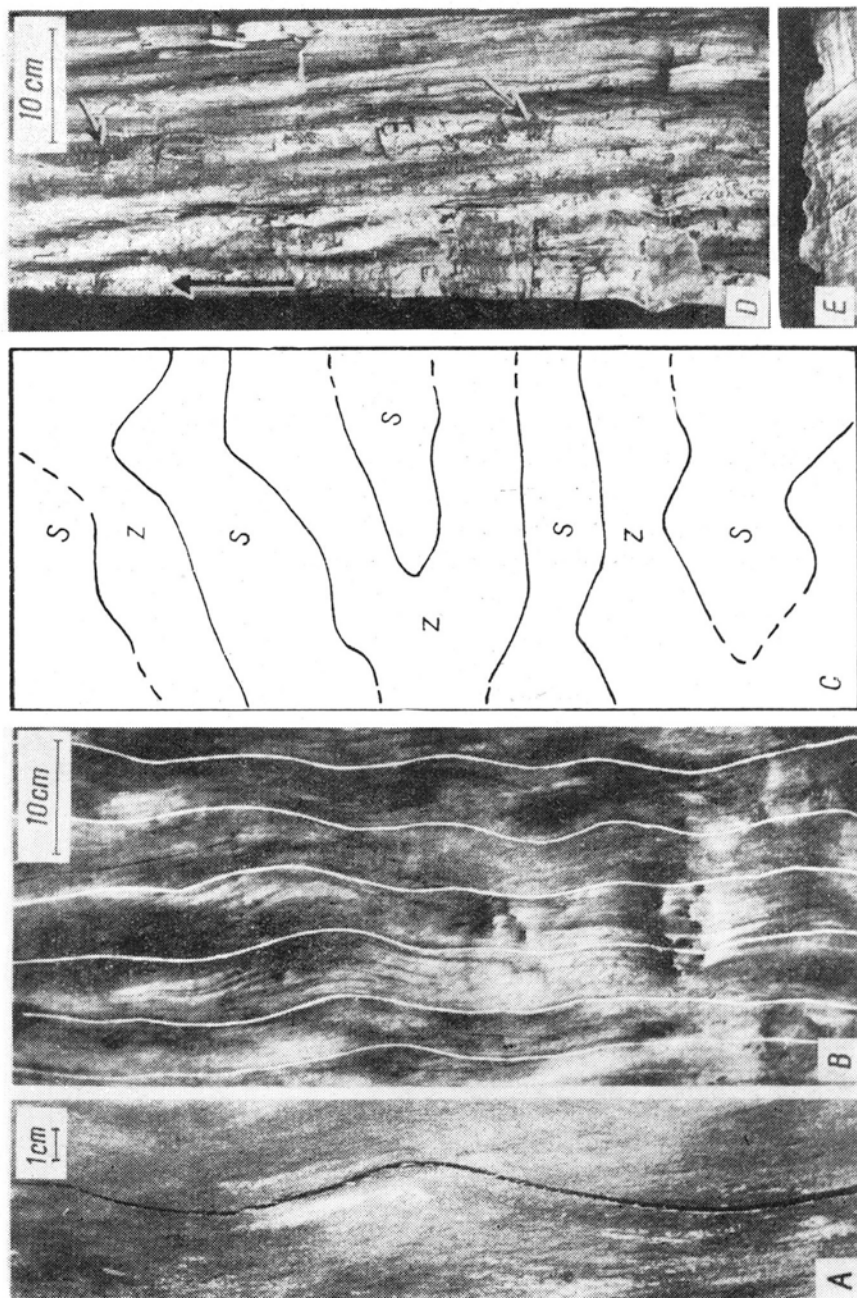


Fig. 1. Wood of *Platanus acerifolia* Willd. A-C — tangential surface, D — radial section, E — transverse section. A — fragment of a debarked wood surface with serpentine check. B — serpentine course of grain; white stripes were drawn on the wood surface along the grain. C — the same surface as in B showing the areas with grain of Z and S type. D — radial split surface. The trunk segment was split from its top. The thick arrow on the side of the last annual ring and is oriented acropetally. Thin arrows indicate xylem rays. The segment contains approx. 100 annual rings. There were 162 rings in the trunk. E — lower edge the same radial split as in D but seen from the bottom

split and appear wavy. Fig. 1E. This indicates that interlocked grain is present in the wood, i.e. that fibres are alternately inclined to the right and left with respect to the bole axis in successive groups of annual rings. The radially split surface of a segment of trunk is shown in Fig. 1D. Ridges and valleys, which appear as light and dark stripes under unidirectional light, are visible. The stripes correspond to groups of annual rings containing wood fibres inclined in the same direction, either Z or S. Successive segments of individual rays belong alternately to darker and lighter stripes, that is to the regions containing wood of the Z and S type respectively. The stripes slant outward forming an angle about 85° with the rays. This indicates that regions of the cambium which differed in the slope of cells move upward as successive annual rings were formed. The grain pattern in *Platanus* wood appears to be a result of the preservation in the wood of the wavelike changing of orientation of cambial initial cells during the formation of the wood.

2. Domain structure of the cambium

Veneers can be cut approximately tangential to the annual rings over moderately large areas. Even so, different layers of an annual ring are included and the ray arrangement on the veneer surface is useful in delineating cambial domains only if the arrangement revealed there is a valid record of the arrangement existing in the cambium when the various xylem layers were formed. Therefore it was necessary to determine whether changes in *Platanus* ray arrangement within annual rings resulted from changes in cambial initials or whether they appeared during the differentiation of xylem elements. In the latter event changes would occur locally within annual rings and would not be recorded in the terminal late xylem (TLX) layers. These layers are known to include near replicas of cambial cell arrangement (Hejnowicz and Krawczyński, 1969). The correct alternative was selected after microscopic analysis of temporal series of tangentially cut microtome sections. Each series included several annual rings. These analyses indicated that evidence of splitting and uniting of rays found in any layer of the annual ring always corresponded to an event recorded in the TLX layers. This is evidence that ray splitting or uniting events actually occurred only in the cambial cell layer and not in the differentiating xylem. Thus veneers can be used to delineate domains over relatively large areas of cambium.

Domains were delineated at two loci of the trunk: sites I and II. Surfaces of veneer that were approximately tangential to the annual rings were used for this purpose. Maps of ray changes at site I (14×5 cm) in six consecutive annual rings are shown in Fig. 2. Each mark on the map represents three proximate events, either splitting or uniting

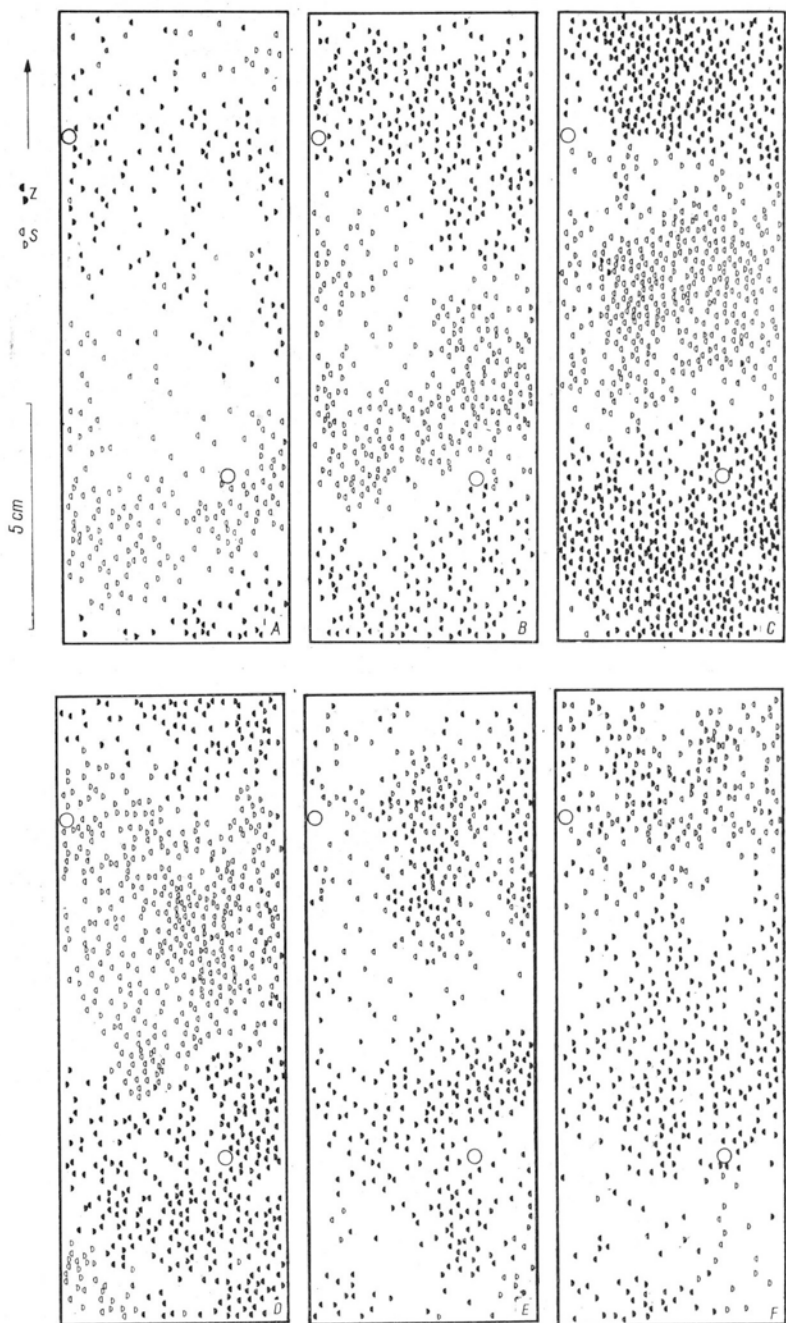


Fig. 2. Maps showing the direction of splitting and uniting of rays on the same area of cambium during the formation of 6 successive annual rings at site I.

The left semicircles represent splitting, the right ones uniting of rays. The arrow indicate the top of the wood. Circles represent small knots which serve as reference points. The thickness of the layer of wood analysed was 11,2 mm.

of rays. Three single points each representing an individual event on a photograph of a veneer surface were joined, and the center of the triangle thus formed was approximately determined and marked on the map. Ray splitting of the Z-type is accompanied by the formation of new strands of fusiform cells oriented to the right; union of the Z-type — by the disappearance of the strands oriented to the left. Events of the S-type include the formation of new strands of cells oriented to the left and the disappearance of old strands oriented to the right. It is clearly evident (Fig. 2) that on the area of cambium examined the ray splitting or uniting events are oriented uniformly to the right (Z) or left (S) in large areas, which, according to the definition, may be considered as domains of the Z and S type. Boundaries between domains are quite distinct. The axial distance between them (domain height) is approximately 8 cm. The transverse dimension of the domain exceeds the examined area.

In Fig. 3, simplified maps of the *Platanus* cambium surface at site II

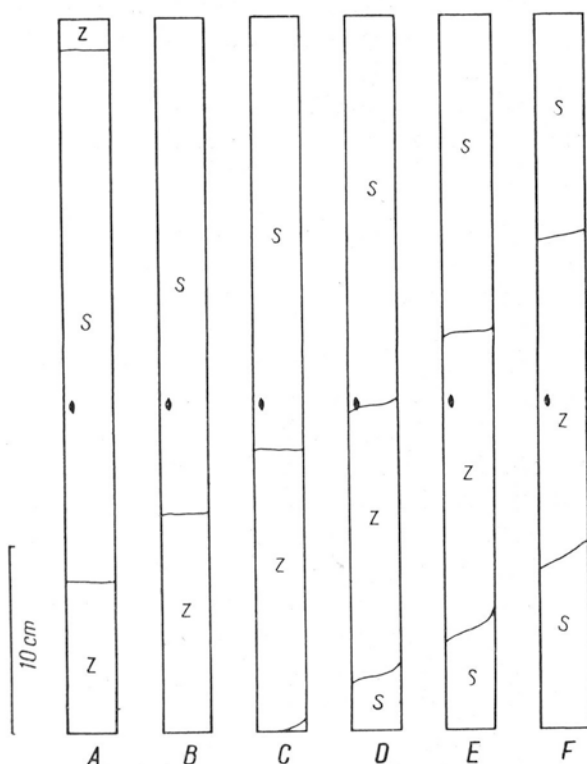


Fig. 3. Simplified maps of changes in the cambium at site II during the formation of successive annual rings.

The lines represent boundaries between domains. A small knot is marked as a reference point. The analysed layer was 16.8 mm thick

are shown. The area of cambium investigated at this site was 38.5 by 2.5 cm. Horizontal lines mark the boundaries between Z- and S-type domains. It is seen that the domains are much higher here than at site I (Fig. 2); their height is approximately 17 cm and 28 cm.

3. Upward movement of the domain pattern

The comparison of consecutive maps A—F in Figs 2 and 3 indicates that domains move upward with respect to cambial cells as consecutive annual rings are produced. The rate of domain movement was approximately 6—7 mm per radial mm of xylem produced at site I and approximately 12 mm per mm at site II. Different parts of the same boundary did not move at the same rates, consequently the shape of domains changed slowly (Fig. 2). Because domains move, each site in the cambium is alternately occupied by Z and S type domains and produces wood the elements of which, viewed tangentially, change their orientation from right to left and *vice versa* many times during the life of a tree. A given site of the cambium may be occupied for longer or shorter times by a domain depending upon domain height and rate of movement. Since the height and the velocity may vary, the rate of change in xylem structure may also vary along the ray.

4. Frequency of ray events within domains

All rays in those sections of veneer studied were analyzed. The density of marks on maps thus indicates the frequency of ray splitting and uniting in the cambium. As may be seen in Fig. 2, the frequency is not uniform; the density of the marks decreases near boundaries between domains. It must be noted here that the annual rings analysed were not uniform in thickness. For this reason the density data were converted into more accurate expressions of frequency of ray splitting and uniting events by dividing the number occurring per cm^2 of cambial surface in a particular annual ring by the thickness (mm) of that ring. Frequency data thus represent the number of events occurring per cm^2 of cambial surface during formation of 1 mm of xylem. The frequency of ray splitting and uniting events was computed separately for the vicinity of domain boundaries and for remaining parts of the domains. The histograms in Figs. 4 and 5 indicate that the frequency of events varies in space and time. Spatial variation is related to distance from domain boundaries — the events are less frequent near them. Change in time — increase or decrease of frequency — occur simultaneously in all domains. (Fig. 4). In general the frequency of events was greater at site I than at site II.

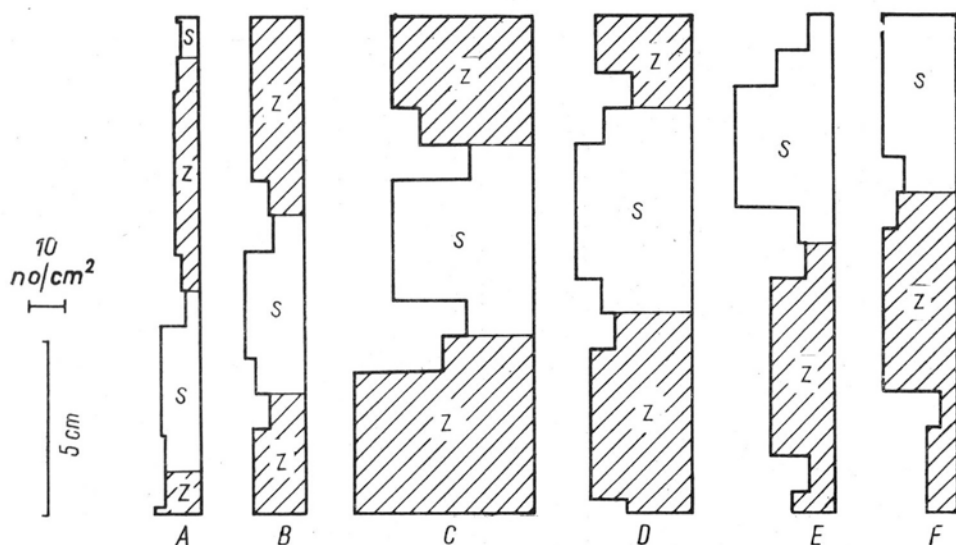


Fig. 4. Frequency of changes in rays in *Platanus* domains on the 1 cm wide zones near the boundaries and of the remaining, central parts of domains at site I.

The localization of domains is marked on the perpendicular axis, horizontal lines represent boundaries between them; Z type domains are lined. Rectangle width correspond to the frequency of changes in rays. The frequency is the joint number of splits and unions of rays per 1 cm² of cambium surface during the formation of a xylem layer 1 mm thick.

A — F represent 6 successive annual rings.

5. Interdependence of domain and grain patterns

Areas with Z and S type arrangement of wood elements were delineated on veneers the domain patterns of which had previously been analyzed. The relation between domain and grain patterns at site I is shown in Fig. 6. Surfaces of consecutive annual rings were marked a, b, c, etc. and maps of the domain pattern occurring in the cambium during the period of production of the xylem located between these limits are marked as a-b, b-c, etc. At the outset, on surface a, the grain is straight. During the deposition of wood layers a-b areas differing in the orientation of wood elements become visible on surface b in keeping with orientational domain in the cambium. Areas of Z and S sloping grain appear in the places which were occupied by Z and S domains, respectively, though the boundaries between them are shifted slightly downwards with respect to the boundaries between domains. Further comparison of domain and grain patterns indicates that generally both move in the same direction with approximately the same speed. The fact that boundaries between areas of Z or S sloping grain are retarded in movement with respect to cambial domains is remarkable.

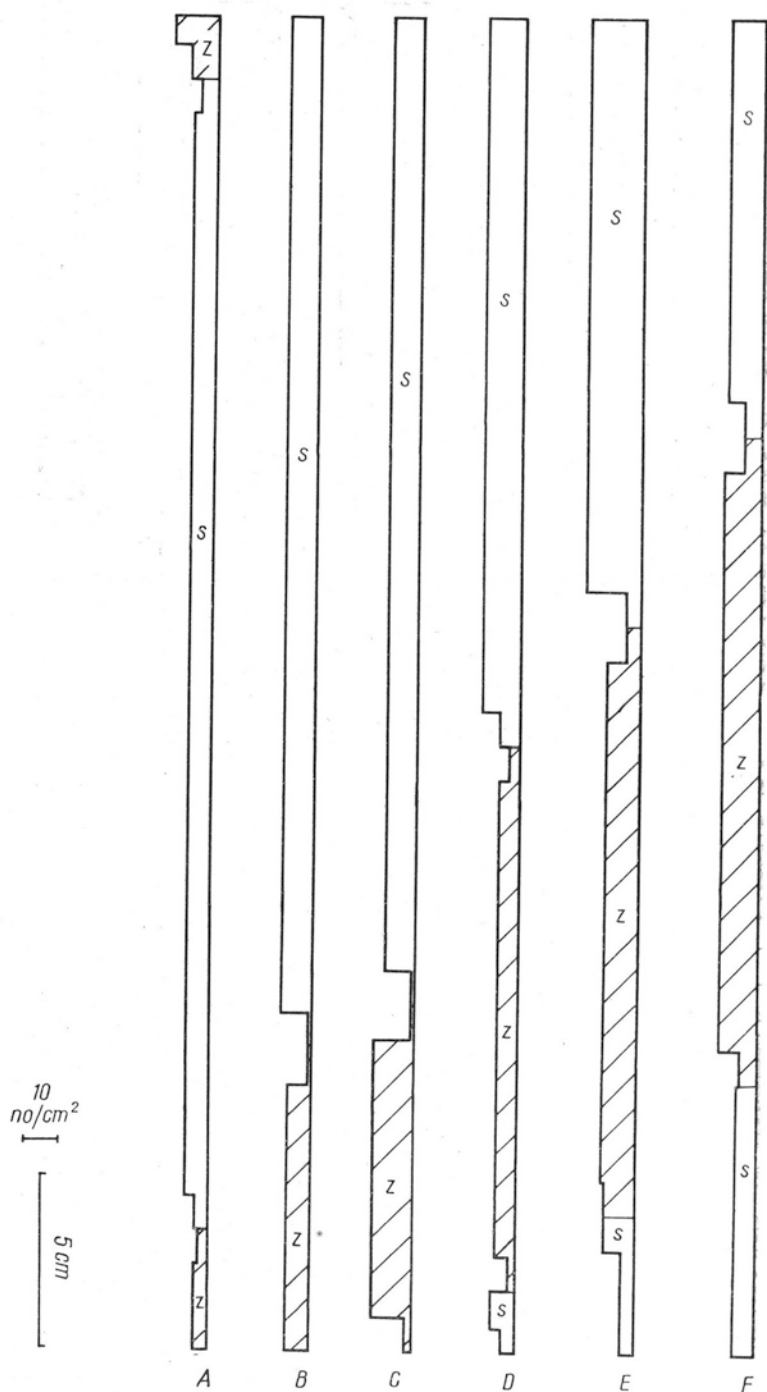


Fig. 5. Frequency of changes in rays in *Platanus* domains at site II.

For explanations see Fig. 4

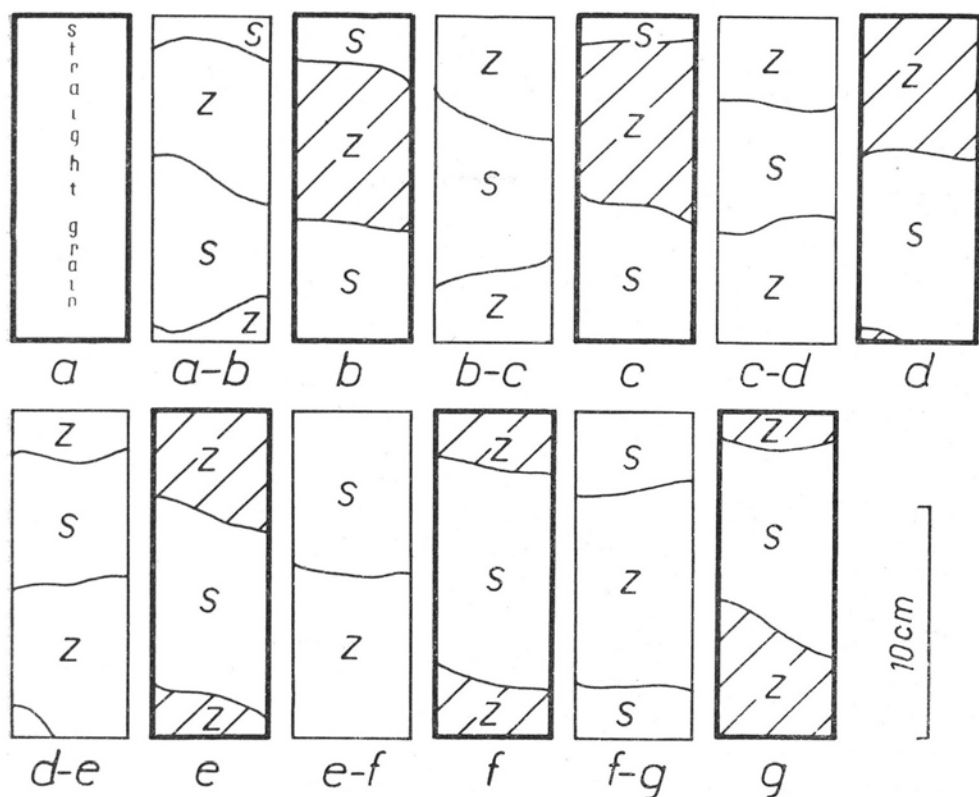


Fig. 6. Interdependence between grain and domain pattern in *Platanus* wood at site I.

Maps in thick frames represent the actual state in the grain on the surface of successive annual rings a, b, c etc. and those in thin frames — domain patterns occurring in the cambium during the formation of successive annual rings a-b, b-c, c-d etc. Areas with Z type grain are lined.

Fig. 7 shows the relation between grain pattern and domain pattern at site II. The orientation of the grain on the surface of consecutive annual rings is shown on histograms a, b, c, etc. Dark areas on the right side of the axis correspond to areas with Z inclined fibers, light areas on left represent areas with fibers of S inclination. The width of each rectangle corresponds to the mean inclination of the grain to the right or left. On maps a-b, b-c, c-d etc., domain patterns occurring in the cambium during the formation of successive annual rings are shown. A tall zone with Z inclined grain occurs in the upper part of the studied area, and a smaller one of S inclination in the lower part. The Z inclination is on the average 7° , and S is approximately 3.5° , thus at the outset the Z pattern is dominant. Comparison of successive histograms indicates that distinct changes occur in the grain pattern. On surface b the Z-type

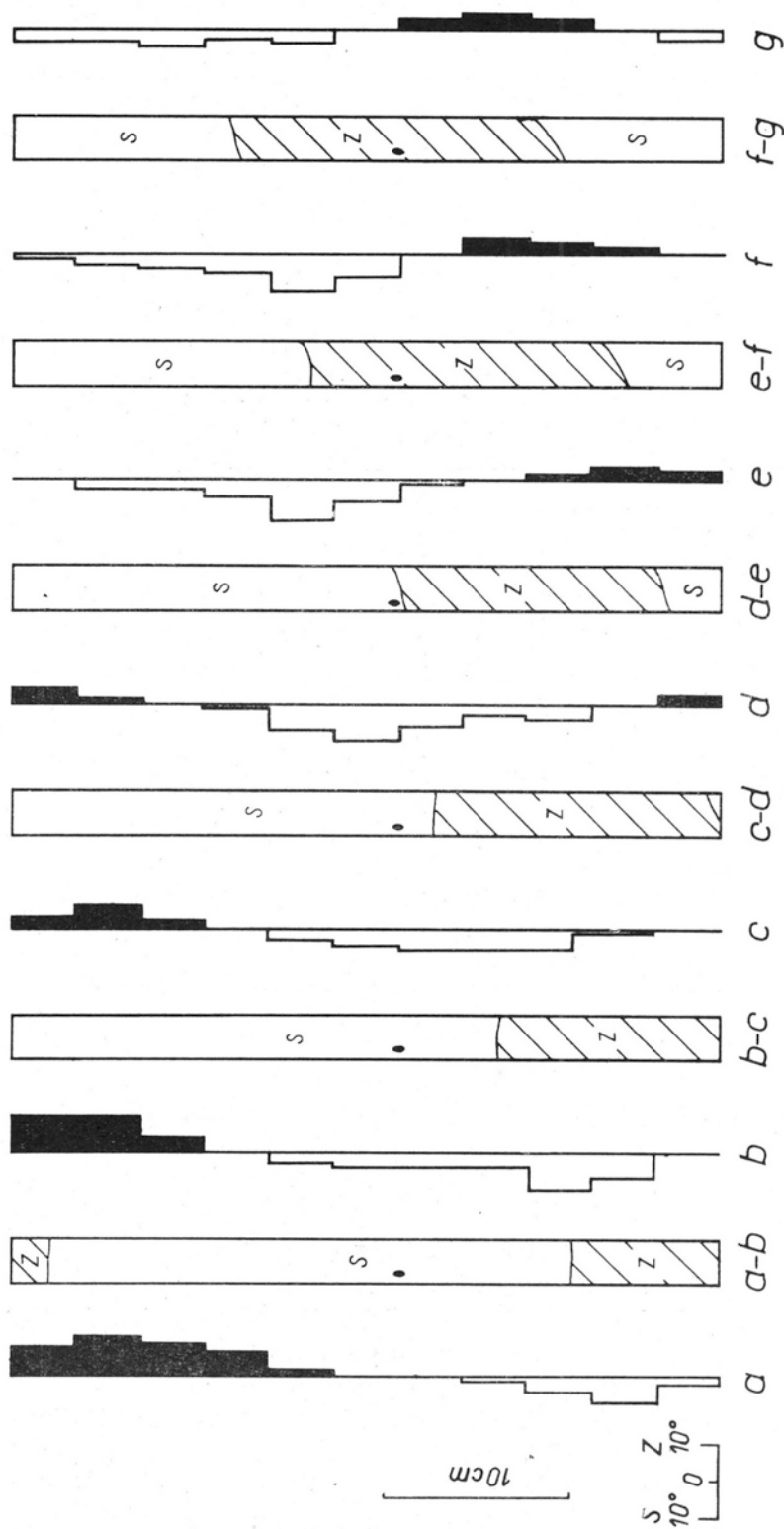


Fig. 7. Interdependence between domain and grain pattern in *Platanus* wood at site II where domains with unequal axial dimensions occur.

The histograms a, b, c etc present grain on the surface of successive annual rings; the localization of areas with Z type grain (shaded) is marked on the right side of the axis, with S type — on the left. The width of the rectangles corresponds to the extent of inclination of the grain to the left or right in different parts of the zones. Maps a-b, b-c, c-d etc, show domain patterns which occur in the cambium during the formation of successive annual rings. Domains of the Z type are lined.

patterns cease to be dominant. This is related to the presence of a tall, S-type domain in the cambium during the formation of the a-b xylem layer. On surfaces a to e the boundary between Z and S grain inclination areas moves upwards, which in localities originally having Z sloping grain means the recession of the grain from a Z-inclination and a subsequent inclination in S direction. Consequently S inclined grain becomes dominant. In the lower part of surface d a new zone of Z inclined grain appears, which moves upwards like the preceding one, but is initially much less tall. The inclination of the grain in this short zone is less than the neighboring tall S zone. The Z inclined zone is preceded by a Z orientational domain only half as wide as the S type domain. The domains migrate in the same direction and at similar rates as zones of grain inclination. Boundaries between orientational domains precede boundaries between grain inclination zones as in the example illustrated in Fig. 6. This indicates that the relationship between domains in the cambium and zones of grain is one of cause and effect: existence and efficacy of orientational domain causes zones of grain inclination to become manifest. The fact that grain inclination in the short Z zone formed by a short domain is in general less than that in the tall S type zone formed by an S domain should be noted. This indicates that migration of domains of unequal height through a given area of the cambium results in inclination of grain in the direction corresponding to the type of the taller domains.

Figs. 6 and 7 also indicate that the actual inclination of the grain in a given area is not the same as the type of domain that was present in the cambium during the formation of that layer of xylem. The type of domain only determines the direction of change in the slope of grain. When the actual inclination of grain is opposite the domain type, the grain withdraws from the initial inclination, passes through vertical, and only later attains the inclination conforming with the domain type.

DISCUSSION

The data hitherto obtained in many studies indicate that a domain structure of the cambium is widespread in both coniferous and deciduous trees. In most of these studies the orientation of cellular processes was examined at particular sites of the cambium or in small areas of its surface, giving no basis for delineating boundaries between domains (Hejnowicz 1964, 1968; Bannan 1966 and earlier works; Hejnowicz and Krawczyshyn 1969). Even in those instances in which the examined areas were fairly large, the boundaries between domains within these areas could not always be delineated due to the low frequency of cellular events in cambium which normally produces

non-wavy wood (as in the case of *Aesculus*, see Hejnowicz and Krawczyszyn 1969). More advantageous conditions for research on domain structure exist in cambium which produces wood having a changing orientation. In these cases the boundaries may be delineated due to a higher frequency of cellular events. Such data have been obtained for cambium producing wavy-grained wood in *Picea* (Hejnowicz 1971) and in *Fraxinus*, *Acer* and *Betula* (Hejnowicz and Romberger 1972).

Platanus, which has a changing grain orientation, is a good object for the study of domain structure in the cambium. Previous investigations by the author of the cambium of this tree (Krawczyszyn 1971) indicated that not more than one boundary between domains occurs on an area 35×60 mm. Therefore the present investigations were carried out on larger surfaces. The conclusion is that the axial dimensions (height) of the domains in *Platanus* is at least 8 cm, which agrees with the result of the previous work.

It is known that the type of domain encompassing a given site in the cambium changes with time (Hejnowicz 1964, 1968; Bannan 1966 and earlier works; Hejnowicz and Krawczyszyn 1969). Investigations of the behavior of boundaries between domains have shown that this change is due to the migration of domain pattern along the trunk with respect to cambial cells during the formation of wood (Krawczyszyn 1971; Hejnowicz 1971; Hejnowicz and Romberger 1972). In all examined cases these boundaries are perpendicular or slightly inclined with respect to the bole axis. For this reason a given site in the cambium is successively occupied by domains of alternate type. The length of time during which a domain includes a particular site depends on the height of the domain and the velocity of its movement.

A correlation appears to exist between height of domains and velocity of domain movement, that is, the taller the domain the faster it moves. This can be seen in the Table:

Grain type in wood	Tree	Domain height (mm)	Velocity of domain movement (mm/1 mm of xylem produced)
curly	$\left\{ \begin{array}{l} \textit{Acer} \\ \textit{Fraxinus} \end{array} \right.$	2-8	~ 0.1
(wavy)	$\left\{ \begin{array}{l} \textit{Betula} \\ \textit{Picea} \end{array} \right.$	~ 10	~ 1.0
interlocked	<i>Platanus</i>	80-280	6.5-12

This table, and the fact that in all instances mentioned domains are arranged in a similar fashion with respect to the bole axis, indicate that only quantitative differences exist between cambia producing curly — (wavy-) and interlocked-grain wood. In cambium producing the first

type of grain the domains are relatively short and their movement slow. Cambium which produces interlocked-grain wood contains wide, rapidly moving domains. In all cases presented in the table domains move upward. P y s z y ń s k i (1972), however, has noted a downward movement in *Aesculus*.

The change in orientation of xylem cells is caused by a corresponding change in the cambial initial cells which produce the xylem. The latter change is a result of unidirectional cellular events such as oblique anticlinal divisions, intrusive growth and ray splitting and uniting and therefore depends on the frequency with which they occur. The orientation of cellular events is determined by the type of domain present in a given part of the cambium. Therefore it is understandable that domain pattern may be reflected in the arrangement of cells, provided that the frequency of cellular events is high enough to change cell orientation to a detectable extent during the period of existence of one domain in particular site. Thus the domain pattern determines the possibility of changes in cell orientation in the cambium and xylem. The frequency of cellular processes within domains determines how these possibilities will be realized. Hejnowicz (1971) and Hejnowicz and Romberger (1972) have shown that cambium producing straight-grained wood differs from that producing wavy-grained wood only by the frequency of processes within domains. It is low in the former case and high in the latter. In *Platanus* wood samples in which changes in grain orientation occur the frequency of splitting and uniting of rays is considerably greater than in straight-grained wood of other genera. Since the frequency of the events concerning rays seems to be proportional to the frequency or more basic cellular events, such as anticlinal divisions and overlapping of cells tips occurring during intrusive growth of cambial cells, the latter frequency is higher also, and surely high enough to change appreciably the orientation of cambium and wood cells in *Platanus*. The fact that this frequency varies in time in a similar way in domains of opposite types is of interest (Fig. 4). If this frequency were considerable decreased for a long period of time and if the initial orientation of cambial cells were straight, the cambium would probably produce a straight-grained wood, which is atypical for *Platanus*. P a n s h i n (1933) and L i m a y e (1954) have reported that both interlocked and straight-grained wood can occur within one species.

Domain movement prevents excessive inclination of cells and causes cyclical changes of domain type at each site in the cambium. Each domain opposes the effects of the previous one, and as result cambium cells oscillate to the right and left with respect to the trunk axis.

The waviness of grain on a tangential surface of an annual ring reflects a wavy arrangement of cambium cells during the formation of this ring. Domains which are perpendicular to the trunk axis (assuming

that cellular processes in the cambium occur with a high frequency) cause perpendicular zones with grain inclined in the Z or S direction to occur on the surfaces of annual rings. These zones are displaced with respect to each other in successive annual rings as a result of domain movement. Oblique undulations on the radial split surface and oblique light and dark stripes on polished radial split faces depend on the arrangement of cambium cells and their changes during the formation of successive annual rings. The above-mentioned stripes are a result of differences in the reflection of light by differently cut grain in the xylem. They occur in wood with grain of the curly or wavy type, forming the so-called curly or wavy figures (Brown et al. 1949) and in wood with interlocked grain forming the so-called ribbon figure (Brown et al. 1949; Limaye 1954). In curly or wavy figures these strips may be arranged almost horizontally and in ribbon figures — almost vertically in respect to the bole axis. In both cases the formation of the figures is based on a domain pattern of the cambium and on the migration of domains. The inclination of the above-mentioned stripes with respect to the bole axis or with respect to the rays depends on the rate of domain movement. Slow movement causes an almost horizontal arrangement and rapid movement an almost vertical one. Passage from slightly inclined to nearly vertical stripes occurs within a fairly narrow range of velocities. Fig. 8 illustrates the dependence of the slope of stripes on the velocity of domain movement in the cambium per mm of xylem formed. This can be expressed as the ratio of length of the path travelled by a domain along the trunk to the thickness of the xylem formed, that is the tangent of the angle between the stripes on a radial section and the rays. It can be seen that the passage from an almost horizontal (curly or wavy figure) to an almost perpendicular (ribbon figure) arrangement occurs in the range of velocities between approximately 0.1—5 mm per mm of xylem.

Brown et al. (1949) and Limaye (1954) consider that interlocked grain is a type of spiral grain (i.e. on the surface of a single annual ring wood elements are inclined in a uniform way with respect to the bole axis) which repeatedly changes direction of spiral among growth ring. Martley (1920) and Webb (1967) however, state that in this type of grain the direction of spiral changes among growth rings as well as within single growth ring; thus the spiral character of grain is obscured giving rise to serpentine configurations. In the *Platanus*, as these investigations have shown, grain is composed of a series of superimposed serpentine curves with peaks displaced upward one to the other when traced ring by ring from the centre outward. A similar arrangement of wood elements occurs in many tropical timbers, among others in the genus *Entandrofragma* (*E. cylindricum*, *E. angolense*, *E. candollei*) which are described as having interlocked grain (see Panshin 1933). The

author has observed these timbers in the veneer factory in Dobroszyce near Wrocław (Poland). Their surfaces show serpentine grain. The shortest waves observed were between 5 and 10 cm long, the longest

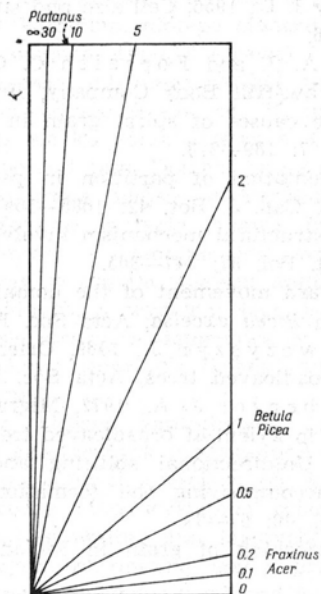


Fig. 8. Relation between the velocity of domain movement in the cambium and the inclination of stripes on the radial surface of wood with grain of the curly, (wavy) and interlocked type.

The numbers correspond to the velocity of domain movement in mm per 1 mm of xylem produced.

2—3.5 m. Stripes visible on smooth quarter-sawn boards were not strictly perpendicular to the rays, but some were nearly so. On segments, 2—4 m in length, it could be seen that the stripes were inclined with respect to the vessels and growth rings. A comparison of the grain pattern of *Platanus* and of tropical timbers of interlocked grained type clearly indicates that differences between them lie primarily in the length of grain waves and the displacement of the waves in successive growth rings. Since only quantitative differences also exist between curly or wavy and interlocked grain in *Platanus*, it may be concluded that interlocked grain is a special type of wavy grain in which the waves are long and the displacement of their peaks in successive growth ring is large.

The guidance of Prof. Dr. Z. Hejnowicz is gratefully acknowledged. Thanks are extended to Dr. J. A. Romberger for valuable cooperation.

This investigation was supported in part by a grant of the United States Department of Agriculture under P.L. 480.

REFERENCES

- Bannan M. W., 1966, Spiral grain and anticlinal divisions in the cambium of conifers, *Can. J. Bot.* 44: 1515—1538.
- Bannan M. W. and Bayly I. L., 1956, Cell size and survival in conifer cambium, *Can. J. Bot.* 34: 769—766.
- Brown H. P., Panshin A. J. and Forsaith C. C., 1949, *Textbook of wood technology*, Vol. I. McGraw-Hill Book Company, Inc. New York.
- Harris J. M., 1969, On the causes of spiral grain in corewood of radiata pine, *New Zealand J. Botany*, 7: 189—213.
- Hejnowicz Z., 1964, Orientation of partition in pseudotransverse division in cambia of some conifers, *Can. J. Bot.* 42: 1685—1691.
- 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., and Krawczyszyn J., 1969, Oriented morphogenetic phenomena in cambium of broadleaved trees, *Acta Soc. Bot. Pol.* 38: 547—560.
- Hejnowicz Z. and Romberger J. A., 1972, Migrating cambial domains and the origin of wavy grain in xylem of broadleaved trees, *Amer. J. Bot.* (in press).
- Krawczyszyn J., 1971, Unidirectional splitting and uniting of rays in the cambium of *Platanus* accompanying the formation of interlocked grain in wood, *Acta Soc. Bot. Pol.* 40: 57—79.
- Limaye V. D., 1954, Interlocking of grain in Indian timbers, *Indian Forester*. 80: 6—9.
- Martley J. F., 1920, Double cross-grain, *Annals of Applied Biology* 7: 222—268.
- Newmann I. V., 1955, Miscellaneous notes on inclination of grain in *Pinus radiata* D. Don. and *Pinus sp.* Laboratory Report No. 1, Forest Products Laboratory, CSIRO.
- Panshin A. J., 1933, Comparative anatomy of the wood of the *Meliaceae*, Sub-family *Swietenioideae*, *Amer. J. Bot.* 20: 638—668.
- Pyszyński W., 1972, Downward movement of the domain pattern in *Aesculus* cambium producing wavy grained xylem, *Acta Soc. Bot. Pol.* 41: 511—517.
- Webb C. D., 1967, Interlocked grain in *Liquidambar styraciflua* L. XIV IUFRO Kongress München, Section 22/41: 398—411.

Mechanizm tworzenia falisto-zaplecionego układu włókien w drewnie platana

Streszczenie

Drewno platana charakteryzuje się falistym i zaplecionym przebiegiem włókien. Falistość wyraża się tym, że na powierzchni przyrostu rocznego, posuwając się wzdłuż pnia, natrafiamy na obszary, w których włókno jest nachylone kolejno na prawo i lewo. Ich długość wynosi 4—15 cm, a maksymalne odchylenie włókna od pionu w falach waha się w granicach 3—20°. Zaplecenie polega na tym, że w grupach kolejnych słoików drewna fale są przesunięte względem siebie, w związku z czym włókno rozpatrywane wzdłuż promienia oscyluje na prawo i na lewo względem osi pnia.

Na seriach cienkich (0,8 mm), stycznych warstw drewna typu forniiru badano promienie drzewne pod względem kierunku rozszczepień i łączeń. Stwierdzono występowanie obszarów, na których powstają nowe pasma włókien nachylone na prawo (lewo) jako rozszczepienie promieni typu Z (S) i zanikają pasma nachylone na lewo (prawo) jako wyraz łączenia się promieni typu Z (S). Ponieważ zmiany w promieniach zachodzą w kambium, dlatego stwierdzone obszary jednokierunkowych zmian odpowiadają domenom typu Z (prawe) i typu S (lewe) w kambium. Domeny układają się poprzecznie lub nieco ukośnie względem osi pnia. Ich wysokość mierzona wzdłuż pnia wynosi 8—28 cm. W miarę jak kambium odkłada drewno, domeny przesuują się ku górze drzewa o 6,5—12 mm w ciągu odkładania warstwy drewna o grubości 1 mm. Domeny przesuują się względem komórek kambialnych i w rezultacie każde miejsce w kambium jest zajęte przez kolejne domeny typu Z i S, wielokrotnie w życiu drzewa. Intensywność procesów wpływających na orientację komórek w kambium jest wewnątrz domen na tyle duża, że w czasie trwania domeny w danym miejscu kambium zmienia się uchwytne orientacja inicjałów kambialnych, a wyrazem tego jest zmiana orientacji włókna w drewnie. Przesuwająca się struktura domenowa w kambium, przy dużej intensywności procesów przebudowy wewnątrz domen, wyjaśnia tworzenie falisto-zaplecionego włókna w drewnie.

Porównanie drewna z włókien zaplecionych („interlocked”) występujących u platana i licznych drzew egzotycznych (np. mahoni) oraz drewna z włókien falistych występujących w odziomkowych częściach pni liściastych (np. klonu, jesionu i brzozy) wskazuje, że między nimi występują tylko ilościowe różnice. W obu przypadkach włókno układa się wzdłuż linii falistych, które są przesunięte względem siebie w kolejnych przyrostach drewna, lecz w przypadku włókna zaplecionego długość odcinków o jednakowym nachyleniu włókna jest większa, a ich przesunięcie względem siebie jest szybsze.

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