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Discontinuous lines on the radial face of wavy-grained xylem as a manifestation of morphogenic waves in the cambium

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Abstract

There appear in the wood of *Entandrophragma*, beside the basic interlocked grain, local minute undulations of grain the manifestation of which are checkered figures, either slanting or horizontal, on the radial face of boards. In reference to the model the slanting checkered figure is interpreted as the result of sudden appearance in the cambium of a wave of orientational tendency (morphogenetic wave) of relatively short wavelengths and stabilized amplitude from the moment of its appearance, moving vertically. This wave induces undulations in the arrangement of cambial initials. The undulation pattern also moves, however, its rate is half that of the morphogenic wave rate. The amplitude of the undulations oscillates between a maximal value and null which means that in successive wood layers there is wavy grain alternating with straight grain. The horizontal checkered figure may be explained by a local shift of the prase by one half of the period of the morphogenic wave of relatively long wavelengths underlying the interlocked grain formation.

INTRODUCTION

Domain pattern and morphogenic waves in cambium

A constant and commonly occurring property of the cambium of coniferous and dicotyledonous woody plants is a migrating domain pattern (H e j n o w i c z, 1971, 1973a, b; H e j n o w i c z, R o m b e r g e r, 1973; K r a w c z y s z y n, 1972). This pattern consists of domains or areas in which the direction of inclination of the fusiform initials is the same — to the right (type Z domain) or to the left (type S domain) in reference to the stem axis.

The cellular events leading to a change in cell inclination are anticlinal, pseudotransverse divisions in non-storeyed cambium and oriented intrusive growth of initials growing after division (H e j n o w i c z, 1964, 1968; H e j n o w i c z, K r a w c z y s z y n, 1969; K r a w c z y s z y n, 1971), whereas in storeyed cambium — the change of position, due to intrusive growth, in respect to one another of the cell ends pointing in opposite directions at the boundary of the storeys (H e j n o w i c z, Z a g ó r s k a-M a r e k, 1974). The above mentioned events are of oriented character, that is they may occur in two configurations: right (Z) or left (S). In a domain one configuration appears. The occurrence of events with the same configuration leads to a undirectional change in the inclination of cells in the given cambium region if the frequency of events is sufficiently high. Frequently domains Z and S are distributed alternatingly one under the other, and the whole pattern shifts vertically in apical direction, although sometimes basipetally migrating patterns may be seen (P y s z y ń s k i, 1972). On account of the shift of the pattern a periodical change of the type of domain occurs at the given site of the cambium.

Domain patterns differ in migration velocity and axial dimensions of the domain. There is, however, a definite relation between these values: the higher the domains the faster the pattern migrates. The duration of a domain at a given point of the cambium is more or less constant for various patterns and does not depend on the domain length (H e j n o w i c z, 1973a, b; H e j n o w i c z, 1974, 1975).

At a sufficiently high frequency of events in the domains there appear on the cambium surface patterns with opposite (i.e. Z and S) inclination of initials, forming a migrating wave of cell inclination.

According to one concept (H e j n o w i c z, 1973a, 1974, 1975) the domain patterns are a manifestation of the existence of waves of oriented tendency of cellular events occurring in the cambium, waves decisive for the arrangement of initial cells, which may, therefore, be referred to as morphogenic. Certain features of the domain pattern such as length, frequency of events in the domains, duration of the domain at a given point on the cambium surface would correspond according to this concept to such parametres of the morphogenic wave as length (λ), amplitude (A), period (T) (see Table 1). The wave interpretation of the domain pattern is confirmed among other things by the phenomenon of pulsation of the domain length in *Fraxinus* cambium (H e j n o w i c z, 1974), which can be explained by the superposition of two morphogenic cambial waves differing in length and velocity, but having the same duration period.

Table 1

Relation between the features of a domain pattern and an undulation line and the hypothetic morphogenic wave in cambium

Morphogenic wave	Domain pattern	Grain
A (amplitude)	frequency of cellular events	maxima Z or S deviation of grain from direction indicated by stem axis (on tangential surface of wood)
λ (lenght)	length of domain equal to λ/2	height of areas with Z or S inclination of grain (on tangential surface of wood)
V (velocity)	velocity of pattern migration	inclination of wave front to rays (on radial split of wood)
T (period)	duration of two successive domains at given point on cambium surface	radial distance between two succesive wave fronts (on radial split of wood)

Wavy-grain figure in wood

The wavy arrangement of cambium cells induced by the domain pattern is the cause of formation by this cambium of wood with wavy arrangement of xylem elements. Wavy grain is manifested in:

(a) appearance on the tangent surface of each wood layer of a longitudinal wave composed of Z and S regions of grain inclination;

(b) appearance on the radial split face of wood of oblique wave fronts.

The axial dimensions of Z and S inclination regions of the grain forming a wave visible on the tangential face of the wood depends upon the length of cambium domains. The inclination of the wave fronts visible on the radial split face arises because the longitudinal grain wave on the tangential faces of the successive wood layers (from pith to cambium) is vertically consistently shifted upwards (downwards). This shift and the inclination of the wave fronts to the rays is the result of migration of the domain pattern in the cambium and is the more pronounced the faster the migration of the pattern (the longer the domains).

In agreement with the above mentioned relation between the domain length and the velocity of pattern migration, the curly-grained wood exhibits a slight inclination of the wave fronts to the rays. This is produced by cambium with short slow-moving domains. When waves on the tangential surface of the wood are very long, the wave fronts visible on the surface of the radial split face run almost vertically. The grain is then of interlocked type — in the successive wood layers the grain inclination alternates. This type of grain is connected with the presence in the cambium of a fast-migrating pattern composed of very long domains (Krawczyszyn, 1972).

Betweeen curly and interlocked grain there exist intermediate forms of grain waviness of various length in various tree species (Hejnowicz, Romberger, 1979).

As a specific case of wavy wood with zero amplitude of grain waviness may be considered straight-grained wood produced by cambium when the frequency of events in the domains is insufficient. Cases are also known of overlapping of various wood figures, sometimes rather complicated ones (moiré, checkered) resulting from the coexistence in the cambium of at least two domain patterns. One of the possible cases is a long wave on which a short wave is superposed (Hejnowicz, 1974; Hejnowicz, Zagórska-Marek, 1974; Pyszyński, 1977; Hejnowicz, Romberger, 1979).

The common basis for formation of the above mentioned grain patterns are changes in cell inclination in the cambium, induced by morphogenic waves (Hejnowicz, Romberger, 1979).

Mathematic model of relation between morphogenic wave and wood grain

An S or Z cell inclination of initials, finding further its reflection in the inclination of the grain is a cumulative effect of oriented cellular events in the cambium. If we assume that the moving morphogenic wave is of harmonic character we can write

$$\alpha = \int_{t_0}^{t} a\,A \cos(\omega t - kz)\,dt \tag{1}$$

where: α — angle of inclination change of grain in time $t - t_0$;

a — dependence coefficient between frequency of oriented cellular events and velocity of grain inclination;

A — frequency of events (amplitude of wave of orientational tendency);

$\cos(\omega t - kz)$ — general equation of moving wave;

t — time;

ω — angular velocity; $\left(\omega = \frac{2\Pi}{T}\right)$ where T — period;

k — wave number $\left(k = \frac{2\Pi}{\lambda}\right)$ where λ — wavelength.

Case I

When A does not differ much from 0 then:

$$\alpha = \int_{t_o}^{t} a\,A \cos(\omega t\text{-}kz)\,dt \cong 0$$

In this case cambium will produce wood with straight grain, on account of the very small amplitude of the wave (under the condition that at t_o the cell arrangement in the cambium was straight).

Case II

A gradually increases so that the wave of orientational tendency of events existing in the cambium can be manifested in the grain. On the cambium surface there appears a wave in the arrangement of initials which we will futher refer to as mother wave of grain.

Let us assume that A increases lineary with time:

$$A = ct$$

then

$$\alpha = ac \int_{t_o}^{t} t \cos(\omega t\text{-}kz)\,dt$$

if we assume $t_o = 0$, and a, c are constants, we get after integration

$$\alpha = \frac{act}{\omega} \sin(\omega t\text{-}kz) + \frac{ac}{\omega^2} \cos(\omega t\text{-}kz) - \frac{ac}{\omega^2} \cos kz \qquad (2)$$

In eq. (2) we can substitute in the factors of amplitude type $\omega = \frac{2\Pi}{T}$.

We then get eq. (2) in the form:

$$\alpha = \frac{actT}{2\Pi} \sin(\omega t\text{-}kz) + \frac{acT^2}{4\Pi^2} \left[\cos(\omega t\text{-}kz) - \cos kz\right]. \qquad (2a)$$

Let us now discuss this equation in respect to t:

a) when $t \gg T$ then in eq. (2a) the first member dominates. This means wavy grain with increasing maximal angle of grain.

b) when $t \cong T$, in eg. (2a) the first member also dominates since its amplitude is 2Π times larger than that of the second member. The amplitudes of both members are, however, small what means a small angle of grain.

Case III

A drastically increases in time t_o from 0 to a value at which the wave of orientational tendency may be manifested in the grain. We can assume that, for $t > t_0 = 0$, A is constant and large and then:

$$\alpha = aA \int_0^t \cos(\omega t\text{-}kz)\,dt = aA\left[\frac{1}{\omega}\sin(\omega t\text{-}kz) - \frac{1}{\omega}\sin(\text{-}kz)\right] =$$

$$= \frac{2aA}{\omega}\cos\left(\frac{\omega t}{2} - kz\right)\sin\left(\frac{\omega t}{2}\right). \qquad (3)$$

Its results from eq. (3) that, owing to the sudden increase of the frequency of events oriented according to the direction of the moving morphogenic wave, there appears on the cambium surface a modulated mother wave moving at a velocity one half the velocity of the morphogenic one, but having the same wavelength. Modulation consists in that, at intervals equal to one period (T), the mother wave straightens out (disappears). It is most pronounced on the cambium surface at the middle of each period. In successive layers of wood produced by such cambium there would occur gradually more pronounced and gradually disappearing wavy grain alternating with straight grain.

MATERIAL AND METHODS

A radially sawn board of *Entandrophragma* was divided into sticks with a long knife applied to the upper transverse surface of each stick (along the rays), and by striking the knife from above delicately with a hammer the stick was split. Cleavage followed the course of the fiber. The split sticks were then arranged in their original orientation and sequence. The waviness of the grain visible on the recomposed split surface was then analysed as regards such features as: longitudinal (along growth ring boundary) and radial distance between successive wave fronts, inclination and continuity of the fronts. After analyzing the recomposed split surface, two sticks were chosen for investigation, on account of the peculiar character of their waviness characterized by the occurrence of curly grain superposed on interlocked grain. From these sticks blocks were cut from sites of curly grain and from them series of tangential sections were prepared. The series was cut with a sliding microtome. In order to soften the wood before cutting, the blocks were boiled for many hours in water with glycerol added. The successive tangential sections 30 µm thick were stuck with Haupt's adhesive on slides. The chosen sections were analysed with the use of a reading apparatus (Dokumator — Lesegerät DL II) and the course of the grain was drawn.

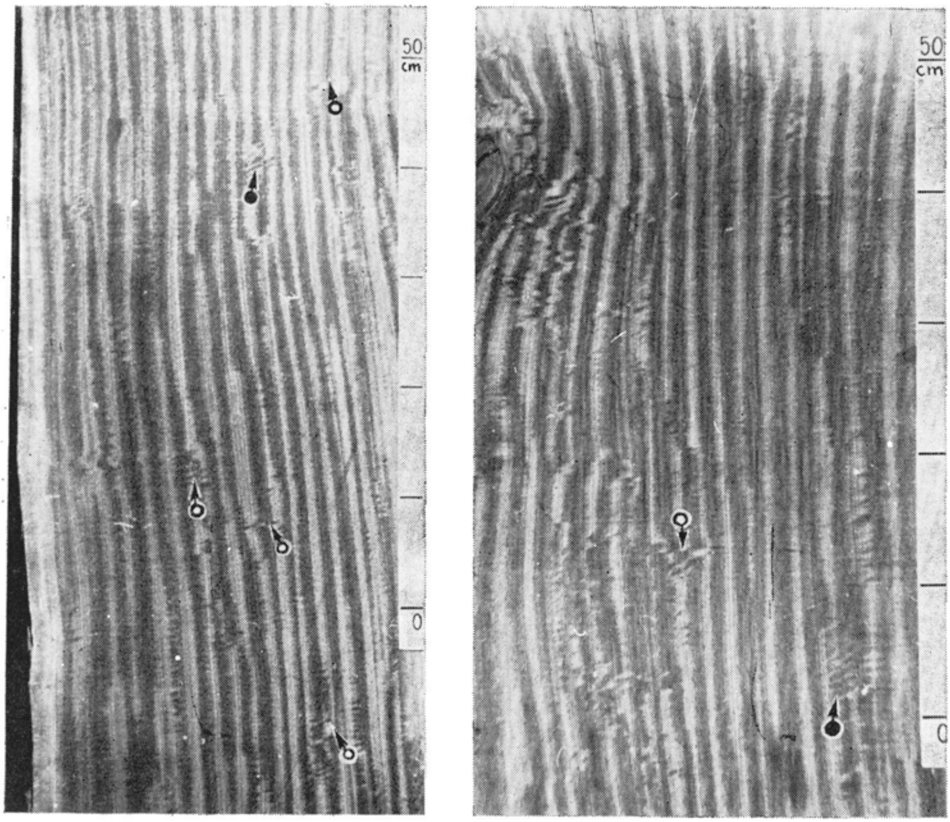


Fig. 1. Radial surface of two *Entandrophragma* boards with characteristic figure: over the basic ribbon figure are superposed at some places stripes of a minute curly figure, slanting (dark circles) or horizontal (clear circles)

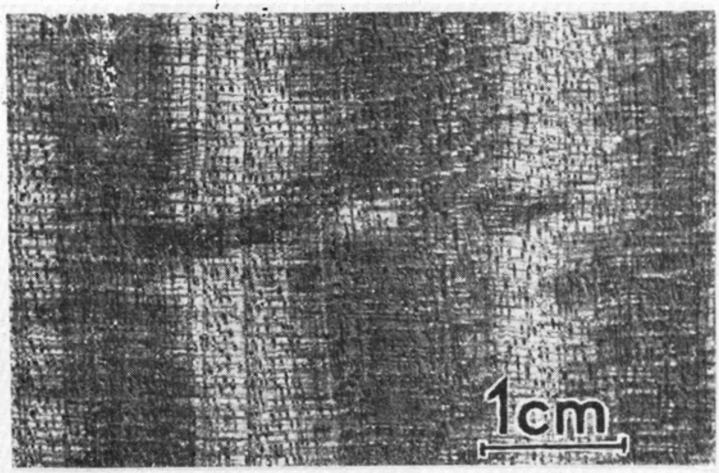


Fig. 5. Radial surface of *Entandrophragma* board with pattern of horizontal checker board type. Against the ribbons of the basic pattern a single series of spots parallel to the rays is visible in the sequence: light spot on dark background, dark spot on light background. Longitudinal dark lines represent growth ring boundaries, horizontal short lines — wood rays

RESULTS

In the examined wood of *Entandrophragma* two basic types of grain waves are found: of long wavelength ($\lambda > 1$ m) to which in general the interlocked character of the grain of this wood is due, and of short wavelength (λ 3-10 mm). The latter occur locally, being superposed on the basic long wave. The local character of the short (curly) grain wave of *Entandrophragma* indicates that the cambial phenomena which are the cause of this wave are limited in space and time: they appear and disappear locally.

The presence of two types of waves finds its reflection in the pattern visible on the radial surface of *Entandrophragma* boards (Fig. 1). The pattern arises owing to the varying light reflection by xylem elements inclined at various angles to the plane of section, that is the board surface. The basic pattern of light and dark bands (ribbon figure) forms because the wave fronts of long waves visible on the radial surface run almost vertically, transecting the growth ring boundaries at an angle smaller than 5°. In connection with this the inclination of the grain is Z and S alternatively in the successive wood layers about 1 cm thick each (interlocked grain).

The basic ribbon figure is disturbed in some places of the slightly inclined or horizontal series of light and dark stripes forming characteristic oblique or horizontal checkered figures (Fig. 1 — arrows). To stripes correspond on the surface of the radial split the curly wave fronts which may be (1) inclined or (2) parallel to the rays. A peculiarity of these curly wave fronts in *Entandrophragma* is their discontinuity. In the first case the fronts are discontinuous along the inclination line, and in the second, along the rays. Since the discontinuity of the fronts is a so far unknown character of the grain waves, both the above described cases of curly wave fronts were studied on series of tangential sections.

In the case of inclined fronts (Fig. 2) a striking agreement was found between the properties of grain waves in the fragment studies with the conclusions resulting from analysis of case III in the model presented above. It is seen in Figure 2 that:

1) at intervals equal to one period the curly grain figure disappears (section L), owing to straightening of the grain;

2) the curly grain figure is most pronounced in the middle of the period (section H);

3) during one period (sections from B to L), that is from the appearance to the disappearance of the curly grain figure, the latter shifts by as little as on half wavelength, this corresponding to the expectation expressed in the model by eq. (3). It also means that on

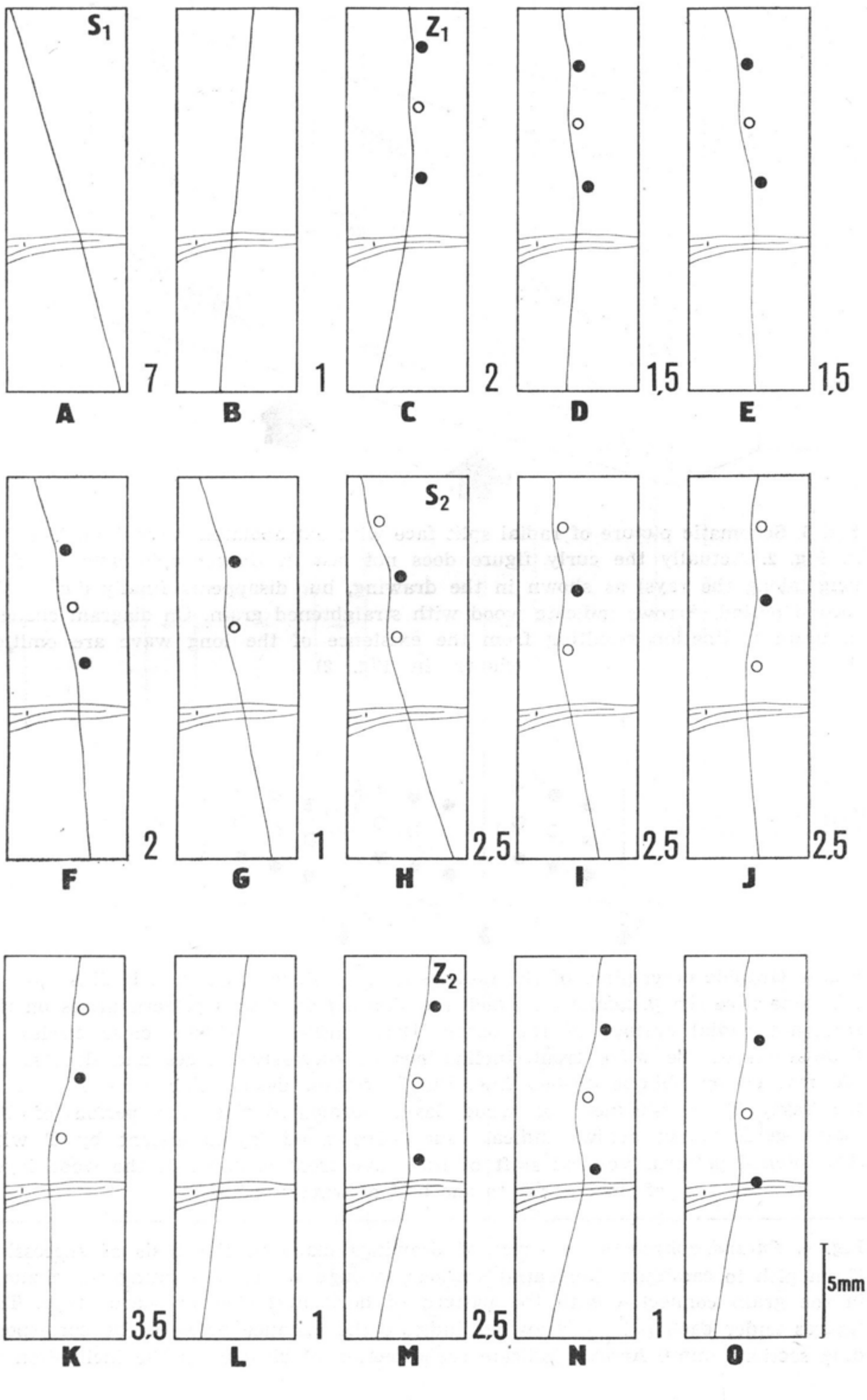
the radial split the inclination of the wave front in the checkered figure is smaller than in the case of the continuous fronts of curly waves of the same length (such fronts shift within one period by a segment equal to its length);

4) after straightening of the grain the curly grain figure returns, however, the figure appearing along the wave fronts is a mirror image of that which existed before the straightening. This means that — when the cell pattern in the cambium straightens out, forming at this moment a straight-grained wood layer — the morphogenic wave is already shifted by its whole wavelength. In consequence, after a transient straightening of the grain a depression appears (Fig. 2, clear circles) in the prolongation of the previous ridge (dark circles) and vice versa.

The property of the curly figure described under (4) is the cause of discontinuity of the undulation lines on the radial split: along the inclination there appear and disappear alternating ridges and depressions (Figs 3 and 4). Owing to this, on the smoothed surface of *Entandrophragma* boards a pattern arises of the type of a slanting checkerboard (Fig. 4) in which on the prolongation of the inclined dark spot there appears a light one, then a dark one and so on. The tangent of the inclination angle (in Fig. 4 angle B), between the wave fronts — the line along which the spots of the pattern lie — and the ray is by one half smaller than the tangent of the angle which would correspond to the existence of continuous wave fronts of the same wavelength.

It should be stressed that the periods of the long and short wave are the same in *Entandrophragma,* this indicating a synchronism in the oscillatory processes underlying both waves (Fig. 2).

Fig. 2. *Entandrophragma* — series of drawings made on the basis of successive tangential sections through wood, illustrating the changes in curly figure which on the radial board surface give the effect of a slanting checkered figure. Drawings A to O are ordered centrifugally (from pith to cambium). The figures under each pair of drawings give the distances between the corresponding sections (mm). The horizontal lines serve as markers indicating the position of the chosen ray storeys (the rays in *Entandrophragma* are stratified). The continuous line running from upper to lower edge of each drawing shows the grain course on the section corresponding to the given drawing. The curly grain figure appearing towards the end of the general change of grain inclination from S_1 to Z_1 (change resulting from the morphogenic wave of long wavelength) disappears after the lapse of the full cycle of long wave. During the change from Z_1 to Z_2 the curly grain figure moves vertically by one half of its length. Atfer straightening out it appears again, its extreme points (marked by clear and dark circles) occupying the same positions as at the beginnig of the undulation (see sections C and M). The grain inclination connected with the long wave is shown by the longitudinal line in the region below the horizontal radial lines, which is outside the curly figure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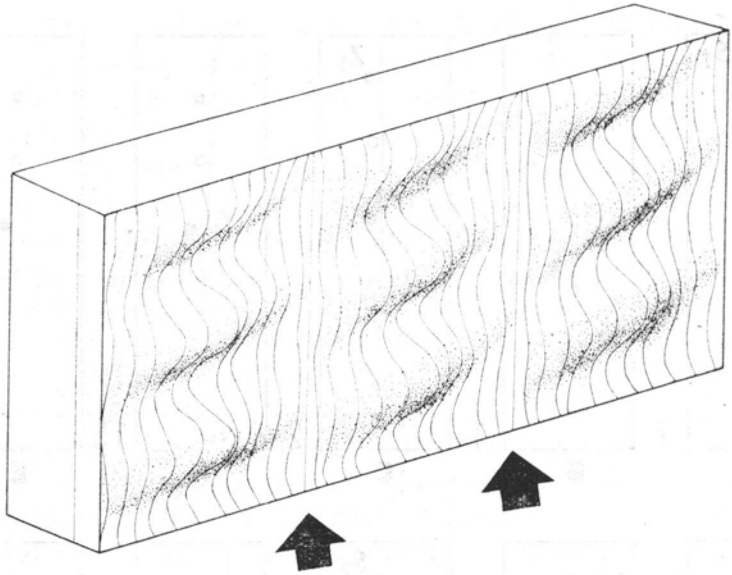

Fig. 3. Schematic picture of radial split face with extrapolated wave front like that in Fig. 2. Actually the curly figure does not last in *Entandrophragma* wood so long (along the rays) as shown in the drawing, but disappears finally during the second period. Arrows indicate wood with straightened grain. On diagram changes in grain inclination resulting from the existence of the long wave are omitted (shown in Fig. 2)

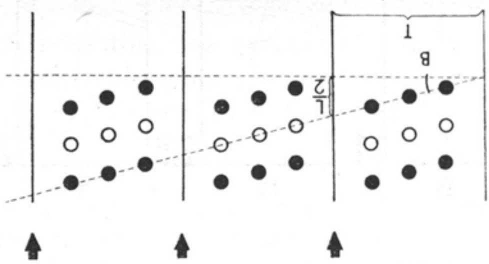

Fig. 4. Graphic description of the radial split face shown in Fig. 3. It illustrates at the same time the principle on which the slanting checkered pattern arises on the smoothed radial surface of the board. Dark circles — ridges, clear circles — depressions of the wave front. Inclinations of successive ridges and depressions are marked by oblique dashed line, the horizontal dashed line runs parallel to the rays; T — thickness of wood layer formed during one period of the morphogenic wave; arrows indicate successive wood layers distant by T with straightened pattern. Vertical shift of the wave front is equal in the wood layer of thickness T to one half of wavelength ($\lambda/2$)

Fig. 6. *Entandrophragma* — series of drawings made on the basis of successive (from pith to cambium) tangential sections through wood, illustrating the changes in the grain connected with the pattern of horizontal checker-boards type. The figures under each pair of drawings indicate the distance between the correspon-ding sections (mm). Arrows indicate the direction of changes in the inclination in

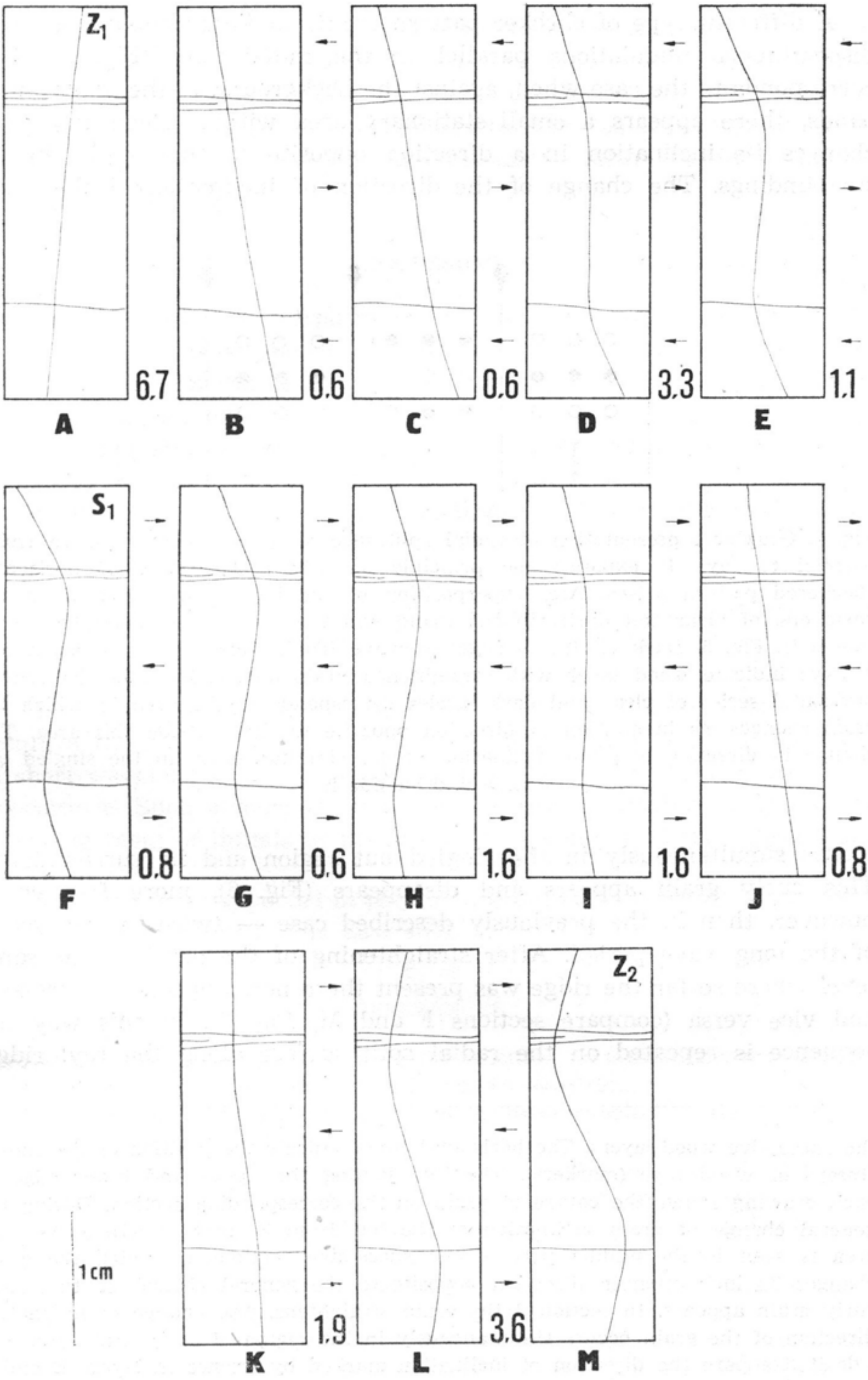

Fig. 6. Explanations on the pages 58 and 60

A different type of checker pattern occurs in *Entandrophragma* with discontinuous undulations parallel to the radial lines (Fig. 5). This corresponds to the case when, against the background of the longitudinal bands, there appears a small stationary area within which the grain changes its inclination in a direction opposite to that taken by its surroundings. The change of the direction of inclination of the grain

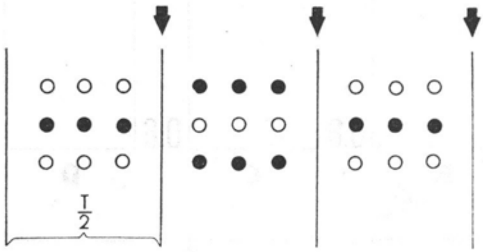

Fig. 7. Graphical presentation of radial split face with discontinuous wave fronts parallel to rays. It explains the principle on which the effect of horizontal checkered pattern arises. Afer superposition of the here shown pattern on the basic one of clear and dark ribbons (band width equal to T/2) the effect is as shown in Fig. 5. Dark circles — ridge of wave front, clear circles — depression. Arrows indicate wood layer with straightened grain distant by T/2. The central horizontal series of clear and dark circles corresponds to the area in which the grain changes its inclination in direction opposite to that outside this area. The change in direction of grain inclination occurs simultaneously in the singled out area and outside it

occurs simultaneously in the singled out region and its surroundings. This curly grain appears and disappears (Fig. 6), more frequently, however, than in the previously described case — twice in the course of the long wave period. After straightening of the grain at the same level where so far the ridge was present there now appears a depression and vice versa (compare sections F and M, Fig. 6). In this way the sequence is repeated on the radial split surface along the ray: ridge,

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the successive wood layers. The horizontal lines indicate the position of the chosen storeys of wood rays (markers). The line joining the upper and lower edge of each drawing shows the course of grain on the corresponding section. During the general change of grain inclination to the left from Z_1 to S_1 (sections A-F) an area is seen in the middle part of the successive sections in which the grain changes its inclination in direction opposite to the general change, so that local curly grain appears. In section J the grain straightens. The change of inclination direction of the grain occurs simultaneously in the region of curly grain and outside it (compare the direction of inclination marked by arrows in layers E and F and in layers F and G). The curly region remains at the same level and does not move vertically depression, ridge, giving an impression of discontinuity of the horizontal fronts (Fig. 7). On the radial surface of the boards there arises in this way a horizontal checkered pattern.

The above described case may be explained as a change of phase by T/2 in the oscillation processes associated with the formation of long-wave grain.

DISCUSSION

The hypothesis of morphogenic waves in the cambium allows the explanation of many phenomena concerning cambium itself and grain pattern. So far, on the basis of this hypothesis, the following phenomena have been elucidated:

1) migrating simple domain patterns in the cambium (Hejnowicz, 1973a; Krawczyszyn, 1971);
2) inclination of the wave fronts visible on the radial split face of wood (Hejnowicz, Romberger, 1973, 1979; Krawczyszyn, 1972; Pyszyński, 1977);
3) domain length pulsation in the cambium producing complex wavy wood in the superposed grain waves (Hejnowicz, 1974);
4) moiré and checkered figures (Hejnowicz, Romberger, 1979).

The present paper explains on this basis the checkered figure as the result of the sudden appearance in the cambium of a morphogenic wave of short wavelength with a stabilized amplitude from the moment of its appearance. Such a morphogenic wave induces a moving curly pattern of arrangement of initials in the cambium, which periodically disappears.

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REFERENCES

Hejnowicz Z., 1964. Orientation of the partition in pseudotransverse division in cambia of some conifers. Canad. 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., 1973a. Morphogenetic waves in cambia of trees. Plant Sci. Let. 1: 359-366.

Hejnowicz Z., 1973b. Domain pattern in cambium and formation of spiral grain. Proc. Vol. 2; IUFRO South Africa pp. 459—466.

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

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

Hejnowicz Z., Krawczyszyn J., 1969. Oriented morphogenetic phenomena in cambium of broadleaved trees. Acta Soc. Bot. Pol. 38: 547-560.

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

Hejnowicz Z., Romberger J. A., 1979. The common basis of wood grain figures is the systematically changing orientation of cambial fusiform cells, (in press).

Hejnowicz Z., Zagórska-Marek B., 1974. Mechanism of changes in grain inclination in wood produced by storeyed cambium. Acta Soc. Bot. Pol. 43: 381-398.

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.

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

Pyszyński W., 1972. Downward movement of the domain pattern in *Aesculus* cambium producing wavy-grained xylem. Acta Soc. Bot. Pol. 41: 511-517.

Pyszyński W., 1977. Complex wavy grain in the stem of *Aesculus*. Acta Soc. Bot. Pol. 46: 231-249.

Nieciągłość grzbietów falistej włóknistości na powierzchni promieniowej drewna jako przejaw fal ukierunkowania zdarzeń komórkowych w kambium

Streszczenie

W drewnie *Entandrophragma* oprócz podstawowej włóknistości typu interlocked grain istnieją lokalnie drobne zafalowania włóknistości przejawiające się w drobnej szachownicowej wzorzystości na powierzchni promieniowej desek. W oparciu o model matematyczny interpretujemy w niniejszej pracy skośne szachownicowe wzory jako wynik nagłego pojawienia się w kambium krótkiej fali ukierunkowania o amplitudzie ustalonej od chwili pojawienia się. Biegnąca pionowo fala wzbudzając przesuwające się dwa razy wolniej zafalowanie układu komórek inicjalnych nie stabilizuje tego zafalowania, lecz powoduje jego okresowe zanikanie. W kolejnych pokładach drewna występuje wówczas włóknistość falista na przemian z włóknistością prostą. Na przełupie promieniowym takiego drewna nachylone do promieni grzbiety drobnej falistości są nieciągłe wzdłuż linii nachylenia.

Poziome szachownicowe wzory będące przejawem drobnej falistości o grzbietach nieciągłych i równoległych do promieni można objaśnić lokalnym przesunięciem fazy o T/2 w oscylacyjnym procesie związanym z długą falą w kambium i tworzeniem „interlocked grain".