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Pulsations of domain length as support for the hypothesis of morphogenetic waves in the cambium

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Abstract

The domains in the cambium may be of different length and each domain varies then in length cyclically with time. Such pulsating domain patterns have been described in *Fraxinus*. A common basis to understand the different aspects of domain pattern — the arrangement of domains, reversals of domain type at a particular site, and the pulsation of domain length — is offered by the hypothesis that there are waves of orientational tendencies in the cambium. The domain pattern itself would represent the spatial aspect of the wave, the reversals of domain type at a particular site in the cambium would represent the time aspect of the wave, while the pulsation of domain length would be due to superposition of waves which differ in length and velocity.

INTRODUCTION

Morphogenetic events and domain pattern in the cambium.

Several types of events occurring in the cambium make possible changes in the orientation of cells with respect to the stem axis (Hejnowicz 1968, Hejnowicz and Romberger 1973). These are: pseudotransverse anticlinal divisions of fusiform initials, overlapping of intrusively growing tips of the initials, changes in the overlap of two oppositely directed tips, splitting and uniting of rays. The events may occur in two alternative orientational forms: Z (right) and S (left), Fig. 1. Since they affect in some way the cambial form, we shall call them morphogenetic events.

Earlier studies have established that the orientation of these events is non-random. There are in the cambium areas within which one of the alternative orientations prevails (Hejnowicz 1961, 1964, Bannan 1966). These areas are called domains, each is either of Z or of S type. The domain pattern in the cambium is a common phenomenon both in broadleaved trees and conifers (Hejnowicz and Krawczyszyn 1969, Hejnowicz and Romberger 1973, Krawczyszyn 1971, Hejnowicz 1973), though often it does not manifest its presence unless the orientation of morphogenetic events is determined.

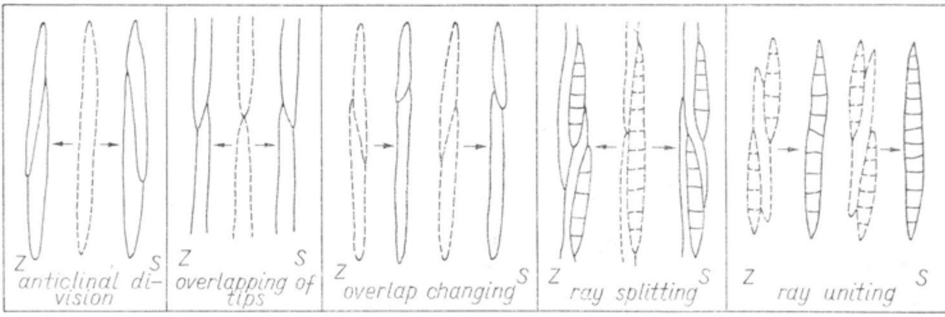
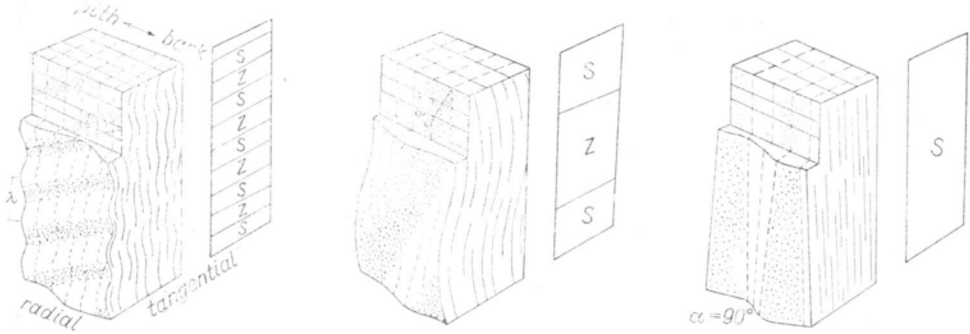


Fig. 1. Alternative (Z or S) orientational types of five different classes of morphogenetic events in the cambium.

The domain pattern migrates in respect to the cells within it, what causes reversals of domain type at each particular site in the cambium (Hejnowicz 1971, Krawczyszyn 1971, Hejnowicz and Romberger 1973). The velocity of this migration depends upon the domain length; the longer the domains the faster the migration (Hejnowicz and Romberger 1973, Krawczyszyn 1972). The domain pattern in the form of alternate transverse bands migrates along the stem.

Grain pattern in wood

The term grain refers to the orientation of the longitudinal axes of wood cells when considered en masse (Panshin and de Zeeuw 1970). To give its a specific meaning this term must be preceded by a qualifying adjective such as straight, spiral (helical), wavy. The grain pattern on the surface of a particular annual ring reflects the pattern of alignment of cells in the cambium which in turn depends on: 1. the relative size and arrangement of domains currently and previously; 2. the frequency of the morphogenetic events within the domain; 3. the rate of domain migration (Hejnowicz 1968, 1971, Hejnowicz and Romberger 1973, Krawczyszyn 1972). If the frequency is low, the domain pattern will have little effect on the alignment of cambial cells and the grain will remain straight if it was originally straight. However, where the domain pattern is accompanied by a high frequency of the morphogenetic events, it elicits a wavy or serpentine pattern of cell arrangement in the wood, Fig. 2. The radial split face of such wood shows grain undulations which run at some angle with respect to the rays owing to the migration of the domain pattern in cambium (Hejnowicz 1971, Hejnowicz and Romberger 1973, Krawczyszyn 1972). The finished radial surface exhibits then dark and light streaks corresponding to the undulations (zones of differently cut wood elements). The longer the domain, the faster the migration of domain pattern and the steeper the undulations (streaks). In extreme case the undulations run parallel to annual rings (Fig. 2 C). In such cases only one domain stretches out over the whole trunk length, and this distance is covered by the border between two domains in less than 1 year. In such a case the grain within a particular annual ring is spiral, however, owing to changes



A B C

Fig. 2. Blocks of wavy-grained (A, B) and interlocked-grained (C) wood with tangential surface forward. The radial surface is formed partly by longitudinal splitting of the disc from which the block derived. The undulations in the radial surface form an angle α with the rays. The blocks differ in wave-length λ and in the value of α. In C the λ is infinitely long and α is about 90°

of domain type there are periodical changes of spiral direction in successive groups of annual rings. The grain is then said to be interlocked and the figure formed by the streaks on the radial surface is said to be ribbon or striped (Panshin, de Zeeuw 1970). When domains are short, the resulting figure is said to be curly or wavy. All intermediate forms between the interlocked and wavy grain as well as combinations of the two types of grain are possible. Such a combination, in the case of high frequency of the morphogenetic events generally results in a mottled figure, i.e. the ribbon figure broken by the less steep streaks which correspond to shorter waves (Panshin, de Zeeuw 1970). Additional diversity of grain pattern arises from the transverse component of the migration of domain pattern when there are longitudinal borders between the domain in the pattern.

Migrating domain pattern as a moving wave phenomenon

In a physical sense a wave is any disturbance which is the cyclic function of distance and the same function of time i.e.

$$\psi(z, t) = a\psi(z+\lambda, t+T)$$

where ψ stands for the function of time (t) and distance (z) which describe the shape of the wave, T is the period, λ is the length of the wave, and a is a proportionality factor which differs from 1 when the amplitude of the wave is modulated. An example of wave is provided by a disturbance of fixed shape which moves with constant velocity.

In the case of domain pattern the orientation of the events changes cyclically both in space and time; at a particular moment it changes with distance, at a particular site — with time. It seemed thus reasonable to propose the hypothesis that there is a wave of orientational tendency in cambium which is called a morphogenetic wave (Hejnowicz 1973).

A moving wave is characterized by the length λ, the velocity v, and the period T. These three parameters are interrelated: v is the conversion factor of the wave from space course to time course; $\lambda = vT$. The length of the morphogenetic wave in the cambium corresponds to the length of two successive domains. The velocity of the wave is represented by the velocity of the migration of the domain pattern.

The proposed morphogenetic wave is a manifestation of unknown process within the protoplasm. What we may infer is that the process itself occurs as a wave $\psi(t, z)$ characterized by the known λ and v, we do not know, however, the shape of this wave, i.e. we do not know the function ψ. We may distinguish at the level of the morphogenetic events only two classes of orientation either Z or S but this does not imply that there are only two states in the process. It is more probable that something in the process changes gradually with time and distance. As a working hypothesis we shall consider the shape of the wave as a simple harmonic function of time and distance:

$$\psi(t, z) = A\cos(\omega t - kz)$$

where ω is the angular frequency, $\omega = \frac{2\pi}{T}$, k is the wave number, $k = \frac{2\pi}{\lambda}$, and A is the amplitude. We assume also that the orientation, either Z or S is determined by the sign of this function as it is diagrammatically illustrated in Fig. 3.

λ and v may be determined from the series of maps of the domain pattern. However, sometimes they may be also estimated on the basis of macroscopic studies of wood with wavy grain. In the case of regular wavy grain, λ corresponds to the blngth of the wave in cell alignment, v is represented by the tangent of the angle eetween the rays and the undulations seen on the radial split face, Fig. 2.

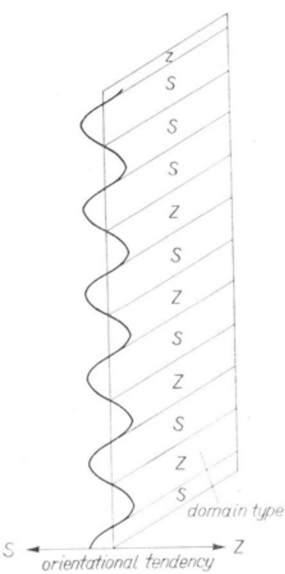


Fig. 3. Model of sinusoid wave of orientational behaviour and the corresponding domain pattern in the cambium. The domain pattern is constructed with the assumption that the domain type is determined by the sign of the wave.

Where two or more waves of different λ and v occur in the same cambium the waves should produce a domain pattern according to their superposition. Let us consider what domain pattern should be expected in the case when there are two waves differing considerably in length but of similar period in the cambium. Fig. 4 shows the unidimensional model of the interference of two such waves and the corresponding domain pattern in successive periods of time. As seen the domain are of different length at a particular moment and each domain varies in length with time till temporary disappearance sometimes.

The occurrence of two or more waves in the same cambium may be expected in those cases where the grain pattern seems to be a combination of two simpler patterns, for instance where the figure on the radially sawn surface of wood is of

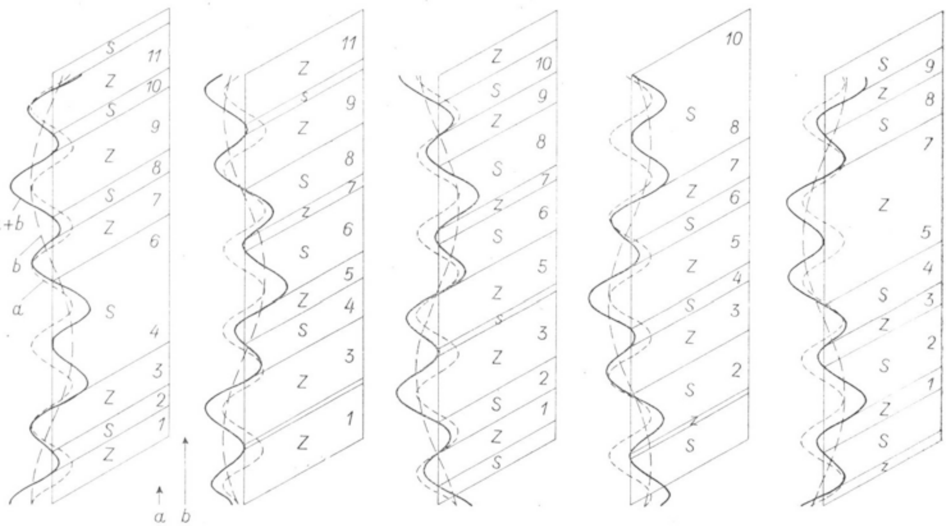


Fig. 4. Model of two waves (dashed lines) superposed, the resulting wave (continuous line) and the corresponding domain pattern in the cambium, at five equidistant times. During a unit period (the period which passes between two successive stages shown in the figure) the component waves are displaced by the indicated vectors v. The vectors are chosen so that the quotient which gives the period of the wave is the same for both waves; $\frac{\lambda_a}{v_a} = \frac{\lambda_b}{v_b}$. The domains are numbered to facilitate their identification. Fluctuation of domain length is seen.

mottled type. The present work was undertaken to locate spatially the splitting and uniting of rays and assign them to S or Z classes in wood characterized by complex grain so as to delineate domain maps in the cambium which produced the wood, and to see whether the domain pulsated. The splitting and uniting of rays were chosen because their configuration, either Z or S, is representative for the domain within which they occur, and they are the easiest to identify among the morphogenetic events.

MATERIAL AND METHODS

The wood samples in the form of segments of radially sawn boards from two trunks of *Fraxinus excelsior* characterized by a complex grain pattern were collected at the sawmill at Dobroszyce, Poland. The segments provided blocks of xylem appropriate for microtome sectioning. The sections were 30 μ thick. Only sections from the terminal layers of xylem in annual rings were taken (Hejnowicz and Krawczyszyn 1969), the remaining sections were discarded. Those left were affixed to slides with Haupt's adhesive. They were then dried, immersed in boiling alcohol to expel air from the cell lumina, passed through xylene and mounted in Canada balsam. Images of the sections were projected into photographic paper with a Zeiss Documator. Enlargement was 35 to 1. The photographic images of the terminal layers of annual rings were the direct object of our study.

RESULTS

One of the samples was taken from the log at about 3-m distance from its base. The log was 50 cm. in diameter at this distance. The wood was wavy grained at least along the 3-m. segment of the log, as it was seen on the radially sawn board of this length. The main pattern of the grain consisted of close and nearly transverse undulations ($\lambda = 5.5$ mm., $\alpha = 3°45'$, Fig. 5). The radial span of one undulation was 85 mm. (T_{r1} in Fig. 5). This is the width of the wood layer produced during the period T. The pattern had appeared during the formation of about the 15th annual ring and continued for the life of the tree.

Within the segment of the board which was taken to the laboratory a second wavy pattern was disclosed when the segment was cut transversely into radial sticks 3 cm. wide and each stick was split radially by applying the edge of a long knife to the upper transverse surface. The cleavage followed the course of the fibers. The second wavy pattern became manifest in the sinuous radial fracture on the lower transverse surface (Fig. 5). The radial span of the wave, i.e. the length of one cycle in the sinuous fracture, T_{r2}, was 80 mm. (18 annual rings). When the split stick halves were set up in the original sequence a secondary undulation was seen on the recomposed split face. The undulation was inclined in respect to the rays by about 80° (α_2). From the radial span T_{r2} and the α_2 λ_2 can be calculated. The latter amounts to 45 cm. which is more than the length of the segment cut into sticks. It should be pointed out that the radial span of undulation in the two patterns was the same in spite of large differences in v and λ. It could not be ascertained whether the second pattern was a local phenomenon in the trunk at the place from which the board segment was derived or whether it was as extensive as the first pattern. The block for microtome sectioning contained the whole S phase of the longer wave between the parts of the Z phases. A series of 14 domain maps was prepared each for a 1-year period at the same site of the cambium (Fig. 6). Each map shows the spatial distribution of Z- and S-oriented ray events and hence delineates the domains. The latter

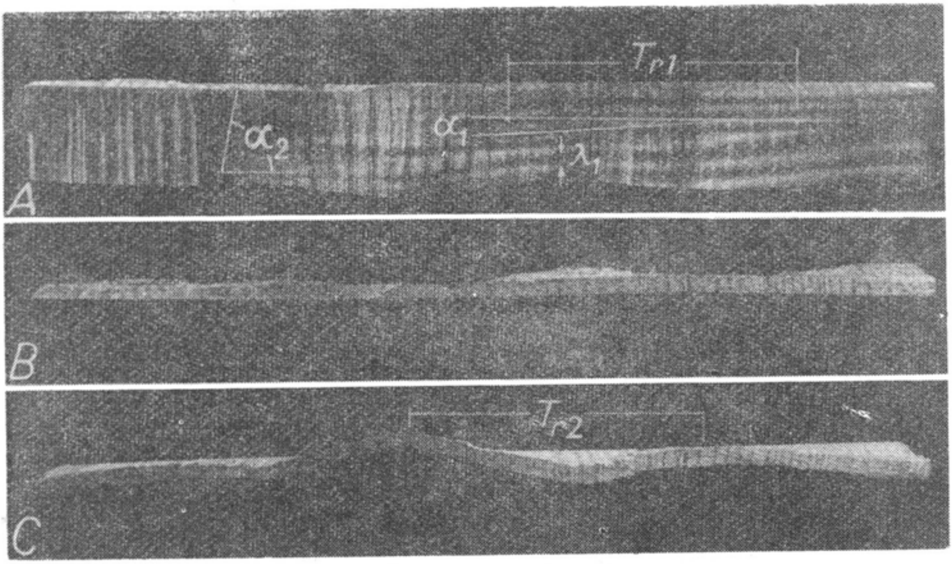


Fig. 5. *Fraxinus excelsior*, sample 1. Different views of a plate of wood split off radially from a 30 mm. broad stick sawn transversely off the radial board. A — face view of the radial surface with nearly transverse, close undulations; B — upper transverse surface to which the edge of a long knife was applied; C — view of the lower transverse surface showing the sinuous fracture due to the second wavy pattern of grain. T_r — radial span of the undulation, — the angle between the undulation and the rays. The very end of the plate at the left consists of pith.

were the basis for the development of the close undulations in the grain as it may be observed when comparing the maps with the outlines of the grain pattern shown at the beginning and the end of the series in Fig. 6. Comparison of successive domain maps allows to observe changes in time. It is evident from Fig. 6 that the domain pattern migrated slowly upward. Surely this migration was reponsible for the inclination of the close undulations of grain. The migration rate, v_1, was 0.68 mm. during the formation of 1 cm of wood while $tg\alpha_1$ is 0.065. Thus v and α fit well as they should.

It is evident also that the dynamics of the domain pattern involved not only migration but also pulsations of domain length; domains of one type increased their length at the cost of domains of the other type. In the first three maps in Fig. 5 Z domains prevail both as regards the area which they occupy jointly and the summated number of events. In the next eight maps the prevailing domains are those of S type, thereafter again Z domains become predominant. This pulsation of the domains resulted in the formation of the second wavy pattern of grain. Maps no. 4 and 12 correspond to the limits of the S-phase of this pattern.

The second sample of ash wood taken from basal part of a trunk about 80 cm. in diameter. It had similar complex wavy grain as the first one, only the radial span of one undulation (T) was shorter. One pattern of the grain consisted of close nearly transverse undulations ($\lambda_1 = 7$ mm., $\alpha_1 = 7°$). The radial span was 57 mm. The second pattern was characterized by much longer undulations inclined by about 80° with

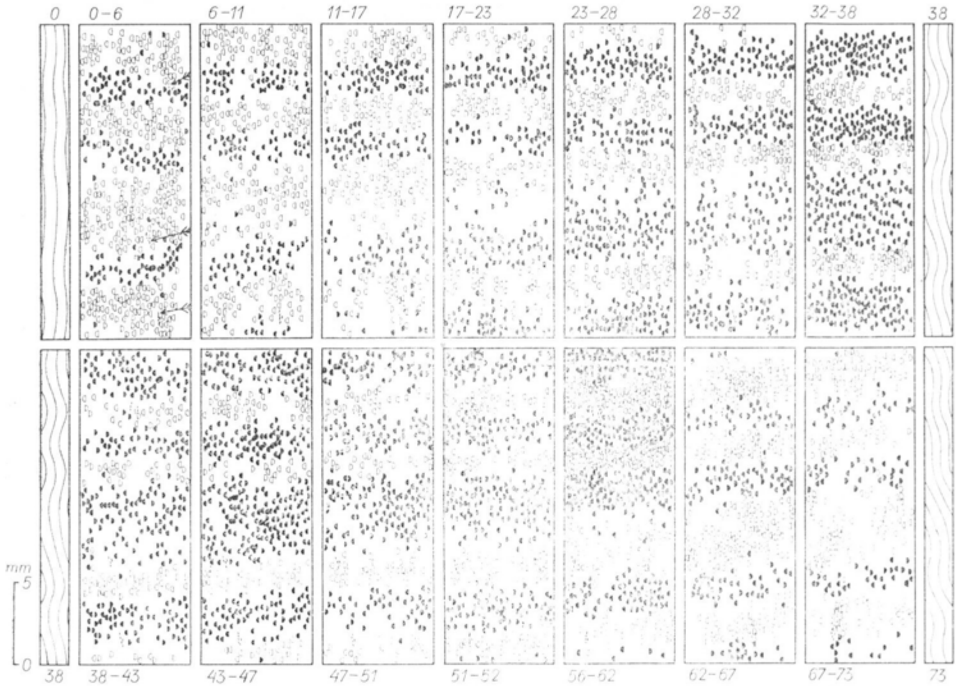


Fig. 6 *Fraxinus excelsior*, sample 1. Wide rectangles with semicircles denote ray splitting and uniting, respectively. Full symbols denote S events, empty symbols Z events. Some rays used as position indices are shown, indicated by arrows on the 1st map. The successive maps are displaced slightly transversely to the right but are not displaced longitudinally, thus upward displacement of the domains represents the migration of the domain pattern. Pulsation of the domains in length may be seen. The figures show the position, in mm., of the annual rings with respect to the inner border of the 19th ring (from the pith). The narrow maps show the course of grain at the indicated positions (0, 38, 73 mm).

respect to the rays. The radial span of one undulation in this pattern was 55 mm., as determined on the radial fracture of a narrow stick sawn transversely off the end of radial board. Thus the calculated λ_2 in the second pattern is 312 mm. A series of maps for the 7-year period corresponding to one cycle of the second grain pattern is shown in Fig. 7. A pronounced pulsation of domain length may be seen. The S domain which on the first map occupied about one half of the map area decreased to a very narrow strip on the sixth map.

Pulsation of the domains may lead to the complete disappearance of a domain as shown in Fig. 8. The maps in Fig. 8 were drawn on the basis of sections cut from the wood block taken from sample no 2 at the point where general orientation of grain changed very fast to the right.

The pulsation of the domains changes the overall proportion of Z to S events within a larger area. A corresponding change in the general course of the wavy grain may be observed by comparing the outlines of grain pattern in successive rings shown in the narrow rectangles in Fig. 7 and 8. This change is related to the

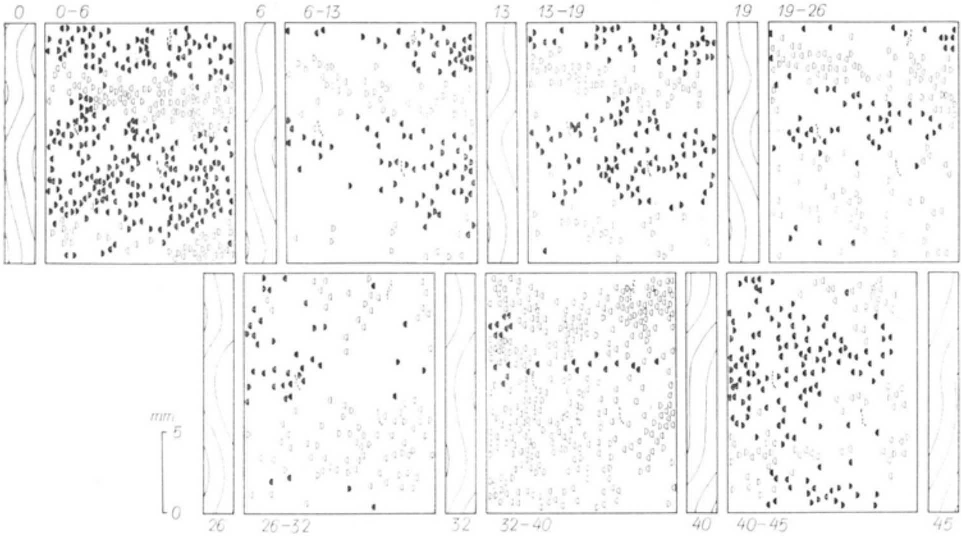


Fig. 7. *Fraxinus excelsior*, sample 2. Events occurring during the formation of the annual rings No. 50—56. Legend as in Fig. 6.

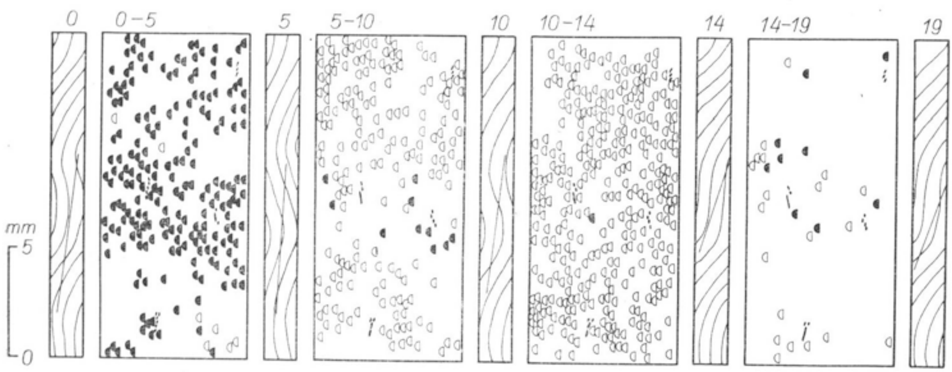


Fig. 8 *Fraxinus excelsior*, sample 2. Ray splitting events during the formation of the annual rings 52—55, 10 cm below the site to which corresponds the series in Fig. 7. The density of the events was so high in the first 3 maps that ray uniting events were not mapped, however, their distribution was the same as that for ray splitting. Legend as in Fig. 6.

pattern of grain with higher values of λ and v. For instance the prevalence of domains of *Z*-type in Fig. 8 resulted in a change of the general course of grain to the right.

DISCUSSION

The foregoing pages have made it clear that the domain pattern in the cambium not only migrates, as has been described earlier (Hejnowicz and Romberger 1973), but may pulsate as well. The common basis for understanding the different aspects of the domain pattern: the arrangement of domains, reversals of domain type at a particular site in the cambium owing to the migration of the domain pattern, the pulsation of domain length — is offered by the hypothesis that there are waves of orientational tendencies in the cambium. According to this hypothesis the pulsation of domain length would be due to superposition of waves which differ in the length and velocity.

We do not know the oscillatory process in cambial protoplasm which underlies the waves, neither do we know the mechanism which reveals the waves and determines the orientation of morphogenetic events. However, we may try to understand the basic nature of the waves from the fact that the different waves which may be superposed in the same cambium have the same period. This fact indicates that the waves are developed in populations of oscillators each oscillating essentially by itself but with some sort of interaction between them in a population. The period is then determined by the nature of the oscillator, the velocity, and hence the length of the wave, is governed by the nature of the interaction. This kind of waves may be of special interest for the morphogenesis because they produce a stationary pattern of beats as it has been pointed out in an earlier paper (Hejnowicz 1973) and will be discussed exhaustively in another paper.

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Pulsacje długości domen jako poparcie hipotezy o występowaniu fal morfogenetycznych w kambium

Streszczenie

Wiadomo z poprzednich badań, że w kambium drzew występują domeny czyli obszary ukierunkowywania na prawo (Z) albo na lewo (S) takich zdarzeń komórkowych jak: skośne podziały antyklinalne, zachodzenie na siebie przeciwnie skierowanych końców komórkowych rosnących intruzywnie, rozszczepianie i łączenie promieni. Wzór domenowy przesuwa się względem komórek w związku z czym typ domeny w danym miejscu kambium zmienia się cyklicznie. Zaproponowano hipotezę, że w kambium występują fale ukierunkowywania zdarzeń, czyli fale morfogenetyczne. Hipoteza ta wyjaśnia wzór domenowy jako przestrzenny przejaw fali, zaś jego przesuwanie i zmianę typu domeny w danym miejscu kambium jako czasowy przejaw fali. Na podstawie tej hipotezy można przewidzieć pewien typ zachowania się wzoru domenowego w przypadku gdy kilka fal o różnej długości i prędkości współistnieje w tym samym kambium. W niniejszej pracy odtworzono wzór domenowy w kambium Fraxinus które produkowało podwójnie faliste drewno. Stwierdzono, że w kambium tym występują pulsacje długości domen, takie jakich można było oczekiwać na podstawie interferencji dwu fal morfogenetycznych o różnej długości i prędkości. Występowanie zjawiska interferencji wskazuje na słuszość hipotezy o istnieniu fal morfogenetycznych w kambium.