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Upward movement of the domain pattern in the cambium producing wavy grain in Picea excelsa

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Abstract:

The cambium which produces wavy-grained xylem in spruce differs from normal cambium by a higher frequency of oblique anticlinal divisions and a higher rate of intrusive growth of fusiform initials. Since the orientation, either to the left or to the right, of the divisions and the overlaps achieved by the growting tips is uniform within the areas called domains, the domain pattern of the cambium is reflected in the pattern of grain undulations in the xylem. The domain pattern moves longitudinally about 0.7 mm during the production of 1 mm of xylem. A visible expression of the movement is the obliquity of undulation lines on the radial face of the wavy xylem.

INTRODUCTION

On one site in the Tatra Mts. a number of old spruce trees was found with scattered lenticular-circular patches of wavy-grained xylem in their trunks. The patches showed clear cut boundaries and were easily recognizable on debarked logs (Fig. 1B). They often occurred in clusters on more or less prominent elevations which extended into the normal wood. The pattern of the grain was rather irregular on the tangential surface (Fig. 1B, C) while on the radial faces of split blocks of the wavy xylem it appeared as undulations oriented obliquely (Fig. 1A). The lines of the undulations formed an angle with the xylem rays, which indicates that the orientation of cells was cyclically changing in particular area of the cambium producing the wavy xylem.

In a cross section of the trunk of a tree about 90-year-old, the sector of abnormal wood extended radially beginning in the 10th ring from the pith which contained wound tissue. Probably the cambium had been wounded in the young tree and in some way its cells had changed to a state of production of abnormal xylem. The abnormality consisted of wavy grain and a lower mean length of tracheids —

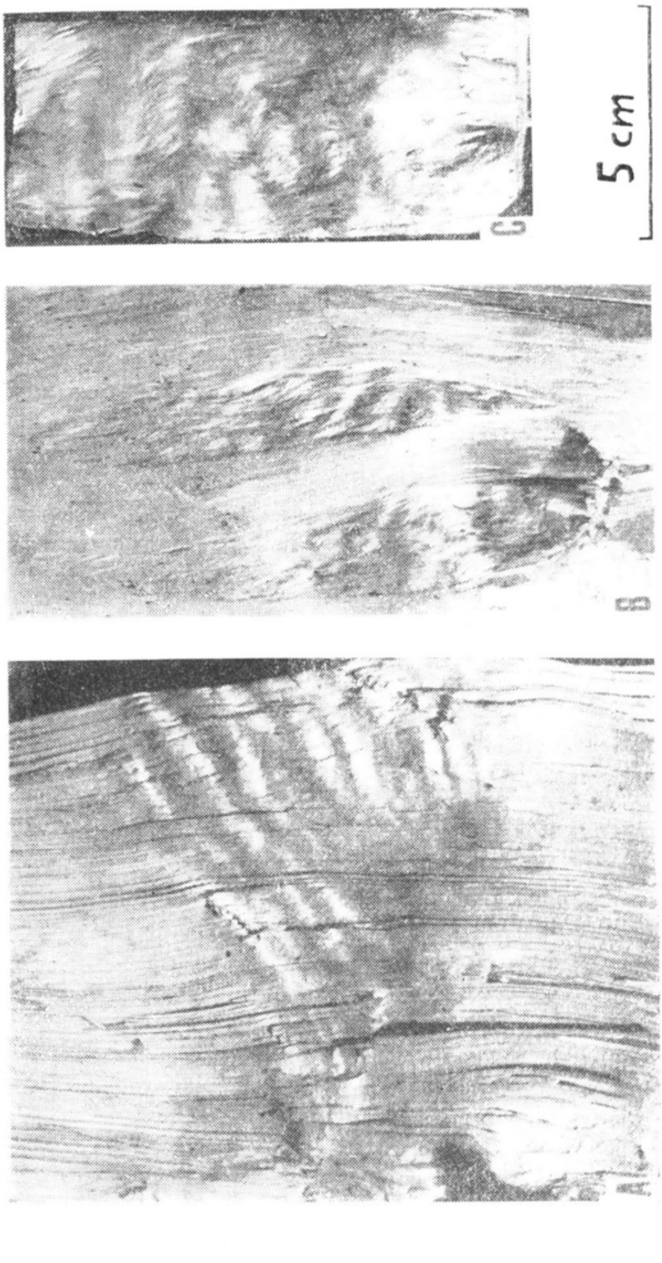

Fig. 1. Wavy xylem in *Picea excelsa*. *A* — radial face, *B* and *C* — tangential surface

about 1 mm as compared with about 3 mm in normal xylem. The area of abnormal cambium was slowly expanding both longitudinally (Fig. 1A) and tangentially.

The variable orientation of tracheids in successive layers of xylem reflects a corresponding reorientation of cells in the cambium which produced these layers (Newman 1955; Harris 1969). Previous studies indicate that this is caused by preferentially oriented, either to the right (Z) or to the left (S), oblique anticlinal divisions, overlapping of intrusively growing tips, and splitting of rays (Bannan 1966, Hejnowicz 1968). The orientation of these events is non-random; one of the alternatives prevails within a particular area (Bannan 1966; Hejnowicz 1968). The areas which differ in the type of prevailing orientation are called domains of Z or S-type (Hejnowicz 1964). The domain pattern is dynamic; reversals off the prevailing orientation in particular area of the cambium were observed (Bannan 1954, 1966; Hejnowicz 1968). In the cambium producing straight-grained xylem, the effect of non-randomly oriented events is minimized by their low frequencies. On the contrary, one may suppose that, when the effect of the domain pattern is not minimized, the pattern will be reflected in a pattern of grain in xylem, and that, if the grain is differently inclined in various regions of the wood surface this is dependent on the domain pattern. This was the guiding idea in choosing the wavy xylem for studies.

MATERIALS AND METHODS

Complete segments of logs containing patches of wavy xylem were cut from 3 trees, additionally small samples of wavy xylem were collected from 34 trees of *Picea excelsa*. The segments provided blocks of wood for microtome sectioning (wavy and normal xylem). The small samples were used to examine the undulations on the radial face. Serial tangential sections 30–40 μ thick were cut along the radial distance up to 30 mm covering more than 10 annual rings. The sections were attached to slides with Haupt's adhesive, dried, immersed in boiling alcohol to remove air from cell lumina, passed through xylene and, mounted in Canada balsam. Images of the sections were projected onto photographic paper by means of a Zeiss Documator. The set of serial sections from each sample was divided into subsets of 20 – 40 sections. For studies of the orientation of anticlinal partitions, every section of some subsets was photographed at a ×49 enlargement. For studies of the reorientation of tracheids, the terminal sections of all subsets were photographed at an enlargement of ×18. The photographs (×18) were used to draw lines parallel to the tracheids on translucent paper. The sheet of paper with a set of lines in black was adjusted to the next photograph by using fusiform rays as reference points and another set of lines was drawn in red. The areas in which the red lines intersected the black ones in one direction, either Z or S, were then delineated. The principle of the procedure and the ways of representing the Z and S-areas on a map are illustrated in Fig. 2.

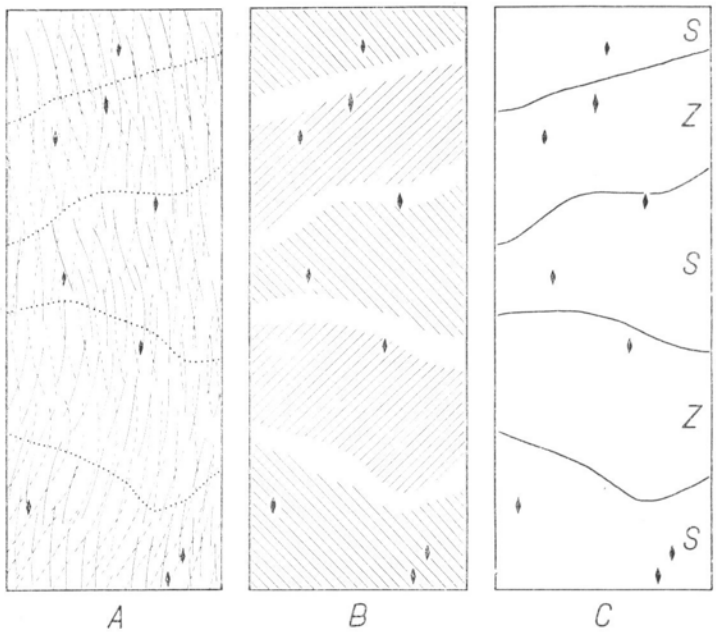

Fig. 2. *A*— the principle of procedure used in delineating the areas which differ in direction of reorientation of cambial cells. Full and dashed lines are parallel to tracheids on two sections 2 mm radially apart, the former corresponding to the section more distant from the pith. Dotted lines separate the areas in which full lines intersected the dashed one in alternative directions; *B* and *C* — — different ways of representing the areas. Some fusiform rays are indicated as reference points

RESULTS

The tangential views of the studied xylem are shown in Figs. 1 c and 3. The orientation of the tracheid axes varied in different areas from S inclination to Z inclination and at some boundary line between them passing through the vertical. The "wavesn" in cell arrangement formed a mosaic pattern with the wave fronts running either obliquely or transversely.

Serial tangential sections showed different orientation of the tracheids in the same area. Fig. 4 illustrates the changes in tracheid orientation and the constancy of the relative positions of fusiform rays. Keeping in mind that the inclination of tracheids in a tangential section reflects the inclination of their parental cambial initials, the variable orientation of tracheids in successive sections must be interpreted as the reorientation of cambial cells during the production of xylem. Although the cells were reoriented uniformly within a particular area of the cambium, this was not due to the twist of the area as a whole, since the position of the rays in relation to the stem axis was preserved.

The reorientation varied in intensity and the direction in which it proceeded in different areas. During the production of a particular layer of xylem, there were areas in which cell orientation was changing at a given moment and others in

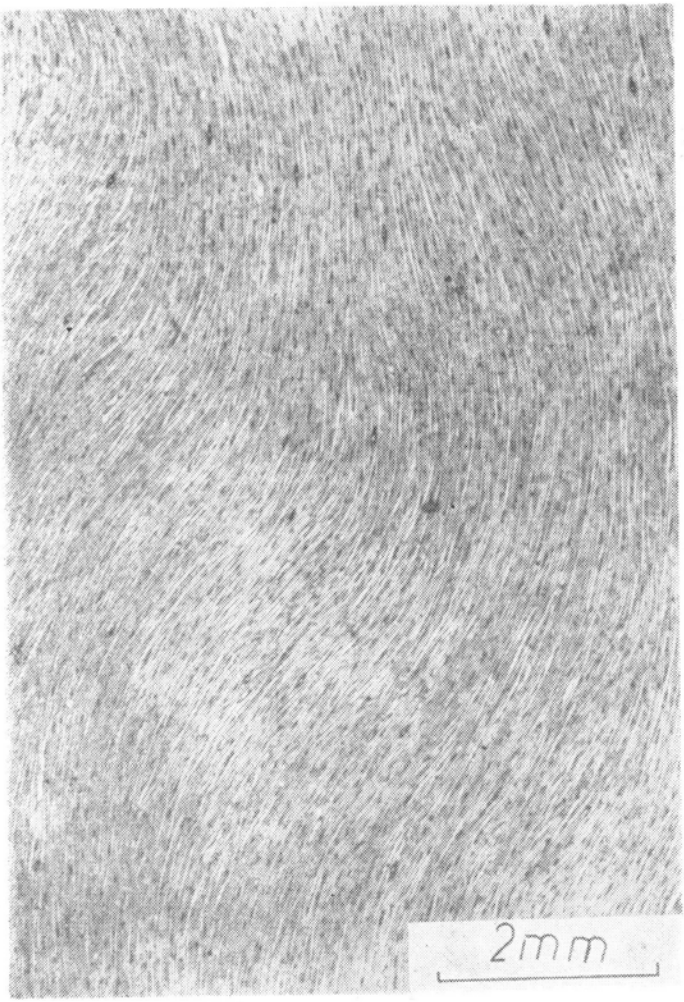

Fig. 3. Tangential view of the studied xylem

which at the same time no change were noticeable. These areas will be referred to as active and neutral, respectively. The active ones were either of Z or S type; they were delineated by the procedure illustrated in Fig. 2. The pattern of the areas of reorientation, called AR-pattern is illustrated in Figs 5 and 6. It should be emphasized that in defining the type of the active area, not the angle of inclination, but the direction in which this angle was changing was taken into account. The cells may be inclined to the right (Z), but if they are with drawing from this inclination they will be considered as belonging to the area of S-type. For instance the fusiform rays within the middle part of the maps in Fig. 5 are inclined to the left although this part belongs actually to a Z-area of the AR-pattern.

Studies of successive sections showed that the anatomical basis for the changing of cell orientation involved the following types of events: 1. Oblique anticlinal divisions

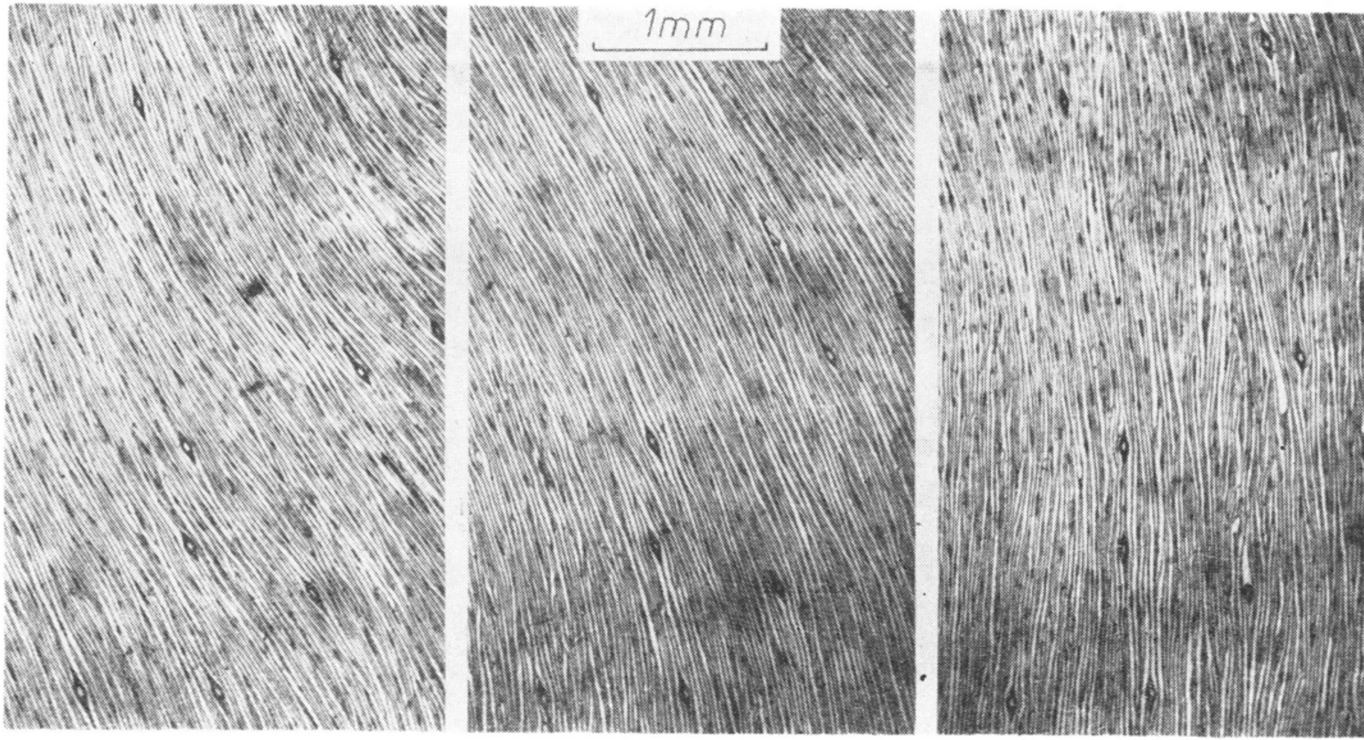

Fig. 4. The same area in three sections, each pair 3 mm apart. Observe constant position of fusiform rays in spite of pronounced changes in tracheid orientation

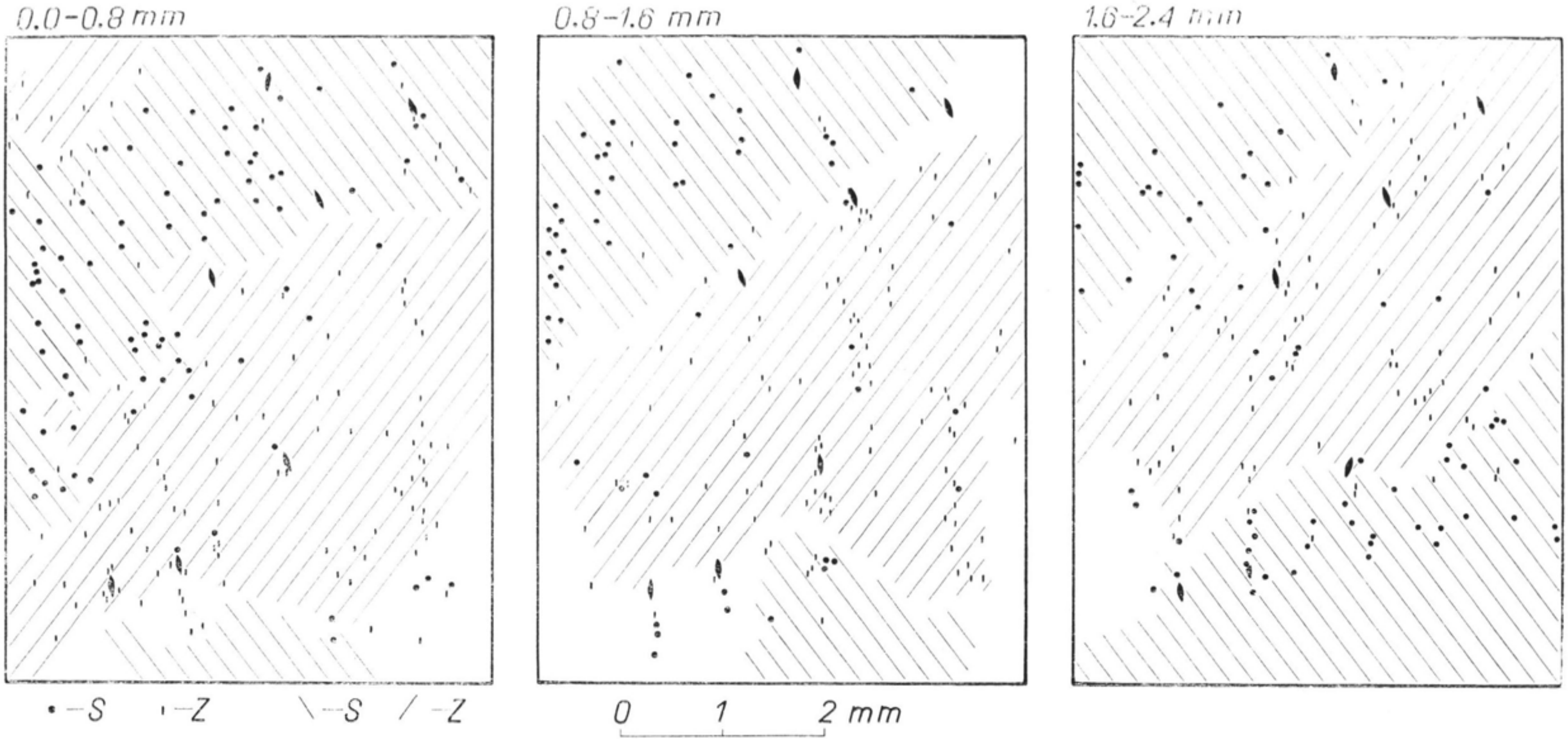

Fig. 5. Maps showing the areas of reorientation and the distribution of newly formed anticlinal partitions of S and Z type in three successive time intervals. The positions of the inner and outer surfaces of the xylem layer produced during an interval in respect to the inner surface of the first layer are indicated above upper margin.

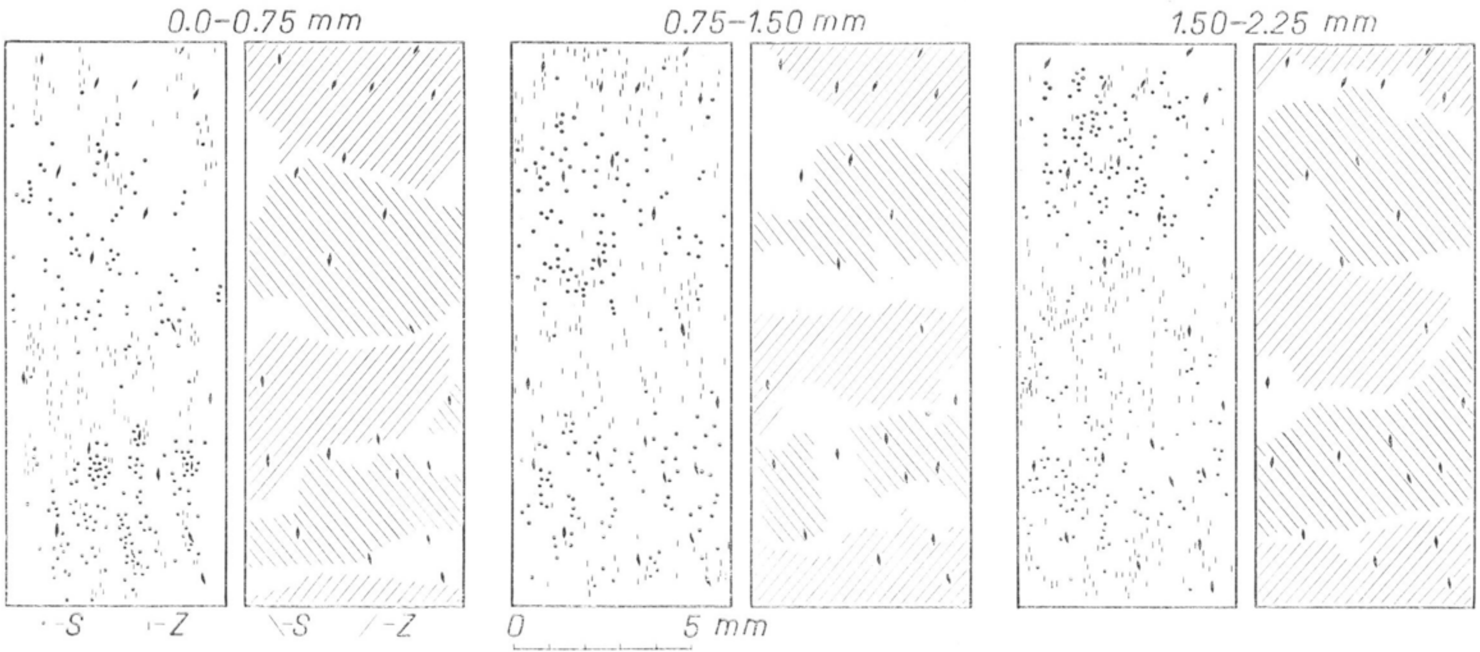

Fig. 6. Three pairs of maps showing the domain pattern and the pattern of the areas of reorientation in successive time intervals

of fusiform initials; 2. overlapping of oppositely directed tips of initials, lapping of the tips over the rays, and splitting of the rays, all due to intrusive growth of the tips of fusiform initials; 3. elimination of certain initials from the cambium following

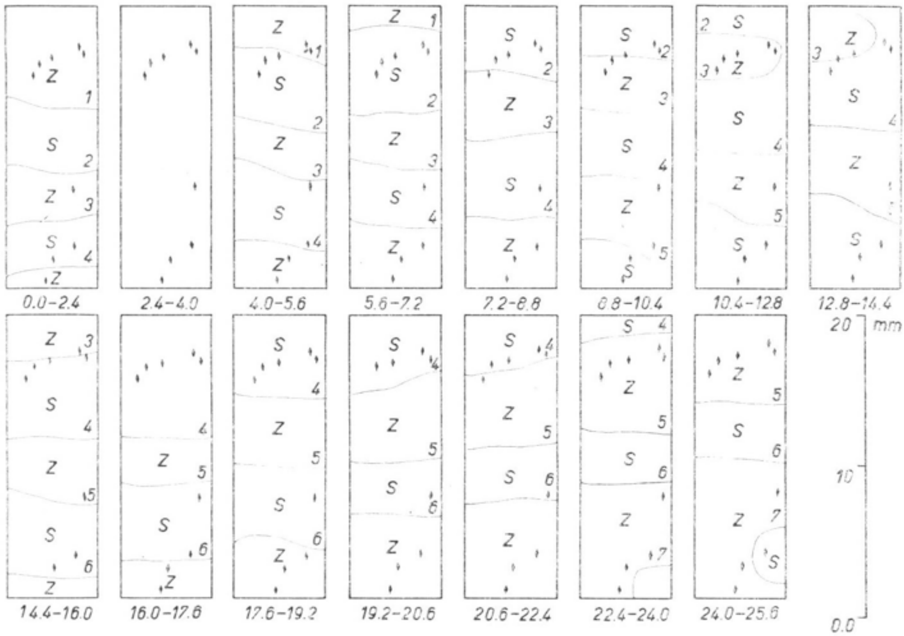

Fig. 7. Domain pattern during formation of successive layers of xylem which jointly extended for 25 mm radially. The borders between the domain are numbered, their gradual displacement is seen. During formation of the 2.4–4.0 mm. layer no perceptible change in cell orientation occurred

divisions and intrusive growth of persisting initials. The anticlinal divisions and the effects of intrusive growth occurred in two alternative forms Z and S. One form prevailed within a particular area of the cambium, i.e. domains of Z and S-type occurred. The Z-areas of the AR-pattern were Z-domains, and similar correspondence occurred between the S-areas and S-domains (Figs. 5 and 6). The correspondence was maintained during the production of the xylem when the patterns moved slowly in respect to cambial cells (Figs 5 and 6). On the strength of the similarity between the two patterns, the movement of the domain pattern was studied further by determinig the AR-pattern. Delineation of the latter was much more efficient than that of the former.

The movement always had a longitudinal and often also a transverse component. In the sectioned material the former was directed. Consistently upward, and the latter was rather erratic either to the left or to the right. In Fig. 5 the displacement of the borders upward and probably to the left is seen. The longitudinal movement was uniform enough to determine its rate (Figs 7 and 8). It was about 0.7 mm during the formation of 1 mm of xylem, or about 1 mm per year. Sometimes the successive borders between the domains or different parts of the same border varied in the rate of movement so that the shape of the domain changed with time.

The specific result of the longitudinal movement of the domain pattern is the inclined undulations on the radial faces of the blocks of wavy xylem (Fig. 1A).

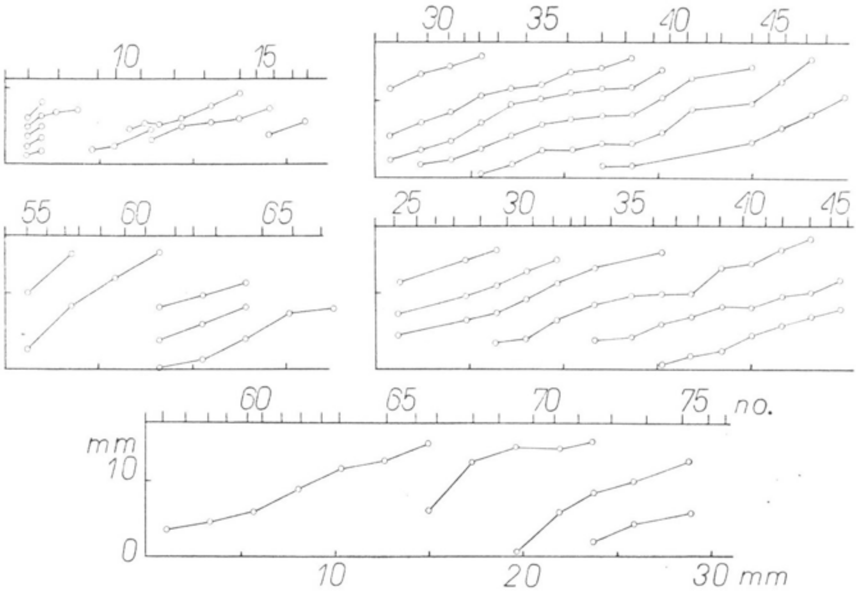

Fig. 8. Graphs showing the movement of the borders between domain in the studied samples of wavy xylem. The lower horizontal axis represents radial distance, the upper one — the annual rings numbered centrifugally starting with pith. The vertical axis represents the longitudinal distance. The successive inclined lines in the graph show the position of successive borders between the domains

In the samples which provided the sectioned material the undulations rose at about 35° from horizontal which is consistent with the rate of 0.7 mm per 1 mm of xylem produced.

The question arises whether the upward direction on the longitudinal movement observed in sectioned material is general. I tried to find an answer by examining the inclination of the undulations on the radial faces of additional samples of wavy xylem from 34 spruces. In 28 samples, each from another tree, the undulations were inclined upward centrifugally which means that the domain pattern moved upward during the production of xylem in these trees. The slope of the undulations appeared to vary from 20 to 50°. It could not be estimated accurately, for most of the samples were not big enough. In four samples the radial faces were covered with local elevations and depressions not aligned in undulations. In other single samples from four trees, the undulations were inclined downward when traced centrifugally, which means that downward movement of the domain pattern occurred there. From one of these trees two additional samples were cut from other

Table 1

Comparison of cambia producing wavy and normal xylem

	Mean frequency of cell division* no. per cell** per 1 mm of xylem	Mean rate of intrusive growth mm per cell per 1 mm of xylem	Mean length of tracheids
Active wavy cambium	1.48	0.77	0.87
Neutral wavy cambium	0.65	0.53	1.15
Normal cambium	0.45	0.40	2.49
	Mean frequency of cell division no. per 1 mm of cell length per 1 mm of xylem	**Mean rate of intrusive growth mm per 1 mm of cell length per 1 mm of xylem**	
Active wavy cambium	1.70	0.88	
Neutral wavy cambium	0.57	0.46	
Normal cambium	0.18	0.16	

* Cell division — oblique anticlinal division in fusiform initial.
** Per cell = per one fusiform initial.

patches of wavy xylem; however the inclination was upward in them. Thus at least in this one tree, the downward movement of the domain pattern was a local phenomenon.

The similarity of the domain pattern and the pattern of areas of reorientation indicates a causal relationship between the two patterns. However, the domain pattern is known to occur also in cambium which produces straight xylem, i.e. which does not show any reorientation of its cells. The domain structure occurred in the neutral areas of the wavy cambium also but the cambium did not reorient its cells, e.g. during the formation of the 2.4–4.0 mm layer shown in Fig. 7. How is the lack of the reorientation in these cases to be explained? The answer appears when the frequency of anticlinal divisions, the rate of intrusive growth, and the mean length of fusiform cells are compared in the various cambia. The data, obtained by the same method as in the previous paper (Hejnowicz 1968) are shown in Table 1. The wavy cambium differed from normal cambium in having lower mean length of fusiform initials. The active wavy cambium showed the highest frequency of anticlinal divisions and also the highest rate of intrusive growth. The difference in the frequency and rate between the cambia became more pronounced when recalculated per 1 mm of cell length. It should be mentioned that strong prevalence of one orientation of anticlinal divisions occured in the cases specified in Table 1. Thus, the explanation of the fact that cambium may be non-active in reorienting its cells in spite of the occurrence of a domain pattern seems to be a low rate the oriented events within the domains and higher mean length of fusiform initials.

DISCUSSION

The causal relation of unidirectional anticlinal divisions to the changing slope of grain was postulated by a few anatomists (see Hejnowicz 1968). Good evidence of this relation is provided by the present paper in the form of the similarity between the domain pattern and the pattern of areas differing in the direction in which the reorientation of cells proceeded. However, it should not be forgotten that the unidirectional anticlinal division represents only one factor in the mechanism of changing of cell orientation in the cambium. The other factors are: overlap of tips of fusiform cells growing in opposite directions, overlap of the tip over a ray, and splitting of rays, all of which are oriented similarly to the anticlinal divisions within the domains. Thus the above mentioned similarity between the pattern should be considered as evidence for causal relation between all unidirectionally oriented events and the changing slope of grain.

The domain pattern is a basis for the orientation of cellular processes in the cambium. Since uniform orientation is necessary for reorientation of cells to occur, the domain pattern is also a basis for this reorientation. However, the very occurrence of the domain pattern is not a sufficient requirement for the reorientation. Nothing will happen if there are but few events in the cambium. Thus in order that the reorientation can take place the occurrence of the events must be frequent enough. Comparison of the occurrence of anticlinal divisions in active wavy cambium, on the one hand, and the neutral wavy and normal cambia, on the other, is illustrative in this respect.

In the previous paper (Hejnowicz 1968) a mathematical relation between the rate of change of the slope of grain, $\Delta\alpha/\Delta R$, and the frequency, p, of unidirectional pseudotransverse divisions was established: $\Delta\alpha/\Delta R = ap^2 + bp$. This relation emphasizes the importance of the quantitative aspects of the phenomenon. Though the rate of intrusive growth, e, does not occur in the relation explicitly, it causes p to be in the second power. Namely e is related to p through the mean length of cambial cells, and thus may be expressed in terms of p. One can, however, also express p in terms of e, and then the equation would contain only e.

The movement of the domain pattern explains the occurrence of periodic reversals in the orientation of anticlinal divisions in a particular locality of the cambium. Thus of the two possible mechanisms of the reversals — gradual movement of the borders between the domains or abrupt rebuilding of the domain pattern — the former acts in the cambium producing wavy xylem. An important question is whether the movement is a general property of cambium or a specific property of the wavy cambium. There are indications that the first alternative is correct both in conifers (unpublished data of Hejnowicz) and in broadleaved trees (Hejnowicz and Krawczyszyn 1969; Hejnowicz and Romberger 1972).

It is known that intrusive growth may be faster at the apical tips of fusiform initials than at the basal tips (Bannan 1968; Brański 1970). One may ask whether the movement of a domain can be due to upward spreading of a population of cambial cells characterized by specific orientation of anticlinal divisions and other growth processes. The rate of intrusive growth listed in Table 1 for the active cambium may be resolved into apical and basal components: 0.42 and 0.35 mm per tip per 1 mm of xylem produced, respectively. Thus, the absolute mean rate of growth of the apical tip was lower than the rate of domain movement. Moreover, the cells grew also at their basal tips, so the population spread not only upward but also downward. It should be also pointed out that the whole population of cells which constituted the patch of wavy cambium spread both upward and downward. We have also direct evidence that the borders between the domains moved with respect to the fusiform initials. The question raised above cannot be answered affirmatively.

The movement of the domain pattern may be considered as a factor which prevents the excessive tilt of the cells in a particular area. This factor together with the low frequency of oriented events minimizes the effect of the domain pattern in cambium producing straight xylem. It is more efficient the higher the rate of the movement as compared with the frequency of the events in the cambium. An interesting effect of the movement of the domain pattern may be anticipated when the frequency of the processes is much higher in the domains of one type than in those of the alternative type; the movement of the domain pattern will lead then to a uniform tilt of cells throughout the cambium.

Summarizing we can enumerate the factors upon which the pattern of grain directly depends: 1. the domain pattern, 2. the frequency of the oriented events in the cambium and the pattern of frequency distribution and, 3. the rate of movement of the domain pattern. A mosaic domain pattern may thus lead to every type of pattern depending upon the two other factors indicated.

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Przesuwanie się wzoru domenowego w kambium wytwarzającym faliste drewno u Picea excelsa

Streszczenie

Kambium świerka wytwarzające faliste drewno charakteryzuje się strukturą domenową, to znaczy występują w nim obszary ,,prawe'' i ,,lewe'' pod względem ukierunkowania skośnych ścian z podziałów antyklinalnych i wzrostu intruzywnego wrzecionowatych komórek inicjalnych. Od kambium wytwarzającego normalne drewno różni się większą intensywnością ukierunkowanych procesów w domenach. Względna łatwość badania wzoru domenowego w tym kambium umożliwiła odkrycie jednostajnego przesuwania się domen postępującego ku górze z szybkością około 0.7 mm na okres tworzenia 1 mm warstwy drewna.

Falistość układu elementów drewna jest skutkiem struktury domenowej w kambium i dużej intensywności procesów komórkowych wewnątrz domen. Wyrazem przesuwania się wzoru domenowego jest skośne ustawienie linii sfalowań widocznych na powierzchni promienistego przełupu.