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The structural mechanism involved in the changes of grain in timber

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The grain in timber, i.e. the arrangement of tracheids or fibres at the surface of wood is a property of the wood layer derived from the arrangement of cambial cells. It may change with the successive growth increments. The changes of the angle of grain inclination in the successive increments reflect the changes occurring in the cambium.

There has been much speculation in the literature on the causal agents of spiral grain (see Nicholls 1965 and Bannan 1966) but they will not be reviewed here as we shall be concerned with the structural aspects of the mechanism of the change in grain rather than with the factors which initiate such a change. As regards the structural mechanism, it seems that we are on the right trail to its understanding. This way has been opened by Braun as early as 1854 by the suggestion that development of spiral grain results:

1. from anticlinal divisions of cambial initials in which the partitions are inclined in one direction instead of being transversely oriented, and 2. from elongation of cells in which the tapering ends overlap the neighbouring cells immediately above them always on the same side. However Braun did not present supporting evidence for the occurence of anticlinal divisions inclined in one direction, neither did he succeed in his search for uniformity in the relative position of overlapping tracheid tips. Hartig (1895) reported a general agreement between inclination of the cross walls separating sister cells formed in multiplicative divisions of fusiform initials, and the direction of grain change. Neef (1914) showed that "gliding" growth of cambial cells was polar in experimentally treated cambium rebuilding the arrangement of its cells. This polar "gliding" growth resulted in a change of cell inclination. An important suggestion has been made by Kohl (1933) that spiral grain depends for the most part upon oblique anticlinal divisions followed by gliding growth. According to him the oblique anticlinal walls determine the path of cell elongation and the maintenance of unidirectional divisions produces a spirality increasing with age. No spiral is apparent if the direction of divisions changes. Seifriz (1933) states that "there can be no question as to the possibility from the point of view of structural

mechanics that spiral grain in trees is due to the gliding growth of cambium cells with oblique transverse walls". He considers the oblique transverse walls and the polar gliding growth as the means by which a general protoplasmic tendency to develop the spiral habit is able to manifest itself. Newman (1955) was the next who expressed the opinion that change of grain depends upon the multiplicative division in the cambium. Random direction of inclination of the pseudotransverse walls will result in the general line of the grain, but any preponderance of one direction of inclination will lead to the appearance of inclination of grain in the predominating direction. That the direction of inclination of the anticlinal partitions tends not to be random has been shown by Bannan (1950—1966) and by Hejnowicz (1962, 1964). The partitions laid down in pseudotransverse anticlinal divisions tend to be inclined in the same direction in neighbouring cells and this is a general phenomenon found in stems producing either straight or spiral grain. A sector or domain in the cambium in which the same direction prevails may vary in size (Bannan 1964a, 1966; Hejnowicz 1964). The direction of tilt of the partitions is not maintained indefinitely in the given sector but undergoes reversals so that the domain pattern in cambium changes with time. A general agreement between the direction in which the grain becomes inclined and the direction of the pseudotransverse division in cambium was observed by Jones (1963) and by Bannan (1964a, 1966). The last author (Bannan, 1966) observed also that the orientation of the overlap achieved by elongating cell tips (direction of cell elongation) was usually the same as that of the anticlinal partitions. According to Bannan the oriented divisions and cell elongation are important factors alterating the slope of grain, he expressed the opinion, however, that the alteration of slope may be restricted to a low degree by periodic reversals in the orientation and by the extensive cambial cell loss which prevents the maintenance of the cell configurations instituted by polarity. Bannan (1966) found that in species with grain tilted in one direction, the intervals between reversals in tilt were longer for the inclination in this direction. This inequality of the intervals produces the predominance of one direction of the inclination, and consequently brings about a change in the slope of the grain.

There are two concepts in the literature which do not belong to the above reviewed theory. Priestley (1945) introduced a concept of spiral which increases its slope passively as a geometrical result of expanding of the diameter of the helix predetermined in the young cambium. This kind of change of angle probably occurs in the bast in which active growth has ceased, however, it seems that, as Newman (1955) has pointed out, Priestley's concept is not applicable to a labile system such as cambium. Preston (1949, 1964) attempted an explanation of spiral grain based on observations made on *Nitella* in which internodal cells twist as they elongate. According to him an elongation of the spiral structure present in cell walls in cambium will result in tilting the grain away from the vertical. However, this kind of twisting would require the cambium to expand longitudinally as a whole, while in fact there is local elongation at the cell tips only. This can result directly in nothing more than in twisting of the cell tips about the cell axes, provided the tips are free to twist.

Returning to the first theory reviewed which relates the change in grain slope to anticlinal divisions and so on, we can say that so far we have no more than some qualitative hints about the problem. The purpose of the present paper is to gain pertinent quantitative data and to develop the theory so as to gain an understanding of the relationship between the rates of the processes involved.

We assume that the cellular changes causing the alteration of slope in cambium are similar during the development to different types of grain tilted in tangential plane. What type of grain will develop in a particular case depends upon the size of the surface area on which the changes take place, upon the rate of changes, upon the duration of the interval during which the grain is tilted in one direction etc. For instance, spiral grain will develop if tilting in one direction is sufficently extensive in space and time.

MATERIAL AND METHODS

The anatomical changes occurring in cambium during the development of inclined grain were reconstructed on the basis of studies of wood. This was possible since we dealt with conifers in which the arrangement of cells on the tangential section of wood replicates the arrangement of cells in the cambium.

The material used were blocks of peripheral wood in which the slope of grain changed with the distance from the stem centre, from basal parts of logs about 30 cm in diameter from two trees of *Pinus silvestris* (denoted as pine A and pine B) and one specimen of *Picea excelsa*. Pine A and the spruce furnished one block each and pine B furnished two blocks denoted as B_1 and B_2. The logs and then the blocks were so selected as to provide material with rapid alteration of grain slope. The blocks were cut into tangential sections $40\,\mu$ thick and attached on slides in succession with Haupt's adhesive. The series consisted of about 200 sections each in the case of pines A and B_1, 350 from B_2 and 600 from the spruce. The section were dried, immersed in boiling alcohol to remove the air from the tracheid lumina, passed through xylene and mounted in Canada balsam. They were projected onto photographic paper by the use of a Zeiss Documator so that one photograph (negative) covered surface area of 4×10 mm on the section. The series of photographs obtained provided the material for direct studies. Each series was divided into groups of 10—50 sections depending upon the rate of changes in the xylem. On each photograph a line transverse to grain was drawn through a chosen fusiform ray. It will be referred to as the null line because its position was taken as zero and the position of the tips of the cells studied was measured in respect to it. On the photograph of the first section in the group (numbered from the centre) the tips of a cell intersected by the null line were pricked with a needle and marked with a number on the back of the photograph. The cells belonging to the same radial file were identified on the successive photographs and their tips were pricked and marked with the same number. If in the radial file an anticlinal partition appeared, the new tips were pricked beside the old tips and the sister cells obtained new numbers. The number of the section on which this was observed and the orientation of the partition were noted. The partition was called *Z* or *S* depending if it was inclined as the diagonal in *Z* or *S* (Z inclination corresponds to a spiral inclined to the right). Similar notation was used to describe the orientation of overlap achieved by two tips directed oppositely or by a tip past ray. If the traced radial file of cells ended (failing of the cambial initial which had produced the radial file) note of it was taken. After tracing the lineal series belonging to the first chosen cell the lineal series belonging to a neighbouring cell intersected by the null line was traced and so on until 50 cells were marked on the first photograph. Then a table was filled out with the following columns:

1. cell no.;

2. direction of anticlinal partition, no. of the section on which the partition first appeared, the numbers which were given to the derived cells;

3. the section on which the cell was last visible if failing of the cell occured;

4a and 4b. initial position of the upper (a) and lower (b) tip of the cell in respect to the null line measured on the first photograph or on the photograph where the cell formed in a pseudotransverse division first appeared;

5a and 5b. the same as 4 but final position, measured on the last photograph or on the photograph on which an anticlinal partition appeared;

6. cell length on first photograph, calculated from 4a and 4b;

7. cell length on last photograph, celculated from 5a and 5b;

8a and 8b. positive and negative shifts of the upper cell tip, calculated from 4a and 5a. Not filled in if the cell perished;

9a and 9b. as 8 but for the lower cell tip, calculated from 4b and 5b;

10. length of anticlinal partition, calculated from 4a and 4b;

11. length of lost cell, the same value as in 6 or if the cell was formed in anticlinal division calculated from 4a and 4b.

From the data presented in the table the following values were determined:

1. the mean rate of pseudotransverse division inclined in the same direction, p_z or p_s. It was determined according to the formula $p_z = \frac{N_{pz}}{N\Delta R}$ where N_{pz} — the number of new pseudotransverse partitions inclined in Z — direction, N — mean number of the cells traced on a section, ΔR — the thickness of xylem sectioned (in mm.). Only potentially multiplicative divisions, i.e. appearing in cells showing no sign of decline, were counted. It should be mentioned that this way of calculation of the rate of pseudotransverse division differs from that used by Bannan (1964a) and yields lower values than Bannan's method (see "Discussion");

2. the mean rate of intrusive elongation, E, which was calculated according to the formula: $E = \frac{\Delta L_e}{N\Delta R}$ where ΔL_e = the sum of positive shifts of the tips (columns 8a and 9a of the table);

3. the mean cell length, H, determined from the columns 6 and 7;

4. the ratio of cell loss, F, expressed as the percentile ratio of total length of the cells lost during the production of 1 mm of xylem to the mean total length of cells in the portion of cambium considered, $F = \frac{\Delta L_f 100}{NH\Delta R}$ where ΔL_f = the sum of lengths of the cells which were completely lost (column 11) and of the negative shifts of the cell tips (columns 8b and 9b).

RESULTS

The events in the cambium underlying the change in the slope of grain in the investigated specimens were: pseudotransverse divisions, intrusive elongation, cell loss and changes of mean cell length.

1. Slope of grain

The first section in each of the investigated series showed grain roughly parallel to the stem axis. Other sections showed grain more or less inclined. The fusiform rays rotated during the change of grain about their centres, however, the relative position of their centres remained constant. The narrow rays rotated as well keeping relative positions, however, during more abrupt changes of grain or between more distant sections they were split by intrusively growing tips of fusiform initials, or were joined together. An example of the alteration in the slope of grain

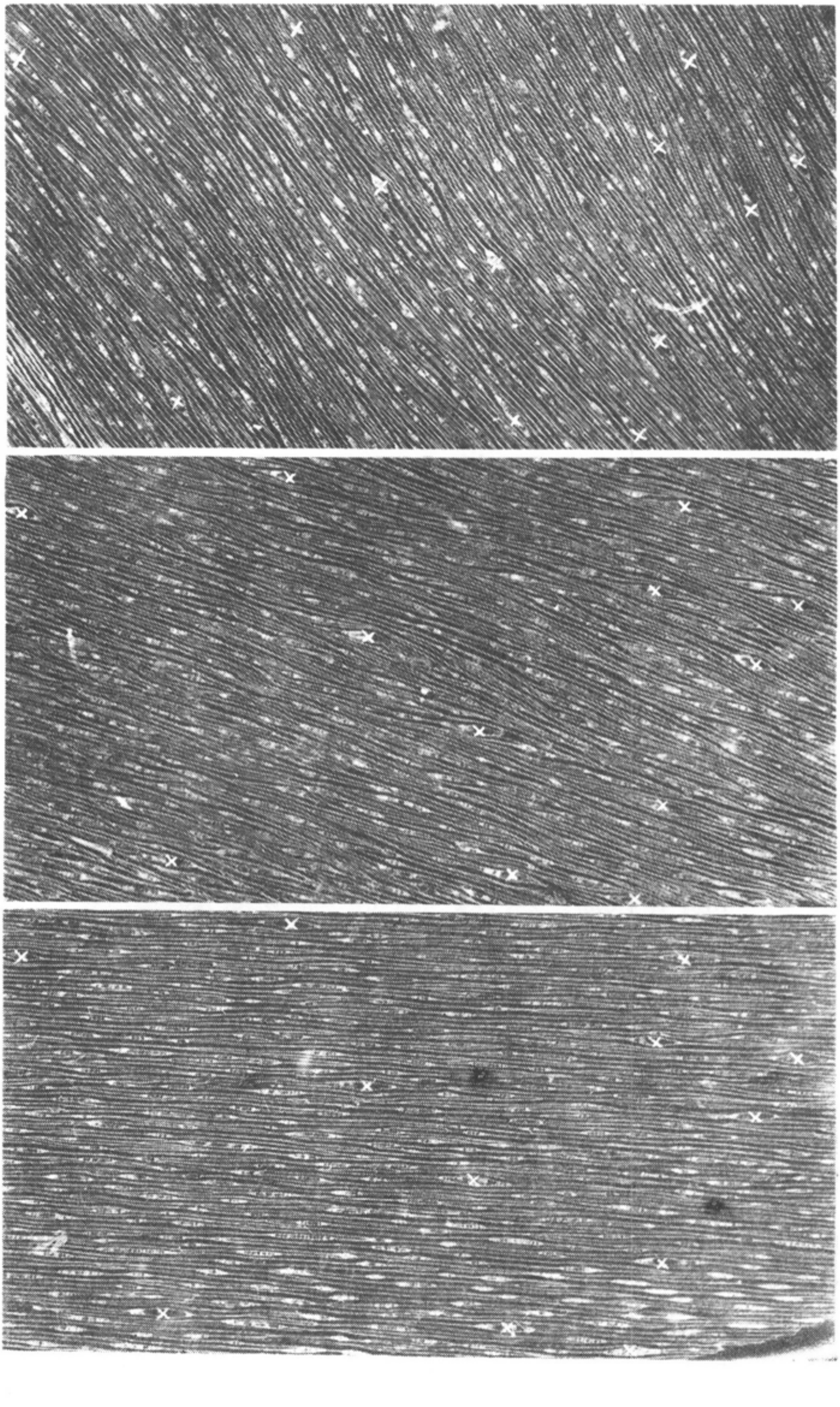

Fig. 1. Tangential sections showing a change in the slope of grain and the constancy of relative position of the centres of fusiform rays (circles)

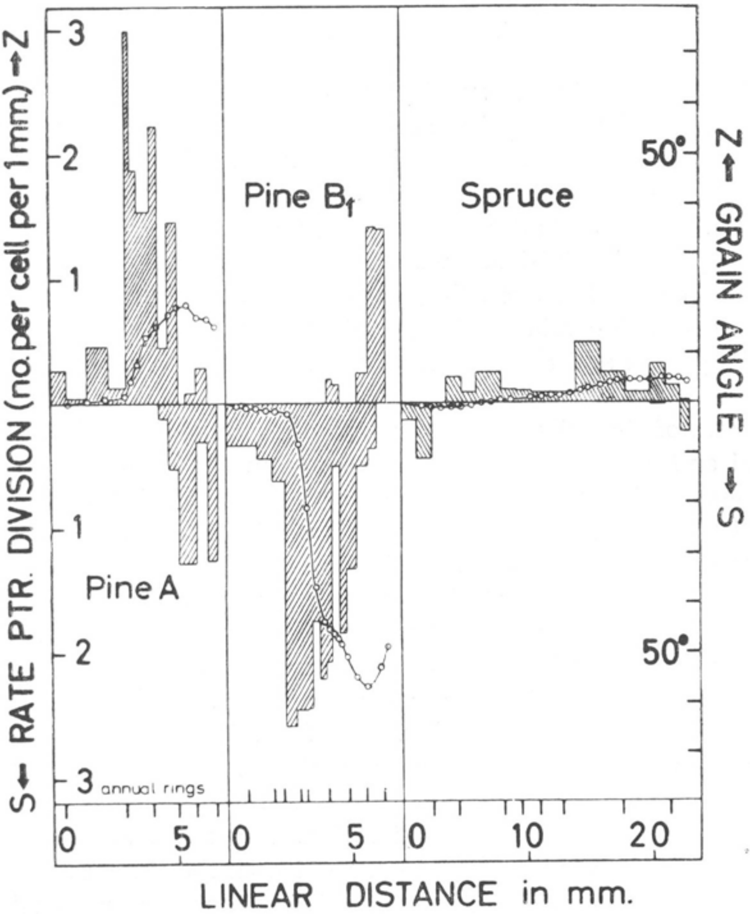

Fig. 2. Radial distribution of the rate of pseudotransverse division (bar-diagrams, Z-division above and S-division below the horizontal axis) and of the angle of grain (circles). The borders between the annual rings are shown at the bottom.

is shown in Fig. 1. The pronounced changes in tracheid arrangement and the constancy of the relative position of fusiform rays are visible.

Owing to the constancy of the relative position of the fusiform rays these rays were used as points of reference in measuring of the grain inclination. The inclination was taken as zero at the first section in each of the specimens. The radial distribution of the inclination is shown in Fig. 2. The rate of alteration in slope varied within an amazingly wide range, from zero to 25° during the production of 1 mm of xylem (see also Table 1). In spruce the slope changed initially in *S*-direction and then in *Z*-direction passing through the zero inclination. The final grain was of *Z*-type. In both the pines the reversals in slope alteration occurred when the rate of alteration was very high and inclination of grain was much advanced. The final grain was of *Z*-type in pine A and of *S*-type in pine B.

2. Anticlinal divisions

Nearly all the anticlinal divisions observed were of a pseudotransverse type, i.e. the partitions ran obliquely between two lateral walls of the mother cell. Nearly all these divisions took place in the cambial initials as evidenced by the continuation of the lineal series derived from both sister cells. The eventual pseudotransverse divisions of xylem mother cells ("temporary" divisions) were not counted for the estimation of division frequency, however, they constituted less than 0.5% of the anticlinal divisions. The relative length of the partitions was about 15% of the dividing cells and about 25% of the mean length of the cells in the section.

The fates of the cells formed by anticlinal divisions varied, some cells elongated and redivided, some were lost from the cambium although at the moment of their formation there was no indication of failure. The partitioning of apparently failing cells was disregarded.

The partitions laid down in anticlinal divisions were mostly oriented in the same direction, *Z* or *S* in a given group of sections. Simultaneous occurrence of both types of orientation was observed only in few groups of sections which derived from the parts of the specimens where the reversal in tilt of the anticlinal partition occurred. An example of oriented anticlinal divisions is shown in Fig. 3a and 3b. The orientation of pseudotransverse partitions was in accord with the direction of alteration in the slope of grain, i.e. if the divisions were of *Z*-type the grain progressed in *Z*-direction or reversed from *S*-direction. The reversals in tilt of the pseudotransverse divisions were concurrent with the changes of the direction of grain alteration. There is no doubt that there was a causal relation between the direction of pseudotransverse divisions and the direction of slope alteration.

The radial distribution of the rate of pseudotransverse division is shown in Fig. 2 and Table 1, beside the distribution of grain inclination, separately for the *Z*- and *S*-divisions. The higher rate of pseudotransverse division was concurrent with the higher rate of the alteration in slope. The alteration rate was not linearly proportional to the rate of unidirectional divisions (Fig. 4), but increased faster than the latter. Apparently the effect of unidirectional division was augmented by intrusive elongation and cell loss.

The reason of the wide fluctuations of the rate of the division could not be established. No clear seasonal periodicity in the rate was observed.

3. Intrusive elongation

An illustration of the intrusive elongation in cambium in the course of change of grain is shown in Fig. 3, the cell parts formed by intrusive

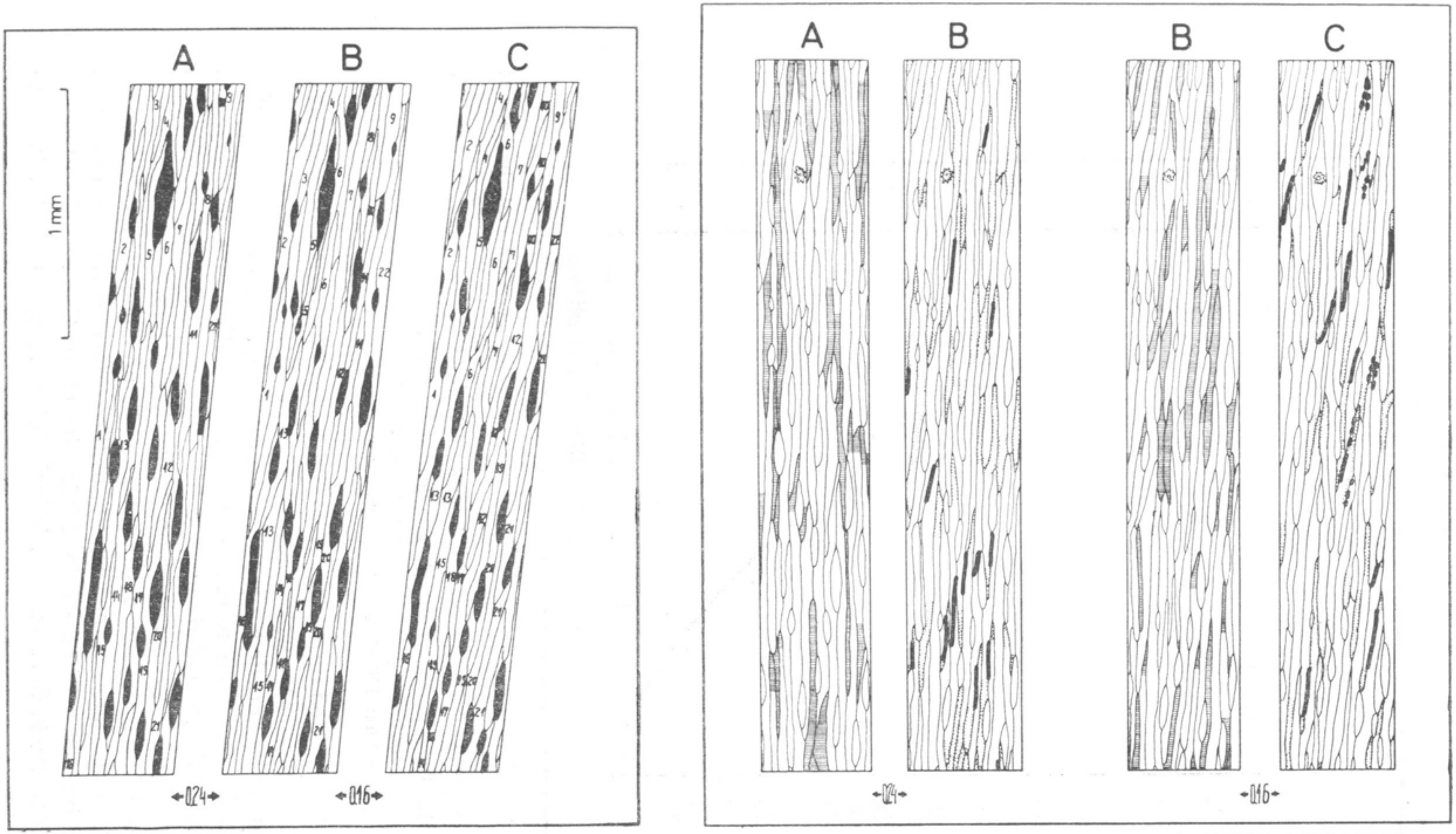

Fig. 3. *a* — The same sector of xylem on three tangential sections. The distance between the sections is given at the bottom (mm.) The rays are shown in black. Some lineal series of cells are numbered to facilitate their identification. *b* — The same section as in *a* but redrawn in pairs to specify the changes which occurred in cambium during the formation of the xylem layer between the sections. The cells which disappeared (or their parts) are striped, the cell parts which were formed by intrusive elongation are dotted, the new formed anticlinal partitions are shown by heavy segments. It the new formed partition was split by the intrusively growing tip it is shown by an interrupted heavy line

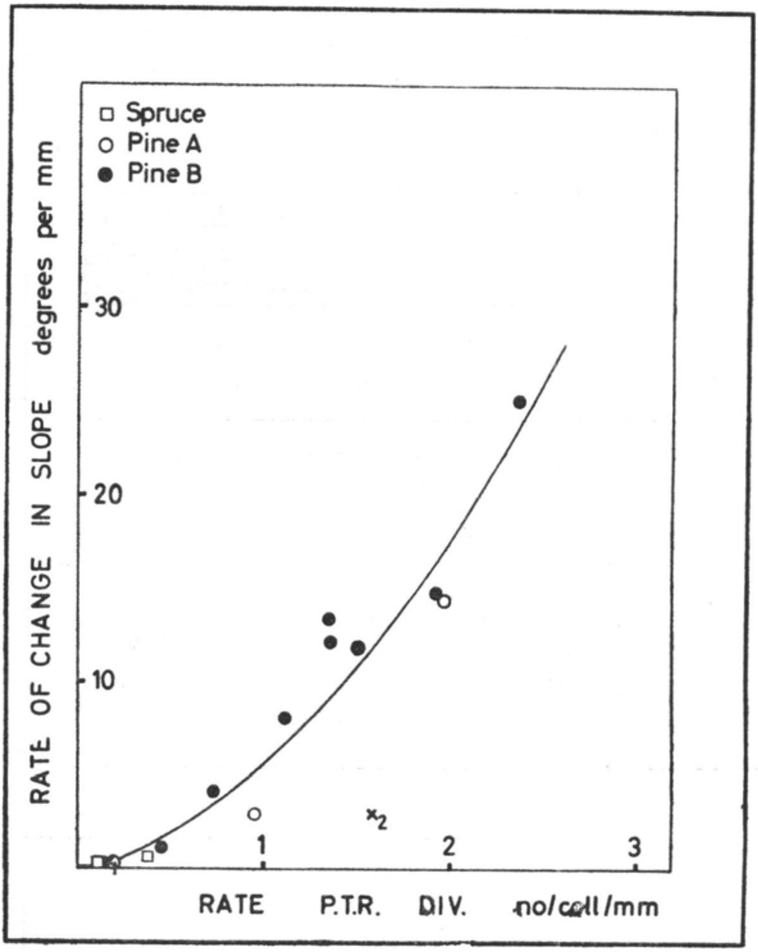

Fig. 4. Relationship between the rate of change in slope of grain and the rate of pseudotransverse division. The data has been fitted by the line $\frac{\Delta a}{\Delta R} = ap + bp^2$ by means of the least-squares method. For comparison two points (crosses) corresponding to the relationship observed by Bannan are shown, x_1 for *Pseudotsuga* (Bannan 1964a) x_2 for *Pinnus contorta* (Bannan 1964b)

elongation are dotted in Fig. 3b. We did not study the course of elongation of individual cells as we were concerned with the general state of cambium which required a knowledge of the mean rate only. The rate of elongation varied widely from cell to cell during the formation of a thin layer of wood. Some cells elongated very much while others remained unaffected. Very often the fast-growing cells occurred in clusters.

The radial distribution of the mean rate of elongation is shown in Fig. 5 which also shows other aspects of the change in cambium (see also Table 1). The increase in the rate of intrusive elongation was simultaneous with the increase in the rate of anticlinal division. Apparently the increase

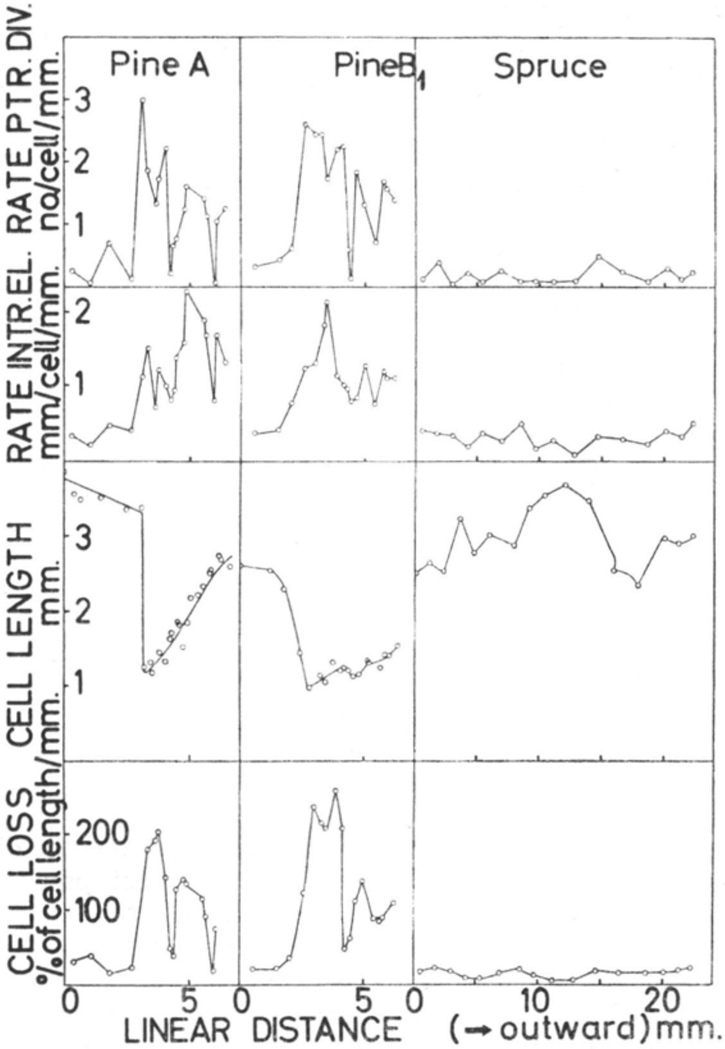

Fig. 5. Radial distribution of the rate of pseudotransverse division (both directions), the rate of intrusive elongation, the mean length of cells and the percentual ratio of total length of lost cells during the production of 1 mm of xylem against the total length of cells in the considered sector of cambium

of the rate of division brought about an increase of the mean rate of intrusive elongation. We know that the rates of intrusive elongation and of anticlinal division are interrelated through the mean length of cells (Hejnowicz 1967a): an increase of the elongation rate increases the mean cell length, an increase of the division rate decreases this length. The increase in elongation rate following the increase of division rate may be therefore considered as the means by which the tendency of cells toward a characteristic length in the cambium is able to manifest itself.

The intrusively growing cell tip overlapped the tips of neighbouring cells immediately above or below, or overlapped the rays. The orientation of the overlap was the same as that of the anticlinal divisions being in accord with the direction of grain alteration. In the case shown in Fig. 3 the orientation of overlap was of Z-type (for instance in the cases of the upper tips of cells no. 2, 12, 20, 21 and the lower tips of cells no. 2, 6, 13).

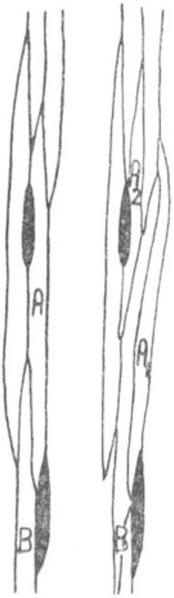

Fig. 6. Cooperation of pseudotransverse division and intrusive elongation in the change of the cell angle (see text). Cell width is exaggerated

When the tilt of anticlinal divisions was reversed so was the direction of overlap. This conformity indicates subordination of pseudotransverse division and of elongation of cell tips to a common control. Sometimes the overimposed tracheids showed noncorforming overlap initially, however, on the subsequent sections the overlap changed and remained later as a conforming one in the same lineal series. Probably the oriented overlapping is an attribute of intrusively growing fusiform initials but not necessarily of the xylem mother cells which can grow intrusively to some extent during their development. The partitions laid down in the anticlinal divisions were immediately accessible to the intrusively growing tips and in this way they could determine a diagonal path of elongation.

The rate of intrusive elongation was estimated separately for the upper and lower tips in search for an eventual polarity in elongation. No regularity in this respect was observed (Table 1).

4. Loss of fusiform initials

The loss of fusiform initials from the cambium compensated the formation of products of intrusive elongation and of anticlinal divisions, since the cambium could not increase significantly in area during the

Table 1

Data obtained from studies of the specimen B_2 of *Pinus silvestris*

Section no.	ΔR	N_1 N_2 N	H_1	H_2	E_u E_1 E	F	N_{ps}	p_s	N_{pz}	p_z	$\Delta\alpha$	D
22—33	0.44	50 59 54	3.02	2.48	0.22 0.35 0.57	45	20	0.89	0.0	0.0		
35—45	0.40	50 80 65	2.31	1.34	0.58 0.69 1.28	147	66	2.54	0.0	0.0	26.5°	14.7
51—79	1.12	50 27 38	0.96	1.34	0.50 0.50 1.00	115	67	1.57	0.0	0.0		
80—94	0.56	50 51 50	1.31	1.21	0.45 0.45 0.90	73	34	1.21	0.0	0.0	11.5	8.2
93—114	0.84	50 48 49	1.32	1.28	0.34 0.34 0.68	91	42	1.02	0.0	0.0		
118—129	0.44	49 47 48	1.31	1.21	0.50 0.80 1.30	178	34	1.61	0.0	0.0	16.0	13.3
130—144	0.56	50 45 47	1.31	1.24	0.44 0.62 1.06	154	30	1.14	0.0	0.0		
171—205	1.36	100 93 96	1.53	1.45	0.34 0.43 0.78	93	104	0.80	36	0.28		
206—240	1.36	50 36 43	1.30	1.32	0.27 0.26 0.53	97	4	0.07	50	0.86		
248—263	1.00	50 36 43	1.45	1.64	0.08 0.18 0.27	23	0	0.0	0.0	0.0		
264—283	0.76	50 44 47	1.65	1.67	0.60 0.47 1.08	110	0	0.0	23	0.64	19.0	4.2
285—328	1.72	100 95 97	1.67	1.58	0.26 0.35 0.61	69	0	0.0	124	0.74		
329—353	0.96	100 77 88	1.60	1.86	0.40 0.36 0.76	80	0	0.0	62	0.73		

Legend:

ΔR – thickness of xylem sectioned;

N_1, N_2, N – mean initial, mean final and general mean length of cells;

E, E_u, E_1 – mean rate of intrusive elongation of whole cell, of upper tip and lower tip, respectively, during the production of 1 mm of xylem, mm.;

F – total length of lost cells during the production of 1 mm of xylem expressed as percentage of total length of investigated cells on a section;

N_{ps}, N_{pz} – number of observed partitions of S- and Z-type respectively;

p_s, p_z – mean rate of divisions oriented in one direction; number of divisions during the formation of 1 mm of xylem per 1 cell;

$\Delta\alpha$ – change in slope of grain in degrees;

$D = \frac{\Delta\alpha}{\Delta R}$ – rate of change in slope of grain, degrees per 1 mm of xylem.

formation of a xylem layer a few millimeters thick in a log about 300 mm in diameter. It was thus natural that the increase of elongation and division rates brought about an increase of the intensity of cell loss. An illustration of the occurrence of cell loss is presented in Fig. 3. Usually the failure of fusiform initial started with a shortening of the initial from one or from both ends. However, the cells which became shorter did not always continue this process till complete disappearance but some of them recovered. It was observed that in the instances of fast progressing change in the slope of grain the failing cells occurred in groups while other groups of cells were dividing and elongating. It appears that, owing to this concentration of failing cells, the groups of surviving ones can be very effective in changing the arrangement of their constituent cells by oriented divisions and elongation. The intensity of cambial cell wastage may be characterized in different ways. One way is to express the total length of lost cells in the given sector of cambium during the formation of 1 mm of xylem as the percentual ratio of the total length of the cells in the given sector. The radial distribution of cell wastage expressed in this way is shown in Fig. 5, lower row. As seen, the total length of cells lost during the production of 1 mm of xylem was about 200% of the total length of the cells in the given sector of cambium during the fastest changes in the cambium. This made possible a considerable rebuilding of this tissue. No wonder that the grain could then change by about 20°.

5. Cell length

The mean length of cells diminished abruptly at the beginning of the rapid changes in the cambium and thereafter increased gradually (Fig. 5, Table 1). Apparently this decrease was a result of a drastic increase in the rate of anticlinal divisions. The successive increase of intrusive elongation opposed this effect so that the relative decrease of the mean length was much lower than the relative increase of the division rate. A lower mean length of the cells means higher density of cell tips which can grow intrusively, it means also higher density of cells which can divide anticlinally in oriented manner. In this way the diminution in mean cell length doubtlessly facilitated the alteration in the slope of grain.

DISCUSSION

Let us consider first how do the pseudotransverse divisions and the intrusive elongation bring about the change of grain angle. Each pseudotransverse division causes a tilt of the axis in two sister cells. The resulting change of the grain angle during the production of ΔR of xylem will be proportional to the difference between the rates of the Z- and S-divisions, i.e.

$$\Delta a_p = K_1 (p_z - p_s) \Delta R$$

(Z-direction is assumed as positive), where K_1 = proportionality factor which depends on the magnitude of the tilt caused by one pseudotransverse division and on the ratio of loss of new formed cells to the frequency of anticlinal division.

The intrusive elongation causes inevitably overlapping of the tips oppositely directed. The overlap may be of Z- or S-type, it may be achieved by two old tips or by an old tip and a new one formed in pseudotransverse division. In the case of the overlap concerning old tips the elongation will contribute to the change of grain angle if the probabilities of Z- and S-overlaps are unequal, i.e. if $k_z \neq k_s$ ($k_z + k_s = 1$). This contribution will be proportional to the rate of intrusive elongation, i.e.

$$\Delta a_e = K_2 E (k_z - k_s) \Delta R \tag{2}$$

where K_2 = proportionality factor.

In the case of the overlaps concerning new formed tips the elongation will contribute to the grain angle even if the probabilities of Z- and S--overlaps are equal unless the direction of pseudotransverse divisions is random. The elongation will be then favored in the predominating direction. In this case we have to do with a cooperative effect of pseudotransverse divisions and intrusive elongation on the grain angle. Since it depends on the presence of the pseudotransverse partitions and the occurrence of intrusive elongation it will be proportional to the rate of intrusive elongation and to the difference between the rates of Z- and S-divisions, i.e.

$$\Delta a_{p,e} = K_3 E (p_z - p_s) \Delta R \tag{3}$$

How does the intrusive elongation amplify the pseudotransverse divisions in their effect on grain angle is illustrated in Fig. 6. If there was no oblique partition in cell A the upper tip of B would grow to the left side of A. The partition of Z-type in A offers a possibility for the tip to pass on the right side of A. If cell B grows along the partition its axis will be tilted from the initial direction. Simultaneously, cell A_1 will grow on the left side of B which means that this cell will be also tilted in the same direction. Similarly, cell A_2 may be deflected when it grows upwards.

The total effect of the anticlinal divisions and intrusive elongation on the grain angle is a sum:

$$\Delta a = \Delta a_p + \Delta a_e + \Delta a_{p,e} \tag{4}$$

Introducing 1, 2, 3 into 4 we obtain:

$$\frac{\Delta a}{\Delta R} = K_1 (p_z - p_s) + K_2 E (k_z - k_s) + K_3 E (p_z - p_s) \tag{4a}$$

This formula gives the rate of change in the slope of grain as a function of p_z, p_s and E. However, these variables are not independent (Hejnowicz 1967a). The mean rate of intrusive elongation E is related to the mean rate of pseudotransverse division, $p=p_z+p_s$, by the mean cell length. In the first approximation we can assume that the mean length is proportional to E and inversely proportional to p, i.e. $H=C\frac{E}{p}$ where C — proportionality factor. Introducing E from this relation into 4a we obtain after rearrangement:

$$\frac{\Delta a}{\Delta R}=K_1(p_z-p_s)+K_{20}(p_z+p_s)(k_z-k_s)+K_{30}(p_z^2-p_s^2) \tag{4b}$$

where $K_{20}=\frac{K_2 H}{C}$, $K_{30}=\frac{K_3 H}{C}$

If the pseudotransverse divisions are inclined in only one direction let us say in Z-direction and the overlap runs only in this direction, i.e. when $p_s=0$, $k_s=0$, $k_z=1$, we have,

$$\frac{\Delta a}{\Delta R}=K_{10}\,p_z+K_{30}\,p_z^2 \tag{4c}$$

where $K_{10}=K_1+K_{20}$.

We see that the rate of unidirectional pseudotransverse divisions enters the equation for the rate of slope alteration in the second power. This is consistent with the shape of the empirical curve describing the relationship between the rates in Fig. 4. We can consider this agreement as a reason to expect that the nonlinearity in the relationship between the rate of alteration in slope and the rate of unidirectional pseudotransverse division observed in pine is generally valid.

The numerical values of the coefficients in equation 4c may be estimated from the parabola in Fig. 4. For this purpose a parabola determined by the least-squares method was fitted to the empirical points in Fig. 4. Its equation is, $\frac{\Delta a}{\Delta R}=3.3\,p^2+2.2\,p$. It follows that $K_{10}=2.2$ and $K_{30}=3.3$.

Bannan (1964a, 1964b) studied fragmentarily the relation between the rate of unidirectional pseudotransverse division and the rate of change in the slope of grain. He reported a 10° increase in the slope associated with a succession of 7.7 pseudotransverse divisions in the production of 3.4 mm of xylem in lodgepole pine and a rate of change in slope 2.5° per 1 cm accompanied by a mean rate of pseudotransverse divisions of 2.3 per 1 cm in *Pseudotsuga*. Do these data fit our parabola in Fig. 4? First, it should be remarked that Bannan calculated the rate on the basis of succession of the divisions in cambial cells (Bannan 1964a), while our definition of the rate is: the number of pseudotransverse divisions in the cambium sector considered during the production of ΔR of xylem per mean number of cells in this sector per thickness ΔR. To compare these two methods we used them parallelly on the same material (specimen B_2). In general our method gave a rate of about 70% of the rate obtained by Bannan's method.

There is an illustration of the basis for the calculation of the division rate in the form of diagrams for a group of radial files of cells in one of Bannan's papers (1964a, p. 611). One may prove that his method gives the rate of 2.8 in this case, while our method only 2.2 per 1 cm.

To compare Bannan's data for *Pinus* and *Pseudotsuga* with ours we corrected his data by decreasing the division rate by 30% and plotted them in Fig. 4 along with ours. It is seen that the relation between the division rate and the rate of change in slope observed by Bannan in *Pinus contorta* differs much from that observed by us in *Pinus silvestris*. Maybe this is due to some interspecific difference in the effect of cell loss on the change in grain. Whether the parabolic relation between the division rate and the rate of change in slope holds for the lodgepole pine remains to be determined.

In the previous paper (Hejnowicz 1967b) which presented preliminary results from studies on spiral grain development it was mentioned erroneously that our studies had showed no preference of the overlap for any side. This erroneous conclusion was drawn from the observations made on sections from the middle part of the specimen A where grain was clearly inclined (region 4—5 mm in Fig. 2), but where the direction of pseudotransverse division changed what was not known at the time. Further extensive studies showed that the direction of overlap was of one type, wherever the pseudotransverse divisions were unidirectional. Bannan's paper on spiral grain (1966) in which the oriented overlap was discovered was not available at the time when the previous paper was prepared.

According to our theory the effectiveness of intrusive elongation in changing of grain slope is augmented by oriented overlap, however, it will not be zero even if the direction of overlap is random, unless the orientation of pseudotransverse division is random.

An important factor modifying the rate of change in grain seems to be the loss of cambial cells. Bannan (1966) suggested that extensive cambial cell loss is acting against the effect of the oriented divisions and elongation. It became apparent, however, that in the specimens studied here the cambial cell wastage did not offset the effect of oriented divisions and elongation. Probably it was so because the failing cells were not randomly dispersed in cambium but occurred in groups.

SUMMARY

The anatomical events in the cambium of pine and spruce related to the development of inclined grain were studied by an analysis of the xylem. The rate of alteration in slope of grain in the investigated specimens varied within the range

0—25° during the production of 1 mm of xylem. The orientation of pseudotransverse divisions was in accord with the direction of the alteration in slope. The reversals in tilt of the divisions were concurrent with the changes of the direction in which the slope was altered. The increase in the rate of pseudotransverse division was accompanied by an increase in the rate of intrusive elongation and in the intensity of cell loss. The orientation of overlap achieved by intrusively elongation tips was the same as the orientation of anticlinal division. The failing cells occurred in groups. The possible relations between the rates of the change in slope, pseudotransverse division and intrusive elongation are formulated mathematically. It is shown that the rate of change in slope is related to the square of the rate of unidirectional divisions. This is consistent with the shape of the empirical curve describing the relation between the rates.

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Strukturalny mechanizm powstawania skośnie włóknistego drewna

Streszczenie

W niniejszej pracy zajmowano się anatomicznymi procesami zachodzącymi w kambium w czasie powstawania w nim skośnego układu komórek inicjalnych. Procesy te odtwarzano na podstawie badań drewna. Szybkości zmian w nachylaniu komórek w badanym materiale zawarte były w szerokich granicach, od 0 do 25° na 1 mm odkładanego drewna. U podstaw zmian kąta nachylenia komórek stały następujące procesy: skośne podziały antyklinalne nachylone w jednym kierunku, zorientowany wzrost intruzywny i eliminowanie niektórych komórek inicjalnych z kambium. Podziały antyklinalne nachylone były zgodnie z kierunkiem zmiany kąta. Wzrostowi częstotliwości podziałów towarzyszył wzrost szybkości wydłużania intruzywnego komórek oraz wzrost natężenia procesu eliminowania komórek z kambium. Kierunek zachodzenia na siebie rosnących intruzywnie końców komórkowych był taki sam, jak kierunek podziałów antyklinalnych. Eliminowane komórki występowały w grupach. Możliwe zależności między szybkością zmiany kąta a częstotliwością podziałów i szybkością wydłużania sformułowano matematycznie. Okazało się, że ze względu na współzależności, jakie istnieją między częstotliwością podziałów a szybkością wydłużania (poprzez przeciętną długość komórek), częstotliwość podziałów w równaniu na szybkość zmiany kąta występuje zarówno w pierwszej, jak i w drugiej potędze. Tego samego typu zależność między szybkością zmiany kąta a częstotliwością podziałów stwierdzono w badanym materiale.