The relationship between the arrangement of rays in secondary phloem and grain inclination in the wood of *Pinus silvestris* L. and *Picea abies* Karst.

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Abstract

The arrangement of rays in cross sections of secondary phloem and the wood grain on the tangential and radial surfaces of wood columns from *Pinus silvestris* and *Picea abies* was studied. It was found that in most cases the rays were slanted and deviated from the geometric radius in either the S-direction (to the left) or in the Z-direction (to the right) when the cross section of the stem was observed from above. The S-type deviation dominated in those stems in which the wood grain in the peripheral parts was of the S-type (left-oriented), whereas the deviation of rays in the Z-direction was found to dominate in those objects, in which the wood grain in the peripheral parts of the stem was of the Z-type (right-oriented).

Key words: secondary phloem, arrangement of rays, spiral grain

INTRODUCTION

Cross sections of conifer stems show the cambium, xylem and conducting phloem cells arranged in regular, radial series. This regular arrangement is usually disturbed in the non-conducting phloem with the phloem rays and radial rows of cells of the axial system deviating from the geometric radius either to the right or to the left. The rays in these layers often have an almost tangential arrangement. Hejnowicz (1973a) observed cases of uniformly slanted arrangements of rays on the periphery of phloem in *Pinaceae*. Similar tendencies to form arrangements of uniformly slanted rays were observed by this author in broadleaved trees, eg. in *Aesculus* (Pyszyński 1980). We found

that rays slanting in the Z-direction dominated in this tree, that is, they slanted to the right in respect to the geometric radius when the transsected stem was seen from above.

It should be noted that although the general structure of the bark of trees from the *Pinaceae* family is rather well known, still not enough attention is being paid to studying the mechanisms involved in the formation of the details of this structure.

The cell arrangement in non-conducting phloem is undoubtedly affected by such factors as the decreasing thickness of the phloem layer resulting from the dying of conducting elements and the effect of radial and tangential pressure from the tissues being added by the cambium, the tangential expansion during growth of the periphery, the dilatation growth of rays and parenchyma cells of the longitudinal system, as well as sclerification (see Holdheide 1951, Whitmore 1962a, 1962b, 1963, Srivastava 1963, Esau 1964, 1969, Hejnowicz 1973b, Lotova 1987). The effect of these factors does not, however, explain the mechanism responsible for forming a uniformly slanting arrangement of rays on the entire periphery or even of one showing only a tendency towards arrangement in one direction.

Hejnowicz (1973a) presented a supposition that the slanted arrangement of rays may result from torsion of the wood column in relation to the shield formed by the external hard tissues and from the pulling of the phloem rays along with it (see Fig. 1). Uniformly slanted arrangements of rays would be, in turn, associated with the unsymmetrical reversal of the wood column caused by the unidirectional, helical arrangement of fibrils in the main S2 layer of the cell wall of elements of the longitudinal system (Hejnowicz 1973a, b).

Fig. 1. A diagram of a cross section through a stem, illustrating the torsional inclination of rays in the secondary phloem. A -- wood column, B -- layer of soft tissues, C -- the external shield of sclerified tissues

These suppositions have been confirmed in the case of *Aesculus* (Pyszyński 1977, 1980). In *Aesculus* the fibrils arrangement in the S2 layer of secondary cell walls is always of the Z-type (Pyszyński 1977) and the wood grain is also always of the Z-type (Schmucker 1924, Hejnowicz and Krawczy-szyn 1969, Krzysik 1974, Pyszyński 1977). It has also been found that

young *Aesculus* stems show asymmetric properties in response to torsion. After the stems had been twisted to the right, the residual torsions were greater than after twisting them to the left (Pyszyński 1977).

Helical symmetry on cellular and tissue level commonly occurs in conifers. This is represented on the cellular level by the helical arrangement of fibrils in the cell wall and most of the cases described in literature have the Z-direction of the fibrillar helix in the S2 layer of the cell wall (Sanio 1863, Schmucker 1924, Pyszyński and Hejnowicz 1972). Helical symmetry on the tissue level is expressed as spiral grain. The grain pattern may be uniformly slanted or it may, after reaching a maximum in one direction, return through a straight pattern and begin to slant in the opposite direction (Loverly 1966).

Due to changes in the direction of the grain during ontogenesis, the grain direction in peripheral growth rings can differ on various levels of the same stem (Noskowiak 1963). The questions arise: 1) what is the direction of the phloem rays at different heights of a tree, and 2) is there a correlation between the direction in which the rays deviate and the helical structure of the wood grain.

MATERIAL AND METHODS

The study was conducted on 7 pine trees and 4 spruces. Transverse discs were taken at breast height and higher. The samples were taken in such a manner that the second disc was about mid-way between the tree crown and base, the next one from the crown. Table 1 presents detailed characteristics of the samples.

The material used for studying phloem was prepared as follows: the surface of the phloem and bark was wet and smoothed with a razor blade. If necessary, the surface of the phloem was treated with phloroglucinol + HCl in order to increase the contrast between the rays and neighboring areas. The surface was photographed and the rays in the phloem were analysed on the positive.

For detailed analysis of the direction of the rays, the phloem was divided into sectors in the tangential direction, with each corresponding to 0.5 cm of the circumference, and into zones in the radial direction. In *Pinus*, the secondary phloem is thin (on average 1 mm), and was therefore divided into two zones: A — which included a phloem layer 0.25 mm from the cambium and B — which included the rest of the layer which reached all the way to the last peridermis layer. In *Picea*, the phloem is thicker (2-3 mm) and was therefore divided into three zones: A — which included the phloem layer 0.25 mm from the cambium, B — the phloem layer up to 1.5 mm from zone A and zone C — which included even further layers reaching the last peridermis layer.

After determining the orientation of phloem rays, the bark was removed and the angles of inclination of the wood grain on the tangential surface of each

Table 1
Characteristic of examined trees

Species	Provenance of tree	Tree number	Tree height (m)	Disc	Level at which disc was taken (m)	Number of annual rings on disc	Circumference of phloem (m)	Thickness of bark (cm)	Type of wood grain on surface of wood column
<i>Pinus silbestris</i> L.	Vicinity of Szprotawa	1	17.0	a	1.3	31	0.40	0.6	S
				b	6.0	22	0.35	0.35	S O
				c	12.5	14	0.28	0.3	S O
		2	21.0	a	1.3	51	0.47	0.9	S O Z
				b	12.5	42	0.38	0.5	S O Z
	Vicinity of Żagań	3	20.0	a	1.3	53	0.51	1.0	S O Z
				b	6.0	28	0.34	0.4	S O
				c	12.5	14	0.24	0.2	S O Z
		4	24.0	a	1.3	78	0.79	1.0	S O Z
				b	7.0	69	0.63	0.6	S
				c	16.5	34	0.38	0.5	S
				d	21.0	22	0.27	0.3	S
	Vicinity of Żagań	5	14.0	a	1.3	127	0.76	1.4	S O Z
				b	5.0	117	0.71	0.5	S O Z
				c	8.0	96	0.68	0.4	S O Z
<i>Picea abies</i> Karst.	Vicinity of Szprotawa	8	17.7	a	1.3	26	0.46	0.6	S O
				b	4.6	23	0.43	0.7	S O Z
				c	10.7	12	0.29	0.3	S O
	Vicinity of Szprotawa	9	17.0	a	1.3	34	0.43	0.7	S O Z
				b	4.1	28	0.40	0.6	S O Z
				c	10.2	17	0.29	0.3	S O
	Vicinity of Żagań	10	23.0	a	1.3	38	0.66	0.7	S
				b	7.0	27	0.54	0.6	S
				c	14.0	16	0.37	0.4	S
		11	24.0	a	1.3	110	1.01	0.7	S O Z
				b	12.0	77	0.70	0.6	S O Z
				c	19.0	37	0.36	0.4	S O Z

disc were measured. The surface of the wood was divided into sectors which exactly matched the phloem sectors. The measurement was made using a horizontal microscope equipped with a goniometric eyepiece. Only the rays

Fig. 2. Photographs of the smooth transverse surface of phloem, cambium and external layers of wood show the direction of the arrangement of rays in the phloem: A and B — *Pinus silvestris* L., C, D and E — *Picea abies* Karst. In A — the direction of the rays is S; in B — Z in zone A and ZS (zigzag) in zone B; in C — the ray direction is S in all of the zones; in D — Z in all but zone C; in E — T in all zones

running through the middle of the sector were taken into account. Next, the discs were split radially along two mutually perpendicular planes intersecting the core. The radial pattern of the wood grain was determined on the basis of the position of the outline of the lower edge of the split in respect to the projection of the upper edge.

The direction of the slanting of the fibrils in the S2 layer of secondary cell walls of the tracheids was determined on the basis of the orientation of the pit apertures in macerated material (Pyszyński 1977). The samples used for maceration were taken from the external wood rings.

RESULTS

Our preliminary results showed that the overall direction of a ray in a given sector can be: 1) uniformly slanted – Z-type or S-type; 2) ZS-type (zigzag) which changes its direction several times in respect to the geometric radius; 3) T-type in which the phloem rays coincide with the geometric radius (Fig. 2).

Fig. 3. Diagrams illustrating the distribution of areas with orientations of rays in the secondary phloem, outlines of the radial splits of wood columns going through the pith and the direction and size of the angle of inclination of wood grain on the surface of this column. Diagrams on the left: A, B and C represent discs from tree no. 1 – *Pinus silvestris*. Diagrams on the right: D, E and F represent discs from tree no. 10 – *Picea abies*. Areas where S rays occurred are marked in black, Z-rays are dotted, white marks T and ZS (zigzag) rays. The Arabic numerals on the edges of the

Fig 4. A diagram of the disc from an approx. 110-year old *Picea abies* tree taken at breast level, in which rays deviating in the Z direction dominate. Legend as in Fig. 3

The distribution of the areas having different ray orientations on the phloem periphery is varied. In most of the discs, areas in which the rays deviated in the S-direction dominated, as shown in the diagrams on Figs. 3A, D, E, F. There also were discs in which rays slanting predominately in the Z-direction were found, as shown in Fig. 4, as well as those in which neither direction was seen to prevail (Fig. 5A).

In addition, it was also possible to observe that in those discs in which the wood core had a wavy contour with distinct ridges and depressions, the rays on both sides of the maximum were arranged in opposite directions (Fig. 5B).

In order to gain information on what general direction the rays tended to take in the particular zones and on what the general direction in the entire periphery was, the percentage of sectors having different orientations of phloem rays in each zone of each disc was determined and presented in graphical form on histograms (Figs. 6 and 7). For *Pinus* these data are as follows: In zone A, 9 discs were found in which S-type sectors predominated over Z-type (discs: 1a, 1b, 1c, 2b, 3b, 3c, 4a, 4b and 4d) in 9 discs, Z-type sectors dominated in this zone (discs: 2a, 3a, 4c, 5a, 5b, 5c, 6a, 6b and 7). In zone B of 9 discs there were more S-type sectors than Z-type (discs: 1c, 2a, 2b, 3c, 4a, 4b, 4c, 4d and 5a) and in 8 discs, Z-type sectors were more numerous than S-type (discs: 1a, 1b, 3a, 3b,

wood column indicate the absolute value of the angle of inclination of the wood grain at that given spot of the column, while the lines perpendicular to the circumference demark the regions of the respective angle. The letters Z — mark the areas with Z-type wood grain on the surface of the column. The letters S — areas with S-grain, while O denotes straight grain. The Roman numerals denote the successive quarters of the split. The height (h) at which the disc was cut is given in the lower right hand corner of each diagram. The scale applies only to the wood. Magnification was used for the phloem (for *Pinus* approx. 10×, for *Picea* approx. 15×)

Fig. 5. A — A diagram of the disc from an approx. 140-year-old *Pinus silvestris* tree taken at breast level, in which no distinct domination of areas of any one orientation of rays is visible. B — A diagram of a disc from a 129-year-old *Pinus silvestris* tree with a wavy wood column contour.

Legend as in Fig. 3

5b, 5c, 6a and 7). In disc 6b the number of S-sectors was equal to the number of Z-sectors. In *Picea*, S-sectors dominated in three zones of the following discs: 8a, 8b, 8c, 9a, 9b, 9c, 10a, 10c and 11c, while Z-type sectors were prevalent in three zones of disc 11a.

In general, it can be noticed that a very distinct dominance of S-type sectors is found in discs from the highest levels, both in pine and in spruce in all zones. It can also be seen that in older trees, especially in tree A, at breast level, the differences between the size of areas with opposite orientations of rays are only slight and cases of Z-type dominance in sectors are noted.

CHARACTERISTICS OF WOOD GRAIN

The grain pattern on the surface of the column

Examination of the direction and size of the angle of inclination of wood grain on the surface of cores have shown that on 7 discs on the entire circumference, the direction of the grain was S-type (see Table 1 and Figs. 1C,

Fig. 6. Histograms representing the percentage of areas with various ray orientations in the phloem of the individual zones of a given disc and the average angle of inclination on the surface of the wood column of the individual disc of *Pinus silvestris*. The capital letters denote the particular zones, the small letters under the line indicate the disc number, the numbers above denote the tree number. The dotted bars represent the areas having Z rays, black bars — S rays, white bars ZS or T rays. The diagonal rays with numbers drawn next to the bars in zone A indicate the direction and size of the mean angle of inclination of the grain in the individual discs. The lines slanting to the left with a minus sign (—) denote the S-direction, whereas those slanted to the right with a plus (+) denote the Z direction

D, E and F). In 7 discs the wood grain was of the S-type and straight (Figs. 1A, B, Fig 4 and Figs. 5A and 5B), in 16 discs, three types of grain occurred — Z-type, S-type and straight (Figs. 4, 5A and 5B). As can be seen, in none of the studied trees, even in over century-old ones, did a uniform, Z-type spiral grain ever occur.

The mean angle of inclination of the wood grain in the entire periphery in each of the discs was calculated based on the data from the individual sectors (Figs. 6 and 7). A decided majority (22 discs) had an S-type mean angle of inclination of the wood grain, with only 8 Z-type discs (obtained mainly at breast level).

Fig. 7. The histograms present the percentage of areas with various orientation of rays in the phloem and average inclination of the wood grain on the surface of the wood column of discs from *Picea abies*. Detailed legend as in Fig. 6

Changes in the type of wood grain along the radius

These changes were determined on the basis of radial splits, and they were found to be as follows: In all of the discs from both species of trees, S-type spirals were formed with the angle of grain inclination increasing for a period of over ten years. After reaching the S-type maximum, the angle in this direction usually decreased. In most of the discs, the S-type grain was maintained until the last annual ring. Locally, in some of the discs, this angle first decreased within a certain segment, then increased again, eg. in the disc on Fig. 3A (between quarters II and IV) and on Fig. 4 (between the II and IV quarters). Changes in the direction of the grain to Z-type on large sized samples occurred usually in the oldest discs (mainly from breast height) eg. on the discs on Figs. 4 and 5A.

A comparison of the arrangements of phloem rays with the direction of the wood grain

On comparing the data on the general tendency of arrangement of phloem rays on the cross section of the entire stem periphery with the general tendency of the orientation of the wood grain on the surface of the column, that is, the

mean value of the angle of inclination of the wood grain on the surface (Figs. 6 and 7), it is possible to notice that, most noticeably in zone A, most of the rays deviate in accord with the direction of inclination of the mean angle of the wood grain on the surface of the column. In pine, in a total of 18 discs, 15 of them demonstrated such an agreement, in spruce 11 out of the 12 discs. S-type correspondence, that is, with a predominance of S-type sectors of phloem rays with the S-type mean grain inclination angle occurred in 9 discs from pine in zone A (1a, 1b, 1c, 2b, 3b, 4a, 4b and 4d), while in zone B, in 8 discs (1c, 2a, 2b, 3c, 4a, 4b, 4c and 4d). In the spruce, S-type correspondence occurred in all of the discs from trees no. 8, 9 and 10 over the entire thickness of the phloem, in tree no. 11 in the disc from the highest level, 11c, in zones A and B. Z-type correspondence occurred in the pine in zone A in 6 discs (5b, 5c, 6a and 7). In the spruce, Z-type correspondence occurred in the three zones of disc 11a.

Lack of correspondence in the dominant direction of phloem rays and the direction of the mean angle of grain inclination, expressed as a predominance of Z-type ray direction along with a S-type mean angle of inclination in the pine occurred in zone A in three discs (2a, 3a and 4c), in zone B in 4 discs (1a, 1b, 3a and 3b). In the spruce such a lack of correspondence occurred only in zone C of disc 11c.

Lack of correspondence in which most of the rays were in the S-direction while the mean angle of inclination of the wood grain was Z-type occurred in two discs, in the pine in zone B of disc 5a, in the spruce in the three zones of disc 11b.

The orientation of fibrils in the S2 layer of the secondary cell wall

Analysis of the flattened pit apertures shows that their direction of slanting in the tracheids was always type Z, that is to the right in respect to the cell axis when the cell is looked at from its external surface. This is the same direction that the cracks in layer S2 of the secondary cell wall were also slanted. Because the direction of the flattening of the pit apertures and the cracks in layer S2 are in agreement with the arrangement of the fibrils in this layer, it may be concluded that in both species the fibrillar helix in the S2 layer of the secondary cell wall was Z-type.

DISCUSSION

On the basis of the presented results of the arrangement of phloem rays and the type of wood grain in the wood of *Pinus silvestris* and *Picea abies*, it can be stated that the rays showed a clear tendency to be arranged in one direction and that there is a relationship between the general direction of the arrangement of rays on the circumference of phloem and the direction of the grain in the peripheral parts of the wood core.

The following questions arise: 1) What is the mechanism by which these slanted phloem ray arrangements are formed in the studied objects? 2) What is the basis of the relationship between the direction of the grain inclination and the direction in which the phloem rays deviate? 3) What factors may cause a deviation from the general rulee.

It is obvious that the cambium is the first factor which determined the spatial relationships between the cells in a functional secondary phloem. Later, in the non-conducting secondary phloem, these relationships are modified through the tertiary anatomical changes in the phloem itself and the stresses caused by the activity of the cambium. There is also no doubt that external, mechanical factors acting on the tree, especially wind acting on the crown and causing torsional moments, can modify the arrangement of rays in the phloem.

Let us now consider the possible reaction of a growing tree subjected to torsional moments due to winds acting on its crown. The wood core of the stem of a growing tree, twisted by the wind, can be considered to be a bar in which torsional moments occur when one end is immobilised at the base of the tree and a twisting couple of forces is applied to its other end (crown). The angle of inclination of rays is changed as the result of the applied torsional moments. This angle (φ) is the torsional measure. Its magnitude is directly proportional to the torsional moment (M_s) and the length of the bar (L) and inversely proportional to the so-called torsional rigidity of the bar ($G I_o$); thus $\varphi = 2M_s L / G I_o$. Stiffness, in turn, is dependent on the elasticity coefficient (G) and the polar moment of inertia I_o , which is dependent on the radius of the twisted bar and equals $\pi r^4 / 2$. The science of mechanics tells us that in the twisting of bars, an important part is played by the strength of the outer layers because there the greatest tangential stresses occur; $T = M_s r / I_o$. In the stem, this part is undoubtedly played by the peripheral zone of the wood column. The mechanical properties of this zone therefore have a significant role in the deformation of the stem. It should be added that the relationships presented above apply to bars having a circular cross section, while a wood column usually is more or less wavy. In non-circular bars, the distribution of stresses is not uniform. Experience shows that eg., in an elliptical bar, the greatest tangential stress on twisting occurs on the short axis of the ellipsis, in bars with wavy cross sections, it reveals on the depressions the outline (Jakubowicz and Orłowski 1970). Mechanics also shows that if a ferro-concrete column is equipped with structural members that are twisted in one direction, it is resistant to torsional moments having the same sign. In order for a construction to be perfect in respect to resistance to torsional moments having opposite signs, it should be equipped with structural members oriented in the opposite direction (Kobiak and Stachurski 1960).

Taking into account the results presented in this paper on the structure of phloem and wood and the principles involved in the twisting of bars presented above, the results may be interpreted as follows. In the young stems of both

species at crown level where the S-type wood grain always occurred, the mean angles of inclination of the grain in the outer layers of the column were relatively large, the rays showed a very distinct tendency to deviate in the S-direction in spite of the fact that the direction of the fibrillar helix in the S2 layer of the secondary cell walls was always type Z.

If we accept the hypothesis about the unsymmetrical reversibility of the torsion of a rotated wood column and that the phloem rays are "pulled" along with it, we can suppose that in the case of the studied pine and spruce trees, the type of asymmetry of the mechanical properties of the column subjected to torsion was determined in the most part by the grain spiral, which in turn was determined by the predominance of events in the cambium. Once the wood grain spiral is formed by the cambium, it may be reinforced by the wind acting on the crown until the cambium undertakes compensatory activity which leads through the straightening of the grain followed by a change in its direction to type Z.

On the lower levels, where the angle of grain inclination usually decreases in the S-direction (more or less in the middle of the stem) the predominance of S-sectors of phloem rays on the periphery usually decreases. In the lowest studied parts of the stem (breast height) in which the change in grain inclination to Z-type occurred, the predominance of one direction of deviation of rays is either very slight or the Z-direction starts to dominate. It is very probable that due to the change in the direction of the grain from S to Z, the residual torsions in the wood column may be null, and therefore the relative amounts of rays with opposite signs is about the same. The lack of dominance of one direction may also be caused by the small torsional angle (φ) at breast level. As was mentioned earlier, this angle is directly proportional to the length of the bar (L) and inversely proportional to the torsional rigidity (GI_0). L is small at breast height, while the rigidity increases because, on the one hand the coefficient of elasticity (G) is greater due to the greater amount of late wood and, on the other, the radius is greater than at higher levels.

In these studies, as well as in ones conducted earlier on *Aesculus* (Pyszyński 1980) it was found that in the area of waviness of the wood column contour, the phloem rays deviated in opposite directions on both sides of the maximal ridge or depressions. Such patterns may be related to the unequal distribution of radial and tangential pressures caused by the unequal pressure from the tissues added by the cambium and also during the twisting of the stem. There is no doubt that the cell arrangement in the peripheral layers of phloem may be modified by the initiating periderm.

In general, the results of this study argue in favour of the relationship between the direction of ray deviation and the direction of the spiral grain of the peripheral layers of the wood column. The mechanism of the formation of slanting arrangements of rays may be as follows: Due to the action of wind on the tree crowns, torsional moments arise and cause rotation of the crown and

the wood column too. The spiral grain of the wood column causes asymmetry of the mechanical torsional properties. Asymmetry of the mechanical properties of the external layers of the column may cause accumulation of residual torsional moments of one type — S in columns of S-type wood (left-oriented), Z-type in columns of Z-type wood (right oriented) due to which it rotates in the direction of the grain spiral. During this rotation, the soft phloem layers (which contain weak conducting elements which lose their turgor and obliterate which are between the column and the rigid shield of external tissues, are pulled by it and, in effect, rotate around the geometric radius.

Due to the change in the direction of the grain inclination in the peripheral layers of the wood column along the stem, the direction of the deviation of the phloem rays in one and the same stem at various heights may be different. In the upper parts of the stem, where the spiral grain was always S-type, S-type arrangements of rays dominated in the phloem, whereas at breast level, where the direction of the grain inclination changed to Z-type, the Z-type arrangements of rays dominated in the phloem.

Exceptions from the general rule occur most often on the waviness of the wood column contour and in the external layers of the nonconducting phloem. It cannot be excluded that other, unknown factors also come into play here. It is also not known how a young pine or spruce stem behaves when it is alternately twisted in opposite directions. Studies on the deformations of young stems of these species will be the subject of further studies.

In conclusion, it must be added that in detailed, systematic studies on the spatial patterns of tissue systems in the bark and in studying the mechanisms of their formation, the pattern of ray arrangement on the cross section should be taken into account, since it is an indicator of the geometry of stresses causing the transposition of tissues and has a significant influence on the formation of tissue patterns on the rhytidome and surface patterns of bark cracks.

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Związek między układem promieni w łyku wtórnym i włóknistością drewna w pniach Pinus silvestris L. i Picea abies Karst.

Streszczenie

Badano układ promieni w przekrojonym poprzecznie łyku wtórnym oraz włóknistość drewna wzdłuż promienia i na powierzchni stycznej kolumny drewna na kilku poziomach pnia *Pinus silvestris* i *Picea abies*. Stwierdzono, że większość promieni miała przebieg skośny i odchyłała się bądź w kierunku S-owym (na lewo), bądź Z-owym (na prawo) względem promienia geometrycznego gdy patrzymy na przekrojony pień z góry. Okazało się, że przewaga S-owego kierunku odchylenia się promieni występowała w tych pniach, w których włóknistość drewna w obwodowych partiach kolumny drewna była S-owa (lewoskrętna), natomiast przewaga kierunku Z-owego wystąpiła w obiektach, w których włóknistość drewna była Z-owa (prawoskrętna) w zewnętrznych warstwach kolumny. Większe odchylenia od reguły występowały na terenie zafalowań konturu kolumny drewna oraz w zewnętrznych warstwach łyka nieprzewodzącego w pobliżu perydermy.

Zaproponowano następujący mechanizm tworzenia skośnych układów promieni w łyku wtórnym: Wskutek działania wiatru na koronę powstają momenty, które powodują skręcanie się korony, a tym samym kolumny drewna. Dyssymetria strukturalna kolumny (skrętna włóknistość) powoduje asymetrię właściwości mechanicznych na skręcanie. Asymetria właściwości mechanicznych kolumny drewna może powodować nagromadzanie skręceń resztkowych jednego rodzaju

(S-owych w kolumnach lewoskrętnych, Z-owych w prawoskrętnych), w związku z czym obraca się ona zgodnie ze skrętem drewna. W trakcie obracania się kolumny drewna miękkie warstwy łyka znajdujące się między kolumną i sztywnym pancerzem zeskleryfikowanych tkanek zewnętrznych są przez nią pociągane i w rezultacie odchylają się względem promienia geometrycznego. A zatem: gdy skręt włóknistości jest S-owy promienie łykowe odchylają się w kierunku S-owym; gdy skręt jest Z-owy promienie odchylają się w kierunku Z-owym.