Mechanism of formation of spiral grain in *Aesculus* stems: dissymmetry of deformation of stems caused by cyclic torsion

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Abstract

The reversibility of deformation of young (3-10-year-old) *Aesculus hippo-castanum* stems was investigated after subjecting them to alternate torsion to the right and left as well as the orientation of the microfibrillar helix in the main S_2 layer of the secondary cell wall in fibres. The studies demonstrated that residual torsions to the right are larger than to the left. The orientation of the fibrillar helix is always Z-wise. The dissymmetry of the mechanical properties of the stem may be responsible for the formation of Z (right-oriented) spiral grain in the stem of a tree undergoing torsions in various directions under the action of winds.

INTRODUCTION

The notion spiral grains of wood denotes such grain in which the long cell axes are arranged along a helical line in respect to the stem axis (P a n s h i n et al., 1970).

The spirality of the stem is a phenomenon occurring commonly both in conifers and in broadleaved trees (S e i f r i z, 1933a, b; R a o, 1954; N o s k o w i a k, 1963; N i c h o l s, 1965; S a c h s e e, 1965; B a n n a n, 1966).

There are two kinds of spiral grain — Z (right oriented) and S (left oriented). In geometry dealing with symmetry helical structures are referred to as dissymmetric.

In *Aescsulus* there always is a Z-spiral cf. S c h m u c k e r, 1924; K r z y s i k, 1957; H e j n o w i c z and K r a w c z y s z y n, 1969; Py-s z y ń s k i, 1977).

Wavy grain with long and short wave may be superposed in *Aesculus* stems on spiral grain. Superposition of long waviness related to

interlocked grain does not change the Z-orientation of the grain to S in respect to the stem axis, it only changes the angle of grain inclination (P y s z y ń s k i, 1977).

A helical course of fusiform cambium cells and of the vascular elements can be observed as early as the first annual ring. The investigations of M i s r a (1939) on *Pinus longifolia*, of Priestley (1945) on *Sambucus nigra* and *Syringa vulgaris* and of H a r r i s (1969) on *Pinus radiata* demonstrated that spiral grain in the first annual ring is connected with the arrangement of leaves and leaf traces along the parastichies, that is with phyllotaxy. Thus the first inclination would be determined by the type of the apical meristem structure.

The wood grain is the reflection of the cambial grain. For the orientation of cells in the cambium is responsible in turn the type of events occurring in it such as: oblique anticlinical division in fusiform initial cells, the direction of intrusive growth, of splitting and uniting of rays. The orientation of events in the cambium is not accidental. Areas may be distinguished here called domains in which one type of events (Z or S) occurs. The domain pattern in the cambium is responsible for the grain pattern in the wood (B a n n a n, 1966; H e j n o w i c z, 1971; 1973a, b, c; 1974, 1975; K r a w c z y s z y n, 1971, 1972, 1973; P y s z y ń s k i, 1972, 1977; H e j n o w i c z and R o m b e r g e r, 1973).

The relation between spiral and interlocked grain is discussed in the literature. B r o w n et al. (1949), K a d a m b i (1951) and L i m a y (1954) consider that interlocked grain is a peculiar case of spiral grain. H e j n o w i c z (1973c) treats spiral grain as a variety of interlocked grain in which the changes in the inclination of the grain in one direction are more pronounced than in the other. This view results from investigations on the domain pattern in cambium producing wavy and spiral grain wood. The difference between these types of wood consists probably in that in the case of spiral grained wood the rapidly shifting domains are very high and exert a nonuniform influence on the grain type.

Examination of the cambial events in *Aesculus hippocastanum* showed that domain patterns are responsible for the wavy grain pattern (P y s z y ń s k i, 1972, 1977). As far as spiral grain is concerned, the case of *Aesculus* cannot be interpreted against the background of data concerning the prevalence of events as the factor determining cell orientation, since in the wood of this species only Z spiral grain was observed, whereas in cambium an S-type of events markedly prevails (H e j n o w i c z and K r a w c z y s z y n, 1969; P y s z y ń s k i, 1977).

The discrepancy between the type of cambial events and the orientation of grain in wood was also noted in conifers (B a n n a n, 1966; H e j n o w i c z, 1971).

The general prevalence of events of S-type in spite of the sustained

occurrence of a Z spiral in *Aesculus* indicates that some other factor, so far not taken into account, must be responsible for the orientation of spiral grain. It is not the prevalence of Z events that is decisive as they do not occur.

Hejnowicz (1973a, c) advanced the hypothesis of the unsymmetric reversibility of torsion caused by wind. He believes that the whole stem of *Aesculus* is twisted Z-wise (to the right). This torsion causes inclination of xylem cells in the same direction. Torsion of the stem would be associated with a unidirectional helical arrangement of micro-fibrils in the S_2 layer of the secondary cell wall. Random torsion of the crown due to wind would be unsymmetric as regards reversibility and consequently irreversible changes would gradually cumulate.

The possibility of some connection between the type of spiral grain and the type of the microfibrillar helix was pointed out by Champion (after Noskowiak, 1963) and Seifriz (1933a, b). Certain grounds to the supposition that such a correlation may exist are supplied by the data of Jaccard and Frey (1928). The authors found in *Picea excelsa* a fibrillar helix of S-type in S spiral-grained wood and of Z-type in Z and S or Z in straight-grained wood. On the other hand, Hejno-wicz (1964) did not note such a correlation in *Larix* sp. Neither was such a correlation found between the type of spiral-grained wood and the type of microfibrillar helix in *Abies alba* and *Picea excelsa* (Py-szyński and Hejnowicz, 1972), in which among 340 trees 80 per cent exhibited a distinct microfibrillar helix of type Z, and only samples from 3 trees showed the S-type, whereas the type of grain varied. The negative results of investigations do not, however, exclude the existence of such a correlation in other tree species.

The unidirectionality of the fibrillar helix in the S_2 layer of the secondary cell wall may have a marked influence on the mechanical properties of wood. The dissymmetry of the cell wall structure may cause a dissymmetry of the mechanical properties of the whole stem, leading in this way to torsion.

The possibility of the influence of winds as the factor producing torsion in tree stems was mentioned by Wentworth (1931), Cahn (1931), Yeager (1931) and Howard (1932). According to these authors the prevailing direction of winds leads to an assymmetry of the tree crown and this, in turn, results in a unilateral torque. The unilateral torque induces spiral grain formation. On the other hand, Jacot (1931) and Herrick (1932) negate the influence of the prevailing winds because of the change in the direction and oscillations of the angle of grain with the age of the stem. Noskowiak (1963) taking the foregoing data into account considers, however, that winds increase the angle of spiral grain inclination.

The present study was undertaken to elucidate the mechanism of

spiral grain formation in *Aesculus* stems. The chief aim was the verifi-
cation of the hypothesis of H e j n o w i c z concerning the unsymmetric
reversibility of stem torsions caused by wind. In this connection the
reversibility of deformations in young straight-grained trees was in-
vestigated. The orientation and size of the angle of inclination of the
fibrillar helix was also investigated.

MATERIAL AND METHODS

1. Measurement of deformations caused by torsion of stem

Several-year-old (3—10) *Aesculus hippocastanum* trees were cut
down at the base and the upper part of the stem was cut so as to leave
an 80-cm segment (the diameters of the stems are given in Table 1,

Table 1

The dimension of the diameter and the values of load applied for stem
torsion

1	2	3	4
No of stem	Diameter of the base cm	Diameter of the end cm	Loading kg
I	1.9	1.3	0.2
II	2.1	1.3	0.2
III	2.3	1.8	0.3
IV	4.2	2.7	2.0
V	4.4	2.8	2.3
VI	4.2	3.2	2.3
VII	3.4	2.9	2.3
VIII	3.6	2.8	2.3
IX	2.0	1.4	0.2
X	2.1	1.0	0.2
XI	3.3	2.2	1.0
XII	3.6	2.4	2.3
XIII	2.2	1.6	0.2
XIV	2.1	1.5	0.3
XV	3.2	2.6	2.3
XVI	2.0	1.3	0.2
XVII	1.8	1.1	0.2
XVIII	4.4	3.0	2.3
XIX	4.3	3.4	2.3
XX	2.0	1.4	0.2

columns 2 and 3). The cut surface was covered with grafting wax to
protect the stem from drying up during the experiment. Immediately
after this operation the examined stem segment was mounted in the
device shown in Fig. 1. The stem base was fixed in clamp A of the

stand, whereas the upper end was inserted into the ball bearing in stand B. The upper end was accurately adjusted to the ball bearing. The mirror C was attached to the apical end of the stem. A beam of light from source D fell on the mirror. The light was reflected at an 90° angle onto a scale 230 cm distant. The scale had a millimetre graduation (1 mm on the scale = 1,5′). Close to the ball bearing a bracket
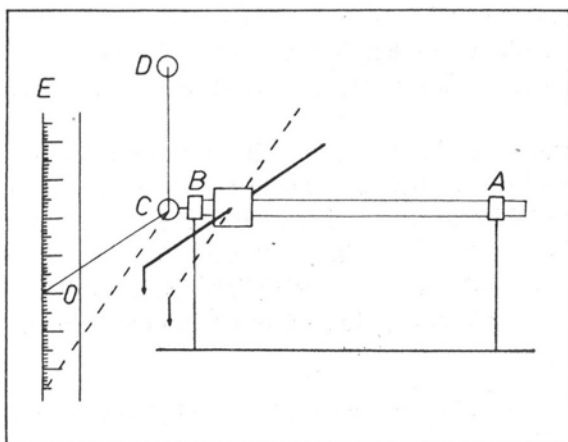

Fig. 1. Scheme of device for measurement of stem torsion
AB — stand (in clamp A fixed stem, in clamp B ball bearing), C — mirror, D — light source, E — scale. Close to clamp B two arms are attached o stem

was fixed on the stem with two horizontal arms (each 25 cm long). The mirror was adjusted so that the beam of reflected light fell onto the point 0 on the scale. At first, without application of any torsion moment, is was checked on the scale if no spontaneous torsions occur within 1/2 hour. If they did not, the experiment proper was started. A weight was placed on the end of one of the arms for 5 min (the loads are given in Table 1, column 4). The angle of light beam deviation was read on the scale 10 sec and 5 min after the application of the load. The weight was then removed and the stem was left for 5 min without any loading. The value of the recovery of the deviation angle was read after 10 sec and after 5 min from the moment of weight removal. Then the weight was placed on the opposite arm to twist the stem in the opposite direction for 5 min, and the next 5 min the stem was left without load. The measurements were performed as before. Thus, one measurement cycle lasted 20 min. The cycle was repeated several times.

Since the stems are not ideally straight, the moment of torsion to one side may be larger that to the other. Therefore, after the first series of measurements (after the first several cycles) the stem was rotated round its axis by 180° in the ball bearing A and further cycles of measurements were performed in the new position.

2. Orientation of microfibrillar helix

The samples were collected from 50 several-year-old trees and 50 old trees growing in various parts of Lower Silesia (among the 50 young trees 20 had been examined in reference to torsion). Samples from old trees were taken from the outer annual ring at a height of 1.5 m from the base (on the southern side of the tree).

From one 85-year-old tree 27 samples of 1 cm length were taken along the radius from the pith to the cambium.

The experiments were carried out on macerated material. For maceration a mixture of hydrogen peroxide and acetic acid 1:1 was used at 100°C.

In examination of the material the direction of inclination of the pit apertures and the course of cracks in the cell wall were taken into account. Ten neighbouring tracheid fibers were chosen, lying on the diametre within the field of vision. When there were pits on only one of the walls it was difficult to establish from which side the wall is seen. The direction of inclination of the elongated apertures was, there-

Table 2

Average of the inclination of the residual torsional lines

| No. of stem | Inclination of the line | | Torsion |
	before reversion	after reversion	
I	Z	Z	First Z-torsion
II	S	S	
III	Z	S	
IV	Z	Z	
V	Z	—	
VI	S	O	
VII	O	S	
VIII	O	S	
IX	Z	O	
X	Z	Z	
XI	O	O	
XII	Z	Z	First S-torsion
XIII	Z	Z	
XIV	Z	Z	
XV	Z	Z	
XVI	S	O	
XVII	Z	Z	
XVIII	Z	Z	
XIX	Z	Z	
XX	Z	Z	

Z — signifies that the line is inclined in Z direction (positive)
S — signifies that the line is niclined in S direction (negative)
O — signifies that the line is parallel to the O axis, — lack of data.

fore, determined only in such cells in which there were pits on the opposite walls. After establishing the type of the helix, the angle of its inclination was measured with a goniometric eyepiece. The angles between the lines tangent to the pit apertures were measured in the upper and lower wall. The value of this angle was divided by two and in this way the angle between the cell axis and the microfibrillar helix in layer S_2 of the cell wall was obtained (Fig. 2).

Fig. 2. Determination of orientation of extended pit apertures and angle of aperture inclination

The pits lie on opposite walls. The pit belonging to upper wall (closer to the observer) is Z-inclined (to the right). The interesecting lines run tangentially to the flattened apertures. Angle between cell axis (O) and tangent to apertures is equal to $\dfrac{2\alpha}{2}$
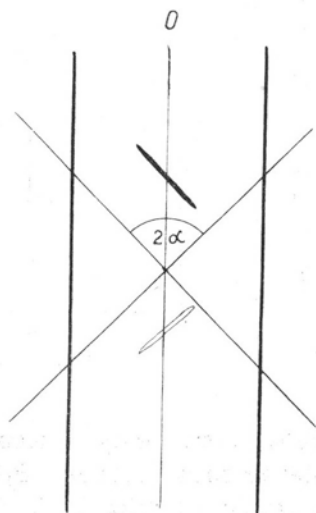
RESULTS

1. Stem deformation due to alternating cyclic torsion to the right and left

When a torsional force starts to act on the stem at t_o, instantaneous torsion OA sets in rapidly. Under the influence of continually acting force further deformation occurs which may be termed delayed torsion AB. When the force ceases to act at moment t_1 part of the deformation is quickly liquidated (instantaneous recovery BO) and then a delayed recovery occurs. After cessation of the action of the force there may remain a residual torsion (Fig. 3).

Short lasting alternate torsion of the stem to the right and left was applied in the experiment. Fig. 4 shows the course of the torsions. Oa_1 corresponds to instantaneous torsion to the left (S), that is to the angle by which the stem was twisted after application of the torsional moment to the arm on the left side of the stem (viewing the stem from the base). This value was read on the scale 10 sec after application of torsional force. The arc a_1b_1 corresponds to delayed torsion, that is to the angle by which the stem was twisted under the influence of continued action of the force. Segment b_1c_1 corresponds to instantaneous

recovery, that is 10 sec after the moment of load removal. Arc c_1d_1 represent the course of delayed recovery between 10 sec and 300 sec after removal of the load, and the segment between point d_1 and the axis shows residual torsion. When subsequently the second arm is loaded on the opposite side (right), there first occurs instantaneous torsion
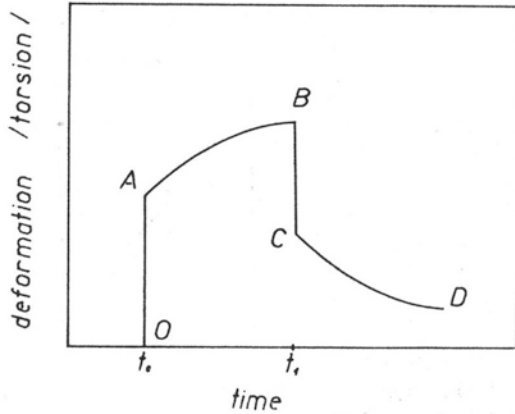

Fig. 3. Diagram of deformation course in torsioned stem
OA — instantaneous deformation (torsion), AB — delayed deformation (torsion), BC — instantaneous recovery, CD — delayed recovery

d_1A_1, then delayed torsion A_1B_1 and after removal of the load instantaneous recovery B_1C_1 and delayed recovery C_1D_1. There remains a residual torsion D_1d_1. Five minutes after removal of the load the stem was torsioned in S direction (left) to start a second cycle D_1a_2 and so on. The next arcs of the course of delayed torsion in the successive cycles after torsion in S direction are denoted on the diagram with small
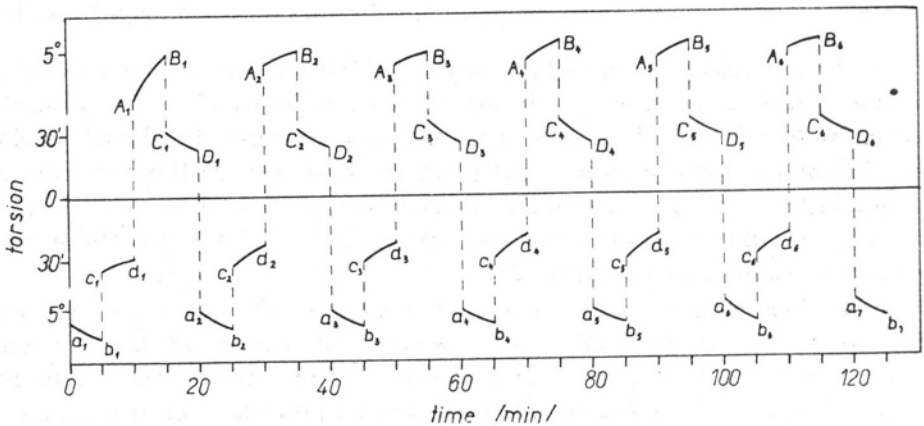

Fig. 4. Diagram of torsion for 6 cycles in alternate stem torsion
Negative values of ordinates denote torsion angle after stem twisting to the left, positive values denote stem torsion to the right: OA_1 — instantaneous torsion after torsion to the left, a_1b_1 delayed torsion, b_1c_1 — instantaneous recovery, c_1d_1 — delayed recovery, d_1 — axis — residual torsion, d_1A_1 — immediate torsion after twisting of stem to the right, A_1B_1 — delayed torsion. Capital letters wih consecutive numbers denote the respective phases of torsion to the right, small letters denote torsion to the left

letters and successive figures a_2b_2 etc., the delayed recoveries by c_2d_2 and so on, and with torsion in Z direction (right) by capital letters A_2B_2, C_2D_2 and so on.

The diagram (Fig. 5) presents the course of torsion in an enlarged scale from the first cycle. As seen, the most essential deformations occur instantaneously and in the first 2—3 minutes following the application of torsional moment. In this connection the end value of delayed torsion was read after 5 min and the end value of delayed recovery, that is residual torsion after a further 5 min. Thus, the period from force application to the moment of reading the value of residual torsion to one side was 10 min. On the other hand, the entire cycle with alternate torsion lasted 20 min.
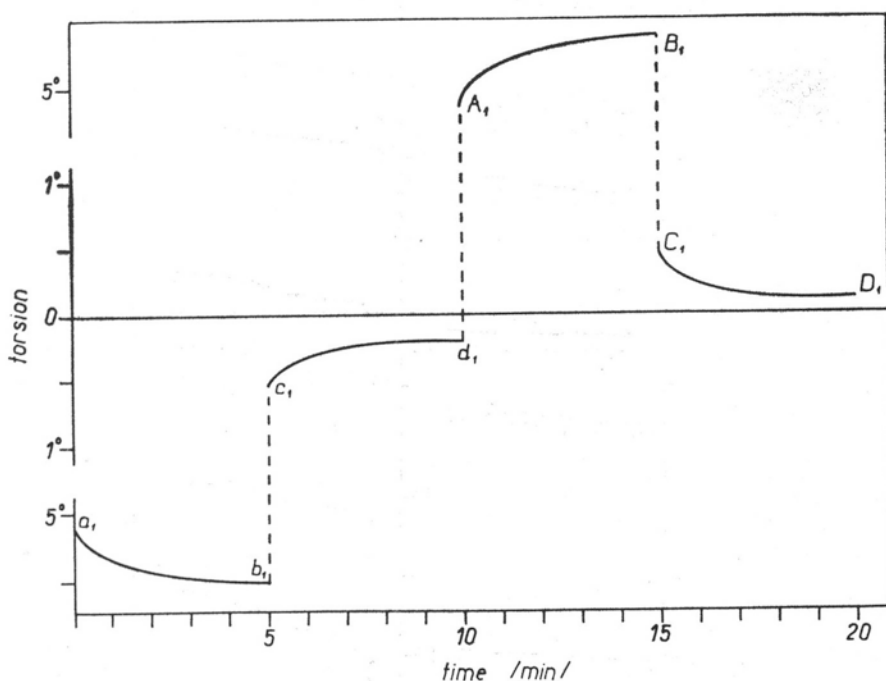

Fig. 5. Diagram of torsion course in first cycle. Most pronounced angle changes in delayed torsion and recoveries occur in the first three minutes of the respective phase

As already mentioned, the stems were not perfectly straight, so the moment of torsion to one side could be smaller than to the other. The size of the torsion angle would, therefore, be dependent on the shape of the stem. In order to obtain measurements independent of these factors, after the first series of measurements, that is after 5—6 cycles the stems were rotated around their axis by 180° so that the position of the two arms was exchanged.

The diagrams in Fig. 6 show as example data for stem no. I. In the lef column denoted A are data for the first position of the stem immediately after its fixation in the device. Column 3 gives diagrams after rotation of the stem by 180°. On these diagrams the points corresponding to the same phases of the successive cycles are joined,
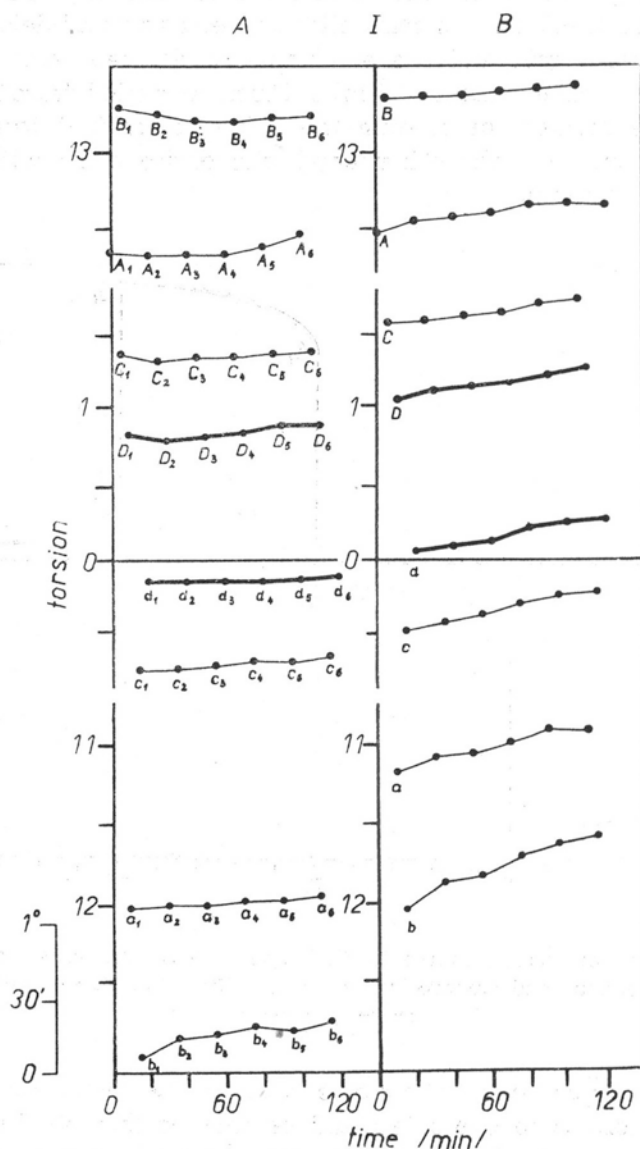

Fig. 6. Course of torsion in stem I as the consequence of alternate twisting
Bold lines join points of residual torsion, denoted D, after twisting to the right, those denoted d after twisting to the left. Lines joining points A or a denote instantaneous torsion values, B or b — delayed torsion values, C or c — instantaneous recovery values. The curves in the left columns (A) represent torsion values in the first position of the stem, in right columns (B) after rotation of stem by 180°

for instance points a_1, a_2 and so on or A_1, A_2 and so on give values of instantaneous torsion 10 sec. after application of the load; points b_1, b_2 and so on or B_1, B_2 give the end values (after 5 min) of torsions occurring under the influence of loading (end values of delayed torsions). The lines running from points c_1, c_2 and so on or C_1, C_2 and so on join values of instantaneous recovery (10 sec after removal of the load), and the lines joining points d_1, d_2 and so on or D_1, D_2 and so on joins values of residual torsions (5 mm after removal of the load).

In the detailed analysis of the character of the course of deformations occurring in time as the result of alternate torsion of stems particularly noteworthy are the data concerning residual torsion. These data for all the stems examined are given in Fig. 7. The diagram consists of two columns. In the left one (I) curves are shown for stems in which the first torsion was S-wise, and in the second column (II) for stems with first torsion Z-wise.

In the first cycle the first residual torsion values in both positions of the stem may be shifted further in the direction of the torsion than those in further cycles. Beginning with the second cycle the values of residual torsion change smoothly in one direction.

The results concerning the direction of inclination of the particular curves in relation to the O axis, that is to the initial position for both positions in each of 20 stems are as follows: in 11 stems the points representing residual torsion (curves d and D), independently of the position of the stem and direction of the first torsion, shifted Z-wise (stems I, IV, X, XII, XIII, XIV, XV, XVII, XIX and XX). In stem V for which measurements were taken only in one position, both curves (D and d) are shifted in Z-direction. In the stems (III, VIII and XVI) the direction of inclination of curves D (torsion to the right) was opposite to that of curves d (torsion to the left) in both positions of the stem (III and XVI) or only in one position (VIII). In one stem (XI) the upper curve (D) is inclined in Z direction and the lower one (d) runs parallely to axis O in the initial position of the stem, whereas after rotating the stem by 180° curve D is parallel to axis O, and curve d is inclined in Z direction. In four stems one curve shifted S-wise and the other was parallel to axis O. Such a combination could be seen in stem II in both positions (upper curve inclined in S direction) and in stems VI and XVI in their initial positions. In stem VI, D and d were parallel to axis O after rotation.

To reveal the general tendency of changes in the residual torsion values in the given stem, a mean direction of inclination was determined for both curves from residual torsion to the right and left. The mean direction of inclination was determined on the basis of the inclination of the line (ab) running in the middle between the two curves representing values of residual torsions when the stem was twisted in opposite
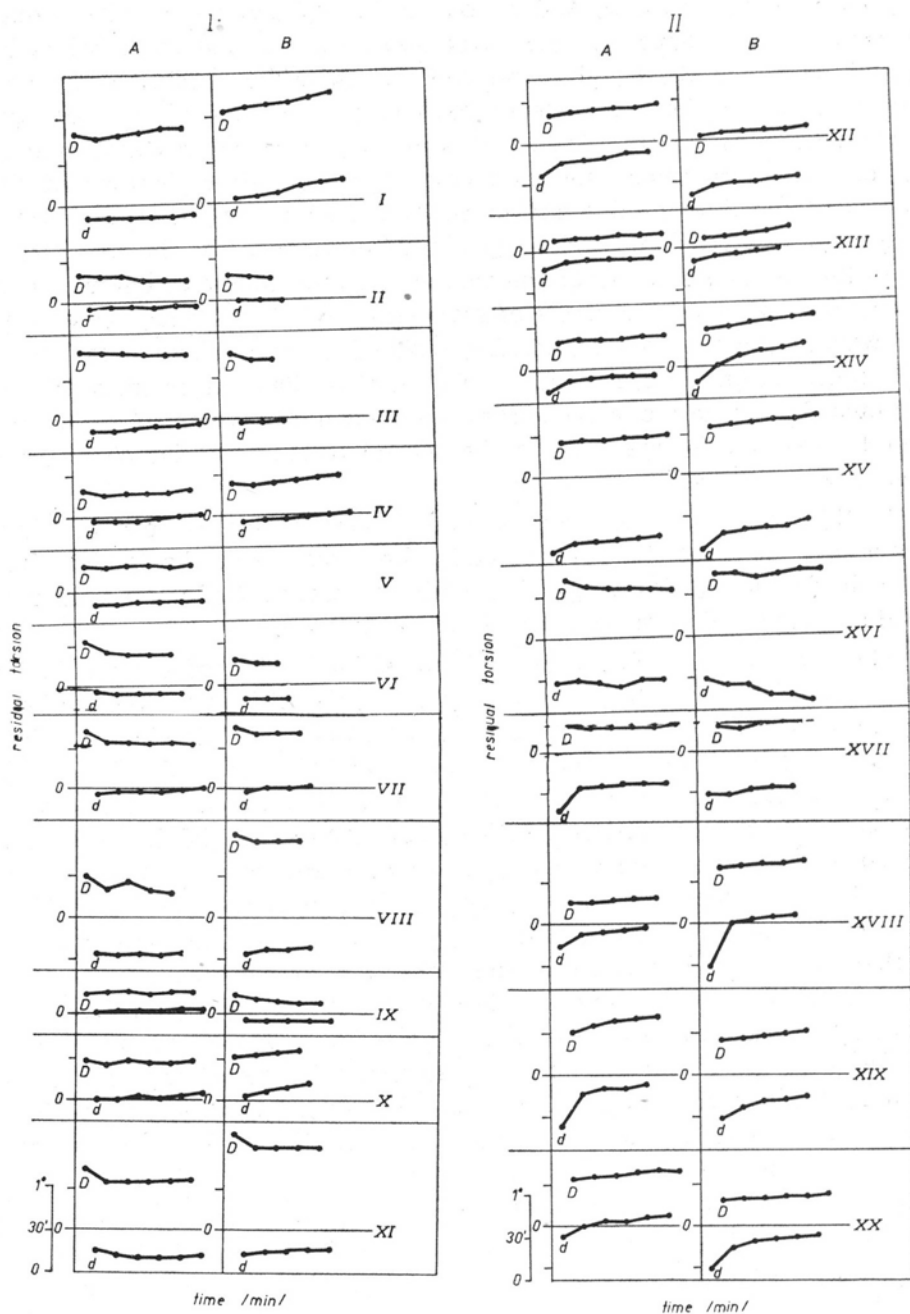
Fig. 7. Residual torsion: on left side in column I (stems I—XI) data for stem in which first torsion was Z-wise (right), in column II (stems XII—XX) — data for stems in which first torsion was S-wise (left)

directions. The "ab" line was traced as in Fig. 8 by joining the point of intersection (middle) between the values of residual deformations in the second cycle (D_2, d_3 intersecting with D_3d_2) with the point of intersection determined in the same way for the values of the last cycle. The mean direction of inclination of the curves of residual deformation are shown in table 2 on page 506. It results form the above given data that the mean direction of inclination was positive (Z-wise) in 14 stems in the first position and in 15 stems in the second position. Three stems in the first position and four stems in the second position showed no tendency to an inclination of the line ab. The inclination was S-wise in two stems in the first position (VI and XVI) and in two stems in the second position (III and VIII). Only in one case, in stem II the mean direction of inclination was S-oriented in both positions of the stem.
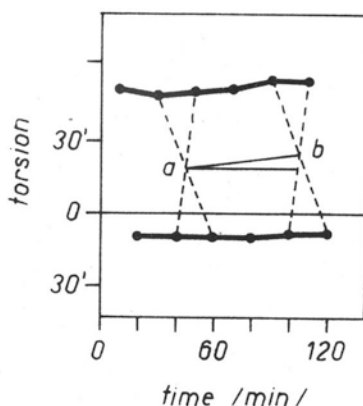

Fig. 8. Determination of mean direction of inclination of residual torsion curves. Mean direction is Z (positive) since segment ab is inclined in positive direction in relation to segment traced from point a and running parelely to axis

As seen the direction of the first torsion and the position of the stem had no influence on the direction of inclination of the residual torsion curves. When the first torsion was of S-type, in 8 of 9 stems the direction of the inclination of the particular curves and the mean directions of inclination of the residual torsion curves were Z-oriented in each case. Only in one stem (XVI) a change in orientation occurred after rotation by 180°. When the first torsion was Z-wise the stems showed a greater tendency to a shift of residual torsion in S direction. To sum up, in spite of certain differences resulting from the direction of the first torsion and position, the residual torsions are in general of type Z. This means that the value of the latter is higher when the stem is twisted to the right than in opposite direction, and that with the application of alternate torsion they gradually were torsioned to the right (in Z direction).

2. Orientation and angle of inclination of microfibrils in the S_2 layer of the cell wall of fibres

It results from analysis of the orientation of extended pit apertures that their inclination in fibre tracheids was always Z-wise. Cracks in the S_2 layer of the secondary cell wall were inclined in the same direction. Since the orientation of the flattened apertures and cracks in the S_2 layer is concurrent with the arrangement of the microfibrils, it may be concluded that in each of the cells examined in *Aesculus* the microfibrillar helix in layer S_2 of the secondary cell wall was of Z type.

The size of the angle formed by the microfibrils with the cell axis is variable as seen from the diagram (Fig. 9); for young trees it is contained in the range of 10—45°. Most frequent are cells with fibril angle of 25—35°.
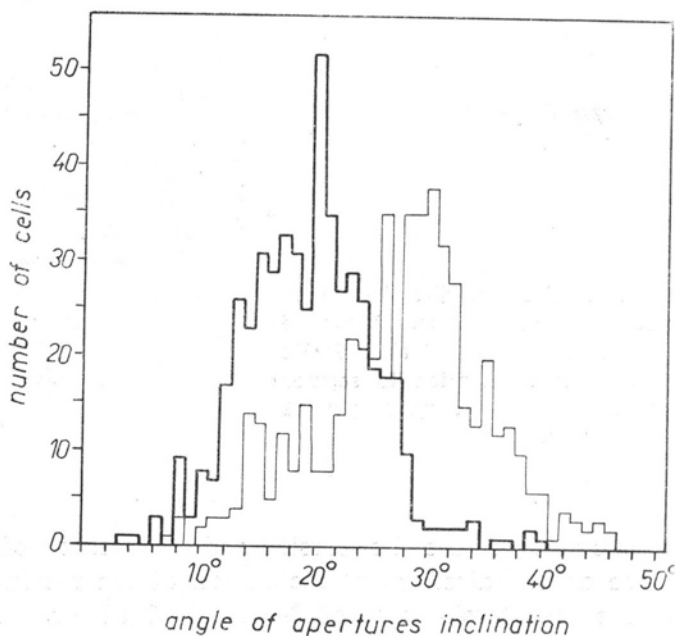

Fig. 9. Angle of inclination of flattened apertures of pits in tracheids of *Aesculus hippocastanum* wood
Bold line denotes size of angle of inclination of pit apertures for cells from old trees (from outer annual rigs). Thin line denotes inclinations of pit apertures in tracheids of young trees

In old trees the values of the microfibril angles lay within the range of 3—40° in the outer annual rings. Cells with a microfibril angle 19—21° were most frequent.

The change of the angle along the radius in the ontogenesis of the stem is shown in the diagram (Fig. 10). In the first years the microfibril
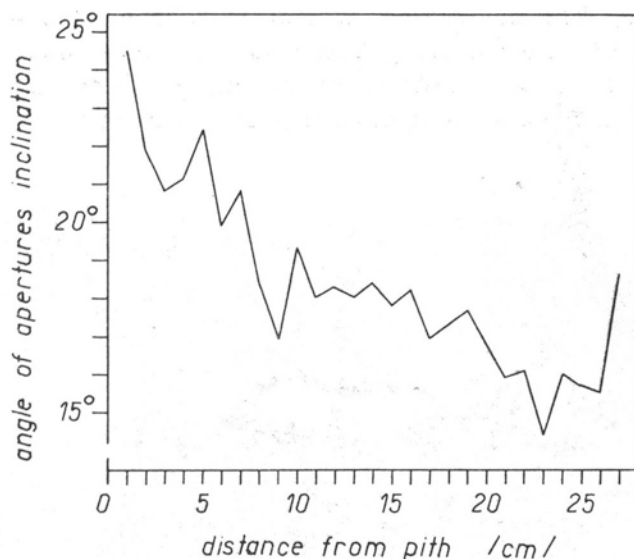
Fig. 10. Angle of inclination of flattened pit apertures in various positions along radius of 85-year-old *Aesculus hippocastanum* tree

angle is large reaching about 25°. Then, at a distance of 10 cm from the pith it gradually decreases to about 16°.

3. A hypothesis and its verification

The dissymmetry of the mechanical properties in torsion of young *Aesculus* trees supports the hypothesis that the upper part of the stem is torsioned by winds in counter-clockwise direction (looking down on the tree). This would mean that the branches are twisted in the same direction. If the stem torsion would be greater than it actually is, the changes in the position of the branches could be ascertained by direct observation. However, since the torsion is slight, of a dozen or so degrees in trees aged several score of years, it would be necessary to carry on observations for many years. One can, however, deduce indirectly whether the stem is torsioned and in which direction, on the basis of the position of the branches in relation to other trees or obstacles. It happens, namely, that if the *Aesculus* branches adhere to the stems of other trees, posts, walls or other objects they do this in such a way as if they had shifted onto the obstacle from the right side (Fig. 11). At the site of adherence the branch surface may show distinct signs of strong friction against the obstacle owing to branch pressure. A long lasting unilateral pressure causing abrasion may finally lead to fracture of the pressing branch (see Fig. 12). In one case a tree was observed (Chwalimierz) with a cut thick branch (diameter 30 cm and

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length 40 cm). The cut surface was at a distance of 5—10 cm from a thick trunk of a neighbouring tree. It does not seem possible that this branch could have been situated before cutting in the same place. It is probable that before it was cut it lay on the right side of the neigh-

Fig. 11. Branch of *Aesculus* (Chwalimierz park) adjacent to *Alnus* stem. Contact surface (arrow) strongly abraded

bouring tree. It should be added here that no arrangement of branches was found indicating a torsion of the crown in clockwise direction (looking down on the tree), that is in a direction opposite to that of the spiral grain.

Fig. 12. Broken *Aesculus* branch (Chwalimierz park) as the result of lasting side pressure. On stem of neighbouring *Alnus* abrasion (arrow) is distinctly seen

DISCUSSION

Cambium is directly responsible for the type of wood formed. It results from the literature of the last two decades that orientation of cambial cells depends on the orientation of events occurring in it such as oblique anticlinal division, the direction of intrusive growth and cell elimination. The joint influence of various events of a given orientation causes a corresponding change in the position of the cambial cells.

In *Aesculus hippocastanum* there is a marked prevalence of S-events

(Hejnowicz and Krawczyszyn, 1969; Pyszyński, 1977), nevertheless, the spiral grain is always of type Z. If this is taken into account we come to the conclusion that some other factor not the prevalence of Z events (since it does not exist), lies at the base of the mechanism causing the Z-spiral grain in the *Aesculus* stem.

The problem arise how does a Z spirality develop in spite of the prevalence of S events. Some other factor must be active here which produces Z spirality and which abolishes the influence of S events. The results of the present investigation indicate that torsion of the stem as a whole may be the cause of spiral grain. This is supported by data concerning unsymmetric deformations of the stem in the case of torsion in opposite directions (right and left) and data from the observations of the position of branches on some trees in relation to other ones or some neighbouring immovable object. Experiments demonstrated that deformations of the stem in *Aesculus* are not equally reversible in the case of torsion to the right and to the left.

The following mechanism of formation of spiral grain in *Aesculus* stem could be imagined: owing to the action of winds on the tree crown there arise torques which cause torsion of the crown and thus of the stem. Torsion occurs in both directions alternately. If the *Aesculus* stem would exhibit symmetrical mechanical properties in torsion in opposite directions, the effects of torsion to the right and left would compensate each other. Then, it would probably be the events in the cambium that would decide of the spiral grain. The stems of *Aesculus*, however, exhibited in experimental torsion asymmetry in the reversibility of torsion, it is, therefore, quite probable that in growing trees random torsion of the crown due to winds is not symmetric as regards reversibility. Consequently, irreversible changes gradually cumulate, causing a gradual torsion of the stem in Z direction, and thus changes in the position of xylem and cambium cells in Z direction. This would explain the fact that, in spite of the prevalence of S events, the torsion in *Aesculus* is always of Z type. The prevalence of S events would be a factor counteracting excessive torsion of the grain in Z direction, as pointed out by Hejnowicz and Krawczyszyn (1969).

As already mentioned some authors have called attention to the possibility of the effect of wind causing torsion in tree stems (Wentwort, 1931; Cahn, 1931; Yeager, 1931; Howard, 1932), but the mechanism of torsion formation suggested by them differs essentially from the above described mechanism. These authors, namely, believed that the prevailing winds cause an asymmetry of the crown and this in turn induces a unilateral torque. The prevailing unilateral torque would lead to the torsion in the tree stem.

Trees grow in various surroundings: singly on open areas, in avenues, in compact groups with other trees, in courtyards etc. It should, there-

fore, be borne in mind that the pressure of winds may be exerted from different sides on various trees. In connection with this both prevailing torques — left and right — and both directions of torsion corresponding to them should occur in various trees. The torsion of the stem in the case of *Aesculus*, however, is only of Z type, thus this interpretation is not valid. Nevertheless, it would seem that the prevailing direction of the torque may exert an influence on the extent of spirality. If the tree is, namely, situated so that it is more frequently exposed to wind on one side (e.g. near a house) producing a torque to the right, the torsion will probably be more pronounced, whereas in the case of trees twisted by the prevailing wind to the left, the Z torsion will be weakened.

At the base of the unsymmetric properties of deformations there probably lies the structure of xylem elements. It results from the investigations performed that in each cell the type of the microfibrillar helix in the main layer of the secondary cell wall is Z oriented. This helix is inclined in relation to the cell axis at a relatively wide angle in both young and older tracheids.

The occurrence of unsymmetric deformation in young straight--grained trees and the simultaneous appearance of one type of microfibrillar helix, exclusively, in the S_2 layer of the secondary cell wall seems to confirm the possibility of existence of a relation between the dissymmetric structure of the wall and the dissymmetry of the mechanical properties of the stem as a whole.

Since young straight-grained trees exhibit dissymmetry of their mechanical properties, the question arises to what extent grain spirality in a stem aged many years influences the mechanical properties of this stem. It may be that the structural dissymmetry at the wood level enhances the effect resulting from the dissymmetry of the cell wall structure.

The helical arrangement of the microfibrils in the cell wall and spiral grain in the stem may be compared to the arrangement of fibres in a rope. A single thread in the rope and also the microfibrillar "thread" in fiber and the grain "thread" in the stem may be compared to a spring. Both a spring and a rope show dissymmetric properties in alternate torsion in opposite directions.

If the cell wall were built only of cellulose microfibrils, one could forsee in which direction torsion will be easier, whether concurrently with the course of the microfibrils or in opposite direction. It should, however, be remembered that the cellulose microfibrils in the cell wall constitute only the supporting system, and the interfibrillar space is filled with hemicelluloses and lignin; moreover the particular xylem cells are not free but joined to one another by middle lamellae. In this situation it cannot be foreseen which torsion will be easier, or which

torsion is more reversible. Experiments indicate that the stem of *Aesculus* in which the main cell wall layer (S_2) is characterized by a Z microfibrillar helix exhibits a poorer reversibility of Z torsions.

Passive torsion of the stem should cause a change in the position of the branches. In order to ascertain this, observations would have to be carried on for many years (since the torsion is slight). Since direct observations are lacking there remains an indirect way — deduction whether the stem undergoes torsion and in what direction, on the basis of the position of the branches in reference to other surrounding objects. It should, however, be borne in mind that the arrangement of branches in the crown is dependent above all on the growth of the particular branches. In general, the postulated changes in the position of the branches due to stem torsion are not conspicuous. There sometimes occur, however, branch arrangements confirming the above named hypothesis. Positions of branches have been observed, namely, in which the branches of one tree were leaning against the stem of another tree or against some other object as if they had shifted onto it owing to crown torsion in Z direction. In such position the *Aesculus* branches exerted a pressure on the stems of other trees in conformity with the orientation of the spiral grain in *Aesculus* .

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Mechanizm powstawania skrętnej włóknistości w pniach Aesculus: dysymetria odkształceń młodych drzewek przy naprzemiennym skręcaniu w prawo i w lewo

Streszczenie

W pracy niniejszej badano odwracalność odkształceń kilkuletnich drzewek *Aesculus hippocastanum* stosując krótkotrwałe naprzemienne skręcenia w prawo i w lewo.

Badania wykazały, że skręcenia nie są jednakowo odwracalne. W większości przypadków średnie skręcenia resztkowe są typu Z-owego.

Badano również kierunek nachylenia helisy fibrylarnej w warstwie S_2 wtórnych ścian komórkowych cewek włóknistych na podstawie orientacji spłaszczonych wlotów do jamek. Stwierdzono, że we wszystkich zbadanych komórkach kierunek nachylenia wlotów był Z-owy. Można stąd wyciągnąć wniosek, że helisa fibrylarna w każdej zbadanej komórce jest typu Z-owego.

Opierając się na powyższych wynikach można wyobrazić sobie następujący mechanizm powstawania skrętu w rosnących drzewach *Aesculus:* wskutek działania wiatrów na koronę powstają momenty obrotowe, które powodują skręcanie korony, a tym samym pania. Skręcanie to odbywa się w obu kierunkach, raz w prawo drugi raz w lewo. Gdyby pień *Aesculus* wykazywał symetryczne właściwości mechaniczne przy skręcaniu w przeciwnych kierunkach, wówczas efekt skręcania w prawo byłby znoszony przez efekt skręcania w lewo, a o kierunku włóknistości skrętnej decydowałyby same zdarzenia w kambium. Łodygi *Aesculus* w eksperymentalnym skręcaniu wykazywały dysymetrię odwracalności skręceń, jest więc bardzo prawdopodobne, że również w drzewach rosnących losowe skręcenia korony pod wpływem wiatrów nie są symetryczne pod względem odwracalności. Te nieodwracalne zmiany stopniowo kumulują się, powodując zwiększanie skrętu pnia w kierunku Z-owym, a tym samym zmiany położenia komórek drewna i kambium również w kierunku Z-owym.

Przedstawiony mechanizm powstawania skrętu tłumaczyłby fakt występowania włóknistości skrętnej typu Z-owego w pniach *Aesculus* pomimo wyraźnej przewagi zdarzeń typu S-owego w kambium.