ACTA SOCIETATIS
BOTANICORUM POLONIAE
Vol. 49, nr 4: 415—422
1980

Pattern of ray arrangement on cross section of bark of *Aesculus*

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(Received: November 5. 1979)

Abstract

The arrangement of rays within the phloem and rhytidome was studied in *Aesculus* stems. It was found that on the cross section most rays in the stem deviate in Z-direction, that is to the right from the geometric radius. The mechanism of Z-arrangement of the rays may be as follows: owing to the action of wind on the crown torques arise causing the torsion of the wood core. The dissymmetry of the mechanical properties of the *Aesculus* wood core leads to accumulation of residual Z-torsion, and as consequence of this wood core torsion to the right occurs when seen from above. In the course of this torsion the soft phloem layers lying between the column and the rigid shield of the outer tissues (rhytidome and outher sclerified phloem layers) are drawn by the core and this results in their deviation to the right in respect to the geometrical radius.

INTRODUCTION

The rays in functioning secondary phloem retain in general the arrangement that prevailed in the cambium, whereas in nonfunctioning phloem they frequently undergo buckling, owing to the reduction of the phloem layer thickness. This is due to the degeneration of the sieve elements (and adjacent cells) and their crushing. In phloem crushing occurs because of radial pressure from the side of addition new layers produced by the cambium tangential stretching when the periphery increases and dilatation growth of rays and axial parenchyma (Holdheide, 1951; Esau, 1969; Hejnowicz, 1973a).

On the basis of literature data (Holdheide, 1951; Srivastava, 1963; Esau, 1964, 1969; Hejnowicz, 1973a) and the author's own observations on segments of coniferous and deciduous trees two principal types of ray-parenchyma cells arrangement in secondary phloem can be distinguished: these in which on cross section through the nonfunctioning phloem rays run in zigzags in relation to the radius and these in which the whole course of the ray is slanting.

In coniferous plants the phloem rays are frequently slanting or even almost tangentially arranged, all oriented in the same direction (H e j n o w i c z, 1973a).

Earlier investigations of the present author on the mechanism of formation of spiral grain in *Aesculus* demonstrated that in stems aged several years, after alternate torsion to the right and left, the torsions were not equally reversible. In most cases the mean residual torsions were of Z-type. Experimental data indicate a dissymmetry of the mechanical properties of the *Aesculus* wood core. It may be concluded on the basis of these data that in growing trees, under the action of wind on the crown, there remain residual torsions to the right (P y s z y ń s k i, 1977b), (even when the sum of right and left torsion moments is equal to zero).

H e j n o w i c z (1973a) advanced the supposition that the slanting arrangement of rays may be caused by unidirectional torsion of the tree crown, and with if of the wood core in relation to the rhytidome.

The finding that the wood core revolves in *Aesculus* allows the supposition that in growing trees, owing to torsion of the wood core, the phloem rays in the soft secondary phloem layer between the wood core and the stiff shield of rhytidome and external sclerified phloem layers are drawn by the core and consequently become inclined in relation to the radii. If we would be dealing with a round stem in which the wood core revolves to the right that is in counter-clockwise direction (when looking from above on the stem cross section), the phloem rays between the core and the shield of external tissues would be drawn by the core and would deviate in the direction of torsion as shown by the model in Fig. 1.

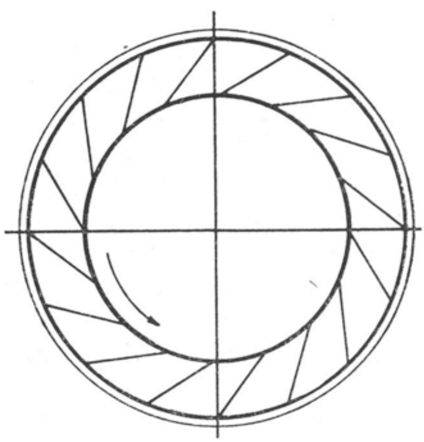

Fig. 1. Scheme of torsional inclination of rays in the bark

It is but little probable that the shield of external tissues would revolve by the same angle as the wood core in the course of development of spiral grain, owing to accumulation of residual torsions to the right. In connection with this it is to be expected that, if the hypothesis of torsion of the core is correct, there will appear in the *Aesculus* phloem a deviation of rays to the right. Investigations on the arrangement of rays on the phloem and rhytidome periphery were performed and the results are presented below.

MATERIAL AND METHODS

Investigations on the arrangement of phloem rays were carried out on two felled stems in the Wrocław University Botanical Garden. In both stems the mean grain inclination was about 10° to the right in reference to the stem axis.

A characteristic of the material is given in detail in Table 1. The rasor-smoothed upper surface of the bark on the disc was treated with phloroglucinol + HCl to increase the contrast between phloem rays and sclerenchyma and to make the annual rings in the bark more distinct. The successive parts of the bark surface were then photographed with a „Microtar" 6.3/90 ap. 0.80. The positives enlarged ×10 were recomposed. The course of rays was discernible on the photographs. The composite photographs were used for analysis of the ray course.

Table 1

Characteristic of stems examined

	Age of tree, years	Height of tree, m	Lenght of stem from base to crown, m	Level at which studied disc was located, m	Circumference of bark at level examined, m	Lenght of circumference of preserved bark, m
A stem no. 1: *Aesculus carnea* Hayne	75	17	2.5	1.0	1.46	0.95
A stem no. 2: *Aesculus hippocastanum* L.	150	20	10.0	1.5	1.52	1.52
	,,	,,	,,	7.0	1.30	0.95

The direction of phloem ray inclination to the right of the radius as in Fig. 1 is denoted as Z-wise, and inclination in the opposite direction as S-wise. The rays superposed on the radius are referred to as T-rays and those with wavy arrangement around the radius as SZ-ones.

RESULTS

It is seen in preliminary observations of ray arrangement and the phloem cross section that on the periphery there are areas in which all rays are inclined in the same direction in reference to the radius, in all layers. The direction of this deviation is frequently Z-wise (Fig. 2). In some areas, however, it is S-wise. There also are regions where it is not uniform, but SZ-wise. It cannot therefore be determined simply whether there is a general tendency of orientation or whether this orientation is accidental.

For analysis in detail of the rays course on the periphery, the phloem surface was divided into sectors in tangential direction and zones in radial direction. On the photographs the successive sectors in tangential direction (along the periphery) correspond to 1-cm sections. In radial direction the phloem was divided into 4 zones: A — of 1 mm corresponding to the latest (youngest) rings, B — comprising the 10 preceding annual rings, C — with successively 10 years older rings and D — from the outer border of zone C to the latest (youngest) periderm. The rhytidome zone denoted as zone E was also taken into account. The results of the investigations are listed in Tables 2 and 3.

In stem no. 1 in all zones the Z-wise direction prevails. It is particularly well visible in zone A in which along 95 cm of periphery with preserved cells the rays are inclined Z-wise in 73 sectors (77 % of the examined periphery). In further zones the proportion of Z to S direction is lower, nevertheless Z-wise direction prevails to the end.

Table 2

Course of phloem rays in secondary phloem and rhytidome on cross section through stem no. 1 (*Aesculus carnea* Hayne)

Course of rays	Number (N) and per cent of sectors with given orientation of rays in particular zones									
	A		B		C		D		E	
	N	%	N	%	N	%	N	%	N	%
Z	73	77	46	48	43	47	35	45	20	65
S	17	13	29	31	26	23	19	25	4	13
SZ	0	0	15	17	12	13	8	10	3	9
T	5	5	4	4	11	12	15	20	4	13
Total	95	100	95	100	92	100	77	100	31	100
N*	0		0		3		18		64	

N* — number of missing zones or those unsuitable for investigation

In stem no. 2 at a level of 1.5 m from the base Z-wise direction prevails in zones A and B, while in C S-direction dominates and in zone D both appear in equal numbers. In the same stem at the level of 7 m Z-sectors prevail in all zones.

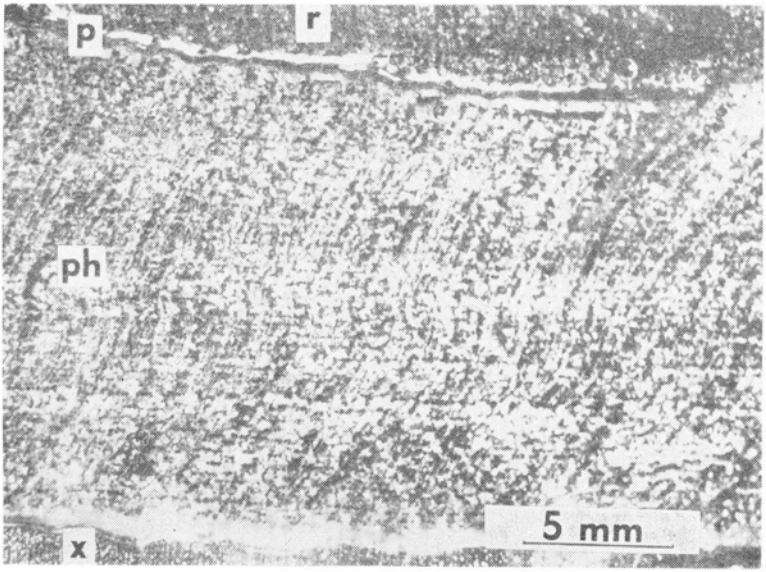

Fig. 2. Example of photograph of transverse surface of bark of *Aesculus* stem (ray course of Z-type)
x — xylem, ph — phloem, p — periderm, r — rhytidome

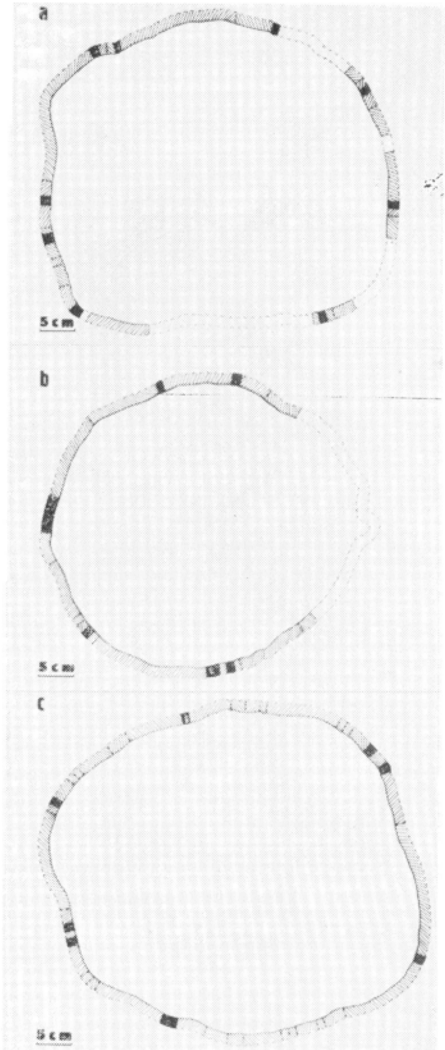

Fig. 3. Graphical representation of general tendency of ray orientation in bark of *Aesculus* stem. The inclination of rays in respect to radius indicates the resultant orientation of rays in all zones of the given sector

a — stem no. 1, disc from 1.0 m level, b — stem no. 2, disc from 1.5 m level, c — stem no. 2, disc from 7.0 m level

Black segments denote areas in which the resulting orientation of rays is T- or SZ-wise. White segments denote missing areas or unsuitable ones for examination

It should be stressed that in stem no. 2 at both levels examined the prevalence of Z-areas over S-ones occurs in zone A similarly as in stem no. 1.

As far as the frequency of rays of SZ- or T-type is concerned, it may be said in general that as compared with the Z- and S-rays they are relatively not numerous and usually their joint proportion does not exceed 25 per cent with the exception of zone D in stem no. 2 at the 7 m level.

Table 3

Course of phloem rays in secondary phloem and rhytidome on cross sections through stem no. 2 (*Aesculus hippocastanum* L.)

	Course of rays	Number (N) and per cent of sectors with given orientation of rays in particular zones									
		A		B		C		D		E	
		N	%	N	%	N	%	N	%	N	%
Level 1.5 m	Z	96	64	82	55	64	42	56	37	60	44
	S	37	25	57	38	70	46	56	37	52	38
	SZ	0	0	0	0	13	9	34	23	12	8
	T	17	11	11	7	5	3	4	3	13	10
	Total	150	100	150	100	152	100	150	100	137	100
	N*	2		2		0		2		15	
Level 7 m	Z	59	63	58	61	45	47	34	36	35	47
	S	19	20	25	26	32	34	27	28	26	34
	SZ	0	0	0	0	4	4	31	33	8	10
	T	16	17	12	13	14	15	3	3	7	9
	Total	94	100	95	100	95	100	95	100	76	100
	N*	36		35		35		35		54	

N* — number of missing zones or those unsuitable for investigation

In order to determine the prevailing general tendency of ray orientation in each sector, the resultant ray orientation in zones A, B, C, D and E were determined graphically (Fig. 3).

In both stems sectors with resultant ray orientatoin Z are more numerous than the S-oriented ones.

Fig. 3 also allows to recognise the distribution of regions with resultant ray orientation in various parts of the periphery. As seen, areas of Z-, SZ-, or T-followed by S-areas then SZ- or T-areas and once more Z-type alternate. Moreover, at the sites of ridges or depressions in the periphery SZ- or T-type areas are frequently localised. In general on the right side of ridges lie S-areas and on the left side Z-ones, whereas in the depression on the right from the minimum point Z-areas occur and to the left S-ones.

DISCUSSION

It results from the present investigations that phloem rays on the cross section through secondary phloem and rhytidome of the examined *Aesculus* stems characterised by the presence of spiral Z-oriented (to the right) grain show a tendency to deviation in Z-wise direction in respect to the radius. The direction of ray deviation agrees thus with the torsion of the wood core according to the hypothesis concerning the mechanism of stem torsion (H e j n o w i c z, 1973a, b; P y s z y ń - s k i, 1977b).

In the inner phloem layer as much as 77 per cent of rays deviated in Z direction in stem no. 1 and 6 and 63 per cent in stem no. 2 at levels of 1.5 and 7 m. In older layers variability was higher, nevertheless prevalence of Z-areas continued with the exception of zones C and D at the 1.5 m level in stem no. 2.

The question arises what may be the cause of deviation from the expected orientation.

In the stems examined rays with resultant course opposite to the expected one (S-wise) occurred mainly in the areas where the periphery was wavy, with ridges and depressions. In the ridges the S-patterns were localised usually on the right side of the radial plane passing through the ridge maximum, and in the depressions on the left side of such a plane passing through the maximum of depression.

It seems that local distorstion of the ray arrangement at the wavy site are due to varying stresses, both torsional arising during torsion of the core and radial and tangential ones occuring owing to cambium activity. In the former case waviness of the periphery may be an obstacle to the wood core revolving in relation to the outer tissue shield. In this connection the extent and directions of the stresses may be different on the right and left side of the ridge (depression) and may cause local modifications in ray arrangement. In the latter case, that is during extension growth of the periphery the radial and tangential stresses are no doubt higher in the ridges where increase in size is larger than in the neighbouring parts of the periphery and in the neighbouring areas. Consequently passive drawing of the rays towards the ridges may occur. In this case the rays on the right side of the radial plane passing through the maximum of the ridge deviate slightly in S-direction and those on the left side of the same plane deviate in Z-direction.

It is possible that if we were dealing with an ideally circular stem in which the cylindrical wood core would revolve freely in respect to the outer tissue shield, the phloem rays would run a uniform course, at least in the younger phloem layers.

Considering the interaction of various factors which may affect the course of rays in the secondary bark, it may be stated in general that in the examined stems slanting Z-patterns prevailed, not only in zone A, but also in the further ones and even in the rhytidome zone. The prevalence of Z-pattern confirms the correctness of the supposition advanced at the beginning that the rays are drawn by torsion of the wood core. This in turn supports the hypothesis of torsion of the core to the right, owing to the dissymmetry of its mechanical properties in *Aesculus* stems (Pyszyński, 1977b) and of formation of spiral Z--oriented grain, in spite of S-events in the cambium (see Hejnowicz, Krawczyszyn, 1969; Pyszyński, 1977a).

Acknowledgments

The author is indebted to Prof. Z. Hejnowicz for helpful advice throughout the study.

The present investigations were supported in part by a grant of the Department of Agriculture of the United States under P.L.480.

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Układ promieni w łyku wtórnym i martwicy korkowej w pniach Aesculus

Streszczenie

Przebadano układ promieni łykowych na obwodzie łyka i martwicy korkowej w pniach *Aesculus hippocastanum* L. i *A. carnea* Hayne. Na przekroju poprzecznym większość promieni odchylała się w kierunku Z-owym, tj. na prawo względem promienia geometrycznego. Mechanizm tworzenia Z-owego układu promieni może być następujący: wskutek działania wiatru na koronę powstają momenty obrotowe, które powodują skręcanie korony a tym samym kolumny drewna; dysymetria właściwości mechanicznych kolumny drewna *Aesculus* powoduje nagromadzenie Z-owych skręceń resztkowych, w związku z czym obraca się ona w prawo; w trakcie obracania się kolumny drewna miękkie warstwy łyka znajdujące się między kolumną a sztywnym pancerzem tkanek zewnętrznych (martwicy korkowej oraz zewnętrznych zeskleryfikowanych warstw łyka) są przez nią pociągane i w rezultacie odchylają się w prawo względem promienia geometrycznego.