Domain pattern in the cambium of young *Platanus* stems

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Abstract:

In the vascular cambium of *Platanus* Z and S domains appear in the course of formation of the first annual ring. Their arrangement is connected with the division of the stem into nodes and internodes. In each node a domain of Z and of S type occurs. The longitudinal boundaries between them run along the middle leaf trace and on its opposite side, and the transverse boundaries lie in the nodes. Z-type domains are found on the right below the base of the nearest upper leaf, and S-type domains on the left. As the young cambium forms further rings, the size and shape of the domains changes.

INTRODUCTION

Z- and S-type orientational domains occur in the vascular cambium. They are delineable areas in which oblique anticlinal division and such effects of intrusive growth and fusiform initials elimination as splitting and uniting of rays are observed in the alternative "right" (Z) and "left" (S) forms (Bannan 1966; Hejnowicz 1964, 1971; Hejnowicz and Krawczyszyn 1969; Hejnowicz and Romberger 1973; Krawczyszyn 1971, 1972).

Domains are commonly found in the cambium of coniferous and broadleaved trees, although they are most pronounced when the cambium produces wavy or interlocked-grained wood. In such cases Z and S domains alternate in the form of transverse stripes perpendicular to the stem axis. Their axial dimensions (height) varies in dependence on the tree species from several millimeters to several score centimetres (Krawczyszyn 1972; Hejnowicz and Romberger 1973). The domain type at the given site in the cambium changes many times during the life of the tree owing to the migration of domains in respect to the

cambial cells along the trunk. This migration, calculated to 1 mm of xylem produced, varies from about 0.1 mm to above 12 cm. It is correlated with the height of the domain — greater for higher domains (Krawczyszyn 1972). The domains migrate as a rule upward (Krawczyszyn 1972; Hejnowicz and Romberger 1973), less frequently downward (Hejnowicz 1971; Pyszyński 1972).

It is not clear so far when domains first appear in cambium development, whether at the moment of appearance of this tissue or only later as secondary xylem is formed. Until now domains have been only observed in mature cambium forming rings distant from the pith. Neither is the origin known of the striped domain pattern commonly found in mature cambium of broadleaved trees which are capable of forming wavy- or interlocked-grained wood. For investigations in this field *Platanus* is a very convenient object. The author's earlier investigations (Krawczyszyn 1971, 1972) demonstrated that in the cambium of this tree species the highest of all so far known domains occur, migrating with the greatest velocity that has ever been measured. These domains are easy to delineate by analysing the splitting and uniting of rays.

MATERIALS AND METHODS

The studies were performed on the stems of *Platanus acerifolia* Willd. taken from the crown of a tree growing in the Botanical Garden of the Wrocław University. A description of the wood samples is given in Table:

Stem No.	Characteristic of material investigated and kind of examination
1	Segment of ca. 20-year-old stem. Length ca. 3 m. Wood grain was analysed
2	Segment of 12-year stem growing more or less horizontally, length ca. 20 cm. Segment included one whole internode and one half of neighbouring ones. Domain structure of the cambium was analysed in the course of 8 first annual rings formation on the upper side of the stem in an area comprising ca. 0.1 of its circumference.
3	Segment of 6-year stem, length ca. 20 cm. Domain structure of cambium was analysed in the course of formation of first 4 annual rings on the entire circumference of the stem on a segment comprising two whole internodes and fragments of neighbouring ones.

Various parts of stem no. 1 were cut serially into disks about 3.2 cm high. Each disk was radially split along the same side of the stem and after piecing together the surface of radial splits through the stem segments was obtained. From stems nos 2 and 3 blocks for cutting on a sliding microtome were taken. They were boiled in water and then cut into tangential section 35—40 μ thick by means of the sliding microtome. The sections from the boundaries between the consecutive annual rings

were chosen for further investigations. These layers preserve the arrangement of cambial cells (cf. Hejnowicz and Krawczyzyn 1969). The sections were attached to slides with Haupt's adhesive, dried and deaerated by alternative immersion in boiling and cold absolute alcohol and then transferred to xylene and embedded in Canada balsam.

The sections were projected onto photographic paper with a Zeiss "Documator". Enlargement was about 15x. On photographs of the successive terminal xylem layers (TLX) all xylem rays were analysed and the points marked at which they underwent splitting or uniting, so that maps of ray splitting in the course of successive annual ring formation were obtained.

RESULTS

Fig. 1 shows the radial split surface of a 20-year-old stem of *Platanus*. Longitudinal undulations are visible, arranged somewhat slatingly in relation to the stem axis. It is known from earlier investigations (cf. Krawczyzyn 1972) that the occurrence of such undulations is associated with migration of domain patterns in the cambium.

For delineating the domains in the cambium the ray splittings and unitings were analysed, first in a narrow sector of a 12-year-old stem (stem no 2), and then on the entire circumference of a 6-year stem (stem no 3).

In a 12-year-old stem changes in the rays on its upper side were examined within an area comprising about 0.1 of the stem circumference. Fig. 2 shows the situation of this area in relation to the enclosed leaf scars, thus in relation to the leaves still present on 1-year-old green stem, and Fig. 3 gives maps recording the splitting and uniting of rays during formation of 8 annual rings. As seen the splitting or uniting events are oriented nonrandom in the rays: there are areas in which changes of one type prevail, corresponding to domains of either Z or S type. The domains are already distinct at the time of first annual ring formation. In the centre of map A lies a domain Z and on both its sides fragments of S domains are visible. The transverse boundaries between the domains correspond to the nodes.

It should be mentioned that for delineation of the domains in the 1-year-old cambium (map A) rays were compared in the earliest layer of secondary xylem and in the first terminal layer of xylem (TLX). In the former the rays are very tall, but later with formation of xylem they split forming many low rays.

The comparison of consecutive maps in Fig. 3 indicates that the domain pattern in the cambium site considered undergoes considerable changes.

In a 6-year-old stem, changes in the rays were examined on the

Fig. 1. Radial split surface, 20-year-old stem of *Platanus acerifolia* Willd. Vertical arrow is oriented acropetally, horizontal arrows mark the level of enclosed leaf scars, thus in nodes. X — pith. Figures indicate number of annual rings. Block A taken from lower part of stem no. 1, B — from upper part; distance between A and B is ca 20 cm.

Fig. 2. Scheme showing situation of xylem segment in 12-year-old stem in relation to leaves appearing in first year. The dots at A and B denote the nodes in the 1-year-old stem

Fig. 3. Map showing orientation of splitting and uniting of rays during formation of eight successive annual rings (A — H) in segment shown in Fig. 2. Left semi-circles denote splittings, right — unitings of rays. Vertical arrow is oriented acropetally. Horizontal arrows on map A show nodes (the same ones as in Fig. 2). Some rays as reference points for position are shown. The transverse dimension of the maps is enlarged three times as compared to the longitudinal one.

Fig. 4. Map indicating orientation of ray splitting on the entire periphery of the cambium cylinder during formation of first annual ring. The line shows the way the two parts of the map are joined. Vertical arrow is oriented acropetally. A, B, C denote the successive nodes; a, b, c — leaf traces entering the corresponding nodes. The thickness of ring studied was 2.5 mm.

surface of the entire cambial cylinder. For this purpose each disk of wood was split radially into 8 blocks including the whole circumference of the stem. Then the changes in the rays were analysed in all the blocks. After piecing together the partial maps (from the successive blocks) maps of the entire cambium periphery were obtained. On the map for the period of first annual ring formation (Fig. 4) two domains Z and S in each internode are seen. One longitudinal boundary runs between them along the median leaf trace, and the other parallelly to the first one but on the opposite side of the cambial cylinder. Horizontal boundaries between the domains are in the nodes. In each internode the domains are regularly arranged in respect to the nearest leaves: the horizontal boundary of domain Z lies right of the base of the upper leaf, and a similar boundary of domain S — left of the leaf base. Owing to such a distribution of domains in relation to leaves, and in view of the spiral phyllotaxis in *Platanus* stem, if we move up the stem 1-year-old cambium, we successively find Z and S domains. When, however, the whole cambium surface is considered, the domains do not form a striped pattern as in old cambium but a chequered pattern. It should be mentioned that all rays were analysed on the cambium surface presented in Fig. 4. The nonuniform density of the marks on the map indicates an unequal frequency of ray splitting. The frequency increases acropetally in each domain and reaches maximum in its upper part that is at the base of the leaf.

The question now arises, how do the domains appearing in cambium during the first annual ring formation (Fig. 4) behave, as the successive annual ring are formed. An answer is found in Fig. 5 presenting simplified maps of domains on the whole cambium surface in the course of formation of 4 annual rings (wood sample same as in Fig. 4). These maps were drawn so that the cambial cylinder circumference would be constant in the course of the formation of successive annual rings (thus longitudinal scale in Fig. 5 does not apply to the transverse dimensions of the maps). The outset situation has already been described (Fig. 4). During formation of the next annual rings the domains change their shapes and surfaces occupied at first in the cambium. In map B a certain extension of domains Z is seen as compared with map A. The horizontal boundaries between the domain sare, however, shifted upwards indicating an acropetal migration of the domains. On the next map C one of the boundaries between the domains runs more or less horizontally and closes forming a ring so that the domains begin to encompass the whole cambium circumference. During formation of the successive annual ring D, domains S expand and Z ones shrink considerably forming only small patches. This indicates that the domain pattern appearing in one-year cambium of *Platanus* undergoes modification as further rings are formed.

Fig. 5. Simplified maps of ray changes on entire circumference of the cambium cylinder in the course of formation of four first annual rings (see text). Map A presents a simplification of the map in Fig. 4. The lines show the boundaries between Z and S domains. The thickness of the successive annual rings is: 2.5; 2.6; 4.0 and 3.5 mm.

DISCUSSION

The present paper is the first to give a description of domain patterns in the cambium during the formation of the first and several subsequent annual rings. As an indicator of the orientation of morphogenic events occurring in the cambial initials (i.e. pseudotransverse anticlinal divisions of fusiform initials and overlapping of intrusively growing cell tips) is considered the splitting and uniting of rays. It was, namely, known that in cambium the direction of ray splitting is determined by the domains type (Hejnowicz and Krawczyszyn 1969). Up till now domains were outlined in this way only in mature cambium of *Platanus* (Krawczyszyn 1971, 1972) and other broadleaved trees (Hejnowicz and Romberger 1973) characterized by rather low rays. It is doubtful, however, whether in the case of splitting of very high rays extending through entire internodes during formation of the first annual ring, the orientation of the splitting is determined by the domain type. Perhaps the orientation of splitting of such rays is not connected with

Fig. 6. Fragment of tangential earl secondary xylem (section taken at the base of the leaf). Vertical arrow is oriented acropetally, horizontal arrows indicated some ray splittings. The circle denotes the node level. As seen, the rays are inclined to the right and left in relation to the stem axis and type Z and S splittings.

the domain structure of the cambium, but rather with the direction of transport. These doubts may arise if we study Fig. 6 showing the arrangement of rays on a tangential section of xylem derived from the site where previously a young leaf and bud grew: It is seen that on both sides of the leaf gap (filled with parenchyma) there occur high rays inclined in relation to stem axis to the right and left in dependence whether they arise on the right or left side of the gap (these rays run, namely, along the leaf trace). It would seem that during the transition of the *Platanus* stem from the primary to the secondary body the high rays converging to the leaf base are an obstacle in longitudinal water

transport (in xylem) and of assimilates (in phloem) to the newly formed leaves. On account of their primary inclination these rays can be split only as shown in Fig. 6. No doubt the reservation here considered is justified. It should, however, be borne in mind that the inclination of high rays is marked only close to the leaf base. On the opposite side of this base (in the nodes), like on the remaining dominating surface of each internode, the high rays are almost parallel to the stem axis, therefore they would not be an abstacle in longitudinal transport. Nevertheless, these nonslanting rays are split in the same way as the inclined ones occurring close to the leaf base. It seems, therefore, that ray splitting occurs according to some other principle than the primary inclination of rays, namely, the domain principle. That the pattern of splitting of high rays is actually a domain pattern is indicated by the fact that the domain pattern in 2-year-old cambium where there are no more high rays can be derived from the migration of the initial pattern (Fig. 5).

How can the relation between the distribution of domains in 1-year-old *Platanus* cambium and leaf distribution be explained? Fig. 6 suggest that the domain pattern in young cambium adjusts itself to the course of high rays close to the leaf base so as to make possible appropriate splitting according to the requirements of conduction. Whether it is so can be established in experiments with disturbance of the conducting pathways in 1-year and several-year-old *Platanus* stems, for instance by various cuttings and investigation of their influence on ray splitting and formation of the domain pattern in young cambium. It is also possible that the domain pattern observed in 1-year cambium is earlier determined in the procambium, since procambium and cambium are two developmental stages of the same meristem (Esau 1943) and there is no clear-cut criterion by which they can be separated (Fahn et al. 1972).

The present investigations indicate that in 1-year cambium of *Platanus*, domains Z and S form a chequered pattern (Fig. 4), whereas in old cambium of the same tree (Krawczyszyn 1972) as well as that of other broadleaved trees (Hejnowicz and Romberger 1973) striped patterns are observed. The difference between the pattern here described and the striped one consists mainly in that in the former the vertical boundaries between the domains (i.e. the boundaries parallel to the stem axis) and in the latter the horizontal boundaries (perpendicular to the axis) are most pronounced. It is as yet not clear whether the chequered pattern is specific for 1-year cambium of *Platanus* or whether it is common to young cambium of broadleaved trees. In the case of *Platanus*, in the ontogenesis of cambium a transition from the chequered to the striped pattern is to be expected. In the light of the data in Fig. 5, however, the mode of this transition is not clear, since the domain

pattern in young *Platanus* cambium undergoes too fundamental modification. Domains of one type expand, of the other type shrink, and at the same time the shapes of the domains change.

It is noteworthy that in 1-year *Platanus* cambium, horizontal short boundaries between the domains lie in the nodes (Figs 3 and 4). If during formation of this ring the domains would migrate upwards with the same velocity as they do in old cambium (ca 10 mm/1 mm xylem, cf. Krawczyński 1972), then after formation of this ring (ca. 2 — 3 mm thick) the horizontal boundaries between the domains would be shifted in relation to the nodes by about 2 — 3 cm. The lack of such a shift points to a more static character of domains in young cambium. It is possible that domain migration is in some way inhibited by the young stem segments still deprived of cambium or by the leaves. In the course of the first three years of cambium activity it is not easy to analyse domain migration on account of the changes occurring at this time in domain height (Fig. 5) later, however, acropetal domain migration must take place as indicated by the slanting undulations of xylem occurring on the radial split face of older stems (Fig. 1).

Changes in domain height (i.e. expansion of domains of one type and shrinking of those of the opposite type) in young *Platanus* cambium (Figs 3 and 5) are particularly interesting. A similar phenomenon was observed by Hejnowicz (1973) in mature cambium of broadleaved trees forming wavy-grained wood. This interesting finding is interpreted by the author on the ground of the hypothesis that in cambium specific morphogenetic waves of the orientation of cellular events occur. (Wave is defined, in the physical sense, as a cyclic change of state spreading in space and time with a certain velocity; a wave has two aspects — a spatial and temporal one.) In the case of cambium, according to Hejnowicz, the spatial aspect of the wave consists in the occurrence of domains Z and S, that is of areas with processes of "right" and "left" type, and migration of domain patterns in the cambium in relation to cambial initials is the temporal aspect. This author believes that expansion of domains of one type and shrinking of those of the opposite one is caused by superposition of two or more waves differing in length and velocity in the same cambium. On this basis we may suppose that on the domains pattern characteristic for 1-year-old cambium of *Platanus* some other pattern originating from the older cambium is superposed which changes the primary dimensions and shapes of the domains.

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REFERENCES

- Bannan M.W. 1966, Spiral grain and anticlinal divisions in the cambium of conifers, *Can. J. Bot.* 44:1515-1538
- Esau K. 1943, Origin and development of primary vascular tissues in seed plants, *Bot. Rev.* 9:125-206
- Fahn A., Ben-Sasson R., Sachs T. 1972, The relation between procambium and the cambium, in *Research Trends in Plant Anatomy*, A. Ghouse and M. Yunus (ed), Tata Mc-Graw Publ. Comp. Ltd, N.Delhi India
- Hejnowicz Z. 1964, Orientation of partition in pseudotransverse division in cambia of some conifers, *Can. J. Bot.* 42:1685-1691
- Hejnowicz Z. 1971, Upward movement of the domain pattern in the cambium producing wavy grain in *Picea excelsa*, *Acta Soc. Bot. Pol.* 40:499-512
- Hejnowicz Z. 1973, Morphogenetic waves in cambia of trees, *Plant Science Letters* 1:359-366
- Hejnowicz Z. and Krawczyszyn J. 1969, Oriented morphogenetic phenomena in cambium of broadleaved trees, *Acta Soc. Bot. Pol.* 38:547-560
- Hejnowicz Z. and Romberger J.A. 1973, Migrating cambial domains and the origin of wavy grain in xylem of broadleaved trees, *Amer. J. Bot.* 60: 209-222
- Krawczyszyn J. 1971, Unidirectional splitting and uniting of rays in the cambium of *Platanus* accompanying the formation of interlocked grain in wood, *Acta Soc. Bot. Pol.* 40:57-79
- Krawczyszyn J. 1972, Movement of the cambial domain pattern and mechanism of formation of interlocked grain in *Platanus*, *Acta Soc. Bot. Pol.* 41:443-461
- Pyszyński W. 1972, Downward movement of the domain pattern in *Aesculus* cambium producing wavy-grained xylem, *Acta Soc. Bot. Pol.* 41:511-517.

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Domeny w kambium młodych łodyg Platanus

Streszczenie

Domeny Z i S tj obszary „prawe” i „lewe” pod względem orientacji skośnych ścian z podziałów antyklinalnych i wzrostu intruzywnego komórek wrzecionowatych, a także rozszczepień i łączów promieni, występują w kambium platana już w czasie odkładania pierwszego słoja drewna wtórnego. Ich układ nawiązuje do podziału łodygi na węzły i międzywęzła. W każdym międzywęzlu występuje domena Z i S a granice między nimi biegną podłużnie: jedna wzdłuż środkowego śladu liściowego, a druga — po jego przeciwnej stronie. Poprzeczne granice między domenami znajdują się w węzłach. Domeny Z występują na prawo, poniżej nasady najbliższego górnego liścia, a domeny S — na lewo. Dzięki temu, jak i ze względu na spiralny układ liści w łodydze, posuwając się wzdłuż 1-rocznej łodygi platana natrafiamy na kolejne domeny Z i S. W miarę odkładania przez młode kambium dalszych słoików drewna domeny zmieniają rozmiary i kształty.