Cambial domain pattern in the root and root collar of *Platanus*

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Abstract

The grain pattern in wood and the pattern of orientation of ray splitting and uniting were studied in roots and root collar of *Platanus acerifolia*. In roots the interlocked-grain wood was observed as in the stem. An analysis of changes in xylem rays indicates that the cambial domain pattern exists and migrates upward there. In the root collar the grain in wood was straight although cambial domains were noted too. The domain pattern is characterized by relatively wide variations of the domain length and by pulsation: expanding some domains and reducing others so that it does not become manifest in the grain.

INTRODUCTION

The occurrence of cambial domains in many woody plants is rather common. Domains (S- and Z-type) are local areas in the vascular cambium within which oblique anticlinal divisions and other cellular events, including some effects of intrusive growth and elimination of fusiform initial cells, occur predominantly in either S ("left") or Z ("right") orientation.

Domains form horizontal or slightly oblique stripes that alternate along the bole, each from some millimetres to a few score centimetres (or even more) in height and migrating along the stem (Bannan 1966; Hejnowicz 1964, 1971, 1974, 1975; Hejnowicz and Krawczynszyn 1969; Hejnowicz and Romberger 1973; Pyszyński 1972; Krawczynszyn and Romberger 1975).

Cambial domains are also known to occur in *Platanus*, as it has been shown in earlier studies (Krawczynszyn 1971, 1972, 1973). They are the highest of all so far known domains and migrate with the highest

velocity that has ever been measured. They appear during the formation of the first annual ring of wood.

Uptil now domains have been observed in the cambium of stems only i.e. in above-ground tree parts. Nothing is known of cambial domains in the roots. Neither are data available in the literature on the occurrence of wavy- or interlocked-grain wood in roots. Therefore we decided to study the domain patterns in the roots of *Platanus*.

MATERIALS AND METHODS

Wood samples were taken from three mature (c. 110, 80 and 30-years-old) *Platanus acerifolia* Willd. trees, cut down in Wrocław. They consisted of fragments of root collar with adjacent tree parts, taproots (i.e. main roots in the central rooting area) and lateral roots (i.e. main roots that expand laterally in the external rooting zone). These roots were taken at a depth 50–60 cm.

A radially-sawn board c. 1 m long, including root collar and adjacent parts of the tree was taken. It was divided into series of radial segments, each 3 cm high. The segments were split radially from the same side and pieced together to obtain the grain pattern on the radial split surface. Roots were also cut into several discs, split and joined together to obtain the surface of radial splits.

Smaller blocks of wood with tangential faces $1-1.5 \times 3$ cm were formed and, after boiling in water, cut into tangential sections (30 μ) with a sliding microtome. Sections of a terminal late xylem (TLX) from successive annual rings were selected and attached to slides with Haupt's adhesive. These layers contain a record of cambial cells behaviour (Hejnowicz and Krawczyszyn 1969).

The sections were dried, deaerated by immersion in boiling and cold absolute alcohol and then, after passing through xylene, mounted in Canada balsam. The sections were projected onto photographic paper (enlargement 15). On TLX photographs from successive annual rings, all xylem rays were analysed. The points where rays underwent splitting or uniting were marked so that maps of ray changes during formation of successive annual rings were obtained.

RESULTS AND DISCUSSION

In general, interlocked-grain wood occurs in the roots of *Platanus*. This is indicated by undulations on the radial split surfaces in such wood (Fig.1). The undulations run centrifugally upward. This pattern resembles that in the stem of this tree. It is a manifestation of inter-

locking in wood and migration of domains in the cambium, as shown in earlier studies (Krawczyński 1972, 1973).

Only in the root collar in *Platanus* there is a local area without undulations so that the grain is rather straight (Fig. 1E). This straight-grained area occupies about 20 cm in an axial dimension. It is something unusual for the wood of *Platanus* which is normally considered to have interlocked grain (Panshin et al., 1970).

Main and the lateral roots representing both central and lateral rooting areas were taken for the study of cambial domains. In general, roots appeared as rather difficult material for such a study because the boundaries between successive rings are sometimes not clearly defined. This refers especially to all roots in the central rooting area and to lateral roots in the external rooting area. The TLX existing there at the border between annual rings is very narrow and not pronounced enough (see also Fayle 1968, Süss et al., 1973). So, it was almost impossible to recognize the TLX layers from the same annual rings on several adjacent root fragments, which will be necessary to establish the dimensions of cambial domains. Because of this, we were able to note only small fragments of domains that occurred in the taproots and the lateral roots. In both types of roots cambial domains seemed to be similar.

Fig. 2 illustrates a series of domain maps in taproot. The occurrence of domains is obvious here, though the studied area was much shorter than one domain. On map A there is a fragment of Z domain at the top and a fragment of S domain at the bottom. The border between domains is inclined to the right. On the next map, B, the whole studied area is covered by S domain which may be considered as a result of an upward migration of the domains. Such a direction in cambial movement is also consistent with further changes on the studied area. But there is also another direction in the domain movement: from right to left. This may be seen from a comparison of maps E and F. The period of cyclic change of the domain type is rather short, lasting about 5 years, in accordance with what is seen on the radially split face through the wood in Fig. 1.

Fig. 3. presents series of cambial domains accompanying the formation of four successive annual rings in the main root from the side rooting zone. (Material illustrated in Fig. 1 A). It can be seen that cambial domains still exist and change rapidly from year to year. Almost the whole area in map A is covered by the S domain and only small parts of Z-type domains occur at the bottom and the top. The pattern occurring in the next map, B, may be considered in general as a result of upward migration of the domains. The changes in the domain pattern on the following maps, C and D, are difficult to interpret because no direction in cambial movement is pronounced enough.

It is noteworthy that the velocity of domain movement in roots considered in Figs. 2 and 3 is higher than in this tree stem. This may be also seen from the radially split surfaces (Fig. 1A—C). The undulations on the radial split face are more steeply inclined upward than in the stem (see Krawczyŝyn 1972, 1973). The radial distance between two ridges of the undulations is 4—5 rings in roots, and about 10 rings in the stems.

The density of marks in domains, denoting ray splitting and uniting in roots is also rather higher than in stems. This shows that the frequency of changes in rays and some other basic cellular events is higher in roots than in above-ground organs in this tree. Maybe, this is related to the fact that in the *Platanus* root the ray tissue is more abundant than in the stem (Süss et al., 1973).

As mentioned previously, in the root collar the grain is rather straight although below it in the roots and above in the stem the grain is interlocked. Analysis of TLX showed that cambial domains are still present there. These domains, however, are characterized by wide variations in shape and axial dimensions as well, and undergo extremely rapid rebuilding. Some domains expand while others diminish or even disappear.

Fig. 4 illustrates such a situation. The domains are presented on simplified maps only and those of the same origin are numbered. The grain course in wood in initial and final rings, *a* and *e*, is also marked.

Initially, in map *A*, there was a long Z domain (no. 6) in the central part and also fragments of long S-type domains (nos. 1 and 10) in the upper and lower part of the map. Between these domains there were some other much shorter domains, of both S and Z type. This pattern changed rapidly during the formation of subsequent rings. It involved an upward migration and other phenomena:

- expanding or diminishing of domains,
- disappearance or shifting of some domains from the studied area,
- reappearance,
- union of domains of the same type or splitting of domains by those reappearing.

On map *B* domains nos. 3 and 5 of S-type are smaller while those of Z-type nos. 2 and 4 are larger and united. In the lower part of this

Fig. 1. *Platanus acerifolia* Willd. Undulations on a radial split wood face in root and root collar

A — taproot; B-C, lateral roots; D-F — tree base with root collar (E) and adjacent root with outer rooting zone. A, B, C were taken from various trees, C-E — taken from the same side of one tree.

Vertical arrows are oriented towards the tree crown. Vertical lines denote the same numbered annual rings and horizontal lines in C-F denote the rays. Brackets in A, E, denote places where cambial domains which occur during formation of successive annual rings were studied

Fig. 2. Maps showing the direction of splitting and uniting of rays on the same small cambial area during formation of nine successive annual rings in the taproot. The left semicircles denote the splitting, the right ones the uniting of rays. The arrow indicates the tree crown. Some rays were used as reference points

Fig. 3. Maps indicating orientation of ray splitting and uniting on the same cambial area during the formation of four successive annual rings (the area between brackets in Fig. 1A) in root from external rooting zone.

The thickness of the wood layer analysed was 18.5 mm. Legend as in Fig. 2

Fig. 4. Simplified maps of splitting and uniting rays during formation of five annual rings in the root collar (the area between brackets in Fig. 1E) Z and S letters denote domains of Z and S-type, and numerals — the domains of the same origin. The rays were marked as orientational points. The arrow indicates the tree crown. The vertical lines in map a and E illustrate the grain course in the first and the last annual ring

map the Z-domain no. 11 reappeared so that the domain no. 11 was split into parts a and b.

The maps C and D indicate the expansion of Z-domains at the bottom and the expansion of S-domains at the top of the map.

On the last map *E* domains more or less uniform in size prevail.

The question arises: why does the rebuilding of cambial domains in the *Platanus* root collar occur so rapidly, otherwise than in the bole of this tree (see Krawczy szyn 1972)?

Probably this is associated with two factors:

1. reduction of the cambial area due to the thickening of the concave side of the tree basis;
2. superposition of domain patterns that migrate into the root collar from several roots.

In the root collar there is a transition from vertical orientation in the stem to more or less horizontal in roots from the external rooting area. The cambial cylinder must, therefore, undergo shortening there (which can be followed in the course of the rays in Fig. 1E), while it still expands in girth as growth in thickness proceeds. Presumably this shortening is not caused by a simple disappearance of delineated cambial areas but rather by the cambial cells intruding in between. Such a phenomenon has been noted by Jost (1901) in branch crotches. This process must depend on intrusive growth and elimination of cambial cells. At any rate there is good reason to believe that cambial domains also undergo shortening in the root collar.

The superposition of domains in the root collar is obvious if we consider every root as a source of domains that migrate towards this part of the tree (this appears from the occurrence of undulations on radial splits in all roots studied). Thus, in the root collar of *Platanus* domains gather as in a "domain sink". These domains interact with each other and pulsate. A model for such pulsation has already been offered by Hejnowicz (1974, 1975) based on the hypothesis that there arise waves of orientational events in the cambium.

According to such a model two or more domain patterns differing in domain height and in velocity of movement can exist in the cambium. Therefore, place in the cambium can be occupied at the same time by domains of both patterns. These domains will interact and pulsate: if domains are of the same type (Z or S) — they expand, if they are opposite (Z and S) — they neutralize one another, and disappear.

In the *Fraxinus* cambium studied by Hejnowicz (1974) two domain patterns may coexist: one with narrow and slowly-moving domains and another with wide and fast-moving ones. Thus, every step in cambial pulsation was rather easy to follow. In the root collar of *Platanus* domains are derived from several roots and they are much wider and quicker than in those of *Fraxinus*. Rebuilding of cambial domains should, therefore, be much more rapid than in the bole of *Fraxinus*. The case described in Fig. 4 seems to be consistent with Hejnowicz's data. This is also in agreement with previous data on young *Platanus* stems (Krawczy szyn 1973), where, on the

domain pattern appearing in young cambium, another pattern originating from older tree parts is superposed.

The rapid rebuilding of the domain pattern does not allow the establishment of a pattern of cell inclination in the cambium so that the grain is straight in the root collar.

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Domeny w kambium korzeni i szyi korzeniowej platana

Streszczenie

Przebadano włóknistość w drewnie oraz orientację zmian w promieniach podczas odkładania kolejnych, rocznych słoików drewna w korzeniach i szyi korzeniowej platana.