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Downward movement of the domain pattern in *Aesculus* cambium producing wavy-grained xylem

W. PYSZYŃSKI

Department of Plant Anatomy and Cytology, Institute of Botany, Wrocław University, Wrocław, ul. Kanonia 6/8

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Abstract

Cambium producing wavy xylem in *Aesculus* is characterised by a domain structure, that is "right" (Z) and "left" (S) areas of orientation of morphogenic processes occur in it. The domain pattern in the form of transversely running stripes of Z and S type moves down the trunk at a rate of 0.2 mm per year or 0.1 mm per 1 mm of produced xylem. The domain pattern finds its reflection in the wavy arrangement of the xylem cells, and the shift of domains is manifested in the oblique course of the undulations on the radial-split face of the xylem.

INTRODUCTION

The morphogenic processes in cambium such as oblique anticlinal divisions, overlapping of intrusively growing cell tips, ray splitting by these tips and elimination of oblique cell strands separating rays occur in two alternative configurations: "to the right" (Z) or "to the left" (S). The orientation of these cellular events is nonrandom and one of the alternatives predominates in a certain area of the cambium, called a domain of Z or S type.

The type of domain in a given part of the cambium changes in time, owing to the migration of the domain pattern in respect to cambial cells, along the trunk during formation of wood (Krawczyszyn 1971, 1972; Hejnowicz 1971; Hejnowicz and Romberger 1972). In the broadleaved trees investigated up- to- date the domain migrated upwards along the trunk (see Hejnowicz 1972).

The domain pattern may be reflected in the arrangement of xylem cells if the frequency of the cellular events in the cambium is sufficiently high. Areas which differ in the slope of grain correspond to the domains. The counterpart of domain migration is the shift of the areas in successive

annual rings, manifested by an oblique course of wood grain undulation on the radial-split face.

The domain pattern of the cambium is not directly visible. It may be outlined on the basis of investigations of morphogenic processes in the cambium. It was found that for domain study objects with interlocked grain or wavy-grained wood, that is those in which the fibre orientations change in time are most suitable (Hejnowicz 1971; Hejnowicz and Romberger 1972; Krawczyszyn 1971, 1972). The cambium which produces interlocked- or way-grain wood differs from cambium forming straight-grained wood mainly in the frequency of cellular events within the domains.

In studies on *Aesculus*, a tree with wavy grain was detected in which the character of the undulations indicated a downward movement of the domain pattern. This pattern was analysed and the present paper reports the result.

MATERIAL AND METHODS

From the outer part of the trunk of a ca. 90-year-old *Aesculus* tree growing in Chwalimierz (Lower Silesia) a xylem sample was taken at a height of 1.5 m from the base. From the sample a series of tangential sections ca. 30 μ thick was prepared. The sections consisting of 13 layers of terminal late xylem (TLX) were attached on slides with Haupt's adhesive, dried and immersed in boilling alcohol in order to expel air from the cell lumens. They were then transferred to xylene and embedded in Canada balsam. Images of the sections were projected onto photographic paper by means of a Zeiss Documator at a 49.5 magnification.

Since the tangential surface of the material investigated was not flat but wavy, the entire TLX area could not be visualised on one section. Therefore TLX fragments were photographed on several successive sections, and these put together gave a photograph of the entire investigated area which amounted to 3.7×7.5 mm.

Analysis of the domain pattern was performed on the basis of the changes occurring in the rays, by comparing them on photographs of the successive TLX layers. The photographs were compared in pairs: the second with the first, the third with the second and so on, and the places where the rays split or united were marked. In this way maps of the domain pattern were obtained. On the same photographs, the lines demarcating areas with different orientation of the fibres were drawn by joining the points at which the fusiform cells were tangent to the vertical edge of the section, which in turn was parallel to the axis of the trunk.

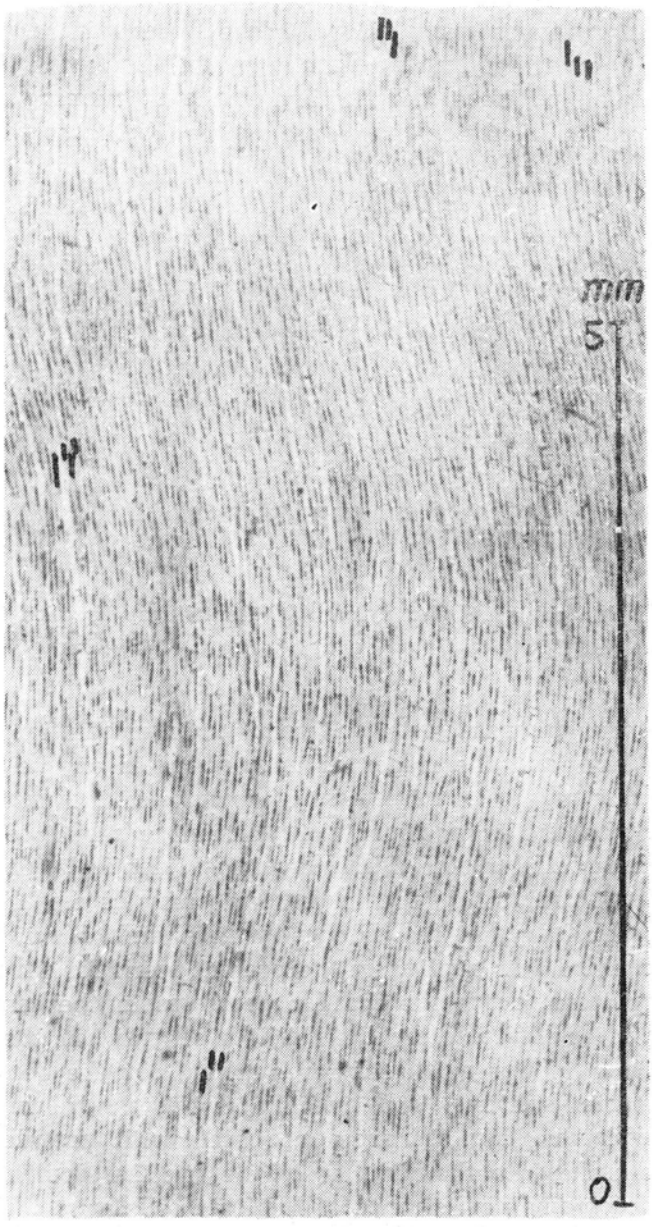

Fig. 1. Tangential section of studied xylem.

RESULTS AND DISCUSSION

The course of the fibres on the outer (tangential) side of the surface of the studied xylem is wavy (Fig. 1). The fibres with a wavy course deviate from the vertical axis maximally by ca. 12° to the left or right.

On the radial-split face "ridges" and "valleys" running obliquely to the rays and centrifugally downards are visible (Fig. 2) so that the same

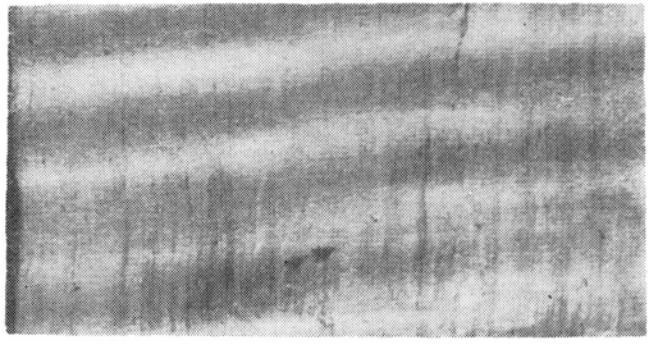

Fig. 2. Radial-split face of studied xylem, × 2. centrifugal direction is to the left.

ray passes through areas with different grain orientation. The angle between the rays and the ridges of undulations is on the average 4°. Such a waviness suggests a movement of domains in the course of xylem formation. Since the arrangement of dormant cambial cells and the adjacent xylem cells in the TLX layer is identical, developmental changes in the cambium of broadleaved tress may be established on the basis of the TLX layers (see Hejnowicz and Krawczyszyn 1969). This method was applied in the present work for investigation of the domain pattern. Since the cellular processes in the cambium were very intensive, as indicated by the changes of grain in the given part of the cambium, it was sufficient for marking out the domain pattern to examine the splitting and uniting of rays. On maps of the surface investigated (Fig. 3), areas are seen with prevalence of ray splitting and uniting to the right or to the left, i.e. domains of Z and S type. In Z domains new strands of fusiform cells arise inclined to the right, and among the old strands those inclined to the left disappear. An opposite situation is observed in S-domains. The borders between the domains run more or less transversely to the stem axis. In the area investigated the Z-domains were higher than the S ones. Comparison of the successive maps shows that with the formation of annual rings the domains move downwards in respect to cambial cells. The mean rate

of this movement is ca. 0.2 mm per year or ca. 0.1 mm per 1 mm of xylem formed. Owing to this movement, the same area of cambium is alternately occupied by Z nad S domains, and xylem is formed, the elements of which gradually change their orientation from left to right and so on. Fig. 3 shows that the borders on the last map are shifted by ca. 2.6 mm downards as compared to the initial position.

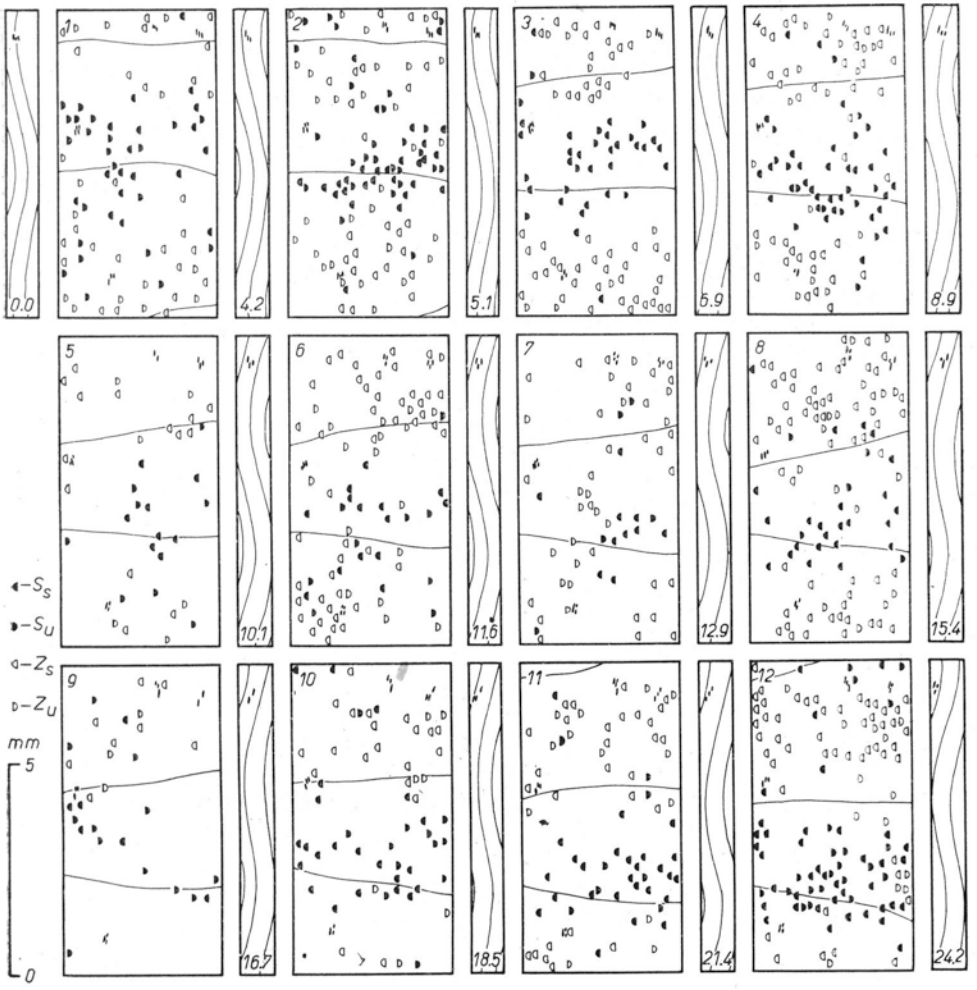

Fig. 3. Maps show occurrence and orientation of splitting and uniting of rays on the same cambium surface in the course of formation of 12 successive annual rings.

Map no. 1 corresponds of the cambium producing annual ring ca. 250 mm distant from the pith. The transversely running lines mark the bordes between areas with different orientation of grain. The narrow rectangular maps ilustrate the grain course on a strip of the studied area. The figure at the bottom of the map indicates the distance in respect to the first TLX layer studied in the series. Hatches denote the same rays in successive annual rings; Z_s and S_s — ray splitting of Z and S type, Z_u and S_u — ray uniting of Z and S type.

In general the areas of the domain pattern are identical with those occupied by the grain pattern.

As already mentioned in the introduction, in all the so far known cases of broadleaved trees (*Fraxinus excelsior, Acer pseudoplatanus, Betula verrucosa* — Hejnowicz 1972 and *Platanus acerifolia* — Krawczyszyn 1972) the domain pattern, and hence the grain pattern, moved up the trunk. In view of these results the case described in the present paper is particularly interesting since migration of the domains occurred downwards here. Maybe that this direction of domain movement is a trait specific of *Aesculus* as indicated by additional observations on other *Aesculus* trees in which the undulations of the radial-split face are centrifugally inclined like in the case here described. The possibility of occurrence of both orientations within a species, or individual as for instance in *Picea excelsa* (Hejnowicz 1971) cannot be excluded.

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Migracja wzoru domenowego w kambium produkującym drewno faliste u kasztanowca

Streszczenie

Kambium kasztanowca produkujące drewno faliste charakteryzuje się wzorem domenowym, tzn. występują w nim obszary „lewe" (S) i „prawe" (Z) ukierunkowania procesów morfogenetycznych. Wzór ten można było badać na podstawie rozszczepień i łączeń promieni ponieważ częstotliwość tych procesów była dostatecznie duża. Wzór domenowy składa się z poprzecznie biegnących pasów typu Z i S. Przesuwa się w dół pnia z szybkością 0.2 mm na rok albo 0,1 mm na jeden mm odłożonego drewna. Wzór domenowy w kambium znajduje swe odbicie w falistym układzie komórek drewna, a przesuwanie się domen znajduje wyraz w skośnym przebiegu falistości na przełupie promienistym.