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Transformation of the domain pattern in the development of *Fagus silvatica* L. cambium

WIESŁAW WŁOCH, PIOTR POPIEL, MAREK RUSIN, ANNA SŁOWIOCZEK

Department of Biophysics and Cell Biology, Silesian University, Jagiellońska 28, 40-032 Katowice, Poland

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Abstract

The domain pattern of cambium during the first year of its function in *Fagus silvatica* L. resembles a checkerboard. The longitudinal line along the leaf trace, its corresponding line on the opposite side of the internode and nodes comprise the domain borders. Starting from the formation of the first annual ring, this checkerboard pattern begins to undergo gradual transformation. A transitional domain pattern appears during the first few years; in each internode, due to the alternate disappearance of *Z* and *S* domains, a fragmentary domain of one type and an expanded domain of the opposite type occur in pairs. After further transformations, a regular pattern of transverse bands of domains moving along the stem appear on older stems (over ten years-old). This pattern is commonly found in other studied species of trees.

Key words: cambium, domain pattern, transformation

INTRODUCTION

Cellular events occur in cambium in one of two possible configurations: right [*Z*] or left [*S*] (Hartig 1901, Klinken 1914, Tupper-Carey 1930). Areas with a specific configuration are called domains (Hejnowicz 1964). Domains form characteristic domain patterns on the surface of the cambium (Hejnowicz 1975). The work of Krawczyszyn (1973a) shows that in *Platanus* cambium, *Z* and *S* domains, that is, right and left zones in terms of the orientation of the oblique walls formed through anticlinal divisions and intrusive growth of fusiform cells, as well as through the splitting and uniting of rays, already exist during the formation of the first annual ring. Their pattern reflects the differentiation of the stem into nodes and internodes. A *Z* and *S* domain occurs in each internode and the borders between them run longitudinally: one through the middle leaf trace, the other opposite it. The transverse borders between them are in the nodes. *Z* domains are found on the right, below the base of the closest upper leaf, *S* domains to the left of it. Because of this and the spiral arrangement of leaves, when moving along a one year-old *Platanus* stem we find alternating *Z* and *S* domains. As the young cambium deposits successive rings of wood, the domains change their sizes and shapes.

In *Fagus*, similarly as in *Platanus*, domains undergo transpositions and transformations. Because it is possible to identify domains on the basis of events in broad primary rays (Włoch and Szendera 1992), we can trace the transformations of domains over relatively large areas and long periods of time. The aim of the study presented in this paper was to describe on the basis of events in primary rays the process of transformation of the checkerboard domain pattern into the band pattern in the cambium of *Fagus silvatica* L.

MATERIAL AND METHODS

This study was carried out on sections of branches and stems of *Fagus silvatica* L. trees aged from a few to over ten years. The splitting of primary rays was analyzed on a series of tangential sections through the wood and on the surface of the wood after debarking. The borders between domains, that is, the areas with opposite configurations (*Z* or *S*) of ray splitting, were drawn directly on the debarked stem segment. The drawing was etched with a chisel and a plasticine impression made. This was then cast in plaster. The casts were photographed. Prints were made from the casts. The migration of domains was analyzed on the basis of the changes in the configuration of events in the primary rays, on the wood surface and read from the series of tangential sections.

RESULTS

Analysis of the configuration of splitting of the broad, multiseriate primary rays of *Fagus silvatica* L. makes it possible to determine the configuration of events on relatively large areas of wood surface and, as a consequence, to determine the domain pattern of the cambium.

On analyzing the splitting of primary rays in the cambium of the beech, we can see the characteristic domain patterns on a debarked stem. Initially, a checkerboard domain patterns is found, that is, one in which pairs of *Z* and

S domains occur in each internode, arranged on both sides of the leaf trace, always in a way so that a *Z* domain is formed on the right and an *S* domain on the left. A diagram of domain distributions based on ray splitting in 1 year-old stems is shown in Fig. 1.

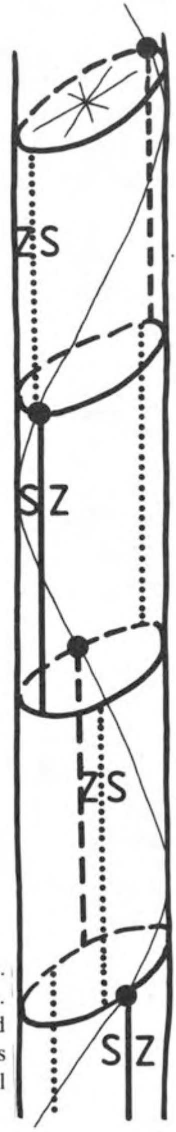

Fig. 1. Diagram of a checkerboard domain pattern in a one-year segment of a stem. The dotted line marks the vertical domain borders on opposite sides of a leaf trace. The continuous or dashed lines mark the domain borders along the leaf trace. *S* and *Z* denote *S* and *Z* domains, respectively. The position of transverse domain borders in the neighborhood of the node are marked by the oval. The position of the lateral bud is marked by a dark circle

After completion of elongation, we can see on a debarked stem that the bands of primary rays do not run parallel to the stem axis but, in agreement with the wood grain, along a spiral. The direction of the turn of the spiral changes in successive internodes and the angle of the turn increases as the stem's circumference increases. If, in one internode the rays turn to the left, then they split in configuration *S* and the *Z* domain disappears. In the neighboring internode, the rays usually turn right, split in configuration *Z* and the *S* domain disappears. The way in which strands of primary rays split in stems indicates that the surface of the cambium does not grow uniformly. Namely, the cambial surface develops more at the node level, opposite the point where branching occurs. This greater development is not, however, uniform in both directions. Upon following the strand of primary rays on the surface of the stem we can see that the rays slant to only one side in a given node and that is the basis on which we draw conclusions on the more intense growth of cambium in the peripheral direction. The direction of this more intense growth alternates in successive nodes. This causes the lateral buds, which initially were positioned more or less alternately, to turn more towards one side of the stem. This is visible both on

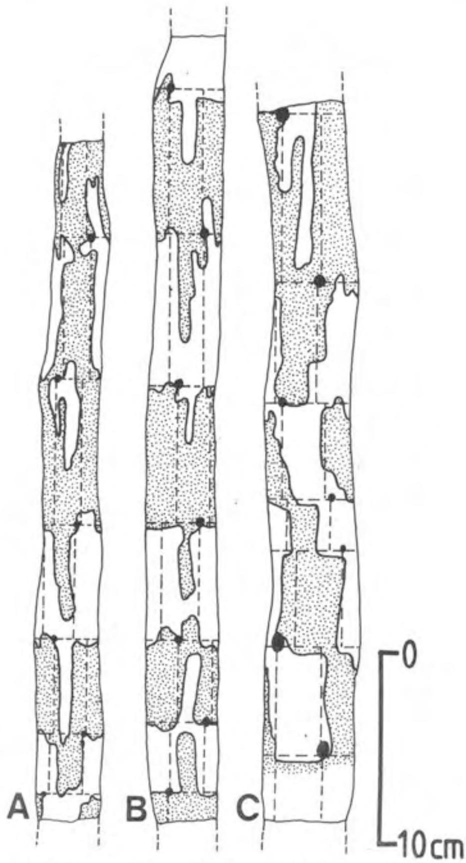

Fig. 2. The domain pattern of the cambium surface of sections of *Fagus silvatica* L. stems: A and B — two year-old stems, C — four year-old stem. The dashed lines mark the initial domain borders in the checkerboard pattern. The black dots denote branch bases of different sizes. The shaded area — *S* domain, unshaded area — *Z* domain

stems as well as on branches. It often becomes impossible to distinguish between several-year-old sections of stems and branches, with the only trait differing them being the smaller size of the annual rings in the latter. As a result of the occurrence of chiral grain and uneven cambial growth, as the distance increases from the stem apex, domains *Z* and *S* begin to alternately dominate, with the other gradually disappearing. This is well visible during the first several years of secondary growth (Figs. 2A, 2B, 3A and 3B). This leads to the establishing of a domain pattern in the form of transverse bands — one type of domain occurs per internode in an alternating fashion (Figs. 3C and 4). This pattern can be maintained even for a number of years, especially when the lateral branches growing out from the buds of each leaf axil develop uniformly. Normally, however, some branches develop more, others less, still others die. Because, of the nonuniformity of lateral branch development, the band pattern of domains is modified so that one domain can encompass even several primary internodes or, several domains can occur in one internode (Fig. 5).

The transformation of the domain pattern described above can be distorted in branches that are very shaded and growing slowly out of large tree trunks — it can then more or less be similar to the band pattern (Fig. 6A). Usually, however, in quickly growing lateral branches the formation of the band domain pattern is similar to that in stems. Figure 6B shows that, on the basis of primary ray arrangement, the rapid development of the cambial surface near the nodes opposite the branches can be observed, once to the right, once to the left of the successive nodes.

Comparing the actual domain pattern on the surface of a stem with the primary checkerboard domain pattern, it usually can be seen that the younger the studied stem, the greater the agreement (Table 1). The exceptionally high degree of agreement visible in a four year-old section of a slowly growing stem (Fig. 2C) is the result of the lower intensity of events in rays and, due to this, the only slight transformation of the initial pattern.

Table 1

Degree of correspondence of domain types with the initial checkerboard domain pattern

Stem segment	Age (years)	% Correspondence with theoretical *S* region	% Correspondence with theoretical *Z* region	% Correspondence $\frac{S+Z}{2}$
A (Fig. 2)	2	74.69	67.19	70.94
B ”	2	66.86	59.54	63.22
C ”	4	79.89	74.39	77.14
A (Fig. 3)	5	59.12	57.44	58.28
B ”	6	67.36	55.42	61.39
C ”	6	48.98	54.93	51.96

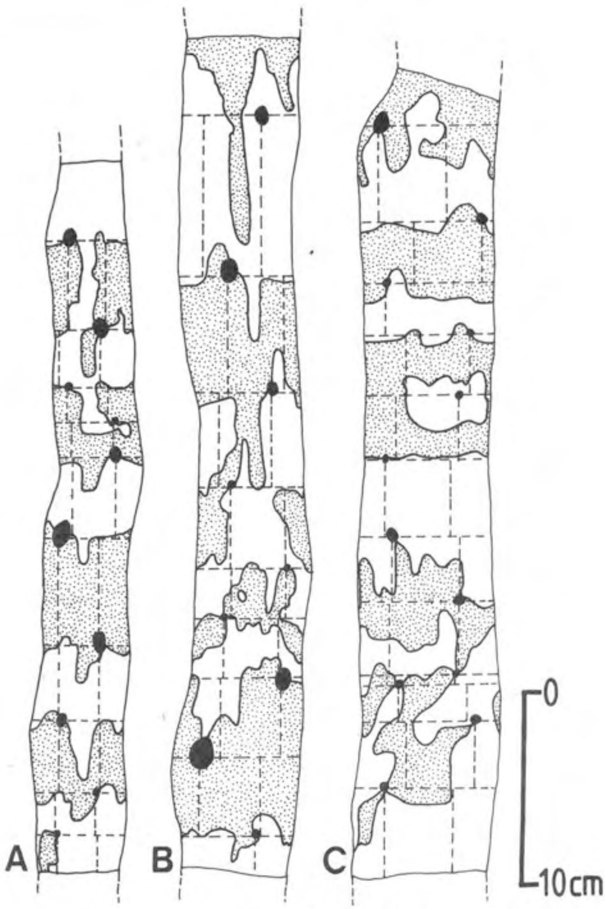

Fig. 3. The domain pattern of cambium surfaces of sections of *Fagus silvatica* L. stems: A — five year-old stem; B and C — six year-old stems. The dashed lines mark the initial domain borders in the checkerboard pattern. The black dots denote branch bases of different sizes. The shaded area — *S* domain, unshaded area — *Z* domain

DISCUSSION

The studies by K r a w c z y s z y n (1973a, b) on *Platanus* have shown that in one year-old branches, a correlation exists between the checkerboard pattern of domains and the arrangement of leaves and buds. Longitudinal wavy grain can be seen on the surface of radial splits in older *Platanus* branches. This grain is somewhat slanted in respect to the branch axis, in a much similar way as on the radial surface in a mature trunk characterized by interlocked grain in the wood and a band domain structure in the cambium (K r a w c z y s z y n 1973b). It can

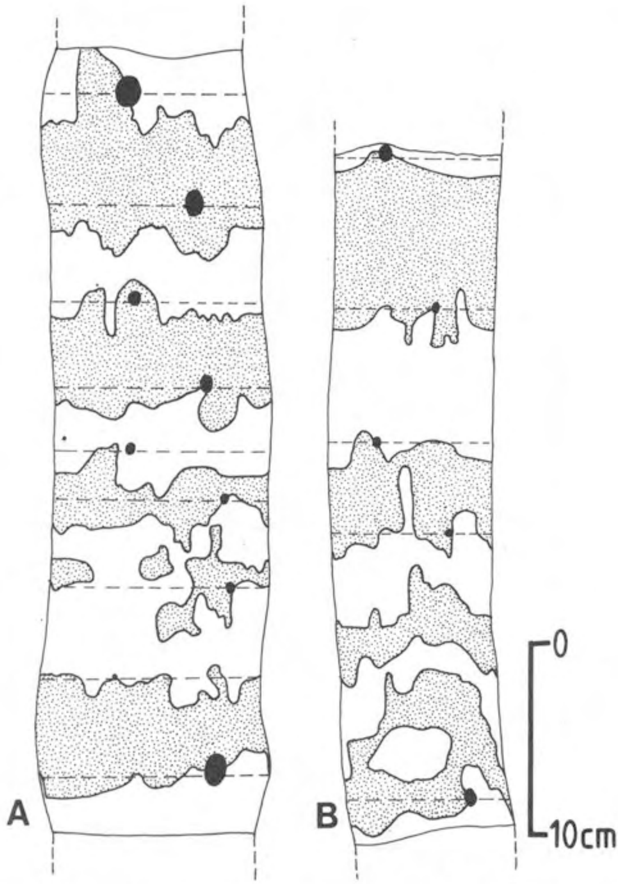

Fig. 4. The domain pattern of cambium surfaces of sections of seven year-old *Fagus silvatica* L. stems: A — growing freely, B — growing in the lower forest floor. The dashed lines mark the initial domain borders in the checkerboard pattern. The black dots denote branch bases of different sizes. The shaded area — *S* domain, unshaded area — *Z* domain

be concluded on this basis that the wood in older branches is also characterized by interlocked grain and that the cambium which deposited it has a band domain structure. On the basis of observations of domain growth in *Platanus* trunks and branches, it can be supposed that a transformation occurs of the checkerboard domain pattern of one-year branches into the domain pattern in the form of transverse bands migrating along the stem.

In this study, on the basis of observations of the events in primary rays of variously aged *Fagus silvatica* L. stems and branches, we found such a transformation of the domain pattern. On the other hand, however, in older stems and branches, we did not find wavy wood grain, which was probably the result of the low intensity of cellular events in the cambium.

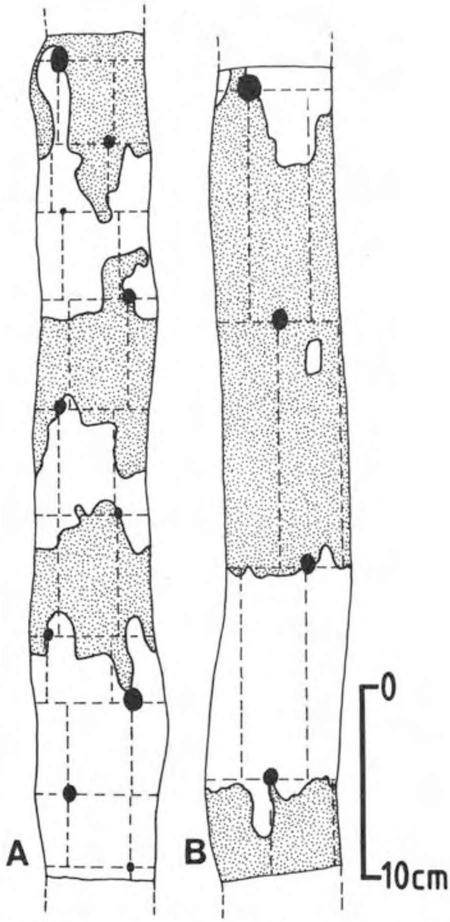

Fig. 5. The domain pattern of cambium surfaces of sections of stems of a century-old *Fagus silvatica* L.: A — nine year-old stem, B — four year-old stem. The dashed lines mark the initial domain borders in the checkerboard pattern. The black dots denote branch bases of different sizes. The shaded area — *S* domain, unshaded area — *Z* domain

Young leaves and buds are the main source of auxin in plants (A v e r y et al. 1937, J a c o b s 1956, D i g b y and W a r e i n g 1966). The direction of cell growth can be explained by the direction of auxin transport (S a c h s 1984, H a r r i s 1973, 1989, Z a g ó r s k a - M a r e k and L i t t l e 1986). The direction of the local flux of auxin probably affects the direction of growth of cells and tissue pattern in a young stem, e.g. the pattern of primary rays, which below the bud do not run parallel to the stem but separate at a certain angle and form a symmetrical pattern around that axis (K r a w c z y s z y n 1973b). In the next annual rings of the stem the tissue pattern is modified, primary rays are split by intrusively growing (along the axis of the main stem) fusiform cambium cell

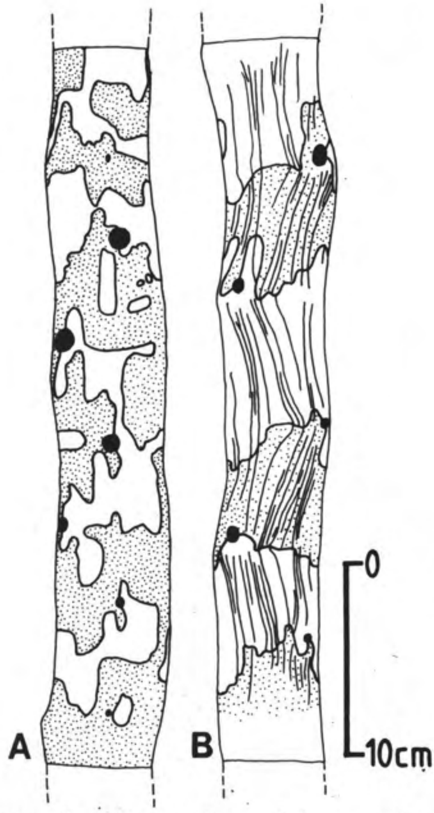

Fig. 6. The domain pattern of cambium surfaces of six year-old sections of *Fagus silvatica* L. branches: A — a section of a branch growing from the trunk of a several-hundred year-old tree; B — a section of a branch growing from the trunk of a tree ten-odd years old (the vertical lines denote strands of split primary rays). The black dots denote branch bases of different sizes. The current borders are delineated with continuous lines. The shaded area — *S* domain, unshaded area — *Z* domain

initials: to the right of the leaf trace splits in configuration *Z* occur and a *Z* domain is formed, while to the left, splits in configuration *S* lead to the formation of an *S* domain. In the first annual ring of a stem, a domain pattern is formed which reflects the node/internode structure of the stem. This initial pattern called the checkerboard pattern undergoes transformation due to the disappearance of the vertical borders among the domains.

It is not known what causes the unequal growth of the cambium surface in the transverse direction so that the lateral branches begin to be oriented more or less to one side of the stem, turning once to the right once to the left. The change in the orientation of cambium cells that is associated with this may thus bring about the change from the checkerboard to the band pattern. Stem elongation does not usually occur straight up, but under a certain angle. The orientation then of lateral branches more to one side of the stem (the upper side) causes their alternate twisting and appears to be the phototropic reaction of the plant.

After the migrating band domain pattern is established, as can be seen on the basis of the interlocked grain of the older *Platanus* branches, changes in the configuration of events in a given site of the cambium become cyclic. In the process of transformation of the domain pattern from checkerboard to band, the configuration of events becomes so ordered that a regular wavy pattern of changes in the configuration of these events is formed. It seems then, that a similar process exists in *Fagus*, although interlocked grain in older branches was not observed, due to the low intensity of cellular events.

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Transformacja wzoru domenowego w rozwoju kambium Fagus sylvatica L.

Streszczenie

W pierwszym roku funkcjonowania kambium *Fagus sylvatica* L. układ domen przypomina szachownicę. Linia podłużna wzdłuż śladu liściowego i odpowiadająca jej linia po przeciwnej stronie międzywęźla oraz węzły wyznaczają granice domen. Ten szachownicowy układ począwszy od pierwszego roku przyrostu ulega stopniowo transformacji. W ciągu pierwszych kilku lat tworzy się przejściowy wzór rozmieszczenia domen; w każdym międzywężlu, w wyniku zanikania na przemian raz domeny *Z* i raz *S*, występują parami: szczątkowa domena jednego typu i rozrośnięta domena typu przeciwnego. Po dalszych przemianach pojawia się na starszych kilkunastoletnich pniach regularny wzór poprzecznych pasów domen przesuwających się wzdłuż pnia. Taki wzór występuje powszechnie u innych badanych gatunków drzew.