Observation of changes of cambial domain patterns on the basis of primary ray development in *Fagus silvatica* L.

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Abstract

The high multiseriate primary rays that occur in young stems of *Fagus silvatica* L. undergo splitting during cambium development. Segments of the split primary rays remain close to each other and form characteristic strands. Within these strands, sections can be observed in which the rays are split in the same direction, either in configuration Z or S. The configuration of other cambial cellular events neighboring the primary rays under consideration is in agreement with the configuration of the splitting of these rays. The arrangement of the rays on the surface of the wood after debarking a young stem makes it possible to decipher the domain pattern on a surface of any given size. As the stem segment ages, the borders between domains migrate and new borders are formed, changing their course from longitudinal to transverse.

Key words: primary rays, pattern of domains, splitting and uniting of rays

INTRODUCTION

In studies on the rays of woody dicotyledons, attention is paid to average height and serration, the ratio of the surface of ray initials to that of fusiform initials in the cambium (Ghouse and Yunus 1976, Catesson 1980, Paliwal et al. 1984, Iqbal and Ghouse 1990) and to the arrangement of rays on the surface of the cambium (den Outer 1986).

The listed properties of cambium can change significantly during its development. In most trees, the width of rays increases with age (Barghorn

1940, 1941, Krawczyzsyn 1973, Iqbal and Ghouse 1987, Carlquist 1988, Włoch and Szendera 1989).

Very high primary rays, which split into smaller segments after initiation of secondary growth, can be found in some woody species (Krawczyzsyn 1973). Other high rays are found in the older branches and trunk of *Fagales*; Carlquist (1988) describes them as an exceptional example of aggregation of rays where the aggregating rays are transformed into a uniform mass lacking tracheal elements (including, in this case, fibers). This does not have, however, any relation to the formation of high and wide primary rays in *Fagus silvatica* L. which arise from the interfascicular regions of the stele of the primary body.

The splitting of rays may occur through the intrusive growth of fusiform cambial cells between the ray cells, or by means of transformation of ray initials into fusiform initials (Barghoorn 1940, Hejnowicz and Krawczyzsyn 1969) as well as by both means (Evert 1961). Rays can also fuse, either through elimination of the fusiform initials separating the rays or through the transformation of fusiform initials into ray initials (Krawczyzsyn 1971, Hejnowicz and Romberger 1973).

Splitting and uniting of rays occurs in one configuration, Z or S, over a certain area called a domain. The configuration of these events is in agreement with that of neighboring events in the cambium (Hejnowicz 1975, Dormer 1980).

The configuration of ray splitting corresponds with the configuration of other cellular events in the neighborhood of the rays under consideration, such as diagonal anticlinal divisions and overlapping of the ends of intrusively growing fusiform cells (Hejnowicz and Krawczyzsyn 1969, Krawczyzsyn 1971, 1972, Włoch and Wawrzyniak 1990).

The objective of this study was to see if it is possible to read the domain pattern over large areas of the cambium on the basis of cellular events in broad primary rays and to apply these studies to the tracing of the domain pattern associated with the development of cambium in *Fagus silvatica* L. branches.

MATERIAL AND METHODS

Selected samples of wood from *Fagus silvatica* L. stems and branches were degassed and softened by placing in alternating cold and boiling water-glycerin baths. The samples were then cut into a series of tangential sections about 30 μ m thick. The sections were attached to microscope slides using Haupt's adhesive, degassed and dehydrated by placing in alternating cold and boiling ethanol. They were then rinsed in xylene, submerged in Canadian balsam and photographed under a microscope. The arrangement and development of primary rays was analyzed in each series. The arrangement of these rays was also studied over large sections of stems after debarking them with the aid of a stereoscopic microscope.

RESULTS

During the formation of the first annual ring in stems and branches, primary rays are broad and very high, extending along the organ axis over numerous internodes reaching lengths of over ten centimeters. From the time they are formed, these rays undergo splitting and uniting. However, as wood is built up, rays begin to split more frequently than unite. This leads to the generation of increasingly shorter segments, which after several or several-odd years, attain average lengths of about 1 mm. In this paper we will term segments those fragments of a ray that had earlier undergone splitting and which are identifiable on tangential sections through the wood. As the surface of the cambium grows, new multiseriate rays, of about the same length as the segments of primary rays, arise from numerous short uniseriate rays.

Segments visible on the wood surface of young shoots were formed by the splitting of high primary rays and remain near each other forming strands. In this paper, we will term strands those characteristic serial arrangements of segments of a split primary ray which resemble beads on a string. Figure 1a shows a fragment of wood surface from a second annual ring with three sections of primary ray strands. A single split in configuration *S* can be seen in the center of the widest strand on the right. Several divisions in both configurations can be seen in the middle, most narrow strand. Three divisions in configuration *Z* can be seen in the strand on the left. Each of the splits of the primary ray occurred here as the result of the intrusive growth of only one fusiform cell. In the same fragment of the wood surface, but as early as in the seventh annual ring (the same in height but wider, corresponding to the enlarged cambial surface), the primary rays, split in configuration *S* by cleats of fusiform cells, have formed well visible strands of segments of initially very high primary rays (Fig. 1a'). We will term as cleats the groups of fusiform cells visible on tangential sections through wood, separating rays into two segments, as long as they are increasing in size and as long as such a situation is discernible. The growth of a cleat takes place through the intrusive growth and divisions of cambial fusiform cells in between segments. In Fig. 1a', the middle, narrow primary ray underwent splitting more quickly and, due to the growth of cleats, lost its strand structure (in the seventh annual ring it is only slightly visible).

When observing long fragments of primary ray segment strands, consistent splitting of rays in either configuration *Z* or *S* can usually be seen (Fig. 1b and 1b'). The width of the cleats of fusiform cells separating the segments of rays is taken to be an indicator of the time when the split occurred during the development of the cambium (Fig. 1c and 1c'). Changes in the configuration of ray splitting between successive segments and thus, in the configuration of the cleat, informs us of the change in domain type. Points between neighboring cleats of opposite configurations are well visible even by naked eye and make it possible to quickly delineate domain borders (Fig. 1d). A low intensity of cellular events

does not change the orientation of fusiform cells — the wood usually remains straight-grained, although the configuration of the cleats indicates the domain type (Fig. 1e).

As the stem gets older and the cambium surface expands, the ray segments separate as the result of cleat growth. Strands of split rays are still visible in stems that are more than ten or even twenty years old. These rays are usually alternately split in successive internodes, once in configuration *Z* (to the right), once in configuration *S* (to the left). This is especially visible when the domain borders move very slowly. In this way, as the cambium cylinder grows, the strands acquire a wavy structure along the stem (Fig. 2). In older stems, the wavy arrangement of these strands can be seen by naked eye, which facilitates tracing the splitting of primary rays in the appropriate configuration of events, thus enabling the domain arrangement to be determined.

Changes in the configuration of primary ray splitting and uniting take place during secondary growth in relation to the migration of domain borders. Modifications of a primary ray over a ten year period of cambium activity are shown on a fragment of wood photographed near a branch trace (Fig. 3). Changes in the orientation of uniting and splitting (middle ray on photograph A), from configuration *Z* to configuration *S* can be seen. In the transitional phase (photograph B), events in

Fig. 1. Photographs a and a'. A fragment of the tangential surface of wood illustrating changes in the primary rays during seven years of cambium activity. a — A fragment of the tangential surface of wood after completion of the second annual ring. *Z* configuration splits of the primary ray are visible. The narrow middle ray is split more frequently. a' — The same fragment of the tangential surface of wood after 5 years of cambial activity. Strands arising after splitting of rays in the *S* configuration are visible. The middle strand created as the result of splitting the narrow primary ray is partially masked due to the expansion of neighboring low wood rays. Photographs b and b'. A fragment of the surface of the trunk of a 7 year-old tree after debarking. Visible is a section of a strand that arose through the splitting of a primary ray where a change in configuration occurred at a certain site. This site is visible on photograph b' in greater magnification — wide cleats of fusiform cells separating the rays are visible. Photograph c and c'. A fragment of the wood surface of a 9 year-old portion of the trunk of a tree over ten year-old. A strand of segments of the primary ray is visible. The particular segments are separated by fusiform cell cleats of variable width (magnified fragment — photograph c'). Photograph d. A fragment of the wood surface of a 9 year-old portion of the trunk a tree over ten year-old. The primary rays are split in some sections into segments in configuration *Z*, while in others, in configuration *S*. The etched-in lines denote the domain borders. Photograph e. A fragment of the wood surface from a trunk over ten year-old. The primary rays are divided into segments in configuration *S*. The split crack is visible in the central part of the photograph. The bar in the lower right-hand corner equals 1 mm

both configurations are visible. Figure 4 presents a more detailed photograph of changes in the orientation from configuration *Z* to *S* in a selected fragment of a ray strand over a three-year period of cambium activity. Changes in the orientation of events are shown on 12 photographs from every fourth successive section of wood. Photograph 1 shows the splitting of a primary ray in three places in configuration *Z*. On photograph 2, the fusiform cells which split the ray and are visible in the central part of photograph 1, disappear. As the cambium develops, intrusively growing fusiform cells appear and split the ray in configuration *S* (photographs, 3, 4, 8 and 9). Photographs 5, 6 and 10 show vessel segments in a cleat of fusiform cells.

Fig. 2. The quasi-wavy arrangement of segments of split primary rays on the surface of the wood of seven-year (A) and four-year (B) sections of the stem. Domain borders are marked with a continuous line on photograph A. Natural size

Fig. 3. Three fragments of tangential sections through the wood of a beech. After two- (A), five- (B) and ten-year (C) periods of cambium development. The configuration of the splits of the primary ray on these sections changes from Z (photograph A) to S (photograph C). The bars indicate the same level of the primary ray as where the split was noted

Fig. 4. A fragment of a split primary ray in a series of tangential sections through a 3-year layer of wood of a several year-old segment of a stem. During this period, transformation of the configuration of ray splits from Z (photograph 1) to S (photograph 12) occurred. Segments of vessels are also seen in the strands of cells separating the rays

Figure 5 presents a series of photographs from successive tangential sections through the wood from a two-year period. The gradual transition of ray splitting from configuration S to Z can be observed. This takes place through the intrusive growth and elimination of cambial fusiform cells. The tracheal elements dividing the ray are usually fibers, but they often differentiate into vessel segments, as can be seen on photographs 20, 22 and 28. The central fragment of the cleat of cambial fusiform cells splitting the ray did not undergo elimination in spite of the change in the configuration of events.

Fig. 5. A fragment of a split primary ray in a series of tangential sections through a two-year layer of wood of a several-year-old segment of a stem. The change in the orientation of splits from configuration S to Z is visible. Segments of vessels are visible on photographs 20, 22, 28 and 29. The middle fragment of the fusiform cell layer splitting the ray did not undergo a change of orientation

DISCUSSION

The primary rays of the earliest layer of secondary wood of *Fagus* are not split and are inclined in the direction of the bud towards its lower side. On tangential sections through the wood in nodes from the side of the leaf gap, that is, through positions where the buds had been set, the rays are inclined in respect to the stem axis to the left at the right side of the gap and to the right at the left side of the gap. The inclination of these rays follows that of the vascular bundles which, in the primary stem, had entered the bud. From the very moment of initiating secondary growth, these rays undergo splitting in either configuration *Z* (to the right) or *S* (to the left), depending on their initial inclination. In the first annual ring to the right of the leaf trace, the rays are always split in configuration *Z*, and to the left, in configuration *S*. In this way, in each internode, one *S* domain and one *Z* domain are formed and their borders run vertically, one border along the leaf trace, the other along the opposite side of the shoot. The domains end in nodes with transverse borders. The spiral arrangement of leaves induces a checkerboard array of domains. A similar pattern of domains was observed by K r a w c z y s z y n (1973) who studied one-year-old branches of *Platanus*.

Young cambium domains change their shapes and sizes in successive annual rings of *Platanus* branches. The vertical borders disappear, diagonal borders appear, thanks to which *Z* and *S* domains can now encompass the entire circumference of the cambium cylinder (K r a w c z y s z y n 1973). It is interesting to note that in *Fagus*, the primary domain pattern, at least in the initial period, undergoes similar transformations.

Both in *Platanus* and in *Fagus*, a high intensity of events is observed in those primary rays which are in the vicinity of the lower side of buds and these events are always in configuration *Z* to the right of the bud and in configuration *S* to its left.

In most trees, rays are split either through the intrusive growth of cambial fusiform cells or through the transformation of ray cells into fusiform cells. The rays of the storeyed cambium of *Tilia* split and unite in a specific way. The directional intrusive growth of the tips of fusiform cells at the story borders generates changes in the contacts among the cells of neighboring stories, which leads to the splitting even of multiseriate rays without eliminating entire fusiform cells. This same intrusive growth leads to the uniting of the previously split rays in another arrangement, also without eliminating entire fusiform cells (W ł o c h 1985, 1987, W ł o c h and S z e n d e r a 1989).

It has been observed that as the surface of the cambium increases, the narrow rays in *Tilia* are split with increasing frequency and separate quickly, which makes it impossible for them to reunite (W ł o c h and S z e n d e r a 1989). In this study it was found that in *Fagus* the narrow primary rays also split faster and more frequently and that as early as in the first annual ring strands composed of segments of primary rays can be seen.

The quicker separation of segments of narrow primary rays causes the strands made up of them to vanish earlier; they become indiscernible as early as in rings that are only a few years old. In the case of *Platanus*, where the primary rays are usually seriated, these strands already are indiscernible in the second year of wood growth (KrawczyŹyn 1973).

The segments arising from the splitting of wide primary rays of *Fagus*, which are often more than 20 cells wide, retain their strand pattern for a considerably longer time and remain visible even in annual rings formed after more than ten years. It seems, then, that *Fagus* is a good subject for studying the transformation of the domain pattern in young branches on the basis of the events occurring in primary rays.

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Obserwacje zmian wzoru domenowego na podstawie rozwoju promieni rdzeniowych u Fagus silvatica L.

Streszczenie

Na powierzchni łodyg *Fagus silvatica* L. można obserwować pasma członów podzielonych promieni rdzeniowych w określonej konfiguracji jeszcze w kilkunastoletnich przyrostach rocznych. Z wiekiem kambium zmienia się konfiguracja podziałów promieni rdzeniowych — granice domen przemieszczają się. Śledząc konfigurację klinów (grup komórek wrzecionowatych rozdzielających promienie) jesteśmy w stanie wyznaczyć granice domen bez użycia mikroskopu na dowolnych powierzchniach drewna po okorowaniu łodygi. Ta stosunkowo szybka metoda wyznaczania wzoru domenowego umożliwia badanie transformacji tego wzoru w rosnących młodych łodygach.