Growth activity of fusiform initials in storeyed cambium

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Received: May 16, 1975

Abstract

The intrusive growth of fusiform initials was studied in *Entandrophragma*. This growth makes possible a change in the position of the cell ends of one storey in respect to those in the neighbouring storey, and this in turn leads to changes in the orientation of cambial initials. The growth activities of the oppositely directed ends of the same initial are not the same. Not all cell ends are simultaneously active. There are groups of ends distributed alternately in a storey which are active or inactive, so that a pattern of growth activity appears in the cambium. The activity of a particular cell end changes in successive time periods. Owing to this, the rate of creeping of one end past those of the adjoining storey varies. This phenomenon of changes in the activity of cell ends in time may be referred to the phenomenon of the appearance of the growth activity pattern on the cambium surface under the hypothesis of transverse shifting of the elements of this pattern ("active" and "inactive" groups) in relation to the cambial initials.

INTRODUCTION

In a previous study of the changes in cell orientation in storeyed cambium (Hejnowicz, Zagórska-Marek 1974) it was found that in *Entandrophragma cylindrica* cyclic changes of the inclination of the axis of the fusiform initials occurs. The changes result from the intrusive growth of fusiform initials which repeatedly produce a new pointed tip from one side of the existing tip which disappears. This causes a sort of creeping of cell ends of one storey past those of the adjoining storey (Fig. 1). The oppositely oriented ends of an initial creep in opposite directions so that the position of its center remains constant and only the angle between the cell and the stem axis changes. Intrusive growth occurs at one of the two radial lateral edges at the end of the fusiform initial. The choice of the right or left edge takes place according to the re-

quirement of the current direction of cell orientation change. A frequently observed consequence of intrusive growth at the lateral edge is the formation of a characteristic fork at the end of the cell.

Fig. 1. *Entandrophragma*: the same cambium area at two stages of change in cell orientation "to the left", reproduced on the basis of cell arrangement in the terminal parenchyma. The distance between the parenchyma layers is 1.2 mm. The groups of initials between the rays are numbered to facilitate their identification. The oppositely directed ends of initials of neighbouring storeys change their position in relation to one another.

Preliminary investigations demonstrated that the growth activity of various cell ends may be different. It was noted that forking may occur at the ends of several neighbouring cells of the same storey, i.e. in groups (Fig. 2). It was hoped that detailed investigations of the growth activity of initials will give an answer to the following questions:

- 1) is the distribution of growth activity on the cambium surface accidental or does it show some regularity?
- 2) does the activity of oppositely directed cell ends differ?
- 3) what course does the dynamics of the creeping rate of the cell ends take in successive periods of unidirectional change?

MATERIAL AND METHODS

The investigations were performed on the wood of *Entandrophragma cylindrica* from Africa, cut in the sawmill Dobroszyce (Poland) to veneer. The wood was available in the form of radial boards 3-m long from trunks of about 1-m diameter. From a board characterized by interlocked grain, in which light and dark strands visible on the radial surface (corresponding to areas of different inclination of the xylem elements) lay nearly parallelly to the annual rings, a small block was cut for preparing a series

Fig. 2. Fragment of terminal parenchyma with preserved cell arrangement in the cambium. A group of cells is visible with forked ends (arrows).

of tangential sections. This block was taken from the peripheral part of the board (peripheral part of the tree trunk). The mean distance between the successive layers of terminal parenchyma was 1.7 mm. The grain changed twice its inclination in the block along its radius. The orientation of the board in the trunk was not known, therefore it was not possible to establish the apical and basal direction on the sections. One group of ends oriented identically was assumed as the upper ones. The series of tangential sections were prepared as follows: 30- μ m sections were stuck successively on slides and treated with Javel water for clearing, then they were washed with tap water, dehydrated in ethyl alcohol and embedded through xylene in Canada balsam. Photographs were taken of the sections which contained axial parenchyma, by way of direct microscopic projection on photographic paper. These photographs served as basic material for the studies. The photographs included in the paper were prepared routinely with the use of a microscope and a camera.

RESULTS

Investigations of the growth activity of fusiform initials were performed on the basis of a series of tangential sections of wood, taking advantage of the fact that in each axial parenchyma layer the arrangement of cells existing in the cambium at the moment of deposition of this layer

is recorded. The growth activity of the initials in storeyed cambium can be established by analysing the occurrence on the cambium surface of cells with forked ends, or else by applying the criterion of the shift of the cell end, that is by establishing the distance of the shift of the cell end along the border of the storeys.

The first of the above mentioned criteria of growth activity was applied for solving the problem of activity of the upper and lower ends of the initials. The frequency of appearance of forked ends was determined in a population of 1000 cells, upper and lower forked ends being marked separately. It was found that cells with one forked end constitute 18 per cent of the total number of cells, this including 16.8 per cent of cells forked at the upper end. Only 1.2 per cent of cells showed a forked lower end. Cells with both ends forked (Fig. 3) are extremely rare, hence it may be concluded that the forking of upper and lower ends occurs independently (the probability of simultaneous forking of both ends is the quotient of the

Fig. 3. Fragment of terminal parenchyma showing the fusiform initial which grew intrusively at both ends simultaneously as shown by the forking (arrows)

Fig. 4. Cases in which two initials neighbouring vertically have forked ends (arrows).

probabilities of forking of the particular ends). The occurrence of cells with two forked ends is a proof, however, that intrusive growth may take place simultaneously at both ends of one and the same cell.

Cells neighbouring in vertical direction those with forked ends were examined, especially those close to cells with forked upper ends. Such cells were examined in 400 cases and it was found that 35 per cent of cells neighbouring vertically those with upper forked ends are also bifurcated (Fig. 4), as could have been expected on a random basis.

The second criterion was applied for studying the problem of growth activity in the time-space aspect. For this purpose the successive layers of axial parenchyma were compared. Between the terminal parenchyma layers about 1.7 mm distant there occur additional bands of parenchyma, the presence of which makes possible investigation of changes in the arrangement of cambial initials within periods shorter than one year. The

same group of initials may be recognized on bands of the parenchyma distributed at 400- μ m intervals, this corresponding in the material studied on the average to 1/4 of the growing season. In such short periods only some of the cell ends change their position — show activity. By denoting the active and inactive ends with different symbols a pattern of growth activity distribution in the cambium was obtained (Figs 5—7). The distribution of activity on the cambium surface in a given time period is characterized by a definite regularity: the active (inactive) cell ends are distinctly grouped together. The groups with active ends and groups with inactive ends (each consisting of several or a dozen or so cells) are distributed alternately within a storey, forming a pattern of growth activity on the cambium surface (Figs. 6, 7). Such a pattern occurs particularly when the course of the border between the storeys is regular. At a site where this border is deranged, e.g. at a site of splitting of the storey, the pattern either disappears or the active groups become smaller (Fig. 6). The distribution of groups in the successive storeys seems to be independent of one another. Sometimes an active group lies under an active one and vice versa in two neighbouring storeys (Fig. 6), in other places active groups irregularly shifted follow in the successive storeys (Fig. 7). The border between a group of active ends and inactive ones within a storey can be often established on the basis of the configuration of the ends: at the border the ends lie more densely together (Figs. 7, 8).

The rate of creeping of the cell ends along the border of the storeys was investigated for initials belonging to the same storey during the half-cycle of the cell orientation change, i.e. during the time period in which the initials change their inclination in one direction (from maximal inclination of their axis in one direction to maximal in opposite direction). The half-cycle investigated was the one in which the cells inclined to the left. During its duration the cambium formed a xylem layer 19 mm thick which included 12 layers of terminal parenchyma. The cell arrangement in 6 chosen parenchyma layers was compared. These layers were chosen so that the distance between them was more or less equal, amounting on the average to 3.8 mm. In this way the time of unidirectional change of cell inclination could be divided into $5 \pm$ equal periods. The cell arrangement was always compared in two successive layers, thus at the beginning and end of each period. For the chosen cells from various sites of the same storey the shift of their ends was determined in terms of the number of cells by-passed by the shifting end. For each of the 5 periods mean values of the shift were calculated. The mean shift proved to be almost equal in each period (Fig. 9). The mean velocity of end shift was about 0.5 during formation of 1 mm of xylem. For single cells of the studied storey the shift of the end varied in equal time periods. Changes in the velocity of creeping of the same end in the successive time periods were irregularly cyclic, that is the end crept alternately faster or slower

(Fig. 10). The characteristic maxima and minima of creeping velocity of the ends of neighbouring cells were shifted in relation to one another in time (Fig. 10 A). The cause of this shift may lie in the transverse migration of the growth activity pattern within the storey. Such a shift of growth activity was observed in the series shown in Fig. 5 B. The direction

Fig. 5. Three different cambium areas (A, B, C) at the beginning (1) and the end (2) of a period during which the initials changed their inclination, and which is measured in terms of deposited xylem layer (in μm , figure under each pair of drawings). The direction of the change is indicated by arrow in right upper corner of each second drawing in the pair. The cells are numbered for easier identification. Not all cell ends changed their position (were active): clear circles — active ends, full circles — inactive ends. The rays are circumscribed with a heavier line. In B the growth activity of cell ends (indicated by forking of ends) shifted in respect to the cells to the left

of the shift of local maximum activity is not stable and undergoes variations (Fig. 10 B, C, D).

By comparing the cell arrangement in layers I and XII of the terminal

Fig. 6. Distribution of growth activity on cambial surface. Clear circles — active ends, full circles — inactive ends. The activity pattern was delineated for the short period of cell orientation change measured in terms of thickness of deposited xylem layer (in μm , figure on right lower side of drawing). Arrow in right upper corner denotes direction in which the cells change their inclination. Rays are circumscribed with heavier line. In upper part of drawing the course of the storey border is rather regular. Groups of active and inactive cell ends in this part are distinct, active groups of one storey lie under active groups of a neighbouring storey. In the lower part of the drawing the storeyed arrangement is disturbed — the grouping of cells is less distinct

— 0,1mm

450

Fig. 7. Growth activity pattern in which groups of active cell ends are shifted irregularly in the successive storeys. Characteristic configuration of cell ends at the borders of active and inactive groups is marked with asterisks. Clear circles — active ends, full circles — inactive ones. Time of cell orientation change (measured in terms of thickness of deposited xylem layer in μm) is indicated on right lower side of drawing. Arrow in right upper corner denotes the direction in which cells change their inclination. The rays are circumscribed with a heavier line

parenchyma the extent of the total shift (N) of cell ends in the given storey could be determined. Not all cell ends reached equal N during the half-cycle of change in cell orientation (Fig. 11). The mean value was 9.

Fig. 8. Scheme of two possible configurations (A, B) of cell ends when an active end (clear circle) is adjacent to the inactive one (full circle) and when cell inclination changes to the right

Fig. 9. Diagram of mean velocity of creeping of cell ends during half-cycle of cell orientation change. $\bar{P}$ — mean shift of an end in terms of the number of by-passed cells; l — time in terms of thickness of deposited xylem (in mm). Below — the distribution of terminal parenchyma layers in the examined wood fragment. Heavier lines mark the layers chosen for investigation. Still lower arrows indicate the direction of the inclination of xylem elements in the wood fragment

Fig. 10. The shift of an end plotted against time during unidirectional change of cell inclination to the left. The shift (P) is measured in terms of by-passed cells, the time (t) — in terms of thickness (in mm) of xylem deposited. A single graph relates to one end. The groups of diagrams (A, B, C, D) concern groups of successive cell ends. The groups were distant from one another but lay in the same storey, O — denotes the position of the ray in the considered cell group. Arrows and circles indicate maxima and minima of the shift, respectively.

The difference between its maximal and minimal value was 5, thus it was rather wide. Cells characterized by a similar value of N were neighbouring ones within the same storey. In general, groups of cells reaching an N

Fig. 11. Total shift value (N) achieved by successive initials during half-cycle of cell orientation change (in this period 19 mm of xylem were deposited). $\bar{N}$ — mean shift. A and B — two distant parts of the same storey. O — position of the ray in the storey. The cells are successively numbered to the right of each ray. The numbering takes into account the common origin of cells arising by divisions which occurred during the studied period (cells with the same number). Full triangle indicates a cell which was eliminated

value higher than the mean were distributed alternately with groups of cells characterized by N values lower than the mean within the storey. The transition between two successive groups of cells was usually gradual.

DISCUSSION

The results of the studies allow the following conclusions:

- 1) the growth activity of oppositely directed ends of fusiform initials is not equal (the ratio of activity of the ends is 14 : 1);
- 2) there exists a certain pattern of growth activity upon the cambium surface (groups of cells with active ends alternate within the storey with groups having inactive ends);
- 3) the growth activity of the end of a given cell changes with time in an irregular cyclic mode.

The literature pertaining to differentiation of the growth activity of fusiform initials in cambium is rather scarce. The earliest finding was that the mean length of the initials in nonstoreyed cambium increases during the ontogeny of cambium, and that the length increments decrease with time until as a definite size of initials is reached. This is known as Sanio's rule (Spurr, Hyvarinen 1954; Philipson, Ward, Butterfield 1971; Hejnowicz 1973a). The diminution of the increments of the mean cell length are, however, not so much the result of declining growth activity of the intrusively growing cell ends as the result of progressing adaptation of the mean cell length (which is initially below the definitive value) to two opponent factors characteristic for the cambium: mean rate of intrusive elongation and mean frequency of pseudotransverse divisions (Hejnowicz 1967). The differences in rate and amount of interdivisional elongation of the upper and lower ends of fusiform initials were detected by Bannan (1956, 1968). He found that in the cambium of conifers intrusive growth (elongation) of the oppositely directed ends of fusiform initials was not equal. In the case of *Thuja occidentalis* basipetal growth tended to predominate (1956), whereas in *Pinus strobus* cell elongation was predominantly acropetal (1968). Similar results as with *Pinus strobus* were obtained by Brański (1970) in investigations on *Pinus silvestris*. The differences in elongation rate between the two ends of the initial cell were also observed in the cambium of *Liriodendron tulipifera*, however, the authors did not identify in this case the upper and lower ends (Chandle Esau 1964).

The distribution of growth activity on the cambium surface is a problem but little known. It results from the studies of Bannan (1956) that the tendency to elongation of the cell ends in one direction dominates within groups of several neighbouring cells. This author observed sectors on the cambium surface within which elongation of cell ends was predominantly upward, and nearby other sectors where the situation was quite different: the elongation was downward. Bannan believes that such co-ordination of growth among neighbouring initials is the result of specific local conditions. It is interesting that groups of initials in the cambium of *Entandrophragma* (with active or inactive ends) are distributed alternately within the storey. These groups may be considered as the equivalent of the sectors distinguished by Bannan in nonstoreyed cambium, although this author makes no mention of the periodicity of occurrence of these sectors on the cambium surface. The growth activity pattern formed by active and inactive cell groups in the cambium of *Entandrophragma* reminds us of another generally observed pattern — the domain pattern (Hejnowicz 1971, Hejnowicz and Romberger 1973). That a domain pattern exists in the cambium of *Entandrophragma* is indicated by the fact that the wood of this species is characterized by interlocked grain (Hejnowicz, Zagórska-Marek 1974).

As an analogous case may be quoted *Platanus* where a similar wood is formed owing to the fast migrating pattern of long domains (Krawczyński 1972). It may be that the domains in *Entandrophragma* cambium are wide areas of its surface, much larger than the elements of the activity pattern, that is groups consisting of at most a dozen or so cells. In an earlier study (Hejnowicz, Zagórska-Marek 1974) it was observed that there are small undulation in the wood of *Entandrophragma* which probably are the result of superposition of the minute domain pattern so far not characterized, on the basic pattern of large rapidly migrating domains. May be that this minute pattern is connected with the nonuniform distribution of growth activity on the cambium surface.

The domains migrate in relation to the initials in the cambium. No doubt the growth activity pattern moves too as described in the present paper. Transverse movement of growth activity in the storey of initials explains two phenomena: the presence of a regular growth activity pattern on the cambium surface (noted at several different time periods) and the cycle of growth activity of the ends of a single initial. As regards domains, the cyclic change of the domain type at a given site in the cambium is the expression of the time aspect of a moving wave of orientational tendency in the cambium (Hejnowicz 1973b, 1974). If the direction of shift of the local growth activity maximum would be stable within a storey, a moving wave of activity might also be postulated in this case. Since this direction is changeable (Fig. 10 B, C, D) the cyclic change of activity of the ends in time could be due to a standing wave changing its position in the storey in an oscillatory way. Beside the domain pattern and the growth activity pattern, one more example of migrating pattern in the cambium is known: in the cambium of *Carpinus*, namely, the area of aggregated rays is shifted sideways in relation to the cambium cells (Holdheide 1955).

The author wishes to express her deep gratitude to Professor Z. Hejnowicz for his valuable comments and advice in the course of this work.

This investigation was supported in part by a grant of the United States Department of Agriculture, authorized by Public Law 480.

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Aktywność wzrostowa komórek inicjalnych w kambium piętrowym

Streszczenie

W kambium piętrowym *Entandrophragma cylindrica* zachodzą cykliczne zmiany w nachyleniu osi komórek inicjalnych. Zmiany te dokonują się dzięki aktywności wzrostowej końców komórkowych: rosnące intruzywnie (aktywne) końce zmieniają swoje położenie na granicy pięter. Przyjęto dwa kryteria aktywności wzrostowej końca komórki inicjalnej:

1) kryterium rozdwójonego końca — rozdzielenie bowiem jest wynikiem wzrostu intruzywnego bocznej krawędzi promieniowej przemieszczającego się końca i stanowi etap pośredni pomiędzy jego dwoma kolejnymi położeniami;

2) kryterium wielkości przesunięcia końca wzdłuż granicy pięter w czasie zmiany nachylenia osi komórek.

Stwierdzono, że rozdzielenia u większości komórek występują na jednakowo skierowanych końcach z czego wynika, że aktywność wzrostowa końców tej samej

komórki inicjalnej jest niejednakowa — jeden koniec jest częściej aktywny niż drugi.

W krótkich (kilkumiesięcznych) okresach czasu na powierzchni kambium istnieją jednocześnie końce aktywne — te, które zmieniają swoje położenie i końce nieaktywne — nie zmieniające swego położenia. Grupy końców aktywnych i nieaktywnych, składające się z kilku do kilkunastu komórek każda, są rozmieszczone naprzemiennie w obrębie pięter tworząc wzór aktywności wzrostowej na powierzchni kambium. Stwierdzono też, że aktywność wzrostowa danego końca komórkowego zmienia się cyklicznie w czasie — koniec przemieszcza się wzdłuż granicy pięter raz szybciej raz wolniej. Zjawisko zmiany aktywności końców w czasie można połączyć ze zjawiskiem występowania wzoru aktywności na powierzchni kambium przyjmując hipotezę o poprzecznym przesuwaniu się elementów wzoru aktywności (grupy „aktywne” i „nieaktywne”) względem komórek inicjalnych w piętrze.