The storeyed and non-storeyed arrangement of rays in the storeyed cambium of *Tilia cordata* Mill.

WIESŁAW WŁOCH¹, WALDEMAR SZENDERA²

¹Department of Biophysics and Cell Biology; ²Department of Botanical Systematics, Silesian University, Jagiellońska 28, 40-032 Katowice, Poland

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Abstract

Due to restructuring of the cellular arrangement, rays in storeyed cambium undergo transformations, that is, uniting and splitting on the borders of storeys, when their height during development exceeds that of the storeys of fusiform cells. The primordial rays on the cambium surface have a non-storeyed arrangement. Prolonged predominance of splitting over uniting can lead to a situation in which the height of the rays does not exceed that of fusiform cell storeys. A storeyed arrangement of rays is thus formed. The maintenance of a given arrangement of rays in successive annual growths is the result of the cumulation of several traits, such as: 1) the seriation of rays, 2) the magnitude of grain inclination, 3) the rate of the restructuring of the cell arrangement. For example, the quicker a storeyed arrangement of rays will be formed the less the rays are seriated, the quicker the cells are restructured and the greater the inclination of their arrangement. The magnitude of the inclination of the grain and the rate of cell restructuring are traits connected with the arrangement of fusiform cells. The seriate nature of rays, however, is characteristic of rays and, moreover, it is a characteristic individual trait. It seems that the seriation of rays can play a valuable role in taxonomic analysis.

Key words: storeyed cambium, seriation and arrangement of rays

INTRODUCTION

Two kinds of rays occur in linden cambium: low, usually uniseriate and high, mainly multiseriate rays (Włoch 1985, 1987). Ray dimensions, that is, length, width and height, are presented in Fig. 1 (Hejnowicz 1980). The low rays can be seen in various phases of their formation, from only one cell to many. Their height does not exceed that of the fusiform cells within the given storey. The high rays, however, are higher (even by several-fold) than the fusiform cells and can be split on the border of fusiform cells due to the changes in the contacts of the tips of initial cells. The component rays which so arise can reunite if they come into contact again. The low rays incline along with the fusiform cells and do not undergo events; they grow into multiseriate rays and when they reach the storey borders, they can join and become high rays.

Fig. 1. An illustration explaining the terminology used in describing the dimensions of wood rays, using a diseriate ray as an example

The splitting and uniting of rays takes place either in the "S" or "Z" configuration (Hejnowicz and Krawczyszyn 1969, Włoch 1985). Because the uniting of rays is something akin to the inversion of splitting, we shall define "S" uniting as the elimination of the configuration of rays which arises as the result of splitting, in other words, configuration Z, and type "Z" uniting as the elimination of configuration S (Fig. 2). Because of the growth of the cambium surface, the new rays created by the splitting of high rays can unite with other rays in a new, fitting arrangement (Fig. 3).

Fig. 2. A diagram of the possible events occurring in rays in connection with the restructuring of the arrangement of fusiform cells. Dotted regions — rays. Broken lines — borders of storeys of fusiform cells. S_u — uniting in configuration S, S_s — splitting in configuration S, Z_u — uniting in configuration Z, Z_s — splitting in configuration Z.

Fig. 3. A model showing the changes in rays occurring in three successive borders of annual growths in connection with the restructuring of fusiform cells in configuration Z. Large numbers — successive numbers of the annual growths, a-n — rays, small numbers — 1, 2 (used along with letters) denote segments of high rays which fit within the storey of fusiform cells marked in the initial arrangement (see: annual growth border nr. 1). Thin horizontal lines mark the border of fusiform cell storeys. The shaded columns on the left of each ray arrangement illustrate the grain direction. A double broken line is used to mark the splitting and uniting of rays. The rays c, f visible on the first border are high rays, the remainder are low rays. Rays c, f each have two segments. All events in the rays (unitings and splittings) are in configuration Z. In the second growth, uniting predominates, due to the decrease in the angle of inclination of the grain there are four unitings and one splitting. In the third growth the angle of inclination of the grain increases and ray splitting predominates; there is only one uniting for four splittings

The change in the configuration of rays is in agreement with the change in the configuration of the tips of fusiform cells on the storey borders neighboring the rays under consideration (Włoch 1985, 1987, 1988). The change in the configuration of the tips of the fusiform cells on the storey borders leads to changes in the inclination of cells. When there is a cyclic change in the inclination of cells over a large area of the cambium surface, a cycle in the rays also occurs: a predominance of uniting, a predominance of splitting, a predominance of uniting etc. (Fig. 3). As the angle of the inclination of the cells (in

respect to the trunk axis) increases, the number of ray splits also rises. When the maximum inclination is reached, it begins to decrease and the number of unitings of rays increases. When the inclination of cells is large, short rays are usually found. They fit within the limits of storeys, and a more or less pronounced storeying of rays is visible (Fig. 4).

Fig. 4. The terminal parenchyma in tangent section on two borders of annual growths, selected from a sample of wood taken from a linden about 100 years of age. The numbers denote the successive growth border. 93 — the growth border in which the cell arrangement is strongly inclined in configuration S. In some fragments the rays are arranged almost storeylike (arrow). 100 — the border of the last growth. The cells are not inclined, the rays are higher and not storeyed

A large predominance of splitting over uniting can lead to a situation in which the height of the component rays created by the splitting of high rays does not exceed that of fusiform cell storeys, which in turn, leads to a storeyed arrangement of rays. It is understandable, then, that a storeyed arrangement of rays should be expected in a rapidly restructuring cambium. However, no relationship has been found between the arrangement of rays and the rate of changes in the grain orientation. Observations show that the non-storeyed arrangement of rays is also often found in rapidly restructuring cambium.

The uniting and splitting of rays during the formation of annual growths in linden wood causes constant changes in the height and arrangement of rays. It should be said here that the height and arrangement of rays are described in literature as taxonomic traits helpful in the systematics of trees, and therefore are more or less constant for species (Ghouse and Yunus 1976, Ghouse et al. 1980, den Outer 1986, Paliwal et al. 1984).

The purpose of this study was to find such relationships between the structure of rays and the dynamics of the restructuring of the storeyed arrangement of fusiform cells in linden cambium which could account for the storeyed arrangement of rays which is sometimes found there.

MATERIAL AND METHODS

The studies were conducted on 4 linden trunks, aged 25 and 36 years and two specimens about 100 years of age. The samples taken from the chosen trunks were examined for seriation, height and arrangement of rays and the rate of restructuring of the arrangement of fusiform cells. The results were obtained by analysis of tangent sections of successive terminal parenchyma layers from the borders of annual growths. The arrangement of cells in the terminal parenchyma is the same as that of the cambium which was active when these layers were formed. In addition, the seriation of the rays in the terminal parenchyma corresponds to the seriation of rays in cambium and can differ from that which occurs during the formation of annual growths (Gregory and Romberger 1975). The studied samples are described in Table 1, in which the ages of the studied trees (two young and two older), the number of the annual growths where the average rate of restructuring the cell arrangement was studied, and the number of the annual growths photographed in light and stereoscopic microscopes using a dark field condensor, are presented. The seriation and ray arrangement in the studied samples were compared with the rate of cell arrangement restructuring. The height and seriation of rays in the first three samples of wood in the tenth annual growth ring (in the 4th sample, the border of the 10th annual ring was not examined) were also analysed.

Table 1
Wood samples from the linden stems selected for studies

Sample number	Age of tree (years)	The numbers of 15 successive annual growths in which changes in the grain were studied	The numbers of the growths in which seriation and ray arrangement were studied	The numbers of the growths which were photographed	The size of the area of the terminal parenchyma from the tenth growth on which the height and seriation of rays was studied (mm ²)
I	25	11-25	10-25	10 and 25	9.78
II	100	86-100	10 and 86-100	10 and 95	10.30
III	36	21-35	10-36	10 and 29	10.45
IV	100	81-95	61-100	91	—

RESULTS AND DISCUSSION

A storeyed and non-storeyed arrangement of rays can occur in the cambium of *Tilia cordata* Mill. The cambium of different individuals, sampled from the same place of the trunk can have different ray structures (Fig. 5) Fig. 5A shows a predominance of narrow 2-3 seriate rays forming a storeyed

Fig. 5. Tangent sections through the cambium of two 50-year-old lindens (*Tilia cordata* Mill.).
A — storeyed 1-3 seriate rays. Their height does not surpass that of the storeys of fusiform cells.
B — the high rays are 4-5 seriate. Their height exceeds several-fold that of fusiform cell storeys
Photograph A shows more split cell tips

arrangement not higher than the height of a storey of fusiform cells, whereas in Fig. 5B, the high rays are wide, mainly 4-5 seriate and do not fit within the storey of fusiform cells and do not form a storeyed arrangement.

The storeyed and non-storeyed arrangement of rays is found irrespective of the age of the tree. The storeyed arrangement of rays is found both in the trunks of 25 and 100 year-old lindens, the non-storeyed in the trunks of 36 and 100 year-old ones. A non-storeyed arrangement of rays was always found in the first ten-odd annual rings of the studied trees. The storeyed arrangement of

Fig. 6. The relationship between the height and seriation of high rays in the terminal parenchyma from the 10th growth border of three lindens. Low rays below 2.5 seriate were not measured. An empty circle marks the rays in the wood of sample II. Solid circles mark the rays in sample I. The crossed circles mark the rays in sample III. Each circle denotes the means of several points in the ray. The distribution of empty circles forms the set of 1-3 seriate rays. The area of this set is dotted. The distribution of the crossed circles forms the set of the highest, over 3 seriate rays. The area of that set is shaded. The solid lines A, B and C denote the mean height of fusiform cell storeys of the three studied individuals, I, II and III, respectively. The broken vertical line is the seriate border equal to 2.5. Low rays of a seriation exceeding this were also measured

rays was not found anywhere in the terminal parenchyma of the tenth annual growth ring. The height and seriation of rays were measured over a 10 mm^3 tangent sample area of this growth in the three studied trees. The measurements were made on the high rays whose height was greater than that of the average height of fusiform cells and on low rays which were more than 2.5 seriate (the measurements were made in several points of the ray and averaged). It was accepted that the rays having such a seriation were mainly component rays created by the splitting of high rays. It turned out that there was no characteristic height of rays for a given sample. Each ray had a different, variable in time, height independent of other characteristics of its structure. About 80% of the studied rays had a determined, unique height. The seriation of rays, however, is a constant trait and individuals can be distinguished whose rays, irrespective of their height, group together forming assemblies of similar seriation (Fig. 6). It was found that: sample no. I had 2-4 seriate rays, sample no. II had narrow 1-3 seriate rays and sample no. III had wide, over 3 seriate rays (Fig. 7).

In observing the arrangement of rays in the successive growths in all of the studied individuals, it was found that the storeyed arrangement of rays was

Fig. 7. Tangent sections through the terminal parenchyma on the border of the tenth growth of three lindens. Linden I — the high rays are 2-4 seriate, linden II — the high rays are 1-3 seriate, linden III — the high rays are over 3 seriate

established in samples I and II when the tree was already ten-odd years old, while the storeyed ray arrangement did not form at all in samples III and IV (Figs. 8 and 9).

All four samples of wood were characterized by interlocked grain, which was already noticeable when the trees were only a few years old. In each sample the size of the changes of the inclination of the grain in the wood for 15 successive growth ring borders was measured. The average value of this changes was calculated and expressed per year and per 1 mm of growth. The mean value of the change in the angle of grain inclination per year will be denoted by the letter Σ . It was observed that the storeying of rays was related to the seriation of rays and the value of Σ , irrespective of the age of the tree. The smaller the seriation of rays and the greater the Σ , the more pronounced was the storeyed arrangement of the rays (Table 2). However, there was no dependence between the average change in the angle of inclination of the grain, when calculated per 1 mm growth of wood, and the occurrence of a storeyed or non-storeyed arrangement of rays.

In rapidly restructuring cambium, the storeyed arrangement of rays is formed primarily where narrow, 1-3 seriate rays occur. In the first years of growth, such rays are usually high and have a non-storeyed arrangement, but more often than wide rays, undergo splitting during the rearrangement of fusiform cells. Due to the rapid expansion of the cambium surface during this period, the component rays formed by splitting cannot come into renewed contact with each other and reunite. They finally form storeys in such a fashion that their heights rarely exceed the length of fusiform cells (Fig. 10A). Wide rays, usually 3 seriate, in spite of the large changes in the inclination of their grain, do not undergo splitting to such an extent as narrow ones do. In wide rays, a more or less constant frequency of uniting and splitting is maintained during the rapid restructuring of the arrangement of fusiform cells. In extreme cases, when the rays are very wide, they may not undergo splitting at all (Fig. 10B). It seems then, that the storeyed arrangement of rays is a characteristic which is formed gradually during the growth of a tree and is directly associated with the rate of restructuring of the arrangement of fusiform cells. The number of split cell tips per unit surface of cambium also is an indicator of the rate of restructuring. The more such cell tips, the more fusiform cells are currently in the process of restructuring (Fig. 8).

In samples I and II of the studied trees, a storeyed arrangement of rays became established such that the uniting and splitting of high rays due to restructuring the cell arrangement occurred sporadically. In samples III and IV which were characterized by a non-storeyed arrangement of high rays, it can be expected that in the successive annual growths there will be a more or less equal number of ray unitings and splittings.

Fig. 8. The arrangement of rays in the terminal parenchyma on the borders of annual growths in the wood from trunks of different lindens. Tangent sections. I — a 25 year-old linden. A storeyed arrangement of rays mainly 3-4 seriate on the border of the 25th growth. II — a 100 year-old linden. Storeyed rays, mainly 2-3 seriate on the border of the 95th growth. III — a 36 year-old linden. Non-storeyed high rays, mainly 5-6 seriate on the border of the 29th growth. IV — a 100 year-old linden. Non-storeyed high rays, mainly 3-4 seriate on the border of the 91st growth. Frequently split fusiform cell tips on the storey borders are visible on photos I, II and III. On photo IV such cell tips occur infrequently and the cell tips are usually pointed

Fig. 9. The arrangement of rays in the terminal parenchyma of annual growths in the wood of trunks of lindens as in Fig. 8. The photographs of large fragments of tissues were made using a stereoscopic microscope equipped with a dark field condensor

Sample III exhibited a very frequent change in the orientation of the grain (every 2-4 years) and, in spite of the small angle of inclination of the grain, the rate of restructuring was relatively rapid. However, the uniting and splitting of rays took place with a certain lag, so we did not find a dependence between the height or number of rays and the magnitude of the angle of inclination of the grain. A relationship should, however, be seen when the number of rays and their heights are compared (Fig. 11) (Janikowska 1986). It should be noted that only the high rays and those low rays having a width equal to that of the high rays were measured, which allows the latter to be considered mainly as component rays created by the splitting of high rays. Figure 12 demonstrates this relationship well by the appropriate value of the scale having been chosen for the number of rays and their average height in successive annual growth

rings. The number and height of rays are seen to change cyclically, and the cycles of changes are strictly synchronized. An increasing number of rays usually corresponds with their decreasing average height, which points to the predominance of splitting; conversely — a drop in the number of rays corresponds with a rise in their average length, which indicates the predominance of uniting of rays. The uniting and splitting of rays in the context of the configuration of events was also analysed in this sample in the study by Włoch (1987). The cycle of changes in the number and height of rays in this sample is generally comparable to the cycle of changes in the orientation of the grain (Table 2). Probably due to the very large width of the rays (4-5 seriate rays predominate), a storeyed arrangement of rays is not formed in spite of the high rate of restructuring of the cell arrangement. Rapid but small deflections give high values of Σ , but do not necessarily bring about a greater

Table 2

Changes in the angle of inclination of grain, in degrees, for 15 successive growths in four samples of wood from *Tilia cordata* Mill.

I			II		III			IV		
a	b	c	a	b	a	b	c	a	b	c
		-2.0					+0.5			+14
11	0.5	-2.5	86	3.0	21	2.5	-2.0	81	6.0	+20
12	2.5	-5.0	87	2.0	22	3.5	+1.5	82	1.0	+21
13	5.5	+0.5	88	4.0	23	1.75	+3.25	83	0	+21
14	3.0	-2.5	89	5.0	24	4.75	-1.5	84	1.0	+20
15	1.5	-1.0	90	1.0	25	3.25	+1.75	85	0.5	+19.5
16	4.5	+3.5	91	1.0	26	3.0	-1.25	86	0.5	+19
17	1.5	+2.0	92	0	27	0	-1.25	87	1.0	+18
18	2.5	+4.5	93	0	28	1.25	0	88	0.5	+17.5
19	0.5	+4.0	94	4.0	29	2.0	+2.0	89	0.5	+17
20	1.0	+5.0	95	0	30	2.0	0	90	1.0	+16
21	4.0	+1.0	96	0	31	0.5	-0.5	91	2.0	+14
22	4.5	+5.5	97	1.0	32	1.0	+0.5	92	1.5	+15.5
23	0.5	+6.0	98	3.0	33	1.75	-1.25	93	0	+15.5
24	5.0	+1.0	99	5.0	34	1.0	-2.25	94	0	+15.5
25	2.0	+3.0	100	3.0	35	0.25	-2.0	95	0.5	+15
$\Sigma = 2.6$			$\Sigma = 2.13$		$\Sigma = 1.9$			$\Sigma = 1.06$		
0.37*			1.43*		0.49*			1.19*		

I, II, III, IV — number of sample and tree; a — the number of the successive growth border; b — the magnitude of the change of the angle of inclination of grain, in degrees; c — angle of inclination of grain in degrees. The border numbers in bold print denote the places where the photographs in Fig. 8 were taken. Σ — mean change in the angle of inclination of grain per year. * — mean change in the angle of inclination of grain per 1 mm of growth of tree, IIc — data lacking.

Fig. 10. A comparison of the arrangement of high rays in tangent section of straight-grained linden wood (the angle to the trunk axis is 0°) during the first years of secondary growth (A_1 and B_1) with the ray arrangement several years later (A_2 and B_2) when the grain began to incline (the angle to the trunk axis is 15°) and with the arrangement after the next several years when the inclination of the grain is eliminated (A_3 and B_3). In case A, narrow rays occur, in case B — wide rays. The broken line marks the borders of fusiform cell storeys in the terminal parenchyma. The gradually increasing dimensions of rectangles A_1 to A_3 and from B_1 to B_3 demonstrate the increase in the surface of the cambium. After splitting, narrow rays separate and do not return to their initial arrangement; they form a storeyed arrangement. Wide rays (B) after bending return to their initial shape; they do not form a storeyed arrangement

intensity of splitting, especially when the rays are wide. Similarly, the occurrence of deflections but along with a low rate of restructuring does not promote the formation of a permanent storeyed arrangement. Only large deflections in conjunction with a high rate of restructuring influence the intensity of ray splitting, which results in the formation of a storeyed arrangement of rays. Small deviations from the described relationship between the number and height of rays may arise from the fact that part of the high rays also arise from growing low rays.

Fig. 11. The dependence of the number of high rays on their mean height for 26 successive annual growths. Each point denotes the number of rays and their mean height, calculated for an area of 0.65 cm^2 of terminal parenchyma (according to Janikowska 1986)

Fig. 12. Changes in the number of high rays and their mean heights in successive annual growths. The empty circles on the broken line denote the mean height of the rays. The solid circles on the solid line denote the number of rays. Each point marks measurements made on a surface of 0.65 cm^2 of terminal parenchyma from 26 successive borders of annual growth (according to Janikowska 1986)

Because sample IV has large deflections of the cell arrangement, it is possible to study the relationship between the number of rays and the value of the angle of the inclination of the grain (Duda 1980). It turns out that a strict relationship exists only when there is a large inclination of the arrangement, when the value of the deflection angle exceeds 10° . This is understandable due to the fact that rays, particularly the thicker ones, can be split only when the cell arrangement is steeply inclined. Narrow rays can split when the cell arrangement is only slightly inclined and, generally, these rays undergo uniting and splitting more often. Figures 13 and 14 show that the change in the orientation of the wood grain occurred four times during 40 years and that the angle of inclination is relatively large. In this sample, however, in spite of such a large deflection of the grain, the rate of change in the orientation of the grain and, thus, of the rate of restructuring the cell arrangement, is small, Σ averages 2.05 for 40 years. Moreover, there are many-year long periods when Σ is significantly smaller (Table 2). With relatively wide rays this does not give

Fig. 13. a — The dependence of the number of high rays on the size of the angle of inclination in the wood of 36 successive annual growths. Each point denotes the number of rays and size of the angle of inclination calculated for a surface area of 1.65 cm^2 of terminal parenchyma. b — The range of changes in the inclination of grain for 36 successive annual growth borders, examined as in Fig. 13a. The direction of changes is marked by arrows. The Roman numerals denote the successive deviations of the studied cell arrangement. The maximal values of the cyclic changes are given in degrees. About 2 cycles of changes are shown (according to Duda 1980)

a permanent predominance of splitting over uniting for high rays, and the non-storeyed arrangement of rays is maintained.

It was found that the storeyed arrangement of rays becomes established very quickly in a young tree — after only ten-odd annual growths. It can be concluded from this that the component rays formed by the splitting of high rays cannot reunite due to the rapid expansion of the cambium surface. For example, when the trunk of a ten-year-old tree which has a radius of 5 cm grows a further 0.5 cm, the surface area of its cambium increases by 21%. When a 50 year-old linden, whose trunk has a diameter of 25 cm, grows by the same amount, its cambium surface will increase by only 4%. In sample no. 1 the increase of the cambium surface is so great that the storeyed arrangement of rays, with relatively wide rays, is established very quickly — about the 12-13th annual growth.

The transformation of a storeyed arrangement of rays back into a non-storeyed one was not observed. This could occur if the rate of cell rearrangement dropped significantly. In such a case, the component rays of split rays would undergo uniting more frequently than high rays splitting. However, the rate of cell rearrangement in linden cambium does not weaken for long periods of time, moreover, it often increases, making the storeyed arrangement of rays permanent. It can be generalized then, that the storeyed arrangement of rays is a dynamic system. The constant ratio of the number of

Fig. 14. Changes in the number of high rays and angle of inclination of grain in successive annual growths. The empty circles denote the number of rays. The solid circles denote the angle of inclination. Each point marks the measurements made over an area of 1.65 cm³ of terminal parenchyma from 36 successive annual growths (according to Duda 1980)

unitings to splittings of rays is decisive in determining the storeyed or non-storeyed arrangement of rays. If there is a large predominance of splitting over uniting of rays and the number expressing this ratio is larger than the number of newly-formed high rays, this leads to the creation of a storeyed arrangement of rays. The greater the predominance, the quicker the storeyed arrangement of rays is established.

It was mentioned in the introduction that the height of rays is considered to be a characteristic trait for a given genus, family or species (Ghouse and Yunus 1976, Ghouse et al. 1980, Palival et al. 1984). In addition, the arrangement of rays (storeyed or non-storeyed) is also considered to be such a feature, especially when species of trees possessing storeyed cambium are under study (den Outer 1986). In this study, the examination of linden wood with a non-storeyed arrangement of rays indicates that there is a correlation of ray characteristics in this species with: 1) the average height and the number of rays, 2) the number of rays and the magnitude of the change of the angle of inclination of the grain. It results from these correlations that significant variability in the height and number of rays can occur in successive annual growths in one species. The mentioned traits are in turn dependent on the rate of restructuring of the arrangement of fusiform cells. It seems that the height and arrangement of rays are traits acquired during individual development, not characteristic for a species, and so are not good taxonomic characteristics. However, seriation of rays can be a species characteristic and serve in taxonomic analysis.

Greater attention should be paid to the dynamics of the changes occurring during the period of individual development of the cambium when studying the characteristics of rays. This work is an attempt to verify the current evaluations describing the various arrangements of rays in trees. On the other hand, studies on the non-storeyed cambium of *Acacia nilotica* (L.) Del. var. *telia* Troup indicate that the seriation of rays undergoes changes with the age of the cambium and height of the tree trunk (Iqbal and Ghouse 1987). It is likely that various anatomical traits related to the formation of storeyed and non-storeyed cambium also characterize rays.

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Piętrowy i niepiętrowy układ promieni w kambium piętrowym Tilia cordata Mill.

Streszczenie

Badano próbki drewna z pni czterech wybranych lip (*Tilia cordata* Mill.). Dwa osobniki były młode, 25 i 36 letnie, i dwa starsze, około 100 letnie. W miększu terminalnym z granic przyrostów rocznych drewna analizowano rzędowość, wysokość i układ promieni, oraz wielkość wychylenia i szybkość przebudowy układu komórek wrzecionowatych. Zaobserwowano, że pierwotnie układ promieni jest zawsze niepiętrowy i nie zmienia się do pierwszych kilkunastu przyrostów rocznych. Później może pozostawać niepiętrowy lub zmienia się na piętrowy. Dany układ promieni zależy od szybkości i wielkości zmiany nachylenia włókności, oraz od rzędowości promieni i to niezależnie od wieku drzewa. Im większe jest nachylenie włókności i szybsza przebudowa układu komórek wrzecionowatych, a także, im mniej rzędowe (węższe) są promienie, tym szybciej tworzy się układ piętrowy promieni.