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Anatomical studies on the wood of *Pseudotsuga menziesii* (Mirb.) Franco

INTRODUCTION

The wood of Douglas fir, which has found many uses in the region of its natural occurrence is also the subject of interest of foresters and wood technologists in many European countries. Some investigators believe that its technological value is comparable to that of spruce or pine (Göhre 1958). Numerous studies have been devoted to the problem of physical and mechanical properties of the wood (Armstrong 1960, Bodig 1965, Filipovici 1960, Göhre 1958, Kennedy and Warren 1969, Krahmer 1961, Liese and Bauch 1967, Löffler 1966, McKimmy 1966, Wisse 1968 and others). We also know the basic microscopic structure of the wood of Douglas fir, and this particularily thanks to the studies of Göhre (1968), Greguss (1955), Budkiewicz (1961), Phillips (1941) and Pechmann and Courtois (1970). However the variability of individual characters in the ontogenetic development of Douglas fir is less well known. Similarily as in the case of other representatives of the *Coniferae* only the variability of these characters was studied which are responsible for the technological value of the wood. These are, width of annual rings, the proportion in them of late-wood, the length of tracheids and the thickness of tracheid walls.

In Poland the interest of foresters and technologists in the wood of Douglas fir increases steadily. However studies on the microscopic structure of the wood of Douglas fir cultivated in our country are lacking, and the absence of studies on the ontogenetic variability of individual characters is total. The present study is an attempt to fill this gap, and even though the results reported here concern only one stem, the information collected on the nature of the intra-individual variability of a series of microscopic wood characters and relations between them is of interest.

METHODS

The studies were conducted on a stem collected in the Forest District Miradz (Toruń Forest Region). The tree had 35.4 m in height. The green crown started from 17 m above the ground and it was 7 m wide. Samples for the anatomical studies have been collected every 2 m starting from 1 m above the ground and ending at 31 m. From each of the stem dices on the northern side tranverse sections were made for the measurement of annual rings and of both the tracheid diameters. Radial sections were made from only two stem slices (two levels above the ground) and tangential sections from only three. On these the diameter of the bordered pits was measured in tracheids of early-wood and the rays were studied. The length of the tracheids was studied on macerated preparations. Detailed information about the studied stem levels and the rings on which the measurements were taken are to be found in the descriptions accompanying illustriations and tables.

The methods of preparing slides and of measuring individual characters of wood have been described in previous papers (Hejnowicz 1964, 1969). The photographs have been made in a Lumipan microscope with an Exacta camera on a panchromatic film.

RESULTS

The studied stem had at 1 m above the ground 72 growth rings. It proved impossible to determine the exact age of the tree and thus to be able to analyse the stem increment in height since in the latter years of its life conditions for its growth were exceptionally unsatisfactory. This was judged from the rapid decline in the width of annual rings in the external part of the stem at all heights (fig. 1). In some parts of the stem circumference the continuity of the annual rings was broken (figs. 2, 3), which indicates that in some years the cambium cells have remained in the dormant condition throughout the growing season and have resumed growth only in the spring of the next year.

The selection of such a tree was not accidental. The main purpose of this study was to find correlations between the dimensions of wood elements and the rate of radial stem increment.

GENERAL DESCRIPTION OF THE WOOD

The wood of Douglas fir belongs to the group of heartwood timbers. Sap-wood extends only for the 30 outside growth rings. The heart-wood

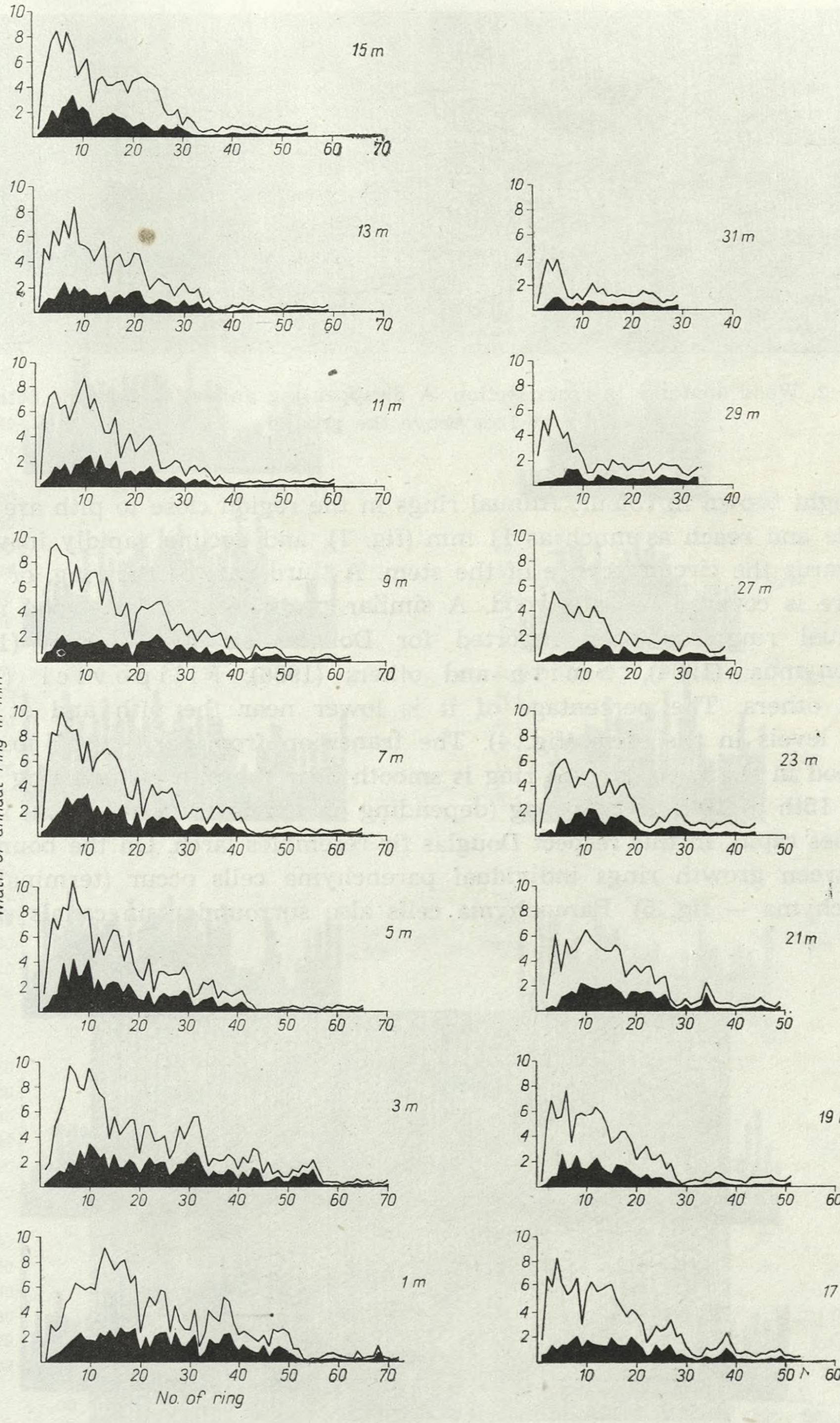

Fig. 1. Variation in width of annual rings and in the width of late wood (darkened area) at various levels in the stem

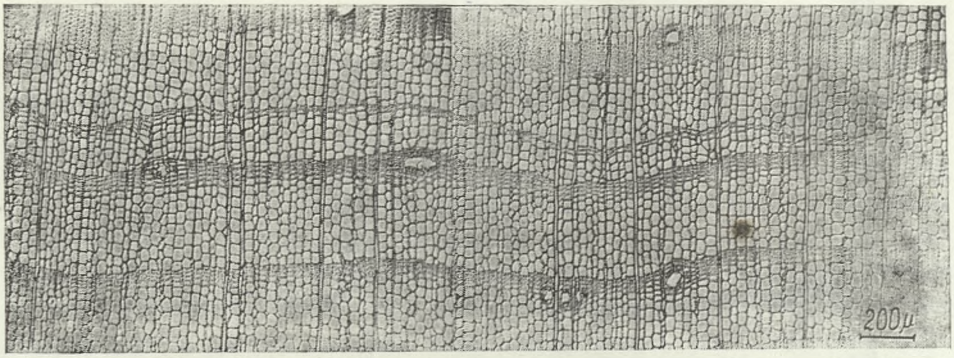

Fig. 2. Wood anatomy in cross section. A disappearing annual ring in the 66th year at 1 m above the ground

is light brown in colour. Annual rings in the region close to pith are very wide and reach as much as 11 mm (fig. 1), and decline rapidly in width towards the circumference of the stem. A third part of the ring, or even more is covered by late-wood. A similar proportion of late-wood in an annual ring has been reported for Douglas fir by Göhre (1958), Anonymus (1964), Smith and others (1966), Filipovici (1960) and others. The percentage of it is lower near the pith and at higher levels in the stem (fig. 4). The transition from early-wood to late-wood in the same growth ring is smooth near the pith but starting from the 15th to 20th growth ring (depending on the level in the stem) it becomes rapid. In this respect Douglas fir resembles larch. On the boundary between growth rings individual parenchyma cells occur (terminal parenchyma — fig. 5). Parenchyma cells also surround resin canals which

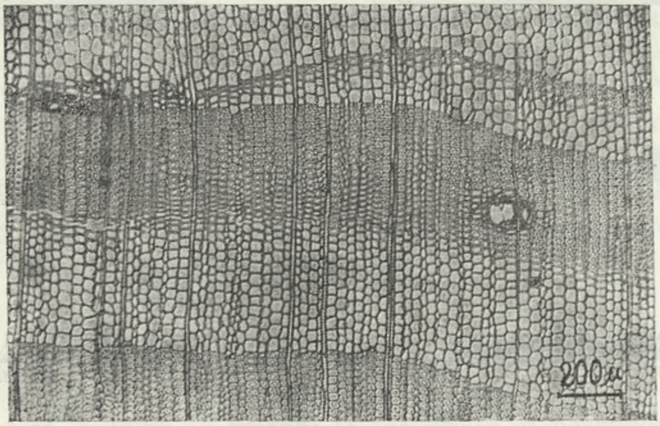

Fig. 3. A disappearing annual ring in the 52nd year at 1 m above the ground

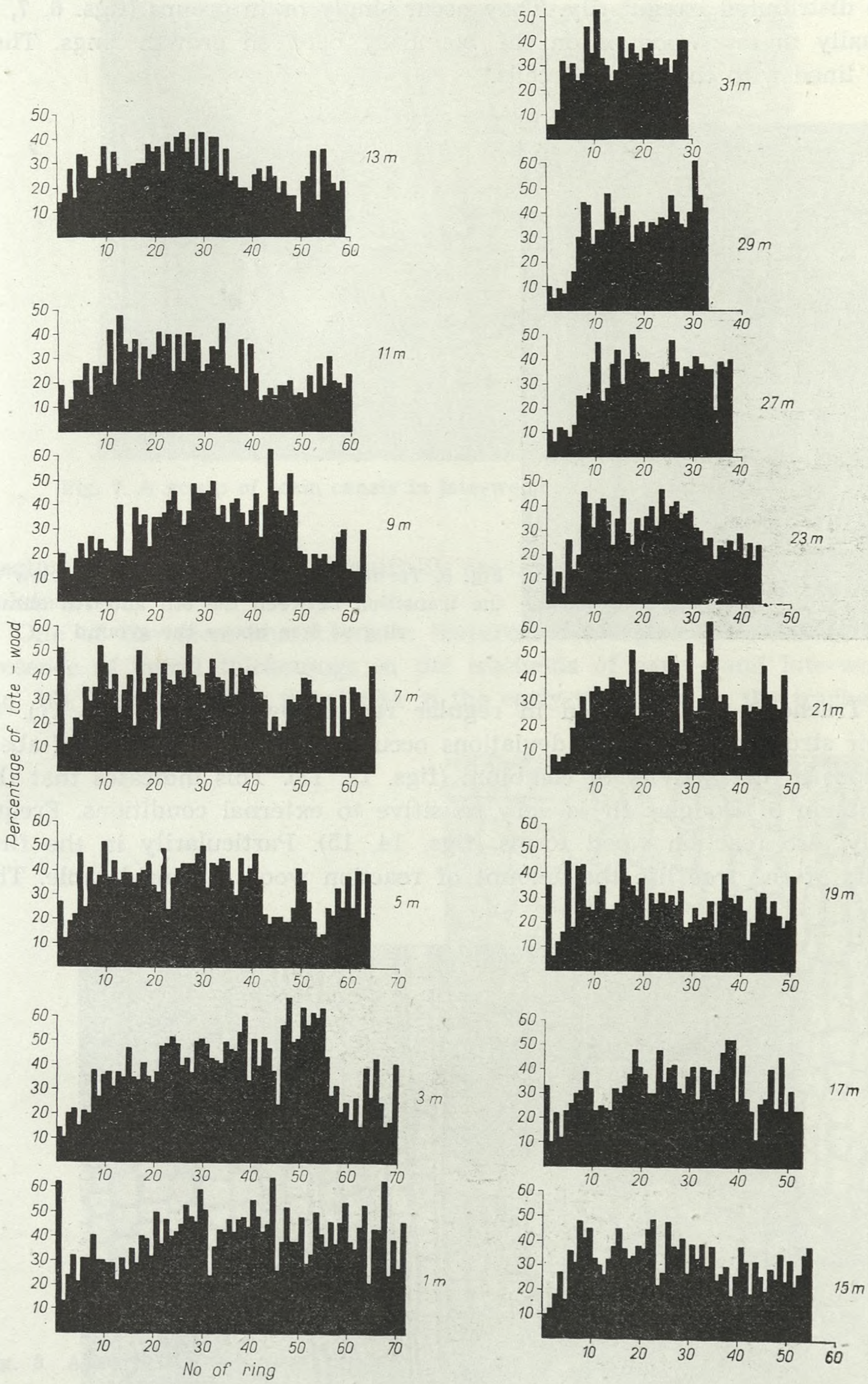

Fig. 4. The percentage of late-wood within an annual ring

are distributed irregularily. They occur singly or in groups (figs. 6, 7, 8) usually in late-wood or on the boundary between growth rings. They are lined with thick-walled cells.

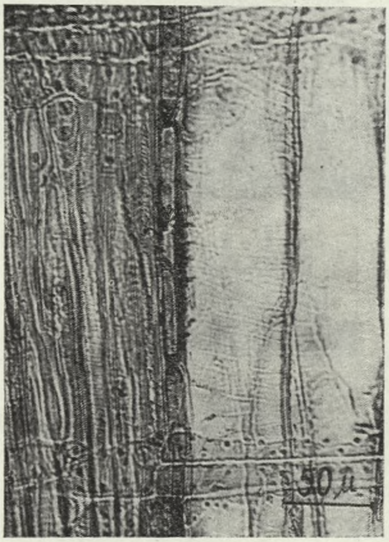

Fig. 5. Terminal parenchyma in radial view on the transition between the 6th and 7th annual ring at 5 m above the ground

Tracheids are arranged in regular radial rows (figs. 9, 10, 11). In their structure frequently deviations occur which are indicative of aberrations in the activity of cambium (figs. 12, 13). This indicates that the cambium of Douglas fir is very sensitive to external conditions. Frequently also reaction wood forms (figs. 14, 15). Particularily in the first years of the tree life the amount of reaction wood is considerable. The

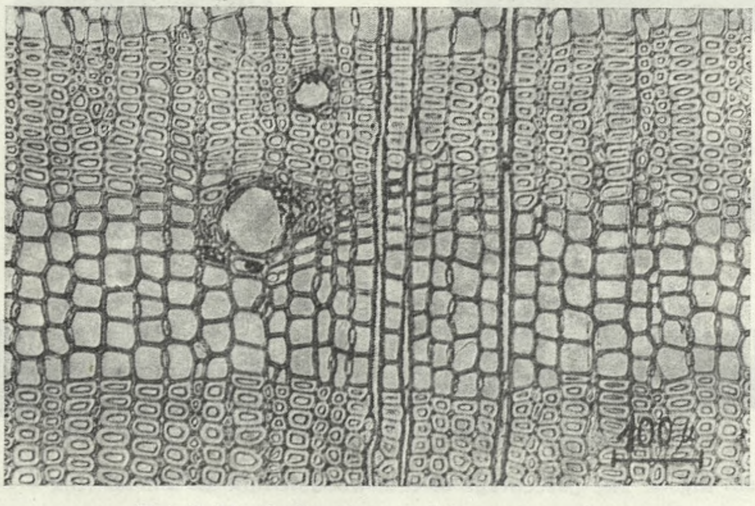

Fig. 6. Vertical resin canal in cross section

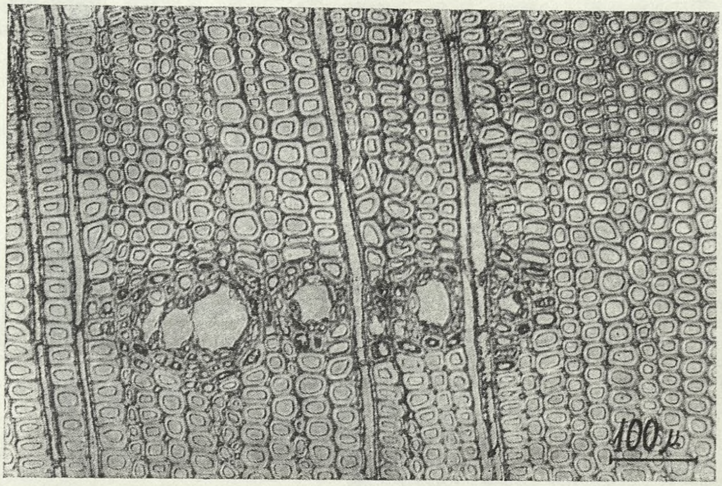

Fig. 7. A group of resin canals in late-wood as seen in cross section

reaction wood forms most frequently on the transition from early-wood to late-wood.

One of the most characteristic features of Douglas fir wood is the presence of spiral thickenings in the tracheids of early- and late-wood (fig. 16). They are most developed in the early-wood and in the tracheids

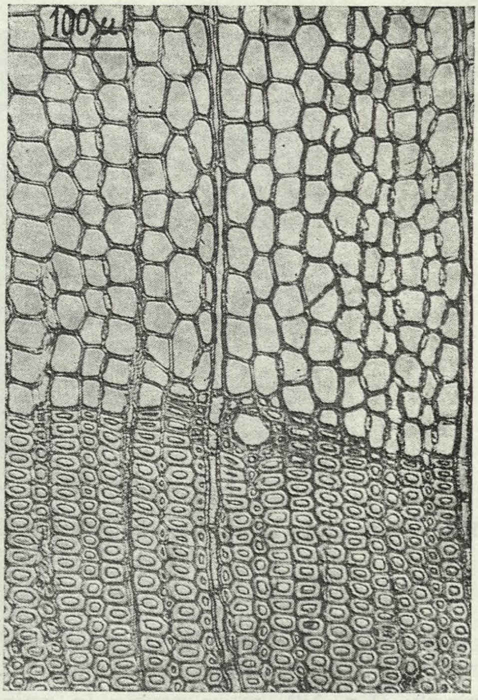

Fig. 8. A vertical resin canal in late wood near the boundary between annual rings

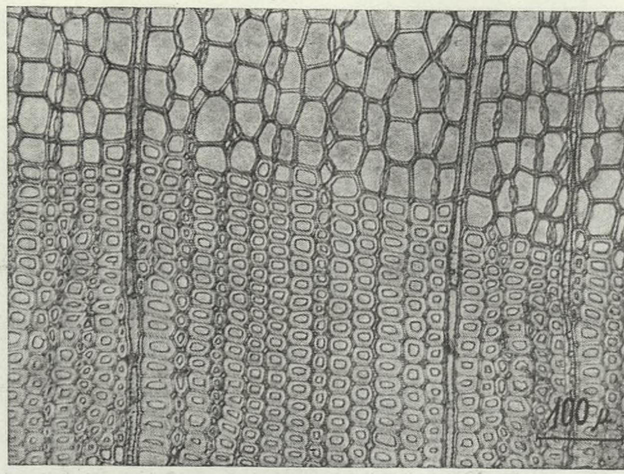

Fig. 9. Boundary between two annual rings in cross section

of late-wood, which lie close to the boundary between growth rings (fig. 17). In the remaining tracheids of late wood they are less developed and become visible only after intensive staining. On unstained sections they are almost invisible. Perhaps it is for this reason that Hollendonner (quoted after Greguss 1955) has described the tracheids lying in the transition zone of late-wood as smooth walled.

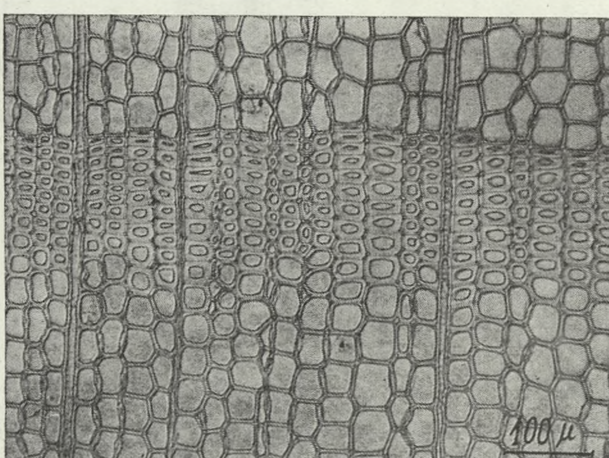

Fig. 10. A sharp transition between early-wood and late-wood within the same annual ring

Bordered pits in mature xylem are distributed unevenly, they agglomerate towards both tips of a tracheid. In early wood they are distributed singly (fig. 18), more rarely in pairs on radial walls of the cells. They

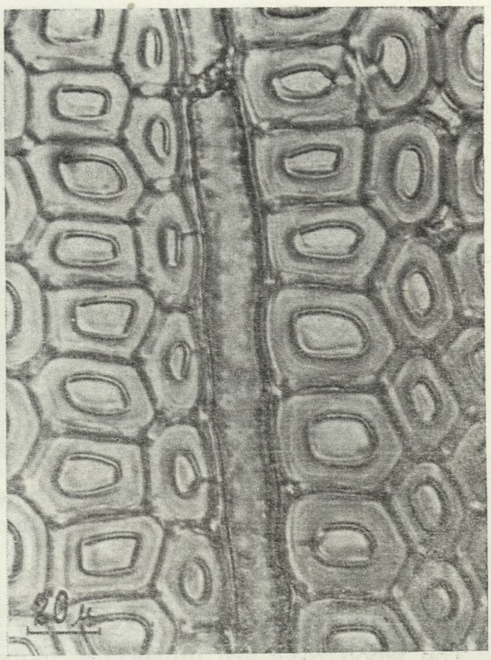

Fig. 11. Late-wood with a uniseriate ray as seen in cross section

occur also on tangential walls, with which tracheids belonging to one group of cells of, common origin, are in contact with tracheids from another such group (fig. 19). In late-wood the pits are distributed singly both on radial walls and on the tangential ones. In particular a large number of small pits are to be found on tangential walls of tracheids in the last border layer of cells.

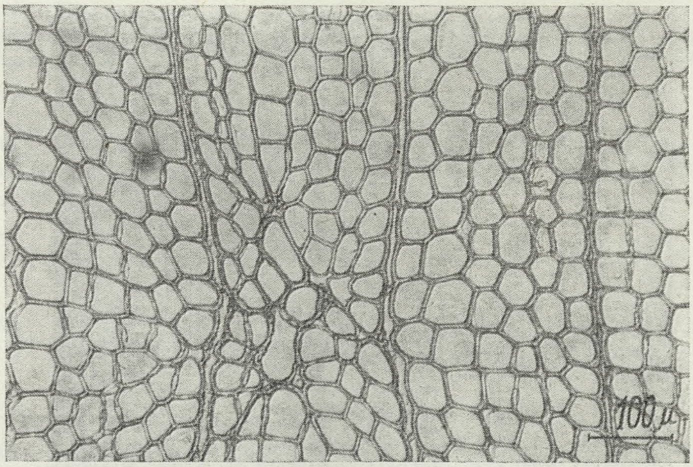

Fig. 12. Early wood formed as a result of aberrations in the function of the cambium. Ring 7 at 15 m above the ground

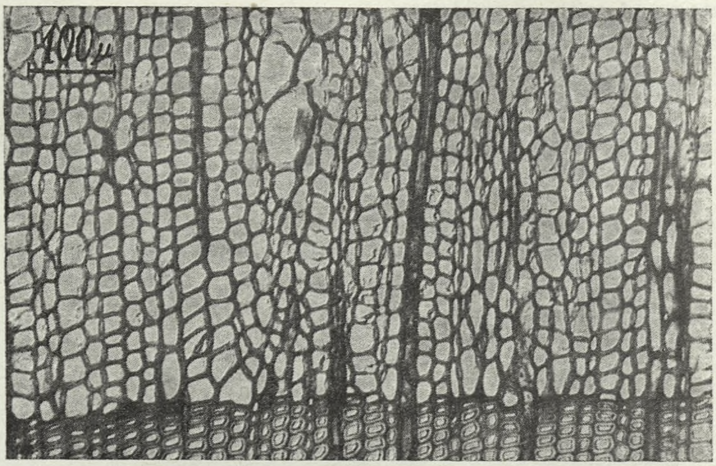

Fig. 13. Aberrations in the arrangement and size of early wood tracheids in cross section

The bars of Sanio are very poorly developed in Douglas fir.

The wood rays are uniseriate, more rarely biseriate and spindle-shaped. Through the middle of spindle-shaped rays run horizontal resin canals. Sometimes in one ray two resin ducts can be found (fig. 20). On margins of rays and more rarely in their centres there lie ray tracheids with numerous bordered pits. The internal surfaces of these cells are dentate. The ray tracheids which were formed as the last ones in a given vegetative season have walls with spiral thickenings (fig. 17).

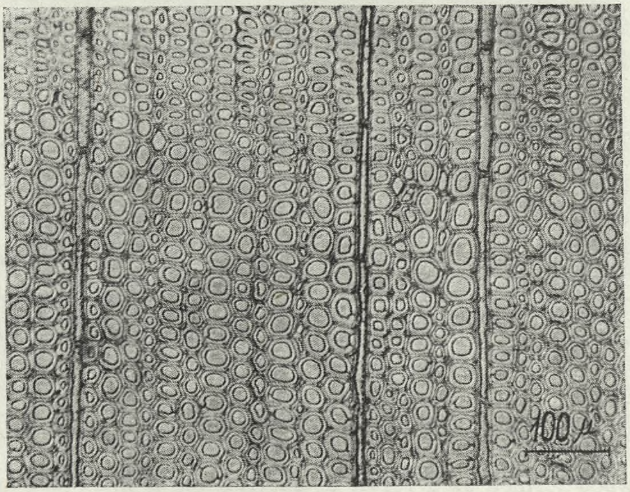

Fig. 14. Reaction wood and its transition to normal late wood in cross section

Table 1

Changes in the tangential dimension of an early and late-wood tracheid along the stem radius and axis, in microns

No. of ring	Distance from ground in m														
	1	3	5	7	9	11	13	15	17	19	21	23	27	29	31
													early-wood		
2	13	15	–	14	17	15	16	16	–	13	14	14	15	15	13
4	18	18	24	25	19	22	19	23	24	22	23	18	18	16	17
6	21	26	26	28	29	25	25	27	27	24	26	24	23	20	23
8	27	27	26	31	29	28	30	29	27	27	27	24	24	25	25
10	28	29	30	31	32	31	31	29	29	31	31	28	30	31	26
15	28	30	31	34	33	32	32	33	31	32	31	30	30	32	29
20	30	31	30	34	32	33	35	32	35	34	30	30	30	30	29
30	33	34	33	34	35	33	32	34	33	35	30	35	35	32	31·
40	30	32	30	33	31	33	34	34	33	33	34	35·	35·	34·	
50	31	30	33	35	33	34	35	36	32	34	35·	32·			
60	29	30	31	33	31	34	34·	32·	33·	36·					
70	28·	32	31·	33·	31·										
													late-wood		
2	18	16	17	16	18	16	18	15	19	17	18	15	14	15	16
4	20	20	24	23	26	22	23	22	25	22	20	20	19	17	22
6	26	24	24	28	30	24	26	24	26	24	22	23	21	21	23
8	25	26	26	31	29	28	28	27	27	28	25	26	23	24	24
10	28	28	29	32	31	29	33	28	27	31	28	27	27	28	26
15	26	30	28	33	30	31	32	28	31	29	30	30	31	28	29
20	30	30	29	34	28	32	34	32	33	33	33	30	29	30	27
30	29	30	28	30	29	31	30	31	33	32	30	33	34	31	29·
40	28	30	31	32	31	34	32	31	32	34	34	32	31·	32·	
50	32	30	33	29	27	34	34	33	31	33	30·	31·			
60	28	30	31	33	31	32	32·	33·	–	33·					
70	25·	30	29·	33·	30·										

N.B. Dots near figures above indicate that the data refers to the last growth rings occuring at the given level, which have the following numbers according to the sequence of levels: 72, 67, 65, 63, 59, 55, 53, 51, 49, 44, 38, 33 and 29.

Table 2

Mean dimensions of an early and late-wood tracheid and the diameter of the bordered pit in an early-wood tracheid, measured on growth rings from the external part of the stem, (from number 20 upwards) in relation to the four groups of growth rings distinguished by width

Ring width in mm	Transverse dimension of a tracheid in microns				Tracheid length in mm		Diameter of a bordered pit, in microns
	radial		tangential				
	early wood	late wood	early wood	late wood	early wood	late wood	
0.10–0.50	42.8	18.7	32.7	32.1	4.12	4.30	21.4
0.51–1.00	45.7	21.2	33.1	31.6	4.41	4.63	22.9
1.10–2.00	49.3	23.2	32.2	31.6	4.05	4.42	22.4
above 2	50.7	23.0	32.3	30.7	3.70	3.97	22.1

CROSS SECTIONAL DIMENSIONS OF A TRACHEID

Dimensions of tracheids within the studied stem change similarily as in other representatives of the *Coniferae*. Thickness of a tracheid, that is its radial dimension, which is measured as the distance between the middle lamellae of the two tangential walls of one cell, increases significantly from the pith to about the 20th growth ring, after which it tends to decline (fig. 21-A). In this respect there are differences between individual levels in the stem and also between the early- and late-wood. At higher levels the radial tracheid diameter after reaching its maximal dimension remains constant. The tangential tracheid dimension changes similarily, but the maximal values are reached here much later, (about he 30th to 50th growth ring, depending on the level in the stem) and do not decline in size in later rings. They decline in size distincly only at the lowest level in the stem (table 1).

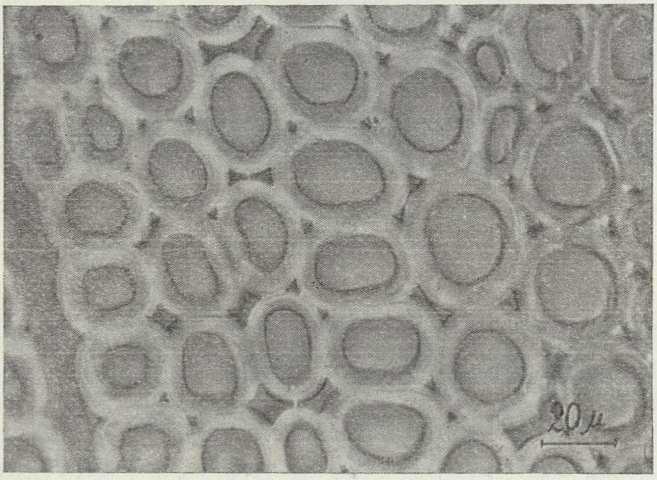

Fig. 15. Reaction wood in cross section

Area of a transverse cross section of a tracheid, that is the product of both its radial and tangential dimension changes in the stem similarily as the radial dimension. In the central part of the stem the largest cells are to be found at its base and the smallest above 27 m (fig. 21 - *B*). A decline in the size of the cross sectional area of a tracheid in the external part of the stem is associated with a decline in the width of the annual rings. These characters are closely related to each other. In a similar way the width of an annual growth ring is also correlated with the radial tracheid dimension, which grows with an increase in the width of an annual ring (table 2). The tangential dimension is correlated negatively with the width of an annual ring.

The ratio of the two dimensions of a tracheid as seen on a cross section (*g/s*) varied in the studied wood samples from 0.5 to 1.1 for tracheids in late-wood and from 1.1 to 2.0 in tracheids of early-wood. The highest *g/s* ratio was observed in a few growth rings closest to the pith and the lowest in tracheids of the external part of the stem and in the highest levels in the crown (fig. 21 - *C*). Values of this character are smaller in narrower growth rings and vice versa. A decisive influence on the existence of this relation is exerted by the radial tracheid dimension, which as has been demonstrated, is positively correlated with the width of an annual ring.

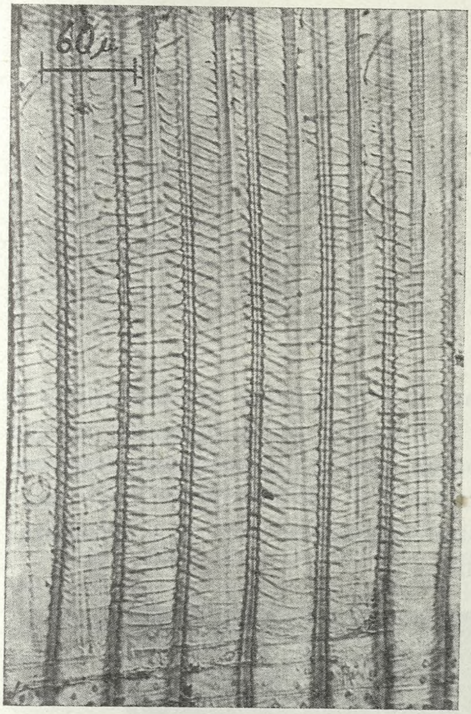

Fig. 16. Spiral thickenings in early wood tracheids as seen in radial section

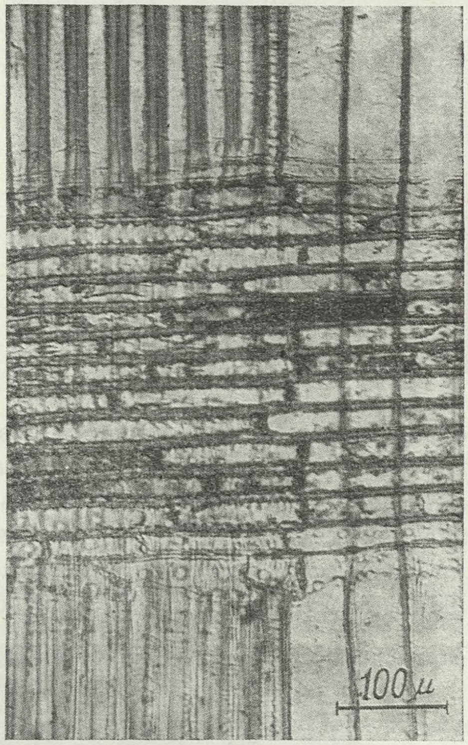

Fig. 17. Wood ray in radial section. In border tracheids spiral thickenings are visible

TRACHEID LENGTH

The average length of a tracheid increases from the pith towards the outside up to about the 30th growth ring (fig. 21 - *D*). On the lowest and highest level in the stem the rate of increase of an average tracheid length from the pith outwards is slower than at other levels. From the 30th growth ring outwards the length of the tracheid does not change in any particular direction but manifests considerable local fluctuations. One

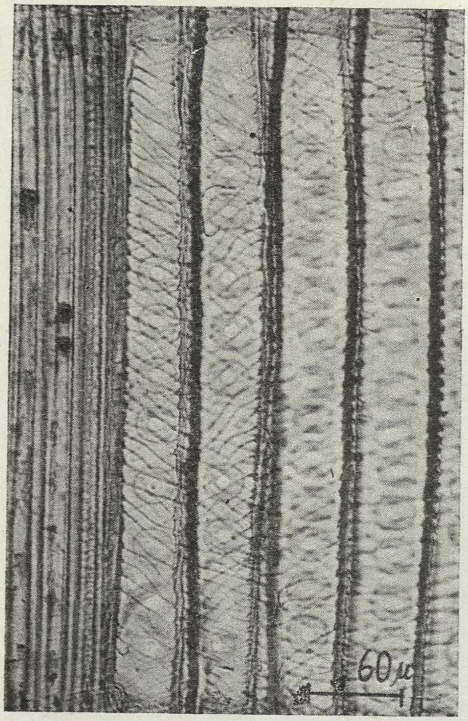

Fig. 18. Boundary between two annual rings in radial section. Bordered pits in early wood tracheids are arranged in single rows

of the reasons for these fluctuations are different types of aberrations in the cambium activity occurring very frequently in Douglas fir, and as a result of which false annual rings occur, as well as traumatic resin canals and other irregularities in the structure of annual rings. These aberrations become reflected in the cell size sometimes even at a considerable distance from the site of their occurrence.

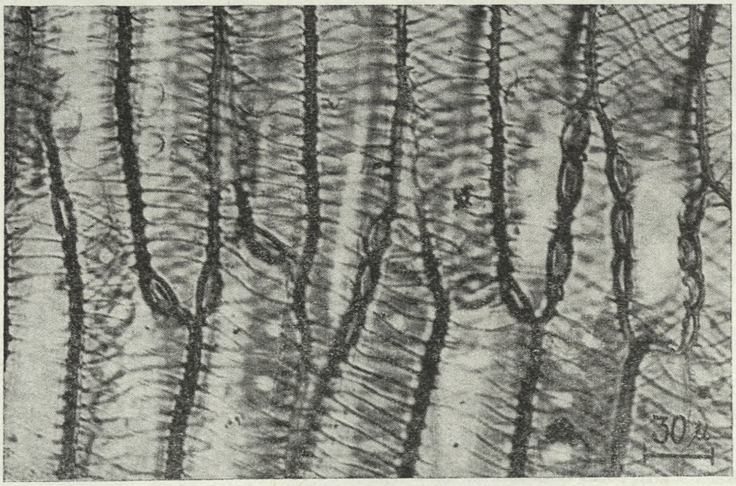

Fig. 19. Bordered pits at tracheid tips in radial section

The length of an early-wood tracheid is as a rule smaller than that of the late-wood. The longest cells occur usually in the first layer of late--wood. Towards the end of the vegetative period the average tracheid length declines (figs. 22, 23).

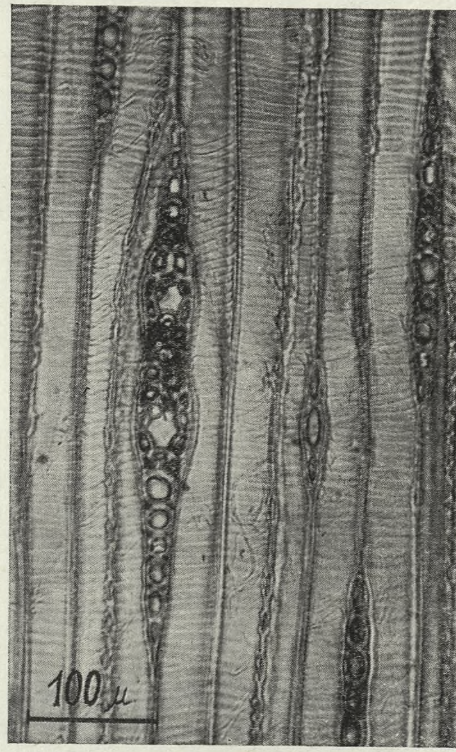

Fig. 20. Fusiform wood ray with two horizontal resin canals as seen in tangential section

The length of a tracheid is correlated with the width of an annual ring; narrower growth rings have longer tracheids (table 2) and vice versa. There is however a certain limit in ring width beyond which the relation between these two characters becomes reversed; with a decline in ring width the length of the tracheid also declines. The longest tracheids occur in growth rings which are 0.51 to 1.0 mm thick and the shorter ones occur in rings below 0.5 mm and above 1 mm in thickness (table 2). A similar relationship has been demonstrated by Bannan (1965) in most of the coniferous species he has studied. The correlation mentioned here was the main reason for the large fluctuations in the average tracheid length in the external part of the stem, where considerable fluctuation in width of annual rings occur.

BORDERED PITS

The mean diameter of a bordered pit in an early-wood tracheid amounts to 21 - 23 microns. This character stabilizes during development relatively early and does not change starting from the 6th growth ring. Tra-

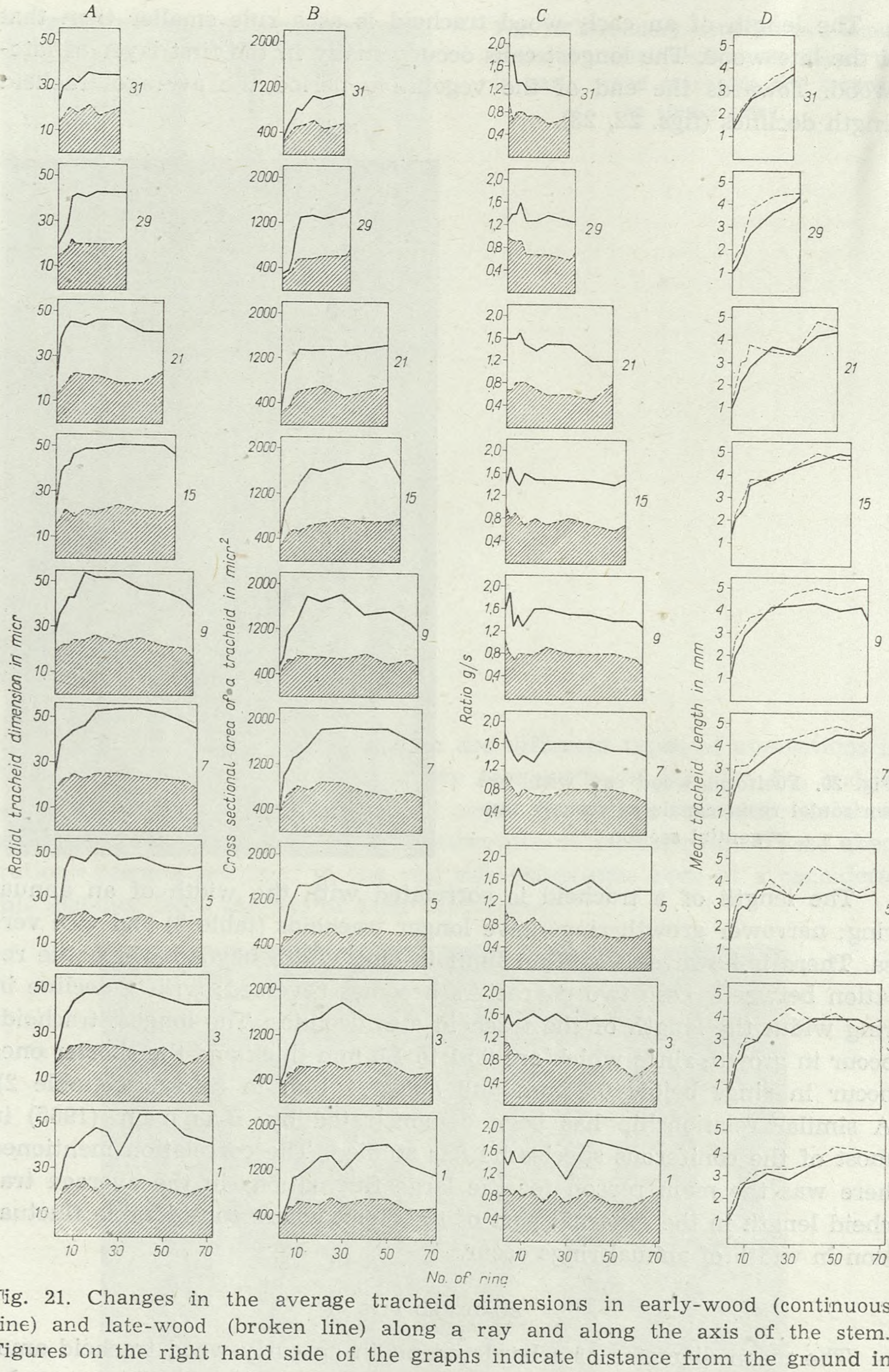

Fig. 21. Changes in the average tracheid dimensions in early-wood (continuous line) and late-wood (broken line) along a ray and along the axis of the stem. Figures on the right hand side of the graphs indicate distance from the ground in meters

A — radial tracheid dimension, *B* — cross sectional area of a tracheid. *C* — ratio between radial and trangential diameters of a tracheid — *g/s*, *D* — tracheid length cheids from higher levels in the stem (27 m) have somewhat smaller bordered pits than tracheids from a lower level (15 m) – fig. 24. There exists a strict relation between the diameter of a bordered pit and the radial dimension of a tracheid and as a result also with the width of an annual ring (table 2, 3). As the tracheid dimension and width of the annual ring

Table 3

Diameter of a bordered pit and a radial dimension of an early-wood tracheid, calculated for growth rings from the external part of the stem (above growth ring no. 20)

Radial tracheid dimention in microns	Diameter of a bordered pit in microns		
	distance from the ground in m		mean
	15	27	
40.0–45.0	22.6	22.0	22.30
45.1–47.0	22.6	22.5	22.55
47.1–49.0	22.4	22.9	22.65
49.1–52.0	22.9	22.6	22.75
above 52	23.3	–	23.30

increase the diameter of the bordered pit also increases. A similar correlation has been observed in the wood of Norway spruce (Hejnowicz 1969).

RAYS

Uniseriate wood rays are formed from 1 - 17 cells. The mean height of a ray varies from 80 to 180 microns. This results from there being on the average 4 to 9 cells per ray (table 4). The lowest ray height is to be found in the first annual ring. Variation in this character at one level in

Table 4

Mean dimensions of uniseriate wood rays at two levels in the stem

Character	Distance from the ground in m	Consecutive ring number counting from pith											
		1	2	4	6	8	10	15	20	30	40	50	60
Ray height	5	77	125	170	141	140	170	–	160	149	139	169	150
in microns	27	125	148	141	162	132	147	150	160	141	132˙		
No. of cells	5	3.6	6.1	8.2	7.6	7.5	8.9	–	8.3	7.4	6.6	8.5	7.7
in a ray	27	6.2	8.0	7.5	8.6	7.4	7.8	7.8	9.0	7.6	6.9˙		
Height of	5	21.5	20.4	20.7	18.6	18.7	19.1	–	19.3	20.1	20.7	19.8	19.9
one ray cell	27	20.2	18.5	18.7	18.8	17.9	18.8	19.2	17.8	18.5	19.1˙		
Width of	5	21.5	14.6	16.8	16.4	14.8	14.7	–	15.4	17.3	16.6	19.2	18.2
one ray cell	27	–	15.7	16.6	16.9	16.6	15.6	16.7	14.9	14.0	17.0˙		

N.B. Dots by the figures indicate that the data refer to the 38th annual ring.

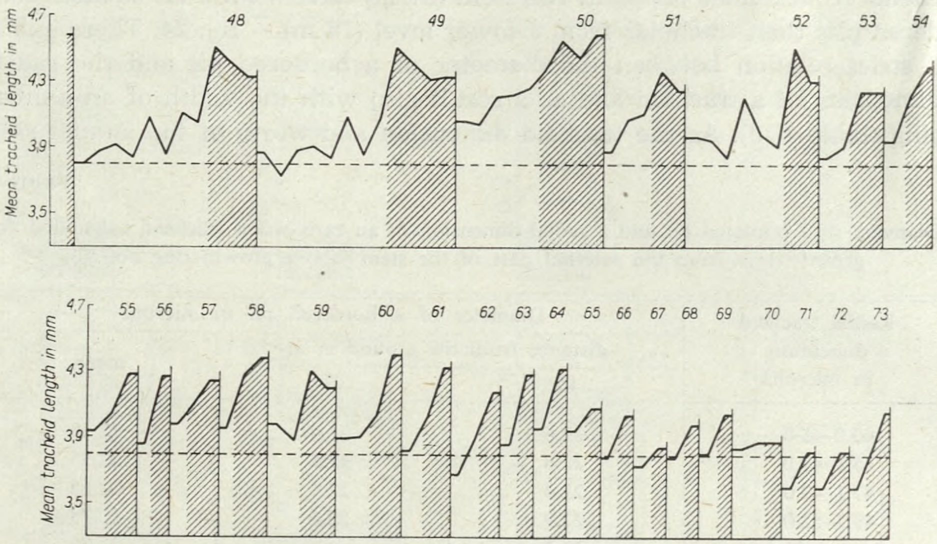

Fig. 22. Changes in the average tracheid length in succesive layers of cells in a growth ring at 1 m above the ground. Shaded area — late-wood, unshaded area — early-wood. The figures above indicate the succesive number of the growth ring counting from pith

the stem are considerable, however individual levels have a similar range of variation. In wider rings, above 2 mm, higher wood rays are to be found (table 6, and fig. 25).

The average height of one ray cell amounts to 18 - 21 microns. Largest cells occur in the first ring around the pith (fig. 26) where the ray height is smallest (table 4). In the lower part of the stem, at levels 5 m and 7 m the average height of a ray cell is somewhat higher than at 27 m. There exists a strict relation between cell height and the height of the whole ray. In smaller rays the cells are taller (table 5), however in rays 7 or more cells tall the dimensions of individual cells remain constant.

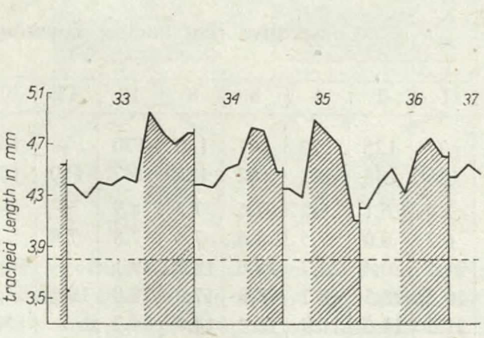

Fig. 23. Changes in the average tracheid length in succesive layers of cells in a growth ring at 27 m above the ground. Explanations as in fig. 22

The average width of ray cells is also highest in the first annual rings, however already from the second annual ring it does not change in any definite direction. Also there are no differences with respect to this character between levels in the stem.

Both the dimensions of they ray cells are lowest in annual rings which are 1.1 to 2.0 mm wide and largest in rings that are wider than 2 mm or narrower than 0.5 mm (table 6). However the difference between the maximal and minimal mean value calculated for various groups of annual ring widths amounts to no more than 5%.

Table 5

A comparison of the height of one cell in a uniseriate ray with the height of the ray as measured by the number of cells it is composed of in the 30th growth ring at two levels in the stem

Distance from the ground in m	No. of cells in a wood ray					
	below 3	4–5	6–7	8–9	10–11	above 12
5	24.5	21.5	21.1	19.4	19.8	18.9
27	–	19.8	18.5	18.1	18.5	–
mean	24.5	20.65	19.8	18.75	19.15	18.9

Table 6

Dimensions of a wood ray and of its individual cells in growth rings of various widths. Means are calculated for data from the whole stems

Studied ray character	Width of annual growth ring in mm			
	0.1–0.5	0.5–1.0	1.1–2.0	above 2
Height in micr.	149	145	143	166
No. of cells	7.6	7.5	7.5	8.1
Height of a cell in micr.	19.6	19.4	19.0	19.9
Width of a cell in micr.	16.0	15.9	15.1	15.9

DISCUSSION

The wood of Douglas fir observed in cross section resembles the wood of larch; the annual rings are similarily constructed with a large proportion of late wood (about 30%), a sharp transition from early- to late-wood in most of the annual rings and with terminal parenchyma in the region of the stem close to the pith. A very characteristic structure, which is not found in other resin conducting representatives of the *Coniferae* is to be found in the wood of Douglas fir on radial and tangential sections.

Both in the early-wood and late-wood tracheids dense spiral thickenings are observable which can also be found in a vestigial form in the wood of larch but only in late-wood in the central part of the stem (H e j n o- w i c z 1964).

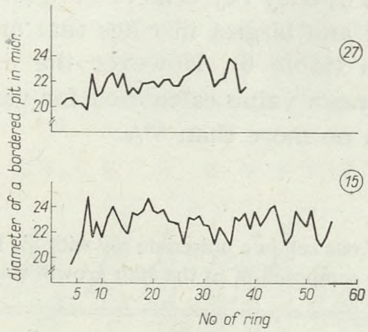

Fig. 24. Changes in the average diameter of a bordered pit in a tracheid of early wood at 15 m and 27 above the ground

The course of changes which the microscopic structure of wood undergoes in the ontogenetic development of Douglas fir is similar to the changes taking place in other species from the class *Coniferae*. In the first years of tree life wide annual rings are formed with little participation of late-wood having short tracheids of small diameter. With age the annual rings become narrower, the proportion of late-wood in them increases and the dimensions of its indvidual elements increase. An exception to this rule are the ray cells, which in the first years of tree life are largest. I was able to show this to be the case in larch (H e j n o w i c z 1964), spruce (H e j n o w i c z 1969) and now in Douglas fir.

The average length of a tracheid during one vegetative season changes in the studied stem of Douglas fir in a similar fashion as in spruce (H e j n o w i c z 1969). It grows in the successive layers of cells in an annual ring up till the transition between early- and late-wood and to-

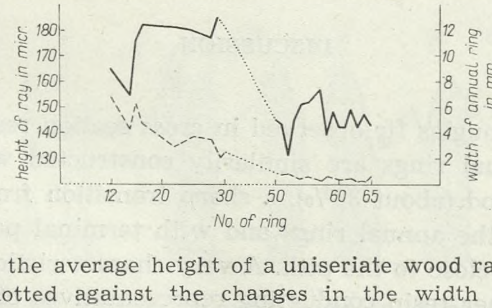

Fig. 25. Changes in the average height of a uniseriate wood ray (continuous line — partially dotted) plotted against the changes in the width of the annual rings (broken line — partially dotted)

wards the end of the growing season it declines. Thus the longest tracheids are to be found in the earliest formed layer of late-wood cells.

Some of the wood characters change also along the height of the tree stem. As a rule, at the base of the tree and in the region of the crown the wood is constructed from smaller tracheids than in the central part of the stem. Also the proportion of late-wood in an annual ring declines away from the stem base. H e g e r (1965) has found in many stems of Douglas fir that in one and the same annual ring, formed during the same calendar year at the base of the trunk more late-wood in formed and less early-wood than is the case higher up in the stem. I was not able to

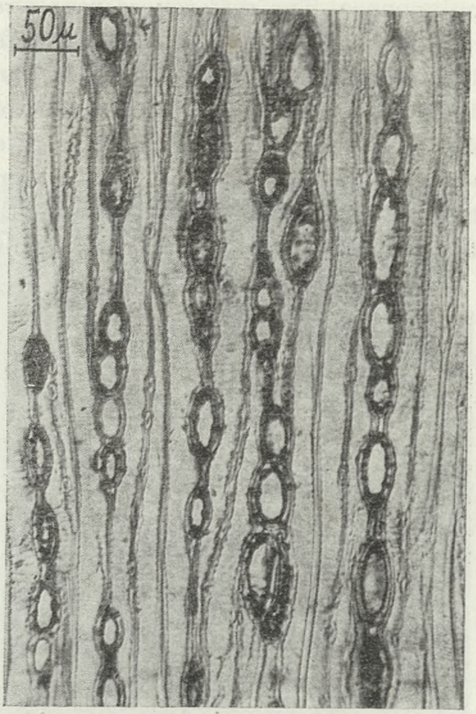

Fig. 26. Wood of the first growth ring, near pith, on a tangential section. Variation in the dimensions of the individual cells of wood rays is visibile

test whether H e g e r' s observation was applicable also to the stem of Douglas fir I have studied, since as a result of the disappearance of certain growth rings in the external part of the tree trunk it was not possible to analyse accurately the growth increments in the lower part of the stem and to determine the true age of each ring.

The dimensions of many wood characters are under genetic control (Z o b e l 1964) however the course of their changes within the trunk is to a large extent determined by site and climatic conditions. It is generally known that photoperiod, drought, light etc can totally change the type of wood being formed (W o d z i c k i 1961, L a r s o n 1964, R i c h a r d s o n 1964, Ż e l a w s k i, and W o d z i c k i 1960 and others).

These factors affect also very strongly the dimensions of the individual wood components. As is known the length of a tracheid increases at one stem level up to a certain age. The age at which these maximal values are reached can be very different even between representatives of the same species. Gerry for example (quoted after Bisset 1949) has found that there exists a continuous increase in the average length of tracheids in a 455 year old stem of Douglas fir. Anderson (1951) observed the same in a 200 year old stem of the same species. Duffield (1964) who studied 20 - 55 year old trees of various origin has observed that the course of change in the average tracheid length at one level in the stem can be very variable even between representatives of the same provenance. The differences concerned both average values for the stem and the rate at which the maximal values were reached (between the 15th and 40th year of life). Lee and Smith (quoted after Bisset 1949) have observed the increment of average tracheid length even after the 50th year of life of the tree after which there was a decline in the value of this character in the further growth rings. Tracheid length as is known is negatively correlated with the cambial activity expressed as the width of the annual rings. This is known among others from the

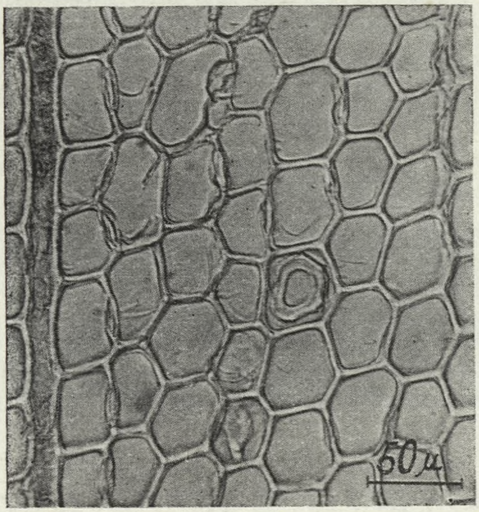

Fig. 27. A thick walled cell in early wood in cross section. The thick tertiary wall is detached from the secondary wall

papers of Bannan (1954, 1964, 1965b, 1967). However when this activity drops exceptionally rapidly in the conditions of suppressed tree growth a decline results in the average tracheid length within one level of a stem. This has been also demonstrated for the Douglas fir stem studied here.

The relation which exists between tracheid length and the width of an annual ring results from a change in the rate of growth and the rate of pseudotransverse and periclinal divisions of cambial cells. An increased rate of cambial cell growth corresponds to an increased frequency of their divisions. There is however a distinct dominance of relative rate of divisions over the rate of growth which results in the cambium cells not reaching their maximal sizes between one division and the next. As a result in wide annual rings, there are shorter tracheids than in narrower ones. There is however a certain limit of the cambial activity, below which together with a strong inhibition of the rate of cambial divisions there is also a strong inhibition in the rate of cambial cell growth. In Douglas fir, in those growth rings, in which the rate of radial wood increment is already so small that the width of an annual ring declines below 0.5 mm, shorter tracheids get formed than in growth rings that are 1 mm thick. In the studied stem of Douglas fir such narrow growth rings have occurred in the external part of the stem and it is for this reason that in the last years of the tree life a decline was observed in the average tracheid length within a level in the tree trunk.

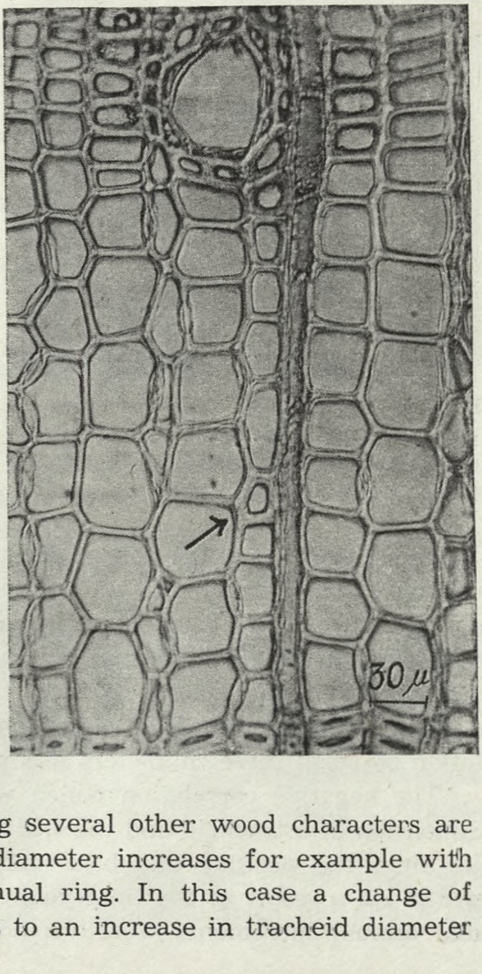

Fig. 28. A thick walled cell in early wood in cross section

With the width of an annual ring several other wood characters are also correlated. The radial tracheid diameter increases for example with an increase in the width of an annual ring. In this case a change of 1 - 1.5 mm in ring width corresponds to an increase in tracheid diameter of about 15%. Conversly a decline in the width of an annual ring corresponds to a decline in the average radial dimension of a tracheid. As a result in the studied stem of Douglas fir the tracheids which were formed in the last years of the life of the tree have had a smaller radial dimension that the tracheids positioned more in the central part of the trunk.

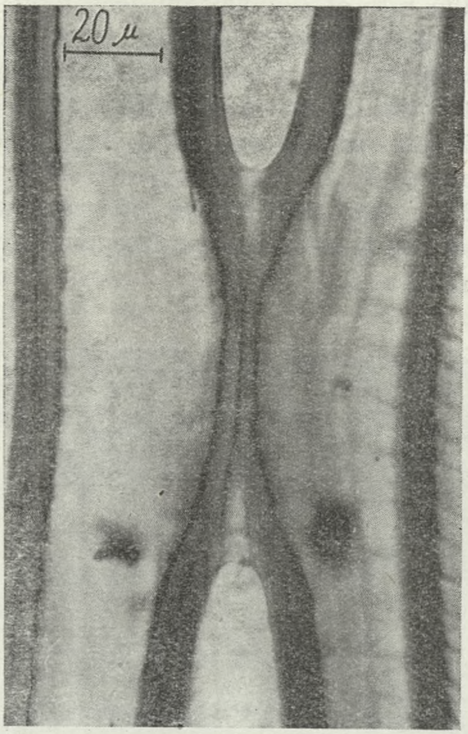

Fig. 29. A part of an early-wood tracheid in radial section. A strong constriction of the cell visible so that the tangential walls contacted each other

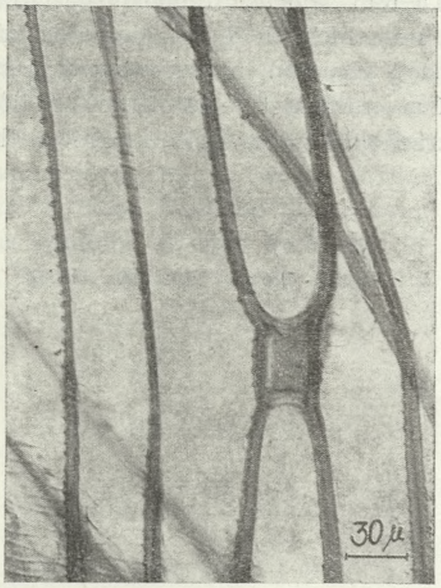

Fig. 30. A part of an early-wood tracheid in radial section

The tangential dimension of the tracheid has a different type of correlation with the width of an annual ring. Wider tracheids occur in the narrower growth rings and vice versa. A negative correlation between the tangential tracheid dimension and the width of an annual ring has been observed by Bannan (1954) in the wood of *Thuja*, however in the other representatives of the class *Coniferae* that he has studied the correlation between these characters was positive.

The negative correlation which was observed between the tangential dimension of a tracheid and the width of an annual ring is however smaller than the positive one between the radial dimension and the ring width. As a result in the final years of the life of the tree when the radial annual increments were very low, the area of the tracheid cross section declined even though the tangential dimension continued to increase uniterruptedly to the last years of tree life.

Of the remaining number of Douglas fir wood characters that were studied a positive correlation with the width of an annual ring was also demonstrated for the diameter of a bordered pit. This character is also positively correlated with the radial dimension of the tracheid from early-wood. A similar correlation was found in the wood of Norway spruce (Hejnowicz 1969). The dimensions of the wood rays are also positively correlated with the width of an annual ring. The height of a ray is stable in rings below 2 mm in width but it is about 14% greater in rings wider than 2 mm.

An interesting observation was made in the wood of Douglas fir by Kennedy and Adamovich (1968). Within thin-walled cells of early-wood they have found single cells with similar diameters but much thicker walls and a smaller lumen than is normal for early-wood cells. In the studies I have conducted, a search for such cells in a large number of sections has resulted in a few such cells being found in the studied stem of Douglas fir (figs. 27, 28). Presumably these are the same cells which on a radial section are illustrated in figures 29 and 30. One can presume that during their development a constriction and mechanical separation of the protoplasm resulted. On both sides of such a constriction wall forming substances were deposited. Thus these were not formed by normal division of a spindle shaped cambium cell. The contact of this layer with the secondary tracheid wall becomes readily broken (fig. 27).

SUMMARY

In a 72 year old stem of Douglas fir, which had very large fluctuations in the thickness of annual growth rings, from 0.1 mm to 11 mm, a study was made of the variability of various characters of the microscopic wood structure along the rays, from the pith to the outside, and along the stem axis from the base towards the tree top. Also the variability of the tracheid characters within one vegetative period has been studied. As a result of these studies it was possible to determine that the mean tracheid length, its radial diameter and its cross sectional area within one level of the tree, increase from the pith towards the outside till about the 30th growth ring. Later the mean length of the tracheids remains unchanged, and the radial diameter and cross sectional area after reaching a maximal value tend to decline.

The tangential tracheid diameter in the lower part of the stem up to about 9 m, increases within one level of the stem from the pith to the

30th - 50th growth ring, after which it somewhat declines. At higher levels it continues to increase till the last growth rings.

Dimensions of the tracheids also grow from the base of the stem to a level of the stem which differs for various growth rings, after which the values decline.

The mean tracheid length within one growing season increases from the early-wood to the first cells of the late-wood after which it declines within the late-wood cells.

Almost all the studied characters of wood correlate with the width of the growth ring. Length of the tracheid and its tangential diameter are negatively correlated with ring width. In narrower rings there are longer tracheids with greater tangential diameters. On the other hand the radial diameter correlates positively with the ring width. In narrower rings there are cells with smaller radial diameters, and vice versa.

The character of the interrelation described above between the tracheid dimensions and the ring width concerns only rings which are wider than 0.5 mm. In narrower rings the tracheids are shorter and with a smaller tangential diameter than tracheids in 0.5 - 1.0 mm wide rings.

Also there is a correlation between the width of the annual ring and the diameter of a bordered pit in the tracheid of early wood. Tracheids in narrower rings have smaller pits and vice versa. This character is also correlated with the radial diameter of the tracheid.

Rays in annual rings up to 2 mm wide are shorter and consist of fewer cells than rays in rings wider than 2 mm.

The height of one cell in a ray is correlated negatively with the height of the ray. In shorter rays there are larger cells and vice versa.

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ALINA HEJNOWICZ

Badania anatomiczne nad drewnem Pseudotsuga menziesii (Mirb.) Franco

Streszczenie

W 72-letnim pniu daglezji wykazującym bardzo duże wahania szerokości pierścieni rocznych, od 0,1 do 11 mm, przeprowadzono badania zmienności wielu różnych cech budowy mikroskopowej drewna w dwóch kierunkach: wzdłuż promienia od rdzenia na zewnątrz i wzdłuż osi pnia od podstawy ku wierzchołkowi. Zbadano również zmienność wymiarów cewki w czasie jednego sezonu wegetacyjnego. W wyniku tych badań ustalono, że przeciętna długość cewki, jej wymiar promienisty i powierzchnia poprzecznego przekroju, rosną na jednym poziomie pnia od rdzenia na zewnątrz do mniej więcej 30 pierścienia. Średnia długość cewki pozostaje potem niezmieniona, a wymiar promienisty i powierzchnia poprzecznego przekroju po osiągnięciu maksimum maleją.

Styczny wymiar cewki w dolnej części pnia do wysokości 9 m rośnie na jednym poziomie pnia w ciągu 30 - 50 lat życia drzewa, a następnie nieco spada. Na wyższych poziomach rośnie nieprzerwanie do ostatnich lat życia drzewa.

Wymiary cewki rosną również od podstawy pnia do określonej, lecz różnej dla różnych pierścieni rocznych wysokości, a następnie maleją.

Przeciętna długość cewki w ciągu jednego sezonu wegetacyjnego rośnie od drewna wczesnego do późnego, aż do początku okresu wytwarzania przez miazgę pierwszych elementów drewna późnego, potem maleje.

Prawie wszystkie zbadane cechy drewna wykazują korelację z szerokością pierścienia rocznego. Długość cewki i jej wymiar styczny są skorelowane ujemnie z szerokością pierścienia; w węższych pierścieniach znajdują się cewki dłuższe i o większym wymiarze stycznym. Natomiast wymiar promienisty cewki wykazuje korelację dodatnią — w węższych pierścieniach występują cewki o mniejszym wymiarze promienistym i odwrotnie.

Opisany wyżej charakter współzależności pomiędzy wymiarami cewki a szerokością pierścienia rocznego dotyczy tylko pierścieni szerszych niż 0,5 mm. W węższych pierścieniach cewki są krótsze i o mniejszym przekroju poprzecznym niż cewki z pierścieni 0,5 - 1,0 mm.

Z szerokością pierścienia rocznego jest skorelowana średnica jamki lejkowatej w cewce drewna wczesnego. Cewki w wąskich pierścieniach mają jamki mniejsze i odwrotnie. Cecha ta koreluje dodatnio także z promienistym wymiarem cewki.

Promienie drzewne w pierścieniach do 2 mm są niższe i składają się z mniejszej liczby komórek niż promienie w pierścieniach szerszych niż 2 mm.

Wysokość jednej komórki promienia drzewnego jest negatywnie skorelowana z wysokością promienia. W niższych promieniach znajdują się większe komórki i odwrotnie.

АЛИНА ХЭЙНОВИЧ

Анатомические исследования древесины Pseudotsuga menziesii (Mirb.) Franco

Резюме

В 72-летнем стволе дугласовой пихты, отличающемся очень большими колебаниями ширины годичных колец, от 0,1 до 11 мм, произведены были исследования изменчивости целого ряда различных признаков микроскопического строения древесины в двух направлениях: вдоль радиуса (от сердцевины наружу) и вдоль оси ствола (от основания к верхушке). Исследовани также изменчивость размеров трахеиды в течение одного вегетационного периода. В результате этих исследований установлено, что средняя длина трахеиды, её радиальная ширина и величина поперечного сечения растут на одном уровне ствола от сердцевины наружу примерно до 30 годичного кольца. Средняя длина трахеиды остаётся потом неизменной, а радиальная ширина и величина поперечного сечения после достижения максимума уменьшаются.

Тангентальный диаметр трахеиды в нижней части ствола, до высоты 9 м, растёт на одном уровне ствола в течение 30 - 50 лет жизни дерева а потом несколько уменьшается. На высших уровнях он растёт непрерывно до последних лет жизни дерева.

Размеры трахеиды растут тоже от основания ствола до определённой, но разной для разных годичных колец высоты, а потом уменьшаются.

Средняя длина трахеиды в течение одного вегетационного периода растёт от ранней древесины до поздней вплоть до начала периода выработки камбием

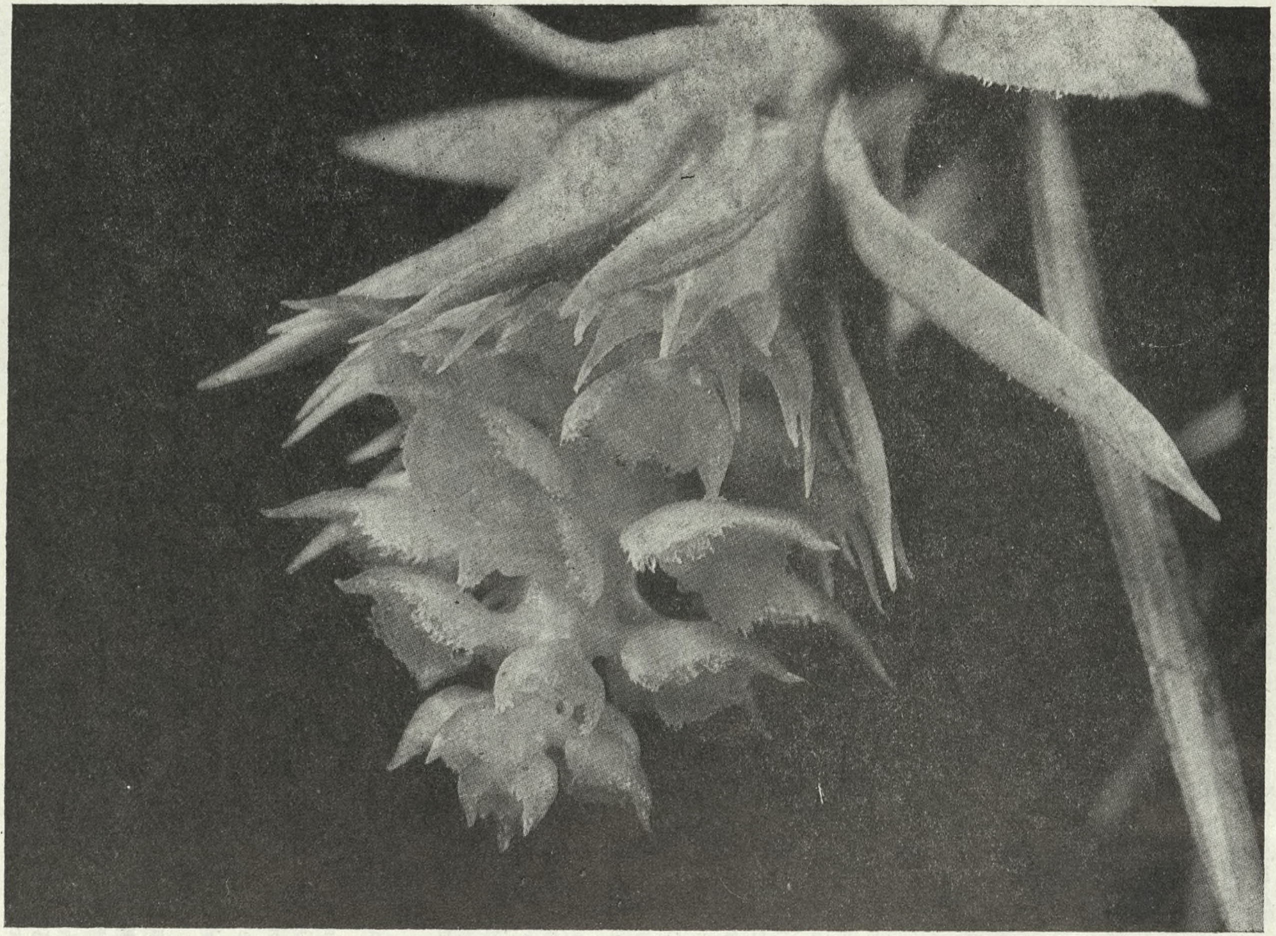
Почти все исследованные признаки древесины показывают корреляцию с шириной годичного кольца. Длина трахеиды и её тангентальный диаметр коррелируются отрицательно с шириной кольца; в более узких кольцах находятся более длинные трахеиды и с большим тангентальным диаметром. Радиальная же ширина трахеиды показывает положительную корреляцию — в более узких кольцах находятся трахеиды с меньшей радиальной шириной и наоборот.

Описанный выше характер взаимозависимости размеров трахеид и ширины годичного кольца касается только колец шириной более, чем 0,5 мм. В более узких кольцах трахеиды короче и с меньшим поперечным сечением, чем трахеиды из колец 0,5 - 1,0 мм.

С шириной годичного кольца коррелируется также диаметр окаймлённой поры в ранней древесине. У трахеди в узких кольцах поры меньшие и наоборот. Этот признак коррелирует положительно также с радиальным размером трахеиды.

Древесные лучи в кольцах до 2 мм являются более низкими и состоят из меньшего числа клеток, чем лучи в кольцах шириной больше 2 мм.

Высота одной клетки древесного луча коррелируется с высотой луча. В низших лучах находятся большие клетки и наоборот.



Fot. K. Jakusz

Cunninghamia lanceolata — kwiatostan żeński