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Variations of length of vessel members and fibres in the trunk of *Populus tremula* L.

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The present report is concerned with variations of length of tracheary elements (tracheids, fibres and vessel members) in the tree trunk. The problem has been the subject of investigations during the past 85 years and the most important results arrived at hitherto can be summarized as follows (a full list of literature was assembled by Bisset (1949) and Spurr (1954):

1. There is a gradient of average length of tracheary elements along the radius of trunk, branches and roots. It consists in an increase in the length of one kind of elements from the pith outwards. In the first dozen or so of annual rings the increase of the average length of elements is rapid, then it drops gradually and when a certain maximum is reached the length of elements remains constant in the majority of cases (Sanio 1872, Pritchard & Bailey 1916, Lee & Smith 1916, Chalk 1930, Desch 1932, Runquist & Thunell 1945, Bisset & Dadswell 1949, Anderson 1951, Hata 1952, Hejnowicz & Hejnowicz 1956). Sometimes the average length increases over many annual rings but it may decrease after the maximum is reached (Sanio 1872 in root, Bailey & Shepard 1915, Kribs 1928, Desch 1932, Bailey & Faul 1934, Nilsson 1945, Boshard 1951), or it may vary greatly along the radius.

2. There is a gradient of element length along the trunk and branches: a) upwards in the same ring and b) upwards at the same number of rings from the pith. In the former case the average length increases from the base upwards to a maximum and then distinctly decreases towards the top (Sanio 1872, Pritchard & Bailey 1916, Bailey & Shepard 1915, Lee & Smith 1916, Chalk 1930, Bethel 1941, Hata 1949, Bisset & Dadswell 1949), the longest elements being formed every time at a higher level as successive annual rings are laid down

(Bailey & Shepard 1915, Lee & Smith 1916, Bethel 1941, Bisset & Dadswell 1949). In the latter type the average length increases distinctly from the base upwards after which there is a slight decrease towards the top (with the exception of the first annual ring where the length tends to be constant) (Sanio 1872, Chalk 1930, Bethel 1941, Bisset & Dadswell 1949).

3. On the whole the length of elements in branches is shorter than in roots (Fegel 1941), whereas, in others in the trunk (Fegel 1941, Lee 1916, Fegel 1941, Hata 1949).

4. The length of elements in roots as compared with the trunk differs in various species. In some species shorter elements have been found in roots (Fegel 1941), whereas, in others in the trunk (Fegel 1941, Lee 1916, Bailey & Faul 1934). The results in this respect depend greatly on the number of rings under consideration; in the first rings the longer elements occur in roots and in the more distant ones in the trunk (Sanio 1872, Hejnowicz & Hejnowicz 1956).

5. Early wood elements are shorter than late wood ones from the same annual ring. This refers equally to fibres, tracheids (Lee & Smith 1916, Lee 1916, Kribs 1928, Chalk 1930, Bisset & Dadswell 1950, Bisset, Dadswell and Amos 1950, Boshard 1951, Chalk & al. 1956), and vessel members in nonstoried wood (Chalk & Chattaway 1935, Bisset & Dadswell 1950, Boshard 1951).

6. In some cases there is a negative correlation between the rate of wood formation and the average length of fibres or tracheids (Bisset & Dadswell 1949, Lee & Smith 1916, Chalk 1930, Helander 1933), but the correlation is by no means always apparent (Sanio 1872, Shepard & Bailey 1914, Hejnowicz A. & Hejnowicz Z. 1956).

7. Compression wood is characterized by shorter tracheids or fibres (there are no reports in this respect on vessel members) than in corresponding normal wood (Lee & Smith 1916, Bisset & Dadswell 1950).

8. Tracheids and fibres are longer in faster growing trees (more vigorous) than in those growing slowly (MacMillan 1925, Nilsson 1945).

It is well known that the length of tracheary elements depends upon 1) the length of cambium initials which form them and 2) the amount of intrusive growth which they undergo during differentiation (Bailey 1918, Bailey 1920). Thus, for the understanding of the facts listed above it is necessary to have a good knowledge of variations occurring within each of these two factors, nevertheless, analyses of that kind were never given much attention in earlier investigations. The only exception in this respect were the researches carried out by Shin-Chen Liang

(1948), and to some extent by B o s h a r d (1951). The results reported by these workers will be considered further on. The present paper is an attempt at analysing all aspects of variations in the length of tracheary elements in an asp-tree trunk frcm the point of view of variations occurring in cambium.

To start with it seems worth while to consider the factors on which the length of tracheary elements depends and also the conclusions resulting from earlier reports on length variations of these elements.

The only problem in the case of vessel members in dicotyledons and of tracheids in conifers is that of the length of cambial initials, as already B a i l e y (1920) demonstrated that in the course of differentiation of these elements there was either no intrusive growth or intrusive growth was only slight. The length of the elements equals the length of the fusiform cambial initials from which the elements developed. Thus, the radial gradient of vessel-member or tracheid lengths shows that the average length of initials increases with age till a maximum is reached.

The average length of initials in nonstoried cambium depends on the rate of intrusive growth of the particular initials and the frequency of their anticlinal divisions. The increased average length of fusiform cambial initials indicates that their rate of growth was greater than the frequency of divisions. A constant average length of initials indicates that anticlinal divisions wholly compensated intrusive growth. Consequently, the radial and longitudinal gradients of length of such elements as tracheids and vessel members show that the proportions of intrusive growth and anticlinal divisions in fusiform initials change (increase) with the age of cambium and that these proportions in cambium of the same age differ on various levels.

The length of wood fibres depends on the length of cambium cells and on intrusive growth occurring in the course of fibre development. To determine the degree of intrusive growth it is necessary to know the length of fibres and cambium cells. The latter value can be replaced by the length of vessel members accompanying the particular fibres. However, there are unfortunately no reports giving the corresponding lengths of fibres and vessel members in the different parts of a tree.

It has been stated beforehand (point 5 of the list of earlier results) that early wood elements are shorter than the late wood ones. This refers to tracheids, fibres, and vessel members (in the last case the statement is true only for nonstoried wood). The question now arises what is the reason for such cyclic changes in element lengths? In the case of fibres the answer may lie in the different rates of intrusive growth during the different seasons. However, in the case of vessel members this factor cannot be taken into account as it is generally accepted that they do not increase in length during their development. Thus, it seems that the cyclic changes of vessel members are caused by cyclic changes in the length of cambial cells.

In 1950 Bannan found that in *Chamaecyparis* anticlinal divisions of fusiform initials of cambium occurred mainly at the end of the vegetative season. The cumulation of anticlinal divisions in one season must of course result in a decrease of the average length of vessel members developed at that time or shortly afterwards. Consequently, the reason for the cyclic changes in the length of vessel members must be looked for in the uneven time distribution of anticlinal divisions.

The circumstance that the average size of cambial initials depends on the number of newly formed fusiform initials is pointed out also by Schin-Chen-Liang (1948).

An earlier paper (1956) reported on preliminary investigations on the length of fibres and vessel members in asp. It was then stated that in rings with the same number (counting from pith) at two different levels the length of vessel members and fibres was distinctly different which obviously was associated with the longitudinal gradient of element length. Namely, in all rings of the trunk except the first one the length of elements at the three-metre level was greater than in the corresponding rings at the thirteen-metre level. On the other hand when the element lengths were related to the linear distance from the pith the difference between the two levels disappeared. At a given distance from the pith the element length was always the same on both levels.

A similar relationship between the length of elements (tracheids) and distance from the pith — the same for all levels except the one just over the ground — was reported by Anderson (1951) in trunks of coniferous species: *Abies concolor, Abies procera* and *Pseudotsuga taxifolia*.

Before any conclusions are drawn from these facts let us make first some definitions of terms which will be used.

The number of a ring counted from the pith defines the time in years which passed from the moment when cambium was formed to the formation of the given ring, or in other words the age of cambium at the time when the ring was forming. This age will be referred to as the absolute age.

The distance of a ring from the pith depends on the number of wood cells laid down beforehand and, consequently, on the number of cambial cell generations preceding the formation of the ring. Now if the transverse or radial size of wood cells differs with the distance away from the pith in the same manner at various levels, then the distance from the pith is the relative measure of the number of cambial generations or in other words the measure of the age of cambium expressed in the number of cambial generations. This age will be referred to as the relative age.

If we now remember that, as has been stated above, the lengths of vessel members in asp trunks and of tracheids in trunks of conifers are the same for various levels at a given distance from the pith and simultaneously differ for rings with the same number, then the following hypothetical assumption can be made: the length of initials depends on the relative age of cambium as measured in the number of generations and not on the absolute age measured in years. The hypothesis was already made in the previous report and this investigation has been primely concerned with checking its validity. Another more direct aim has been to investigate fully the length gradient of tracheary elements in the trunk of an asp-tree many years old. For this purpose it was necessary to measure the length of vessel members and fibres (only these two kinds of elements are present in asp) in successive annual rings along the radius at various levels.

MATERIAL AND METHODS

For measurements the trunk of a straight vertical tree of *Populus tremula* L. was used. The relevant data are as follows: height of tree — 26 m; diameter of trunk one metre above ground — 41—50 cm; age — 53 years; main branches growing out 11 m, 13.5 m (two), and 14.5 m above ground; symmetric crown; habitat in a mixed forest.

The investigation consisted of two stages, one fundamental the other supplementary. The aim of the former stage was to determine the average lengths of vessel members and fibres of the trunk in successive annual rings or in layers thinner than rings at 21 levels along the south radii. In the supplementary stage radial diameters of fibres in successive rings at various levels were determined.

The levels for which measurements were made are listed in Table 1 together with the relevant data and are shown on the longitudinal section through the trunk in Fig. 1.

The procedure was as follows: On the fallen trunk the south side was marked with a long incision in the bark and then at the particular levels discs about 5 cm thick were cut out from the trunk. On every disc the lengths of south and north radii were measured and then narrow radial strips (1 cm wide) were cut out from pith to bark along the south radii. The transversal surface of every strip was planed and transversal sections from the whole of those surfaces were cut off. The width of rings was measured on the sections using a microscope (objective x1, eye piece x6), and then every strip was split into blocks along the planes dividing rings and the blocks were placed in separate glass tubes marked with the

Table 1
Examined levels

Level	Height above ground level metre	Length of south radius (cm)	Number of annual rings	Number of examined ring
A	0,0	20,3	53	all and anew every other
B	1,15	18,2	51	all
C	2,22	20,3	48	all and anew a part of rings with splitting into layers
D	3,31	15,0	46	all
E	4,37	19,4	44	all
H	7,59	23,6	39	all and anew a part of rings with splitting into layers
J	8,66	18,4	37	all
K	9,71	17,0	37	all
L	10,79	21,5	35	all
N	12,95	13,2	31	all
O	14,03	12,8	29	all
P	15,12	11,0	28	all
R	16,22	10,3	26	all
S	17,31	8,9	25	from 10 to 25
T	18,71	4,0	24	all
U	19,86	4,3	20	all
W	20,94	3,4	15	all
X	22,07	2,2	11	all with exception 2 and 4
Y	23,24	1,7	9	all with exception 2,4 and 8
Z	24,04	1,0	6	all with exception 2

number of the ring from which the block was cut out. In the case of levels C and H some of the blocks were further split radially into two parts of which one was divided tangentially into several (2—9) layers. In every block the length of fibres and vessel members was measured.

To measure the length of elements maceration was necessary. For this purpose small chips covering the whole width of a ring or its layer were stripped from the radial side of a block and were macerated for one hour in modified Schultz's fluid (10 c. c. of 80% nitric acid, 0.5 g of $KClO_4$ at 60°C). Maceration was interrupted by adding cold water before the chips were crumbled. The mass was then washed carefully with cold water and broken up into elements by shaking vigorously. Rapid sedimentation of elements was obtained by centrifugation. After decantation glycerin was added and a drop of the sediment was placed on a slide. In the preparations thus obtained there were almost no damaged elements.

From every sample 50 fibres and 50 vessel members were selected. Length measurements were made with a microscope fitted with a x10 objective and a x6 eye-piece. Mean values were computed from 50 measurements. The number of samples examined was 762 for complete rings and 111 for ring layers. The number of fibres and vessel members was 43 000 each, amounting to a total of 86 000 elements.

For measuring radial diameters of fibres in supplementary measurements transverse sections were made from blocks corresponding to the particular rings. From different parts of a ring 5 radial series of fibres with approximately 10 fibres in every series were measured. From the total length of these series and the total number of cells in them the average radial diameter of fibres was computed. Measurements of that kind were made for successive rings from 10 levels (A, E, L, N, O, R, T, U, X, Y).

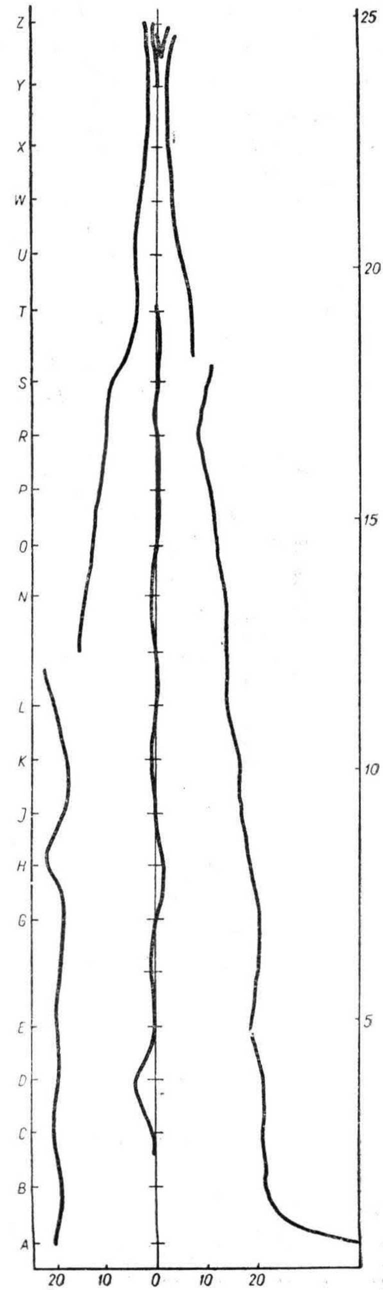


Fig. 1. Schematic diagram showing longitudinal section through trunk in the north-south plane. The letters on the left of the axis show the examined levels. The heights above the ground are marked in metres on the right of the axis. The diameter of the trunk is marked in centimetres

RESULTS

There are three methods of characterizing wood: 1) by the age of cambium involved in wood formation, i. e. by the number of a ring as counted from the pith, 2) by the year of formation, i.e. the number of a ring counted from the bark (e. g. in a fallen trunk the second ring from outside was formed at all levels in the last year but one in the life of the tree), and 3) by the linear distance from the pith. When comparing the length of elements all these three methods of characterizing wood must be taken into account.

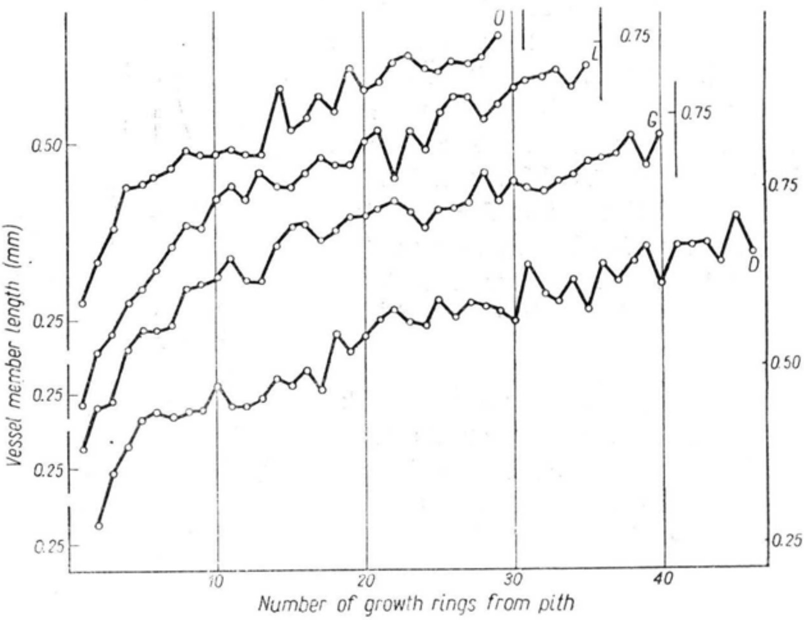


Fig. 2. Gradient of average length of vessel members in annual rings along radius at 4 freely chosen levels. The points joined with straight lines show the average length of vessel members in the particular annual rings· Curves have been displaced successively downwards to prevent overlap

Length gradient of vessel members and fibres along radius

This gradient can be established from average values for the particular annual rings or layers thinner than annual rings. In the former case variations within a ring are eliminated, whereas, in the latter they can be estimated. In this manner either a general or a detailed gradient can be established. As has been mentioned average values can refer either to the number of a ring, i. e. to the age of tissue, or to the distance from the pith. The gradient will then correspond to the age or to the distance from the pith.

General gradient depending on age

The general trend of changes in the average length of vessel members and fibres as the number of rings from the pith increases is of the nature of a logarithmic function. This is shown by the curves in Fig. 2 and 3

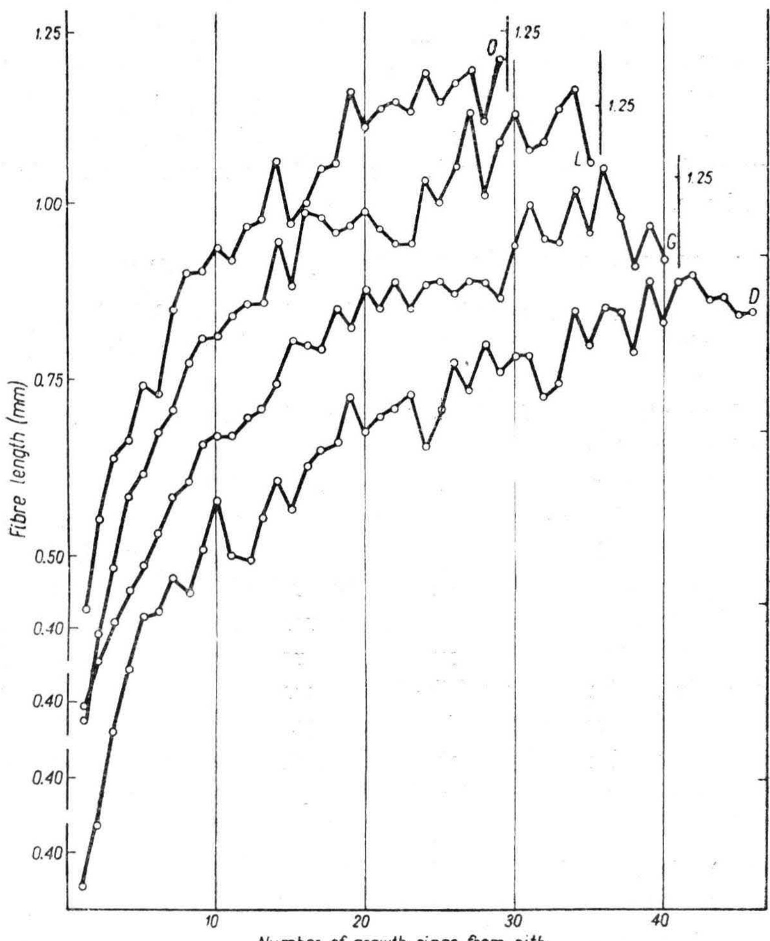


Fig. 3. Same as Fig. 2 for fibres

for several chance chosen levels. It is to be seen that 40 to 50 years is unsufficient for obtaining a constant length of elements.

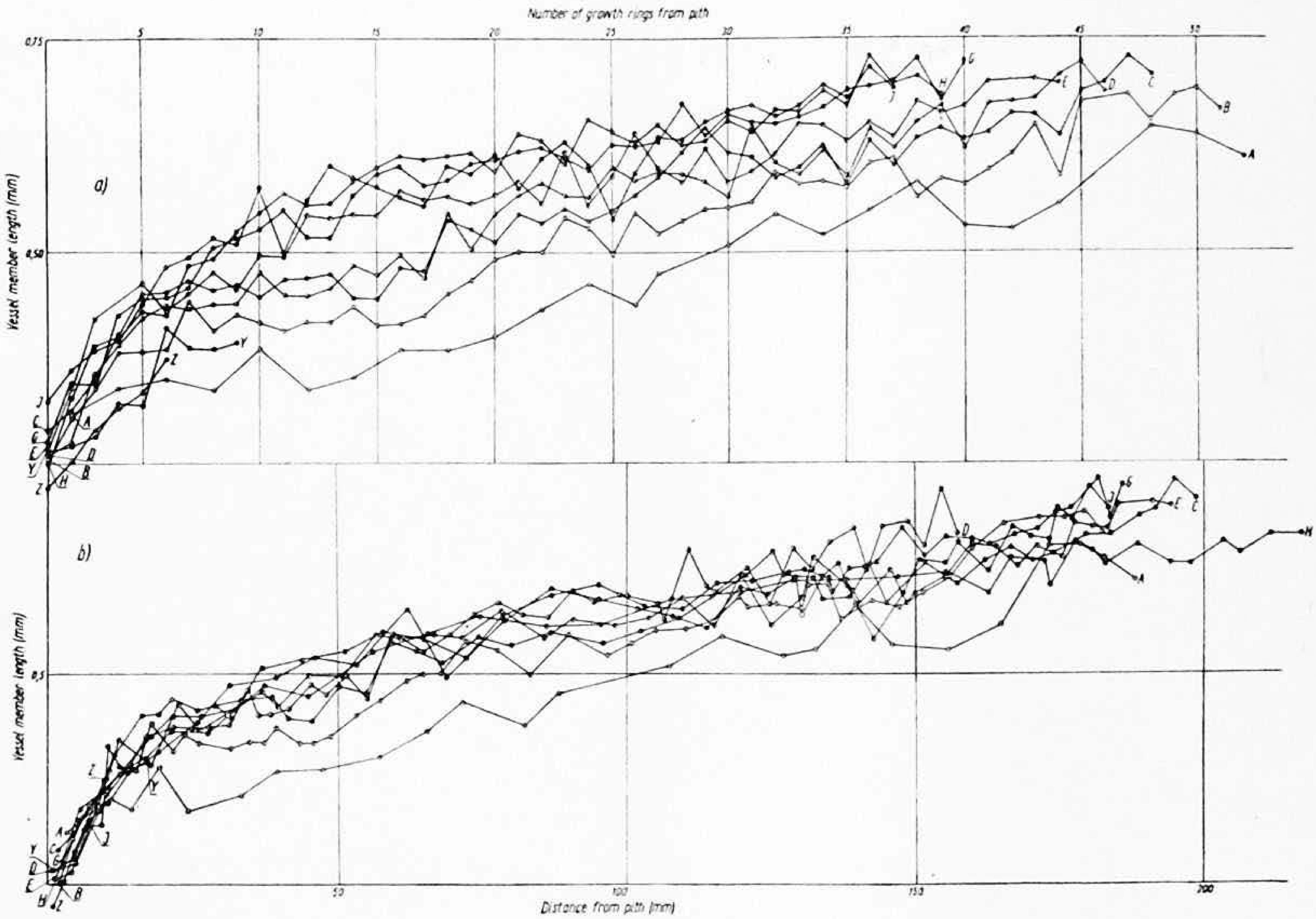
There are considerable fluctuations in the particular average values and consequently the line connecting them has numerous tips and dips. However, there is no need to attach too much significance to these fluctuations at it is quite evident that the mean values used here cannot be considered separately. The reason is of course the small size and the unsufficient representativeness of samples from which the mean values have been derived. The line joining the particular points of the curves is drawn in solely to facilitate visual interpretation.

The changes in length of elements from successive annual rings are on the whole similar and have the same trend on all levels. Nevertheless, in respect to certain details which of course are not associated with fluctuations there are some differences between the particular levels. This is shown by the curves marked with letter *a* in Figs. 4, 5, 6 and 7. Curves from different levels do not correspond. The greatest differences occur between levels from the middle part of the trunk and levels in the crown and base.

General gradient depending on distance from pith

The gradient (curves marked *b* on Figs. 4, 5, 6 and 7) has the same character as the gradient depending on age. This is natural as the difference between the two gradients consists only in small shifts of average values along the horizontal axis. However, a more accurate analysis brings forth some specific peculiarities of gradients depending on distance. When curves *a* and *b* on Figs. 4—7 are compared it is seen that at various levels the gradients depending on the distance from the pith are more alike than the corresponding gradients depending on age. The curves marked *b* correspond more accurately than the curves *a*. In particular, the gradients illustrated by curves *a* for the levels from the crown of the tree lie distinctly outside the range of variations of levels from the middle of the trunk, while in the case of curves *b* the gradients are well within the range of variations (Figs. 5, 7). Only the gradient of the length of vessel members at level A (immediately above ground) behaves in both cases differently than at other levels; vessel members at level A are distinctly shorter than in the rest of the tree.

To check whether the generally shorter length of elements from level A is not a chance result the measurements were repeated for avery other ring. This seemed advisable as level A was the first to be examined and it was, therefore, possible that the difference in respect to other levels was due to unsufficiently refined techniques of maceration and measurement. The repeated results are compared in Fig. 8. The graph shows, moreover, the data for the north radius at level A, because ori-



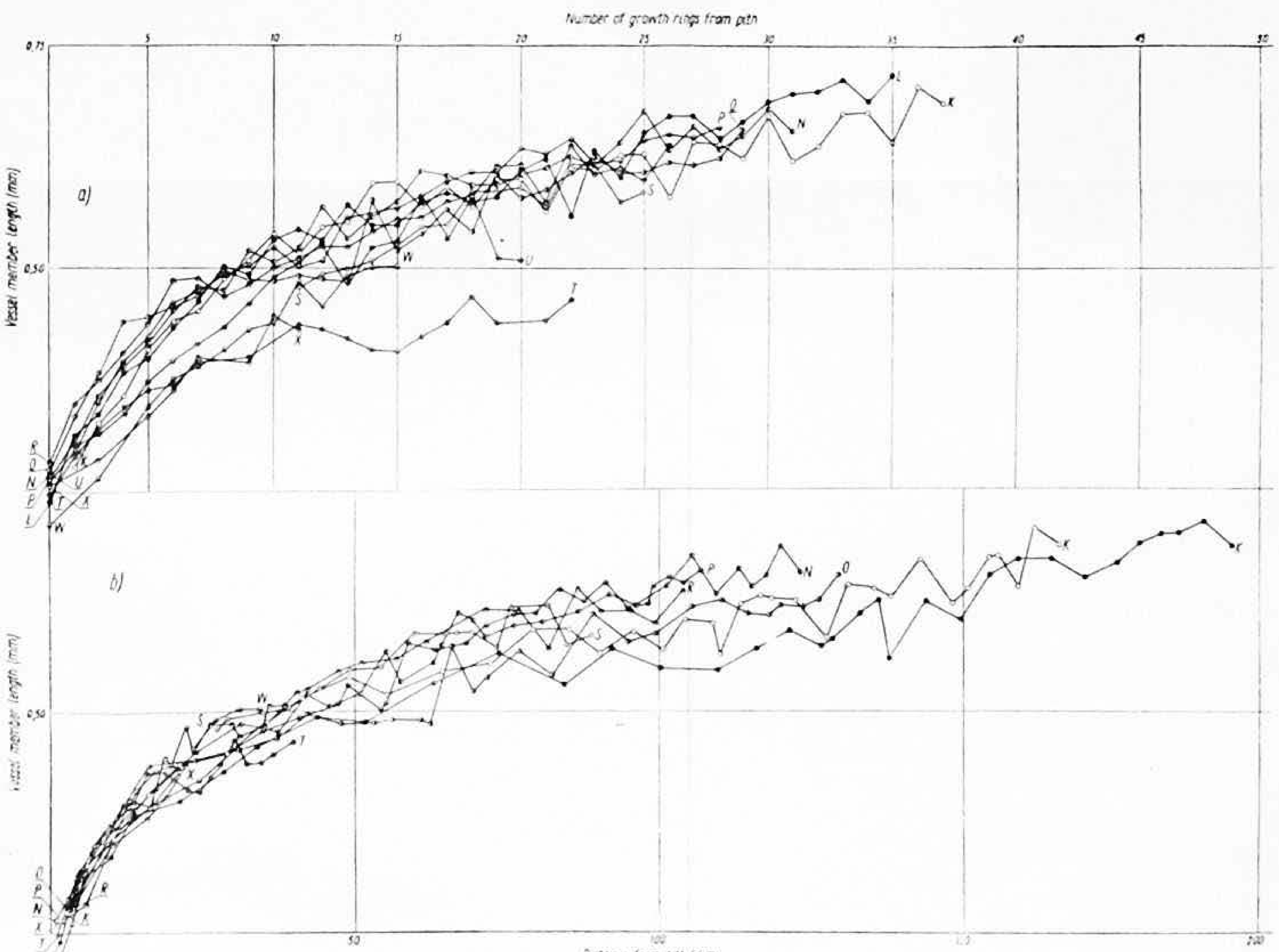
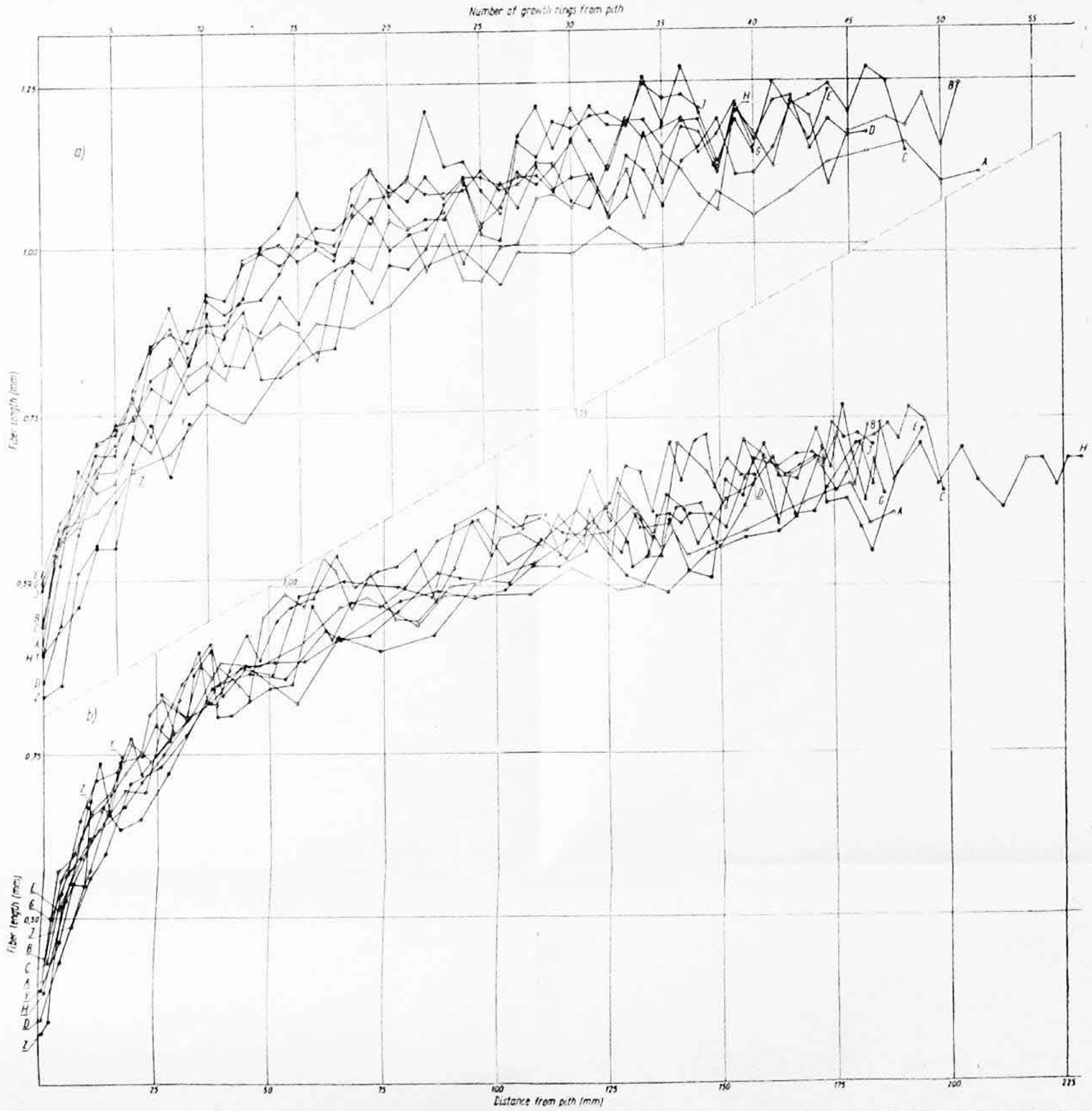


Fig.s 4 and 5. Gradient of average lengths of vessel members in rings along radius at various levels. Points joined with straight lines show the average lengths of vessel members in the particular rings. Some of the levels are shown in Fig. 4 the rest in Fig. 5

a — gradient depending on age (growth rings numbered from pith outwards); b — gradient depending on linear distance from pith



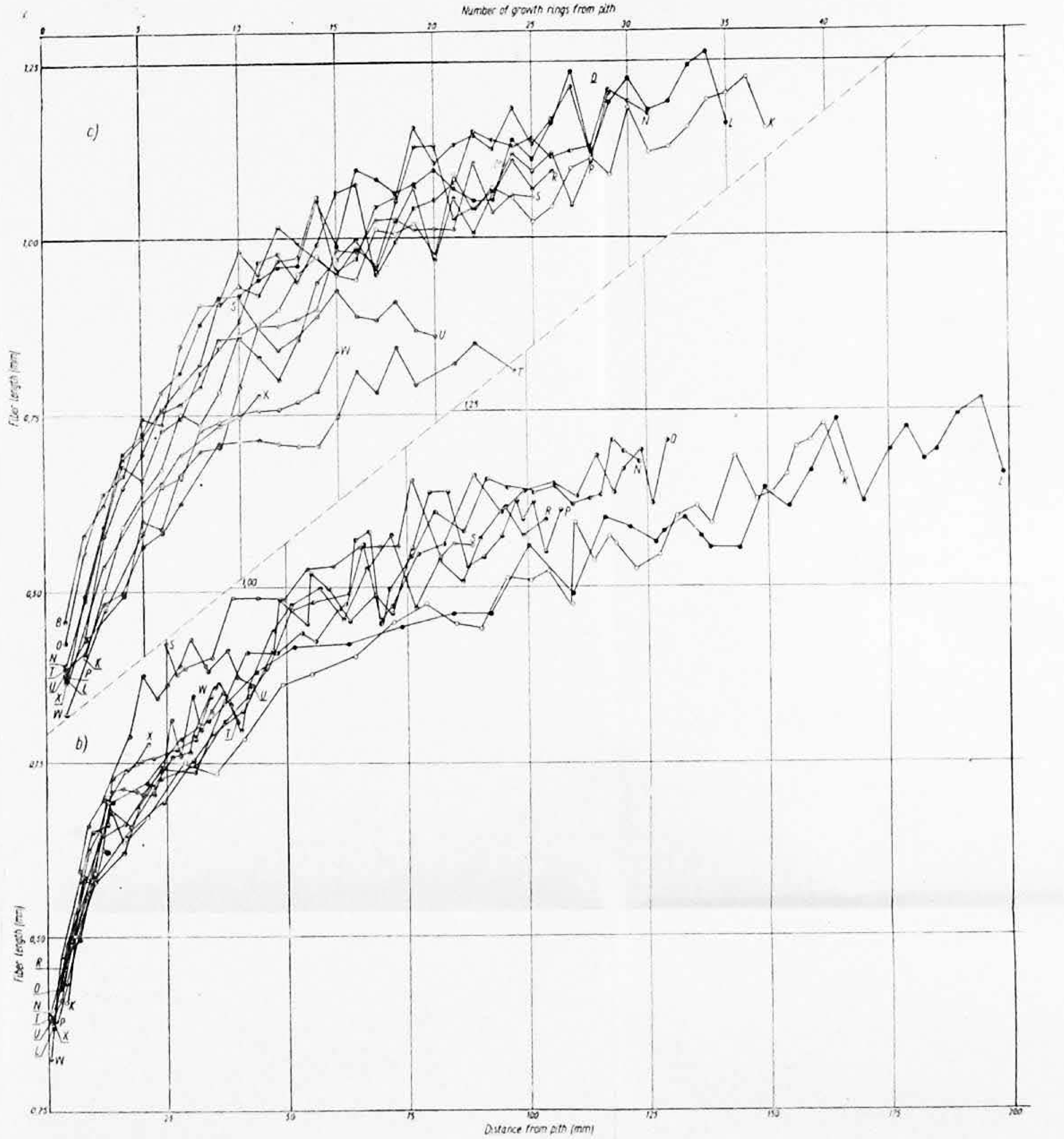


Fig. 6 and 7. Same as in Figs. 4 and 5 for fibres

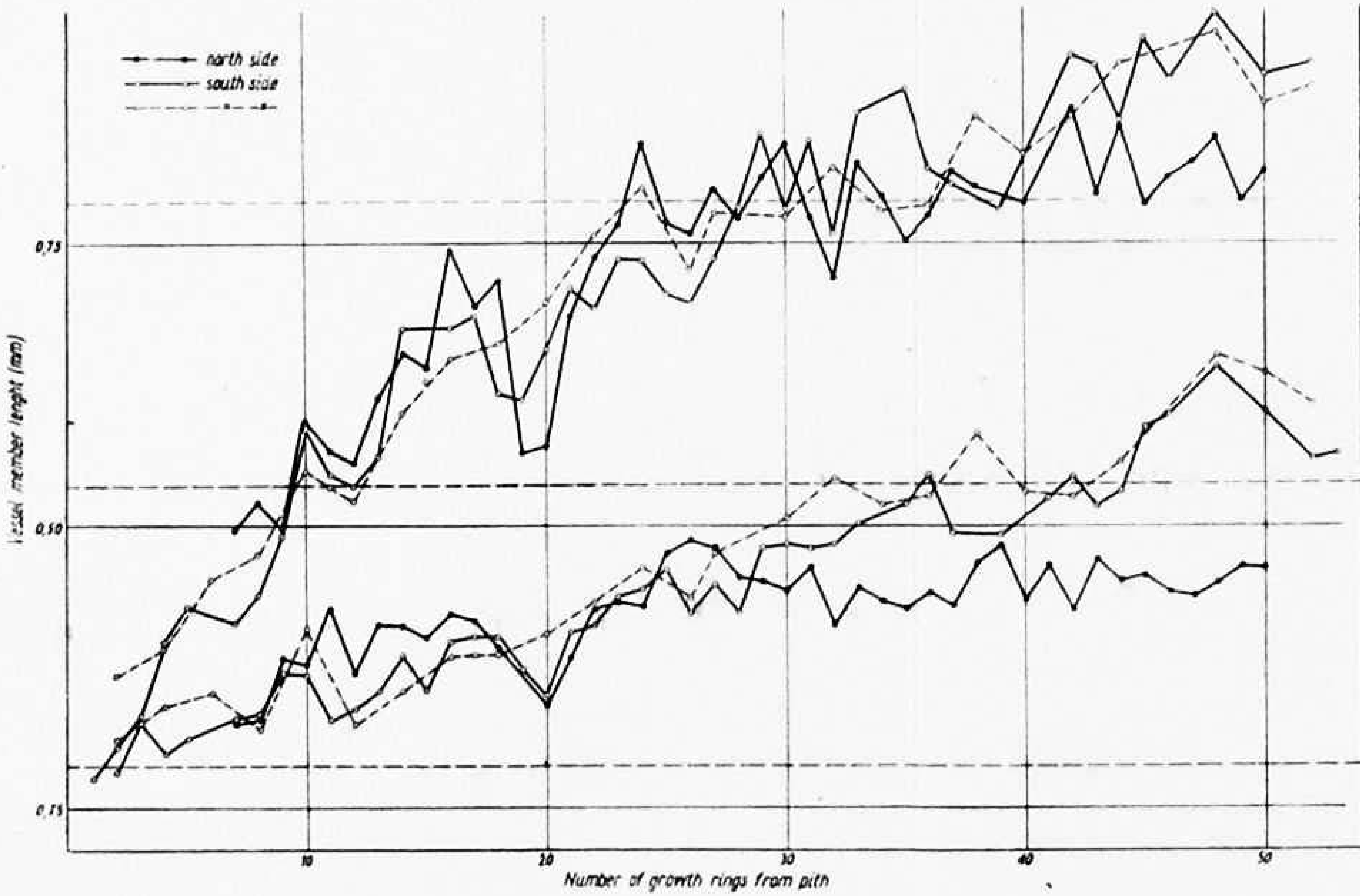


Fig. 8. Gradients of average lengths of vessel members (lower curves) and fibres (upper curves) along radius at ground level on the north and south sides. On the south side measurements were repeated twice

ginally it was planned to examine the element lengths from both sides of the trunk. It follows from Fig. 8 that the first results are absolutely correct.

Detailed gradient depending on distance

The gradient was determined for chosen groups of rings at levels H and C. The following rings were examined: at level H rings 1—11 and 21—24, and at level C rings 1—3, 6—7, 15—16 and 20—21. The number of layers into which rings were split depended on their thickness. The thickness of layers was not uniform and attempts were made to obtain thinner layers near the boundaries of rings. Altogether 111 layers from 25 rings were examined. The results are shown by the curves in Figs. 9—10 (empty circles joined with continuous line).

There is a distinct seasonal regularity in the changes of fibre length (with the exception of the first 2 or 3 rings). The regularity consists in a gradual increase of fibre length within a ring from the first formed early wood to the last formed late wood and a sudden drop in length at the boundary between rings. The difference between the length of fibres of the earliest and latest wood amounts to 24%. In some rings the drop in length of fibres occurs already in the last formed late wood, but it is possible that this drop is due to the manner of splitting up the rings.

Disturbances in the regularity of differences in fibre lengths are apparent in some of the rings from level C, however, it seems likely that the irregularities may be caused by an excessive thickness, as compared with the thickness of rings, of the layers used for measurements.

In the case of vessel members a seasonal regularity, similar to the regularity in changes of fibre length, was recorded only in rings 21—24 on level H. In the other rings of that level and of level C the length of vessel members changed more or less irregularly.

It seemed plausible to suppose that the cyclic variations in the length of vessel members, where they were recorded, were caused by changes in the length of outgrowths at the ends of the segments. To check on this possibility the length of vessel members was measured once again with and without the outgrowths (Fig. 11). The repeated measurements confirm the regularity in the length variations of vessel members and show, moreover, that the regularity is not due to changes in the length of outgrowths but refers too to the thick conductive parts of vessel members.

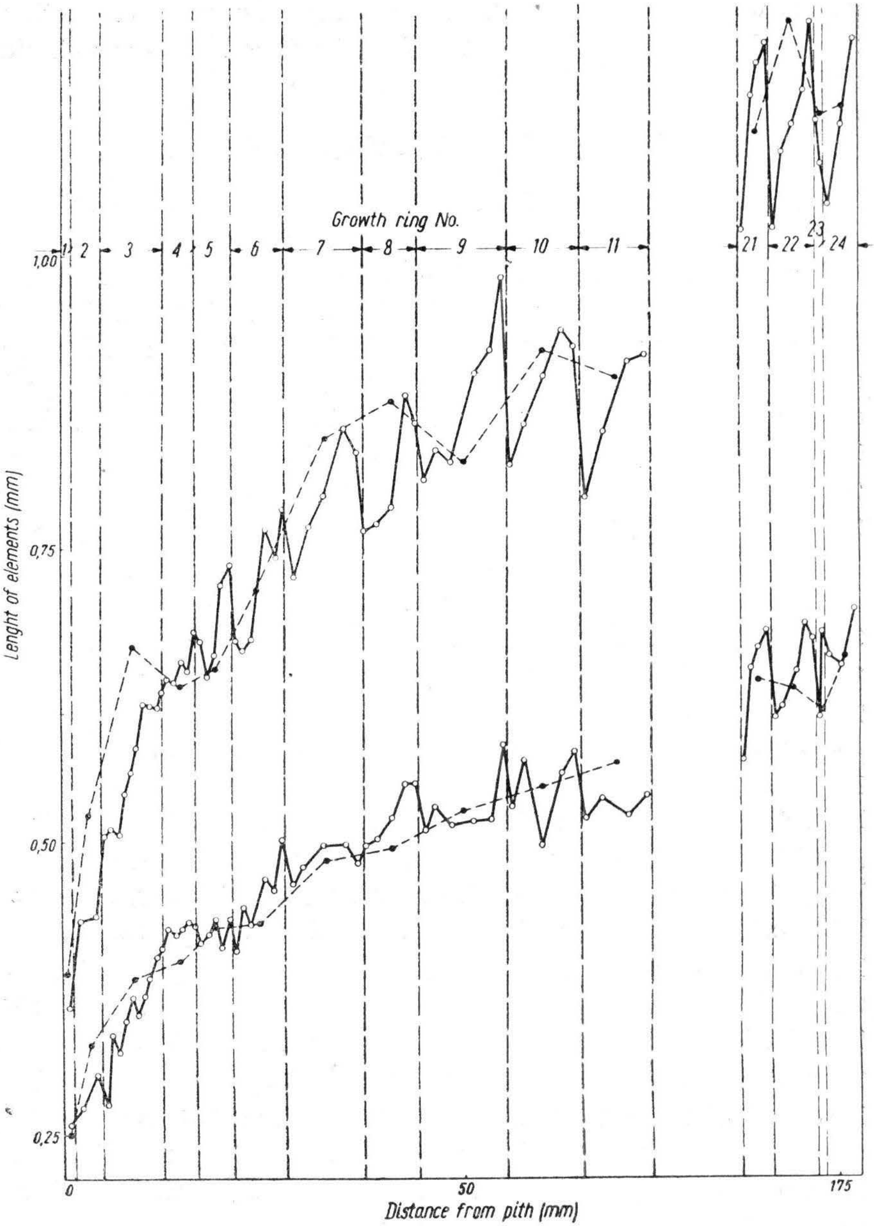


Fig. 9. Detailed gradients of the length of vessel members (lower curves) and of fibres (upper curves) along radius at level H (7,6 m above ground). Points joined with continuous line show the average length of elements in the particular layers into which annual rings were divided. General gradients (points joined with broken line) computed independently of element length in layers within rings are also shown. Vertical broken lines show the boundaries between rings

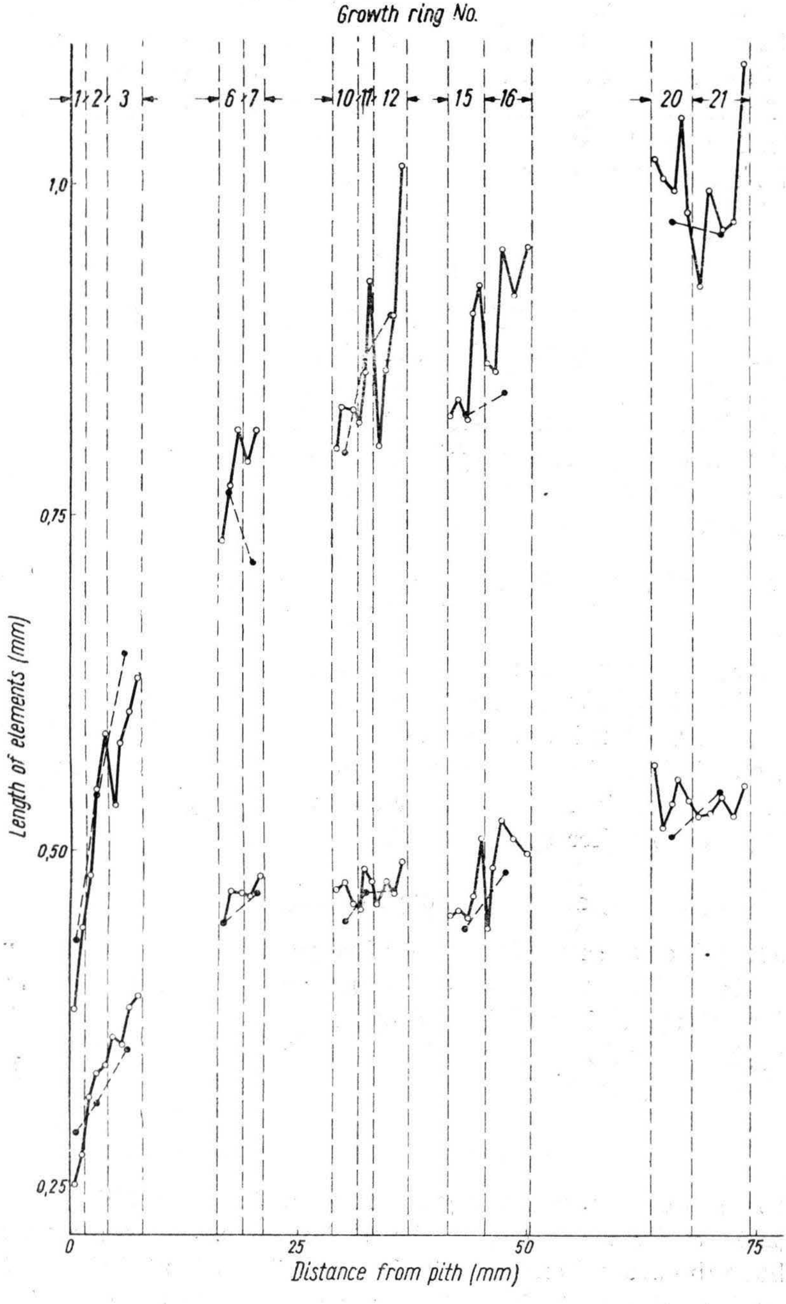


Fig. 10. Same as Fig. 9 at level C

In Figs. 9 and 10 the mean values for annual rings (black dots joined with broken line) are compared with the detailed gradients. Although, the average values lie within the range of variations for the corresponding rings in some cases they refer to elements of early wood, whereas, in others to elements of late wood in spite that care was taken to prepare strips for maceration from the whole radial surface of a ring. Consequently, it is to be stressed once again that not too much significance must be attached to fluctuations of average values within the general gradient.

THE GRADIENT OF LENGTH OF ELEMENTS UP THE TRUNK

This part of considerations is based on essentially the same average values as those already used, however, it has been mentioned beforehand that the average values cannot be compared individually because of the insufficient number of measurements in the particular samples. Consequently new average values were computed for groups of rings, so that groups of rings from the different levels and not the particular rings are now compared.

Upward gradient in the same ring depending on the year of wood formation

The length of elements formed in the particular years at various levels is shown by Figs. 12 and 13. It is to be seen that elements formed in the same year at various levels are of different length. The length of vessel members and fibres increases upwards to a point and in the upper parts of the tree drops distinctly. The level at which elements are the longest lies every year further up the trunk.

Upward gradient in groups of rings of the same age

The length of elements in groups of rings of the same age is illustrated by Figs. 14 and 15. The length of elements increases at first from the ground level upwards and then drops somewhat at the highest levels. The length of vessel members in the older rings increases distinctly up to 10 m above the ground.

Upward gradient depending on distance from pith

The length of elements at a given distance from the pith is illustrated by Figs. 16 and 17. The length of vessel members increases up only to 2 m. above the ground and then is the same throughout the rest of trunk. The length of fibres at given distance from pith is the same in all the levels.

INTRUSIVE GROWTH OF FIBRES IN VARIOUS PARTS OF TREE

When the lengths of fibres and vessel members in the various parts of a tree are known it is easy to calculate the ratio between them. As has been said beforehand that ratio defines intrusive growth in the course of differentiation of libres and is called the coefficient of intrusive growth. To reduce the error in the particular average values the coefficients are computed not for particular rings but for groups of rings (with the exception of the first two). The procedure is to divide the sum of the average fibre lengths in a group of rings by the sum of the average lengths of vessel members. The coefficients are listed in Table 2. It follows from this table that at any particular level the fluctuations of coefficients are rather large which is undoubtedly caused by statistical defects. It seems, nevertheless, that theres is a regular tendency in the changes of the coefficients consisting in their increase over the first 10—15 rings, the rate of increase being greatest in the first and second rings. It is apparent that there are no significant differences between the particular levels with the exception of the first two above the ground where the coefficient of intrusive growth is on the whole somewhat higher.

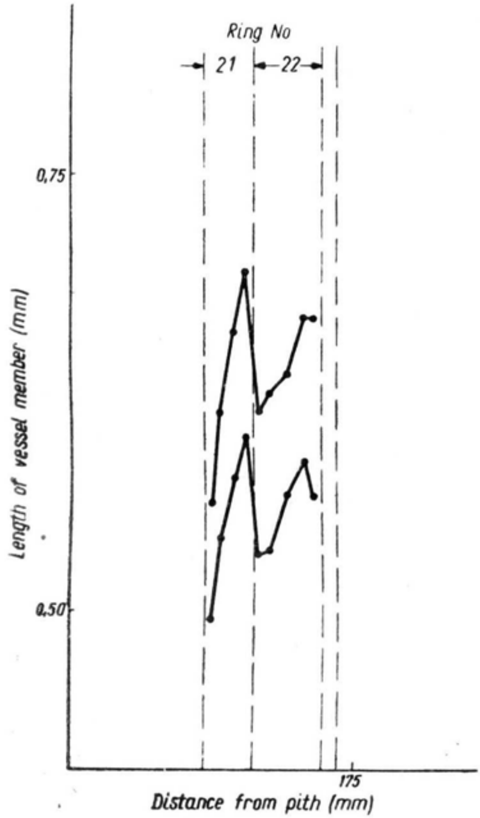


Fig. 11. Length of vessel members with (upper curve) and without (lower curve) outgrowths in successive layers of two rings in which (Fig. 9) cyclic changes in the length of vessel members were recorded

In view of the large volume of data it seems plausible to suppose that, in spite of the considerable errors in the particular mean values, a correlation, if any, could be established between the intensity with which wood was laid down (width of ring) and intrusive growth. However, when the relevant data is analysed by plotting the ratio of fibre length to the length of vessel members against the width of rings (Fig. 18) the above supposition must be rejected; there is no correlation between the width of rings and intrusive growth.

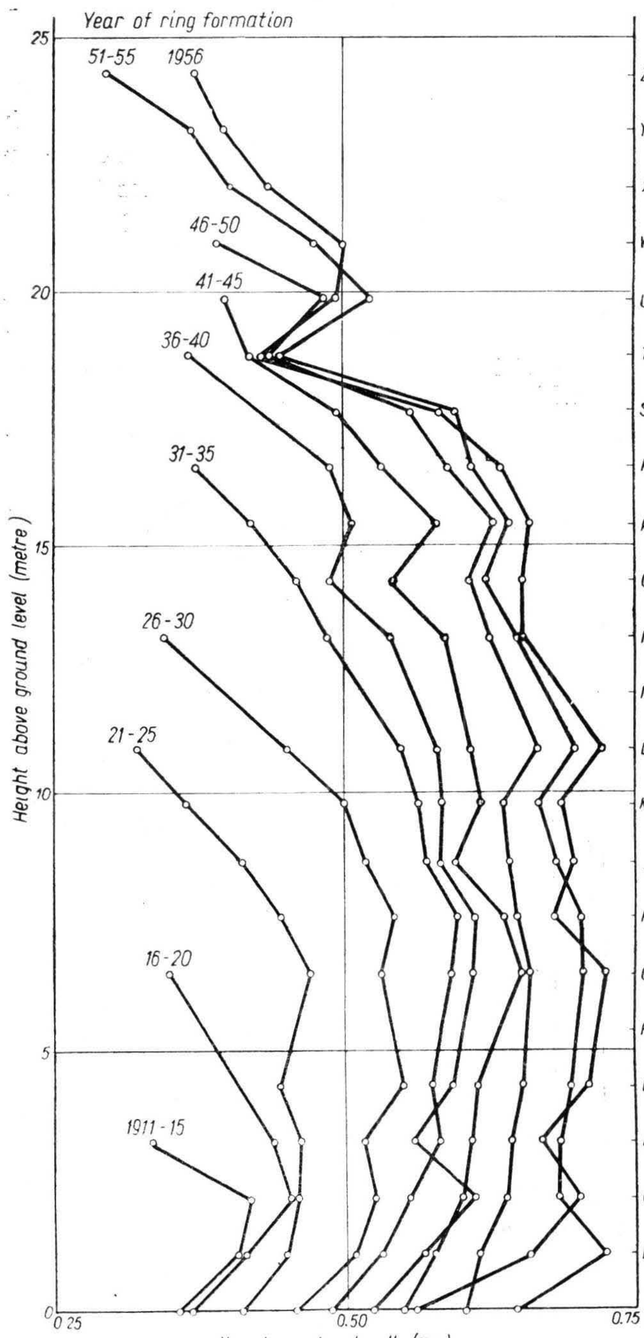


Fig. 12. Length of vessel members in groups of rings produced in the same years at various levels

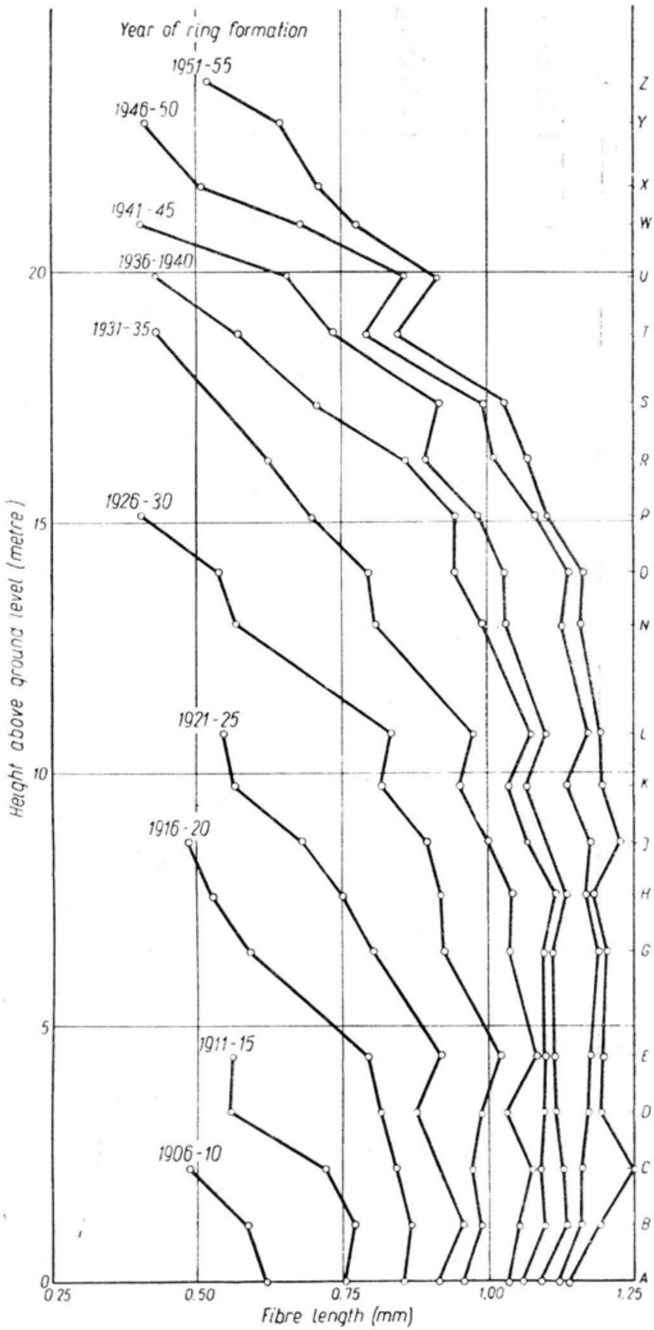


Fig. 13. Same as Fig. 12 for fibres

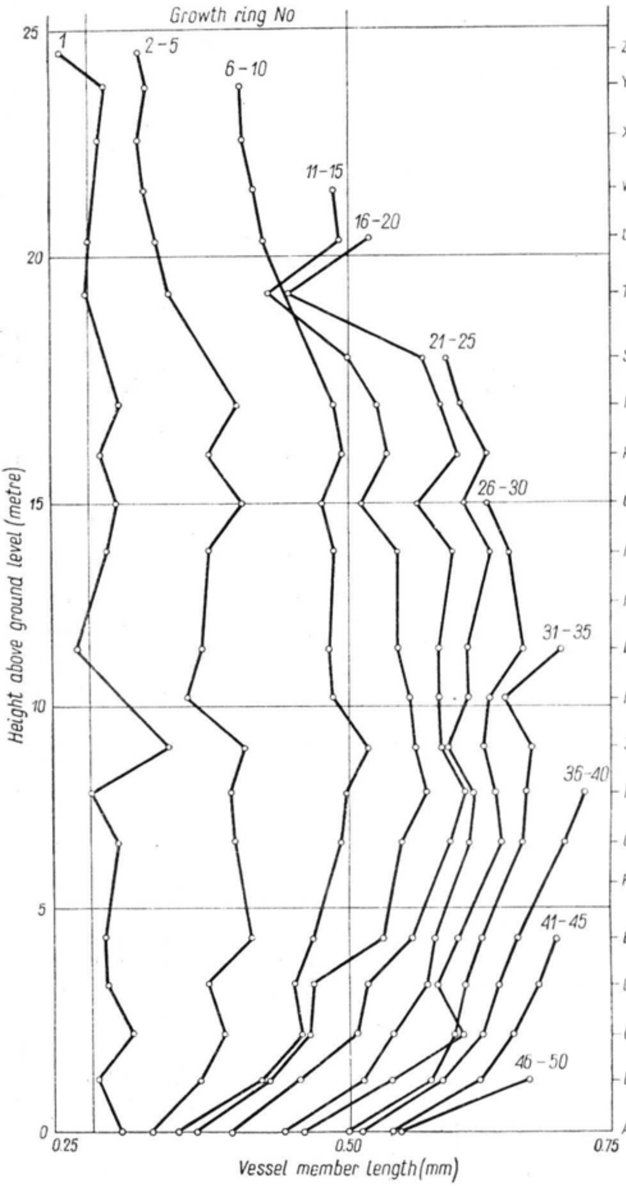


Fig. 14. Length of vessel members in groups of rings of the same age from the pith at various levels

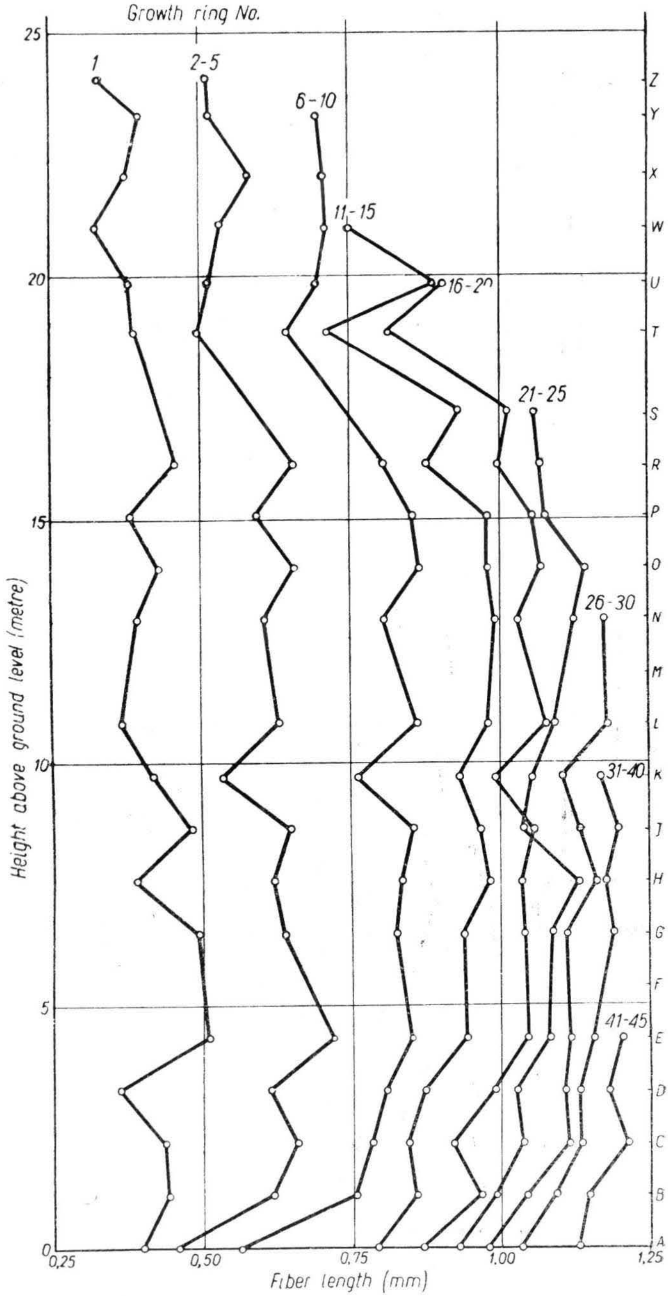


Fig. 15. Same as Fig. 14 for fibres

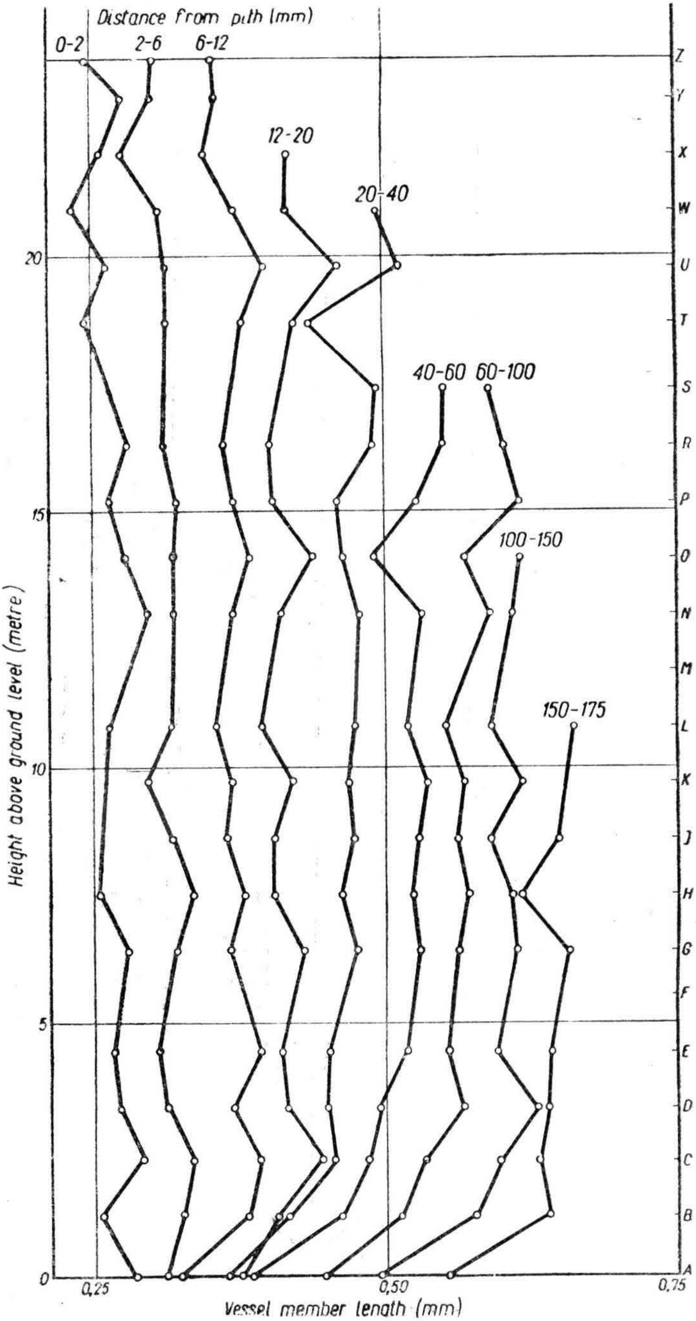


Fig. 16. Length of vessel members in segments of wood of the same distance from pith at various levels

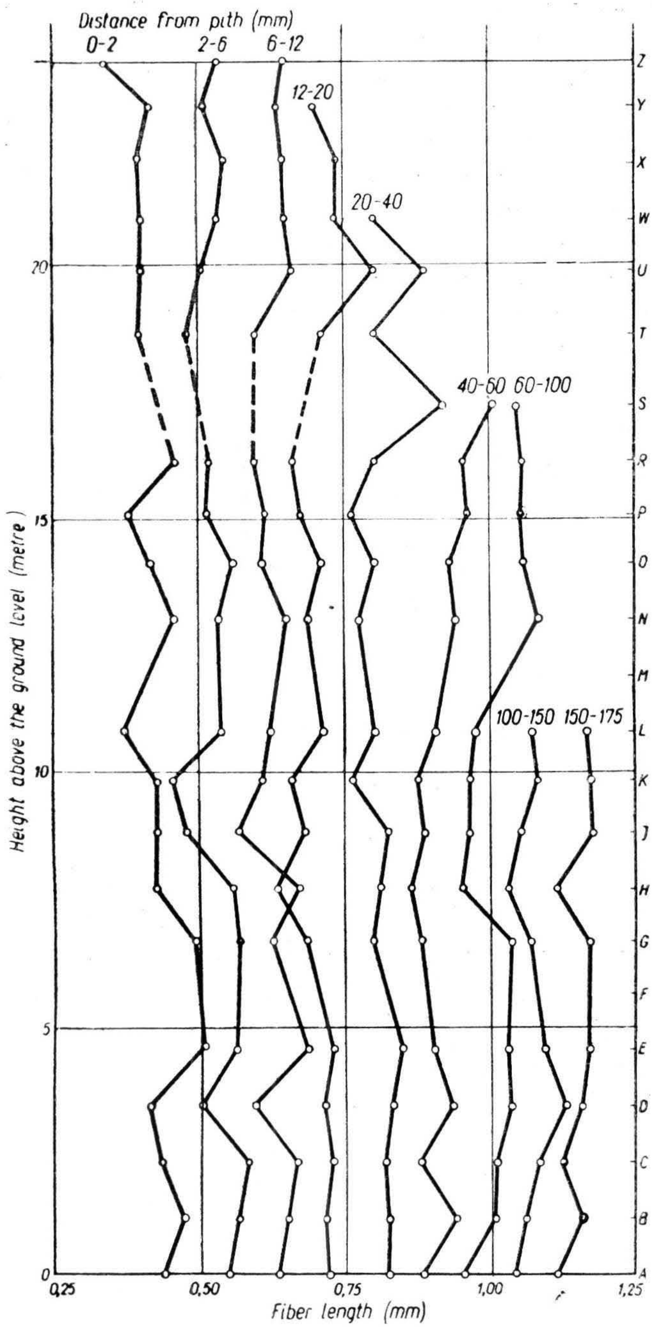


Fig. 17. Same as Fig. 16 for fibres

The data used for plotting the detailed gradient along the radius indicate that there is a cyclic change of fibre length in the successive rings. The question, therefore, arises whether this change is associated with any variations of intrusive growth. In order to find an answer the ratio of fibre length to the length of vessel members was computed for the particular layers within rings, but only for the rings which had been divided into at least three layers. The results are assembled in Table 2 and it is to be seen that the coefficients for late wood are greater than for early wood. The conclusion is, therefore, that the differences in the length of fibres within a ring are at least partly caused by differences in intrusive growth.

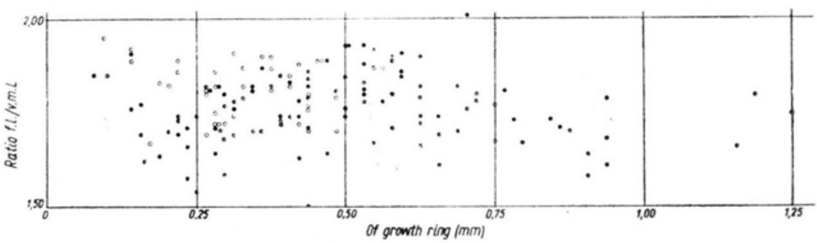


Fig. 18. Diagram illustrating the relation between the coefficient of intrusive growth (ratio of fibre to vessel member lengths) and the width of rings at 4 freely chosen levels

Suplementary measurements — radial diameter of fibres

Data on the radial diameter of fibres are necessary for analysing changes in the length of cambial initials in respect to the relative age of cambium. This problem will now be dealt with.

The results of measurements (average values for groups of rings) are shown in Figs. 19—22.

It follows from Figs. 19 and 20 that the radial diameter of fibres increases outwards away from the pith. The changes of radial diameter when related to the age of rings follow different courses at the particular levels (Figs. 19 and 20). The radial diameter of fibres from groups of rings of the same age increases at first up the trunk then drops a little (Fig. 21). The differences between the particular levels are much smaller when the radial diameter of fibres is related with the linear distance from the pith (Figs. 20 and 22). The radial diameter of fibres in segments of radii equidistant from the pith is in fact the same at different levels.

Table 2

Coefficients of intrusive growth

Level / No. of rings	A	B	C	D	E	G	H	I	K	L	N	O	P	R	S	T	U	W	X	Y	Z
1	1,45	1.72	1,49	1,31	1,93	1,80	1,54	1.49	—	1,58	1,48	1,55	1,46	1,64	—	1,58	1,54	1,56	1.43	1,47	1,47
2	1,60	1,82	1.73	1,57	1,73	1,67	1,60	1,55	1.47	1,59	1,57	1,65	1,46	1,68	—	1,43	1,54	—	—	—	1,36
3—5	1,84	1,72	1,72	1,67	1,57	1,50	1,60	1,64	1,58	1,80	1.67	1,62	1,65	1,72	—	1,57	1,64	1,74	1,89	1,69	1,79
6—10	1,93	1,83	1.71	1,81	1,83	1,68	1,68	1,66	1,57	1.79	1,65	1 83	1,73	1,66	1,83	1,65	1,65	1,73	1,79	1,77	1,78
11—15	2,32	2,05	1.81	1,86	1.76	1,71	1,71	1,72	1,66	1,80	1,80	1.90	1,82	1,66	1,85	1,70	1,79	1,53			
16—20	2,22	2,18	1,79	1,91	1.88	1,75	1,70	1,80	1,69	1.85	1,71	1,89	1,74	1,70	1,77	1,84	1,70				
21—25	2,15	1,91	1,90	1,77	1,87	1,77	1,82	1,76	1,74	1,77	1,77	1.88	1,68	1,75	1,78	1,87					
26—30	2,17	1,92	1,81	1,90	1.85	1,71	1,81	1,80	1,75	1,78	1,80	1.85	1,66								
31—35	2,11	1,82	1,83	1,79	1,84	1,78	1,72	1,78	1,79	1,72	1,79										
36—40	1,98	1,90	1,80	1,80	1,76	1,67	1,61	1,71	1,71												
41—45	2,09	1,84	1,83	1,74	1.72																
46—50	2,08	1,75	1,71	1,74																	

It follows that at various levels the same amount of fibres can be placed along segments of the same length and distance from the pith. Generally speaking variations in the radial size of fibres have the same character as variations in their length.

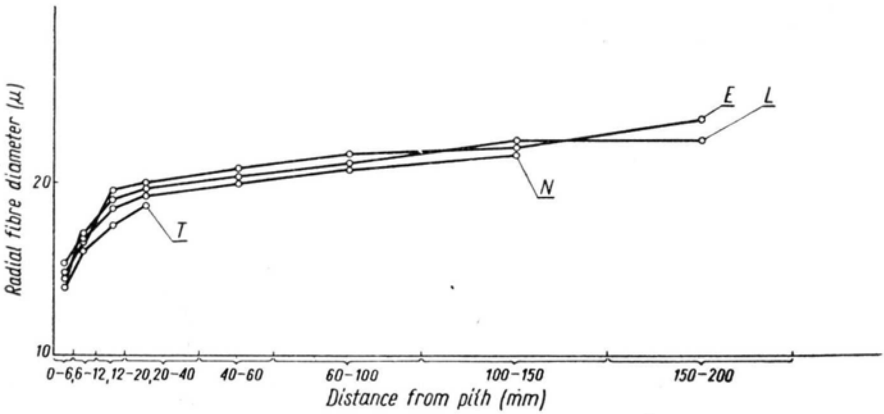


Fig. 19. Radial fibre diameter depending on the linear distance from pith at 4 freely chosen levels

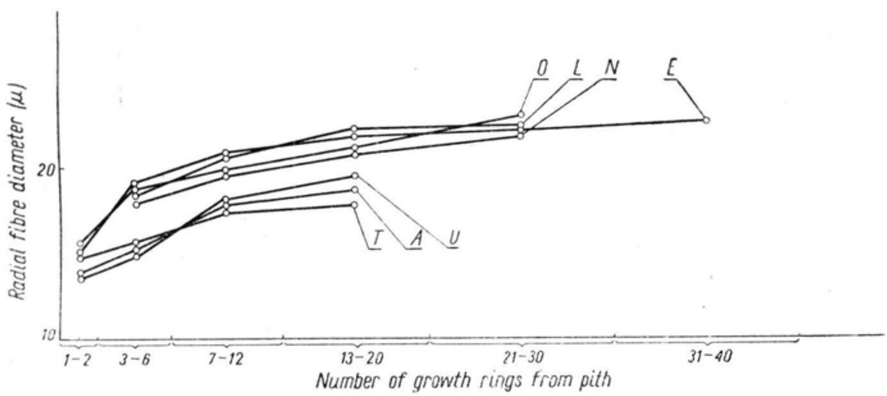


Fig. 20. Radial fibre diameter in groups of rings at various levels

DISCUSSION

It has been pointed out beforehand that the length of tracheids in conifers and of vessel members in dicotyledons depends on the length of fusiform cambial initials. The length of fibres is, moreover, influenced by intrusive growth in the course of their differentiation. However, variations in the length of tracheids, vessel members and fibres are caused chiefly, when disregarding variations within the particular rings, by variations in the length of fusiform initials. The results from the present investigations have shown that intrusive growth, at any rate in asp, is in fact uniform throughout the tree. Thus special attention must be centred here on length variations of fusiform initials.

The present results are in good agreement with the results of other workers referring to various tree species. The regularities described above are of a general nature and their analysis in respect to changes of length of cambial initials will, therefore, have a general character.

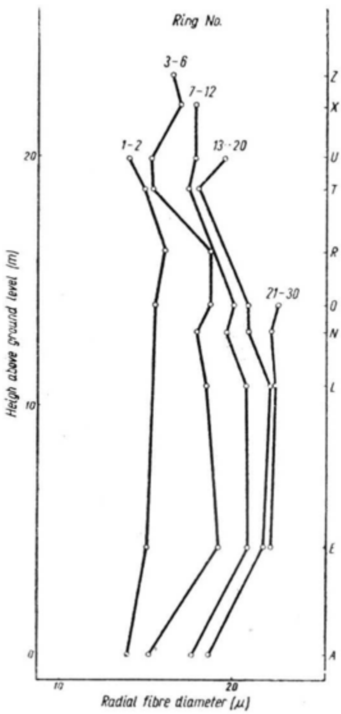


Fig. 21. Radial fibre diameter in groups of rings of the same age at various levels

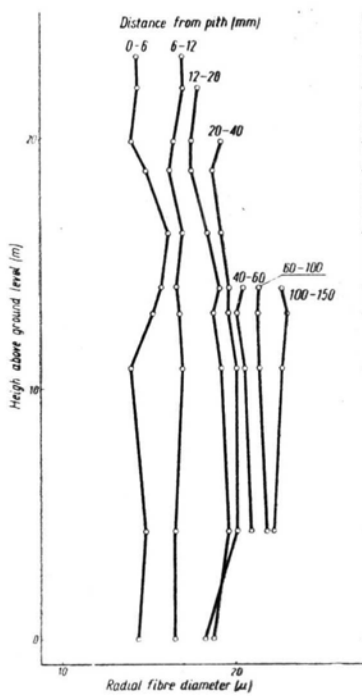


Fig. 22. Radial fibre diameter in segments of wood of the same distance from the pith at various levels

Mention has already been made that the length of cambial initials is the same as the length of vessel members (or tracheids in conifers). Consequently, conclusions on the length of vessel members or tracheids can be extended to the length of fusiform initials. From the data reported earlier in the paper it follows that:

a. fusiform cambial initials increase together with the age of cambium,

b. the length of initials in cambium active in a particular year differs at various levels,

c. the length of fusiform cambial initials of the same age differs at various levels, and

d. the length of cambial initials changes together with the distance from the pith in the same manner throughout the trunk, except for the base.

The last conclusion has already been considered at the beginning of the paper and its significance stressed. It has been stated that the distance from the pith, i. e. a metrical trait, can be replaced by the relative age of cambium, i. e. a biological trait. In point of fact, the distance of cambium from the pith depends on the number of wood cells formed by cambium, that is the number of its cell generations (the generations associated with the production of phloem are not considered). However, according to an earlier assumption the number of cambial generations is the measure of the age of cambium. Thus, there remains only the problem whether the same distance of cambium from pith at various levels represents the same relative age of cambium.

The supplementary measurements show that if fibres are substituted instead of vessels along the radius so as to obtain series consisting of fibres only, the number of fibres corresponding to segments of the same length and distance from the pith will be the same at different levels. On the other hand, it is to be assumed that this number of fibres represents the number of cells formed by cambium along the radius (the large transverse size of the vessels present inbetween fibres is reached at the expense of the fibres by their obliteration and displacement, whereas, the vessels themselves do not contribute to the thickness of the laid down wood layers, at least in the diffuse-porous wood as in the case of asp). The conclusion is, therefore, that the previous question must be answered positively: the same distance of cambium from the pith at different levels represents the same relative age of cambium.

The conclusion arrived at beforehand in point d) seems to have, according to the results reported by Anderson, a more general nature and can be restated in terms more biological in character: the length of fusiform initials is related with the relative age of cambium and changes in the same manner throughout the trunk except for the base. In other words, the length of fusiform initials is regulated by the relative age of cambium without regard for absolute age or the part of the trunk, provided that the part closest to the ground is disregarded.

In asp similarly as in conifers the lower part of the trunk up to 2 or 3 metres above the ground differs from the rest in respect to the changes occurring in fusiform initials. This is not surprising if it is remembered that the influence of the root where the changes in length of fusiform initials have an entirely different character is still strong. Thus, the lower part of the trunk must be considered as a transition zone where the gradient of root influences modifies the relationship between the length of fusiform initials and the relative age of cambium characteristic for the trunk.

Long ago Chalk (1930) pointed out that the different kinds of variations in the length of tracheary elements — in particular longitudinal gradients — could be merely the same phenomenon measured in different ways. From the evidence now available it appears that this fundamental phenomenon is the relationship between the length of fusiform initials and the relative age of cambium (distance from the pith) and near the base of the trunk the modifying influence of roots.

The upward gradients of the length of elements mentioned earlier have a biological basis only in the lower part of the trunk in the form of the gradient of root influences. In the other parts of the trunk the gradients are in a way artificial as at their origin lies the fact of comparing elements produced by cambium of different relative age.

For instance, the upward gradient in a group of rings of the same age results from different rates of wood formation at various levels and consequently the distance of a ring of some particular number from the pith differs at various levels. In other words there is a discrepancy between the relative and absolute age of cambium producing the same ring at various levels. Thus, this gradient consists in fact — in the part of the trunk where there is no influence of roots — in the relationship between the length of fusiform initials on one hand, and the relative age of cambium and the factors causing the difference between the absolute and relative age at various levels on the other.

The upward gradient is simply caused by the fact that the trunk tapers to the top which means that the relative age of cambium decreases from the base upwards.

The relative age of cambium and the influence of the root may be considered as being the main causes of length variations of fusiform initials and consequently too of tracheary elements. Nevertheless, it is evident that alongside of the main causes there may be secondary ones modifying locally the principal variations, e. g. factors causing the formation of compression wood, local injuries etc. However, in the case of asp, similarly as in conifers investigated by Anderson, the disturbances are not sufficiently severe to obliterate the main causes.

Mention must be made briefly of variations within the particular rings. In the case of vessel members in dicotyledons and tracheids in conifers this variation is caused by the uneven distribution with time of anticlinal divisions in fusiform initials of nonstoried cambium. Moreover, it follows from the present results that in the case of fibres there is too the influence of differences in intrusive growth.

SUMMARY

An asp-tree 50 years old was examined and an analysis of 1720 average values for the length of fibres and vessel members showed that variations in the length of these elements in the trunk of the asp-tree were of the same kind as in other tree species examined in that respect. Thus there were: a) the length gradient along the radius (Figs. 2—10) which in the case of fibres and to some extent of vessel members was characterized by cyclic seasonal variations (Figs. 9—10); b) the upward gradient in the same ring; and c) the upward gradient in a group of rings of the same numbers counting from the pith.

These variations — but not the variations within the particular rings — were caused by corresponding changes in the length of the fusiform initials of cambium. Intrusive growth was the other factor influencing the length of elements (fibres) in the course of their differentiation. This factor changed little in the various parts of the trunk.

When the length of elements was related to the distance from the pith the results were the same as those reported by Anderson for conifers; the length of elements at a given distance from the pith was the same throughout the trunk irrespectively of the number of the ring involved, except for the lower part up to 2 m above ground. At the same time it was found that the distance from the pith was a comparative measure of the number of cambial generations involved in wood formation, i. e. a measure of the relative age of cambium. This meant that elements situated at the same distance from the pith at various levels were formed by cambium of the same relative age. Inasmuch as the length of vessel members (tracheids in conifers) was the same as the length of fusiform initials, the consequence of Anderson's relationship was that the length of fusiform initials was determined by the relative age of cambium without regard for its absolute age measured in years. This relation was modified near the base of the trunk by the gradient of root influences.

The relation between the length of initials and the relative age of cambium as well as the gradient of root influences modifying the relation in the lower part of the trunk constituted the essence of the variations in the length of tracheary elements. The upward gradients of the length of elements in the same ring or in a group of rings of the same age in that part of the trunk which was not influenced by the root were due to the difference in the age of cambium which had produced the elements. In particular, the reason for the upward gradient in a group of rings of the same age was the difference at various levels between relative and absolute age of cambium which had formed the ring of a given number.

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