

## FIBRE LENGTH IN STOREYED HARDWOODS

BY

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### INTRODUCTION

The number of cells in the cambial ring is increased in most woody species by anti-clinal divisions followed by elongation of the resulting cells. This must affect the mean length of the fusiform initials and so, presumably, the length of the wood cells derived from them, particularly in the conifers, whose tracheids undergo very little elongation after they are cut off from the cambium. Division of the fusiform initials to keep pace with increasing perimeter has in consequence often been suggested as the underlying reason for the various trends of variation that have been observed in tracheid and fibre length. In woods with storeyed structure, however, the number of cells in the cambium is increased by longitudinal divisions that should not affect the length of the cambial cells at all. These woods, therefore, afford a means by which to check the hypothetical influence of anti-clinal cambial division in other woods. In order to distinguish between changes in the length of the fusiform initials and changes due to elongation of the fibres, measurements were made of the length of the parenchyma strands, which were assumed not to have elongated and therefore to represent the length of the fusiform initials.

Three general trends have been studied. Firstly, the increase in length outwards from the pith first demonstrated by SANIO (1872) in *Pinus silvestris* and observed since in many other softwoods and hardwoods; secondly the negative correlation observed between rapid growth and fibre or tracheid length; and thirdly the more recently discussed (BISSET and DADSWELL, 1950) changes observed within the growth ring. It is not convenient to discuss these trends in the chronological sequence in which they have been established, as variation within the ring and with rate of growth need to be discussed before the larger pattern of increase outwards from the pith, if only for their bearing on methods of sampling.

### MATERIALS AND METHODS

Most of the observations were made on discs of *Pterocarpus angolensis* DC. (Papilionaceae) from Tanganyika. Measurements were also made on specimens from the collection at the Imperial Forestry Institute,

Oxford, of *Aeschynomene elaphroxylon* (Guill. et Perr.) Taub. (Papilionaceae) from Uganda and *Nesogordonia papavifera* (A. Chev.) Capuron (Tiliaceae) from Nigeria.

Macerations for the measurement of fibre length were prepared by the acetic acid and hydrogen peroxide method and were measured directly under a microscope or on a projected image. Fifty to eighty fibres were measured from each sample. The length of the parenchyma strands was measured from tangential sections on a Shand micrometer, which enables the mechanical stage to be moved by either of two screw micrometers reading to 1/100 mm. It is thus possible to obtain a cumulative measure of a number of cells on one micrometer, the other being used for all adjusting movements from the tip of one strand to that of the next. Measurement of 30 strands was found sufficiently accurate for most purposes, but this figure was increased to 80–90 for the comparison between lengths of fibres and parenchyma strands within the same ring.

#### RATE OF GROWTH AND POSITION RING

The literature contains many references to the influence of rate of growth on tracheid length in the conifers. The majority agree that tracheids tend to be shorter in wide rings, though the reverse has sometimes been observed. PRIESTLEY suggested (1930) that, if rapid growth is accompanied by rapid transverse division of the cambium, the time lag before these new cells reach average length could lead to a shorter mean length of the fusiform initials. This conception offers a very plausible explanation of the relation that has been observed in wide rings. It has, however, been shown by WHALLEY (1950) that in *Thuja occidentalis* L. the rate of transverse division is not related to increase in girth of the cambium, being in all cases far greater than is necessary for that purpose, and that readjustment is rapid. BANNAN (1955) has found that in the same species the surge of growth in the spring takes place in a zone of actively dividing and re-dividing xylem mother cells, rather than in the initiating layer, and that only towards the end of the growing season do the initial cells undergo the changes that modify the cellular pattern of the cambium.

This aspect of variation was studied in *Pterocarpus angolensis*, by measuring fibre length in the wide and narrow parts of an excentric ring (6 and 1.8 mm wide respectively). The results are illustrated in Fig. 1. It will be seen that there is remarkably little difference in maximum length and that such difference as there is would point, if it were significant, to an increase in length with increased rate of growth, which is the reverse of the relation usually observed. Measurements were also made of fibre length and ring width in a series of consecutive rings from one disc. These are shown in Table II. No statistically significant regression could be demonstrated between ring width and fibre length from these data.

A point of considerable interest in Fig. 1 is that the variation within the ring is of the same type and of the same order of magnitude as in woods in which this variation has been ascribed to anti-clinal division

of the cambial cells. It may be noted that these curves differ slightly from those obtained by AMOS, BISSET and DADSWELL (1950) for *Eucalyptus gigantea* Hook. f. and by BISSET and DADSWELL (1950) for various hardwoods and softwoods. These authors found a steady increase to the end of the ring and a sudden drop in length which they believed to occur at the actual boundary, though the technical

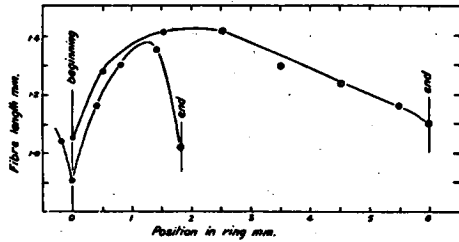


Fig. 1. Comparison of fibre length in the wide and narrow parts of an excentric growth ring in *Pterocarpus angolensis*

difficulties of separation made this difficult to demonstrate. VASILJEVIĆ (1952) found that in various European hardwoods the maximum fibre length occurred somewhere in the middle of the ring. In *Pterocarpus* also there is a maximum in the middle of the ring followed by a slight decline towards the end of the ring, and an abrupt change at the boundary. This point was studied more carefully in the 27th ring and is illustrated in Fig. 2. It will be seen that although there is a distinct decline in the outer part of the ring, this does not reduce the length to that at which the next ring begins; there is a further large and abrupt decrease in length at the ring boundary, as was found by Amos, Bisset and Dadswell.

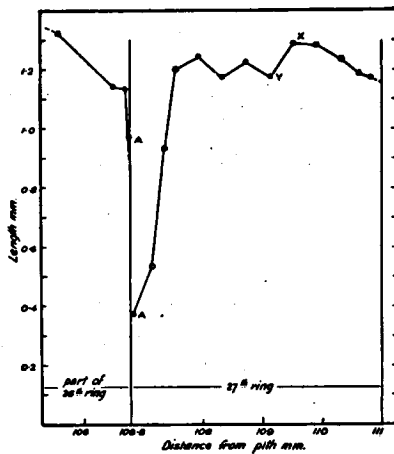


Fig. 2. Changes in fibre length at the ring boundary in *Pterocarpus angolensis*

It is very difficult to believe that transient changes of this magnitude can be the result of changes of length in a storeyed cambium and an attempt was made to show whether any similar changes take place in the lengths of the parenchyma strands. Tangential sections were cut through two complete rings (Rings 8 and 9) and measurements made at nine points in each. The mean lengths of the parenchyma strands at each of these points are shown in the broken lines in Fig. 3. It may be noted that Ring 8, with a width of 4.2 mm, was nearly twice as wide as Ring 9, with a width of 2.4 mm.

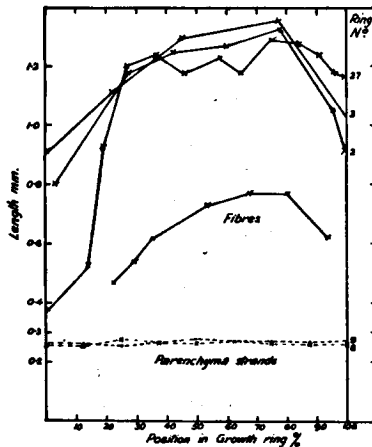


Fig. 3. Variation in length within the growth ring in *Pterocarpus angolensis*. Solid lines = fibres, broken lines = parenchyma strands.

It will be seen that in each ring fibre length rose to a maximum in the middle of the ring, but that the length of the parenchyma strands remained constant. These two types of cell were measured in different rings and it was therefore thought advisable to secure confirmation of these results by making alternating measurements of the lengths of the fibres and of the parenchyma strands along a radius across a single ring. The procedure adopted was to cut three sections, each  $15\mu$  thick, on which to measure the parenchyma strands, followed by one  $335\mu$  thick to provide material for maceration, and to repeat this sequence till the end of the ring was reached. It was arranged that the beginning and end of the ring should be covered by the sections for the parenchyma strands rather than by those for the macerations for fibre length, as it was more important to observe the lengths of the parenchyma strands at these points, the fibres having already been investigated. Consequently the figures for fibre length would not be expected to show the full drop in length that occurs near the boundary. The results are illustrated in Fig. 4. It will be seen that the rise in fibre length in the middle of the growth ring is again independent of any change in the length of the parenchyma strands, and one must assume, therefore, that the changes in fibre length within the ring

are due to elongation of the fibres and not to any changes in the lengths of the fusiform initials from which they are derived. It will be seen from Table I that the amount of elongation of the fibres is considerable,

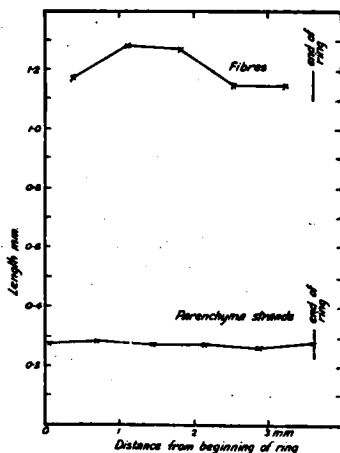


Fig. 4. Comparison of the lengths of fibres and parenchyma strands within a single growth ring of *Pterocarpus angolensis*

being over four times the length when cut off from the cambium. This elongation is greatest in the middle part of the ring.

TABLE I

Lengths of fibres and parenchyma strands within one ring of *Pterocarpus angolensis*

Distance from beginning of ring $\mu$	Length of Fibres $\mu$	Elongation of Fibres $\times$	Length of Parenchyma Strands $\mu$
22			276.5
380	1170	4.24	
737			280.5
1095	1283	4.60	
1452			273.0
1810	1272	4.67	
2167			273.5
2525	1156	4.35	
2882			261.0
3240	1157	4.13	
3597			280.0

VARIATION OUTWARDS FROM THE PITH

The typical increase in tracheid and fibre length outwards from the pith at any one level has usually been expressed in terms of number of annual rings from the pith and correlations sought between length and age. LIANG's observations on *Larix*, published in 1949, however, appear to indicate distance rather than age from the pith as the importance factor. He found a negative correlation between length and 'percentage of increment of perimeter' or the rate at which the

perimeter was increasing. This he expressed as the ratio  $r^2/r^1$ , where  $r^1$  is the radius from the pith to an inner ring and  $r^2$  the radius to an outer ring. This ratio decreases outwards. Marstrand has suggested using the ratio  $2 \frac{r_2 - r_1}{r_2 + r_1}$  to express the increase in the unit girth of the cambium and found significant correlations between this and tracheid length in Liang's data for *Larix* and for data extracted from the figures and photographs published by BISSET, DADSWELL and WARDROP (1951) for *Pinus radiata* D. Don. Liang explained his results in terms of transverse division of the cambial cells on the lines suggested by BAILEY (1923) and PRIESTLEY (1930), the argument being, briefly, that the proportion of newly divided (and therefore shorter) cells decreases outwards from the pith. WHALLEY (1950) as has been mentioned above, has shown that the process is more complex than the hypothetical case propounded by Priestley, but it would still be true that the small number of new, short initials that survive at any stage must represent a smaller and smaller percentage of the cambial ring as the perimeter increases and their effect in reducing length must become progressively less. It is, however, clear from Whalley's drawings that the fusiform initials near the pith increase in maximum, as well as mean, length and that the increase here at least cannot be entirely accounted for by a decrease in the proportion of transverse divisions.

It is of considerable interest therefore to find that in storeyed woods, in which there are no transverse divisions of the cambial cells, there may be a sharp increase in length between the first and second rings, but no further increase in cell length outwards from the pith. In *Pterocarpus angolensis* the large fluctuations within the ring make it necessary to compare whole rings or measurements taken from comparable parts of the ring. In the latter case the most suitable part is

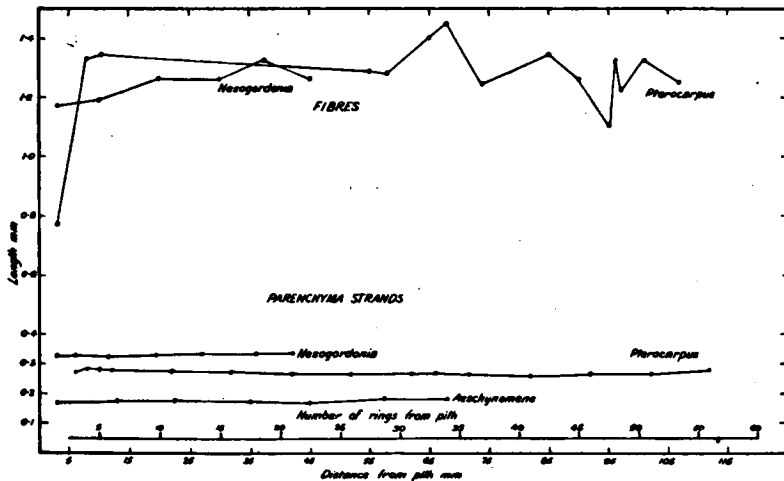


Fig. 5. The lengths of fibres and parenchyma strands from the pith outwards in storeyed woods.

the middle of the ring, which gives the maximum length. A comparison of whole rings is made in Fig. 3, and it will be seen that the fibres in the first ring are distinctly shorter, but that there is very little difference between the middle parts of the second, third and twenty seventh rings. The lengths at the beginnings and ends of the rings are not reliable, as it is technically very difficult to make an accurate separation between one ring and the next and, as the difference between the two may be considerable, the inclusion of some fibres from the wrong ring may appreciably affect the mean.

In Fig. 5 a comparison is made of the fibre lengths at different distances from the pith of *Pterocarpus angolensis* and *Nesogordonia papavifera*, both of them being woods with distinct storeyed structure. Apart from the sharp rise from Ring 1 to Ring 2 in *Pterocarpus*, there is no sign of the type of increase characteristic of non-storeyed woods.

TABLE II

Lengths of fibres and parenchyma strands in *Pterocarpus angolensis*, at different distances from the pith.

FIBRES		PARENCHYMA STRANDS	
Distance mm	Length mm	Ring number	Length mm
3	0.77	3	2.76
8	1.33	4	2.87
10.5	1.35	5	2.82
55.4	1.29	6	2.78
57.7	1.28	11	2.70
65.0	1.42	16	2.69
68.3	1.45	21	2.62
74.3	1.25	26	2.66
84.7	1.35	31	2.65
90.2	1.26	33	2.65
95.0	1.10	36	2.58
96.2	1.33	41	2.55
97.3	1.22	46	2.63
101.4	1.33	53	2.74
106.8	1.25	56	2.80

TABLE III

Lengths of fibres and parenchyma strands in *Nesogordonia* and *Aeschynomene* at different distances from the pith.

PARENCHYMA STRANDS				FIBRES	
<i>Nesogordonia</i>		<i>Aeschynomene</i>		<i>Nesogordonia</i>	
Distance mm	Length mm	Distance mm	Length mm	Distance mm	Length mm
3.1	0.33	3.0	0.17	3	1.17
11.7	0.32	13.0	0.18	10	1.19
19.6	0.33	22.5	0.18	20	1.27
27.0	0.34	35.0	0.17	30	1.26
36.1	0.34	45.0	0.16	40	1.33
42.2	0.32	56.5	0.18	45	1.26
		68.0	0.18		

In the lower part of the graph are the corresponding lengths of the parenchyma strands in these two species and also in *Aeschynomene elaphroxylon*, another species with storeyed wood. The consistency of the lengths of the parenchyma strands in each species is remarkable. The figures for the parenchyma strands of *Pterocarpus* have been plotted against number of rings and not distance from the pith.

The data on which Fig. 5 is based are given above in Tables II and III.

#### DISCUSSION

There appear to be two independent factors causing variation in the length of fibres and tracheids. From the observations given above on variation within the ring it is clear that an increase of 100–300 per cent. can occur between the beginning and end of a season's growth, independently of any change in the length of the fusiform initials. These changes must presumably be due to varying degrees of elongation of the fibres. In the material examined the mean fibre lengths were more than four times the lengths of the corresponding parenchyma strands, so that an elongation even of this order would be possible. BISSET, DADSWELL and AMOS (1950) found that in 11 hardwoods that they investigated the amount of elongation of the fibres was between 22 and 118 per cent. Since the pattern of variation within the ring is the same in both storeyed and non-storeyed woods, it seems likely that the cause may be basically the same. Of possible significance in this connection is the observation of BANNAN (1955) referred to above, that in *Thuja occidentalis* growth in the spring takes place in a zone of actively dividing and re-dividing xylem mother cells rather than in the initiating layer and that only towards the end of the growing season do the initial cells undergo the changes that modify the cellular pattern of the cambium. It is possibly at such a period of maximum activity that conditions are most suited to the growth in length of the cells, not only as regards supplies of food materials and water, but as regards conditions for rapid readjustment of the cell pattern.

The general trend of variation in length from the pith outwards in non-storeyed woods cannot easily be explained on this basis and it is generally accepted that it is related to changes in the length of the fusiform initials. That there is some relation between the commonly observed increase from the pith outwards and the method of increasing the number of cells in the cambium by anti-clinal divisions receives strong indirect support from the absence of any such trend where there are no anti-clinal divisions, as in woods with a storeyed cambium. In woods with storeyed structure the length of the parenchyma strands at varying distances from the pith is quite remarkably constant after about the second ring, and the fibres, though more variable, show no consistent tendency to increase at greater distances from the pith. The fluctuations that occur at different points are possibly due to varying degrees of elongation, such as occur within the ring. Such an explanation could be equally applicable to the similar fluctuations that occur in non-storeyed woods.



The absence of any relation between ring width and fibre length in the storeyed woods, supports the view that in non-storeyed woods the negative correlation that has been observed is due to the method of cambial division. On the other hand, it might be supposed that, if vigorous growth in the middle of the ring leads to longer fibres, wider rings and more vigorous growth generally would also be associated with greater length. In fact, the reverse appears to be true, wide rings in non-storeyed woods being associated with shorter tracheids and fibres. This apparent anomaly can perhaps be explained by assuming that the former is associated with the development and readjustment of the mother and daughter cells, whereas rapid growth generally implies changes in the initiating layer itself.

#### SUMMARY

- (1) Measurements of the lengths of wood fibres and of parenchyma strands were made in three species with storeyed structure, *Pterocarpus angolensis*, *Nesogordonia papavifera* and *Aeschynomene elaphroxylon*.
- (2) Within the growth ring fibre length rose to a maximum in the middle of the ring and dropped abruptly at the ring boundary, but the length of the parenchyma strands remained constant.
- (3) Neither the fibres nor the parenchyma strands showed any general tendency to increase in length from the pith outwards.

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