

ABSTRACT.

Variation in structure of the secondary xylem was studied in the bole, branches and roots of Quercus robur L., Fagus sylvatica L., Acer pseudoplatanus L.

VARIATION IN STRUCTURE OF THE SECONDARY XYLEM IN INDIVIDUAL DICOTYLEDONOUS TREES.

Attention is drawn to the length of the vertical elements, diameters of the vessels and to ray height and volume.

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ABSTRACT.

Variation in structure of the secondary xylem was studied in the bole, branches and roots of Quercus robur L., Fagus sylvatica L., Acer pseudoplatanus L., and Robinia pseudoacacia L. Attention was paid especially to variation in the length of the vertical elements, diameters of the vessels and to ray height and volume.

Vessel-elements and libriform fibres increased in length from the pith outwards at any one level in the bole, branch and root, at first rapidly and then rather slowly. In a specific growth ring these elements increased in length upwards in the bole up to a certain height and later decreased. It is suggested that the fusiform initials of the vascular cambium become larger during the first few years when growth of the tree is most vigorous, thus accounting for increase in length of the derived elements from pith outwards at any one height; further, that successively larger fusiform initials are laid down nearer the apex during the period of greatest vigour so that at this time the longitudinal elements in a ring are longest nearer the apex. After this period

of maximum vigour is past, new fusiform initials are smaller and hence the longitudinal elements of the xylem are smaller above a certain height.

Vessel-elements and libriform fibres within one growth ring are longer in the late-formed wood than in the early-formed wood irrespective of whether the vascular cambium is stratified or not. The variation in the length of the vessel-elements is correlated with the diameter of the vessel, those of the spring wood shortening as a result of the considerable swelling during differentiation. On the other hand, the libriform fibres elongate during differentiation.

Variation in vessel diameters, ray height and ray volume show much the same trend as that of the vessel-elements.

Apart from certain minor details, wood of different ages and that from different parts of the tree, shows no great histological difference.

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INTRODUCTION AND REVIEW OF PREVIOUS WORK.

In any particular tree species, as in other organisms, all the individuals are not identical. Variations may be found in the wood as well as in other parts of the plant and may occur between different individuals and also in one individual for variation in the wood may be due to age and to its position in the tree. Further, internal stresses or external factors such as light, soil, water and temperature with which may be included competition with other organisms which form part of the environment of the tree, may be responsible for the variation in structure of the secondary xylem in a tree. Again changes in such physical properties as colour and grain may be brought about by some pathogens, especially fungi, which may also bring about changes in the chemical composition of the cells. Thus structure of wood varies not only in plants of different taxonomic affinities but also in the different individuals of the same species growing in different localities and even in different parts of the same tree.

Interest in the secondary xylem has generally been associated, if indirectly, with economic considerations and in the past, the necessity for detailed

knowledge of the different types of variations met with in the structure of wood was seldom realised, because timber for commercial purposes was derived mainly from adequate supplies of mature and carefully selected trees. With the increased demand for timber in the recent times, and the more difficult supply position, there has been considerable use of timber derived from comparatively young and vigorously growing plantations. Recent researches, giving adequate information on the variation of growth and structure, would be of immense value to utilize the timber from plantations, thinnings and tops, to best advantage.

The fact that wood from different parts of individual trees is extremely variable has been fully appreciated by some of the recent investigators in their attempts to secure satisfactory criteria for identification and classification of woods, due consideration being given to range of variation of each of the diagnostic characters (Dadswell et al., 1932 and 1934; Chalk et al., 1932, 1933, 1935 and 1939).

Much work, done during the last half-a-century on the problem of variation, relates particu-

larly to tracheid and fibre dimensions throughout the bole of a tree and while there have inevitably been conflicting results, there is, as a whole a very fair measure of agreement on this aspect of variation. Apart from the aspect of utilisation of the wood for the paper and pulp industry, the earlier work on the study of tracheid length variations seems to be purely of academic interest.

A brief review of the previous work on variation in the tracheid and fibre length follows.

Modern interest in the length of the vertical elements of the secondary wood, as related to their position in the tree, dates back to the pioneer work of Sanio (1872) who determined the mean tracheid length in the secondary wood of Scots pine (Pinus sylvestris) in various parts of the trunk and branches. De Bary (1884) summarised Sanio's results as follows:

"(1) In the stem and branches the tracheids everywhere increase from within outwards, throughout a number of annual rings, until they have attained a definite size, which then remains constant for the following annual rings.

(2) The constant final size changes in the stem in such a manner that it constantly increases from below upwards, reaches its maximum at a definite height, and then again diminished towards the summit.

(3) The final size of the tracheids in the branches is less than in the stem, but is dependent on the latter, inasmuch as those branches which arise from the stem at a level where the tracheids are larger, themselves have larger tracheids than those which arise at a level where the constant size is less.

(4) In the gnarled branches of the summit, the constant size in the outer annual ring also at first increases towards the apex, and then falls again; but here irregularities occur, which may be absent in regularly grown branches.

(5) In the root the width of the elements first increases, then falls again, and next rises to a constant amount. An increase in length also takes place, but could not be exactly determined."

Numerous investigators have since studied the problem of variation in length of the vertical elements of the secondary xylem from three different aspects; (1) from pith outwards in successive growth rings at one level in the bole, (2) from base upwards in specific rings of the bole and (3) in the early and late wood of an individual growth ring. It appears to have been tacitly assumed that variation in fibre length in dicotyledons follows the same course as that of the conifer tracheid.

Although all of them confirmed that there was an initial increase in length of the vertical elements in the successive growth rings from pith outwards, there is no agreement among them regarding whether a constant

maximum length was attained by these elements in the later growth rings of a tree at any one level, as stated by Sanio. Shepard and Bailey (1914) reported that tracheid length in Pinus palustris reached its maximum at 160 years and in the older rings decreased comparatively rapidly. Lee and Smith (1916) noticed that tracheid length tended to decrease slightly towards the periphery in Douglas fir, particularly at the base of the bole. An actual decrease in length of the fibres towards the outside, after a ~~3~~ maximum was reached, was reported by Hartig (1885) for Fagus sylvatica and Boshard (1951) for Fraxinus excelsior. On the other hand, many of them reported that tracheid length, or fibre length, as the case may be, continued to increase at any one level in the bole with increasing age of the tree. Gerry (1916) found that in Douglas fir old age had no effect on the tracheid size and the tracheid length was slowly increasing after 455 years. Chalk (1930) reported a regular increase in tracheid length from pith to bark in Picea sitchensis and Desch (1932) that fibre length was gradually increasing after 129 years in Fagus sylvatica, 102 years in Populus serotina, 56 years in Acer pseudo-platanus and Betula pubescens. Contrary to the above

observations Mell (1910) in Pseudotsuga taxifolia, Kribs (1928) for Pinus banksiana, Bethel (1941) for Pinus taeda, Hata (1949) for Pinus densiflora, Pritchard and Bailey for Carya ovata and Bisset and Dadswell (1949) for Eucalyptus regnans recorded the attainment of a constant length in the later part of the growth ring, thus confirming the results of Sanio.

On the aspect of variation in length of the tracheids of gymnosperms and fibres of angiosperms in specific growth rings at different heights in the bole, the conclusions drawn by the various investigators are conflicting. Sanio's conclusions were confirmed for gymnosperms by Mell (1911), Gerry (1916) and Lee and Smith (1916) for Douglas fir; Bailey and Shepard (1915) for Pinus strobus, Pinus palustris, Picea rubra, Tsuga canadensis and Abies concolor; Kribs (1928) for Pinus banksiana; Chalk (1930) for Picea sitchensis; Hata (1949) for Pinus densiflora and Anderson (1951) for Abies concolor, Abies procera and Pseudotsuga taxifolia. On the other hand, Hartig and Weber (1885) found a progressive decrease in fibre length with the height in the tree. Hartig (1894) reported a gradual decrease in fibre length

from the base of the tree upwards in Quercus robur, as did Stauffer (1892) for Betula sp., but Eichhorn (1895) recorded an initial increase and then a decrease in fibre length upwards in certain American oaks. Desch (1932) confirmed that the variation in fibre length at different heights in Betula pubescens, Alnus glutinosa, Fagus sylvatica, Populus canescens, Acer pseudoplatanus and Baikiaea plurijuga, followed the type of variation in tracheid length in conifers described by Sanio and others. Bisset and Dadswell (1949) confirmed this trend in Eucalyptus regnans where they found increasingly longer fibres up to 50 feet level and successively shorter fibres from 50 feet to 166 feet level. Contrary to these findings Pritchard and Bailey (1916) observed that fibre length decreased from the base upwards in Carya ovata, although the length of the vessel elements increased to a certain height and then decreased.

The results of the work of Siriban (1939) on Trema orientalis, Misra (1939) on Pinus longifolia, Bannan (1941, 1942 and 1944) on Thuja occidentalis, Juniperus and Libocedrus decurrens, Bethel (1941) on Pinus taeda, Cortes and Hambananda (1947) on

Columbia serratifolia, Mallotus ricinoides and Parkia javanica, Liang (1948) on Larix and Bergman (1949) on a number of dicotyledons, all showed agreement with Sanio's first two postulates.

Variation between the first and last formed wood of a growth ring has been studied by several investigators with reference to the tracheids of gymnosperms and the results obtained are contradictory. For example, Gerry (1916) reported in Pseudotsuga taxifolia that the tracheids from the late wood were shorter than those from the early wood. But Lee and Smith (1916) working on the same species noted that the tracheids in the late wood were longer than those of the early wood. Similarly Kribs (1928) for Pinus banksiana, and Chalk (1930) for Picea sitchensis, both reported that the tracheids of the late wood were slightly longer than those of the early wood. The results obtained recently by Wardrop and Williams (See Wardrop, 1948) on a rapidly grown specimen of Pinus radiata, seem to agree with those of Gerry (1916) in that the early wood tracheids are longer than those of the late wood. However, the work of Bisset and Dadswell (1950) on a number of gymnosperms including

those mentioned above, indicated that in all instances, where compression wood is not present, the late wood tracheids are slightly longer (about 11%) than those of the early wood, thus confirming the findings of Lee and Smith, Kribs and Chalk.

Fibre length variation within one ring in angiosperms was, first, studied by Bisset and Dadswell (1949) who found that there was a consistent difference in length between early wood and late wood fibres in every ring at all levels of the bole, in Eucalyptus regnans. Subsequently Bisset, Dadswell and Amos (1950) and Bisset and Dadswell (1950) extended these studies to a number of angiosperms. In all the woods, they investigated, which had distinct growth rings, they found a definite increase in the fibre length from the first-formed to the last-formed wood within an individual ring, whether the structure was ring porous or diffuse porous. In those species with no apparent check in growth, they reported little change in fibre length over radial distances which were assumed to cover the growth of several years. Chalk, Marstrand and Walsh (1955) studied the lengths of wood fibres and of parenchyma strands in woods with storeyed

structure, Pterocarpus angolensis, Aschynomene elaphroxylon and Nesogordonia papavifera and reported that, at any one level within the growth ring, the fibre length rose to a maximum in the middle of the ring and dropped abruptly at the ring boundary, but that the length of the parenchyma strands remained constant.

Spurr and Hyvarinen (1954) reviewed the literature on wood fibre length as related to position in the tree and growth from a morphogenetic point of view, giving special attention to the data published, and assessed the possible interrelationships between cell size and developmental factors of growth and senescence.

There seems to be a lack of agreement regarding conclusions arrived at concerning the variation in height and volume of rays. Essner (1883) described a gradual increase in height and decrease in number of rays outward from the pith in Pinus strobus except in the outermost wood, where there sometimes was a slight increase in number. He also found that there was a gradual decrease in ray number per unit of surface at higher levels in the bole. Jaccard (1915) on the other

hand, deduced from his observation on Picea excelsa and Abies pectinata that the maximum number of rays occurred in the bole some 10-15 centimeters above ground; higher in the stem a minimum was reached which was again followed by an increase at the base of the crown*. DeSmidt (1922) found a similar increase in the number of rays higher up at the base of the crown, after a minimum was reached, in Ulmus fulva. Sebestine (1955), on the contrary, reported a slight decrease in height of the rays in the outer wood from that of the inner wood in Pajanelia rheedii, Erythrina stricta, Macaranga peltata, Tabernaemontana dichotoma and Anacardium occidentale. Bannan (1937) correlated the variation observed in the number, height and distribution of rays in the bole and branch wood of a number of conifers (Araucaria, Thuja, Taxodium, Abies, Tsuga, Larix, Picea and Pinus) with such variations as width of growth rings, distance from the pith and, in the branches, the position, i.e. on the upper and lower side. The height and distribution of rays in the root was found to vary more widely and unlike the

* CROWN is interpreted to mean the distal part of the main trunk, from which most of the main branches will, generally, arise.

condition in the stem, the trend of variation differed in the genera studied.

DeSmidt found in Ulmus fulva that the total ray volume was greatest in the root and at the stem base; ray volume remained fairly constant in the bole but increased again in the upper portion of the crown to a second maximum. He ascribed the greater ray volume in the root to the increase in number as well as size of the multiseriate rays. That of the stem, he thought, might be due to an increase in the size of the multiseriate rays, and that of the crown to an increase in the number of rays. Myer (1922) stated that the larger variations in ray volume were due to inheritance and that the smaller individual ones were the result of differences in site, climate, temperature, soil, age in the tree, efficiency of the leaves and the development of the deciduous habit. He found that deciduous trees showed a relatively higher percentage of ray volume than the evergreens. Harlow (1927) found greater ray volume near the base of the bole in Thuja occidentalis than farther up. However, he failed to support the observation of a heightened ray volume in the crown, as found by DeSmidt. Further, he stated that between extremes of site there was no

greater difference in ray volume than might be found between two trees growing on the same site. Bannan (1937) reported that the total ray volume, in some species of conifers studied, was possibly greater in the root than in the outer parts of the tree owing to the larger size of the individual cells.

From the foregoing it is evident that much work was done on the variation in tracheid length in some of the gymnosperms. In view of the comparative lack of definite information regarding fibre length variation in the angiosperms a detailed examination of such variation is undertaken in oak, beech, sycamore and robinia, which were selected to include ring and diffuse porous species and also one with stratified vascular cambium.

Attention so far has been given mainly to variation in the fibre length in the bole of the angiosperms, and the roots and branches have been ignored by recent investigators. So far as is known, variation in the vessel-elements and such other vertical elements as fibre-tracheids and tracheids has not been studied, in any of the angiosperms, by any of

the previous investigators. In the present investigation, attention has been paid especially to variation in length of the vessel-elements, libriform fibres, fibre-tracheids and tracheids in oak and vessel-elements and libriform fibres in beech, sycamore and robinia in the bole, branches and roots. In addition, an attempt has been made to investigate variation in vessel diameter and ray height and volume in sycamore and robinia.

Features investigated in the present work:

(1) Variation in length of the vertical elements of wood (vessel-elements, libriform fibres, fibre-tracheids and tracheids) in successive growth rings from pith outwards at different levels in the bole, branch and root in oak, beech, sycamore and robinia.

(2) Variation in length of vessel-elements and libriform fibres in specific growth rings at different levels in the bole.

(3) Variation in length of vessel-elements and libriform fibres on different radii at different levels in the bole.

(4) Variation of vessel-elements and libriform

fibres within one growth ring between the first and last formed wood, in the bole and root.

(5) Variation in the radial and tangential diameters of the vessels in individual growth rings.

(6) Variation in the height and volume of rays in different parts of the wood in robinia.

(7) Histological features of the four woods and their variation with age. (Treated as an appendix).

As the growth rings were often narrow and sometimes evidence of their formation was less apparent in the roots of these trees, it was not possible to investigate the root as precisely as the bole and branches.

of the roots. MATERIAL AND METHODS.

Material used in this investigation included a tree each of pedunculate oak (Quercus robur L.) (42 years), sycamore (Acer pseudoplatanus L.) (44 years), beech (Fagus sylvatica L.) (38 years) and robinia (Robinia pseudoacacia L.) (63 years). The approximate age of these trees is given in brackets after the name.

Four transverse discs, three inches thick, were cut from each tree trunk as detailed below.

| <u>Tree</u> | <u>Height from the ground level.</u> | | | |
|--------------------------------|--------------------------------------|--------|--------|--------|
| <u>Quercus robur</u> L. | 6" | 6'.6" | 12'.9" | 18'.0" |
| <u>Acer pseudoplatanus</u> L. | 1'.0" | 7'.0" | 13'.6" | 20'.3" |
| <u>Fagus sylvatica</u> L. | 1'.4" | 8'.3" | 16'.3" | 25'.3" |
| <u>Robinia pseudoacacia</u> L. | 1'.6" | 10'.9" | 20'.0" | 29'.3" |

In each tree these discs are referred to as D_I , D_{II} , D_{III} , and D_{IV} respectively.

For root material a single lateral root from each tree was used and discs at three different places, one nearer to the stump, one at the distal end and the other in the middle, were cut out for study. They were designated as R_I , R_{II} , R_{III} respectively for each

of the roots.

| <u>Roots.</u> | <u>Distance from the stump.</u> | | |
|---------------|---------------------------------|-----------------|------------------|
| | R _I | R _{II} | R _{III} |
| Oak | 1'.0" | 2'.6" | ----- |
| Sycamore | 1'.0" | 2'.0" | 4'.6" |
| Beech | 1'.0" | 2'.6" | 5'.0" |
| Robinia | 1'.0" | 3'.3" | 6'.0" |

For measuring the different elements of the wood radial strips, one centimetre wide tangentially, were cut out from the south side of the discs. Hence directional effects, if any, were avoided. Macerations were made from each of the first six growth rings, then every alternate one up to the sixteenth ring and afterwards, every fourth ring.

For determining the variation within one ring small blocks approximately $\frac{1}{2}$ " x $\frac{1}{2}$ " in cross section and $\frac{3}{4}$ " long were cut from wood so as to include the particular growth ring to be studied and small portions of the previous and the next rings. Specimens from bole and root were taken in oak and sycamore and in beech and robinia only from the bole. From each block, which had been previously softened by boiling

in water, transverse sections of 20 μ were cut to determine exactly the width of the growth ring. Serial tangential sections of 80 μ thick were cut of the selected ring on the sliding microtome; such a series included the latest wood of the preceding ring and the earliest wood of the succeeding one. The sections were numbered serially and files of these sections were kept after drying. It was thus possible to select material from any desired position, by checking with the transverse section originally taken for subsequent determination of vessel-element and fibre lengths in different parts of the growth ring.

Maceration of the wood was accomplished by Jeffrey's method. After removing the air, by repeated boiling and cooling, chips of wood were transferred into vials containing equal quantities of 10% chromic and nitric acids and kept in an oven maintained at 50° C. After all traces of acid removed, the different elements were separated by vigorously shaking the macerated material in 70% alcohol. The time taken for complete maceration depended on the material.

From the radial strips of wood used for maceration, small blocks of wood ($\frac{1}{2}$ " cubes) were cut

from pith outwards and numbered them serially. After staining in aniline safranin, permanent canada balsam mounts of the transverse, radial-longitudinal and tangential-longitudinal sections from these blocks were prepared.

Ray height was measured from the tangential-longitudinal sections taken at the second growth ring from the pith and then at regular intervals of one inch from the pith towards the bark.

50 fibres, 50 vessel-elements, 25 fibre-tracheids, 25 tracheids, 25 vessel-diameters (radial and tangential and 100 ray heights were measured from each sample. The choice of these numbers was based on the recommendations of Rendle and Clarke (1934).

The results were expressed as the MEAN and the STANDARD DEVIATION was calculated, according to the

formula
$$\sigma = \sqrt{\frac{\sum (x - \bar{x})^2}{n - 1}} \quad \left(\sum (x - \bar{x})^2 = \sum x^2 - \frac{\sum^2 x}{n} \right)$$

where $\sum x^2$ is the sum of the squares of each of the values; $\sum^2 x$ is the square of the sum of the values and n is the number of observations. As the number of observations was sufficiently large (always more than 20), n was substituted for $n - 1$. The

radial sections on a uniformly thick good quality

standard deviation by itself was not regarded as an expression of the amount by which the extreme sizes differed from the mean, but it was assumed for practical purposes that extremes would not differ from the mean by more than about three times the standard deviation.

Measurement of the different elements, from the temporary glycerine mounts of the macerated material, was carried out with the help of an eyepiece micrometer.

Vessel diameters, both radial and tangential, and ray heights were measured by means of a projection apparatus (Clarke, 1930). This was preferred to the previous method as it avoided the difficulty of aligning the images of the section and the micrometer scale and the considerable error introduced in the measurement of the small vessel diameters. Radial and Tangential diameters of the vessels were recorded to the nearest 5 μ .

In determining the volume occupied by the rays relative to the other elements of the wood, drawings of the rays were prepared from the tangential longitudinal sections on a uniformly thick good quality

paper using a camera lucida. A known area was taken, the rays in it cut out and weighed. Their weight was then compared with the weight of the total area of the portion used. In this way it was possible to obtain the percentage of the ray area in a tangential section, and the proportion between the ray area and the area occupied by the other elements. Since the rays are continuous and vary but little in size as they extend radially, the volume of the block might be considered as a series of tangential sections in which the number of rays and consequently the area of the rays remains fairly constant. Therefore, it might be assumed that the ray area per unit area of tangential section varied directly as the ray volume, which may be indicated by the formula:

$$\underline{\text{Ray area}} : \underline{\text{total area}} = \underline{\text{Ray volume}} : \underline{\text{total volume}}.$$

Care was taken to keep the cut pieces and the residual area of paper in a desiccator for a day before the weight was determined to avoid any differential absorption of atmospheric moisture. A mean of five different weighings from each place was taken. It is realised that errors may have arisen owing to uneven thickness of the paper, but it was felt that by using a good

quality paper this might be minimised and that such inaccuracies as did arise from this source would be relatively insignificant bearing in mind that the results would in any case only give an approximate indication of the proportions. *asus and other elements in the same field five times with five pieces of paper.*

The following two alternative methods were also tried to calculate the volume of the rays. (1) By Photo-electric cell: As in the previous method drawings of the rays were prepared on a good quality tracing paper. The area occupied by the rays was painted black. By passing a beam of light through this area on the paper the amount of light impinging on the photo-electric cell was noted; this was regarded as proportional to the area of the other elements of the wood, in a given area. (2) In the section under examination the rays were considered as indefinite number of parallel strips of each of infinitely small width. It was considered that when sufficiently large number of strips, about one hundred, were measured in a unit area, a figure giving the proportion of the area of the rays present in the wood as a whole could be obtained (Clarke, 1930).

The first method was preferred to the other two

as it proved to be more satisfactory in that the results were more quickly and easily obtained and, it was estimated, with an error of no more than 2-3%. This degree of error was determined by estimating the relative proportions of ray tissue and other elements in the same field five times with five pieces of paper.

mean value of fibre EXPERIMENTAL RESULTS. at random from

measurements of fibre length, except
in the tables 1b and 1c where each value is a mean

(a) Variation from pith outwards: Variation in length of the vertical elements of the wood in successive growth rings from the pith¹ outwards was studied in the bole, a lateral root and a branch in the oak, beech, sycamore and robinia. Vessel-elements, libriform fibres, fibre-tracheids and tracheids in oak, and vessel-elements and libriform fibres in sycamore, beech and robinia were measured in the bole. Vessel-elements and libriform fibres were measured in root wood at different levels and in branch wood from all the four trees. in all the four trees, through approximately the

BOLE: The results obtained are given in the tables² 1, 1a, 1b, 1c, 3, 3a, 5, 5a, 7 and 7a. Each figure in the tables represents in millimetres the

NOTE: 1. The word PITH is used in the present investigation for the sake of convenience. It is, however, realised that, in reference to roots, this term designates the organic centre.

2. Although the measurements given in the tables are expressed in thousandths of millimetres it is recognised that an accuracy of less than 5 u is unlikely to have been attained to by the method used.

mean value of fifty measurements taken at random from macerations of wood from definite growth rings, except in the tables lb and lc where each value is a mean of twenty five observations. In each of these tables the corresponding standard deviation is given opposite to each figure.

With the exception of the vessel-elements of robinia, the different elements were found to increase in length in the successive growth rings from the pith outwards at the four different levels from which observations were made. There was a rapid initial increase in length of the libriform fibres at any one level in all the four trees, through approximately the first 20 growth rings. The vessel-elements showed a similar increase except in robinia, where at any one level little change in length occurred. In robinia a sharp increase in fibre length is noticeable through the first 20 growth rings, whereas in oak, this rapid increase, applicable to both fibres and vessel-elements was observed through approximately the 15 oldest growth rings. In beech and sycamore there was a more irregular initial increase in length of the libriform fibres but this increase in length of the libriform fibres was

greater through about the first 30 rings than later. After this initial increase, some fluctuations occurred although there was an overall, but much smaller increase through the succeeding rings. This feature has been represented in the figure 1, where the mean lengths of the vessel-elements and libriform fibres are plotted against the growth rings. The points in each of the graphs represent the mean length of vessel-elements and libriform fibres given for D_{II} of the tables 1, 1a, 3, 3a, 5, 5a, 7 and 7a.

The results obtained in the present investigation indicate that the relative increase in length varies in the different elements of the wood of an individual tree, and in the different species of trees. For example, in oak the increase in the vessel-elements is relatively smaller than that of the libriform fibres, while the tracheids and fibre-tracheids show a relative increase of length intermediate between that of the vessel-elements and that of the libriform fibres through successive growth rings at a particular level, (Tables 1, 1a, 1b and 1c). The same feature is observed for the vessel-elements and the libriform fibres in sycamore and beech (Tables 3, 3a, 5 and 5a).

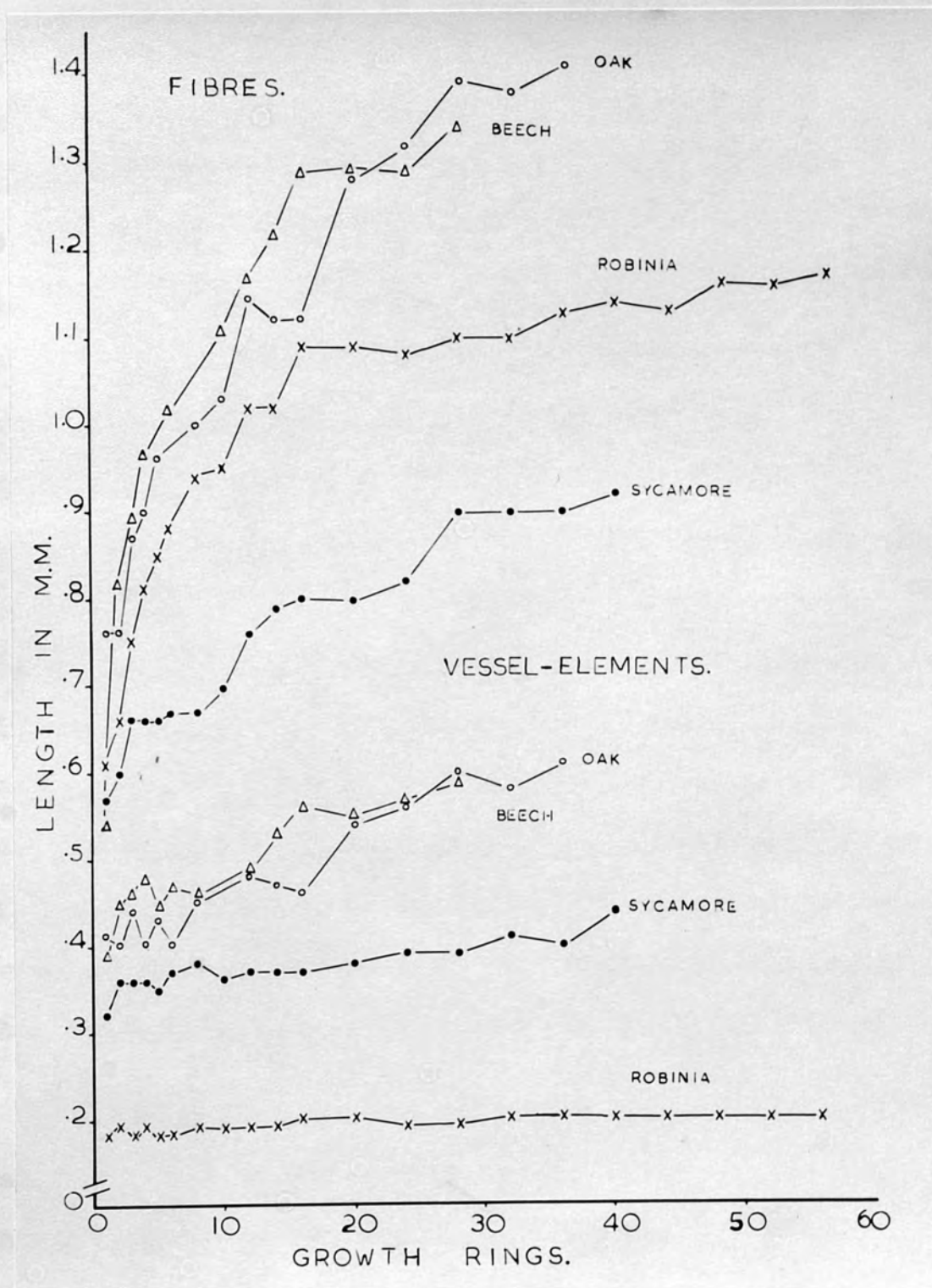


Fig. 1. Variation in vessel-element and fibre length in successive growth rings from pith outwards at one level in the bole of oak, beech, sycamore and robinia.

In robinia there is remarkably little difference in length of the vessel-elements in successive growth rings from the pith outwards at any one level (Table 7). It is tempting to relate the uniformity of length of the vessel-elements in this species to the stratified arrangement of the fusiform initials of the vascular cambium, and to suggest that these cells may not increase in length to any considerable extent and that their derivatives do not elongate, at least by an appreciable amount, during differentiation of the vessel-elements. These were matters which there was not time to investigate and it is clear that without investigation, such an explanation is somewhat facile, for the libriform fibres which are, equally, products of the fusiform initials, finally have a length in the order of about 6 times that of the vessel-elements. This matter is considered more fully in the discussion.

There is a marked amount of variation in the length of the vessel-elements and the libriform fibres in oak, sycamore and beech, and in the libriform fibres of robinia from the first formed rings to the youngest ones at any one level. In oak there was an increase of about 70% in length of the vessel-elements and a

105% in the libriform fibres, in beech a 52% and 160%, in sycamore a 45% and a 85% increase respectively. In robinia there was a 185% increase in the length of the libriform fibres.

It is further seen from the data obtained (Tables 1-8a) that the rate of increase in length of the elements of wood in the successive growth rings from pith, is more gradual in the discs taken near the base of the bole than in those at higher levels.

In all the four trees studied neither the vessel-elements nor the libriform fibres attained a constant maximum length in the later growth rings (except, of course, in the vessel-elements of robinia). This may be due to the fact that the wood of all these trees lay within the period of increasing length, which was stated by Bailey, (1923), to be approximately 60 years. In robinia, as has been already stated, the vessel-elements were observed to be of almost constant length in the later growth rings at any one level.

ROOT: Vessel-elements and libriform fibres were measured at two levels in the root of oak and at three levels in roots of beech, sycamore and robinia.

The mean length in millimeters, of fifty measurements taken at random in the individual rings and the corresponding standard deviations are given in the tables 2, 4, 4a, 6, 6a, 8 and 8a. It is clear from the tables that the pattern of increase in the length of the elements of wood in the roots is similar to that observed in the bole of these trees.

The length of the vessel-elements and of the libriform fibres is distinctly greater in the initial growth rings of the roots than in the growth rings of the same age in the bole. For example, the greatest mean length, in millimeters, of the vessel-elements and libriform fibres in certain growth rings of the bole and root of robinia are shown below:

| <u>Growth ring.</u> | <u>BOLE</u> | | <u>ROOT</u> | |
|-------------------------|-------------|-------------|-------------|-------------|
| | <u>V.E.</u> | <u>Fib.</u> | <u>V.E.</u> | <u>Fib.</u> |
| 1 | .254 | .493 | .289 | 1.276 |
| 10 | .192 | .987 | .261 | 1.670 |
| 20 | .204 | 1.053 | .254 | 1.635 |
| 40 | .197 | 1.085 | .252 | 1.636 |
| 60 | .198 | 1.105 | .251 | 1.719 |

Through the successive growth rings, the length of these elements increased in the same manner as those of the bole, there being an initial rapid increase in length in the first few growth rings after which the increase was rather slow and showed some fluctuation. The mean length of both these elements is greater in the outermost growth rings of the roots than those of the comparable rings in the bole. For example, in robinia, the mean lengths of the vessel-elements and libriform fibres were 0.27 mm. and 1.72 mm., respectively (Tables 8 and 8a), which means that the vessel-elements are 30% and the libriform fibres are about 40% longer than those of the bole. In oak there was no perceptible difference in the length of these elements in the root and the bole. The vessel-elements and libriform fibres were ^{each} 25% longer in sycamore and 16% and 14% respectively in beech in the roots than in the bole. It is a noteworthy feature that the vessel-elements and the libriform fibres are longer in the roots of robinia and sycamore, which, because of their histological features, are regarded as more specialized (Frost, 1930). In oak and beech, however, there is little difference in the maximum mean length of the

vessel-elements and the libriform fibres in the outermost growth rings of the bole and the root. The longest libriform fibres found in the present investigation were those in the root of robinia (Table, 8a). In root_{III} (Table, 8) of robinia the mean length of the vessel-elements is 0.412 mm., in the 8th growth ring, which is about 100% greater than that observed in the comparable ring of the bole (Table, 7). It was observed that the vascular cambium in this root, as evident from the $\$$ configuration of the derivatives, was stratified. This unusual length of the vessel-elements may be attributed to the increase in length of the fusiform initials themselves, perhaps due to of the the vigorous growth/root.

A rapid initial increase in length of the libriform fibres was observed through the first 25 years in robinia, and through the first 15 in beech and sycamore in the older roots studied in this investigation. In oak, however, the increase in length of the fibres was continuous throughout the rings.

Branches: In all the four trees, specimens of the branches with about 25 growth rings were selected for study of variation in length of vessel-elements

and libriform fibres. Instead of studying the successive growth rings, as was done in the bole, the length of these elements in rings 1, 2 and 3, and of the outermost growth ring was measured at one level. The mean lengths of these elements in millimeters are shown in table 9.

One interesting feature observed during the course of the present investigation was that in the bole of all the four trees and in the branches of all except in sycamore, the vessel-elements in the secondary xylem of the first ring were longer than those of the later formed rings. The length of these elements dropped, however, in the second growth ring and from this ring onwards there was a gradual increase. Bailey and Tupper (1919) reported that the elements in the primary wood might be considerably longer than those of the secondary wood, but, so far as is known, this great length of the secondary elements of the first growth ring has not been recorded previously. In contrast to the abnormal length of the vessel-elements the libriform fibres, in the early formed secondary xylem, were not correspondingly elongated in the branch.

Including the first ring, the length of these elements, as can be seen from the table 9, increased in the succeeding rings, except in robinia. The overall length attained by these elements in the last growth ring is much less than that in the comparable rings of the bole at any level in any of the trees. However, the pattern of variation in the length of the vessel-elements and the libriform fibres is the same, apart from the exception just noted, as that observed in the bole and root, in that there is a gradual increase in length from pith outwards in the successive growth rings.

| | | | | | |
|-----|-------------|--|-------------|-------------|-------------|
| | | | .396 ± .073 | .425 ± .075 | |
| | | | .448 ± .072 | .412 ± .072 | |
| 10. | .470 ± .105 | | .473 ± .078 | .428 ± .072 | |
| 12. | .471 ± .088 | | .479 ± .082 | .441 ± .088 | |
| 14. | .453 ± .080 | | .472 ± .070 | .463 ± .073 | |
| 16. | .440 ± .070 | | .450 ± .084 | .435 ± .075 | .578 ± .078 |
| 20. | .428 ± .085 | | .541 ± .084 | .492 ± .083 | .574 ± .084 |
| 24. | .475 ± .074 | | .558 ± .090 | .536 ± .084 | |
| 26. | .375 ± .121 | | .597 ± .084 | .528 ± .096 | |
| 28. | .442 ± .070 | | .577 ± .083 | | |
| 30. | .474 ± .104 | | .606 ± .111 | | |
| 32. | .484 ± .133 | | | | |

TABLE 1a. OAK-BOLE. Mean fibre length in mm.
 TABLE 1. OAK BOLE. Mean vessel-element length
 in mm. and standard deviation at different
 levels.

| Ring No. | D _I 6" from the ground | D _{II} 6' from the ground | D _{III} 12' from the ground | D _{IV} 18' from the ground |
|-------------|---|--|--|---|
| 1. | .350 ± .048 | .409 ± .082 | .430 ± .071 | .273 ± .056 |
| 2. | .362 ± .050 | .401 ± .059 | .442 ± .054 | .313 ± .057 |
| 3. | .428 ± .065 | .438 ± .065 | .447 ± .069 | .403 ± .059 |
| 4. | .422 ± .078 | .403 ± .027 | .449 ± .069 | .439 ± .081 |
| 5. | .392 ± .055 | .433 ± .081 | .457 ± .060 | ----- |
| 6. | .405 ± .075 | .396 ± .073 | .435 ± .073 | .456 ± .049 |
| 8. | .430 ± .072 | .448 ± .072 | .412 ± .073 | .470 ± .027 |
| 10. | .470 ± .105 | .473 ± .070 | .424 ± .070 | .518 ± .106 |
| 12. | .431 ± .089 | .479 ± .084 | .443 ± .056 | .500 ± .085 |
| 14. | .453 ± .060 | .472 ± .070 | .463 ± .075 | .509 ± .058 |
| 16. | .440 ± .090 | .460 ± .084 | .456 ± .079 | .536 ± .098 |
| 20. | .428 ± .096 | .541 ± .084 | .492 ± .085 | .574 ± .065 |
| 24. | .475 ± .074 | .558 ± .090 | .536 ± .084 | ----- |
| 28. | .515 ± .121 | .597 ± .084 | .528 ± .096 | ----- |
| 32. | .512 ± .078 | .577 ± .093 | ----- | ----- |
| 36. | .522 ± .104 | .606 ± .111 | ----- | ----- |
| 40. | .555 ± .113 | ----- | ----- | ----- |

TABLE Ia. OAK-BOLE. Mean fibre length in mm., and standard deviation, at different levels.

| Ring No. | D _I 6" from the ground | D _{II} 6' from the ground | D _{III} 12' from the ground | D _{IV} 18' from the ground |
|----------|--------------------------------------|---------------------------------------|---|--|
| 1 | .684 ± .057 | .763 ± .088 | .828 ± .084 | .572 ± .049 |
| 2 | ----- | .759 ± .074 | .951 ± .095 | .628 ± .068 |
| 3 | .918 ± .113 | .873 ± .082 | .987 ± .091 | .915 ± .098 |
| 4 | .949 ± .079 | .904 ± .087 | .993 ± .084 | 1.160 ± .143 |
| 5 | .944 ± .095 | .961 ± .110 | .996 ± .078 | ----- |
| 6 | .961 ± .061 | 1.014 ± .097 | 1.009 ± .097 | 1.122 ± .114 |
| 8 | .940 ± .084 | 1.002 ± .093 | 1.085 ± .077 | 1.094 ± .074 |
| 10 | 1.082 ± .143 | 1.032 ± .082 | 1.100 ± .120 | 1.184 ± .105 |
| 12 | 1.094 ± .166 | 1.145 ± .107 | 1.153 ± .108 | 1.210 ± .125 |
| 14 | 1.045 ± .120 | 1.117 ± .117 | 1.223 ± .121 | 1.242 ± .111 |
| 16 | 1.110 ± .126 | 1.122 ± .106 | 1.282 ± .147 | 1.247 ± .146 |
| 20 | 1.064 ± .097 | 1.276 ± .155 | 1.297 ± .088 | 1.333 ± .155 |
| 24 | 1.223 ± .116 | 1.320 ± .149 | 1.402 ± .167 | ----- |
| 28 | 1.254 ± .093 | 1.391 ± .195 | 1.401 ± .162 | ----- |
| 32 | 1.215 ± .136 | 1.381 ± .131 | ----- | ----- |
| 36 | 1.251 ± .129 | 1.408 ± .192 | ----- | ----- |
| 40 | 1.375 ± .185 | ----- | ----- | ----- |

TABLE Ib. OAK-BOLE. Mean fibre-tracheid length in mm., and standard deviation at different levels.

| Ring No. | D _I 6" from the ground | D _{II} 6' from the ground | D _{III} 12' from the ground | D _{IV} 18' from the ground |
|----------|--------------------------------------|---------------------------------------|---|--|
| 1 | .600 ± .058 | .632 ± .057 | .618 ± .065 | .412 ± .035 |
| 2 | ----- | .605 ± .057 | .650 ± .049 | .484 ± .037 |
| 3 | .672 ± .091 | .614 ± .053 | .714 ± .054 | .687 ± .058 |
| 4 | .676 ± .072 | .659 ± .041 | .709 ± .057 | .833 ± .090 |
| 5 | .646 ± .066 | .726 ± .085 | .776 ± .051 | ----- |
| 6 | .681 ± .065 | .705 ± .080 | .760 ± .085 | .804 ± .090 |
| 8 | .716 ± .065 | .746 ± .107 | .719 ± .065 | .819 ± .084 |
| 10 | .739 ± .078 | .752 ± .070 | .760 ± .072 | .820 ± .093 |
| 12 | .773 ± .083 | .813 ± .094 | .787 ± .066 | .860 ± .068 |
| 14 | .796 ± .072 | .737 ± .095 | .868 ± .090 | .875 ± .056 |
| 16 | .761 ± .078 | .812 ± .085 | .858 ± .075 | .901 ± .062 |
| 20 | .768 ± .056 | .913 ± .086 | .861 ± .078 | .945 ± .100 |
| 24 | .810 ± .112 | .890 ± .090 | .886 ± .083 | ----- |
| 28 | .836 ± .079 | .992 ± .120 | .914 ± .093 | ----- |
| 32 | .854 ± .093 | .920 ± .085 | ----- | ----- |
| 36 | .796 ± .086 | .949 ± .107 | ----- | ----- |
| 40 | .839 ± .070 | ----- | ----- | ----- |

TABLE 1.c. OAK-BOLE. Mean tracheid length in mm.,
and standard deviation at different
levels.

| Ring No. | D _I 6" from the ground | D _{II} 6' from the ground | D _{III} 12' from the ground | D _{IV} 18' from the ground |
|----------|--------------------------------------|---------------------------------------|---|--|
| | Vessel- elements | Fibres. | Vessel- elements | Fibres. |
| 1 | .391 ± .060 | .466 ± .051 | .478 ± .050 | .329 ± .028 |
| 2 | ----- | .441 ± .036 | .501 ± .048 | .342 ± .043 |
| 3 | .449 ± .070 | .460 ± .045 | .487 ± .050 | .476 ± .046 |
| 4 | .429 ± .056 | .463 ± .038 | .495 ± .044 | .482 ± .044 |
| 5 | .444 ± .057 | .449 ± .045 | .497 ± .046 | ----- |
| 6 | .430 ± .043 | .474 ± .054 | .485 ± .043 | .495 ± .064 |
| 8 | .436 ± .058 | .465 ± .076 | .489 ± .046 | .502 ± .044 |
| 10 | .497 ± .051 | .464 ± .038 | .467 ± .059 | .490 ± .062 |
| 12 | .528 ± .077 | .512 ± .069 | .493 ± .044 | .539 ± .051 |
| 14 | .526 ± .049 | .507 ± .060 | .531 ± .070 | .541 ± .052 |
| 16 | .463 ± .075 | .497 ± .061 | .543 ± .059 | .560 ± .061 |
| 20 | .487 ± .048 | .576 ± .075 | .514 ± .051 | .619 ± .064 |
| 24 | .526 ± .059 | .555 ± .068 | .557 ± .055 | ----- |
| 28 | .595 ± .065 | .573 ± .078 | .555 ± .050 | ----- |
| 32 | .564 ± .058 | .621 ± .064 | ----- | ----- |
| 36 | .556 ± .067 | .622 ± .077 | ----- | ----- |
| 40 | .560 ± .067 | ----- | ----- | ----- |

TABLE 2. OAK-ROOT. Mean vessel-element

TABLE 2. OAK-ROOT. Mean vessel-element and fibre length in mm., and standard deviation

| Ring No. | Root I (28 Growth Rings) | | Root II (16 Growth rings) | |
|----------|--------------------------|--------------|---------------------------|-------------|
| | Vessel-elements. | Fibres. | Vessel-elements. | fibres. |
| 2 | .302 ± .052 | .397 ± .063 | .318 ± .056 | .358 ± .051 |
| 1 | .331 ± .052 | .383 ± .049 | .400 ± .048 | .675 ± .052 |
| 2 | .336 ± .052 | .361 ± .049 | .431 ± .042 | .698 ± .055 |
| 3 | .464 ± .024 | 1.060 ± .086 | .409 ± .044 | .671 ± .050 |
| 4 | .328 ± .053 | .374 ± .061 | .427 ± .031 | .698 ± .043 |
| 5 | .329 ± .068 | .384 ± .055 | .407 ± .030 | .730 ± .024 |
| 6 | .479 ± .055 | 1.147 ± .089 | .442 ± .039 | .733 ± .040 |
| 8 | .475 ± .064 | 1.193 ± .080 | .436 ± .028 | .702 ± .030 |
| 10 | .474 ± .062 | 1.109 ± .060 | .442 ± .044 | .737 ± .052 |
| 12 | .491 ± .060 | 1.151 ± .070 | .445 ± .030 | .780 ± .052 |
| 14 | .478 ± .075 | 1.159 ± .068 | .446 ± .032 | .774 ± .056 |
| 16 | .519 ± .063 | 1.232 ± .112 | .452 ± .057 | .806 ± .037 |
| 20 | .520 ± .076 | 1.270 ± .104 | ----- | 406 ----- |
| 24 | .540 ± .086 | 1.318 ± .100 | ----- | 409 ----- |
| 28 | .539 ± .094 | 1.415 ± .095 | ----- | 396 ----- |

TABLE 3. SYCAMORE-BOLE. Mean vessel-element length in mm., and standard deviation at different levels.

| Ring No. | D _I 1' from the ground | D _{II} 7' from the ground | D _{III} 13'-6" from ground | D _{IV} 20'-3" from ground |
|----------|--------------------------------------|---------------------------------------|--|---------------------------------------|
| 1 | .224 ± .041 | .323 ± .052 | .285 ± .022 | .319 ± .083 |
| 2 | .302 ± .062 | .357 ± .063 | .318 ± .056 | .358 ± .051 |
| 3 | .331 ± .052 | .363 ± .044 | .356 ± .054 | .359 ± .048 |
| 4 | .336 ± .052 | .361 ± .049 | .366 ± .038 | .382 ± .040 |
| 5 | .329 ± .048 | .350 ± .027 | .375 ± .051 | .383 ± .042 |
| 6 | .328 ± .053 | .374 ± .061 | .377 ± .042 | .369 ± .060 |
| 8 | .329 ± .068 | .384 ± .055 | .372 ± .056 | .372 ± .037 |
| 10 | .338 ± .047 | .358 ± .053 | .369 ± .030 | .398 ± .032 |
| 12 | .363 ± .045 | .370 ± .043 | .360 ± .038 | .381 ± .050 |
| 14 | .329 ± .041 | .372 ± .044 | .361 ± .041 | .367 ± .050 |
| 16 | .304 ± .054 | .370 ± .044 | .377 ± .054 | .381 ± .046 |
| 20 | .321 ± .054 | .380 ± .045 | .363 ± .044 | .381 ± .044 |
| 24 | .335 ± .052 | .387 ± .056 | .396 ± .047 | .417 ± .054 |
| 28 | .309 ± .054 | .385 ± .054 | .385 ± .057 | .406 ± .050 |
| 32 | .303 ± .067 | .409 ± .055 | .397 ± .042 | .409 ± .049 |
| 36 | .327 ± .082 | .402 ± .063 | .397 ± .043 | .396 ± .042 |
| 40 | .371 ± .046 | .437 ± .053 | .425 ± .047 | ----- |
| 44 | .344 ± .062 | .----- | ----- | ----- |

TABLE 3 a. SYCAMORE-BOLE. Mean fibre length in mm., and the standard deviation at different levels.

| Ring No. | D _I 1' from the ground | D _{II} 7' from the ground | D _{III} 13'-6" from ground | D _{IV} 20'-3" from ground |
|----------|--------------------------------------|---------------------------------------|--|---------------------------------------|
| 1 | .453 ± .064 | .570 ± .086 | .475 ± .048 | .477 ± .069 |
| 2 | .553 ± .071 | .598 ± .103 | .572 ± .063 | .520 ± .071 |
| 3 | .578 ± .112 | .661 ± .070 | .625 ± .062 | .596 ± .060 |
| 4 | .637 ± .078 | .658 ± .084 | .652 ± .073 | .705 ± .095 |
| 5 | .722 ± .096 | .660 ± .079 | .647 ± .090 | .702 ± .069 |
| 6 | .747 ± .107 | .671 ± .100 | .698 ± .066 | .756 ± .077 |
| 8 | .665 ± .123 | .673 ± .054 | .723 ± .078 | .770 ± .059 |
| 10 | .751 ± .093 | .699 ± .104 | .723 ± .093 | .814 ± .044 |
| 12 | .825 ± .116 | .758 ± .099 | .735 ± .057 | .821 ± .055 |
| 14 | .801 ± .090 | .792 ± .065 | .753 ± .088 | .837 ± .074 |
| 16 | .709 ± .133 | .796 ± .092 | .766 ± .088 | .867 ± .094 |
| 20 | .857 ± .129 | .799 ± .082 | .782 ± .081 | .843 ± .075 |
| 24 | .818 ± .100 | .819 ± .085 | .814 ± .088 | .875 ± .103 |
| 28 | .698 ± .124 | .897 ± .108 | .845 ± .093 | .908 ± .111 |
| 32 | .796 ± .117 | .895 ± .143 | .861 ± .096 | .876 ± .069 |
| 36 | .818 ± .120 | .904 ± .106 | .895 ± .100 | .942 ± .080 |
| 40 | .874 ± .115 | .916 ± .088 | .868 ± .064 | ----- |
| 44 | .857 ± .110 | ----- | ----- | ----- |

TABLE 4. SYCAMORE ROOT. Mean vessel-element length in mm., and the standard deviation.

| Ring No. | Root I 1' from the stump | Root II 2' from the stump | Root III 4'-6" from the stump. |
|----------|-----------------------------|------------------------------|-----------------------------------|
| 1 | .437 ± .019 | .421 ± .071 | .483 ± .066 |
| 2 | .446 ± .047 | .449 ± .072 | .515 ± .033 |
| 3 | .486 ± .064 | .442 ± .056 | .502 ± .052 |
| 4 | .459 ± .055 | .432 ± .067 | .539 ± .034 |
| 5 | .464 ± .055 | .460 ± .071 | .537 ± .036 |
| 6 | .460 ± .056 | .442 ± .071 | .546 ± .047 |
| 8 | .500 ± .056 | .469 ± .057 | .556 ± .048 |
| 10 | .476 ± .056 | .485 ± .063 | .520 ± .052 |
| 12 | .500 ± .062 | .465 ± .052 | .517 ± .026 |
| 14 | .507 ± .056 | .469 ± .059 | .547 ± .027 |
| 16 | .479 ± .055 | .481 ± .057 | .528 ± .036 |
| 20 | .483 ± .057 | .457 ± .046 | ----- |
| 24 | .501 ± .055 | .458 ± .041 | ----- |
| 28 | .504 ± .053 | ----- | ----- |
| 32 | .498 ± .064 | ----- | ----- |
| 36 | .501 ± .052 | ----- | ----- |

TABLE 4 a. SYCAMORE ROOT. Mean fibre length in mm., and the standard deviation at different levels.

| Ring No. | Root I 1' from the stump. | Root II 2' from the stump. | Root III 4'-6" from the stump. |
|----------|------------------------------|-------------------------------|-----------------------------------|
| 1 | .761 ± .063 | .624 ± .097 | .800 ± .082 |
| 2 | .798 ± .052 | .681 ± .061 | .817 ± .083 |
| 3 | .844 ± .063 | .746 ± .069 | .857 ± .074 |
| 4 | .810 ± .056 | .722 ± .030 | .946 ± .099 |
| 5 | .849 ± .050 | .776 ± .027 | .928 ± .098 |
| 6 | .835 ± .047 | .783 ± .076 | .940 ± .101 |
| 8 | .874 ± .045 | .823 ± .069 | .955 ± .049 |
| 10 | .865 ± .058 | .858 ± .071 | .952 ± .107 |
| 12 | .981 ± .068 | .873 ± .074 | .951 ± .081 |
| 14 | .975 ± .065 | .834 ± .061 | .990 ± .100 |
| 16 | .977 ± .057 | .826 ± .051 | 1.001 ± .090 |
| 20 | .923 ± .057 | .832 ± .055 | ----- |
| 24 | .931 ± .052 | .865 ± .051 | ----- |
| 28 | .947 ± .058 | ----- | ----- |
| 32 | .994 ± .064 | ----- | ----- |
| 36 | 1.006 ± .052 | ----- | ----- |

TABLE 5. BEECH BOLE. Mean vessel-element length in mm., and the standard deviation at different levels.

| Ring No. | D _I 1'-4" from the ground | D _{II} 8'-3" from the ground | D _{III} 16'-3" from the ground | D _{IV} 25'-3" from ground |
|----------|---|--|--|---------------------------------------|
| 1 | .393 ± .068 | .389 ± .075 | .361 ± .056 | .344 ± .055 |
| 2 | .382 ± .057 | .446 ± .064 | .383 ± .054 | .387 ± .055 |
| 3 | .434 ± .057 | .460 ± .058 | .418 ± .058 | .439 ± .079 |
| 4 | .435 ± .024 | .484 ± .089 | .419 ± .048 | .439 ± .061 |
| 5 | .429 ± .069 | .453 ± .071 | .431 ± .071 | .435 ± .079 |
| 6 | .454 ± .067 | .472 ± .093 | .406 ± .058 | .435 ± .056 |
| 8 | .478 ± .092 | .456 ± .078 | .468 ± .074 | .444 ± .081 |
| 10 | .492 ± .080 | .469 ± .089 | .483 ± .087 | .452 ± .083 |
| 12 | .482 ± .084 | .494 ± .088 | .472 ± .060 | .466 ± .072 |
| 14 | .476 ± .067 | .528 ± .076 | .533 ± .081 | .485 ± .062 |
| 16 | .473 ± .099 | .555 ± .083 | .519 ± .080 | .488 ± .053 |
| 20 | .521 ± .104 | .542 ± .100 | .519 ± .063 | ----- |
| 24 | .534 ± .091 | .575 ± .088 | .548 ± .078 | ----- |
| 28 | .537 ± .081 | .593 ± .102 | ----- | ----- |
| 32 | .555 ± .086 | ----- | ----- | ----- |
| 36 | .546 ± .105 | ----- | ----- | ----- |

TABLE 5 a. BEECH Bole. Mean fibre length in mm.,
and the standard deviation at different
levels.

| Ring No. | D _I 1'-4" from ground | D _{II} 8'-3" from ground | D _{III} 16'-3" from ground | D _{IV} 25'-3" from ground |
|-------------|--|---|---|--|
| 1 | .496 ± .058 | .535 ± .057 | .568 ± .059 | .656 ± .058 |
| 2 | .601 ± .085 | .824 ± .086 | .561 ± .047 | .702 ± .092 |
| 3 | .703 ± .081 | .896 ± .092 | .639 ± .074 | .930 ± .118 |
| 4 | .714 ± .081 | .977 ± .117 | .671 ± .059 | .960 ± .119 |
| 5 | .759 ± .084 | .993 ± .114 | .751 ± .085 | .955 ± .088 |
| 6 | .833 ± .109 | 1.024 ± .102 | .739 ± .074 | 1.051 ± .098 |
| 8 | .987 ± .117 | 1.008 ± .097 | .936 ± .128 | 1.067 ± .107 |
| 10 | 1.102 ± .142 | 1.105 ± .111 | 1.083 ± .150 | 1.108 ± .069 |
| 12 | 1.129 ± .114 | 1.173 ± .149 | 1.129 ± .107 | 1.057 ± .104 |
| 14 | 1.118 ± .141 | 1.218 ± .160 | 1.207 ± .107 | 1.239 ± .132 |
| 16 | 1.058 ± .115 | 1.285 ± .093 | 1.236 ± .121 | 1.248 ± .119 |
| 20 | 1.229 ± .137 | 1.286 ± .180 | 1.227 ± .130 | ----- |
| 24 | 1.269 ± .118 | 1.291 ± .122 | 1.267 ± .104 | ----- |
| 28 | 1.287 ± .138 | 1.337 ± .135 | ----- | ----- |
| 32 | 1.318 ± .130 | ----- | ----- | ----- |
| 36 | 1.337 ± .107 | ----- | ----- | ----- |

TABLE 6. BEECH ROOT. Mean vessel-element length in mm., and the standard deviation.

| Ring No. | Root I 1' from the stump. | Root II 2'-6" from the stump. | Root III 5'-6" from the stump. |
|----------|------------------------------|----------------------------------|-----------------------------------|
| 1 | .430 ± .073 | .566 ± .062 | .592 ± .097 |
| 2 | | | .640 ± .069 |
| 3 | | .586 ± .086 | .681 ± .109 |
| 4 | .466 ± .084 | .686 ± .074 | .683 ± .098 |
| 5 | .487 ± .076 | .689 ± .078 | ----- |
| 6 | .506 ± .064 | .673 ± .099 | ----- |
| 8 | .535 ± .089 | .711 ± .116 | ----- |
| 10 | .578 ± .093 | ----- | ----- |
| 12 | .579 ± .096 | ----- | ----- |
| 14 | .587 ± .088 | ----- | ----- |
| 16 | .555 ± .098 | ----- | ----- |
| 20 | .620 ± .091 | ----- | ----- |
| 24 | .637 ± .086 | ----- | ----- |
| 28 | .657 ± .081 | ----- | ----- |

TABLE 7. ROBINIA BOLE. Mean vessel-element length in μm , and the standard deviation at different levels.

TABLE 6 a. BEECH ROOT. Mean fibre length in mm., and the standard deviation.

| Ring No. | Root _I 1' from the stump. | Root _{II} 2'-6" from the stump. | Root _{III} 5'-6" from the stump. |
|----------|---|---|--|
| 1 | | | |
| 2 | | | |
| 3 | 1 .709 \pm .067 | .962 \pm .125 | 1.214 \pm .105 |
| 4 | 2 | | 1.382 \pm .192 |
| 5 | 3 | 1.108 \pm .093 | 1.438 \pm .147 |
| 6 | 4 .870 \pm .081 | 1.324 \pm .110 | 1.468 \pm .149 |
| 8 | 5 .961 \pm .092 | 1.335 \pm .140 | ----- |
| 10 | 6 1.069 \pm .104 | 1.432 \pm .147 | ----- |
| 12 | 8 1.165 \pm .123 | 1.443 \pm .157 | ----- |
| 14 | 10 1.227 \pm .118 | ----- | ----- |
| 16 | 12 1.326 \pm .116 | ----- | ----- |
| 20 | 14 1.428 \pm .126 | ----- | ----- |
| 24 | 16 1.433 \pm .094 | ----- | ----- |
| 28 | 20 1.481 \pm .113 | ----- | ----- |
| 32 | 24 1.475 \pm .145 | ----- | ----- |
| 36 | 28 1.532 \pm .126 | ----- | ----- |
| 40 | | | |
| 44 | | | |
| 48 | | | |
| 52 | | | |
| 56 | | | |
| 60 | | | |

ROBINIA BOLE. Mean fibre length in mm.,
 TABLE 7. ROBINIA BOLE. Mean vessel-element length
 in mm., and the standard deviation at
 different levels.

| Ring No. | D _I 1'-6" from ground | D _{II} 10'-9" from ground | D _{III} 20'-0" from ground | D _{IV} 29'-3" from ground |
|-------------|--|--|---|--|
| 1 | .254 ± .051 | .179 ± .050 | .195 ± .019 | .218 ± .024 |
| 2 | .216 ± .032 | .186 ± .019 | .195 ± .025 | .225 ± .024 |
| 3 | .195 ± .025 | .182 ± .022 | .212 ± .021 | .215 ± .021 |
| 4 | .199 ± .024 | .185 ± .041 | .211 ± .021 | .207 ± .021 |
| 5 | .196 ± .024 | .183 ± .061 | .216 ± .020 | .216 ± .019 |
| 6 | .203 ± .011 | .180 ± .029 | .211 ± .015 | .215 ± .018 |
| 8 | .198 ± .019 | .186 ± .014 | .218 ± .016 | .218 ± .020 |
| 10 | .192 ± .017 | .191 ± .017 | .213 ± .018 | .215 ± .019 |
| 12 | .200 ± .018 | .188 ± .016 | .216 ± .018 | .215 ± .021 |
| 14 | .203 ± .022 | .190 ± .016 | .209 ± .012 | .203 ± .017 |
| 16 | .203 ± .022 | .198 ± .018 | .211 ± .012 | .195 ± .018 |
| 20 | .204 ± .014 | .197 ± .014 | .214 ± .013 | .202 ± .017 |
| 24 | .204 ± .017 | .191 ± .017 | .213 ± .013 | .209 ± .015 |
| 28 | .203 ± .022 | .194 ± .012 | .211 ± .013 | .207 ± .012 |
| 32 | .201 ± .016 | .198 ± .015 | .211 ± .013 | .201 ± .018 |
| 36 | .194 ± .015 | .203 ± .015 | .220 ± .016 | .208 ± .015 |
| 40 | .197 ± .013 | .199 ± .017 | .213 ± .015 | .208 ± .012 |
| 44 | .201 ± .018 | .203 ± .013 | .212 ± .014 | .210 ± .014 |
| 48 | .199 ± .019 | .198 ± .015 | .218 ± .017 | ----- |
| 52 | .199 ± .015 | .199 ± .018 | .218 ± .015 | ----- |
| 56 | .201 ± .019 | .202 ± .014 | ----- | ----- |
| 60 | .198 ± .017 | ----- | ----- | ----- |

TABLE 7 a. ROBINIA BOLE. Mean fibre length in mm., and the standard deviation, at different levels.

| Ring No. | D _I 1'-6" from ground | D _{II} 10'-9" from ground | D _{III} 20'-0" from ground | D _{IV} 29'-3" from ground |
|----------|-------------------------------------|---------------------------------------|--|---------------------------------------|
| 1 | .493 ± .088 | .614 ± .064 | .418 ± .046 | .546 ± .044 |
| 2 | .655 ± .112 | .656 ± .154 | .626 ± .086 | .591 ± .060 |
| 3 | .700 ± .108 | .747 ± .085 | .628 ± .037 | .613 ± .054 |
| 4 | .788 ± .141 | .807 ± .052 | .768 ± .090 | .800 ± .063 |
| 5 | .820 ± .115 | .846 ± .090 | .798 ± .078 | .798 ± .083 |
| 6 | .946 ± .131 | .880 ± .088 | .869 ± .081 | .827 ± .103 |
| 8 | .981 ± .130 | .938 ± .079 | .897 ± .104 | .898 ± .086 |
| 10 | .987 ± .029 | .953 ± .088 | .937 ± .098 | .917 ± .101 |
| 12 | .988 ± .099 | 1.024 ± .073 | 1.006 ± .071 | .949 ± .079 |
| 14 | 1.031 ± .135 | 1.019 ± .079 | 1.058 ± .125 | .937 ± .085 |
| 16 | 1.034 ± .115 | 1.087 ± .079 | 1.081 ± .112 | .976 ± .095 |
| 20 | 1.053 ± .143 | 1.085 ± .076 | 1.108 ± .109 | 1.002 ± .079 |
| 24 | 1.084 ± .137 | 1.083 ± .069 | 1.113 ± .111 | 1.079 ± .061 |
| 28 | 1.081 ± .126 | 1.097 ± .133 | 1.110 ± .125 | 1.110 ± .097 |
| 32 | 1.083 ± .105 | 1.104 ± .101 | 1.123 ± .119 | 1.136 ± .099 |
| 36 | 1.082 ± .100 | 1.128 ± .118 | 1.135 ± .072 | 1.135 ± .115 |
| 40 | 1.085 ± .031 | 1.136 ± .105 | 1.172 ± .135 | 1.131 ± .112 |
| 44 | 1.082 ± .103 | 1.129 ± .128 | 1.195 ± .080 | 1.153 ± .097 |
| 48 | 1.084 ± .079 | 1.162 ± .110 | 1.192 ± .111 | ----- |
| 52 | 1.085 ± .128 | 1.160 ± .100 | 1.194 ± .083 | ----- |
| 56 | 1.097 ± .118 | 1.166 ± .106 | ----- | ----- |
| 60 | 1.105 ± .107 | ----- | ----- | ----- |

TABLE 8. ROBINIA ROOT. Mean vessel-element length in mm., and standard deviation.

| Ring No. | Root _I 1'-0" from stump | Root _{II} 3'-3" from stump | Root _{III} 6'-0" from stump |
|----------|---------------------------------------|--|---|
| 1 | .289 ± .129 | .201 ± .027 | .355 ± .055 |
| 2 | .354 ± .146 | .236 ± .019 | .356 ± .082 |
| 3 | .262 ± .033 | .227 ± .029 | .387 ± .053 |
| 4 | .261 ± .036 | .239 ± .024 | .389 ± .036 |
| 5 | .254 ± .024 | .239 ± .025 | .398 ± .071 |
| 6 | .259 ± .030 | .234 ± .023 | .412 ± .044 |
| 8 | .274 ± .036 | .223 ± .023 | .410 ± .051 |
| 10 | .261 ± .020 | .233 ± .023 | ----- |
| 12 | .276 ± .050 | .233 ± .021 | ----- |
| 14 | .265 ± .030 | .234 ± .024 | ----- |
| 16 | .255 ± .040 | .244 ± .017 | ----- |
| 20 | .254 ± .029 | .251 ± .018 | ----- |
| 24 | .277 ± .053 | .245 ± .021 | ----- |
| 28 | .250 ± .024 | .244 ± .018 | ----- |
| 32 | .254 ± .033 | .241 ± .016 | ----- |
| 36 | .256 ± .026 | .245 ± .018 | ----- |
| 40 | .252 ± .021 | ----- | ----- |
| 44 | .257 ± .019 | ----- | ----- |
| 48 | .265 ± .020 | ----- | ----- |
| 52 | .258 ± .021 | ----- | ----- |
| 56 | .263 ± .027 | ----- | ----- |
| 60 | .251 ± .016 | ----- | ----- |

TABLE 8 a. ROBINIA ROOT. Mean fibre length in mm., and standard deviation.

| Ring No. | Root _I 1'-0" from stump. | Root _{II} 3'-3" from stump. | Root _{III} 6'-0" from stump. |
|----------|--|---|--|
| 1 | 1.276 ± .158 | 1.107 ± .062 | .485 ± .030 |
| 2 | 1.332 ± .161 | 1.292 ± .142 | .502 ± .055 |
| 3 | 1.367 ± .151 | 1.415 ± .185 | .586 ± .052 |
| 4 | 1.312 ± .146 | 1.388 ± .153 | .582 ± .035 |
| 5 | 1.491 ± .164 | 1.388 ± .177 | .640 ± .066 |
| 6 | 1.515 ± .172 | 1.395 ± .166 | .665 ± .049 |
| 8 | 1.686 ± .191 | 1.483 ± .087 | .670 ± .056 |
| 10 | 1.670 ± .133 | 1.476 ± .067 | . ----- |
| 12 | 1.665 ± .152 | 1.467 ± .190 | . ----- |
| 14 | 1.676 ± .160 | 1.499 ± .177 | . ----- |
| 16 | 1.656 ± .172 | 1.500 ± .162 | . ----- |
| 20 | 1.635 ± .171 | 1.506 ± .106 | . ----- |
| 24 | 1.605 ± .170 | 1.607 ± .126 | . ----- |
| 28 | 1.627 ± .145 | 1.627 ± .103 | . ----- |
| 32 | 1.573 ± .079 | 1.675 ± .158 | . ----- |
| 36 | 1.639 ± .159 | 1.687 ± .155 | . ----- |
| 40 | 1.636 ± .147 | . ----- | . ----- |
| 44 | 1.663 ± .193 | . ----- | . ----- |
| 48 | 1.607 ± .143 | . ----- | . ----- |
| 52 | 1.645 ± .172 | . ----- | . ----- |
| 56 | 1.600 ± .126 | . ----- | . ----- |
| 60 | 1.719 ± .117 | . ----- | . ----- |

(b) Variation upwards in the bole: Variation in length of the vessel-elements and of the libriform fibres

TABLE 9. Variation on length of the vessel-elements and fibres in the branches of oak, beech, sycamore, and robinia.

Growth rings were numbered from bark inwards in each of the four cross-sectional discs cut at a level in each year.

| NAME | Ring 1 | | Ring 2 | | Ring 3 | | Outermost ring | |
|----------|--------|------|--------|------|--------|------|----------------|-------|
| | V.E | Fib. | V.E. | Fib. | V.E. | Fib. | V.E. | Fib. |
| Oak | .490 | .757 | .362 | .834 | .436 | .926 | .487 | 1.105 |
| Beech | .419 | .492 | .376 | .524 | .488 | .664 | .482 | .928 |
| Sycamore | .268 | .443 | .285 | .465 | .304 | .557 | .333 | .710 |
| Robinia | .257 | .420 | .195 | .482 | .197 | .582 | .185 | .936 |

Oak

Beech

Sycamore

Robinia

(b) Variation upwards in the bole: Variation in length of the vessel-elements and of the libriform fibres was studied in specific growth rings from the base to the top of the bole in all the four trees. Growth rings were numbered from bark inwards in each of the four cross-sectional discs, cut at different levels, in all the trees, so that the rings of particular years could be traced in all the discs. Care was taken to see that all these rings were traced on one side of the bole, that facing due south, in the standing tree.

The relation of the selected rings to the pith was as follows:

| <u>Name</u> | <u>Growth ring</u> | <u>Number of the ring from pith.</u> | | | |
|-------------|--------------------|--------------------------------------|-----------------|------------------|-----------------|
| | | D _I | D _{II} | D _{III} | D _{IV} |
| Oak | 1925 | 10 | 6 | -- | -- |
| | 1939 | 24 | 20 | 14 | 6 |
| | 1956 | 40 | 36 | 30 | 22 |
| Beech | 1928 | 10 | 1 | -- | -- |
| | 1942 | 24 | 15 | 13 | 4 |
| | 1954 | 36 | 27 | 25 | 16 |
| Sycamore | 1922 | 10 | 9 | 7 | 3 |
| | 1936 | 24 | 23 | 21 | 17 |
| | 1952 | 40 | 39 | 37 | 33 |
| Robinia | 1913 | 20 | 15 | 12 | 4 |
| | 1933 | 40 | 35 | 32 | 24 |
| | 1953 | 60 | 55 | 52 | 44 |

Results of the measurements of fifty vessel-elements and libriform fibres taken at random from maceration of individual rings at different heights in the four trees are given in the table 10, where each of the measurements represents the mean value in millimeters.

The figures in table 10, indicate that, in all the trees, there is, generally, an increase in length of the vessel-elements and the libriform fibres from the base of the bole upward, to a certain height, after which there is a decrease toward the top of the trunk. In a few instances, however, as indicated in the table 10, by a frame in broken lines, this relation does not appear to hold. This may, however, be due to the spacing of the discs used, and might not have shown had measurements been made from a series of more closely placed discs; unfortunately time did not permit this. Judged on the data available the vessel-elements and the libriform fibres attained their maximum length at a height of between 6 and 12 feet in the bole of oak, beech and sycamore but in robinia at a height of about 20 feet(cf. Fig. 2). In the figure 2, the mean length of these elements from selected rings,

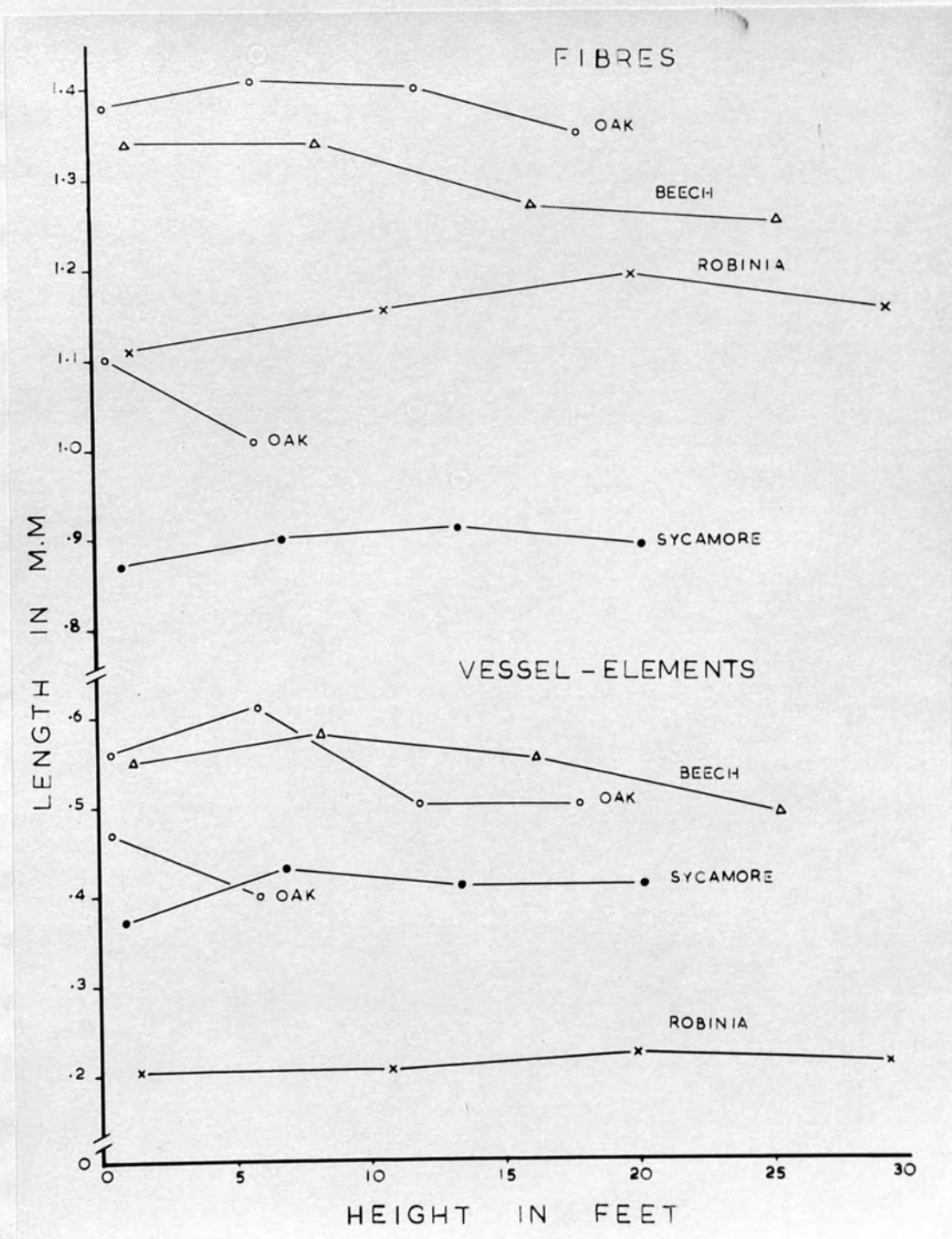


Fig. 2. Variation in vessel-element and fibre length in specific growth rings at different levels in the bole of oak, beech, sycamore and robinia.

is plotted against the height in feet at which the rings were examined in the bole. It cannot, of course, without an examination of a series of discs cut at much closer intervals, be stated at exactly what height in the bole the maximum lengths were attained in specific rings. Moreover, it must not be assumed, without further study, that the maximum length is attained at exactly the same height all round the ring, nor that this height may not differ in different individuals of the same species.

The height at which the maximum length of the vessel-elements and the libriform fibres is attained varied in the different growth rings of the same tree. For example, in the oak the maximum length of these elements in 1925 ring (which was the 10th growth ring from the pith at a height of 6" in the bole) occurred at a height of between 6" and 6' from the ground, whereas in the 1955 ring (which was the 40th ring from the pith at the same height, 6") the maximum length was observed at a height between 6' and 12'. Similar variation is observed in the beech, sycamore and robinia (See table, 10). Hence the height in the bole at which the maximum length of the elements of

wood is attained varies, being higher in those growth rings nearer the bark than in those nearer the pith.

O A K

| Height | Ring 1925-26 | | | | Ring 1939-40 | | | | Ring 1955-56 | | | |
|--------|--------------|-------|------|------|--------------|-------|------|------|--------------|-------|------|------|
| | W.E. | F. | F.T. | T. | W.E. | F. | F.T. | T. | W.E. | F. | F.T. | T. |
| 0'-6" | .470 | 1.082 | .739 | .497 | .475 | 1.223 | .810 | .526 | .555 | 1.378 | .839 | .560 |
| 6'-0" | .396 | 1.014 | .705 | .474 | .541 | 1.276 | .913 | .576 | .606 | 1.408 | .949 | .622 |
| 12'-0" | — | — | — | — | .463 | 1.223 | .868 | .531 | .561 | 1.395 | .941 | .600 |
| 18'-0" | — | — | — | — | .456 | 1.122 | .804 | .495 | .547 | 1.351 | .930 | .593 |

STAGHORE

| | Ring 1922-23 | | Ring 1936-37 | | Ring 1950-53 | |
|--------|--------------|------|--------------|------|--------------|------|
| | Wes. | Pr. | Wes. | Pr. | Wes. | Pr. |
| 1'-0" | .338 | .651 | .335 | .818 | .372 | .674 |
| 7'-6" | .368 | .695 | .388 | .834 | .433 | .902 |
| 13'-6" | .347 | .689 | .363 | .782 | .415 | .911 |
| 20'-3" | .339 | .596 | .351 | .867 | .410 | .859 |

BEOCH

| | | | | | | |
|--------|------|-------|------|-------|------|-------|
| 1'-4" | .492 | 1.102 | .501 | 1.229 | .546 | 1.357 |
| 5'-5" | .389 | .535 | .545 | 1.281 | .575 | 1.357 |
| 16'-3" | --- | --- | .507 | 1.193 | .544 | 1.269 |
| 25'-3" | --- | --- | .439 | 0.960 | .488 | 1.248 |

ROBINIA

| | | | | | | |
|--------|------|-------|------|-------|------|-------|
| 1'-6" | .204 | 1.053 | .197 | 1.085 | .198 | 1.105 |
| 10'-9" | .196 | 1.065 | .201 | 1.123 | .204 | 1.159 |
| 20'-0" | .215 | 1.006 | .211 | 1.123 | .218 | 1.194 |
| 29'-3" | .207 | 0.800 | .209 | 1.079 | .210 | 1.153 |

TABLE 10. Variation upwards in known growth rings in OAK, SYCAMORE, BEECH and ROBINIA.

O A K

| Height | Ring 1925-26 | | | | Ring 1939-40 | | | | Ring 1955-56 | | | |
|--------|--------------|-------|------|------|--------------|-------|------|------|--------------|-------|------|------|
| | V.E. | F. | F.T. | T. | V.E. | F. | F.T. | T. | V.E. | F. | F.T. | T. |
| 0'-6" | .470 | 1.082 | .739 | .497 | .475 | 1.223 | .810 | .526 | .555 | 1.375 | .839 | .560 |
| 6'-0" | .396 | 1.014 | .705 | .474 | .541 | 1.276 | .913 | .576 | .606 | 1.408 | .949 | .622 |
| 12'-0" | — | — | — | — | .463 | 1.223 | .868 | .531 | .561 | 1.395 | .941 | .590 |
| 18'-0" | — | — | — | — | .456 | 1.122 | .804 | .495 | .547 | 1.351 | .930 | .593 |

SYCAMORE

| | Ring 1922-23 | | Ring 1936-37 | | Ring 1952-53 | |
|--------|--------------|------|--------------|------|--------------|------|
| | Ves. | Fr. | Ves. | Fr. | Ves. | Fr. |
| 1'-0" | .338 | .651 | .335 | .818 | .371 | .874 |
| 7'-0" | .368 | .695 | .388 | .834 | .433 | .902 |
| 13'-6" | .347 | .689 | .363 | .782 | .411 | .911 |
| 20'-3" | .339 | .596 | .351 | .867 | .410 | .885 |

BEECH

| | | | | | | |
|--------|------|-------|------|-------|------|-------|
| 1'-4" | .492 | 1.102 | .521 | 1.229 | .546 | 1.337 |
| 8'-3" | .389 | .535 | .545 | 1.281 | .576 | 1.337 |
| 16'-3" | --- | --- | .507 | 1.193 | .544 | 1.269 |
| 25'-3" | --- | --- | .439 | 0.960 | .488 | 1.248 |

ROBINIA

| | | | | | | |
|--------|------|-------|------|-------|------|-------|
| 1'-6" | .204 | 1.053 | .197 | 1.085 | .198 | 1.105 |
| 10'-9" | .196 | 1.065 | .201 | 1.123 | .204 | 1.159 |
| 20'-0" | .216 | 1.006 | .211 | 1.123 | .218 | 1.194 |
| 29'-3" | .207 | 0.800 | .209 | 1.079 | .210 | 1.153 |

A comparative study of the length of the vessel-elements and of the libriform fibres in different parts of the same tree was made in all the four species. For this purpose wood from the outermost growth ring (1956) and from that of the second growth ring from the pith was used from the following parts:

| 2 year old twig | |
|---|-----------------------------|
| Twig (2 Rings) | 25 " " branch |
| From four different heights in the bole | |
| Branch (25 Rings) | From three " levels " root. |

The results are given in the tables 11 and 12 where each figure represents the mean value in millimeters of 50 measurements, taken at random from macerations.

Table 11 gives the lengths of the vessel-elements and the libriform fibres of the same growth ring in different parts of the tree. It will be observed from this table, that these elements are shortest in the twigs, and the longest in the roots, while those of the bole are longer than those of the branch.

Similarly, the vessel-elements and the libriform fibres of the second growth ring in the different

TABLE 11. Variation in length of the vessel-elements and libriform fibres in the outermost growth ring in different parts of oak, beech, sycamore and robinia.

| | Oak | | Beech | | Sycamore | | Robinia | |
|----------------------|------|-------|-------|-------|----------|-------|---------|-------|
| | V.E. | Fib. | V.E. | Fib. | V.E. | Fib. | V.E. | Fib. |
| Twig (2 Rings) | .222 | .310 | .307 | .611 | .240 | .446 | .172 | .416 |
| Branch (25 Rings) | .487 | 1.105 | .482 | .928 | .330 | .710 | .185 | .936 |
| Bole | | | | | | | | |
| D _I | .555 | 1.375 | .546 | 1.337 | .344 | .857 | .198 | 1.105 |
| D _{II} | .606 | 1.408 | .593 | 1.337 | .437 | .916 | .202 | 1.166 |
| D _{III} | .528 | 1.401 | .548 | 1.267 | .425 | .868 | .218 | 1.194 |
| D _{IV} | .574 | 1.333 | .488 | 1.248 | .396 | .942 | .210 | 1.153 |
| Root | | | | | | | | |
| R _I | .539 | 1.415 | .657 | 1.532 | .501 | 1.006 | .251 | 1.719 |
| R _{II} | .452 | .806 | .711 | 1.443 | .458 | .865 | .245 | 1.687 |
| R _{III} | -- | -- | .683 | 1.468 | .528 | 1.001 | .410 | .670 |

TABLE 12. Variation in length of vessel-elements and libriform fibres in the 2nd growth ring from pith of different parts of oak, beech, sycamore and robinia.

| | Oak | | Beech | | Sycamore | | Robinia | |
|----------------------|------|-------|-------|-------|----------|------|---------|-------|
| | V.E. | Fib. | V.E. | Fib. | V.E. | Fib. | V.E. | Fib. |
| Twig (2 Rings) | .222 | .310 | .370 | .501 | .240 | .446 | .172 | .416 |
| Branch (25 Rings) | .362 | .834 | .376 | .524 | .285 | .465 | .195 | .482 |
| Bole | | | | | | | | |
| D _I | .350 | .684 | .393 | .496 | .224 | .453 | .254 | .493 |
| D _{II} | .409 | .763 | .389 | .535 | .323 | .570 | .179 | .614 |
| D _{III} | .430 | .828 | .361 | .568 | .285 | .475 | .195 | .418 |
| D _{IV} | .273 | .572 | .344 | .656 | .319 | .477 | .218 | .546 |
| Root | | | | | | | | |
| R _I | .464 | 1.060 | .430 | .709 | .437 | .761 | .289 | 1.276 |
| R _{II} | .400 | .675 | .566 | .962 | .421 | .624 | .201 | 1.107 |
| R _{III} | -- | -- | .592 | 1.214 | .483 | .800 | .355 | .485 |

parts of these trees showed the same type of variation as that exhibited by those of the growth ring 1956. In studying the second growth ring from the pith, the actual growth rings examined were:

| | <u>Oak</u> | <u>Beech</u> | <u>Sycamore</u> | <u>Robinia</u> |
|---------------------|------------|--------------|-----------------|----------------|
| Twig | 1956 | 1956 | 1956 | 1956 |
| Branch | 1933 | 1933 | 1933 | 1933 |
| Bole D _I | 1917 | 1920 | 1914 | 1895 |
| D _{II} | 1921 | 1929 | 1915 | 1899 |
| D _{III} | 1927 | 1931 | 1917 | 1903 |
| D _{IV} | 1935 | 1940 | 1921 | 1911 |
| Root R _I | 1930 | 1930 | 1922 | 1898 |
| R _{II} | 1949 | 1950 | 1934 | 1922 |
| R _{III} | -- | 1954 | 1942 | 1950 |

It is evident from these two methods of study of the growth rings that the initial as well as the maximum length of the vessel-elements and the libriform fibres is different in the different parts of the bole. Further, if it is accepted that the length of the vessel-elements gives the indication of the length of the fusiform initials of the vascular cambium, then these latter vary in length, increasing through the successive growth rings at any one height and attaining to different maxima in twig, branch, bole and root.

(c) Variation within one growth ring: The variation in length of the vessel-elements and libriform fibres in different parts of one growth ring, at one level, was investigated in the bole of all the four trees and in the roots of oak and sycamore. For the investigation care was taken to examine these elements, as nearly as possible, along one radius and not indiscriminately. Specimens from three positions (six in sycamore bole) were selected from each growth ring under examination: (1) from the first-formed wood, (2) from the middle of the ring and (3) from the last-formed wood. Measurements of the lengths of 50 vessel-elements and 50 libriform fibres made at random from macerations are shown in table 13, where each figure represents the mean value in millimeters.

It will be observed from the table 13, that the vessel-elements and the libriform fibres are shorter in the early wood of a growth ring than in the late wood in the bole of all the trees and in the roots of the oak and sycamore. The relative difference in length of these elements between the early-formed wood and late-formed wood of a ring varied in the bole of the different trees and also in the bole and

TABLE 13. Variation in the vessel-element and fibre lengths within one growth ring between the early-formed spring wood and lateformed summer wood in OAK, SYCAMORE, BEECH and ROBINIA.

| Name of the Tree | BOLE | | | ROOT | | |
|------------------|-------------|-----------|--------|-------------|-----------|--------|
| | Growth ring | Ves. Ele. | Fibres | Growth ring | Ves. ele. | Fibres |
| OAK | 1944-45 | .568 | 1.414 | 1954-55 | .502 | 1.240 |
| | | .388 | 1.128 | | .389 | 1.063 |
| | 1945-46 | .474 | 1.249 | 1955-56 | .455 | 1.145 |
| | | .591 | 1.399 | | .491 | 1.078 |
| | 1946-47 | .410 | 1.113 | 1956-57 | .412 | 1.078 |
| SYCAMORE | 1930-31 | .389 | .825 | 1955-56 | .470 | .928 |
| | | .358 | .731 | | .441 | .819 |
| | | .350 | .725 | 1956-57 | .466 | .889 |
| | 1931-32 | .363 | .734 | | .476 | .939 |
| | | .364 | .780 | 1957-58 | .454 | .806 |
| | | .356 | .795 | | | |
| | | .373 | .746 | | | |
| | 1932-33 | .365 | .746 | | | |
| BEECH | 1947-48 | .612 | 1.323 | | | |
| | | .504 | 1.080 | | | |
| | 1948-49 | .527 | 1.130 | | | |
| | | .607 | 1.308 | | | |
| | 1949-50 | .493 | 1.071 | | | |
| ROBINIA | 1942-43 | .204 | 1.075 | | | |
| | | .157 | 0.931 | | | |
| | 1943-44 | .181 | 1.013 | | | |
| | | .191 | 1.087 | | | |
| | 1944-45 | .154 | 0.919 | | | |

root of the same individual (Table, 14). This difference was greater in the bole of the ring porous oak than

TABLE 14. Difference in length between the early and late wood elements expressed as percentage of length of early wood elements.

| | <u>BOLE</u> | | <u>ROOT</u> | |
|--------------------|-------------|-------------|--------------------|-------------|
| | <u>V.E.</u> | <u>Fib.</u> | <u>V.E.</u> | <u>Fib.</u> |
| Oak (1945) | 52% | 24% | Oak (1955) | 26% 18% |
| Beech (1948) | 20% | 21% | ----- | --- --- |
| Sycamore (1931) | 4% | 11% | Sycamore (1956) | 8% 15% |
| Robinia (1943) | 22% | 17% | ----- | --- --- |

in the diffuse porous beech and sycamore. It is particularly remarkable in sycamore for woods of the genus Acer show very even growth throughout the ring. However, the type of variation observed in all the four trees in the present investigation is essentially the same, irrespective of whether the vascular cambium is stratified or not.

The difference in length of the vessel-elements in a growth ring in the bole of oak, about 52%, is

much greater than that of the other trees, as might be expected from the large size of the vessels in the pore ring. In robinia, although the vessels of a pore ring are as large as those of oak, the difference in length of the vessel-elements between the early and late wood of a ring in the bole is smaller than those of the latter (see below).

The libriform fibres show (Table, 14) a similar type of variation to that of the vessel-elements, in all the four trees, irrespective of whether the vascular cambium is stratified or not. These elements are much longer than the vessel-elements at any position in a growth ring.

The vessel-elements in a growth ring of the dicotyledons, especially those in which the secondary xylem is more specialised structurally, are supposed to have approximately the same length as the cambial initials from which they are derived (Bailey, 1920). The distinct difference in length of the vessel-elements within a ring between the early and the late wood, as observed in the present investigation, may be due to the shortening of the early-formed vessel-elements as a result of varying degrees of distension.

This shortening of the vessel-elements in the early wood is more marked in the ring porous woods than in the diffuse porous and is more in the bole than in the root. The mean values given in the table 15, of the radial and tangential diameters of the vessels of the corresponding growth rings in which the variation was studied, indicate that in the ring porous oak and robinia the radial diameters of the vessels in the early wood are nearly 350% to 400% greater than those of the late wood vessels.

TABLE 15. Difference in radial and tangential diameters of the early and late wood vessels expressed as percentage of diameters of the late wood vessels.

| | <u>Radial Diameter.</u> | <u>Tangential Diameter.</u> |
|-------------|-----------------------------|---------------------------------|
| <u>BOLE</u> | | |
| Oak | 382% | 385% |
| Beech | 33% | 19% |
| Sycamore | 18% | 12% |
| Robinia | 394% | 360% |
| <u>ROOT</u> | | |
| Oak | 50% | 42% |
| Sycamore | 43% | 29% |

On the other hand, in the diffuse porous beech and sycamore there is comparatively little difference between the diameters of the early and

late wood vessels. In beech the radial diameter of the early wood vessels is about 33% and in sycamore about 18% more than those of the late wood vessels.

The difference in the diameters of the vessels in the early and late wood of a growth ring in the roots of oak and sycamore is smaller (Table, 15).

It would seem that the considerable lateral swelling of the vessel-elements produces a corresponding shortening of these cells (Priestley 1930, and Chalk and Chattaway 1935), as might well happen in extensible elastic walls. Such shortening might account for the difference in length of the vessel-elements of the early and late wood of a growth ring observed in the present investigation in all the four trees; indeed this is believed by the writer to^{be} the explanation of the phenomenon.

It is remarkable that in robinia the difference in length of the early and late wood vessel-elements in a growth ring is considerably less than that in oak (Table, 14), although the difference in the diameters of the early and late wood vessels is greater in robinia than in oak (Table, 15). Hence the suggestion that

the difference in length is to be accounted for by a shortening of the early wood element as it becomes distended transversely, needs further consideration.

Two possible explanations may be advanced either or both of which may account for this apparent anomaly.

1. That, apart from the fluctuations within a ring (cf. p.27) the fusiform initials in oak are gradually increasing in length from the pith outwards at any one height for a considerable number of years, so that in any one ring the initial from which a vessel-element of the earliest formed wood is derived, is shorter than that giving rise to an element at the end of the ring. In robinia, on the other hand, the length of the fusiform initial, as judged from the average length of the vessel elements of a ring remains remarkably constant from ring to ring (cf. Fig.1) and hence it may be assumed that the first and last formed vessel-elements of a ring arise from fusiform initials of the same length.

2. That there is a difference in the pitting of the vessel-element may make a difference in the amount of stretching which can occur before there is a com-

compensating decrease in length. (which are also the derivatives of these initials) were about 4 to 3 times as long as the vessel-elements.

In oak the pits are irregularly distributed, and not always very close to one another, so that there are areas of wall devoid of pits. In robinia the pits are very closely packed and no areas of wall devoid of pits have been observed. It seems not unreasonable to suggest that robinia has in consequence a greater area, occupied by pits or primary pit fields, which is more extensible than the rest of the wall and consequently that in the vessels of this tree length of the elements is less affected by their dilation than in oak.

Unfortunately, time did not permit of full investigation of these two points so that they are advanced very tentatively as possible explanations of the differences. graphically represented in figures 3-6.

The variation in length of the libriform fibres, on the other hand, appears to have been brought about by an altogether different factor. These fibres show different degrees of elongation in the early and late wood of a ring in the four trees studied. For example in robinia, assuming that the length of the vessel-elements indicate an approximate length of the fusiform

initials, the libriform fibres (which are also the derivatives of these initials) were about 4 to 5 times as long as the vessel-elements.

The proportionate increase in length of the libriform fibres as between the early and late wood of a ring may be due to a strong intrusive growth taking place on either end of the derivatives of the vascular cambium during differentiation (Figs. 14-16). These fibres, as shown in the figures 14 and 15, possess the same body length as that of the strand parenchyma, and possibly due to the strong intrusive growth from either end, are transformed into long libriform fibres.

The variation observed in the vessel-elements and the libriform fibres between the early and late wood of a ring is graphically represented in figures 3-8. In each of these figures, the mean length of these elements is plotted against the width of the ring in millimeters. The limits of the particular ring under examination are indicated by broken lines. The points in each of the graphs represent the exact position in the growth ring from which these elements are measured. Figures 3 and 4 represent the variation

in a growth ring in the bole and root of oak, figure 5 that of the bole of beech, figures 6 and 7 those of the bole and root of sycamore and figure 8 that of the bole in robinia.

From these figures it will be observed that the increase in length of the vessel-elements and the libriform fibres is gradual from the early wood to the late wood in a growth ring. From the number of samples taken in each of these rings, it is not possible to indicate exactly where the different elements of wood attained maximum length in that particular ring. However, the graphs in the figures 3-8 indicate that these elements were longest beyond the middle of the growth ring.

There is a distinct decrease in the length of these elements in the transition from the late wood of one growth ring to the early wood of the succeeding growth ring. As the elements of the late wood of one growth ring and the early wood of the succeeding ring sometimes occurred in the same 80 μ tangential longitudinal sections, it was not possible to observe whether the decrease in length of the vessel-elements and the libriform fibres was gradual or sudden from

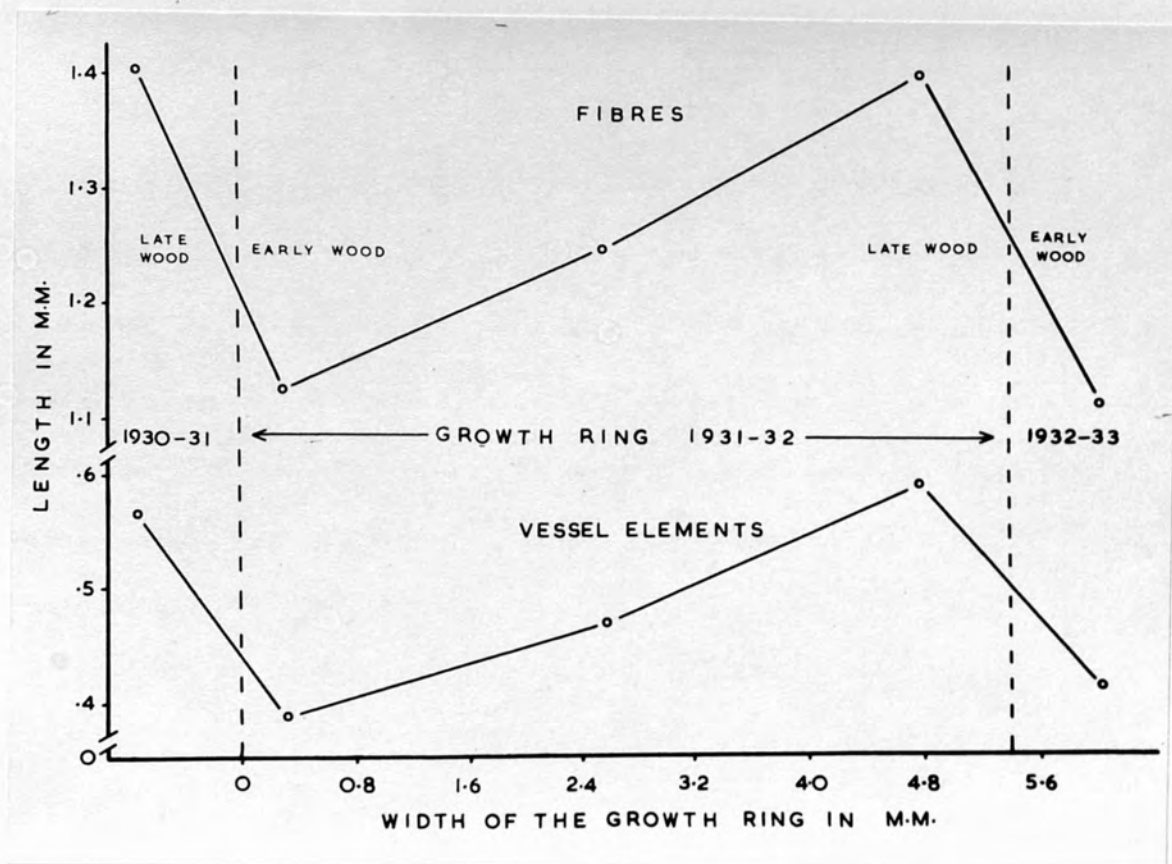


Fig. 3. *Quercus robur*. Variation in vessel-element and fibre length within one growth ring in the bole.

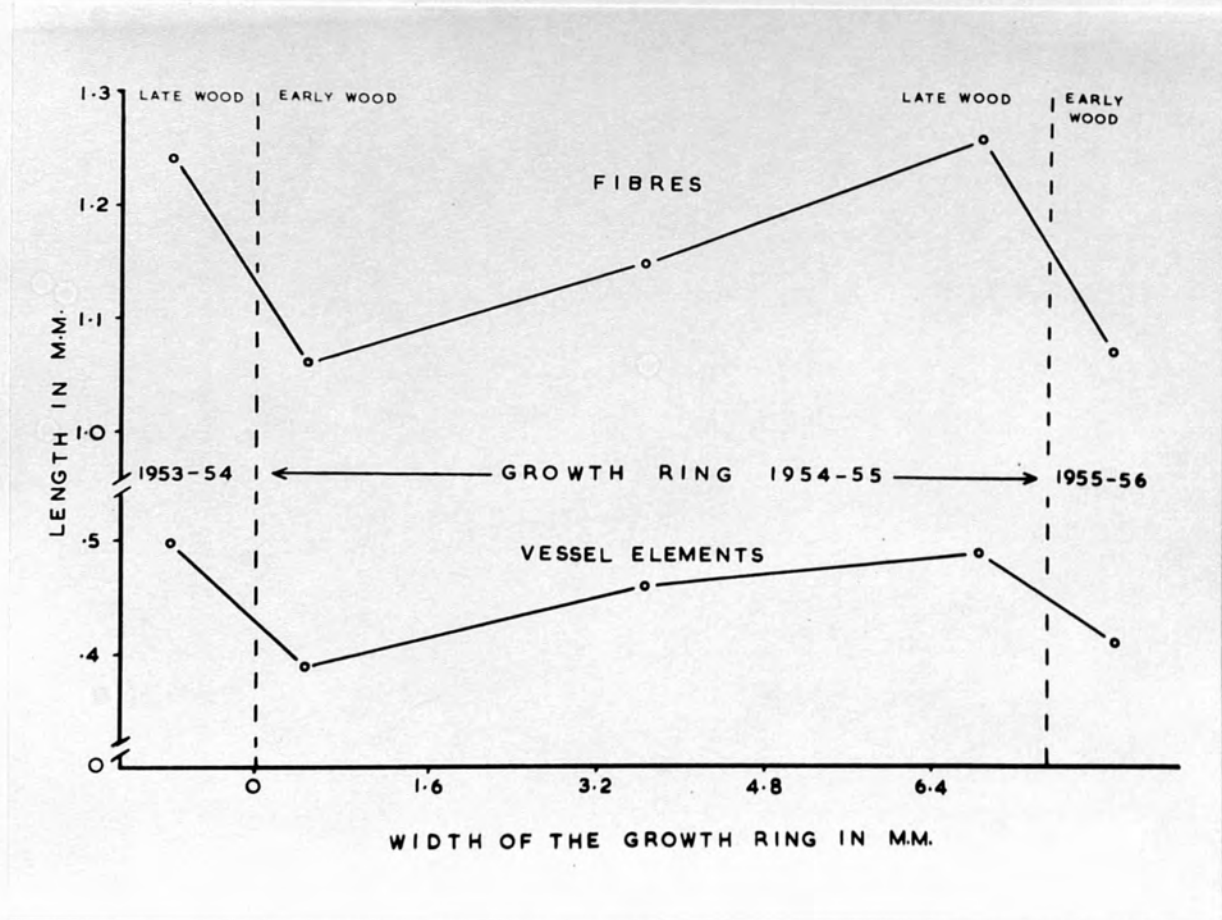


Fig. 4. *Quercus robur*. Variation in vessel-element and fibre length within one growth ring in the root.

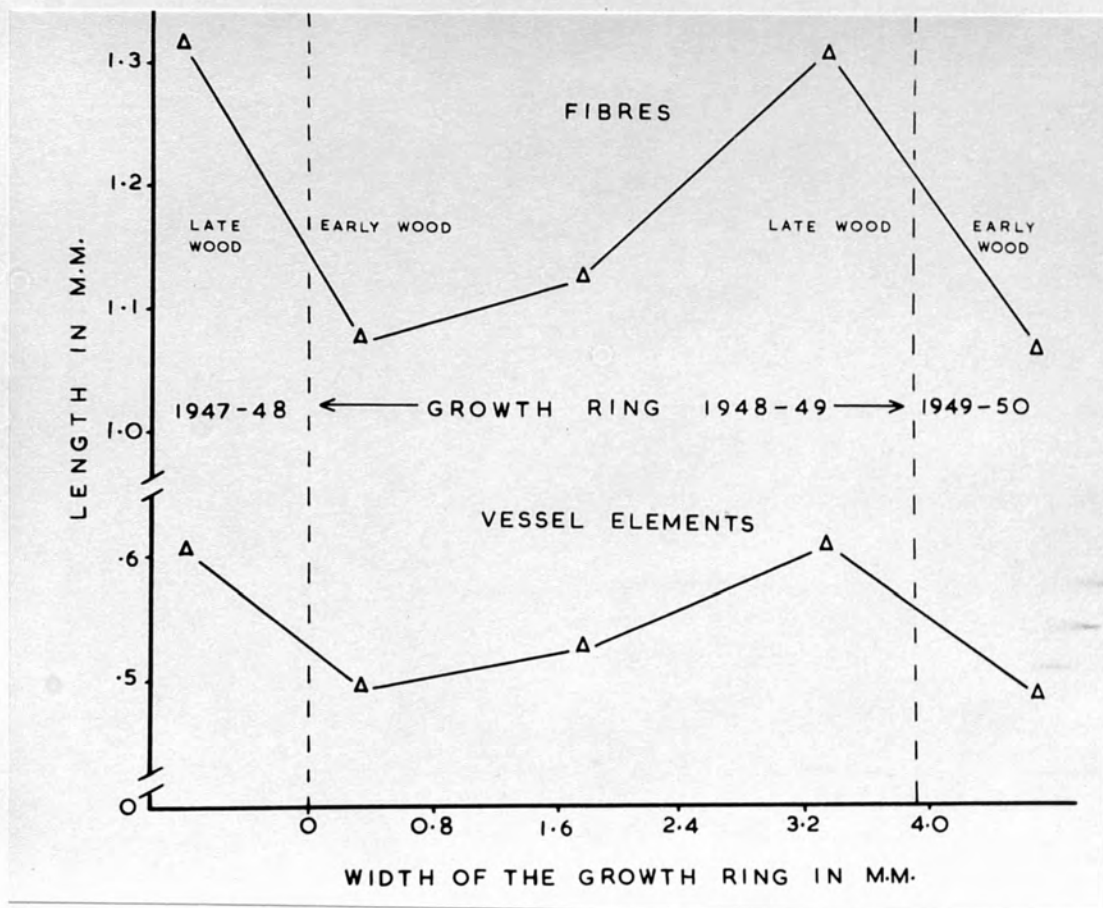


Fig. 5. *Fagus sylvatica*. Variation in vessel-element and fibre length within one growth ring in the bole.

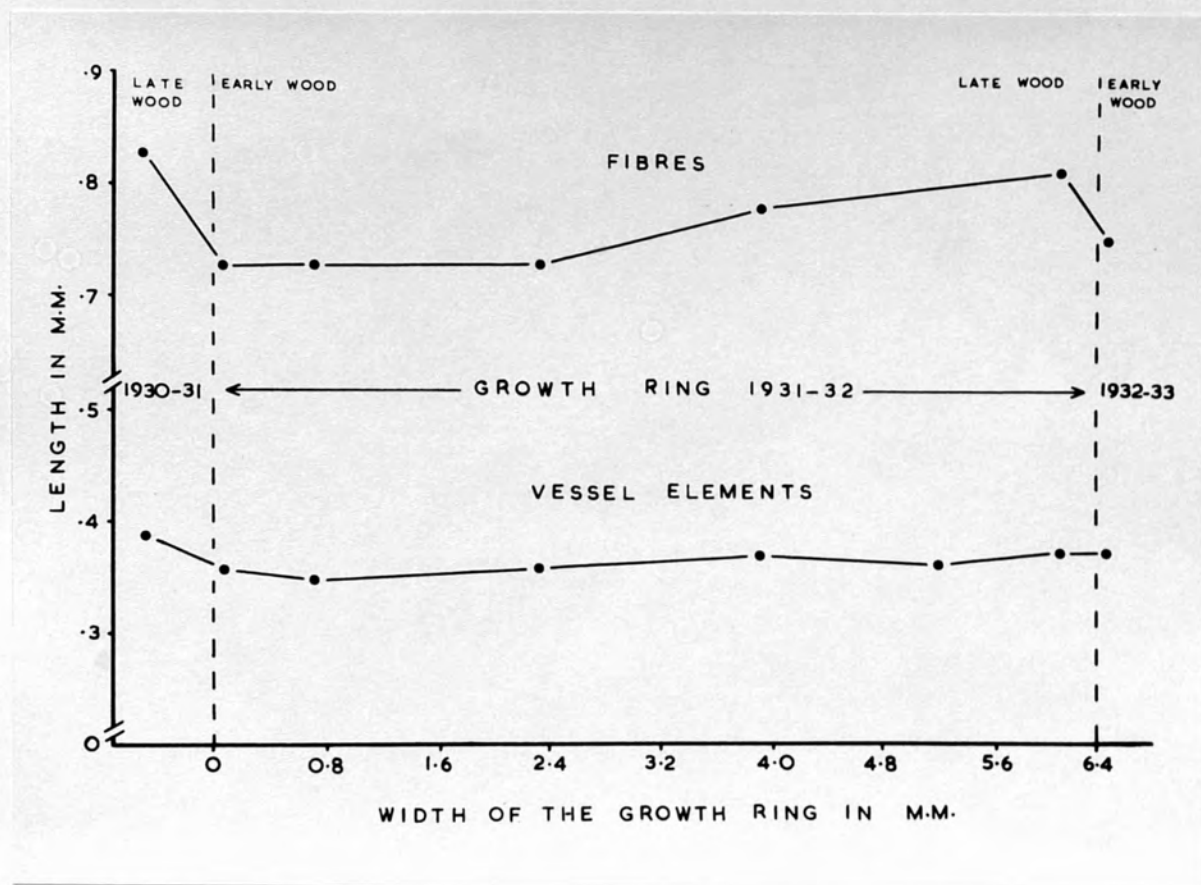


Fig. 6. Acer pseudoplatanus. Variation in vessel-element and fibre length within one growth ring in the bole.

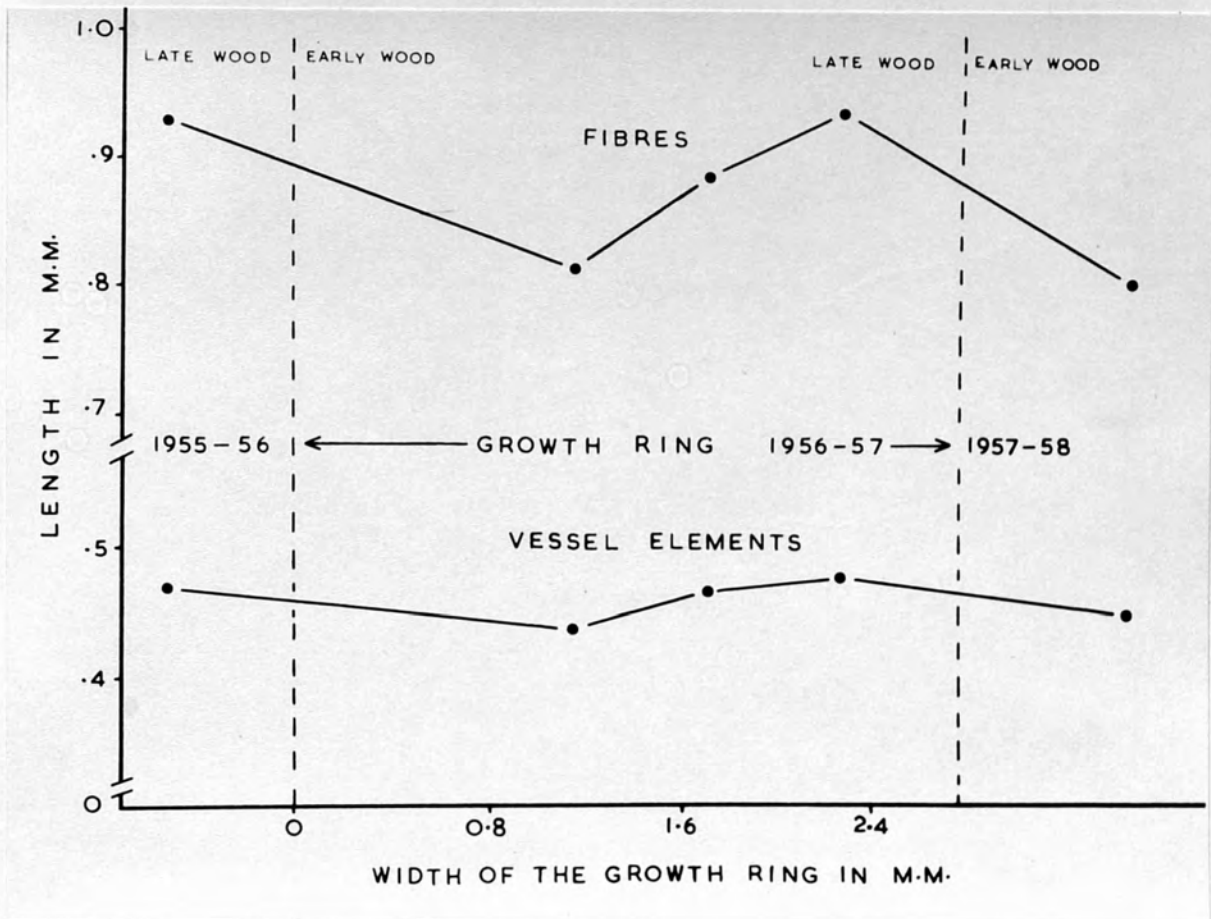


Fig. 7. Acer pseudoplatanus. Variation in vessel-element and fibre length within one growth ring in the root.

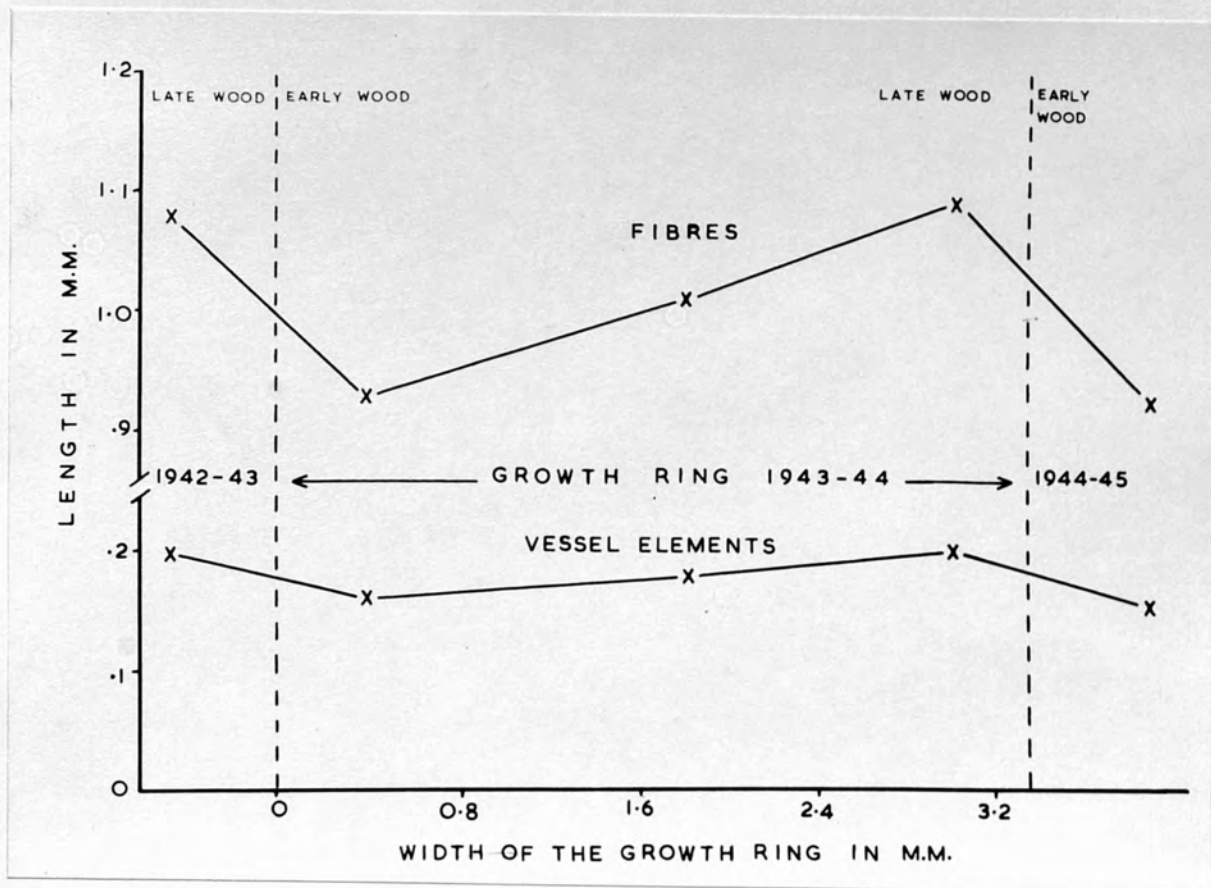


Fig. 8. *Robinia pseudoacacia*. Variation in vessel-element and fibre length within one growth ring in the bole.

(d) Variation around the stem: Variation in the length of the vessel-elements and the libriform fibres has so far been considered in the successive growth rings from the inner to the outer--due to decrease in length of these elements is generally rather abrupt from the last-formed late wood of one ring to the first-formed early wood of the succeeding ring both in the bole and root. However, a comparison on the variation in the length of these elements in certain growth rings on the opposite side (north radius) of the bole at the different levels was made in oak and sycamore. The results are given in table 16. Each figure in the table represents the mean value in millimeters of fifty measurements taken at random.

It is evident, from the data given in the table 16, that there is little variation in the length of the vessel-elements and libriform fibres in the growth rings studied on the two radii at any one level in the bole. This may indicate that results obtained for one radius will apply generally for the other radii as well, but it is realised that much more work is necessary on this aspect of the investigation before any generalisation would be justified. Unfortunately time did not allow of a fuller investigation.

(d) Variation around the stem: Variation in the length of the vessel-elements and the libriform fibres has so far been considered in the successive growth rings from pith outwards on one radius--due south--at different levels, in the boles of all the trees. However, a comparison on the variation in the length of these elements in certain growth rings on the opposite side (north radius) of the bole at the different levels was made in oak and sycamore. The results are given in table 16. Each figure in the table represents the mean value in millimeters of fifty measurements taken at random.

It is evident, from the data given in the table 16, that there is little variation in the length of the vessel-elements and libriform fibres in the growth rings studied on the two radii at any one level in the bole. This may indicate that results obtained for one radius will apply generally for the other radii as well, but it is realised that much ^{more} work/is necessary on this aspect of the investigation before any generalisation would be justified. Unfortunately time did not allow of a fuller investigation.

TABLE 16. Variation in vessel-element and fibre lengths in particular growth rings on the north and south sides of the bole in OAK and SYCAMORE.

| Height | | Ring 6 from pith | | Ring 16 from pith | | Ring 24 from pith | | Outermost ring | |
|--------------------------------------|--------|------------------|-------|-------------------|-------|-------------------|-------|----------------|-------|
| | | North | South | North | South | North | South | North | South |
| O A K | | VESSEL-ELEMENTS | | | | | | | |
| | 0'-6" | .383 | .405 | .429 | .440 | .446 | .475 | .522 | .555 |
| | 6'-0" | .410 | .396 | .483 | .460 | .525 | .558 | .599 | .606 |
| | 12'-0" | .441 | .435 | .473 | .456 | .525 | .536 | ----- | ----- |
| | 18'-0" | .447 | .456 | .523 | .536 | ----- | ----- | ----- | ----- |
| | | FIBRES | | | | | | | |
| | 0'-6" | .905 | .961 | 1.070 | 1.110 | 1.177 | 1.223 | 1.221 | 1.321 |
| | 6'-0" | .994 | 1.014 | 1.180 | 1.122 | 1.371 | 1.320 | 1.504 | 1.408 |
| 12'-0" | 1.056 | 1.009 | 1.181 | 1.282 | 1.458 | 1.402 | ----- | ----- | |
| 18'-0" | 1.081 | 1.122 | 1.214 | 1.247 | ----- | ----- | ----- | ----- | |
| S Y C A M O R E | | VESSEL ELEMENTS | | | | | | | |
| | 1'-0" | .307 | .328 | .328 | .304 | .369 | .335 | .369 | .344 |
| | 7'-0" | .352 | .374 | .379 | .370 | .413 | .387 | .425 | .437 |
| | 12'-6" | .376 | .377 | .367 | .377 | .394 | .396 | .403 | .425 |
| | 20'-3" | .340 | .369 | .382 | .381 | .408 | .417 | .401 | .396 |
| | | FIBRES | | | | | | | |
| | 1'-0" | .637 | .747 | .765 | .709 | .858 | .818 | .881 | .857 |
| | 7'-0" | .686 | .671 | .761 | .796 | .828 | .819 | .876 | .916 |
| 12'-6" | .682 | .798 | .783 | .766 | .860 | .814 | .902 | .868 | |
| 20'-3" | .667 | .756 | .873 | .867 | .835 | .875 | .870 | .942 | |

(Each figure represents the mean value of fifty measurements, in millimeters)

TABLE 17. Variation in the radial and tangential diameters of the vessels

II. Variation in the radial and tangential diameters of the vessels

Variation in the radial and tangential diameters of the vessels was studied in the bole of sycamore and robinia. The diameters of the vessels were measured from canadabalsam mounts, in growth rings 1-5, 10 and in every 10th ring afterwards, on one radius, due south, at four different levels. The results obtained are given in the table 17, where each figure represents the mean value in millimeters of twenty five measurements. In both woods these diameters were taken from the early spring wood vessels, i.e. in sycamore the vessels in the first third of the growth ring and in robinia from the pore ring.

There is a marked increase in the diameters of the vessels in both these trees, in the successive growth rings from pith outwards. This increase is rapid through the first five to ten growth rings after which there is a more gradual increase. Both the radial and tangential diameters of the vessels show this increase. Owing to the age of the specimens it was not, unfortunately, possible to ascertain if this increase is continuous throughout the life of the tree.

TABLE 17. Variation in the radial and tangential diameters of the vessels in successive growth rings at different levels in the bole.

| Ring No. | D _I | | D _{II} | | D _{III} | | D _{IV} | |
|-------------------|----------------|------|-----------------|------|------------------|------|-----------------|------|
| | RD | TD | RD | TD | RD | TD | RD | TD |
| S Y C A M O R E . | | | | | | | | |
| 1 | .052 | .043 | .068 | .053 | .068 | .048 | .061 | .052 |
| 2 | .078 | .058 | .091 | .070 | .080 | .060 | .077 | .059 |
| 3 | .078 | .067 | .093 | .068 | .093 | .068 | .085 | .066 |
| 4 | .076 | .065 | .090 | .068 | .092 | .072 | .088 | .072 |
| 5 | .080 | .070 | .090 | .073 | .089 | .072 | .112 | .081 |
| 10 | .088 | .074 | .109 | .086 | .098 | .080 | .105 | .080 |
| 20 | .102 | .082 | .108 | .080 | .109 | .082 | .106 | .084 |
| 30 | .095 | .079 | .110 | .084 | .106 | .090 | .101 | .080 |
| 40 | .095 | .081 | .105 | .085 | .112 | .091 | -- | -- |
| R O B I N I A . | | | | | | | | |
| 1 | .100 | .082 | .079 | .064 | .087 | .063 | .082 | .064 |
| 2 | .135 | .120 | .129 | .107 | .138 | .115 | .134 | .105 |
| 3 | .174 | .156 | .194 | .177 | .192 | .162 | .156 | .137 |
| 4 | .208 | .185 | .212 | .179 | .230 | .179 | .169 | .135 |
| 5 | .238 | .215 | .203 | .168 | .221 | .168 | .217 | .180 |
| 10 | .224 | .203 | .254 | .233 | .284 | .217 | .266 | .217 |
| 20 | .256 | .208 | .260 | .210 | .290 | .246 | .282 | .230 |
| 30 | .275 | .227 | .300 | .244 | .287 | .250 | .292 | .239 |
| 40 | .274 | .232 | .300 | .268 | .309 | .271 | .293 | .262 |
| 50 | .287 | .220 | .320 | .250 | .326 | .272 | -- | -- |
| 60 | .273 | .246 | -- | -- | -- | -- | -- | -- |

The curves for both trees, in figure 9, suggest that constant dimensions may be attained. The radial diameters of the vessels were always greater than the tangential ones. But this observation may be more apparent than real, since tangential shrinkage of wood as it dries is always greater than radial shrinkage, and apart from normal drying out, of the disc from which the sections were taken, in the laboratory, dehydration of the sections in the preparation of balsam mounts may have exaggerated this differential shrinkage. The overall increase of the diameters of the vessels in the growth rings nearer the bark compared with those of the first formed growth rings was 307% on the radial diameter and 325% on the tangential in robinia and 115% and 112% respectively in sycamore.

In figure 9, the mean diameters of the vessels are plotted against the growth rings. The measurements were made in disc III, i.e. at 13' 6" from the ground in sycamore and 20' in robinia.

Variation in the radial and tangential diameters of the vessels also was investigated in robinia in one growth ring (ring 1956) from the base of the bole upwards at different levels. From the data of the

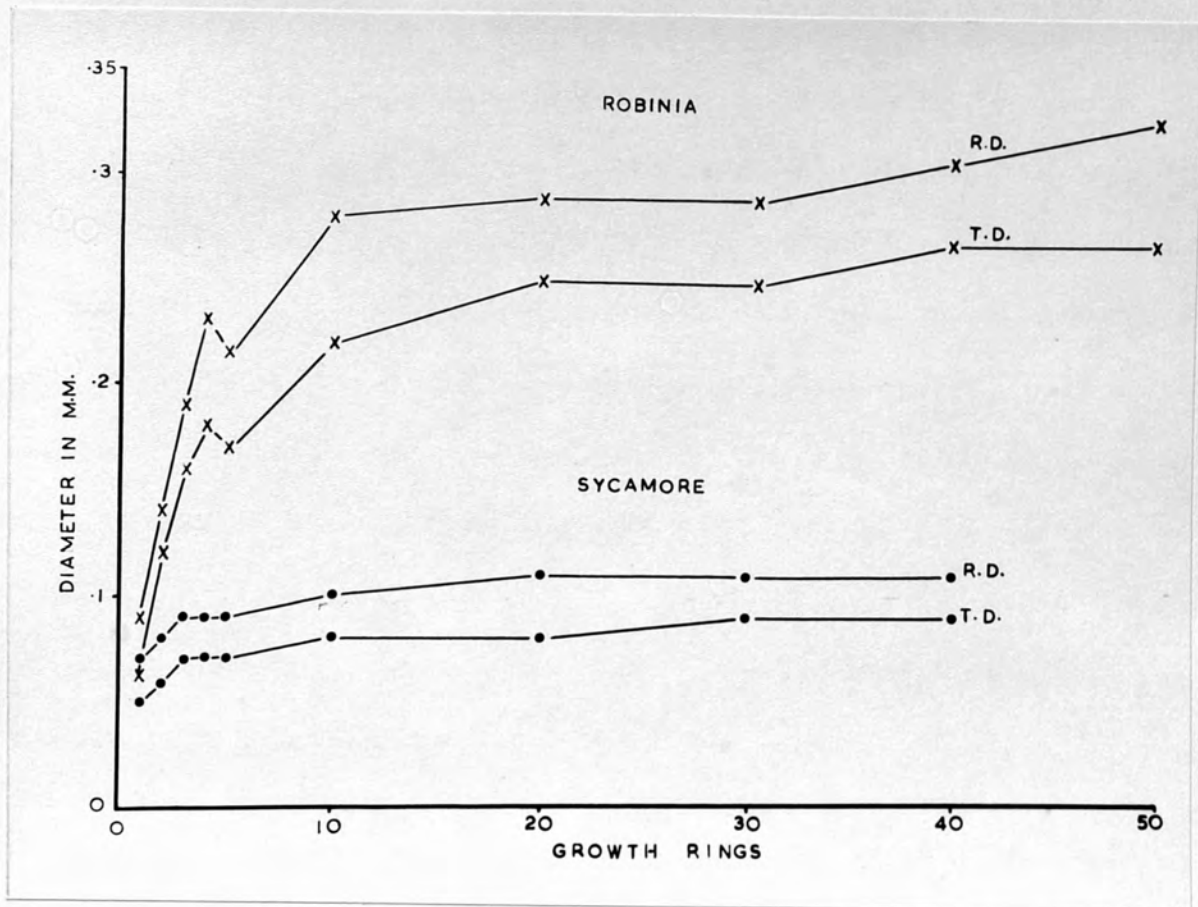


Fig. 9. Variation in the radial and tangential diameters of the vessels in successive growth rings from pith outwards in the boles of sycamore and robinia.

mean diameters given in the table 18, it is clear that there is a marked increase in the radial as well as the tangential diameters of the vessels of the same growth ring up to a particular height in the bole, after which there is slight decrease. This decrease is appreciable

TABLE 18. ROBINIA. Variation in the radial and tangential diameters of vessels in a specific growth ring (1956) at different levels in the bole.

| Height | Mean R.D. in mm. | Mean T.D. in mm. |
|------------------------------|---------------------|---------------------|
| D _I (1' 6") | .268 | .252 |
| D _{II} (10' 9") | .300 | .260 |
| D _{III} (20' --) | .331 | .288 |
| D _{IV} (29' 3") | .317 | .284 |

in D_{IV} in the radial diameter but very small on the tangential diameter and it is doubtful if the difference recorded for tangential diameters between discs III and IV can be regarded as of any significance. It would have been better if a further disc taken from a higher

level of the bole could have been investigated, but disc IV was taken at the top of the bole just before it forked.

III. Variation in the rays.

Variation in ray height and volume was studied in bole, branch and root of robinia. Robinia was preferred to the other three trees as the rays in the mature wood are mostly multiseriate, with only a few uniseriate ones, and are uniformly distributed, whereas, in the other three trees, they are of two distinct types (multiseriate and uniseriate) and their arrangement as seen in tangential section is more irregular.

HEIGHT: Ray height was measured from the tangential longitudinal sections of the second growth ring from the pith and then at regular intervals of one inch outwards towards the bark, at four different heights in the bole, and at one level each in the branch and the root. One hundred measurements were taken at each place and the mean values in millimeters are given in the table 19.

The average height of the rays was greater near the pith and 2nd growth rings) the rays were exclusively uniseriate but in the later growth rings with a few uniseriate ones. During this trans-

the bark than near the pith in all these organs.

TABLE 19. ROBINIA Variation in height of the rays from the centre towards the bark in the bole, branch and root wood.

| Ring 2 | Distance from the centre. | | | | | | | | | |
|-----------------------------|---------------------------|------|------|------|------|------|------|------|------|------|
| | 1" | 1.5" | 2" | 3" | 4" | 5" | 6" | 7" | 8" | |
| | mm | mm | mm | mm | mm | mm | mm | mm | mm | |
| <u>BOLE</u> | | | | | | | | | | |
| D _I (1' 6") | .421 | .348 | -- | .312 | .384 | .410 | .401 | .449 | .491 | .486 |
| D _{II} (10'9") | .331 | .309 | -- | .365 | .340 | .432 | .467 | .511 | -- | -- |
| D _{III} (20'--) | .422 | .312 | -- | .385 | .403 | .437 | .441 | .483 | -- | -- |
| D _{IV} (29'3") | .314 | .272 | -- | .341 | .390 | .436 | .440 | .462 | -- | -- |
| <u>ROOT</u> | | | | | | | | | | |
| R _I | .492 | .568 | .574 | .618 | -- | -- | -- | -- | -- | -- |
| <u>BRANCH</u> | | | | | | | | | | |
| | .252 | .259 | -- | -- | -- | -- | -- | -- | -- | -- |

In the "juvenile" wood (1st and 2nd growth rings) the rays were exclusively uniseriate but in the later growth rings/with a few uniseriate ones. During this trans-

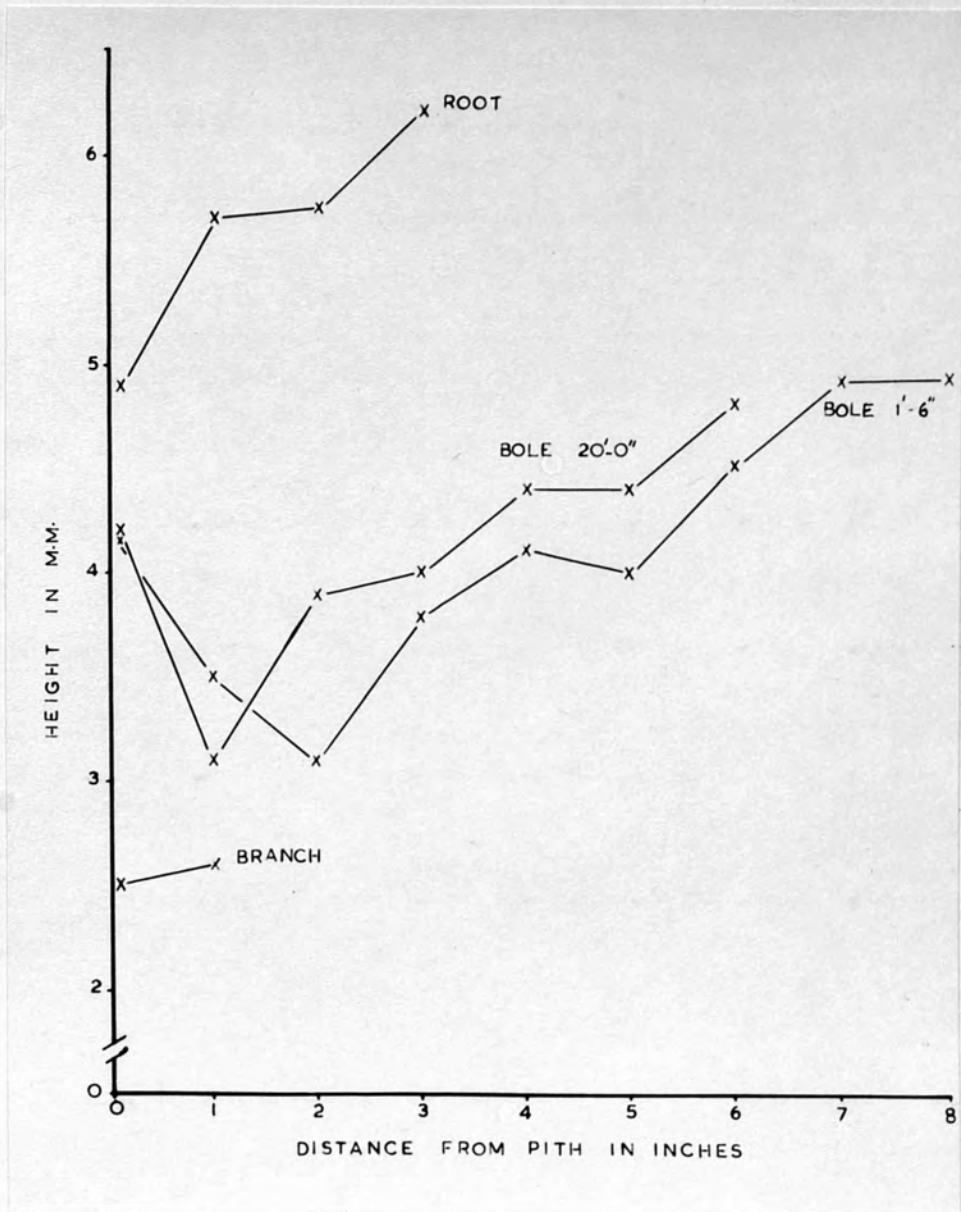


Fig. 10. *Robinia pseudoacacia*. Variation in height of the rays from centre outwards.

formation from uniseriate to multiseriate rays, there is a considerable decrease in the average height of the rays, but afterwards there is a steady but slow increase in height towards the bark at any one level in the bole. In the branch and root, however, this initial decrease in height of the rays is not noticed (Fig. 10).

The overall increase in ray height near the bark was about 55% in the bole and 26% in the root. In the branch the increase in ray height is very slight. The rays are higher in the root and lower in the branch than in the bole. The individual cells of the rays are larger in the root and smaller in the branch than in the bole (Fig. 11).

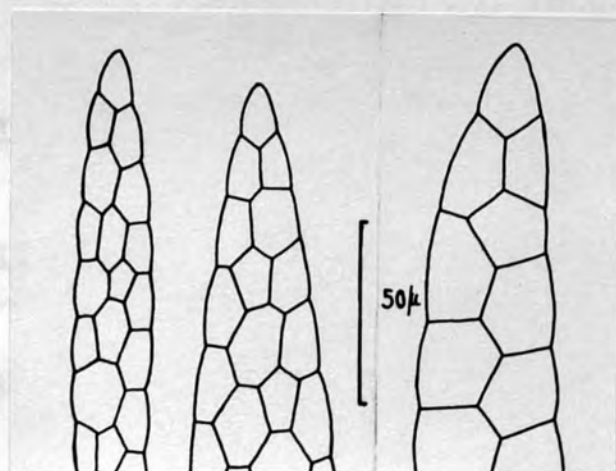


Fig. 11.

ROBINIA. Size of the cells of the rays.
(Left to Right--Branch, Bole, Root)

VOLUME: The percentage of a unit area of wood occupied by the ray tissue was determined by the weighing method (see page 20). Determinations were made in robinia at four levels in the bole and at one level in branch and root wood, from pith outwards, the results being given in table 20.

TABLE 20. ROBINIA. Variation in volume of the rays in the bole, branch and root.

| Height above ground. | Percentage of the Ray Area | |
|------------------------------|----------------------------|-------|
| | Inner (Ring 2) | Outer |
| <u>BOLE</u> | | |
| D _I (1' 6") | 11.84 | 21.33 |
| D _{II} (10' 9") | 8.57 | 18.08 |
| D _{III} (20' --) | 9.06 | 9.58 |
| D _{IV} (29' 3") | 9.18 | 9.27 |
| <u>ROOT</u> | | |
| R _I | 14.19 | 12.43 |
| <u>BRANCH</u> | | |
| (22 Rings) | 6.78 | 5.28 |

It is realised that volume determinations would have been preferable, but unfortunately no satisfactory method could be devised for measuring ray volume and it was assumed that the area occupied by ray tissue in a unit area could be regarded as proportional to the volume of ray tissue in a unit volume (see page 21).

These results indicate that the volume of the rays relative to the other elements of the wood, is at maximum in the base of the bole both near the pith and the bark. The sections from the lower part of the bole were 1' 6" above the base. At this level the volume of the rays increased from pith outwards by about 90%. A gradual decrease was observed in the ray volume upwards and outwards in the bole and ultimately at the top of the bole the volume of the rays was the same both near the pith and the bark (Fig. 12).

In the root the volume of the rays is higher near the pith than in the bole. On the contrary, the ray volume decreased from the centre outwards by about 14%. The greater volume of the rays is due to the larger size of the individual cells of the rays rather than the number of rays per unit area. The

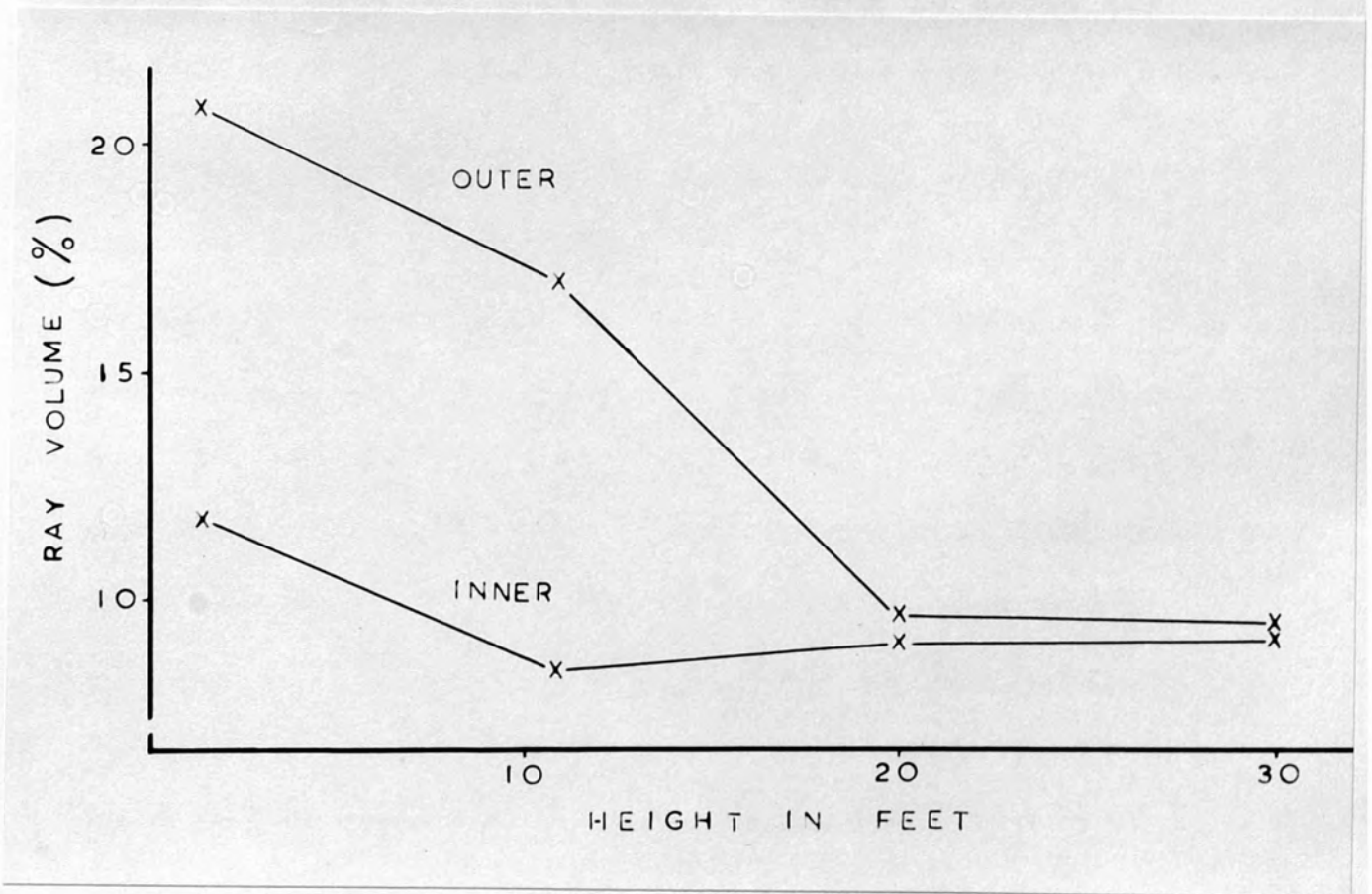


Fig. 12. Robinia pseudoacacia. Variation in ray volume in the bole at different levels.

volume of the rays is lowest in the branch in spite of the presence of the largest number of rays per unit area. This is thought to be due to the smaller size of the individual cells of the ray rather than the number of rays per unit area. There is about 16% decrease in the volume of the rays near the bark over that near the pith in the branch.

DISCUSSION.

It is clear that the several types of variation studied in the present investigation are not all due to the same cause. Variation in length of the vessel-elements and libriform fibres from the pith outwards along one radius is associated with the activity of the same fusiform initials throughout, i.e. with initials which originated at one time in the life of the tree. Variation in a single ring throughout the bole is, on the other hand, to be associated with the different fusiform initials, which have been formed over a long period in the life of the tree. Variation within a single ring at one level may be due to seasonal environmental effects on the differentiating wood tissue but it must also be related to the overall variation from pith to the bark, and this may be assumed also to apply to variation in the diameter of the vessels. Variation along different radii at one level, if it occurs, might be expected to be associated with differences in environment on different sides of the tree, but if gravitational effects differ, i.e., if the bole is not vertical, complexities probably involving the distribution of auxins and leading to the

localised formation of reaction wood, may also play a part. Variation in different parts of the tree--bole, branches and roots--would seem at first sight to be connected with the environment although there may be inherent differences in the primary meristems of roots and stems which through the vascular cambium produce, or help to produce, the differences. The causes underlying variation in the rays might be expected to be those affecting variation in the longitudinal elements. Unfortunately, there was not time to study the rays in as much detail as the longitudinal elements but their variation in the bole from the pith outwards at any one level, from the pith outwards at several levels and also their variation in the root, bole and branch wood were all investigated.

It will be evident that such a complex of factors cannot all be considered simultaneously, but in the following discussion an attempt has been made to integrate and group the types of variation as far as this appears possible.

Variation from pith outwards: Results obtained in the present investigation indicate that there is a

period of rapid initial increase in length of the vertical elements of the secondary xylem in the first few growth rings. This period of rapid increase in length of the vessel-elements and the libriform fibres was about 10-15 years in the oak, beech and sycamore and 20 years in the robinia, as compared with 20-25 years in Carya ovata (Pritchard and Bailey, 1916), 5-10 years in Fagus sylvatica, Populus serotina, Acer pseudoplatanus, Betula pubescens and Baikiaea pluri-juga (Desch, 1932) and 8-10 years in Eucalyptus regnans (Bisset and Dadswell, 1949). The duration of this period of rapid increase of the vertical elements of the secondary xylem, however, appears to be much longer in conifers. For example Lee and Smith (1916) report it as 50 years for Pseudotsuga taxifolia although Gerry (1916) states that it is 20 years in this tree and Pinus palustris, while Harlow (1927) finds the period of initial rapid increase to be up to 100 years in Thuja occidentalis. Bailey (1923) stated that the length of the longitudinal elements of the secondary xylem is largely dependent on that of the fusiform initials from which they are derived and, further, that these initials increase in length over the first 100 years in conifers and for about the first 50-60 years

in dicotyledons, after which their length remains constant.

(1955) observed that in these species of dicotyledons with starved structures, when the beech three of the four trees used (Oak, and sycamore) were less than 50 years old. However, it was observed that the vessel-elements and the libriform fibres increased in length through successive growth rings from pith, or centre outwards, at any one level in the bole, branches and roots of all the trees, with the exception of vessel-elements of robinia. No constant maximum length was attained by these elements, at any one level, in any of the trees studied except in robinia where the vessel-elements attained to a constant length in the younger growth rings. This remarkably constant length of the vessel-elements in robinia, at any one level in the bole, branches and roots, is probably due to the stratified cambium, where, according to Bailey (1923), the size of the fusiform initials remains almost constant at any one level in the life of the tree. On the other hand, the fibre lengths in all the four trees showed a similar type of variation in that there is an initial rapid increase in length and subsequent fluctuations in

the later growth rings at any one level in the bole, branches and roots. Chalk, Marstrand and Walsh (1955) observed that in three species of dicotyledons with storeyed structure, when due attention was paid to the position in the ring, "Neither the fibres nor the parenchyma strands showed any general tendency to increase in length from the pith outwards." This statement finds no support from the results obtained in the present investigation, in reference to variation of fibre length in robinia (Table, 7a) where the vascular cambium is also stratified.

In the present work variation of the vessel-elements and the libriform fibres, through successive growth rings from the pith outwards, has been attributed to the progressive increase in length of the fusiform initials of the vascular cambium from which these elements are derived (Bailey, 1923). He, further, stated that because the frequency of the anticlinal divisions and the elongation of the fusiform initials is not constant, the size of these initials fluctuates in different parts of a tree with non-stratified vascular cambium, while, on the other hand, no change in

length and configuration of these initials takes place in plants with a storeyed vascular cambium. Indeed, it is difficult to imagine how such a change could take place in a storeyed vascular cambium without disarranging the regularity of the vertical tiers of initials or involving buckling of their longitudinal walls.

Several explanations have been put forward regarding the principles involved in the elongation of the fusiform initials of the vascular cambium. For example, Priestley (1930) has suggested that normally occurring radial pressures in the expanding stems may cause an increased length of the fusiform initials from pith outwards. Further, from some of Bailey's data (1923) on Pinus strobus, he showed that elongation of the fusiform initials proceeds slowly, allowing ample time for gradual mutual adjustment of a "symplastic" nature. He concluded that not more than four successive anticlinal divisions would be necessary to produce the requisite number of initials in 60 years. However, the objections of Wardrop (1948) and Whalley (1950) appear to be important in this respect. Wardrop concluded that the radial pressures normally occurring

upon the growing cambium are not responsible for the progressive increase in length of the fusiform initials, but that this is to be attributed to the seasonal flow of growth hormones accompanying the opening of the buds and the resumption of apical growth. Whalley (1950) stated that the increase in girth of the cambium was not accomplished by an orderly and well regulated anticlinal division of the fusiform initials, as stated by Priestley, but by such rapid multiplication of the initials so as to produce a superfluity, if all survived.

Increase in length of the vessel-elements and the libriform fibres from pith outwards was observed to be more gradual nearer the base of the bole than at higher levels in the trees studied in the present work. This feature, which was also reported by Lee and Smith (1916), Chalk (1930) and Bisset and Dadswell (1949), is discussed subsequently (p.108).

In studying variation along a radius at one level in the bole of the oak and sycamore. This is probably due to the different environmental conditions prevailing in the locality in which the trees grew. On the other hand, it does not follow that differences in the environmental conditions in different parts of

relate this rapid increase to youthful vigour of the tree, for it is well known that growth is faster in the juvenile tree than when it becomes older. Similarly Lee and Smith (1916), MacMillan (1925) and Desch (1932) all associate the initial rapid increase in length of the vessel-elements and libriform fibres with the period of juvenile vigour and this is, in the opinion of the present author, a satisfactory explanation of the rapid initial increase in length of these elements. It should be observed, however, that in sycamore the overall increase in the vessel diameter is less than that of robinia. While there appears to be no simple explanation of this difference, it is possible that it represents an inherent difference between diffuse porous and ring porous woods.

It has been already stated that there was little difference in length of the vessel-elements and the libriform fibres of a ring on different radii at one level in the bole of the oak and sycamore. This is probably due to the uniform environmental conditions prevailing in the locality in which the trees grew. On the other hand, it does not follow that differences in the environmental conditions in different parts of

of the bole will necessarily produce visible differences in histological details of the secondary xylem. Bailey and Shepard (1915) and Chalk, Marstrand and Walsh (1955) have both proved that, where reaction wood is not present, there is no significant difference in fibre length on different radii in eccentric growth rings. Nevertheless, as found by Mell (1910) MacMillan (1925) and Harlow (1927), individuals inhabiting widely different environments may show considerable differences in the length of the longitudinal elements of their secondary xylem.

Variation of the rays in robinia, which showed a gradual increase in height and volume and decrease in number from pith outwards at any one level in the bole, is in agreement with the type of variation found by Essner (1883) and Bannan (1937) in some of conifers. On the other hand, Jaccard (1915) in Picea excelsa and Abies pectinata and De Smidt (1922) in Ulmus fulva*

* While the ray size, as given by De Smidt, may perhaps be used relatively indicate differences in different parts of the bole, it seems certain that the sizes given in his paper are erroneous. Thus Ulmus fulva is reported as having rays of a mean maximum height of 30.23 mm., and a minimum height of 14.59 mm., sizes out of all proportion to the size of elm rays. The present author examined a number of specimens of elm wood and found in authentic material of Ulmus fulva that the maximum height of the multiseriate rays was 0.449 mm.

reported another increase in number of rays higher up the bole in the crown, after a minimum was reached.

Comparison of the variation along one radius at one level in bole, branches and roots of oak, beech, sycamore and robinia showed that the vessel-elements and libriform fibres were shortest in the branches and longest in the roots, that branch wood vessels had the smallest diameters and the shortest and least bulky rays while the longest vessel diameters and tallest rays with the biggest volume were found in the root.

The present writer concludes that the different variations so far dealt with are related ultimately to the size of the cambial initials from which the wood has arisen. At a particular level the xylem cells, whatever their position on a radius, are all formed from the same initials, i.e. those which were formed when the vascular cambium became differentiated at the particular level in the tree. The initial rapid increase in length of the libriform fibres and vessel-elements is thought to be due to juvenile vigour, the fusiform initials enlarging rapidly and thus giving rise to larger derivatives. Although the rate of this

enlargement slows down it evidently continues for many years and in the material examined it is assumed that the increase had not ceased because the libriform fibres and vessel-elements became increasingly longer toward the periphery. The vessel-elements of robinia formed an exception for here a maximum size was reached in the second growth ring and after this the size remained constant. This has been related to the constant length of the fusiform initials which, in a stratified cambium, could not increase in length without disarrangement of the regular tiers of initials and a consequent loss of stratification. The libriform fibres of robinia, however, evidently increase considerably in length during differentiation, their ends pushing between the other elements and thus, for the libriform fibres the stratified arrangement is lost.

It might be argued that attention should be also given to the possibility that differentiation of the derivatives of the fusiform initials may not itself be constant and that a libriform fibre produced, in say the twentieth ring, may become longer than one produced in the second ring, even were the initial which produced both of them, to remain the same size.

Bailey's work (1920), however, shows that the size of the differentiated derivative does appear to be related to the size of the initial.

Considering variation along different radii at a particular level, the elements on different radii owe their origin to different fusiform initials, but, nevertheless, to initials which are all produced simultaneously in the life of the tree. It would not seem surprising, therefore, if they had a uniform length and this may explain the uniform length of the vessel-elements and libriform fibres in a ring but on different radii at one level.

The differences in length of the libriform fibres and of length and diameter of the vessel-elements in the bole, branch and root wood may be due to inherent differences in the cambial initials laid down by the apical meristems. The more uniform environment of the root and the variable environment of the branches may play its part, if indeed this may not be the main cause of the difference. It may not be without significance that the roots are nearest the water supply of the tree and the branches most remote from it.

and then decreases towards the top of the bole. It has already been stated that, for position, where the rays also are produced by the same ray initials and it might be expected that variation would be concerned with increase in cell size when, in fact it appears to be due to increase in cell number and presumably, therefore, in the number of ray initials. So far as the author knows, no attention has been given to the ray initials and to their behaviour as the cambium increases in age. Variation among the rays of root, bole and branch may probably be accounted for in the same manner as that just suggested for the longitudinal elements.

Variation within one growth ring was studied in all four trees, (1) vertically, at four different heights in the bole and (2) horizontally, when comparisons were made between the first and last formed wood of one ring and at the transition zone between the late wood of one ring and the adjacent early wood of the succeeding one.

Variation vertically: The present study, like many previous ones, has shown that in any one growth ring the vessel-elements libriform fibres increase in length from the base of the bole upwards to a maximum

and then decreases towards the top of the bole. It has already been stated that the position, where the maximum length of the vessel-elements and the libriform fibres occurs, is the highest in those rings furthest from the pith. Kribs (1928) in Pinus banksiana and Bisset and Dadswell (1949) in Eucalyptus regnans, have both demonstrated that there is a high correlation between age from the pith and the length of the tracheids, or fibres as the case may be, in their higher levels of the tree. Thus the two factors, age of the growth ring and height in the tree, appear to be responsible for the type of variation in specific growth rings at different levels. If, however, the rate of increase in length of these elements outwards from the pith were the same at all levels in the tree, one would expect that any definite age (i.e. number of growth rings) from the pith, the different elements of wood would be of constant length, irrespective of the height of the tree.

In attempting to explain the differences in length of the longitudinal elements of the secondary xylem in different parts of the bole and in the bole in relation to other parts of the tree, it is assumed

that the actual length of an element like a tracheid reflects the length of the fusiform initial from which it arises. During the early life of the tree, when growth is most vigorous, it has already been suggested that any fusiform initial gradually becomes larger, until, with slower growth of the tree it ceases to increase further in size. Further, during the period of greatest vigour of the tree, it might be supposed that successively larger fusiform initials would be laid down as new vascular cambium is formed, so that during this period, the fusiform initials nearest the apex of the part would be the longest and those nearest the base shortest, unless these latter with age had themselves increased in size. Consequently, longer elements would be produced nearer the top of the young tree in the first formed growth rings. Thus in any one growth ring the longitudinal elements would be longer the nearer one approached the apex. After this period of maximum vigour was past, the fusiform initials subsequently formed would be shorter, hence the smaller length of the derivatives at the top of the bole in the older trees and the corresponding decrease in length of these elements in a growth ring at higher

levels in the bole.

The steady decrease in length upwards in the tree, as reported by Hartig (1885) in Fagus sylvatica and Quercus robur and Pritchard and Bailey (1916) in Carya ovata, might possibly be due to sampling from the early wood at different heights in the tree rather than to any inherent differences in the species examined.

Variation within one ring horizontally: Results obtained in respect of variation in length of vessel-elements and libriform fibres in the early and late wood of a growth ring are in agreement with the type of variation noted by Bisset and Dadswell (1949), Bisset, Dadswell and Amos (1950) and Amos, Bisset and Dadswell (1950). These elements are distinctly longer in the last formed wood of a ring than in that laid down first.

The amount of elongation of fibres during differentiation, as observed in the present work, may vary in the different types of woods: that in the diffuse porous beech and sycamore is less and that in the ring porous robinia with stratified vascular cambium more

than that in the ring porous oak with non-stratified vascular cambium. For oak, beech and sycamore an increase in length of about 120% to 260% was observed in the last formed fibres of a ring as compared with that of the early formed fibres; Bisset and Dadswell (1950) reported an increase of 200%. In robinia this increase is about 600% to 800% as against an increase of 100% to 300% reported by Chalk, Marstrand and Walsh (1955) for woods with storeyed structure. As has been already stated the proportionate increase in length of the libriform fibres as between early and late wood of a ring may be due to strong intrusive growth from either end of the derivatives of the vascular cambium during differentiation.

In angiosperms Bisset and Dadswell (1950) attributed the variation in length of the libriform fibres within a growing season to a time factor. They suggest that there is not sufficient time for considerable elongation of the developing fibres in the early part of the season when the cambial initials divide more actively. They presume, on the other hand, that more time is available for extension growth as the season progresses and the cambium is less active.

It seems possible that the conditions during the period of active growth and metabolism at the beginning of the growing season may be most suited for the early lignification of the differentiating fibres and that the process of elongation of the fibres may be carried farther before lignification sets in as the season progresses, giving time for the formation of long narrow fibres in the late wood.

It has already been stated that the variation in length of the vessel-elements in the first and the last formed wood within a growth ring is essentially the same in storeyed and non-storeyed woods. The differences in length between the early and late wood vessel-elements (Table, 14) correlated with the increase in the radial and tangential diameters (Table, 15) suggest that these differences are mainly due to the shortening of the vessel-elements brought about by their considerable swelling or distension in the early wood, rather than elongation of those in the late wood. However, it is realised that in oak, beech and sycamore where the vascular cambium is not stratified, the fusiform initials increase in length between the beginning and end of a season's growth, thus bringing about

increased difference in length of these elements of the early and late wood. It seems reasonable to suggest that there may be no elongation of the vessel-elements in the late wood, for a vessel, at its inception, is a vertical chain of parenchyma cells, and if strand parenchyma shows no elongation within a ring (Chalk, Marstrand and Walsh, 1955), it would not be surprising if the vessel-elements behaved in the same way. Further, as shown in figure 32, the vessel-elements and the parenchyma strands are almost of the same length in the late wood of robinia, indicating that there was no elongation in the vessel-elements after they were derived from the fusiform initials.

It has often been recorded that there is a very sudden drop in fibre length from the last-formed late wood of one ring to the first-formed early wood of the succeeding ring (Bisset and Dadswell 1950, Amos, Bisset and Dadswell 1950 and Chalk, Marstrand and Walsh 1955). Such an abrupt decrease in length is also observed in all the four trees of the present investigation in respect of libriform fibres as well as vessel-elements (Figs. 3-8).

In the opinion of the author the sudden decrease in length of these elements at the beginning of a growth ring appears to be independent of the length of the fusiform initials. This may be proved by an examination of the structure of the wood of robinia, where the small late wood vessel-elements and the strand parenchyma of the first-formed early wood are stratified. It is evident that these stratified narrow vessel-elements in the last-formed late wood of one ring and strand parenchyma of the first-formed early wood of the succeeding ring show remarkably uniform length (Fig. 13). It seems reasonable to suggest that the length of the fusiform initials, as indicated by the length of these elements, remains the same at the region of transition from the late wood of one ring to the early wood of the succeeding ring. Further Chalk, Marstrand and Walsh (1955) proved that the strand parenchyma is almost of uniform length of the throughout a growth ring. As the variation in length of the vessel-elements and the libriform fibres from one ring to the other is essentially the same in the storeyed and nonstoreyed woods, it seems reasonable to suppose that the cause may also be the same. This sudden decrease in length of the *libri*form fibres may,

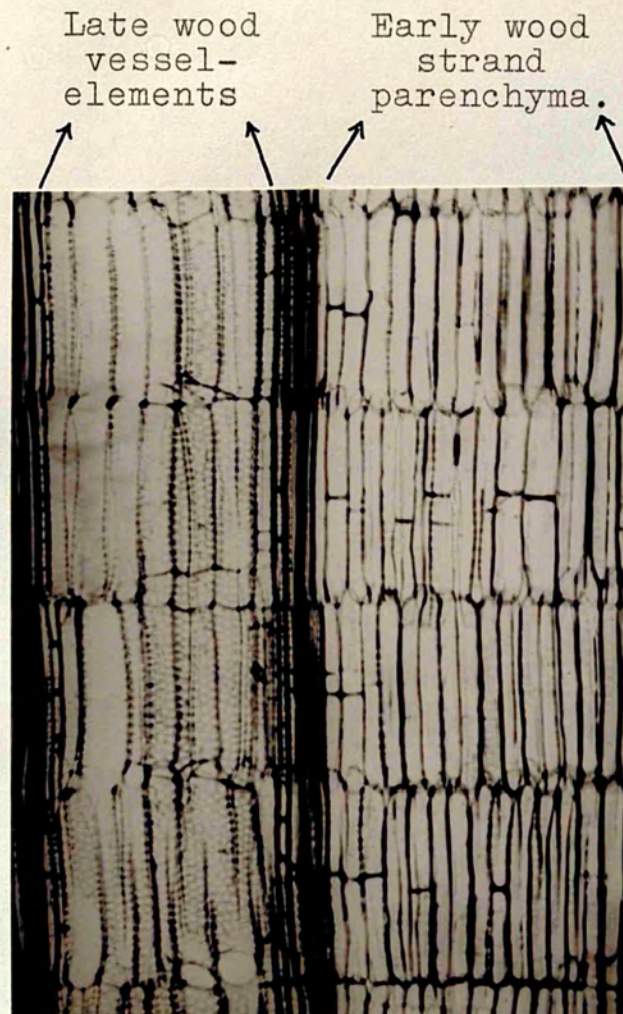


Fig. 13. Robinia pseudoacacia. Photomicrograph of radial longitudinal section of wood from the bole showing the stratified vessel-elements and stratified strand parenchyma. x 125.

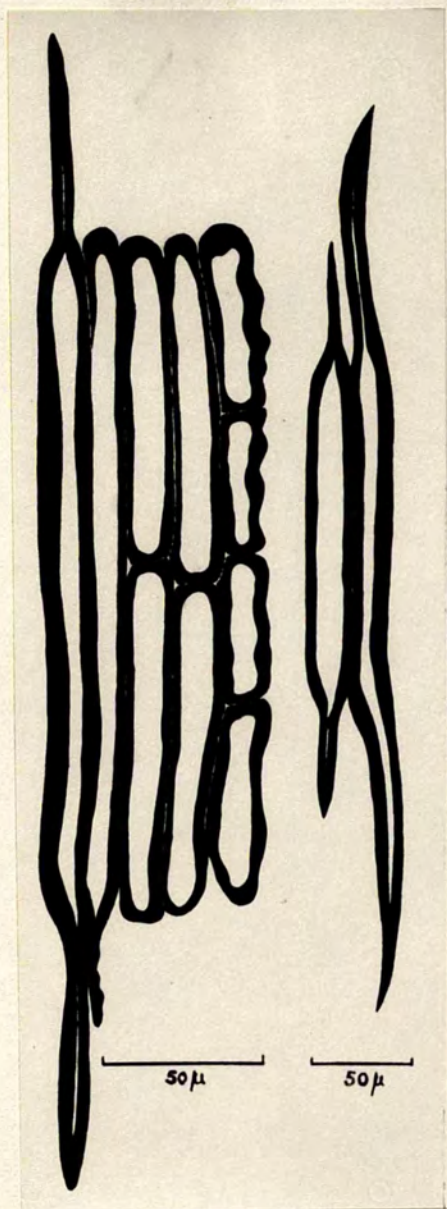


Fig. 14.

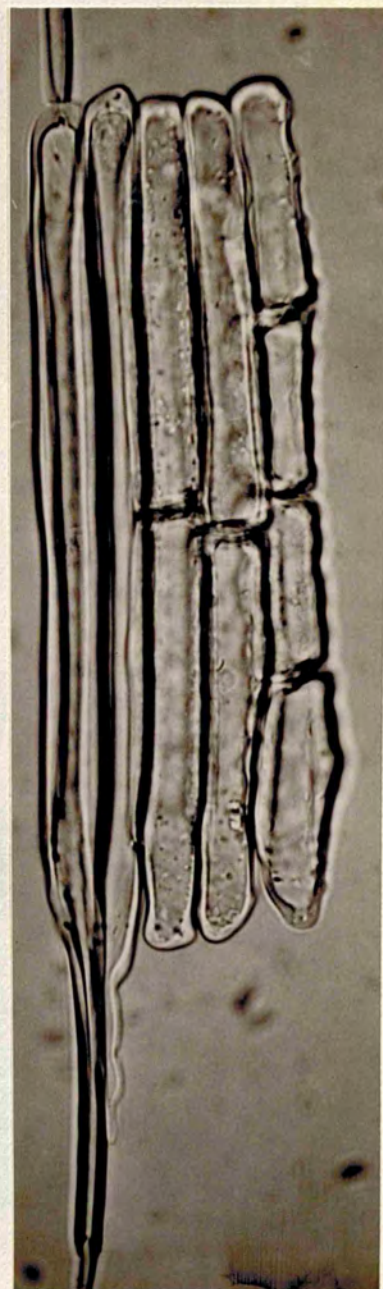


Fig. 15.

Fig. 14. *Robinia pseudoacacia*. Derivatives of the vascular cambium differentiating into libriform fibres and strand parenchyma.

Fig. 15. Photomicrograph of fig. 14. x 510.

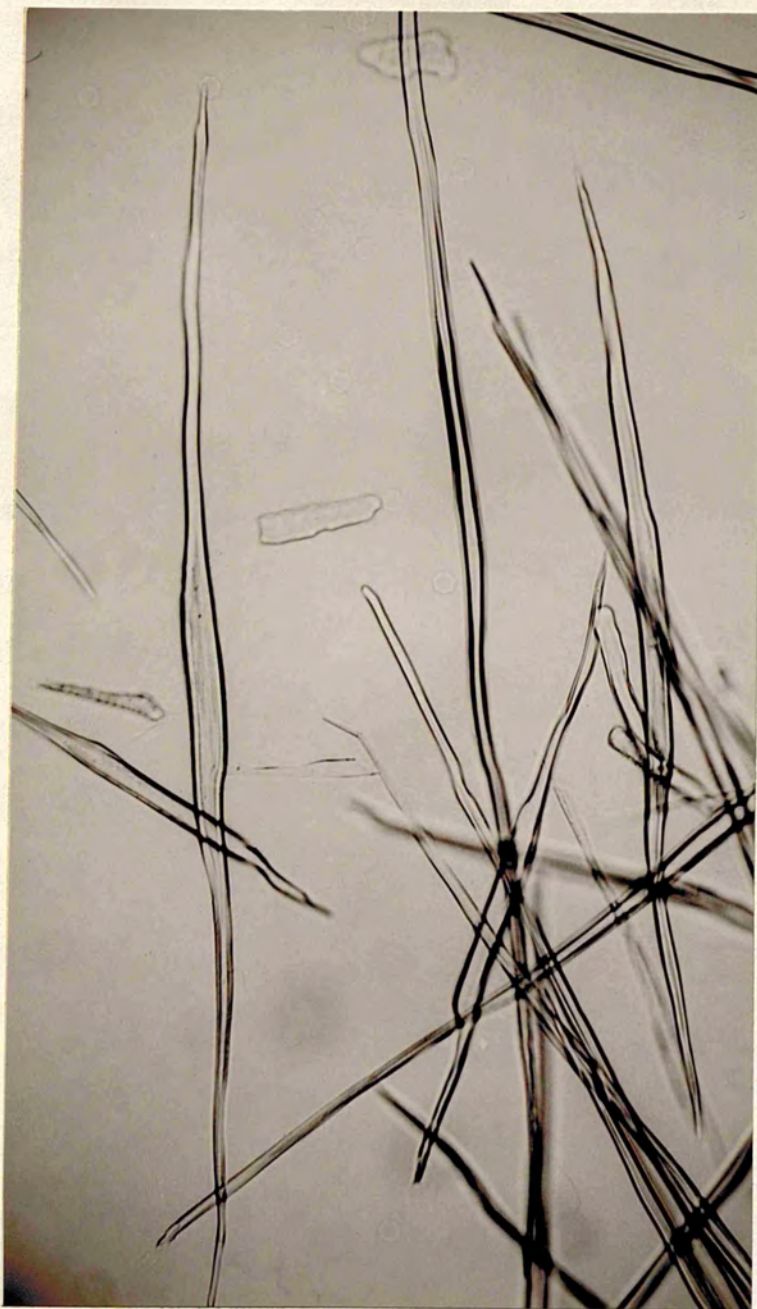


Fig. 16. Robinia pseudoacacia. Photomicrograph showing different stages of elongation of the fibres. x 160

therefore, be due, as suggested on page 71, to earlier lignification and consequent cessation of elongation while that of the vessel-elements may be explained by the shortening of those of the early wood in relation to lateral distension, notwithstanding the length of the fusiform initials.

In conclusion, it may be stated that the variation in length of the vessel-elements and the libriform fibres within a ring vertically in the bole, although studied from the same growth ring at different levels, is, in fact, of that of the derivatives of different fusiform initials formed at different periods in the life of the tree. On the other hand, variation within a ring horizontally may be due to seasonal flow of hormones accompanying the opening of the buds and the resumption of the apical growth as well as to the environmental effects on the differentiating wood tissue.

SUMMARY

1. The vessel-elements and libriform fibres increased in length at first rapidly and afterwards rather slowly at any one level in the bole, branches and roots from the centre outwards in successive growth rings of the oak, beech and sycamore where the vascular cambium is not stratified.

2. In robinia, where the vascular cambium is stratified, the vessel-elements showed remarkably uniform length in the successive growth rings from pith outwards at any one level in different parts of the tree. The libriform fibres showed the same type of variation as those of the other trees.

3. The increase in length of these elements is more gradual through successive growth rings from the pith at the base of the bole than at higher levels.

4. The mean maximum length of these elements is less in the branches and greater in the roots than in the bole.

5. In any growth ring the length of these elements increased from the base of the bole upwards

to a maximum and then decreased towards the top.

The position in the bole where the maximum length of these elements attained is highest in those rings furthest from the pith.

6. The vessel-elements and the libriform fibres are distinctly longer in the last-formed wood of a ring than in that which was laid down first in all the investigated trees.

7. The variation in length of the vessel-elements in a ring is attributed to the shortening of those of the early wood as a result of lateral distension and of the libriform fibres to the elongation during differentiation.

8. Vessel-elements and libriform fibres of a ring varied little in length around the stem at one level.

9. The radial and tangential diameters of vessels of sycamore and robinia increased through successive growth rings at first rapidly and afterwards slowly throughout the life of the trees.

10. Rays showed gradual increase in height and decrease in number from centre outwards at any one level in the different parts of robinia.

11. Ray volume is at a maximum at the base of the bole and root both near the pith and bark and it gradually decreased upwards and outwards in the bole.

12. Apart from certain minor details, wood of different ages and that from different parts of the tree showed no great histological differences.

APPENDIX

The wood of oak and sycamore was differentiated into heartwood and sapwood, whereas there was no such distinct difference in beech and robinia.

The oak and robinia were ring porous and the sycamore and beech, diffuse porous (Figs. 17, 18, 19 and 20). Vessel-elements were either found to large in the spring wood of oak and in robinia and rather small in both the sycamore and beech. In robinia the large early wood vessels were

APPENDIX

vessels were present in both the early and the late wood of a ring. In the sycamore they were usually solitary but occasionally in radial pairs or threes, while in beech they were solitary or in small irregular clusters. In both these woods there was a gradual diminution in size of the vessels throughout the growth ring. Tyloses were often present in the heartwood in oak, robinia and beech. Mean vessel-element length in oak and beech varied between 0.4 mm. to 0.6 mm., in sycamore 0.3 mm. to 0.45 mm., and in robinia there was almost a constant length varying round about 0.2 mm.

HISTOLOGICAL FEATURES.

The wood in oak and robinia was differentiated into heartwood and sapwood, whereas there was no such distinct difference in beech and sycamore.

The oak and robinia were ring porous and the sycamore and beech, diffuse porous (Figs. 17, 18, 19 and 20). Vessel-elements were medium sized to large in the spring wood of oak and in robinia and rather small in beech and sycamore. In robinia the large early wood vessels were solitary but the smaller vessels were clustered in both the early and the late wood of a ring. In the sycamore they were commonly solitary but occasionally in radial pairs or threes, while in beech they were solitary or in small irregular clusters. In both these woods there was a gradual diminution in size of the vessels throughout the growth ring. Tyloses were often present in the heartwood in oak, robinia and beech. Mean vessel-element length in oak and beech varied between 0.4mm. to 0.6 mm., in sycamore 0.3 mm to 0.45 mm., and in robinia there was almost a constant length varying round about 0.2 mm.

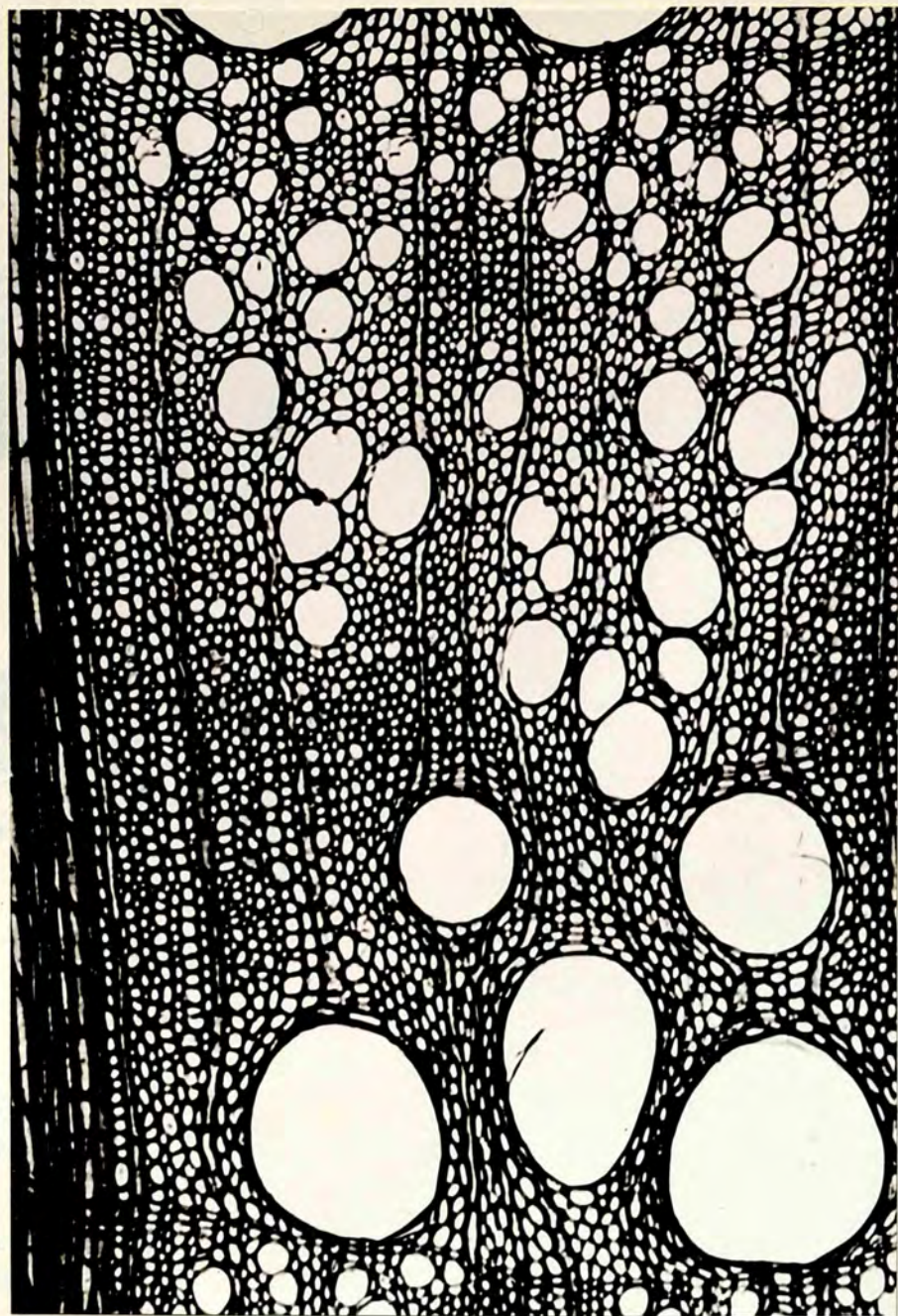


Fig. 17. Quercus robur. Photomicrograph of transverse section of wood from the bole. x 120.

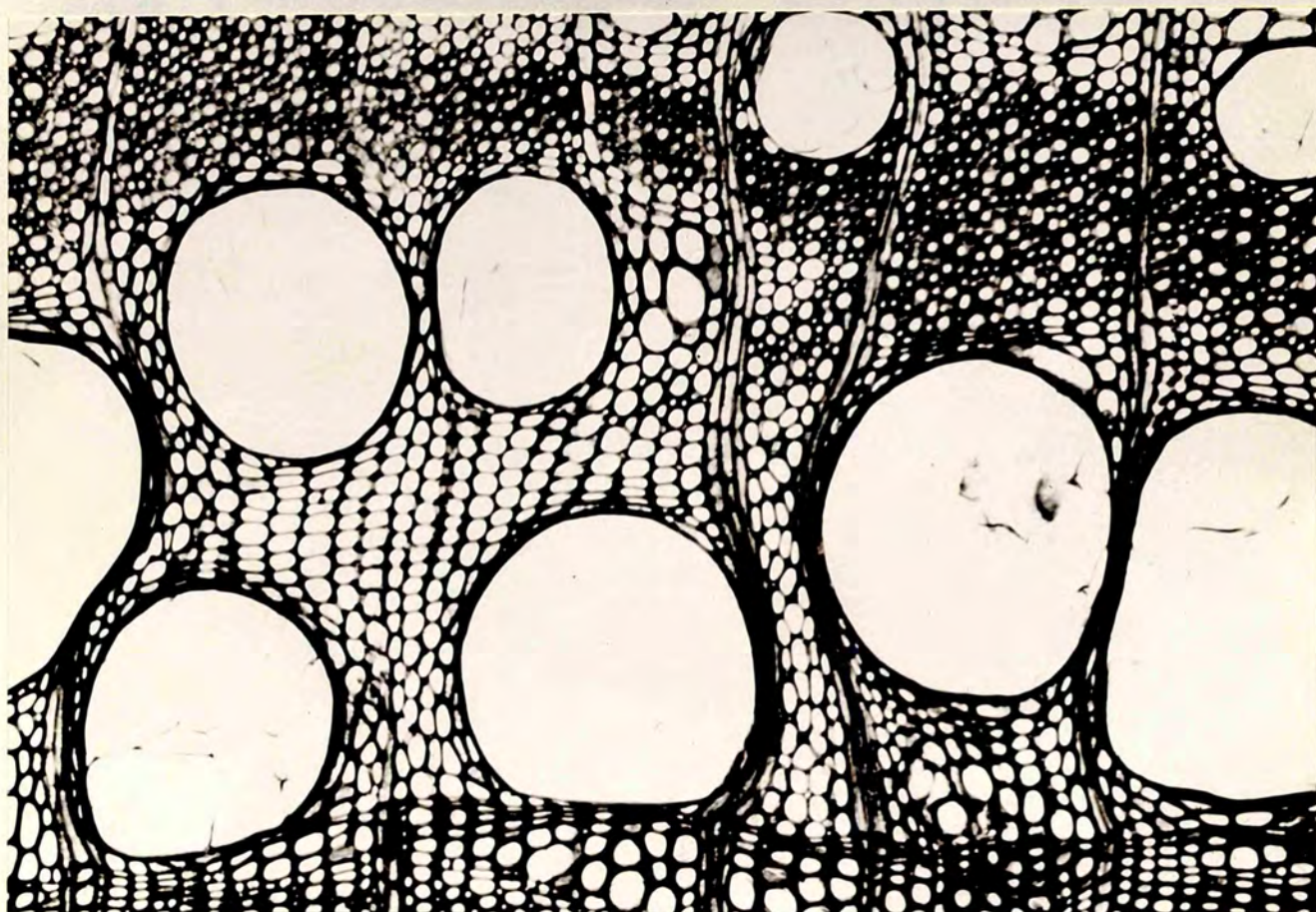


Fig. 18. Robinia pseudoacacia. Photomicrograph of transverse section of wood from the bole. x 140.

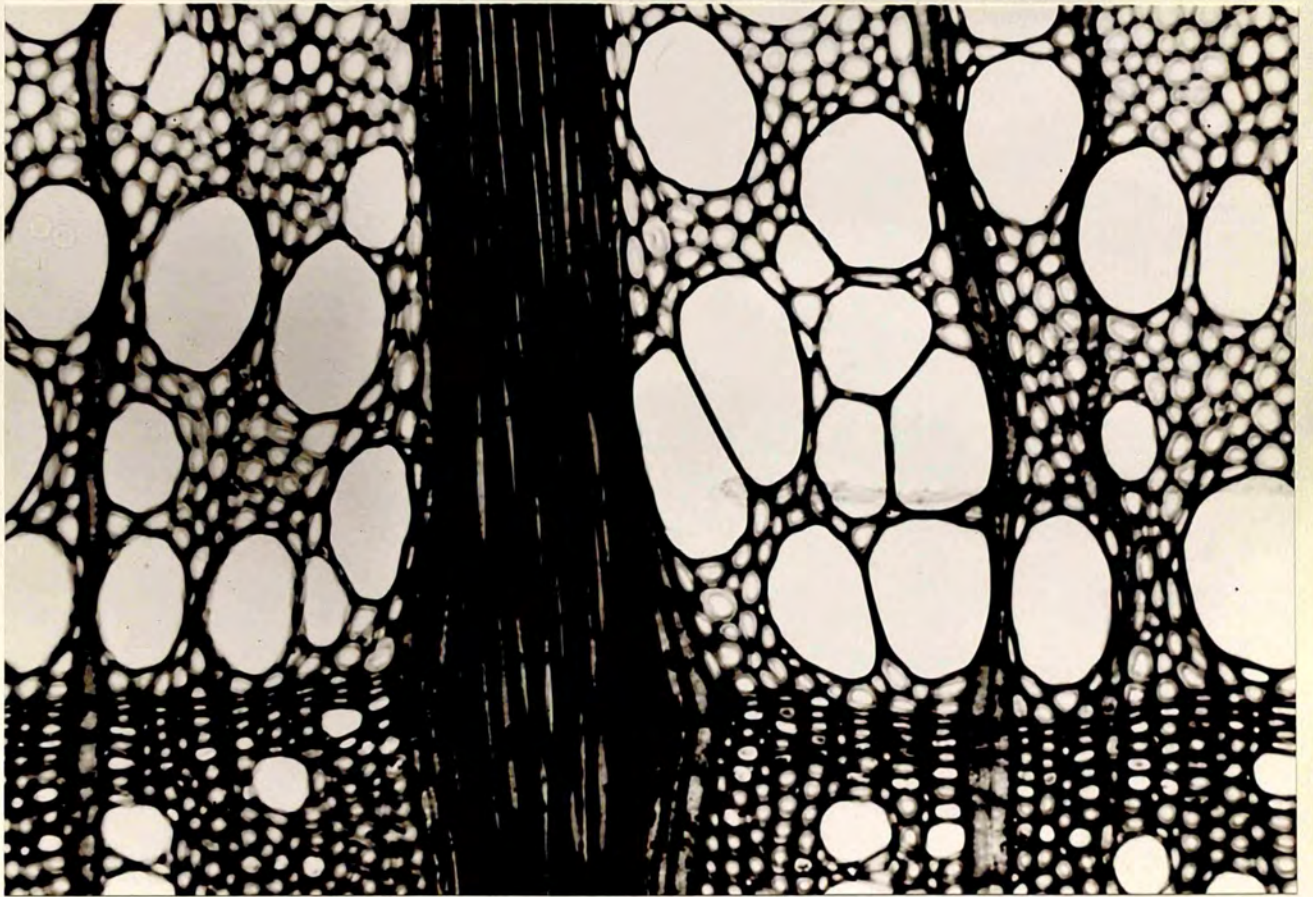


Fig. 19. Fagus sylvatica. Photomicrograph of transverse section of wood from the bole. x 220.

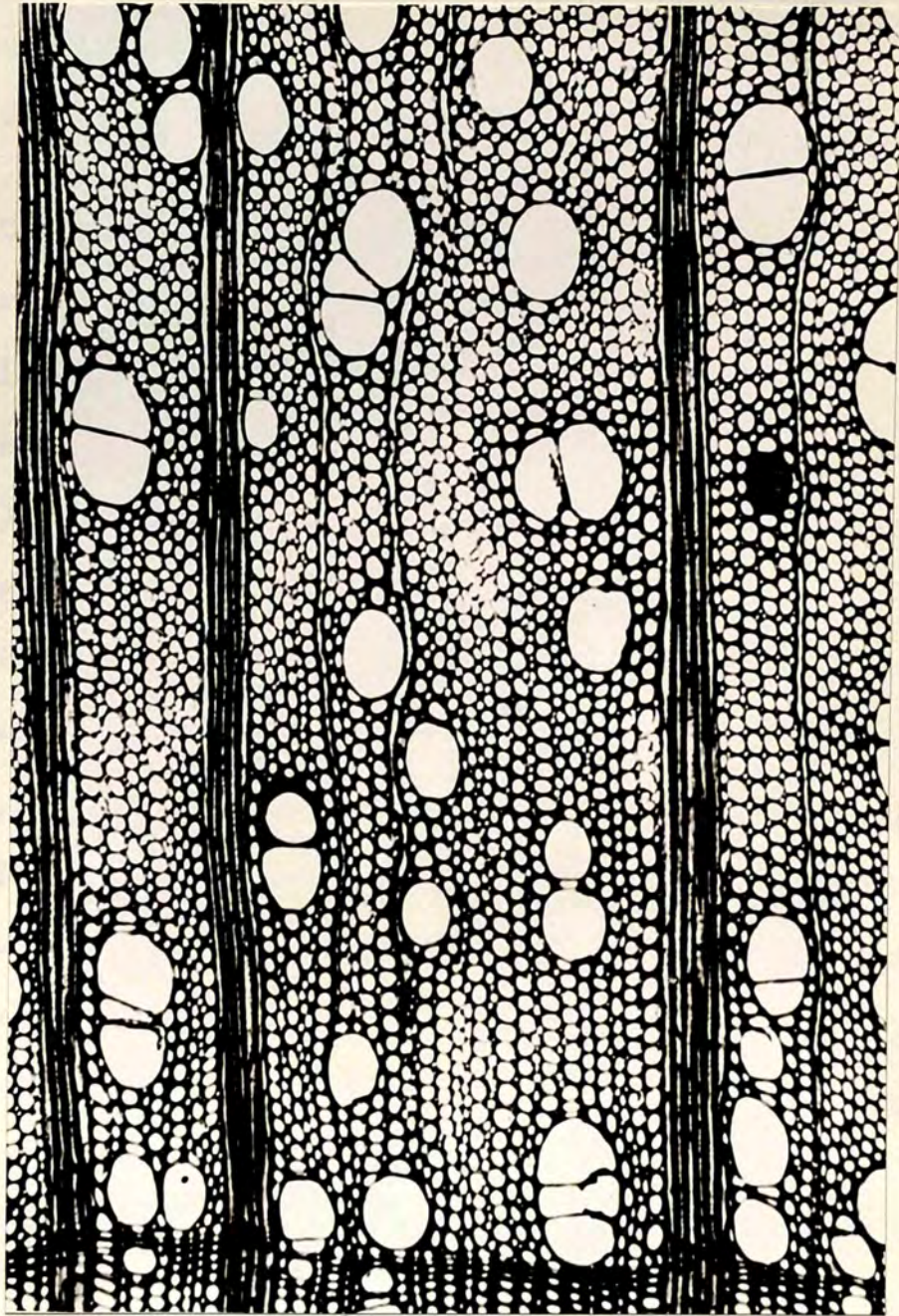


Fig. 20. Acer pseudoplatanus. Photomicrograph of transverse section of wood from the bole. x 120.

Spiral thickening was present in the vessels of sycamore and in robinia it was often limited to smaller vessels; it was not seen in oak and beech.

Intervascular pitting varied between opposite and alternate in oak and beech even in the same vessel (Figs. 21 and 22). In beech, scalariform lateral pitting was occasionally observed in the mature wood (Fig. 22). In sycamore and robinia intervacular pitting was typically alternate and the pits were hexagonal in shape (Figs. 23 and 24). Pits in robinia were vestured (Fig. 25). In robinia and sycamore, pitting between the vessels and vertical parenchyma and or ray parenchyma was similar to the intervacular pitting. In oak and beech these pits were large and elongated, with the long axis mostly vertical in the former and horizontal in the latter (Figs. 21 and 22).

In all four woods perforation plates were predominantly simple. However, occasional vessel-elements with scalariform perforations were found in oak in all parts of the secondary xylem (Fig. 26). In beech scalariform perforations were commonly found in

EXPLANATION OF FIGURES.

- Fig. 21. Quercus robur. Intervascular pitting and pits to ray cells.
- Fig. 22. Fagus sylvatica. Intervascular pitting and pits to ray cells.
- Fig. 23. Acer pseudoplatanus. Photomicrograph showing intervascular pitting. x 500.
- Fig. 24. Robinia pseudoacacia. Photomicrograph showing intervascular pitting. x 595.
- Fig. 25. Same as fig. 24. Vestured pits. x 860.

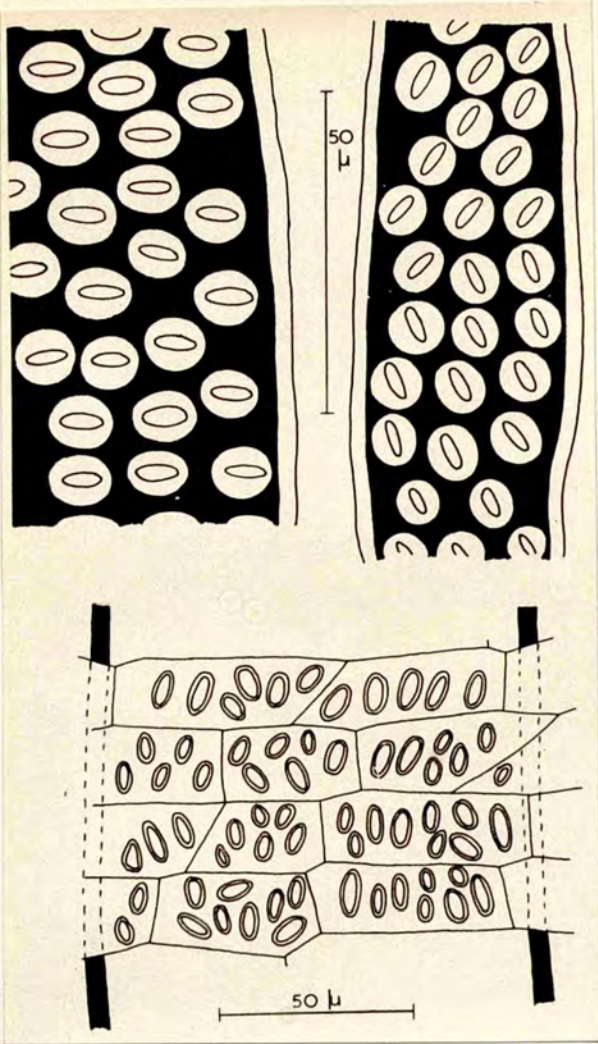


Fig. 21.

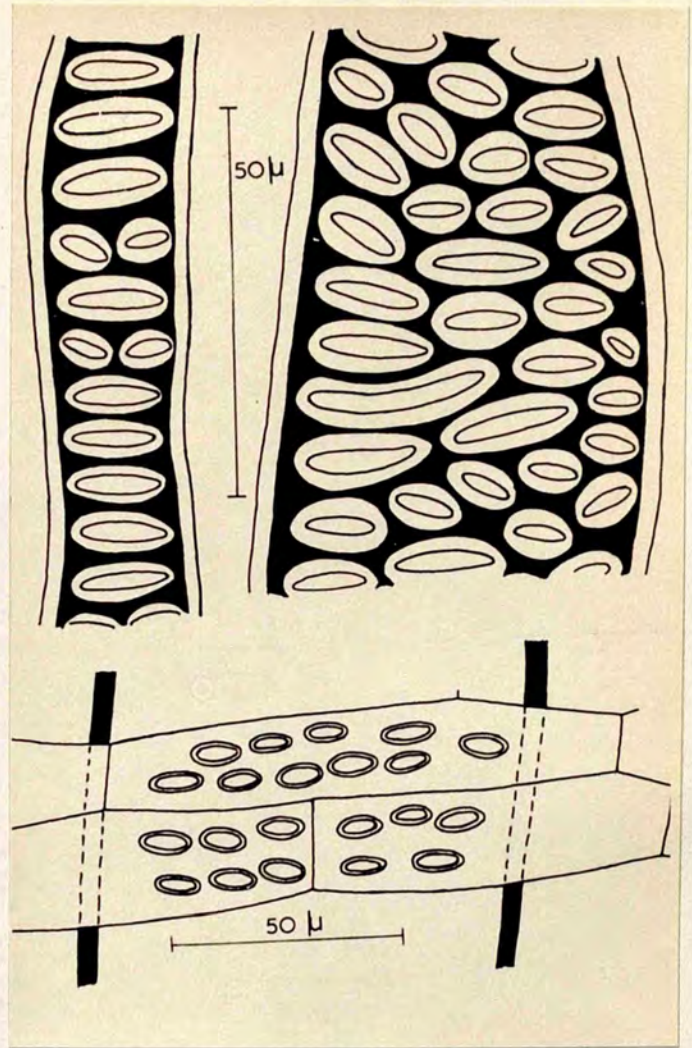


Fig. 22.

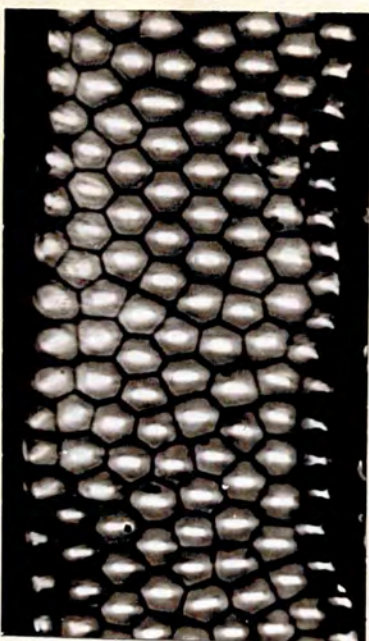


Fig. 23.



Fig. 24.



Fig. 25.

EXPLANATION OF FIGURES.

- Fig. 26. Quercus robur. Scalariform perforation plates on the end walls of the vessel-elements.
- Fig. 27. Acer pseudoplatanus. ' 8 ' --Shaped perforation plates on the end walls of the vessel-elements.
- Fig. 28. Robinia pseudoacacia. Photomicrograph of a vessel-element with scalariform perforation on one end wall and a simple one on the other. x 680.

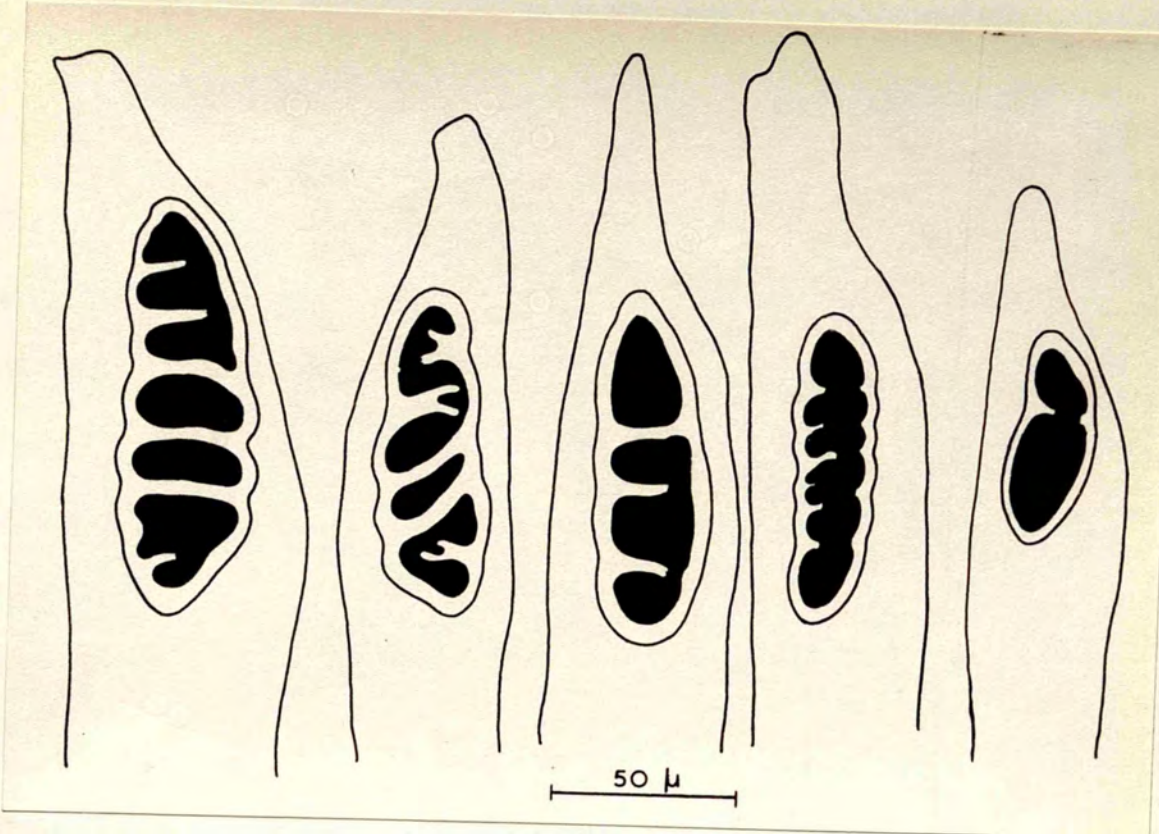


Fig. 26.

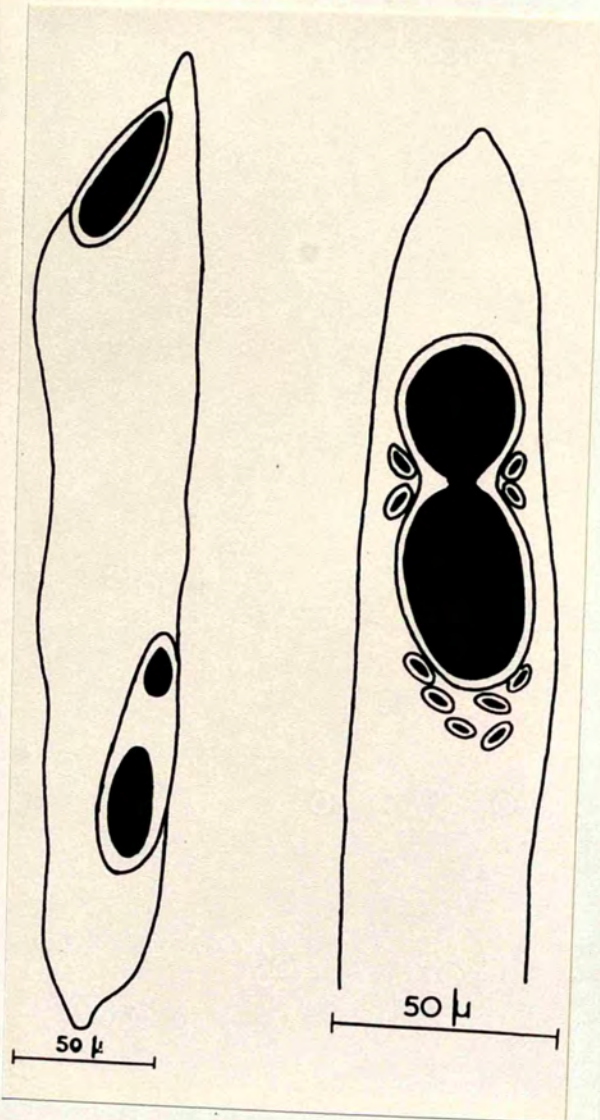


Fig. 27.

Fig. 28.



the narrower vessel-elements. Very rarely, in sycamore perforation plates were observed with '8'-shaped perforations/^{or}with two small ones (Fig. 27), but nearly all the perforations seen in this wood were simple. This latter type would appear to be comparable with the foraminate perforations mentioned by Metcalfe and Chalk (1950) in some of the smallest vessel-elements in sycamore. In robinia one vessel-element of the late wood of one of the later growth rings in the bole, was observed to have a scalariform perforation plate in which some of the bars were forked (Fig. 28), but in all other instances only simple perforations were found in this wood.

The parenchyma was apotracheal in oak and beech occurring as scattered cells or in uniseriate bands. In sycamore, parenchyma was sparse or absent except at the boundary of the growth ring. In robinia the abundant parenchyma was vasicentric and, in the outer part of the growth ring, confluent. The strand parenchyma in the latter genus was most commonly one or two celled; more rarely a strand contained four cells. In oak and beech strand parenchyma was many celled.

In robinia the parenchyma and vessel-elements are storeyed whereas in oak and the others there was no storeyed structure.

Rays were of two distinct sizes in oak, the smaller being uniseriate and the larger multiseriate (Fig.29). In beech, however, there was a complete gradation from the smallest to the largest rays (Fig.30). Multiseriate rays were about 20-25 cells wide in oak and were very high, measuring up to 35 to 40 mm; in beech they were about 20 cells wide and not exceeding 5-8 mm. in height. They were homogeneous in both oak and beech. In sycamore rays were about 5-10 cells wide and were homogeneous (Fig. 31). In robinia the rays were exclusively uniseriate in the early growth rings but mainly multiseriate (Fig.32), with a few uniseriate ones, in the later growth rings. They were short, measuring about 0.5 mm., in height and homogeneous.

The fibres in oak and beech were thick walled with pits more abundant on the radial walls than on the tangential walls. Mean fibre length in beech and oak varied from 0.6 mm. to 1.4 mm. In sycamore,



Fig. 29. Quercus robur. Photomicrograph of tangential longitudinal section of wood from the bole. x 120.



Fig. 30. Fagus sylvatica. Photomicrograph of tangential longitudinal section of wood from the bole. x 220.



Fig. 31. Acer pseudoplatanus. Photomicrograph of tangential longitudinal section of wood from the bole.
x 140



Fig. 32. Robinia pseudoacacia. Photomicrograph of tangential longitudinal section of wood from the bole. x 140.

the fibres have noticeably thicker walls in the neighbourhood of vessels (Fig.20). Mean fibre length in sycamore varied from 0.45 mm. to 1.0 mm. In robinia the fibres were very narrow and thick walled with small pits which were more numerous on the radial than on the tangential walls. The mean fibre length in robinia varied from 0.4 mm. to 1.7 mm.

Fibre-tracheids were abundant in oak and sparse in beech; they were not present in sycamore and robinia. The mean fibre-tracheid length in oak was less than that of the libriform fibres and varied from 0.4 mm. to 0.95 mm.

Vasicentric tracheids were found in abundance in oak but not in the other three woods. They were irregular in shape with thin walls uniformly thickened except for the abundant pits on all the walls. In beech and sycamore a few vascular tracheids were found but these were of very rare occurrence.

Growth rings were distinct in all the woods studied with abrupt transformation from the summer wood to the spring wood (Figs.17-20). The wood of the branches and roots showed marked differences. In

that of the branches the growth rings were narrow and the vessel-elements and libriform fibres smaller and shorter than those of the bole. The extent of late wood was more in the rings of the branches (Figs. 33, 34, 35 and 36). In the roots the fibres and vessel-elements were the longest. The growth rings were narrow with a less well defined transition between late wood of one year and the spring wood of the next; indeed there was no definite ring sometimes (Figs. 37, 38, 39 and 40). The walls of the vessel-elements, fibres and parenchyma were not as thick as in the bole and hence the wood of the roots was of open nature and less dense.

Fig. 33. *Alseodaphne* sp., in branch, transverse section of wood from the branch.

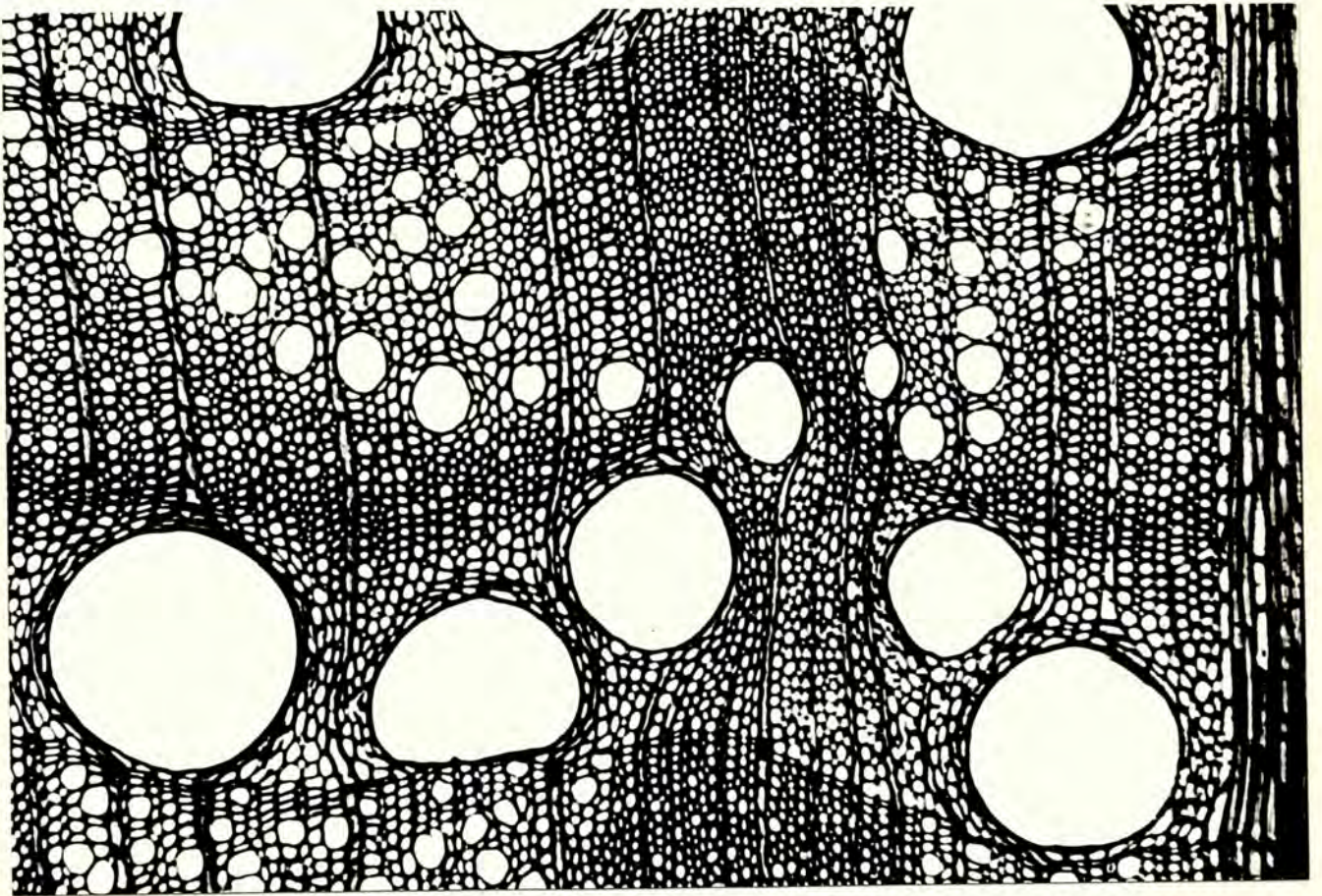


Fig. 33. Quercus robur. Photomicrograph of transverse section of wood from the branch. x 120.

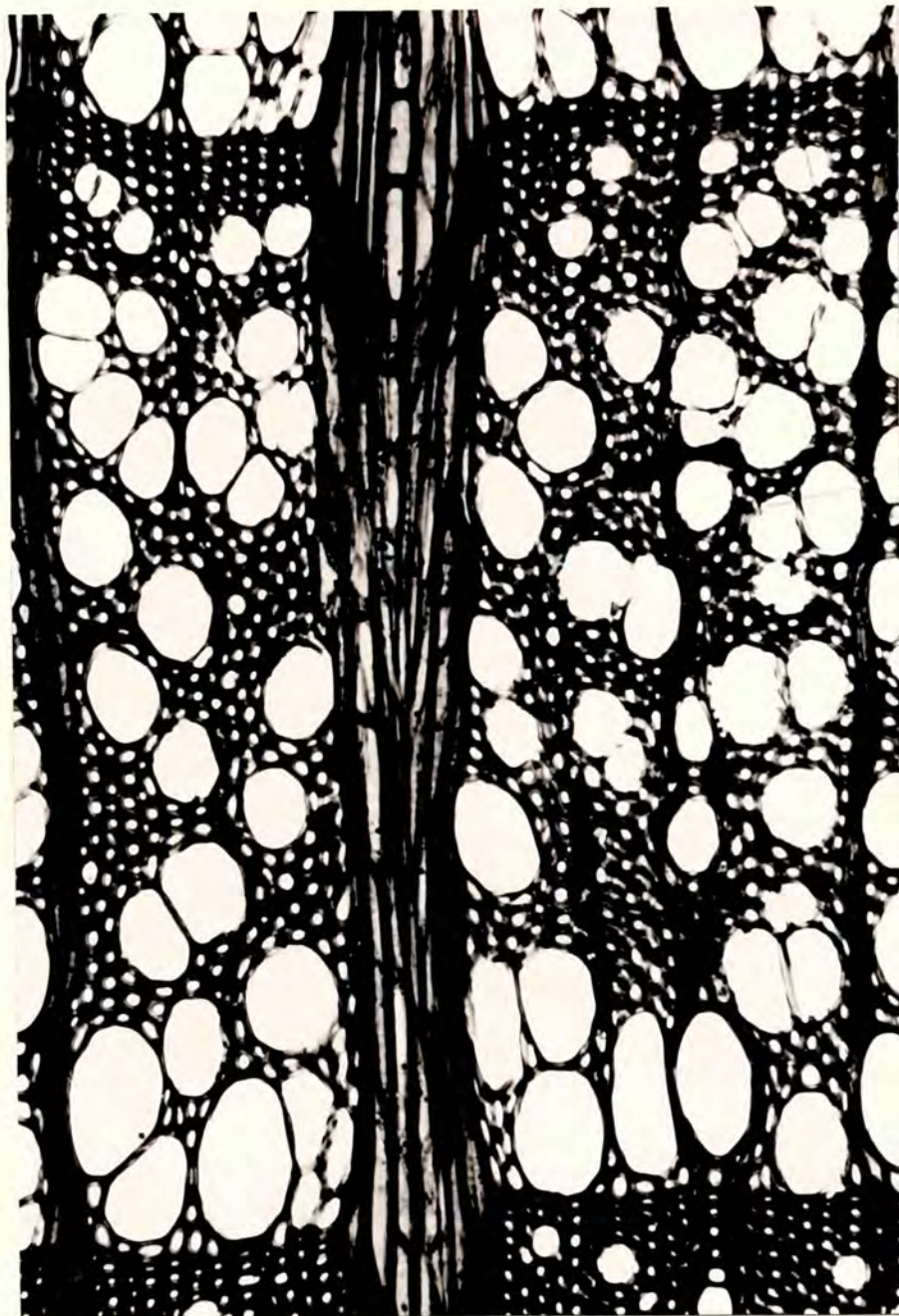


Fig. 34. Fagus sylvatica. Photomicrograph of transverse section of wood from the branch. x 220.

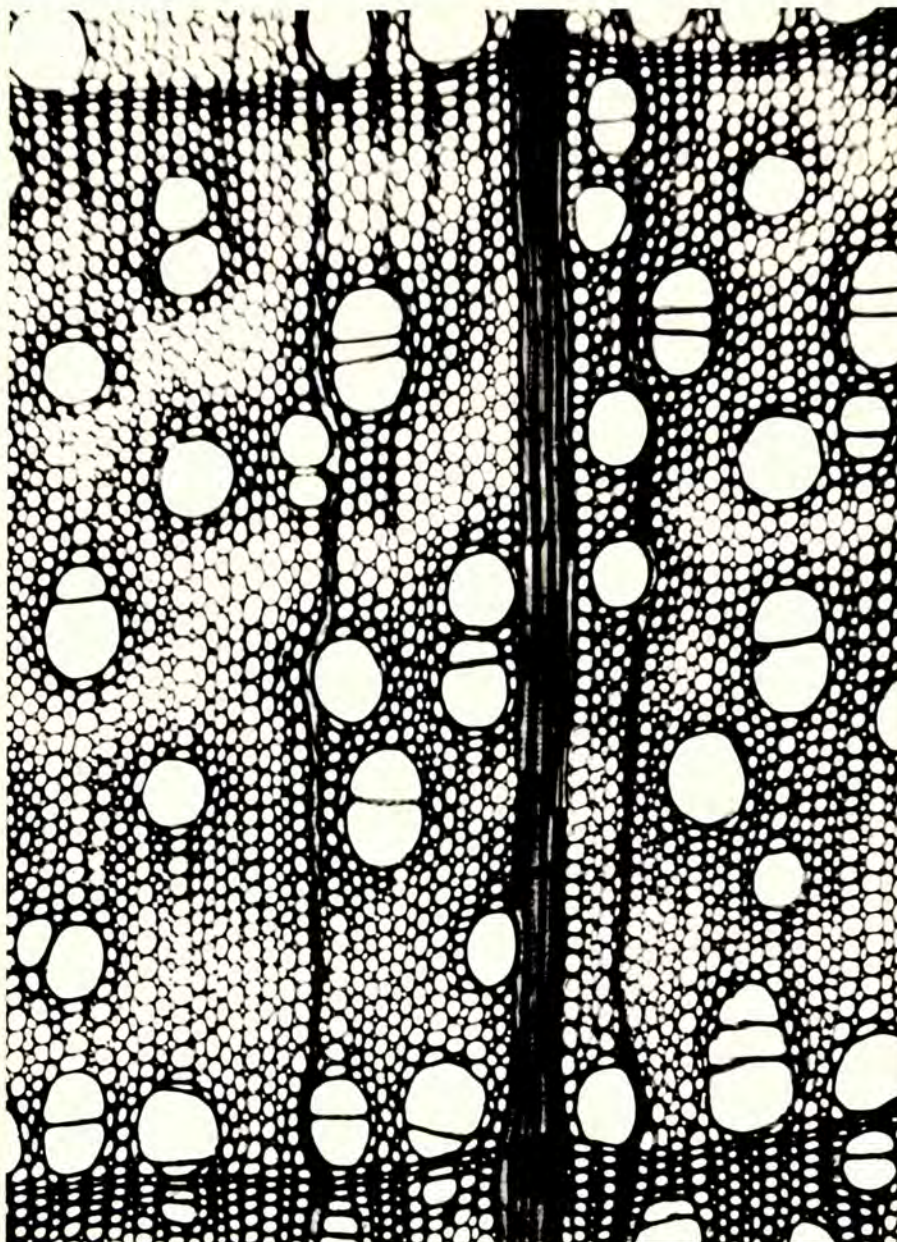


Fig. 35. Acer pseudoplatanus. Photomicrograph of transverse section of wood from the branch. x 140.

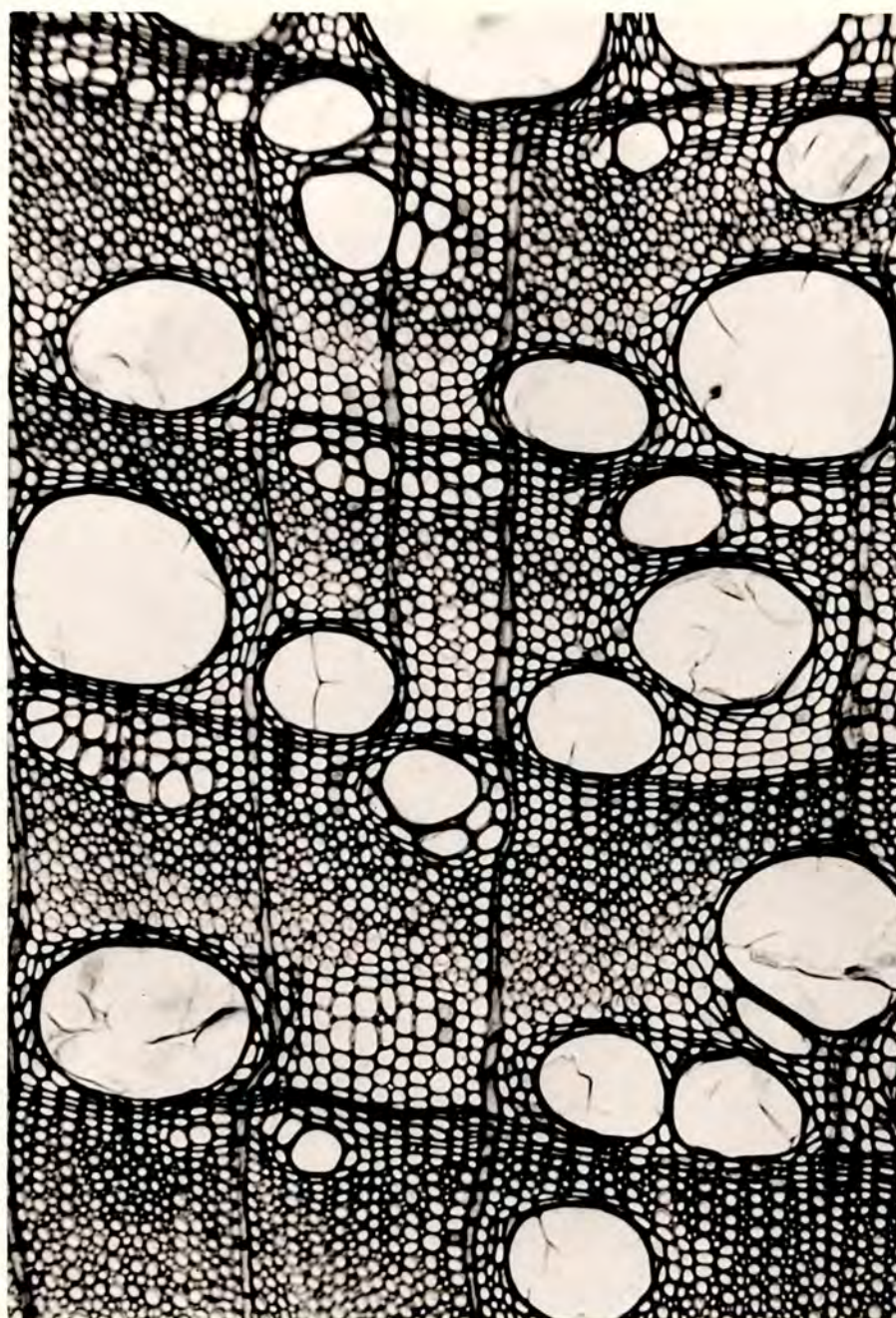


Fig. 36. Robinia pseudoacacia. Photomicrograph of transverse section of wood from the branch. x 140.

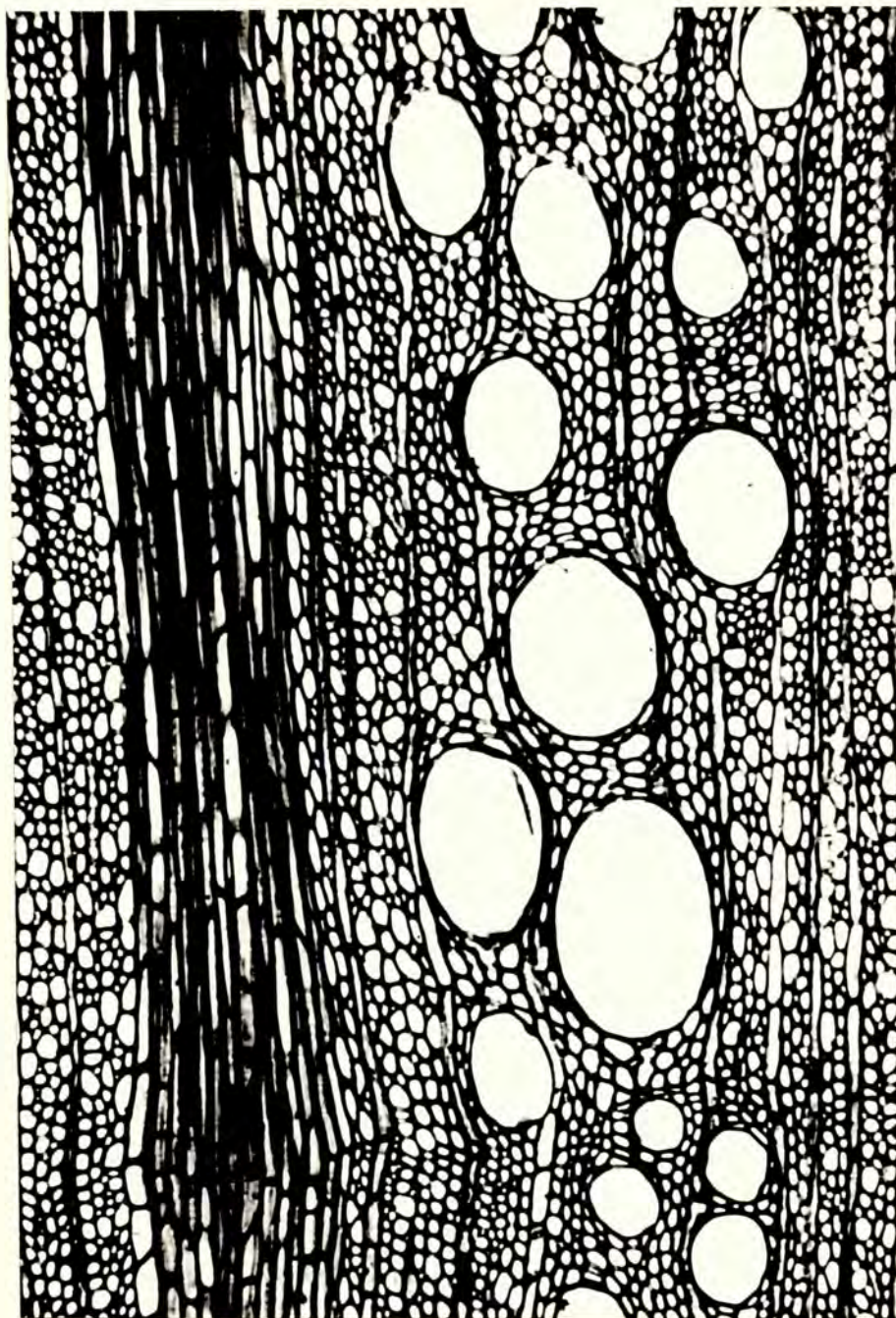


Fig. 37. Quercus robur. Photomicrograph of transverse section of wood from the root.
x 120.

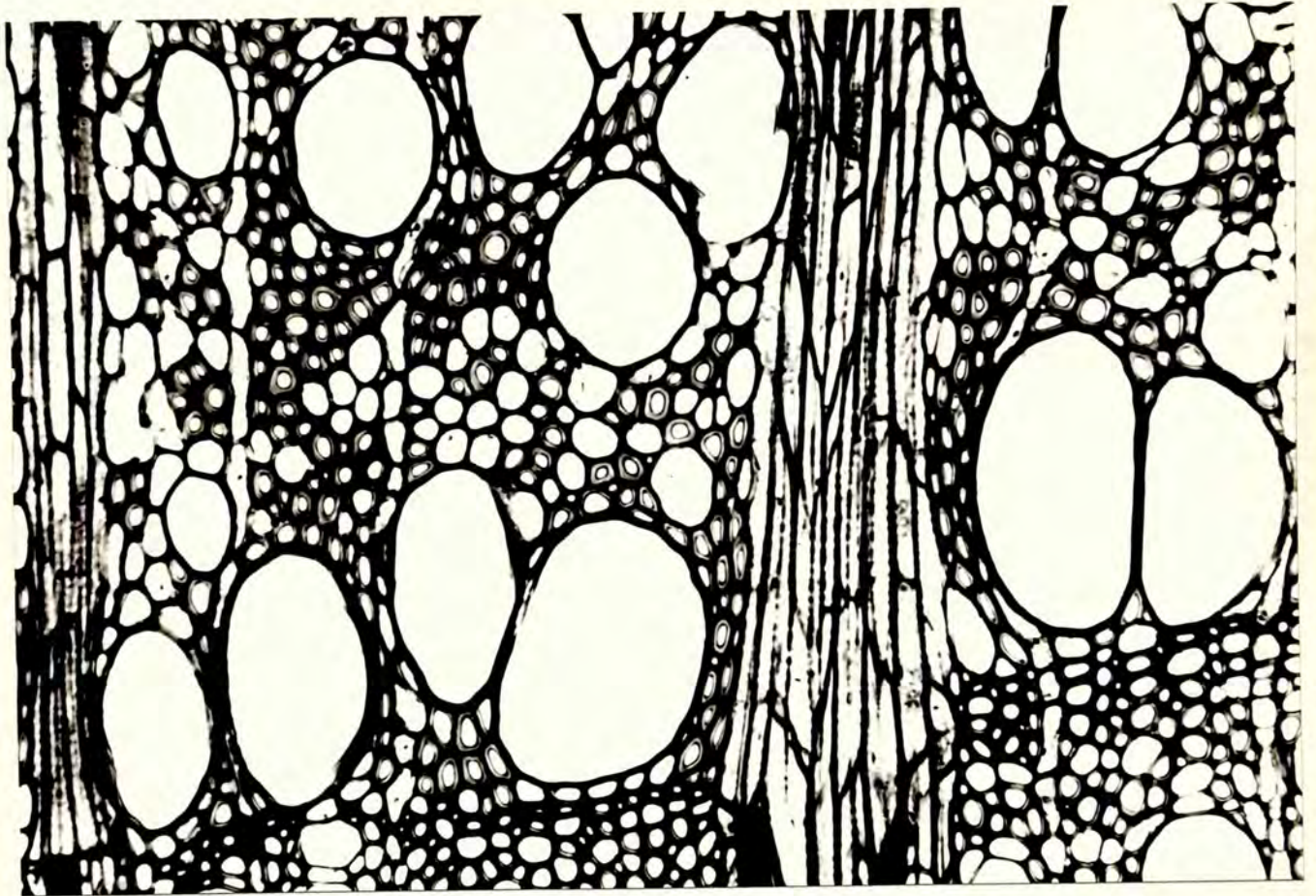


Fig. 38. Fagus sylvatica. Photomicrograph of transverse section of wood from the root. x 220.

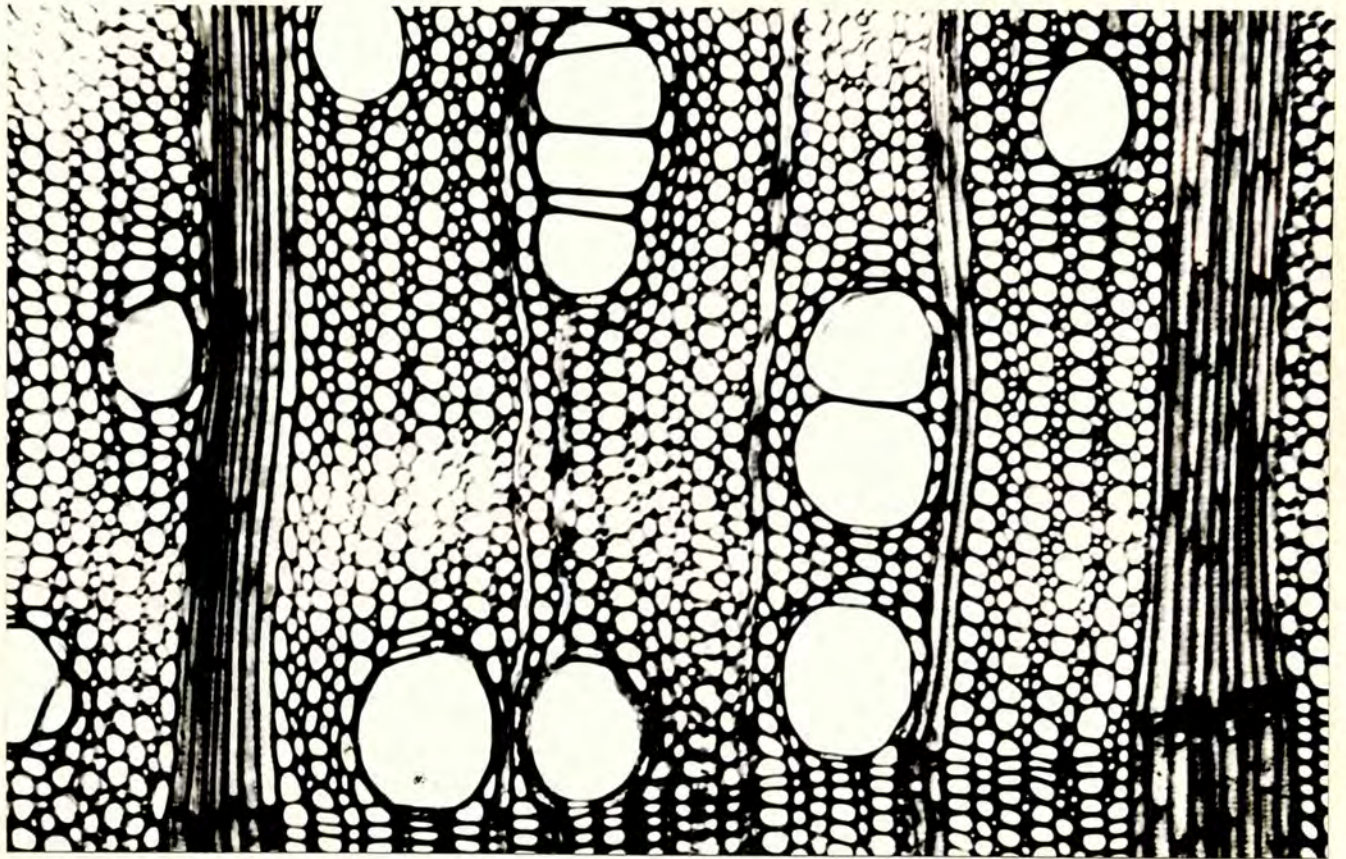


Fig. 39. Acer pseudoplatanus. Photomicrograph of transverse section of wood from the root. x 140.

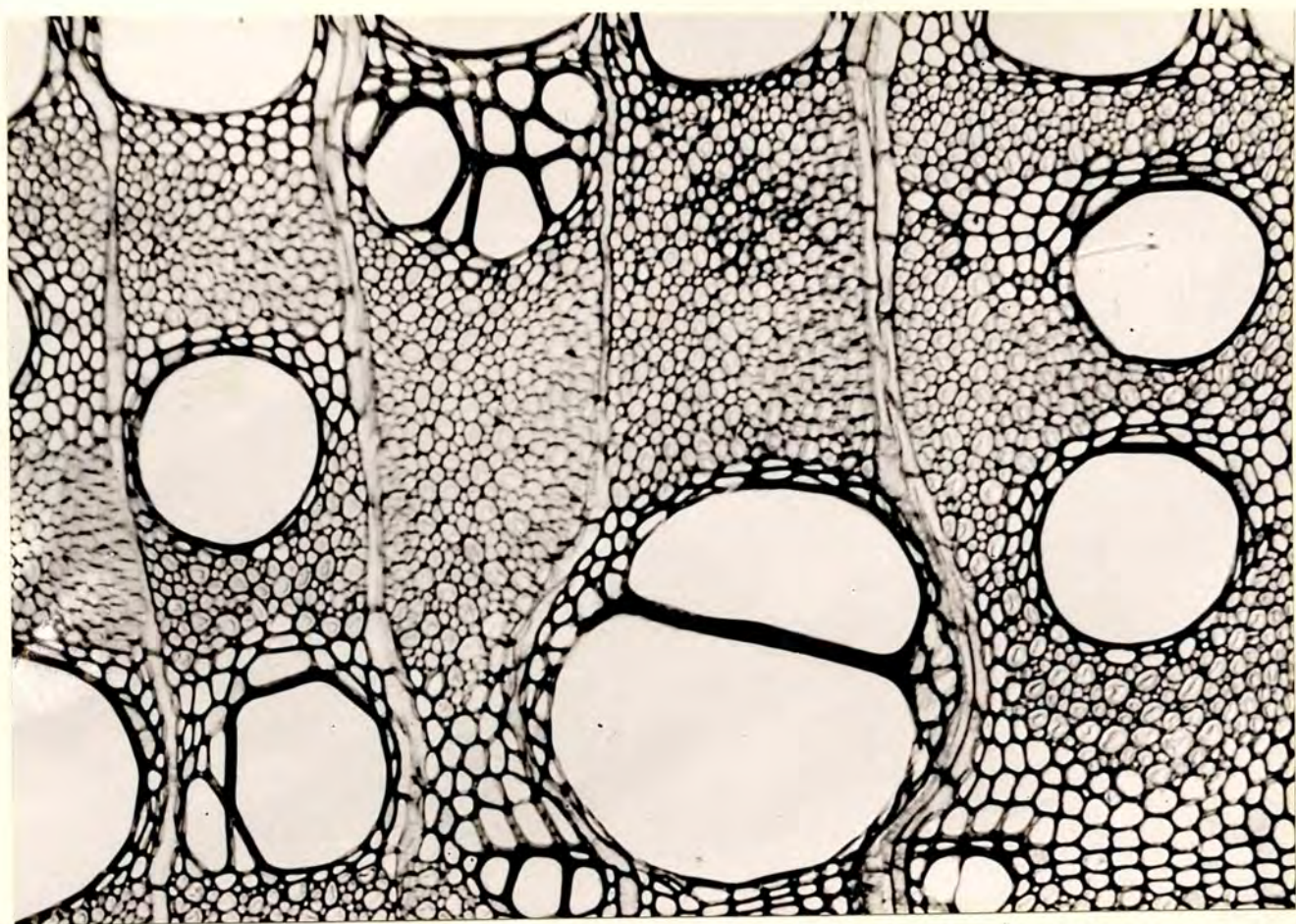


Fig. 40. Robinia pseudoacacia. Photomicrograph of transverse section of wood from the root. x 140.

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