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VARIATION IN ROOT WOOD ANATOMY*

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Summary. Variability in the anatomy of root wood of selected specimens particularly *Fraxinus excelsior* L. and *Acer pseudoplatanus* L. in the Kew reference microscope slide collection is discussed in relation to generalised statements in the literature on root wood anatomy.

INTRODUCTION

Although variability in the anatomical characters of trunk wood has been studied in some detail by various authors, relatively little comparable work has been carried out on root wood. This is probably because root wood is more difficult to obtain, and its economic importance is slight. However, it is often important to be able to identify root samples; it is therefore necessary to know about the possible range of variability in root anatomy so that accurate identifications can be made. Use is made of variability in the root structure of certain fruit trees for the selection of root stocks which will help to regulate the final size of the crown of the tree, and the age at which fruiting begins.

In the above-ground parts of a tree, variability in wood anatomy is often related to the position from which the sample is taken. The juvenile wood of twigs is dissimilar in a number of respects from trunk wood; the length and diameter of cells is usually smaller in twigs, for example, and species with simple perforation plates in vessels of the trunk may have scalariform plates in twig vessels. For this reason, Metcalfe & Chalk (1950) describe twig (or young stem) and mature wood anatomy separately for each family. Samples from near the junction of branches, or near the base of a tree frequently show detailed and sometimes even gross anatomical differences when compared to samples taken from the main trunk. The special features of reaction wood from leaning trunks and from branches have been the subject of extensive study and experiment.

The arrangement of vessels, fibres, tracheids, and parenchyma can vary to some extent, even in adjacent growth rings or within a single ring from opposite sides of a trunk. The numbers of cells of each type per unit area, the size and thickness of their cell walls can also vary. General descriptions of wood anatomy should normally be based on observations made on a number of samples from different specimens taken at a standard position from the trunk. The sizes of cells, their frequency and distribution should be stated only when large numbers of measurements have been made, or counts taken, so that reliable figures have been obtained.

Less easily detectable differences occur between the lengths of cells of successive growth rings in a trunk. The first formed (oldest) axially arranged cells are often shorter than those in more recent rings. There may be a continuous increase in, say tracheid length, in successive new rings throughout the life of the tree, or a maximum may be reached and maintained, or even a fall in length may occur in very old trees. Generally, however, a Sanio curve is found, relating length and age of elements. From the first formed secondary xylem outwards there is normally a steep increase in length which levels off after a short distance, so that the axial elements of subsequent growth rings show only a gradual length increase or hardly change at all. Usually a statistical analysis has to be applied to measurements of cell dimensions before such trends can be appreciated.

In addition to variability within a single tree, there can be considerable differences between the secondary xylem anatomy of samples obtained from trees of the same species grown under different environmental conditions.

It is inappropriate to give a comprehensive list of references here, but the reader will find that the following cover many of the points outlined above: Sanio (1872); de Bary (1884); Chalk (1930); Baily & Faull (1934); Fegel (1941); Bannan (1941–2, 1944, 1952); Bosshard (1951); Spurr & Hyvärinen (1954); Liese & Dadswell (1959); Dinwoodie (1963); White & Robards (1966); Philipson & Butterfield (1968); Yaltirik (1968, 1970); Novruzova (1968); Mariani (1968); Jane (1970); Gottwald (1971); Baas (1973); van der Graaff & Baas (1974).

Root wood anatomy varies in much the same way as wood from the aerial parts of a tree. It seems that variability is frequently more extreme. This may be due to the presence of additional factors such as soil compression, waterlogging, variability in the composition of soil atmosphere and so on, not present in the environment of the aerial parts.

Although much less has been published on the subject of root anatomy than that of aerial parts, as Fayle (1968) points out, there is a considerable amount of information scattered throughout the literature. This often takes the form of short notes in papers dealing largely with other subjects. Fayle's own observations and his literature review cover 57 species or varieties. He was able to make a number of generalisations about root wood anatomy in comparison with trunk wood anatomy. He was careful to state that these were only generalisations and not laws. The statements do form a useful basis for discussion, and are as follows. In roots: (a) pith is absent; (b) parenchyma content is usually higher and fibre content lower; (c) the number of vessels per unit area in hardwoods is usually less; (d) heartwood and tyloses are infrequent; (e) the annual rings generally contain fewer cells and the boundaries between rings are less well defined; (f) cells in the root are generally wider, longer, have thinner walls, and are less lignified; the pits are larger and the number of rows increased with some pitting on tangential walls. Some of these and the observations of other authors will be considered in the section on observations and discussion. Fayle gave a comprehensive bibliography and an extended list of references is unnecessary here. The following papers also relate to the subject: Macdonald (1960); Patel (1965); Pil'shchikov (1969); Rusch (1973); Süss & Müller-Stoll (1973).

THE STUDY OF ROOTS AT KEW

The approach to the study of root anatomy at Kew is essentially practical (Cutler, 1974). Roots removed from the proximity of foundations of buildings showing subsidence damage are sent to the laboratory for identification. Sections prepared from the roots are compared with slides from the references collection, and identified as closely as possible. This is often the only relatively inexpensive way of determining which of a number of different species of trees might be related to some particular structural damage. It is quite evident from this work that root anatomy is very variable. The reference collection contains a number of specimens of roots of each of many of the 190 species or varieties represented; there are about 900 slides in total. The slides resulting from enquiries are also retained following identification; there are about 4,500–5,000 of these. The range of material available for comparative studies is, then, considerable. Very narrow roots with one or two growth increments are represented, as well as much wider roots. The collection has been built up largely in response to the need to identify samples, so the tree species which most commonly cause damage and those which exhibit the widest variability in their root anatomy tend to be better represented than others. The main drawback is that the root samples are not related to trunk wood samples from the same plant. There is a very extensive collection of trunk wood slides. It is not possible to compare the differences between root and trunk wood from the same specimen using these collections, but one can select representative trunk wood slides for comparison, or even in order to compare the range of variability of trunk wood with variability in root wood anatomy from the same species.

The roots in both the reference and enquiries collections are not normally referable to a particular part of a root system. Consequently it is not possible to relate variability displayed to particular types (e.g. lateral, tap) of root.

MATERIALS AND METHODS

Tree and shrub roots of known origin were sectioned on a sledge microtome at 25–30 μm, and stained in the normal way with safranin, safranin and haematoxylin, or safranin and fast green. Sections were dehydrated and mounted in canada balsam. Normally, it was not known from which part of the root system the samples were obtained, but most were lateral and not tap-roots.

Acer pseudoplatanus and *Fraxinus excelsior* were selected for special study since they demonstrate a wide range of variability in root anatomy, and the *Acer* is diffuse porous and *Fraxinus* ring porous in the trunk wood. Representative slides of trunk wood were selected for comparison, and a simple statistical analysis applied so that numbers of vessel elements per unit area, and the radial diameter of vessel elements could be discussed for each sample in a meaningful manner. Radial rather than tangential vessel element diameter was selected for measurement, since Fayle (1968) stated that increase in diameter was likely to be greater in the radial than the tangential diameter for longitudinal elements in root wood, when compared with trunk wood.

Thirty vessel elements, ten from each of three consecutive growth rings, were measured. In *Fraxinus*, where two distinct size categories of vessels could be detected, each was analysed separately, with measurements of thirty elements of each group per root. In *Fraxinus* roots the sixth, seventh, and eighth growth rings were sampled in roots B and D, and in root C which had fewer rings, the fifth, sixth, and seventh were sampled. In *Acer* the third, fourth, and fifth growth rings were examined. The early growth rings with very narrow cells were thus avoided and observations were made on zones where the anatomy was regular for the root being examined.

The number of vessel elements in each of ten unit areas was recorded for each sample, except in *Acer* root D, where only five areas could be taken to avoid overlap because of the small diameter of the root.

The mean and standard deviations were calculated for each set of measurements or counts. Sample size was accounted for using Student's t test, and levels of confidence were worked out at $p = 0.05$ and $p = 0.01$.

The following were examined and are discussed, but no statistical analysis was applied: *Rosa* sp., three roots, *Quercus* (*robur* type), three roots, *Malus pumila*, root and trunk wood, *Populus* sp., one root.

OBSERVATIONS AND DISCUSSION

The roots examined were all rather narrow when compared with those reported on by some authors. Mature root wood had probably not been laid down in any of them, but a regular pattern of cell size and frequency of cell types was apparent in the areas analysed.

The number of root samples examined for each specimen is rather low for generalisations to be made. The particular roots reported on were selected because they showed some abnormality, or represented part of a range of variability. The object was to demonstrate that some of the published generalisations about root anatomy may need critical re-examination.

Plata 1A, B, and C shows three roots of *Fraxinus excelsior* in transverse section (T.S.) These demonstrate part of the range of variability which exists, and they complement the statistical data set out in Fig. 1 in which root C is represented by Plate 1A and root B by Plate 1C.

Patel (1965) stated that in *Fraxinus*, vessels of the 'pore zone' (first formed vessels) are smaller in the roots than in the stem whereas in most diffuse porous species the vessels are normally larger (throughout the growth ring) in the root than in the stem. He considered that ring porous and diffuse porous timbers should be treated separately for the comparative study of cell dimensions. He stated that if the 'pore zone' was regarded as extra, supplementary tissue, and not comparable with other tissues, one should compare the late wood of ring porous species with diffuse porous wood. This seems to be an unnecessarily complicated attempt to reconcile the fact that in some roots of ring porous (and diffuse porous!) species, the vessel elements are narrower than those of the trunk wood. It would appear to be the generalisation which is inaccurate, not the interpretation of the tissues. This is substantiated by the data set out in Fig. 1, which shows a comparison between radial vessel diameter and vessel density in mature trunk wood and the root wood from three samples of *Fraxinus excelsior*. In the mature wood and root C, vessels could be clearly grouped into two distinct size classes representing the 'pore zone' or early wood, and the late wood, although in the root the two zones overlap. In the roots B and D no such distinction could be made. The striking feature is that in roots B and D all vessels ($p = 0.01$) fall within the size range of the smaller vessels of the mature wood; there is no significant difference in

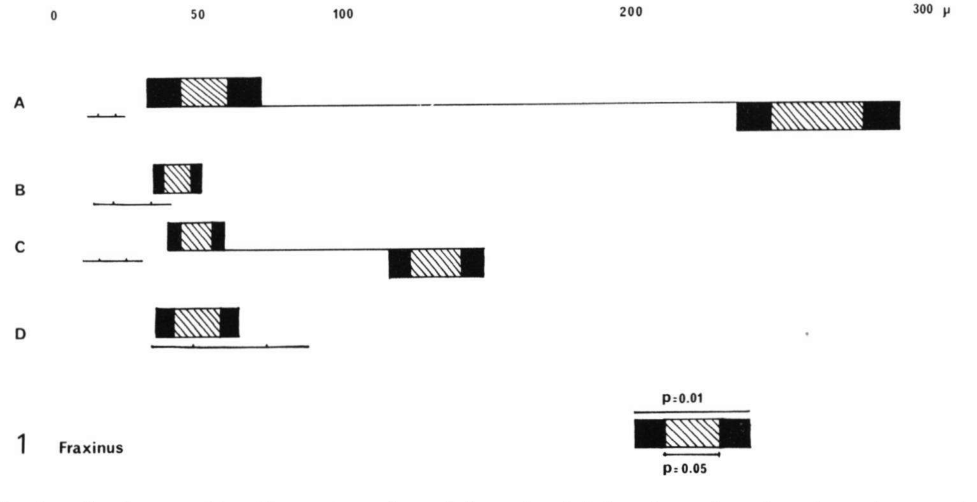

Fig. 1. —*Fraxinus excelsior*. Comparison of vessel element radial diameter and number of vessels per unit area for mature trunk wood (A) and three root wood samples (B, C, and D). Blocks indicate vessel diameter: with $p = 0.05$, cross-hatched, and $p = 0.01$ solid black plus cross-hatched. In A and C, the blocks for early and late wood are joined by a line to indicate that they relate to one another. The separate lines indicate the numbers of vessels per unit area. Total line length, $p = 0.01$; centre portion of line, $p = 0.05$.

size. In root C, the smaller vessels are similar in size to those of the late wood and the larger vessels are significantly smaller than the larger vessels of the spring wood of the mature trunk wood specimen.

The number of vessels per unit area of roots B and C is not significantly different from that of the mature wood, but significantly more (at $p = 0.01$) are present in root D.

Mature trunk wood and four variable roots of the diffuse porous species *Acer pseudoplatanus* are compared in Fig. 2, and photographs (T.S.) of the trunk wood, Plate 2A, root B, Plate 2B, and root C, Plate 2C, together with an additional root, not used in the statistical analysis, Plate 2D give a visual impression of the variability in root wood anatomy.

Root B (Plate 2B) represents the average condition of *Acer* roots from the Kew reference collections. Root C (Plate 2C) was taken from waterlogged ground at a lakeside. The root in Plate 2D came from under foundations of a building on a heavy clay soil.

Referring to Fig. 2 it can be seen that vessel element radial diameter in roots B and D is not significantly different from that in the representative sample of mature trunk wood. The vessels in root E are larger, and taken at the confidence level $p = 0.05$, significantly larger than those of the trunk wood. The elements in root C are significantly smaller than those of the trunk wood at $p = 0.01$.

The numbers of vessels per unit area in trunk wood and root E are not significantly different. Vessel number in samples B and D is significantly greater ($p = 0.05$) as it is in sample C ($p = 0.01$) when compared with the number in the mature trunk wood.

In each of the above examples, it can be seen that roots exist in which vessel elements are significantly narrower than those from a representative sample of trunk wood. In

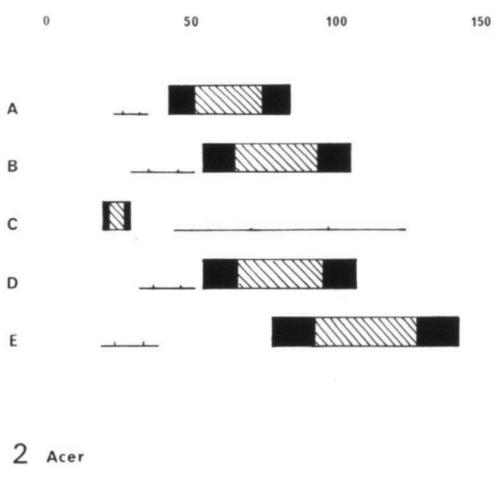

Fig. 2. —*Acer pseudoplatanus*. Comparison of vessel element radial diameter and number of vessels per unit area for mature trunk wood (A) and four root wood samples (B–E). Blocks indicate vessel diameter: with $p = 0.05$, cross-hatched, and $p = 0.01$ solid black and cross-hatched. The separate lines indicate the number of vessels per unit area. Total line length, $p = 0.01$; centre portion of line, $p = 0.05$.

Fraxinus (mature trunk wood ring porous) none of the roots has vessel elements which approach the diameter of spring vessels of the trunk wood sample. In three of the four *Acer* roots (mature trunk wood diffuse porous) vessels show a trend towards being wider than in the mature trunk wood sample. Fayle, Patel, and others suggest that, generally, vessels in roots are wider than in mature trunk wood. The evidence presented here, limited as it is, shows that the number of exceptions may be high enough to warrant further research into the matter.

From collected evidence Fayle also indicates that the number of vessels per unit area in hardwoods is usually less in roots than in mature trunk wood. In four of the seven roots examined here, this is not shown to be the situation, and again some doubt can be cast on the generalisation.

Obviously, the value of the results of this present work is limited since the full range of variability in mature trunk wood for either species was not taken into account, but, as mentioned, care was taken to select samples of trunk wood with average growth ring width, cell size and vessel frequency. Probably of more significance then, is the comparison between the roots themselves where variability has been shown to be extensive.

As noted, *Acer* root 3C came from a waterlogged site. The roots were not actually growing in water but in soil. Evidence presented by Pohl (1926, 1927, reported in Fayle, 1968) shows that for some trees of *Alnus* and *Salix caprea*, the roots growing in water have narrower vessel elements than those growing in soil. The narrow elements in *Acer* root C might, then, be related to the presence of water in all or most of the spaces between soil particles.

In *Fraxinus* growth rings are distinguishable with difficulty in roots of many of the samples in the slide collection. In a number of samples some rings are incomplete. Growth rings are difficult to detect in several of the *Acer* roots; this is in accordance with Fayle's generalisation on growth rings.

A visual comparison of photographs in Plate 2 shows that *Acer* root B (Plate 2B) corresponds well with a number of the generalisations made by Fayle, except that there are more vessels per unit area than in the trunk wood (Plate 2A). Most cells are larger than those of the trunk wood. In *Acer* root C (Plate 2C) and the root in Plate 2D a number of the cells have thicker walls than in the trunk wood, and all cell types appear narrower than in the trunk wood. These roots do not follow the generalised concept in these respects.

Plate 3A, B, and C shows parts of three roots of *Quercus* (*robur* type) in T.S. These are included here because they serve to illustrate several points, but no quantitative analysis has been attempted. The structure in Plate 3C is of interest because this sample was sent to the Laboratory as a root, but could be a sucker shoot arising adventitiously from a root, since it has a pith (not shown). Fayle states that pith is generally absent from roots. The specimen was identified as *Quercus* on the basis of details of cortex anatomy and vessel wall pitting among other things. Rays in *Quercus robur* are either uniseriate or wide, multiseriate; rays of intermediate widths rarely occur. The root shown in Plate 3C is abnormal in this respect when compared with the trunk wood, but apparently many oak roots have abnormal rays (Riedl, 1937). The vessel elements are also abnormal, since they are all narrow. They do show a slight dendritic arrangement, typical of *Q. robur*.

The roots shown in Plate 3A and 3B are more like the majority of oak roots in the reference collections. Even in the mature root (3A) growth rings are indistinct. Apart from the very small vessels of the first growth ring shown in Plate 3B, there is little distinction between the diameters of vessels from early and late wood, and ring porousness is lost. This accords with Fayle's observations.

Species of *Rosa* also have variable roots. Roots of *Rosa* are often encountered when excavations are made close to buildings, since roses are commonly planted near to walls. It is essential to be able to distinguish them from the roots of trees which are more likely to be the cause of structural damage.

The roots shown in Plate 4C and D demonstrate differences in vessel element diameter and number of vessels per unit area. Note also variability in cell wall thickness of fibres and parenchyma. Growth rings are indistinct, the roots fitting well with generalisations in this respect.

Malus sylvestris Mill. also shows some variability in root anatomy, but the example selected in Plate 4B, contrasted with trunk wood (Platc 4A) shows many of the features in which root wood is generally supposed to differ from trunk wood. There are fewer fibres and more parenchyma in the root, and more vessels per unit area. The vessels are, on an average, wider than those of the stem, annual rings contain fewer cells, and the boundaries are less distinct. Mention has already been made of the selection of *Malus* root stocks for dwarfing purposes in horticulture. Pil'shchikov (1969) has reported variation between roots of individual trees. The roots showed variations related to the depth at which they were found growing.

Up to this point, the larger differences of vessel size and number per unit area and the arrangement of cells have been discussed. There are also many finer features which vary in root anatomy, and can give rise to difficulties in making identifications. One of the most apparent of these is the tendency for species in which rays are homocellular in the trunk wood to have roots in which rays may be heterocellular (Lebedenko, 1961, 1962; Shimaji, 1962; both reported in Patel, 1965). This is the situation in *Populus* species. A heterogeneous ray is shown in *Populus*, Plate 1D.

Unfortunately *Populus* and *Salix* are commonly associated with damage to buildings. Whereas the trunk wood is usually readily ascribed either to *Populus*, the majority of rays of which are homocellular, or to *Salix* with exclusively heterocellular rays, the occurrence of larger numbers of heterocellular rays in *Populus* roots makes it impossible to separate the two genera on the basis of root wood anatomy alone.

CONCLUSIONS

From the extensive collections of reference slides of root anatomy held at Kew, the small sample selected serves to indicate that the probable extent of variability in root

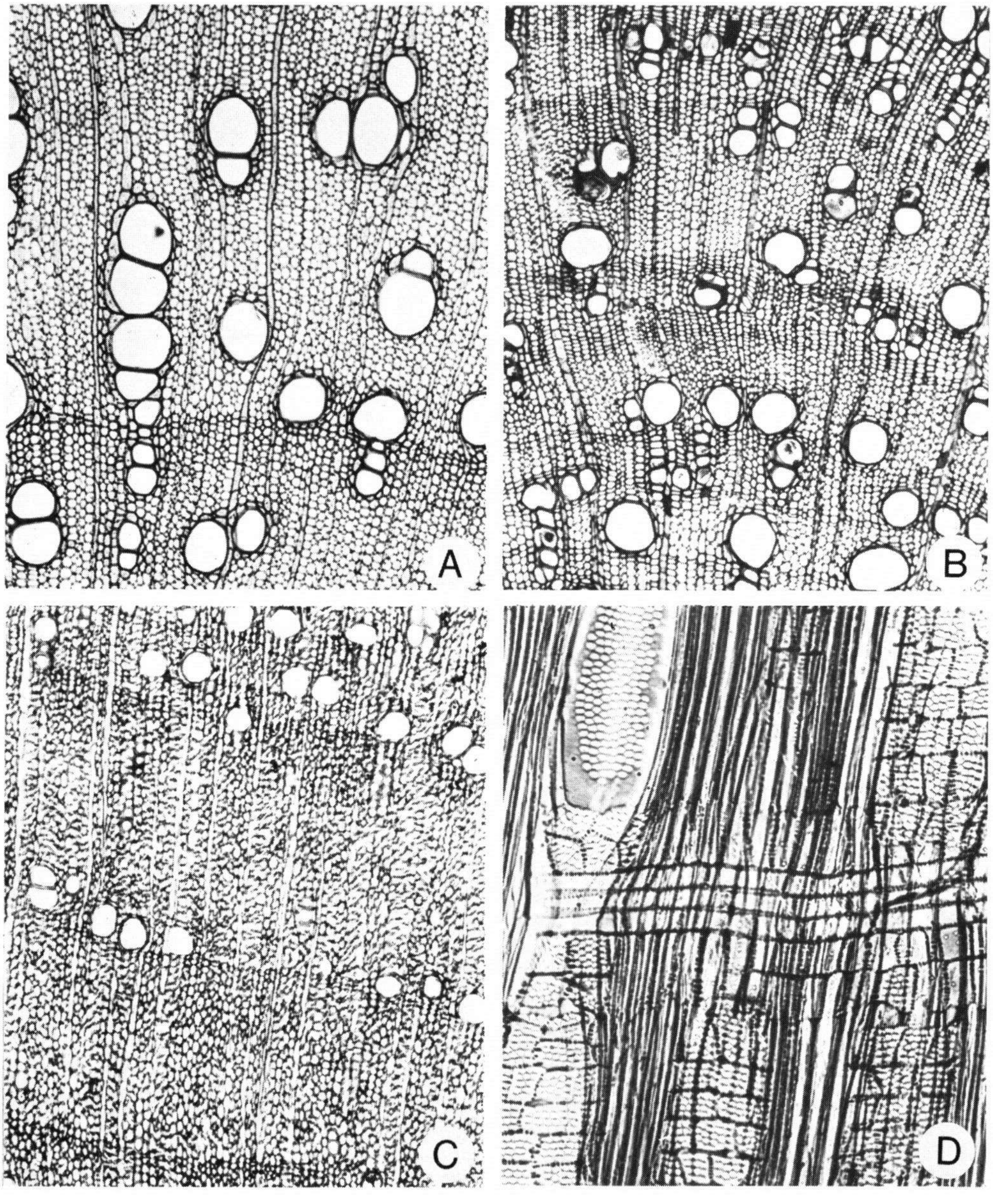

Plate 1. —A–C, *Fraxinus excelsior* transverse sections of roots, to illustrate part of the range of anatomical variability (×65); D, *Populus* sp., radial longitudinal section showing a heterocellular ray (×130).

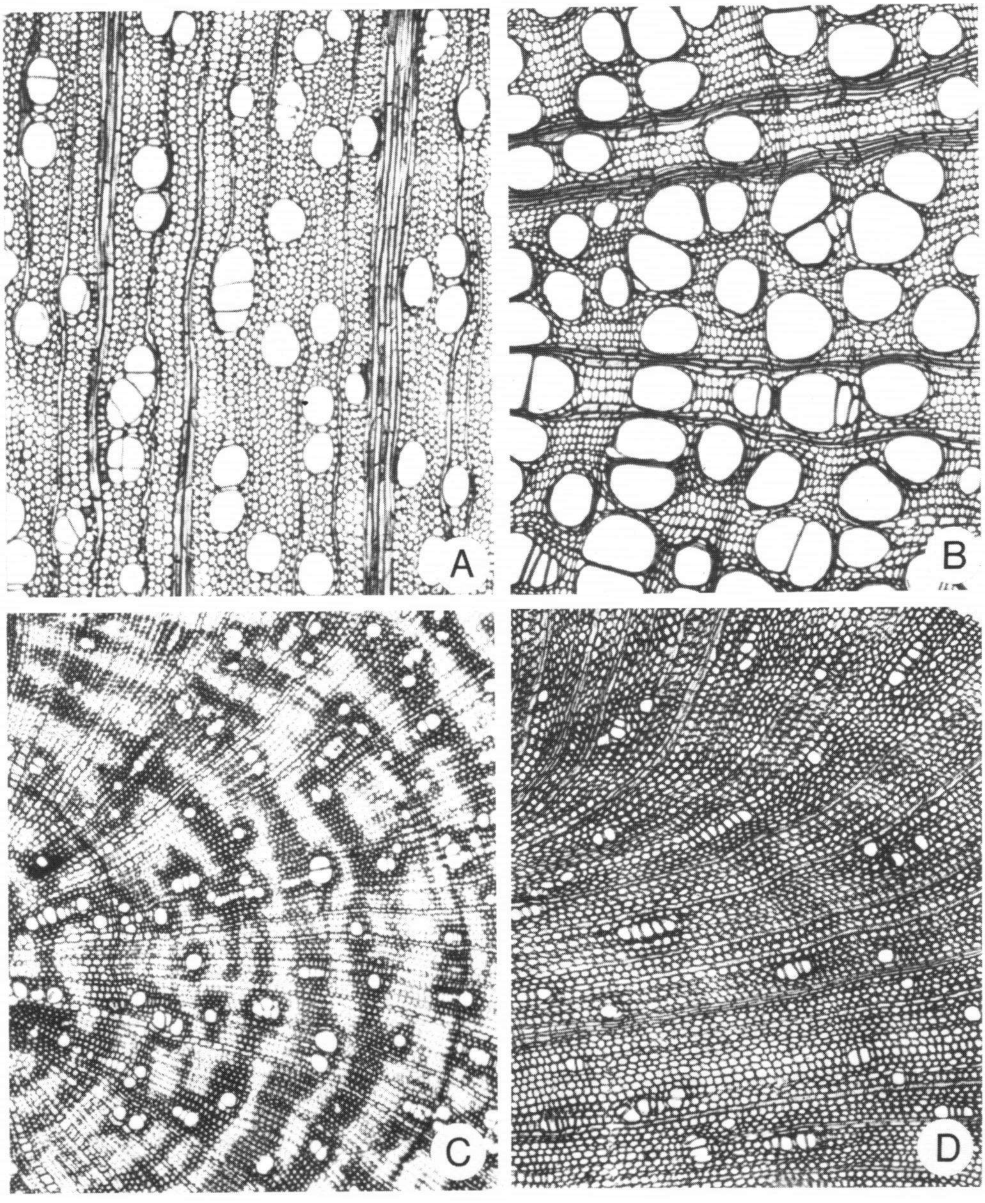

Plate 2. —*Acer pseudoplatanus*. A, transverse section of mature trunk wood; B–D, transverse section of root wood of a range of specimens for comparison with A (all × 65).

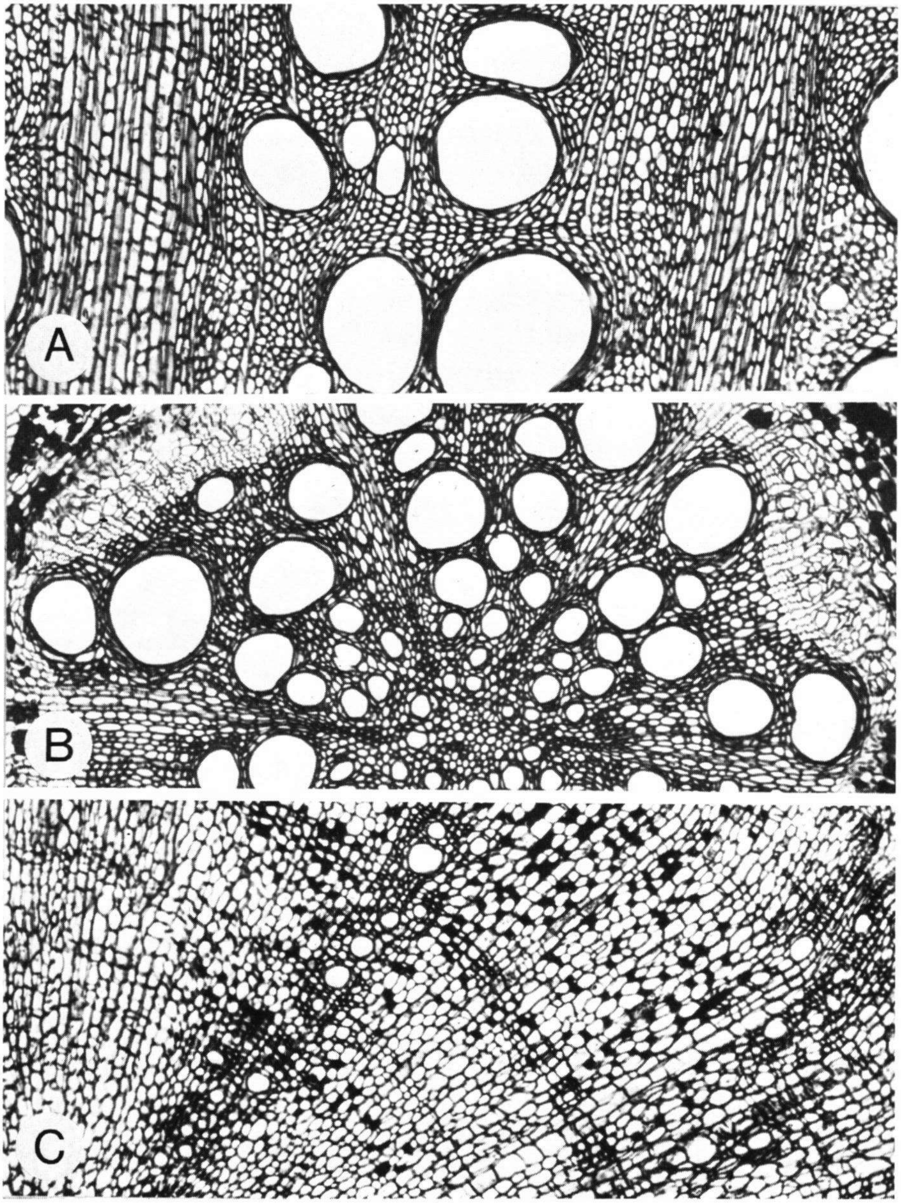

Plate 3. —*Quercus* (*robur* type). A–C, transverse section of roots of different specimens for comparison of anatomy (all ×80).

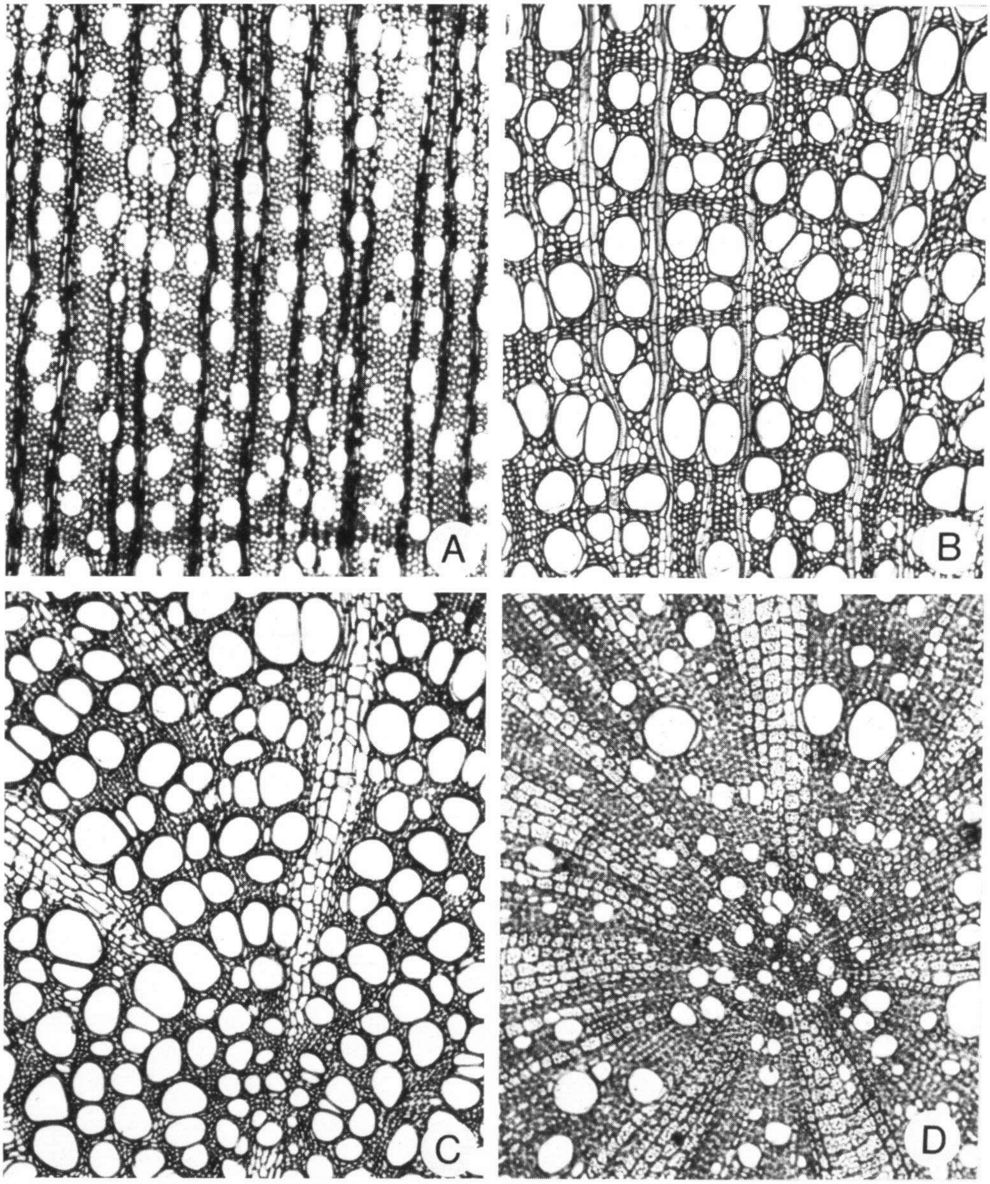

Plate 4. —A, B, *Malus sylvestris*. A, transverse section of mature trunk wood, for comparison with B; B, transverse section of mature root wood; C, D, roots of *Rosa* sp. in transverse section demonstrating part of the range of variability (all × 65).

wood is greater than normally appreciated. Generalisations about root wood anatomy, and in particular, those in which contrasts are made between trunk and root wood, may need revision.

Additional research is required not only from the academic standpoint, but also because of the economic importance of being able to make correct identifications of root samples.

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