ANATOMY OF STEM AND ROOT WOOD OF *PINUS RADIATA* D. DON

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ABSTRACT

Tracheids are much longer and wider in the root wood than in the stem wood of **Pinus radiata** D. Don. The tracheids in the root, in contrast to those in the stem, are larger in the rings close to the organic centre than in outer rings. The occurrence of spiral thickening, callitrisoid thickening, and true axial parenchyma are recorded. The axial resin ducts are associated with a single layer of epithelium together with inner short and outer long parenchyma cells. Compression wood is absent from the root wood. The occurrence of a perforated axial tracheid in a horizontal root is recorded.

INTRODUCTION

The structure of the mature stem wood of radiata pine *(Pinus radiata* D. Don) has been studied and described by several authors at various times during the past 40 years (Welch, 1927; Dadswell and Eckersley, 1935; Phillips, 1948; Greguss, 1955; Jacquoit, 1955; Hudson, 1960). In New Zealand, Barker (1927) made the first intensive study of the secondary wood structure of this species, and during the 1950s and early 1960s several studies were done at the Forest Research Institute on tracheid size.

The genus *Pinus* is separated anatomically from all other conifers by the presence of resin ducts with thin-walled epithelial cells. On the basis of its wood anatomy, *P. radiata* is placed in the ponderosa group which includes amongst others, the commercially grown *P. contorta, P. patula, P. pinaster, P. ponderosa* (see Phillips, 1948). Identification of species within each group by the use of anatomical features is not practicable.

Very little is known about the secondary xylem of gymnosperm and angiosperm roots. Even reference books on plant anatomy give very brief and usually generalised descriptions of root wood structure. In their two volumes totalling 1,500 pages Metcalfe and Chalk (1950) provided a wealth of very useful data on the anatomy of the dicotyledons. These authors, however, make it quite clear in the introductory chapter that it was often necessary to omit the section on roots because information concerning the root structure of many families was lacking. Several years later the symposium on "The Formation of Wood in Forest Trees" held at the University of Harvard, USA (Zimmerman, 1964) revealed our lack of knowledge of secondary growth in roots.

Both the root and stem are morphologically and physiologically important parts of the same unit axis, each organ being dependent on the other. Problems concerning tree growth would be better understood with further knowledge of root wood. Stem and roots perform different functions and normally grow in different environments; therefore some differences in their anatomical structure are expected to occur. Carbohydrates from shoots, growth substances from both shoots and roots, and environment play a decisive role in wood formation. There is some evidence of the existence in roots of highly growth-active unidentified compounds similar to auxins (Street, 1969). It is not known whether growth substances which are required for wood formation in stems and roots are identical. An examination of anatomical differences between stem and root wood could provide valuable leads towards understanding the physiology of wood formation. A few attempts have been made to compare the stem and root wood of dicotyledons (Riedl, 1937; Lebedenko, 1961a, 1962; Shimaji, 1962; Patel, 1965). This problem in some conifers excluding *P. radiata* has been studied by Bailey and Faull (1934), Bannan (1934, 1952, 1954), Riedl (1937), and Lebedenko (1961b). A paper by Fayle (1968) provides an excellent description of radial growth of roots in trees. Large roots are difficult to obtain and it is common knowledge that roots, irrespective of their size, do not produce timber of commercial importance. So it is not surprising that studies in wood anatomy are almost entirely confined to the stems which produce timber.

METHODS AND MATERIALS

Stem and root samples were obtained from *P. radiata* trees, about 37 years old, growing in compartment 1,004, Kaingaroa Forest. The size of these trees is given in Table 1. Stem samples (discs) were obtained 1.2m above ground level. Three buried roots were selected and removed from each tree; from each a transverse disc was obtained at a distance of 30cm from the root origin. Two blocks from each stem disc (one block only in tree 3) and two to seven blocks from each root disc were studied. Transverse (TS), tangential longitudinal (TLS), and radial longitudinal sections (RLS) 18 μ thick were cut from each block. Safranin-stained sections were dehydrated in alcohol, cleared in xylol, and mounted in DePex. Specimens were macerated by boiling small chips of wood in a mixture of glacial acetic acid and hydrogen peroxide. The wood from growth rings 1-2 nearest the pith*, 9-10, and the last two rings nearest the bark were used for measuring cell dimensions. The following measurements and counts were made from the material prepared from each block:

MATERIAL	CELL AND TISSUE MEASUREMENTS
Macerated material	Length of 50 early- and late-wood tracheids
TS of wood	Diameter of 25 early-wood tracheids
	Wall thickness of 25 early-wood tracheids
	4 counts of ray number per mm line
TLS of wood	4 counts for ray number per mm line
	3 counts for ray number per sq mm

* The roots examined do not contain pith, but it is convenient to refer to the true or ontogenetic centre as the "pith".

RESULTS

Stem

Growth Rings distinct (Fig. 1). Axial Tracheids average 38.35 μ in tangential diameter (range 21.80-56.60 μ); average 3.45 μ in wall thickness (range 1.20-6.60 μ); average 2.72mm in length (range 0.73-4.78mm); uniseriate bordered pits present on radial walls; tangential pits rare; spiral thickening very occasional; pits leading to ray parenchyma pinoid (Fig. 2), variable in size and shape; 1-4 per

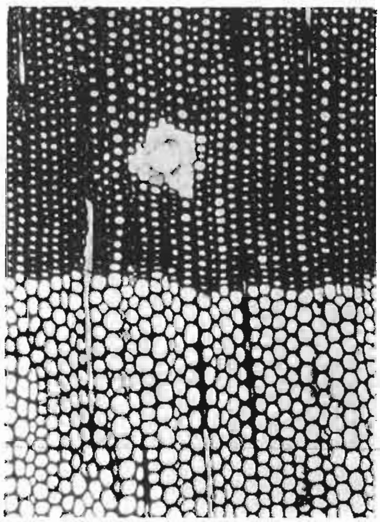

FIG. 1—Stem TS ×50. Distinct ring boundary. The late wood contains resin duct.

FIG. 2—Stem RLS ×325. Pinoid cross-field pits.

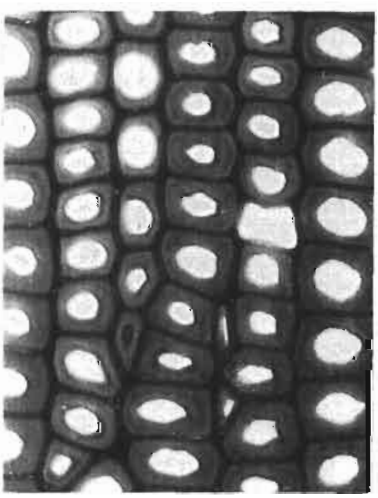

FIG. 3—Stem TS ×325. A thin-walled axial parenchyma cell is shown at left centre.

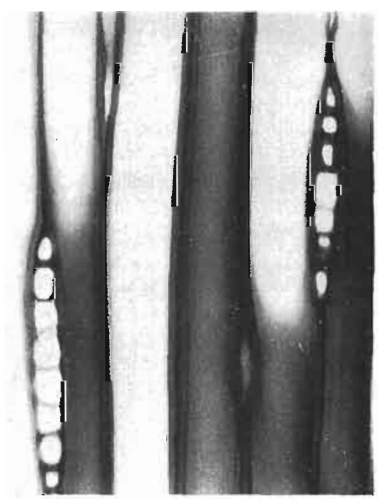

FIG. 4—Stem TLS ×325. Two uniseriate rays can be seen.

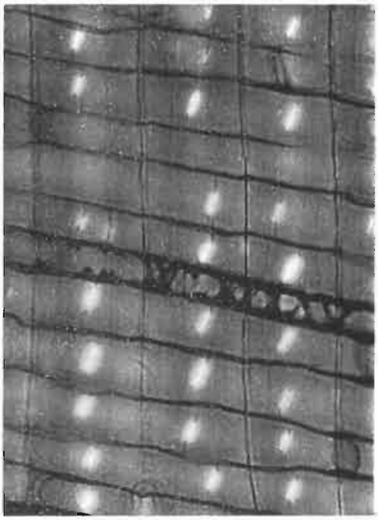

FIG. 5—Stem RLS ×325. Ray parenchyma with thin horizontal walls. A ray tracheid lies across the centre.

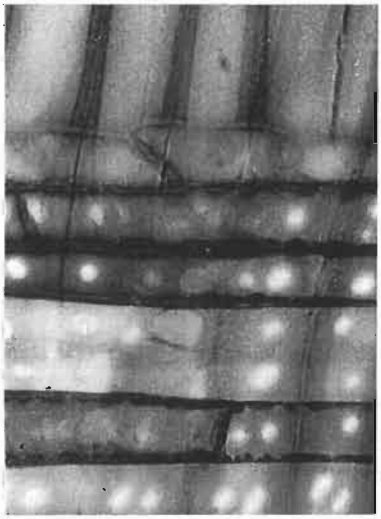

FIG. 6—Stem RLS ×325. Ray parenchyma with thick, pitted horizontal walls.

cross-field. Strand Tracheids associated with resin ducts. Axial Parenchyma sparse (Fig. 3). Axial Resin Ducts lined with thin-walled epithelium with 5-6 cells (range 4-8 cells) as seen in a transverse section; short and long parenchyma cells partly or completely surround the epithelial lining (see Fig. 1). Rays (1) uniseriate (Fig. 4), occasionally biseriate (2) fusiform with horizontal resin duct lined with thin-walled epithelium; average 5.9 per mm line in transverse section of wood (range 4-9); average 5.6 per mm line in tangential longitudinal section (range 4-9); average 31.9 per sq mm in tangential

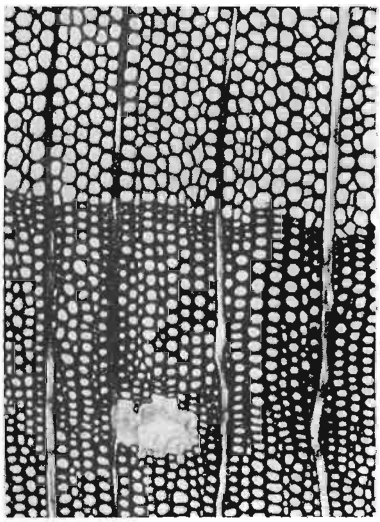

FIG. 7—Root TS ×50. Distinct ring boundary across the centre.

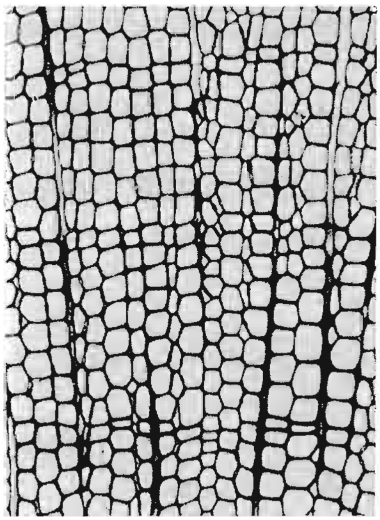

FIG. 8—Root TS ×50. Indistinct growth rings.

longitudinal section (range 18.5-53.5); 1-12 (maximum 17) to 1-21 (maximum 26) cells in height; horizontal walls (a) thin, unpitted (Fig. 5) (b) thicker than (a) and pitted (Fig. 6); ray tracheids present (see Fig. 5), dentate with some reticulation.

Root

Growth Rings distinct (Fig. 7) or indistinct (Fig. 8). Axial Tracheids average 49.68 μ in tangential diameter (range 20.20-88.90 μ); average 3.06 μ in wall thickness (range 1.50-6.30 μ); average 4.52mm in length (range 2.14-9.60mm);

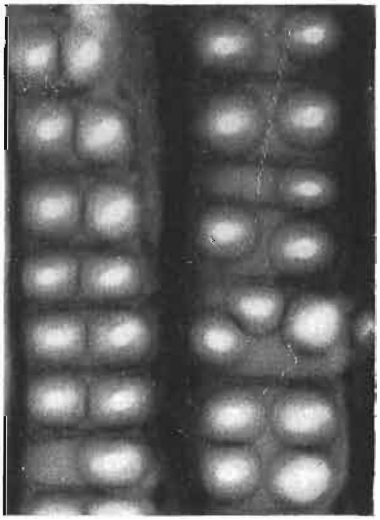

FIG. 9—Root RLS ×325. Biseriate pits.

FIG. 10—Isolated root tracheid ×325. Spiral thickening.

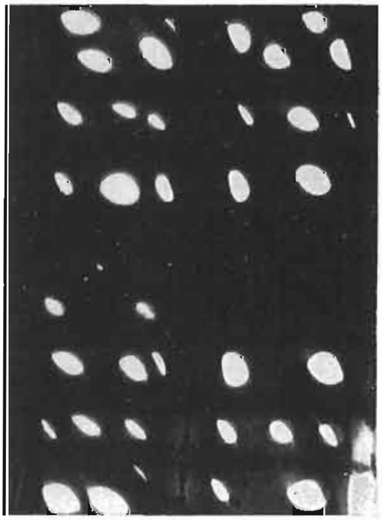

FIG. 11—Root RLS ×325. Pinoid cross-field pits.

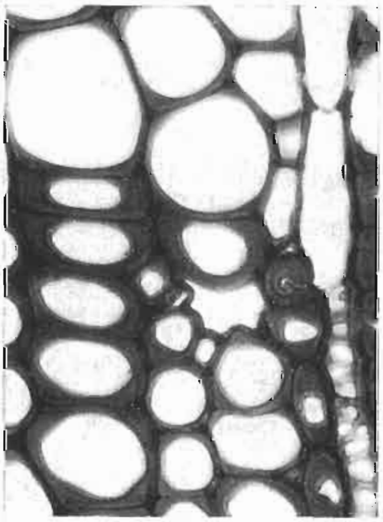

FIG. 12—Root RLS ×325. An axial parenchyma cell with an irregular outline is shown in the late wood.

bordered pits on radial walls in one row, frequently in two rows (Fig. 9) particularly in rings close to the "pith"; tangential pits very sparse; spiral thickening sometimes present (Fig. 10); pits leading to ray parenchyma pinoid (Fig. 11), variable in size and shape, 1-4 to 1-7 per cross-field. Strand Tracheids associated with resin ducts. Axial Parenchyma very sparse to rare (Fig. 12). Axial Resin Ducts lined with thin-walled epithelium with 5-6 cells (range 4-9 cells) as seen in a transverse section; short and long parenchyma cells partly or completely surround the epithelial lining. Rays (1) uniseriate, occasionally biseriate (2) fusiform with horizontal resin duct lined with thin-walled epithelium; average 4.6 per mm line in transverse section of wood (range 2-8); average 4.8 per mm line in tangential longitudinal section (range 3-8); average 22.4 per sq mm in tangential longitudinal section (range 12-36.5); 1-9 (maximum 14) to 1-13 (maximum 22) cells in height; horizontal walls (a) thin, unpitted, (b) thicker than (a) and pitted; ray tracheids present (see Fig. 11), dentate to well developed reticulate.

Various cell and tissue measurements are given in Table 1.

TABLE 1—**Pinus radiata.** Tracheid and ray measurements

Samples	Trees						Tracheids		
	Height	D.b.h.	Age	Early wood Tangential diameter			Length mm		
	m	cm	yr	Range	Mean	CV*%	Range	Mean	CV%
Stem 1	37	56	37	21.8-52.5	37.64	20.99	0.73-4.74	2.70	43.01
Stem 2	35	38	37	24.2-56.6	38.50	20.34	0.75-4.78	2.52	42.98
Stem 3	37	68	37	30.3-53.5	40.00	14.26	2.39-4.14	3.38	15.28
Stem				21.8-56.6	38.35	19.82	0.73-4.78	2.72	40.18
Root 1A			28	28.3-61.6	43.42	17.20	2.71-6.82	4.49	18.39
Root 1B			25	30.3-72.7	47.30	15.69	3.08-6.65	4.84	17.62
Root 1C			30	32.3-72.7	48.96	19.47	2.34-6.96	4.61	21.93
Tree 1 Roots				28.3-72.7	46.56	18.23	2.34-6.96	4.65	19.58
Root 2A			17	32.3-72.7	50.48	17.56	2.18-6.18	3.72	20.30
Root 2B			16	31.3-88.9	47.37	23.08	2.52-6.26	4.05	17.58
Root 2C			18	32.3-63.6	50.44	13.98	2.84-6.87	4.25	19.40
Tree 2 Roots				31.3-88.9	49.43	18.54	2.18-6.87	4.01	19.82
Root 3A			20	43.4-83.8	62.75	14.51	3.24-9.60	5.98	27.28
Root 3B			31	33.3-78.8	50.64	20.59	2.14-7.30	4.24	21.98
Root 3C			17	20.2-79.8	45.81	27.37	2.22-7.38	4.46	21.12
Tree 3 Roots				20.2-83.8	53.06	24.30	2.14-9.60	4.89	29.37
Root				20.2-88.9	49.68	21.51	2.14-9.60	4.52	25.38

* Coefficient of variation.

DISCUSSION

The main differences between the stem and root wood were quantitative and were reflected in the cell size. Although the roots examined were younger than the stems (Table 1), their tracheids were much longer and wider. That the tracheids are larger (longer and wider) in the conifer roots than in the stems is a generally accepted view (Sanio, 1872; Bailey and Faull, 1934; Reidl, 1937; Bannan, 1934; 1965). In the present work the initial tracheid size (i.e., near "pith") in the roots was greater than the final size in the stems (Table 2). As shown by Sanio (1872) and subsequently by many others, the tracheids of conifers are smaller in the inner than in the outer rings of the stems. In contrast to this rule the tracheids in the roots examined were commonly larger and thicker-walled in the growth rings close to the "pith" than elsewhere. Similar trends in the roots were also reported by Sanio (1872) for tracheid length in *Pinus sylvestris;* Bailey and Faull (1934) for tracheid diameter in Abietineae [sic], and by Bannan (1965) for tracheid length and diameter in several conifers. Bailey and Faull (1934),

TABLE 1 (continued)

Early wood Cell wall thickness μ			Rays Number/mm line TS		Rays Number/mm line TLS		Rays Number/sq. mm TLS	
Range	Mean	CV%	Range	Mean	Range	Mean	Range	Mean
2.2-6.6	3.82	32.39	5-9	6.8	4-7	5.6	24.7-53.5	35.8
1.2-6.6	3.10	48.23	4-8	5.4	4-8	5.8	19.7-47.0	32.2
1.9-5.3	3.35	28.06	4-6	5.0	5-6	5.3	18.5-26.5	23.6
1.2-6.6	3.45	39.35	4-9	5.9	4-8	5.6	18.5-53.5	31.9
1.9-4.9	3.04	20.30	4-7	5.4	3-8	5.1	21.2-30.0	24.6
1.9-4.4	3.13	16.44	4-8	5.0	3-6	4.9	18.5-28.5	24.2
1.9-4.9	3.27	19.24	3-6	4.5	4-7	5.1	19.0-26.2	22.1
1.9-4.9	3.15	18.87	3-8	5.0	3-8	5.0	18.5-30.0	23.7
1.9-4.9	3.03	18.44	3-7	5.0	3-6	4.5	19.0-29.0	23.5
1.9-5.8	3.12	22.99	4-7	5.5	4-6	4.8	17.5-25.5	20.8
1.7-4.1	2.92	18.46	2-6	4.2	3-6	4.6	15.2-29.7	22.5
1.7-5.8	3.03	20.27	2-7	4.7	3-6	4.6	15.2-29.7	22.5
2.7-4.9	3.28	13.20	3-5	4.4	4-6	4.6	12.0-24.2	18.8
2.4-6.3	3.67	21.31	3-5	4.1	3-6	4.6	15.2-26.5	19.9
1.5-3.2	2.11	18.43	2-5	3.7	4-6	4.9	21.2-36.5	25.0
1.5-6.3	3.02	28.83	2-5	4.1	3-6	4.7	12.0-36.5	21.0
1.5-6.3	3.06	23.02	2-8	4.6	3-8	4.3	12.0-36.5	22.4

TABLE 2—**Pinus radiata.** Tracheid measurements from pith outwards

Samples		Age (yr)	Tracheids								
			Length (mm)			Diameter (μ)			Wall thickness (μ)		
			Ring number from pith								
			1-2	9-10	Last 2	1-2	9-10	Last 2	1-2	9-10	Last 2
Stems	1	37	1.19	3.41	3.50	29.09	45.42	38.42	2.74	3.50	5.20
	2	37	1.13	3.00	3.41	30.92	41.38	43.20	1.65	2.82	4.84
	3	37	—	—	3.38	—	—	40.00	—	—	3.35
Roots	1A	28	4.78	4.53	4.18	46.76	41.95	41.56	3.04	2.85	3.24
	1B	25	4.75	4.91	4.86	51.91	45.06	44.92	3.31	3.08	3.01
	1C	30	4.95	3.86	5.02	56.00	44.08	46.79	3.35	3.40	3.05
Roots	2A	17	3.92	3.38	3.87	50.91	45.70	54.82	3.16	3.06	2.88
	2B	16	4.34	4.06	3.74	54.33	42.87	44.89	3.68	3.03	2.66
	2C	18	4.68	3.76	4.32	49.57	50.96	50.79	3.28	2.54	2.94
Roots	3A	20	4.62	6.80	6.52	59.42	65.79	63.03	3.49	3.26	3.08
	3B	31	4.97	4.08	3.67	56.80	50.62	44.48	3.93	3.53	3.55
	3C	17	5.11	4.36	3.91	58.82	39.76	38.83	2.01	2.04	2.26

however, noted that in *Sequoia sempervirens* the root tracheids were narrower in the innermost rings than elsewhere in the root.

The occurrence of biseriate pits on the radial walls of radiata pine stem tracheids is rare to occasional (Barker, 1927; Welch, 1927; Phillips, 1948; Hudson, 1960). In the present work biseriate pits, although frequent in a few rings near the "pith" in the root wood became less frequent or even sparse in the wood near the bark. In this respect the outer root wood is similar to the stem wood. The occurrence of biseriate pits on the radial walls of the root tracheids is associated with the wide cells mentioned earlier. Bannan (1952, 1954) and Lebedenko (1961b) also reported frequent occurrence of biseriate pits in the root tracheids.

In conifers spiral thickening occurs as a regular feature in the wood of a few genera, namely, *Taxus, Torreya, Pseudotsuga, Cephalotaxus, Amentotaxus* and infrequently in *Picea* and *Larix.* Penhallow (see Bailey, 1909) and Bailey (1909) observed this feature in *Pinus taeda* and *Pinus attentuata* respectively. The occurrence of spiral thickening in the wood of radiata pine described by Barker (1927) was, in fact, the spiral checking which is associated with an abnormality called compression wood. In the present work the tracheids of radiata pine sometimes showed spiral thickening which occurred irregularly, even within a single tracheid. This thickening was often associated with the bordered pits (Fig. 13). Such thickening which is appropriately known as callitrisoid thickening was reported earlier in the secondary xylem of *Dacrydium cupressinum* (Patel, 1967). Howard and Manwiller* (1969) made similar observations on the stem wood of the southern pines.

It is well known that the axial and horizontal resin ducts which occur in the wood of a few conifers are surrounded by epithelium or epithelial cells. The terms "epithelium" and "epithelial cells" which are synonymous, have been used by several authors when

* This publication was seen after the completion of the present work.

describing the resin ducts (Bailey, 1909; Phillips, 1948; Eames and MacDaniels, 1951; Esau, 1965; Greguss, 1955; Jacquoit, 1955; Jane, 1956a; Tsoumis, 1968). Not one of these authors indicates whether the epithelium is composed of one or more layers of parenchyma cells. Panshin *et al.* (1964), and Kollman and Cote (1968) stated that the epithelium of the axial ducts may consist of one or more layers of parenchyma cells. On the other hand, the Committee on Nomenclature (International Association of Wood Anatomists, 1964) defines the epithelium as "the layer of secretory parenchymatous cells that surrounds an intercellular canal or cavity". Bannan (1936) correctly distinguished the single-layered epithelium from the surrounding parenchymatous cells associated with the axial resin ducts. Engstrom and Back (1959), Nyren and Back (1959), Howard and Manwiller (1969), and Kibblewhite (1969) described the epithelium and the surrounding parenchymatous cells in some detail. According to these authors only the innermost layer of cells lining the resin duct is the epithelium. In the axial resin duct the layer outside the epithelium is composed of short units of parenchyma. The layer surrounding the short units of parenchyma is composed of elongated units of parenchyma. The difference between the length of units of inner and outer parenchyma is considerable (Engstrom and Back, 1959; Nyren and Back, 1959; Howard and Manwiller, 1969).

In the stems and the roots of *Pinus radiata* the one-layered epithelium of the axial resin ducts as seen in transverse section commonly consists of 5-6 cells. The parenchymatous tissue surrounding the epithelium shows marked structural variability which is easily seen in the longitudinal view. The layer of thin-walled parenchyma immediately surrounding the epithelium (average length 57 μ) consists of short units (average length 93 μ). The layer or layers outside the short parenchyma consists of short, as well as long units (average length 280 μ). The outermost layer consists almost exclusively of very long units (average length 623 μ). In other words, the parenchymatous cells associated with the axial resin ducts increase in length from the duct cavity outwards. It is not uncommon to find thick-walled units in all but the short thin-walled parenchyma and the epithelium. Such units have conspicuous simple pits. Only one thick-walled unit with conspicuous simple pits has been seen among the short parenchyma. A few parenchyma cells excluding the epithelial cells gave a positive reaction with phloroglucinol and hydrochloric acid, indicating some degree of lignification.

Strand tracheids which do not form a sheath are present outside the very long parenchyma followed by axial tracheids. It is remarkable that all the axial elements of the secondary xylem of *P. radiata* are arranged almost side by side within a very small distance from the resin duct cavity. This arrangement also demonstrates various changes from the short thin-walled cells with fine, inconspicuous simple pits to the long thick-walled cells with conspicuous bordered pits. The epithelium of the horizontal resin duct is sometimes partly surrounded by a layer of axially and radially short parenchyma cells. The small size of these cells is the only criterion used to distinguish these cells from the ray parenchyma.

In the wood of *Pinus* species axial parenchyma is restricted to that associated with the resin ducts (Bailey, 1909; Phillips, 1948; Esau, 1960, 1965; Isenberg, 1963; Panshin *et al. 1964;* Tsoumis, 1968). In the conifers the parenchyma cells associated with or in the close vicinity of the axial resin ducts are not regarded as true axial parenchyma (Phillips, 1948). True axial parenchyma occurs in several conifers, e.g., *Dacrydium cupressinum, Podocarpus totara, Juniperus virginiana, Sequoia sempervirens, Cryptomeria japonica, Chamaecyparis lawsoniana.* Jacquoit (1955) reported the rare occurrence of axial parenchyma in *Pinus peuce,* a species from the Balkan Peninsula, but he did not indicate whether the parenchyma was close to or apart from the resin ducts. Although Greguss (1955) did not find axial parenchyma in *P. peuce,* he found "thin walled cells which are generally elongated and terminated in a roundish cyst-like growth" in *P. massoniana* which is indigenous to south-eastern China.

The occurrence of sparse, thin-walled cells among the thick-walled late wood tracheids of radiata pine stem wood indicates that true axial parenchyma is present in this species. These cells were not associated with the resin ducts. Two thin-walled cells and their surrounding tissue were studied in a transverse section cut to a thickness of 18 μ. The block of wood from which this section was cut, was observed under stereomicroscope. The cells concerned were spotted and the area in which these occurred was marked on the block. Radial longitudinal sections of this small area containing the cells were cut, and it was thus possible to study the longitudinal view of the cells. The cells were in the form of strands. The presence of transverse walls (one with nodule) and simple pits on the radial walls indicated beyond doubt that the thin walled cells under observation were true axial parenchyma cells (Figs. 14, 15). The pits between

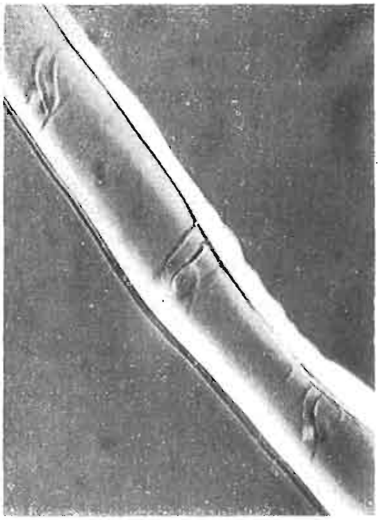

FIG. 13—Isolated root tracheid $\times 500$. Thickening associated with bordered pits.

FIG. 14—Stem RLS $\times 135$. Two axial parenchyma cells with transverse walls are shown in the centre.

the axial parenchyma and the ray parenchyma are simple. A few similar cells which were cut longitudinally all proved to be axial parenchyma. It was difficult to recognise axial parenchyma in the root wood where the late wood was not as well developed as in the stem wood. It is quite possible that axial parenchyma is less common in the roots than in the stem of radiata pine. According to Bannan (1952) axial parenchyma is also less frequent in the roots than in stems of *Chamaecyparis lawsoniana* and *C. thyoides*.

Several permanent slides of the stem wood of *Pinus* species in the Forest Research Institute slide collection were examined and the following species showed thin-walled cells quite apart from the axial resin ducts, and were similar to true axial parenchyma as seen in a transverse section: *P. nigra* var. *austriaca* (Austrian pine), *P. banksiana* (jack pine), *P. elliottii* (slash pine), *P. echinata* (shortleaf pine), *P. muricata* (muricata pine), *P. contorta* (lodgepole pine), *P. palustris* (longleaf pine), *P. resinosa* (red pine), *P. rigida* (pitch pine) and *P. taeda* (loblolly pine).

Compression wood is found mostly on the under side of branches and non-vertical stems of conifers, including radiata pine. The pith is eccentric in such plant organs, and occupies a position above the geometric centre. The three most typical microscopic features of the compression wood are the rounded outlines of the tracheids in transverse section, the occurrence of intercellular spaces, and the presence of spiral checks in the secondary walls of the tracheids. In the nine transverse discs of the horizontal roots examined, the "pith" was towards the upper side in six roots, centric in one and laterally displaced in the remaining two. In spite of their horizontal position and eccentricity of the growth, the roots did not show any evidence of compression wood. Absence of compression wood from the buried roots of several conifers has been reported by Patel (1964), Westing (1965), and Fayle (1968). However, Westing (1965) found compression wood in the buried roots of *Tsuga canadensis*.

Perforated tracheids were found in the secondary xylem of *Sequoia sempervirens* and *Thuja occidentalis* by Jane (1956b) and Bannan (1958) respectively. The perfora-

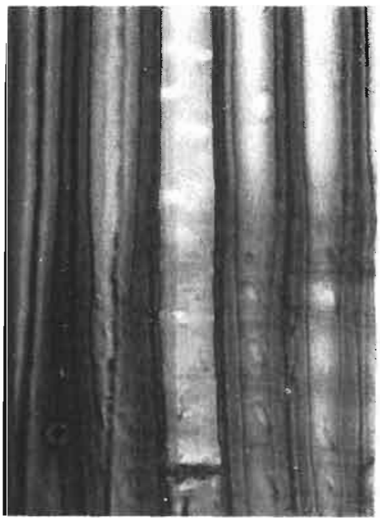

FIG. 15—Stem RLS ×325. An axial parenchyma cell with nodular cross wall and simple pits is shown down the centre of the photograph.

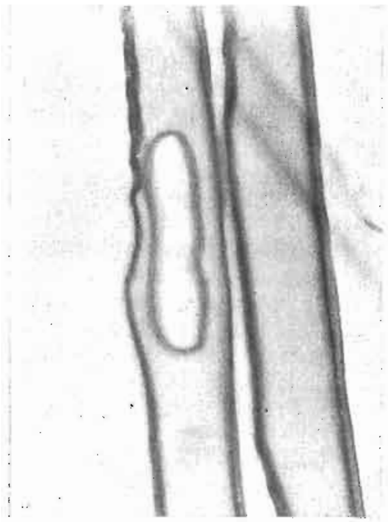

FIG. 16—Isolated root tracheids ×315. A simple perforation is seen on the left hand one.

tions were lateral and were present on the radial side of the tracheids. The occurrence of a simple lateral perforation on the tangential side of an axial tracheid in the macerated material of a 31-year-old horizontal root of *Pinus radiata* is recorded (Fig. 16). The perforated tracheids of *Sequoia* occurred in the area of compression wood (Jane, 1956b). Although Bannan (1958) did not mention this abnormality, Plate 1e of his paper clearly shows two perforated tracheids in association with compression wood tracheids. In the present material not one tracheid showed the characteristics of compression wood. The formation of perforated tracheids is attributed to a local deficiency in the synthesising mechanism concerned with surface growth of the wall (Bannan, 1958).

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