

# THE NATURE OF REACTION WOOD

## II. THE CELL WALL ORGANIZATION OF COMPRESSION WOOD TRACHEIDS

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### Summary

Optical and X-ray methods have been used in the examination of the secondary cell wall of compression wood tracheids from a number of species of gymnosperms. By these methods it has been shown that the cell wall of compression wood tracheids consists of two layers. In the outer layer the micelles are inclined at a large angle to the longitudinal axis of the tracheid, while in the inner layer the micelles are inclined at a relatively smaller angle. In the inner of the two layers there exist radial discontinuities in the spiral micellar structure, which are visible as longitudinal striations in the cell wall. These discontinuities also account for the radial distribution of lignin which is observed in transverse sections of compression wood tracheids. By determining the average tracheid length of the last-formed late wood in the various growth rings of several eccentric stems of *Pinus radiata* D. Don it has been shown that the tracheids of compression wood are appreciably shorter than would be the case if no compression wood were present. A study of the change in micellar orientation with change in tracheid length has indicated that the angle of micellar orientation in compression wood tracheids does not differ significantly from that existing in normal wood tracheids of similar length. In so far as the properties of wood are determined by cell wall organization, it is concluded that comparisons between compression wood and normal wood should be made on material of the same tracheid length and spiral organization. It is suggested that both the reduction in tracheid length and eccentric radial growth in stems containing compression wood are to be attributed to an increase in the number of both transverse and tangential longitudinal divisions of the fusiform initials of the cambium.

### I. INTRODUCTION

A study of the cell wall organization of the tracheids from the compression wood of gymnosperms is of interest, both from the way in which the organization of the normal cell wall has been modified in response to a gravitational stimulus, and from the way in which the properties of the wood change as a result of this modification. Furthermore, the greater anatomical simplicity of the gymnosperms provides a more favourable material for the study of these changes than the corresponding reaction wood (tension wood) of angiosperms, discussed in the first paper of the series (Wardrop and Dadswell 1948). The macroscopic appearance of compression wood and the anatomical details of its constituent tracheids (rounded form and associated intercellular spaces, cell walls somewhat thicker than normal with marked longitudinal spiral striations, and shorter length) have been referred to by numerous workers (Pillow and Luxford 1937;

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Münch 1937-38; Jaccard 1938). The influence of compression wood on the properties of timber has also been described (Pillow and Luxford 1937; Desch 1947; Brown, Panshin, and Forsaith 1949; Dadswell and Wardrop 1949). Chemically, compression wood is relatively higher in lignin content and lower in cellulose than normal wood (Johnson and Hovey 1918; Dadswell and Hawley 1929) and it has been shown by Bailey and Kerr (1937) and Dadswell and Ellis (1940) that the lignin distribution in the cell walls of compression wood tracheids is in a characteristic radial pattern when viewed in cross section in contrast to the more normal radio-concentric pattern of normal wood tracheids.

The secondary wall of the normal tracheids of gymnosperms consists of three coaxial micellar spirals (see Fig. 1(A)) recognizable, when cross sections are examined microscopically between crossed Nicols, as three layers of different optical properties. The micellar organization of these layers is such that, with reference to the longitudinal tracheid axis, the central layer (S2) consists of a steep micellar spiral while the outer layer (S1) and the inner layer (S3), which is adjacent to the lumen, possess a relatively flat micellar spiral (Kerr and Bailey 1934; Wardrop and Preston 1947). The inner layer (S3), however, is not always present. If this conception of the cell wall organization of normal tracheids is accepted, it is pertinent to know in what ways compression wood tracheids differ from the typical organization.

An examination of the literature suggested that the following aspects of the organization of compression wood tracheids required further investigation:

- (i) whether all three of the layers of the secondary wall, S1, S2, and S3, occur in compression wood tracheids (Münch reports only two),
- (ii) the significance of the radial lignin pattern visible in cross section,
- (iii) the nature of the characteristic spiral striations of the cell wall visible in longitudinal section, and
- (iv) the significance of the observation that compression wood tracheids are shorter than comparable normal tracheids.

Each of these aspects will be discussed in the present paper, but it is proposed to refer particularly to the way in which the cell wall organization of compression wood tracheids is related to their length.

It has been well known since the time of Sanio (1872) that the average tracheid length in stems of gymnosperms increases rapidly over successive annual rings during the first 20-50 years of growth and thereafter ceases to increase or increases only slowly. The fundamental investigations of Preston (1934, 1948) have indicated that the micellar spiral organization of the central layer (S2) of the secondary wall can be related to the tracheid length by an equation of the form:

$$\cot \theta = a + bL, \quad \dots \dots \dots (1)$$

where  $L$  is the tracheid length,  $\theta$  is the angle between the tangent to the direction of the micelles and the longitudinal axis of the tracheid, and  $a$  and  $b$  are constants. A similar equation has also been applied to the outer layer (S1) of the secondary wall (Preston and Wardrop 1949).

From these investigations it is obvious that, as the tracheids increase in length over successive growth rings, the micellar spiral angle  $\theta$  becomes smaller, and that short tracheids will possess a relatively flatter micellar spiral angle than long tracheids. This is of considerable significance in relation to compression wood tracheids since it has been reported (Pillow and Luxford 1937; Münch 1937-38) that these tracheids are shorter than comparable normal wood tracheids and that they possess a flat spiral micellar organization. Thus the question is raised as to whether the spiral micellar organization of compression wood tracheids is related to tracheid length in the same manner as is represented by equation (1) or in some other way. Moreover it was felt that some confirmatory evidence regarding the length of compression wood tracheids in relation to normal tracheids was desirable, as statements on this point in the literature are not supported by data, nor do they indicate how comparisons were made. This is important in view of the known variations in tracheid length with distance from pith, and with height in tree. It was therefore decided to examine the changes in tracheid length and associated changes in spiral micellar orientation in eccentric stems containing both normal and compression wood. The results of these investigations together with additional information on points (i) to (iv) above are given in the following sections of this paper.

## II. EXPERIMENTAL

### (a) Details of Cell Wall Organization

Observations were made on compression wood from a variety of endemic and imported species of gymnosperms, including the following:

<i>Pinus radiata</i> D. Don.	}	from plantations
<i>Pinus pinaster</i> Soland.		
<i>Pseudotsuga taxifolia</i> (Lamb.) Britt.	}	branch material from trees growing in the Melbourne Botanical Gardens
<i>Taxus baccata</i> L.		
<i>Taxodium distichum</i> (L.) Rich.		
<i>Araucaria cunninghamii</i> Ait.		
<i>Araucaria bidwilli</i> Hook.		
<i>Athrotaxis selaginoides</i> D. Don.		
<i>Callitris tasmanica</i> Baker and Smith.		
<i>Dacrydium franklinii</i> Hook. f.		
<i>Diselma archeri</i> Hook. f.		
<i>Phaerosphaera hookeriana</i> Archer.		
<i>Phyllocladus asplenifolius</i> (Labill.) Hook.		

Examination of thin cross sections by means of the polarizing microscope using crossed Nicols revealed two definite layers of the secondary wall, both of which showed considerable birefringence. These two layers appeared to be comparable with layers S1 and S2 of Figure 1(A), the layer comparable with S3 being usually absent or only poorly developed (Plate 1, Fig. 1). The birefringence of layer S2 was rather less than that of the outer layer, indicating that, in

this layer, there was a relatively steeper spiral micellar organization than in the outer layer. The sign of birefringence of both of the layers was positive with respect to the cell surface, indicating that the micelles were parallel to the surface.

Visual evidence of the micellar orientation in the two layers has been obtained by crushing isolated fragments of compression wood tracheids from hoop pine (*Araucaria cunninghamii*) in the manner described in the first paper of this series (Wardrop and Dadswell 1948). Part of such a tracheid is shown in Plate 1, Figure 3, in which two distinct directions of striations can be seen—one being almost transverse to the longitudinal tracheid axis, and the other inclined at approximately  $45^\circ$  to this axis. The dichroic properties of these striations made it apparent that they corresponded to true directions of micellar orientation. The characteristic striations normally visible without crushing were very coarse and easy to distinguish in the various species of the genus *Pinus* (cf. Jaccard 1940), but in certain other specimens examined, e.g. *Diselma archeri*, *Phaerosphaera hookeriana*, *Araucaria cunninghamii*, they were extremely fine, although visible under high power. Examination of these striations indicated that there was apparently no other cell wall material between them, since they were often displaced in sectioning (Plate 1, Fig. 4). This observation was confirmed by cutting sections at angles approximately parallel to the direction of the striations when it could be seen that they were ribs of cell wall substance extending through the layer S2 of the secondary wall (Plate 1, Fig. 5).

X-ray examination of various specimens of compression wood was carried out with the beam perpendicular to the tangential face and using  $\text{CuK}\alpha$  radiation and a specimen film distance of 3 cm. (cf. Bailey and Berkley 1942). The spread of the equatorial arcs yielded a value for the angle of the micellar orientation in agreement with that obtained by optical observations (Plate 1, Fig. 6).

In referring to the layers of the secondary wall of compression wood tracheids, Bailey and Berkley have reported that, in *Taxodium distichum* (L.) Rich., there is an intervening layer which is isotropic or feebly birefringent between the two wide layers normally present. They stated that the optical properties of this layer are due—"not to a longitudinal orientation of fibrils, but to the fact that this layer is composed largely of non-cellulosic constituents." In the present investigation, no obvious isotropic layer similar to that depicted by Bailey and Berkley was observed in *Taxodium distichum*. However, in *Pinus pinaster*, *Pinus radiata*, and *Pseudotsuga taxifolia* there was some evidence of an isotropic layer between the two main layers of the secondary wall of compression wood tracheids (Plate 1, Fig. 2), but it was not possible to decide whether this was of the type referred to by Bailey and Berkley.

#### (b) Lignin Distribution in the Cell Wall

In transverse section the distribution of lignin as demonstrated by means of treatment with 72 per cent. sulphuric acid (Dadswell 1931) was observed to be in a radial pattern. This is in contrast with the radio-concentric lignin pattern for normal wood tracheids. Those specimens with coarse spiral striations in the

cell wall, e.g. *Pinus pinaster*, showed a coarse lignin pattern in cross section (Plate 2, Fig. 1); on the other hand, those with fine spiral striations showed a fine lignin pattern in cross section (Plate 2, Fig. 3). Longitudinal sections treated in the same way gave a similar correlation between striations and lignin pattern (Plate 2, Fig. 2). In a specimen of *Araucaria cunninghamii* two striation directions in the lignin pattern were observed when the focus was altered slightly; these presumably correspond to the two layers of the cell wall referred to above and are illustrated in two adjacent tracheids in Plate 2, Figure 4.

(c) *Variation of Tracheid Length and Micellar Organization of the Cell Wall in Stems containing Compression Wood*

For this part of the investigation cross sections of logs taken from three specimens of *Pinus radiata* approximately 20 years old were obtained. Each of these showed compression wood on one side. One was used for the determination of the tracheid length, at 60° intervals around the stem in the late wood of the ninth growth ring, which contained compression wood. The average tracheid length in each case was determined by the measurement of 50 tracheids isolated from longitudinal sections cut from the last-formed late wood. The

TABLE 1  
VARIATION IN TRACHEID LENGTH AT 60° INTERVALS AROUND THE NINTH GROWTH RING  
OF A SPECIMEN OF *PINUS RADIATA* D.DON

Radius	Tracheid Length (mm.)	Ring Width (cm.)	Comments
1 (0°)	3.58	0.80	Comp. wood absent
2 (60°)	3.15	0.80	Comp. wood absent
3 (120°)	2.94	0.95	Comp. wood absent
4 (180°)	2.74	1.20	Comp. wood present
5 (240°)	2.79	1.20	Comp. wood present
6 (300°)	3.39	0.85	Comp. wood absent

results, set out in Table 1, indicate the variation in tracheid length obtained. Ring width and presence or absence of compression wood are also recorded. In the other two specimens a strip of wood was taken along a diameter, in such a manner as to pass through the compression wood bands occurring on one side of the cross sections. The average angle of micellar orientation was determined in the last-formed late wood of the different growth rings from the degree of spread of the 002 diffraction arcs in the X-ray diagrams. The values so obtained corresponded to that existing in layer S2 of the cell wall (Plate 1, Fig. 6). After X-ray examination the specimens of late wood from each ring were macerated and the average tracheid lengths determined. Results of these determinations, together with the corresponding angles of micellar orientation, information on presence or absence of compression wood, and ring width, for both sides of the stem, are shown in Table 2.

TABLE 2  
VARIATION IN TRACHEID LENGTH, MICELLAR SPIRAL ANGLE, AND RING WIDTH IN  
*PINUS RADIATA* D.DON

Specimen	Age in Years	Wide Side			Narrow Side		
		Tracheid Length (mm.)†	Micellar Spiral Angle (degrees)	Ring Width (cm.)	Tracheid Length (mm.)†	Micellar Spiral Angle (degrees)	Ring Width (cm.)
1	1	1.28	53	0.74	—	48	0.60
	2	1.56	—	0.66	1.64	—	0.80
	3	1.77	48	1.00	2.07	50	1.00
	4	2.10	—	0.80	2.13	—	0.60
	5	2.36	45	0.60	2.73	—	0.50
	6	2.84	—	0.80	2.90	39	0.60
	7	2.84	41	0.80	2.72	—	0.40
	8	3.27	—	0.50	3.07	35	0.40
	9	3.13	36	0.70	3.11	26	0.40
	10*	2.61	40	0.80	3.35	29	0.40
	11*	2.53	35	0.60	3.39	31	0.40
	12*	2.89	42	0.70	3.37	29	0.30
	13*	2.92	37	0.80	3.18	24	0.50
	14	3.18	27	0.60	3.30	23	0.10
	15	3.03	—	0.80	3.43	—	0.30
	16	3.35	35	0.70	3.39	25	0.30
	17	2.88	—	1.00	3.52	—	0.30
	18	3.19	—	1.10	3.48	—	0.30
	19	2.96	25	0.80	3.57	23	0.20
	20	3.05	—	0.70	3.50	—	0.30
2	1	1.72	34	1.60	—	—	1.50
	2	—	—	1.35	2.61	31	1.60
	3	2.56	32	1.80	2.71	35	1.85
	4	—	—	1.50	—	—	1.40
	5	3.14	30	1.35	3.33	23	1.25
	6	3.54	24	1.20	—	—	0.85
	7	3.70	24	1.20	3.72	14	0.65
	8	3.89	22.5	1.00	—	—	0.25
	9*	3.98	27	0.85	4.02	13.5	1.00
	10*	2.47	32	1.00	—	—	0.75
	11*	2.67	37	1.05	4.28	15	0.65
	12*	3.13	35	1.05	—	—	0.60
	13*	2.70	22.5	1.00	4.23	16	0.45
	14*	—	—	1.00	—	—	0.60
	15*	3.15	31	0.85	4.40	16	0.50
	16*	—	—	0.95	—	—	0.40
	17*	2.97	33.5	0.75	4.42	12	0.50
	18*	—	—	1.00	—	—	0.55
	19	3.59	28	1.10	4.51	13	0.50

† Average of 50 measurements.

\* Compression wood present.

## III. DISCUSSION

From a consideration of the above evidence it will be apparent that the secondary wall of compression wood tracheids usually consists of only two layers which, from the disposition of the micellar spirals, might be regarded as analogous to the layers S1 and S2 of normal tracheids (Fig. 1(A)). The inner layer corresponding to S3 of the normal tracheids is absent or only feebly developed. The existence of an isotropic non-cellulosic layer between the layers S1 and S2 reported by Bailey and Berkley (1942) cannot be regarded as a characteristic of these tracheids. However, the inner of the two layers normally present in compression wood tracheids differs from the layer S2 of the normal tracheids. There exists a radial discontinuity of structure such that this layer can be imagined to consist of spirally arranged ribbons of cell wall material, the longer, narrow edge of which is attached to the adjacent cell wall layer. From the X-ray and optical evidence it is apparent that the micelles lie parallel to the length of these spiral bands. In terms of this structure it can be seen that the individual cells would appear to have a radial lignin distribution when examined in cross section (Plate 2, Figs. 1 and 3) and a spiral distribution in longitudinal section (Plate 2, Figs. 2 and 4).

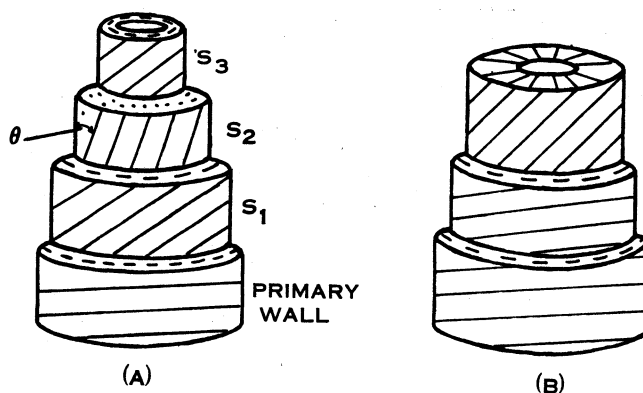


Fig. 1.—Diagrammatic representation of the cell wall organization in (A) a normal tracheid and (B) a compression wood tracheid. The lines represent the directions of spiral micellar orientation only. The texture of the primary wall ("tube structure") differs from that of the secondary wall layers ("fibrous structure").

On the basis of such a model it is also apparent that the optic sign of the wall would be positive with respect to the cell surface. Thus, in contrast to a normal wood tracheid (Fig. 1(A)), the cell wall organization of a compression wood tracheid can be represented by Figure 1(B). As with normal wood tracheids, no evidence of the layer S1 was observed in the X-ray examination of compression wood tracheids. It has been pointed out by Preston (1946) that the meridional arcs (Plate 2, Fig. 6) are to be interpreted as arising from the fusion of the 002 equatorial arcs in specimens of relatively large micellar spiral angle. The fact that the contribution of the outer layer is not apparent in the

diffraction diagram is most probably due to the existence of considerable micellar angular dispersion and to diffuse scattering from other cell wall substances present in this layer (Wardrop and Preston 1947). A further factor is the decrease in the angle of the micellar spiral organization, which takes place in both of these layers with increasing cell length and makes difficult the detection of any contribution from the outer layer (Preston and Wardrop 1949).

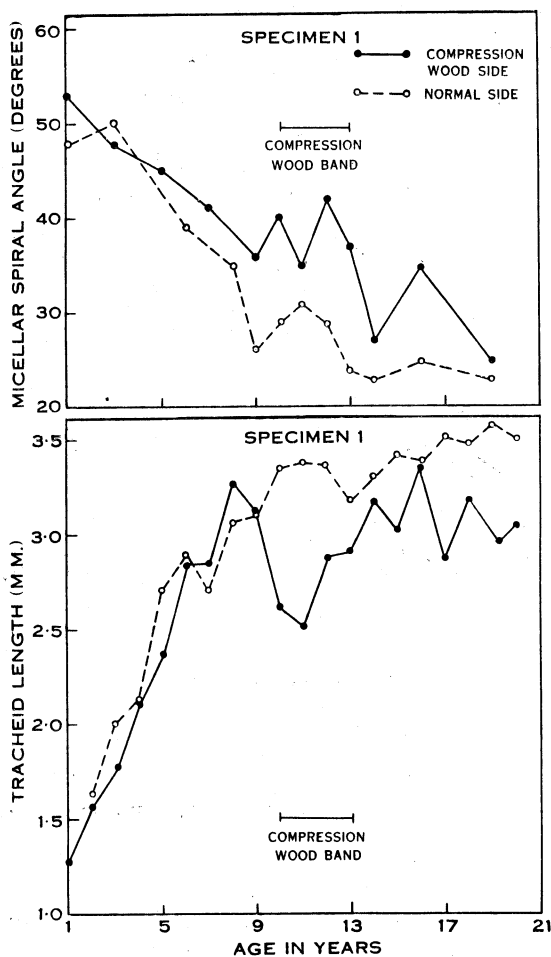


Fig. 2.—Variation of tracheid length and micellar spiral angle with age in *Pinus radiata* D. Don.

It can be seen from Table 2 and Figure 2 that the formation of compression wood is accompanied by a marked decrease in tracheid length and increase in spiral angle. After this sudden change, the tracheid length again increases and the spiral angle again decreases. On the side of the stem opposite to the compression wood, and prior to the formation of compression wood on the side containing it, the tracheid length increases from the pith outwards in the usual



manner (Sanio 1872 and others). Where no compression wood is present this increase is maintained to the eleventh ring (Fig. 2), after which the length attains a more or less constant value. Correspondingly, the spiral angle gradually decreases from the pith outwards, and again where no compression wood is present, it attains a more or less constant value at approximately the thirteenth ring in one specimen and the sixteenth ring in the other. Thus it is evident that the tracheids in the compression wood area are appreciably shorter than they would have been if no compression wood were present, and that this shorter length is accompanied by an increase in spiral angle.

In order to determine whether the micellar organization in compression wood tracheids is significantly different from that in normal wood tracheids, use was made of the relationship developed originally by Preston (1934) and referred to in equation (1) above. The tracheid length and the corresponding value for the cotangent of the spiral angle were plotted for both normal and compression wood growth rings (see Fig. 3). Straight lines were fitted by the method of least squares, firstly to the normal and compression wood results separately, and then to the combined data. Statistical examination showed that the single line gave a satisfactory fit, indicating that the assumption of a common relationship between tracheid length and the cotangent of the spiral angle for both normal wood and compression wood was in accordance with the data.

It was therefore concluded that, so far as the angle of micellar orientation of the layer S2 of the cell wall is concerned, compression wood tracheids are apparently no different from normal wood tracheids of the same length. This conclusion may be of considerable practical value, as compression wood properties are usually compared with properties of adjacent normal wood. If, as seems probable, properties of timber are determined by the cell wall organization (e.g. shrinkage, swelling, strength-properties) then it is clear that comparison should be made between compression wood and wood of similar tracheid length and micellar angle. Thus, from this point of view, compression wood may be regarded as physiologically younger than adjacent normal wood. In this connection it is of interest to note that some preliminary work on *Pseudotsuga taxifolia* (Wardrop 1948) has shown that the Cross and Bevan cellulose content increases in successive rings from the pith; thus, in this specimen a low cellulose content was associated with a shorter tracheid length and relatively large spiral angle. It is therefore significant that compression wood with its short tracheids and associated large spiral angle has also been found to contain less cellulose than corresponding normal wood.

Again, if as has been suggested for wood and demonstrated for cotton (Meredith 1946), the micellar organization is a factor contributing to properties such as tensile strength and possibly shrinkage and swelling, then compression wood might be expected to more nearly resemble in properties the wood near the centre of the stem than that immediately adjacent to it. Support for this view is seen in the facts that compression wood is known to be characterized by high longitudinal shrinkage and that the recent investigations of Pillow (1949), as well as observations in this laboratory, have demonstrated the existence of

high longitudinal shrinkage near the centre of the stem. The poor tensile strength of compression wood in comparison with normal wood adjacent to it may also be explained in the above terms, and experiments along these lines are already in progress in this laboratory.

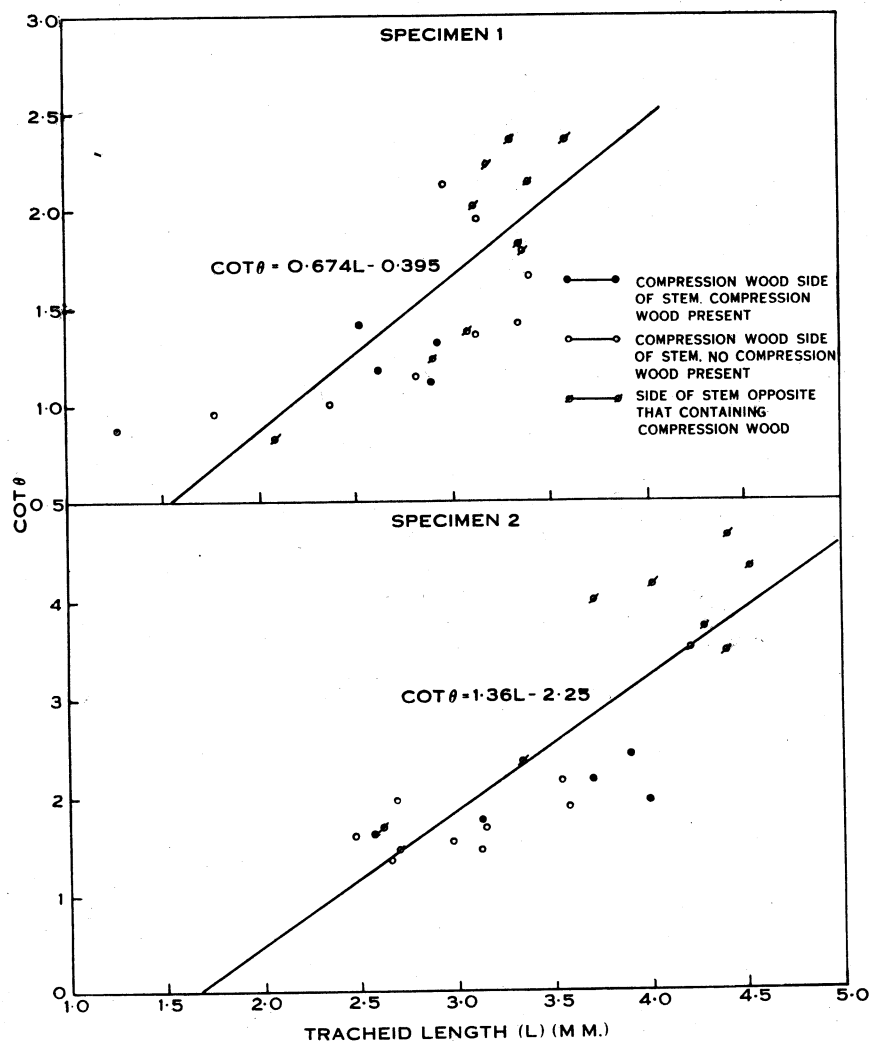


Fig. 3.—Relation between angle of micellar orientation ( $\theta$ ) and tracheid length ( $L$ ) in *Pinus radiata* D. Don.

It is well known that compression wood formation is usually associated with eccentric growth in the stem (Jaccard 1938), and, as can be seen from Figure 2, considerable reduction in tracheid length also takes place. These points are of interest in relation to some considerations put forward by Priestley (1930), who pointed out that vigorous radial growth would mean rapid tangential divisions of the fusiform initials of the cambium. If this were to result in a postponement

of transverse divisions in the cambium, then a wide annual ring would be associated with the formation of long tracheids. If, however, rapid tangential divisions are accompanied by an increased number of transverse divisions, then a wider annual ring would be correlated with the formation of shorter tracheids. This latter possibility obviously seems to present a reasonable explanation of the eccentric growth and shorter tracheid length which accompanies compression wood formation. Support for this view can be seen in Table 1 where the tracheid length and ring width at 60° intervals around one growth ring containing compression wood are listed.

The factors leading to the increased rate of cell division resulting in compression wood formation in stems and branches under gravitational stimulus are not known. The recent experiments of Wershing and Bailey (1942), in which compression wood formation was induced in conifer seedlings with 3-indoleacetic acid, would, however, strongly suggest the operation of some correlative factor such as a redistribution of auxin in the stem, resultant upon the operation of the gravitational stimulus.

In conclusion, it will be apparent that the cell wall organization in compression wood tracheids is to be regarded as a modification of the structure present in normal tracheids, and that this structure is determined by the shorter length of the cells. Although it is probable that this shorter cell length is governed by an increase in the number of transverse divisions occurring in the fusiform initials of the cambium, the way in which the course of cell division in the cambium is governed by the gravitational stimulus remains to be demonstrated.

#### IV. ACKNOWLEDGMENTS

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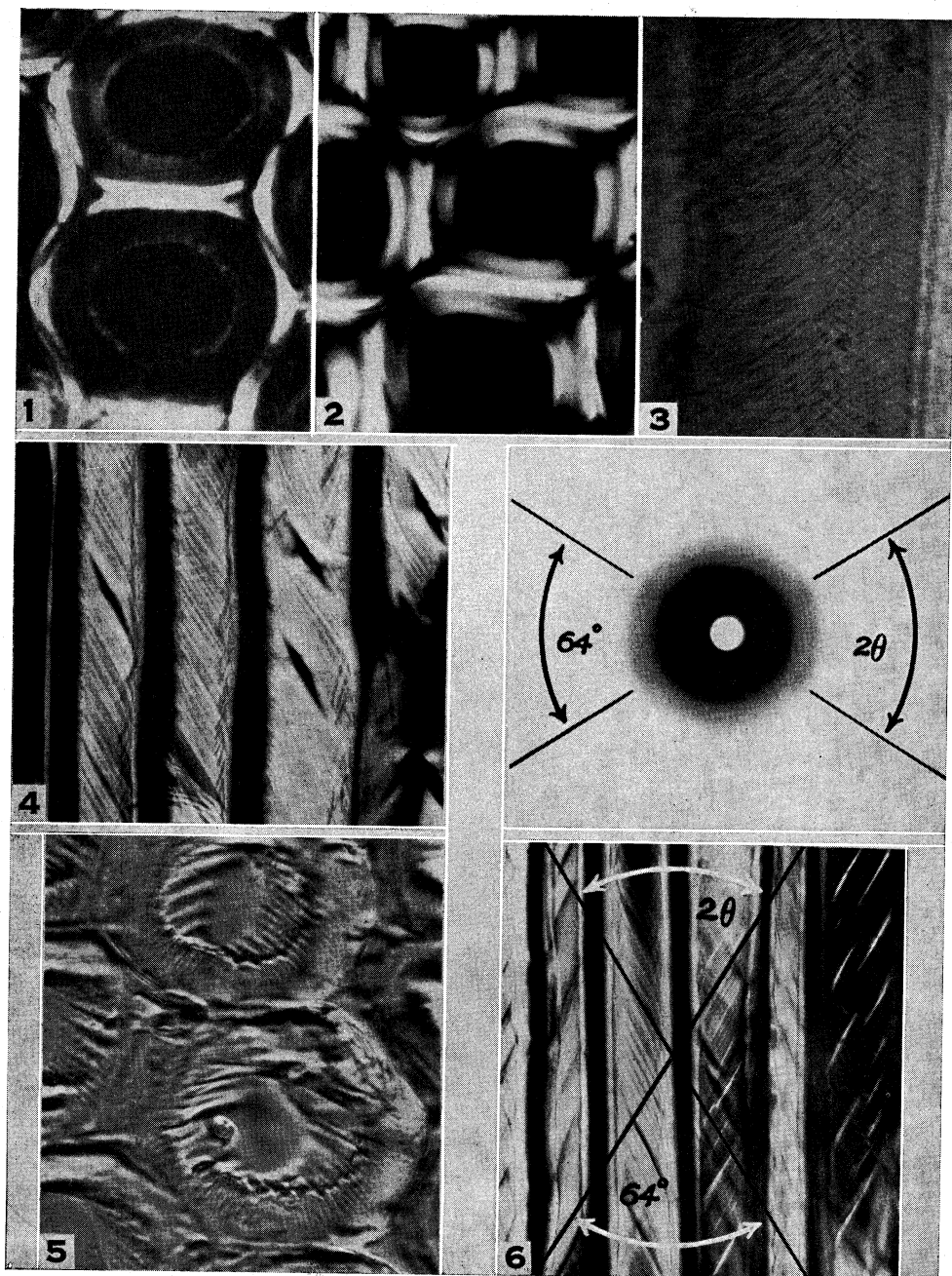
## EXPLANATION OF PLATES 1-2

### PLATE 1

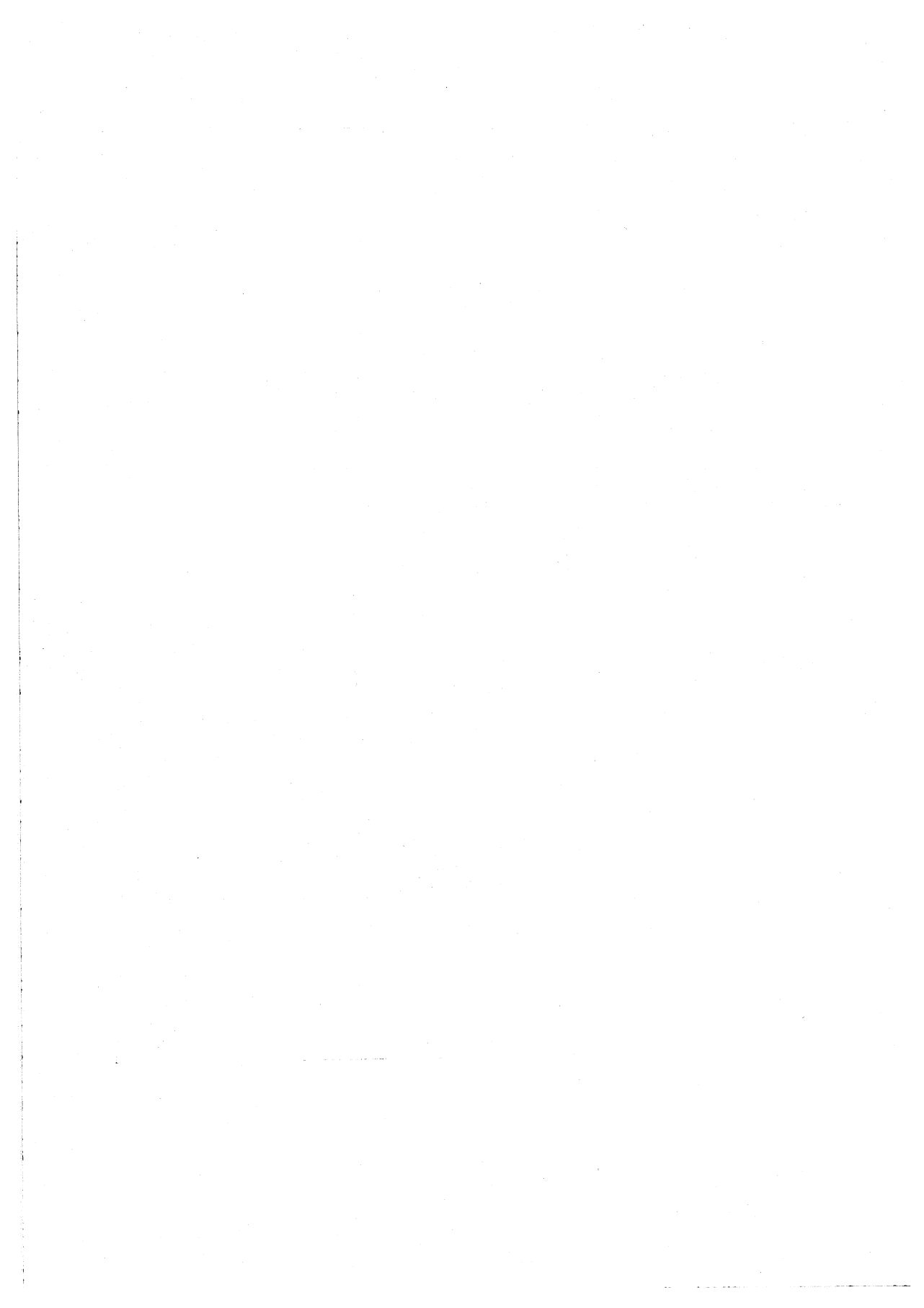
- Fig. 1.—*Pinus pinaster*. Transverse section of compression wood photographed between crossed Nicols showing feeble development of the inner layer of the secondary wall.  $\times 930$ .  
 Fig. 2.—*Pseudotsuga taxifolia*. Transverse section of compression wood photographed between crossed Nicols showing the isotropic layer described by Bailey and Berkley (1942) (see text).  $\times 930$ .  
 Fig. 3.—*Araucaria cunninghamii*. Part of the delignified cell wall of a compression wood tracheid after staining with congo red and crushing. Note the two striation directions.  $\times 930$ .  
 Fig. 4.—*Pinus pinaster*. Radial longitudinal section ( $15\ \mu$ ) of compression wood, photographed between crossed Nicols showing distortion of the pits and spiral striations. Note the displacement of the part of the cell wall in lower part of the centre tracheid.  $\times 410$ .  
 Fig. 5.—*Pinus pinaster*. Section of compression wood ( $15\ \mu$ ) cut approximately parallel to the striation direction and illustrating radial discontinuities of the secondary wall.  $\times 930$ .  
 Fig. 6.—*Pinus pinaster*. Tangential longitudinal section ( $20\ \mu$ ) of compression wood photographed between crossed Nicols ( $\times 410$ ), and the X-ray diffraction photograph of the same specimen. The intense blackening of the X-ray film surrounding the central spot arises from the diffuse scattering which is here exaggerated because of the prolonged exposure with such a thin specimen.

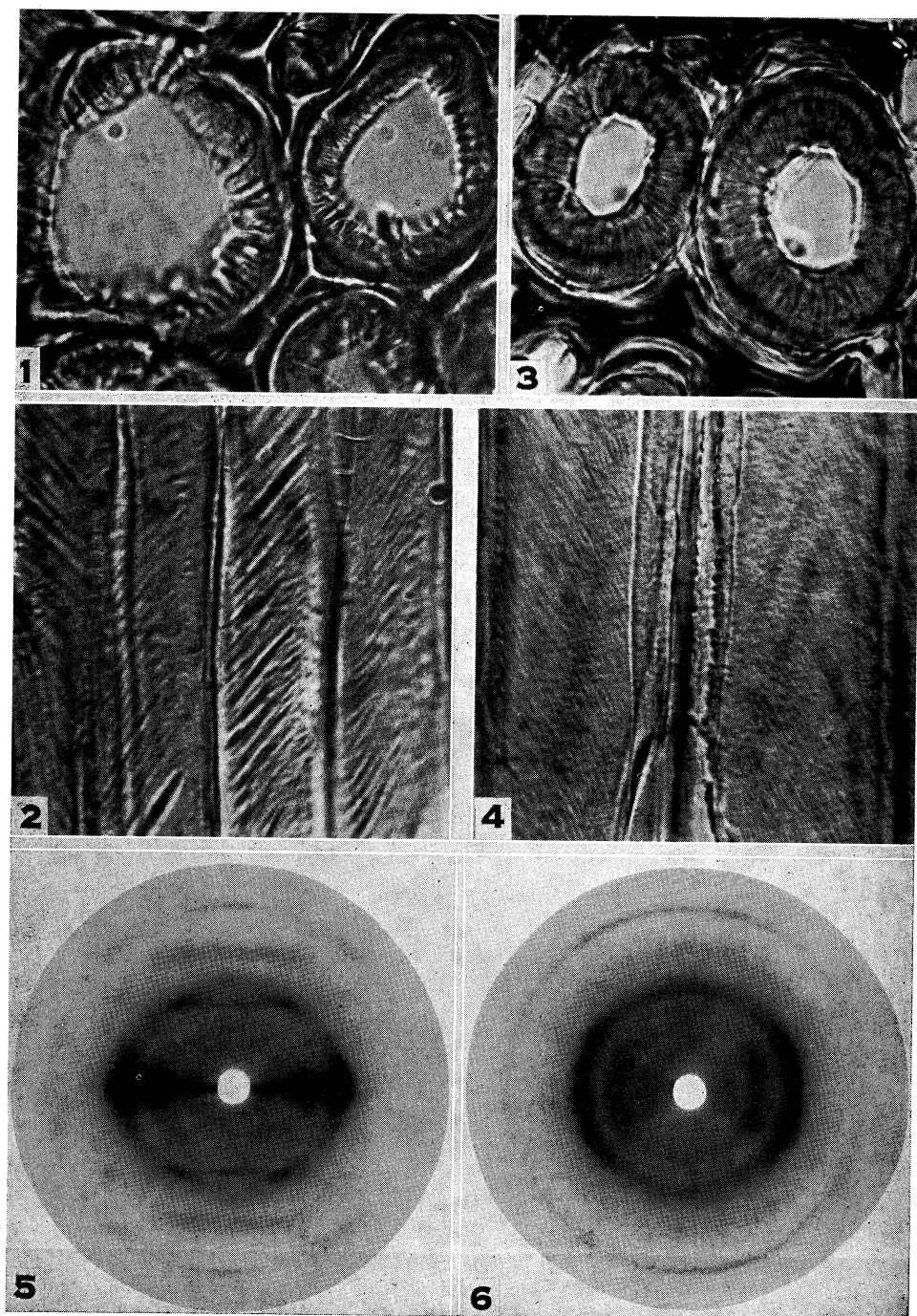
### PLATE 2

- Fig. 1.—*Pinus pinaster*. Transverse section ( $20\ \mu$ ) after treatment with 72 per cent. sulphuric acid, showing radial distribution of lignin in the cell wall.  $\times 980$ .  
 Fig. 2.—*Pinus pinaster*. Tangential longitudinal section after treatment with 72 per cent. sulphuric acid, showing spiral arrangement of lignin in the cell wall.  $\times 430$ .  
 Fig. 3.—*Araucaria cunninghamii*. Transverse section ( $20\ \mu$ ) after treatment with 72 per cent. sulphuric acid, showing fine radial distribution of lignin in the cell wall. Compare Figure 1.  $\times 980$ .  
 Fig. 4.—*Araucaria cunninghamii*. Tangential longitudinal section ( $20\ \mu$ ) after treatment with 72 per cent. sulphuric acid, showing differences in striation direction in the lignin pattern of two adjacent cells. Compare Figure 2.  $\times 980$ .



WARDROP AND DADSWELL.—THE NATURE OF REACTION WOOD. II





WARDROP AND DADSWELL.—THE NATURE OF REACTION WOOD. II





- Fig. 5.—*Pinus radiata*. X-ray diffraction diagram of normal wood from the eleventh annual ring of Specimen 2, taken with the X-ray beam parallel to the medullary rays, using  $\text{CuK}\alpha$  radiation and a specimen film distance of 3.7 cm. Note the small spread of the equatorial arcs indicating a steep spiral micellar orientation  $\theta = 15^\circ$ . Compare Figure 6.
- Fig. 6.—*Pinus radiata*. X-ray diffraction diagram of compression wood from the eleventh annual ring of Specimen 2, taken with the X-ray beam parallel to the medullary rays using  $\text{CuK}\alpha$  radiation and a specimen film distance of 3.7 cm. Note the large angular spread of the equatorial arcs indicating a flat spiral micellar orientation  $\theta = 37^\circ$ . Compare Figure 5.