THE NATURE OF REACTION WOOD

I. THE STRUCTURE AND PROPERTIES OF TENSION WOOD FIBRES

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(Plates 1-4)

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Summary

An examination has been made of the cell wall structure of tension wood fibres isolated from several Australian species including *Eucalyptus regnans* F.v.M., *Eucalyptus gigantea* Hook. f., *Nothofagus cunninghamii* Oerst. and *Acacia melanoxylon* R. Br.

It has been demonstrated that the so-called tertiary or gelatinous layers of these fibres are unlignified and consist almost entirely of a very highly oriented form of wood cellulose.

X-ray, optical, and visual evidence suggests that the secondary wall of tension wood fibres of *Eucalyptus regnans* F.v.M. consists of three layers of different micellar orientation: an outer layer in which the micelles are oriented at 40° to the longitudinal fibre axis, a middle layer where the angle of micellar orientation is 18°, and a broad, unlignified, inner, tertiary layer in which the micelles are oriented at approximately 5° to the longitudinal fibre axis.

Reference has been made to the possible relationship between the abnormal properties of tension wood and the nature of the cell wall: it has been suggested that the lack of lignin in the cell wall may account for the high tensile strength and low compressive strength of tension wood.

No satisfactory explanation of the high longitudinal shrinkage of tension wood has been forthcoming.

Slip planes and minute compression failures in tension wood have been discussed in relation to Chow's claim (1946) that incipient tension failures are present in tension wood fibres.

I. INTRODUCTION

The structure of tension wood fibres is of considerable academic and practical interest, both in relation to considerations of the stimuli which produce them, and to studies of the influence of fibre structure on the properties of the wood as a whole. As is well known, the chief abnormal properties of tension wood lie in its unusually high longitudinal shrinkage, its high tensile strength, and its low compressive strength.

Until recently, perhaps the most detailed study of fibre structure in tension wood was that of Munch (1938). This investigator has pointed out that in tension wood fibres, in addition to the lignified primary and secondary layers,

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there is an additional "tertiary" layer which is relatively unlignified. It is this tertiary layer* which has often been described as the "gelatinous" layer and has frequently led to tension wood fibres being described as "gelatinous fibres" (Rendle 1937). More recently Chow (1946) and Preston and Ranganathan (1947) have described various aspects of the structure of tension wood, and in relation to these studies, the following account of the structure of tension wood fibres from various Australian species should prove of interest.

Before describing the properties of tension wood fibres in detail, it is convenient to consider as a basis of comparison, the structure of normal wood fibres. The most important cell wall constituent is cellulose consisting of long-chain molecules built up from anhydroglucopyranose residues, and measuring 1,000-3,000 Å (1Å $= 10^{-8}$ cm.) in length. These molecules, over certain regions of their length, are perfectly aligned with respect to one another, so as to form a type of crystal lattice. These regions of high molecular orientation in the cellulose are known as micelles and measure, so far as can be ascertained from X-ray data, about 50Å by 60Å by at least 600Å. Between the micelles are cellulose chains in more or less random orientation and also other cell wall constituents such as lignin, hemicelluloses, and mineral matter. Because of the perfect molecular alignment in the micellar regions of cellulose, the cell wall exhibits certain crystalline properties such as optical anisotropy. In a typical fibre or tracheid the outermost layer of the cell wall is the primary wall formed at cell division, and inside this is the much thicker secondary wall. If a cross section of a fibre or tracheid is viewed between crossed nicols, three distinct layers of different optical properties can be identified in the cell wall: a brighter outer and inner layer, together with a dark middle layer (Plate 1, Fig. 1). The primary wall also appears bright between crossed nicols but cannot always be distinguished from the much brighter outer layer of the secondary wall. This difference in optical properties of the various cell wall layers has been interpreted in terms of differences in micellar arrangement within them (Kerr and Bailey 1934; Preston 1934, 1946). It has been established that in the primary wall the micelles are oriented almost transversely to the longitudinal fibre axis, while in the middle layer of the secondary wall they are oriented at only a small angle to the longitudinal fibre axis. In the outer and inner layers of the secondary wall the micelles are, according to Kerr and Bailey (1934), oriented almost transversely to the longitudinal fibre axis, and it is because of this, according to these investigators, that the layers are strongly birefringent between crossed nicols. However, Preston (1934, 1946), working exclusively on conifer tracheids, has ascribed the optical properties of the various cell wall layers to different types of micellar angular dispersion about the spiral axis of the general cellulose chain direction, so that while the micellar angular dispersion differs in the three layers of the secondary wall, the inclination of the cellulose chains to the longitudinal cell axis is almost constant. Preston (1947) has also made a detailed

*Throughout this paper the inner gelatinous layer of the tension wood fibre will be referred to as the "tertiary layer."

study of the optical behaviour of the various cell wall layers and has concluded that, in the secondary wall, no layer exists with transversely oriented chains sufficiently extensive to affect materially the optical properties of the wall. However, from work since carried out by one of us (A.B.W.) in collaboration with Dr. R. D. Preston in the Botany Department at the University of Leeds, it has been established that both orientation and dispersion play a part in determining the optical heterogeneity of the cell wall.

For this purpose an examination was made of the changes in birefringence for the different wall layers in a series of sections cut at increasing angles to the radial longitudinal plane. It was shown that in the outer bright layer, illustrated in Plate 1, Figure 1, the micelles are oriented in a rather flat spiral with respect to the longitudinal cell axis, while in the dark layer the micellar orientation is in the form of a steep spiral (Wardrop and Preston 1947). In both the bright and dark layers, however, there exists considerable angular dispersion about the spiral direction, both in the plane of the wall and, in the case of the dark central layer, in a plane perpendicular to the wall surface as well. The dispersion, together with composition differences, gives rise to rather low values for the maximum birefringence in the various cell wall layers—these are of the order of 0.04 for the dark central layer and 0.02 for the bright outer layer (cf. ramie—0.06). This fact is of importance in determining the micellar orientation in the different cell wall layers. It will be clear, however, that the type of cell wall organization proposed by Kerr and Bailey (1934) is essentially the correct one, and their conception will be employed in the present paper (see Fig. 1A).

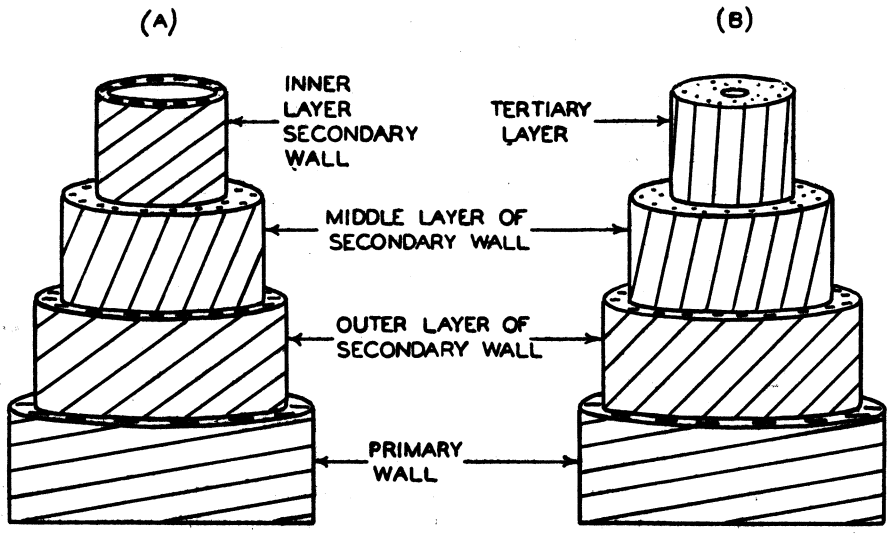

Fig. 1.—Diagrammatic representation of the structure of a normal wood fibre (A) and a tension wood fibre (B) of *Eucalyptus regnans* F.v.M. in which successive cell wall layers are considered partially removed.

In the investigations described below, it was necessary to establish the difference between the structure of the tension wood fibre and that of the normal fibre, especially as regards the relationship of the "tertiary" layer of Munch to the other cell wall layers. Also, in considering the abnormal physical properties of tension wood, it will be apparent that these will depend on three main factors: (i) The fine structure; (ii) the composition of the fibres; and (iii) the arrangement and proportion of the fibres and other tissue elements (rays and vessels) within the wood. It is with these factors, together with a consideration of the comparative cell wall structure of tension wood and normal wood fibres, that this paper is primarily concerned.

II. Form and Thickness of the Tertiary Layers in Tension Wood Fibres

In the present investigation four species were examined:

Eucalyptus regnans F.v.M.
Eucalyptus gigantea Hook.f.
Nothofagus cunninghamii Oerst.
Acacia melanoxylon R.Br.

The tertiary layer is easily distinguished in cross sections of tension wood fibres by its gelatinous appearance and capacity to stain strongly with light green (Plate 1, Fig. 2) and to give a strong positive reaction with cellulose cytological reagents. The thickness of the tertiary layer varies greatly; all stages, from completely normal cells to those in which the lumen is almost completely filled, are observed. This variation in thickness could possibly be related to the duration of the stimulus producing tension wood and to the stage of differentiation of the cells when the stimulus began to be effective.

The tertiary layer when viewed in transverse section sometimes shows slits or cracks suggestive of high shrinkage within the cells themselves. In *Acacia melanoxylon* (Plate 1, Fig. 3) the tertiary layer is peculiar in that it is markedly convoluted and often withdrawn from the remainder of the wall. In view of the extent of these convolutions it is unlikely that this layer could ever have been directly in contact over its whole surface with the other layers of the cell wall.

III. The Chemical Nature of Tension Wood Fibres

(*a*) *The Analysis of Tension Wood and Normal Wood*

The composition of tension wood and normal wood from the same annual ring of a young tree of *E. regnans* is shown in Table 1.

The specimens were removed from discs cut from the trunk by means of a band saw and ground to pass through a standard 60-mesh sieve prior to analysis. The analyses were carried out according to the standard methods of the Forest Products Division of the Council for Scientific and Industrial Research, Australia.

TABLE 1

THE COMPARISON OF NORMAL AND TENSION WOOD

	Normal Wood (%)	Tension Wood (%)
C and B cellulose	55.8	63.5
Xylan* (total)	18.3	11.5
Lignin	22.2	16.0
Alkali solubles	10.7	7.95
Total methoxyl	7.78	5.67
Apparent lignin	27.0	18.7
Xylan in C and B cellulose:		
As cellulose	20.6	9.87
As wood	11.5	4.27
Methoxyl in apparent lignin:		
As apparent lignin	21.4	20.3
As wood	5.71	3.74

*Furfural yield calculated as xylan.

These results are of interest in relation to the statement frequently made that tension wood is less lignified than normal wood, this being based on the apparently low lignin content of tension wood as shown in Table 1. In order to make such a comparison of lignin content, however, it is necessary to determine the relative amounts of lignin in a tension wood fibre compared with a normal wood fibre. This can be done approximately by considering the density of tension wood in comparison with normal wood in relation to the analytical data. Numerous determinations have shown that the densities of tension wood and normal wood in *Eucalyptus regnans* are in the ratio of 4 : 3, the actual figures for the basic density (based on the ratio of oven dry weight to volume when soaked to maximum volume) of tension wood being 40 lb./cu.ft. and of normal wood being 30 lb./cu.ft. Since there is little difference in size between tension wood fibres and normal wood fibres (Chow 1946; see also Plate 1, Fig. 2), and since the analytical data refer to equal weights of tension wood and normal wood, these data will, because of the density difference, cover only three-quarters as many tension wood fibres or parts thereof as normal wood fibres or parts thereof. Thus in the case of lignin which analysis indicates to be present to the extent of 16 per cent. by weight in tension wood and 22.2 per cent. by weight in normal wood, in order to make a fibre by fibre comparison the former value must be corrected by the factor 4/3, thus giving a value of 21.3 compared with 22.2 for the normal wood. These values, which are no longer percentages, represent relative weights of lignin per fibre in tension wood and normal wood respectively. In view of the apparent complete absence of lignin from the tertiary layer as revealed by staining (see below), this result would suggest that the extent of lignification of tension wood fibres and normal wood fibres is approximately the same prior to the development of the tertiary layer in the abnormal fibres (see Discussion).

Further consideration of the data in Table 1, with particular reference to the low xylan content of the Cross and Bevan cellulose in tension wood, and also to the high proportion of this resistant form of cellulose compared with normal wood, suggests that the ratio of crystalline cellulose to amorphous material may be higher in tension wood than in normal wood. Evidence which would add support to this possibility can, in fact, be obtained by the study of the comparative hydrolysis rates of tension wood and normal wood, and of the corresponding holocellulose fractions, using dilute acid (see Table 2). The values were obtained by measuring the loss in weight of the wood or of the holocellulose after hydrolysis for a specified period of time and expressing the result as percentage hydrolysis calculated on the initial weight.

TABLE 2

HYDROLYSIS OF TENSION WOOD AND NORMAL WOOD OF EUCALYPTUS REGNANS AND OF CORRESPONDING HOLOCELLULOSE FRACTIONS USING 2N HCl AT 100° C.

Time of Hydrolysis (min.)	Hydrolysis of Wood (%)		Hydrolysis of Holocellulose (%)	
	Normal	Tension	Normal	Tension
0	0.00	0.00	0.00	0.00
15	22.74	22.50	28.62	27.29
30	25.70	24.20	—	—
60	31.49	28.73	38.06	33.89
120	31.56	29.75	42.92	36.42

It will be noted that the extent of hydrolysis in a given time for tension wood and tension wood holocellulose is considerably less than that for the normal wood or its holocellulose fraction, and this is probably an indication of a higher degree of crystallinity in the tension wood cellulose and is consistent with the X-ray evidence (see below) and low xylan content of tension wood: all this evidence would indeed point to the conclusion that tension wood contains a very highly oriented form of wood cellulose.

(*b*) *The Lignin Distribution in Tension Wood Fibres*

The tertiary layer of tension wood fibres stains strongly with cellulose stains such as light green, while the remaining cell wall layers stain with lignin stains such as safranin. The tertiary layers stain strongly with iodine and sulphuric acid. They are also insoluble in 17.5 per cent. sodium hydroxide, indicating that they consist of chemically resistant cellulose which is relatively unlignified. However, the most striking evidence of lignin distribution in tension wood fibres can be obtained by staining sections using the method of Coppick and Fowler (1939). This method is in fact a modified Tollens reaction; the section is first treated with chlorine water when reducing substances are formed from the lignified tissues and the section is then immersed in an aqueous solution of silver nitrate when silver is deposited in the lignified areas. That the tertiary layer

lacks lignin according to this stain is shown in Plate 1, Figure 4, which is a cross section of *Nothofagus cunninghamii* tension wood. Similar results were obtained with the other species used in this investigation. Thus it will be clear that the tertiary layer of tension wood fibres is almost entirely free of lignin, and this, taken in conjunction with the purely chemical evidence, suggests that the tertiary layer consists of a form of wood cellulose of exceptional purity.

(c) *The Distribution of Pectin in Tension Wood Fibres*

If tension wood was sectioned immediately after removal from the tree the cells stained strongly with ruthenium red (1 : 10,000 aqueous solution) which is reputedly a pectin stain. The staining reaction was localized entirely in the unlignified tertiary layer while the lignified areas gave no reaction (Plate 2, Fig. 1). After digestion with dilute hydrochloric acid at 90°C. for 20 minutes, the sections no longer gave the reaction, presumably due to the removal of pectins or hemicelluloses (Plate 2, Fig. 2). The exact nature of this pectin fraction is difficult to characterize because a positive staining reaction was obtained even after extraction with water, 0.5 per cent. ammonium oxalate (90°C.) and 0.5 per cent. oxalic acid (90°C.), so that apparently considerable hydrolysis was necessary before the material was removed. If this material were pectic in nature (when presumably it would be in combination, possibly as the calcium complex) it is consistent with previous evidence that pectin cannot be demonstrated in any but unlignified tissues of the plant (Onslow 1931).

IV. Evidence regarding the Structure of Tension Wood Fibres

(a) *The Crushing of Isolated Fibre Sections*

Herzog (1939) has employed the technique of crushing various textile fibres as a means of revealing their structure. However, this method, using whole fibres, did not reveal anything as to the layering of the cell wall. In the present work longitudinal sections of tension wood and normal wood were cut sufficiently thin (6 μ - 8 μ) so that in the section no whole fibre was included. The sections were then delignified until equivalent in composition to holocellulose. Treatment of the sections with 0.025 per cent. sodium hydroxide enabled the cells to be easily separated. The fibre sections so obtained were then treated with a 1 per cent. aqueous solution of congo red and crushed by rolling a glass rod over them. The fibres were photographed in green light (Plate 2, Figs. 3 and 4). It would appear from an examination of fibres treated in the above manner that at least two layers of different spiral angle are present in the tension wood fibres. In the outer layer of the cell wall (Plate 2, Fig. 3) the fibres are oriented at approximately 18° to the longitudinal fibre axis while in the inner layer (Plate 2, Fig. 4) the fibrillar orientation is at 15° to the longitudinal cell axis. In the normal wood fibre treated similarly, one prominent set of striations oriented at approximately 20° to the longitudinal fibre axis can be distinguished, together with two less prominent sets oriented at a large angle (see Plate 3,

Fig. 1). However, the striations at a large angle must be regarded with some reserve as an indication of micellar direction since they do not exhibit marked dichroic properties as do the striations oriented at 20° as well as both the layers in the tension wood fibre illustrated in Plate 2, Figures 3 and 4. The orientation of the outer layer of the cell wall in normal wood fibres is probably better indicated by the birefringence measurements of this layer when viewed in transverse section (see below).

It is not considered likely that this crushing technique would greatly alter the orientation of the cellulose within the fibre wall; since the major extinction position did not alter by more than 5° during the crushing process and treatment with alkali.

(*b*) *Optical Properties of Tension Wood Fibres*

The major extinction position was measured using longitudinal sections of tension wood cut at a thickness so as to include only one wall of the fibre and was found to be inclined at 5° - 8° to the longitudinal fibre axis compared with an inclination of 15° - 20° in normal wood fibres, thus indicating that, in tension wood fibres, the micelles are inclined at a considerably steeper angle than in normal wood fibres.

The difference in micellar orientation in the various cell wall layers of tension wood fibres is also revealed by the examination of thin cross sections between crossed nicol prisms (Plate 3, Figs. 3 and 4). Thus the tertiary layer appears dark, and this is consistent with the presence of a steep micellar spiral and presumably the same inner layer as that revealed by the crushing technique in Plate 2, Figure 4. Furthermore, the birefringence of the outer bright layer of the wall in *E. regnans* normal wood was 0.012 while the corresponding layer in tension wood (Plate 3, Fig. 4) was 0.009, indicating that this layer possesses a rather steeper spiral in tension wood than in normal wood (see Discussion).

(*c*) *X-ray Examination of Tension Wood Fibres*

Since the X-ray examination of tension wood fibres has been the subject of a detailed study by Preston and Ranganathan (1947), little need be said concerning the results presented here other than to compare them with those obtained by these investigators. The diffraction patterns of normal wood (Plate 4, Fig. 1) and tension wood (Plate 4, Fig. 2) were obtained from small blocks 1 mm. thick with the medullary rays parallel to the X-ray beam using Cu-K-α radiation and a specimen-film distance of 3 cm. The spread of the equatorial arcs reveals a micellar spiral angle of 23° in normal wood and of 18° in tension wood with respect to the longitudinal fibre axis. While this difference between the values for normal wood and tension wood is rather less than that observed by Preston and Ranganathan in the case of beech, the photographs otherwise show essentially similar features. The higher orientation of molecules with respect to one another in tension wood in comparison with normal wood is evidenced by the better definition of the X-ray diffraction arcs in the former case and is consistent with the chemical data presented in Tables 1 and 2.

(*d*) *External Striations on Tension Wood Fibres*

If longitudinal sections of tension wood are cut at a thickness of about 40 μ and delignified in the manner described in Section IV (*a*) of this paper, then subsequent treatment with dilute alkali enables the separation of whole tension wood fibres. These isolated fibres, when allowed to dry in air, develop marked longitudinal striations inclined at about 5° to the longitudinal fibre axis. A fibre so treated and viewed between crossed nicol prisms is shown in Plate 3, Figure 2. Presumably these striations arise from the crinkling of the outer cell wall layers by the shrinkage of the tertiary layer so that the striations represent the orientation of the tertiary layer in the fibre corresponding to the dark layer in Plate 3, Figure 4, and that illustrated in Plate 2, Figure 4.

V. Discussion of the Structure of Normal Wood and Tension Wood Fibres

From the evidence presented above it will be clear that at least two cell wall layers of different micellar orientation exist in the wall of the tension wood fibre. Both of these, an outer layer oriented at approximately 18° and an inner layer oriented at approximately 5° to the longitudinal fibre axis, were demonstrated by the crushing technique applied to single cell walls. It is to be emphasized that these values represent maxima for the particular layers concerned, since some distortion as evidenced by the change of the major extinction position did occur during crushing and subsequent alkaline treatment. Further evidence of the existence of the layer oriented at 5° is seen in the value of the major extinction position (5° - 8° to the longitudinal fibre axis) and also in the development of fine longitudinal striations on the fibre during drying. It is to be noted that the value obtained from the major extinction position is probably greater than that of the inner layer since the value measured would be intermediate between the cellulose chain directions of the two layers.

On the other hand, the existence of a layer oriented at 18° to the fibre axis, shown in Plate 2, Figure 3, is supported by the X-ray evidence of a similar spiral angle.*

Now both these layers are of a spiral angle steeper than that existing in the middle layer of the secondary wall of a normal wood fibre (about 23° in the case of *E. regnans*) and so presumably would appear dark when viewed between crossed nicols in transverse section; both these layers must then be included in the dark layer of Plate 3, Figure 4. The orientation of the layer appearing bright between crossed nicols can be calculated from the observed values of the birefringence of this layer when viewed in cross section (Section IV (*b*)) and assuming a maximum birefringence of 0.02 (see Introduction) which would indicate that the outer layer in normal wood is oriented at some 49° to the longitudinal fibre axis compared with 40° in tension wood. This is illustrated

*Actually the X-ray diagrams show only that the cellulose chains are dispersed, but do not distinguish between angular dispersion of the cellulose micelles and their arrangement in the cell as a spiral. The evidence is, however, strongly in favour of the latter view, and the angle measured by spread of the arcs is not far removed from the angle determined by other means.

in Figure 1. At the present time there is no evidence of any difference in the structure of the primary wall in tension wood as compared with normal wood although this point is under investigation. It is concluded that the outer and middle layers of the secondary wall in tension wood possess a steeper spiral orientation than do those of normal wood, and that the inner layer of the secondary wall, with its relatively flat spiral angle in normal wood, is replaced in tension wood with the very thick tertiary layer in which the micelles deviate by not more than 5° from the longitudinal fibre axis. These two structures are illustrated for comparison in Figure 1.

Since, in the recent work of Preston and Ranganathan (1947), only X-ray methods were employed, no consideration was given to the possible existence of more than one cellulose spiral existing in the cell wall. It is true that from the X-ray photographs there is no evidence of a spiral at 40° or 49° to the longitudinal fibre axis in either tension wood or normal wood, but, in view of the vastly different composition of the different wall layers, and especially as regards their lignin content and the extent of their micellar dispersion, it is to be expected that any contribution the outer layer may make to the X-ray diagram would be faint and diffuse (Wardrop and Preston 1947). However, apart from this, it will be appreciated that the angle of the micelles to the longitudinal fibre axis, as measured by the spread of the equatorial arcs, will be the greatest of any steep spirals present in the structure. Thus in the present case of tension wood, where two spirals of 5° and 18° are present, that of 18° will be indicated on the X-ray diagram and will effectively mask the smaller spread of the equatorial arcs due to the 5° spiral. In general, therefore, the structural interpretation here presented of the tension wood fibre is consistent with the X-ray, optical, and visual evidence.

The chemical composition of tension wood fibres also presents certain features of interest. Thus the analytical and hydrolysis data of Tables 1 and 2 suggest the presence of a highly crystalline form of cellulose. This fact, in conjunction with the staining reactions of tension wood fibres in cross section (Plate 1, Fig. 4) and the similarity of lignin content in tension wood fibres and normal wood fibres, suggests that the tertiary layer is virtually unlignified and presumably consists of this chemically resistant and crystalline cellulose fraction. This view is supported by the X-ray diagram of tension wood in which there is a marked absence of diffuse scattering by amorphous materials, leading to a generally clearer photograph than is obtained with normal wood.

VI. Relation of Fibre Structure to the Properties of Tension Wood

In view of the abnormal properties of tension wood it is of some interest to consider the possible relationship of these properties to the fibre structure of tension wood proposed above. Two such properties of particular interest are (i) the high longitudinal shrinkage of tension wood and (ii) the abnormal collapse of tension wood as observed in specimens of various eucalypts—in particular *Eucalyptus regnans*.

In the case of the former, Preston (1942) has examined the relation of shrinkage to the angle of inclination of the micelles to the longitudinal fibre axis while Frey-Wyssling (1940, 1943) has focused attention on the nature of the intercellular layer as the major factor involved. While it is probable that both factors are involved to some extent, it was considered of interest to investigate the shrinkage of the wood in comparison with that of the fibre. The high longitudinal shrinkage of tension wood is well established; for the present experiment, blocks from *Eucalyptus regnans* were used to make a comparison between the longitudinal shrinkage of tension wood and of normal wood, and it was again observed that the tension wood had considerably higher longitudinal shrinkage. From matched blocks, fibres were isolated by the holocellulose method and used for determining fibre shrinkage, if any. While the behaviour on drying of an isolated fibre is rather complicated, it can be stated that, in all drying experiments, the fibres from both normal wood and tension wood exhibit similar dimensional changes. Details of the work on fibre shrinkage will be published later. While the conditions of shrinkage of the blocks and that of the fibres are admittedly not the same, it might have been expected that some difference in the amount of shrinkage of the fibres would be detected, and in view of the absence of such evidence, it remains difficult to account for the abnormally high shrinkage of tension wood. Preston and Ranganathan (1947) have pointed to the difference in micellar spiral angle as a possible source of this difference, but admit that it is in itself insufficient to account for the shrinkage properties, and suggest the possibility that angular dispersion about the spiral direction may be an additional factor. While this may well be so it is also probable that the composition of the fibres may also be a pertinent factor. Thus the absence of lignin, which is less hydrophilic than cellulose, in the tertiary layer of tension wood may facilitate intermicellar movement (Preston 1943), and this is consistent with the high longitudinal shrinkage of the low lignin-containing textile fibres, but it is obvious that any conclusion on this problem in the absence of further data would be premature.

The extremely bad collapse of tension wood as observed in the various species of the genus *Eucalyptus* is of the type referred to as "non-recoverable." Neither the standard steaming treatment nor boiling in water induces recovery, and in this respect collapsed tension wood differs from the ordinary collapsed specimen. Here again the cell wall composition may be the responsible factor.

The suggestion in the recent paper by Chow (1946) that the spiral markings observed by him in tension wood fibres are responsible for the high longitudinal shrinkage of the wood demands some comment. These markings (see Plate VI, Figs. 3-5, and Plate VII of Chow's paper (1946) are described by the author as incipient tension failures and are regarded as cracks in the wall substance which, he suggests, close together during drying thus causing the fibre to contract in length. The form, behaviour in polarized light, and preferential staining properties of these deformations described by Chow suggest to the authors that these markings are, in fact, incipient slip planes and compression failures and

are similar to those described by them in tension wood and in a large number of other fibres (Dadswell and Wardrop 1946; Wardrop and Dadswell 1947) (see also Plate 3, Fig. 2). Further, Chow refers to the work of Jacobs (1945) which he claims demonstrates that considerable tensile stresses exist in the growing stem. However, this is only one of two hypotheses presented by Jacobs, the alternative hypothesis being that actually the whole growing stem may be in a state of compression, but the peripheral layers of the wood are in a state of tension relative to the wood nearer the centre of the stem so that the existence of features characteristic of compression in tension wood is understandable. Furthermore, it has been shown that slip planes and compression failures are very common in tension wood (Wardrop and Dadswell 1947), the distinction between these two kinds of deformation being that the minute compression failures extend over a number of fibres in a more or less straight line. It should also be noted that these features are more difficult to detect in whole fibres as used by Chow than in thin sections. Again, the common occurrence of the cell wall deformations in tension wood is quite understandable in terms of the explanation of the occurrence of dislocation marks in textile fibres given by Frey-Wyssling (1936). This investigator suggests that when a compressive stress is applied to a fibre the micelles tend to buckle because of their great length as compared with their lateral dimensions. Thus, in an unlignified fibre similar to that of tension wood, buckling could occur easily, giving rise to the formation of slip planes and minute compression failures. However, in a lignified fibre, lignin, packed between the micelles, resists the tendency of the micelles to buckle, and slip planes and minute compression failures are less common, so that, in heavily lignified cells such as the tracheids of compression wood, slip planes and minute compression failures are not found.

Such considerations also offer an immediate explanation of the extremely low compressive strength of tension wood as compared with normal wood. It will also be apparent that the tensile strength will not be greatly altered since the intermicellar lignin would be without influence on this property and the micellar spiral angle is only one factor in determining the tensile properties of timber. These also depend on the forces of intercellular adhesion, which presumably influence the toughness of the timber. In fact, there is some evidence that intercellular adhesion in tension wood is greater than in normal wood (Wardrop and Dadswell 1947). In conclusion, it will be apparent that while the strength properties of tension wood are readily understandable in terms of the submicroscopic morphology of the fibre, the shrinkage phenomena must, as yet, await further experimental data before a comprehensive explanation is attempted. The next step in this study must now be concerned with the physiological significance of the fibre structures described above in relation to growth regulating factors operating in the tree, and work is now in progress which should throw some light on this interesting problem, at the same time bringing it into the field of investigation of the forester and plant physiologist.

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Explanation of Plates 1-4

Plate 1

Fig. 1.—Cross section of delignified normal wood fibres of *Nothofagus cunninghamii* Oerst. (somewhat swollen) viewed between crossed nicols. X 880.

Fig. 2.—Cross section of *Eucalyptus gigantea* Hook. f. showing both tension wood fibres and normal wood fibres stained with safranin and light green. X 390.

Fig. 3.—Cross section of *Acacia melanoxylon* R.Br. showing typical tension wood fibres stained with safranin and light green. X 390.

Fig. 4.—A cross section of tension wood in *Nothofagus cunninghamii* Oerst. stained according to the method of Coppick and Fowler (1939). Note the preferential staining of the middle lamella zone and the lack of staining in the tertiary layer of the cell wall. X 650.

PLATE 2

Fig. 1.—Cross section of freshly cut tension wood in *Eucalyptus gigantea* Hook. f. stained with ruthenium red. Note the staining on the cell wall layers but not in the middle lamella and adjacent layers. X 390.

Fig. 2.—Cross section of tension wood in *Eucalyptus gigantea* similar to that shown in Figure 1 but boiled with 12 per cent. HCl before staining with ruthenium red. Note lack of staining. X 390.

Fig. 3.—A tension wood fibre isolated from *E. regnans* F.v.M. that has been cut longitudinally and crushed after staining with congo red. Note angle of spiral in cell wall. X 880.

Fig. 4.—Same fibre as illustrated in Figure 3 photographed at different focus showing angle of spiral of innermost tertiary layer. X 880.

PLATE 3

Fig. 1.—Normal wood fibre from *E. regnans* F.v.M. cut longitudinally and crushed after staining with congo red. Note the definite striations oriented at a steep angle to the longitudinal fibre axis corresponding to the middle layer of the secondary wall. X 880.

Fig. 2.—A tension wood fibre isolated from *E. regnans* F.v.M. viewed between crossed nicols. Note longitudinal striations at a very small angle to the fibre axis. X 390.

Fig. 3.—A cross section of tension wood from *E. regnans* F.v.M. treated with Herzberg's stain. The tertiary layers of the cell walls stain a distinctive purple which is not observed in normal wood and is indicative of a high percentage of pure cellulose. X 880.

Fig. 4.—The same section as illustrated in Figure 3 but viewed between crossed nicols. Note the absence of any indication of an inner layer as observed in normal wood fibres under similar conditions—compare Plate 1, Figure 1. X 880.

PLATE 4

Fig. 1.—X-ray diffraction photograph of normal wood of *E. regnans* F.v.M. Cu-K-α radiation specimen-film distance 3 cm.

Fig. 2.—X-ray diffraction photograph of tension wood of *E. regnans* F.v.M. Note evidence of greater orientation. Cu-K-α radiation specimen-film distance 3 cm.

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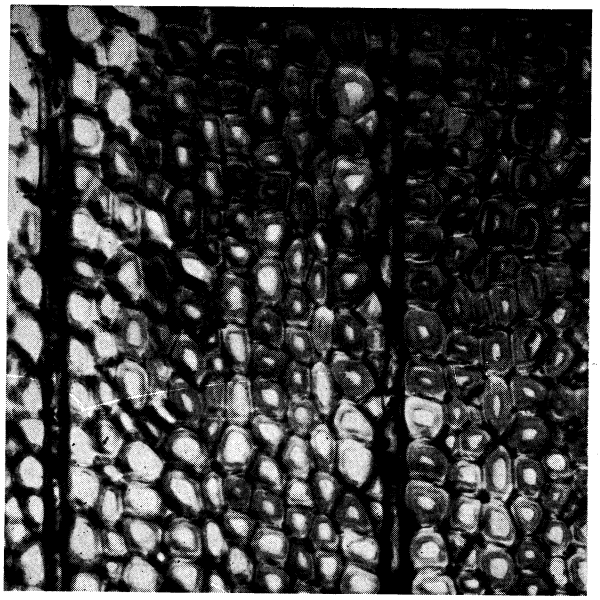

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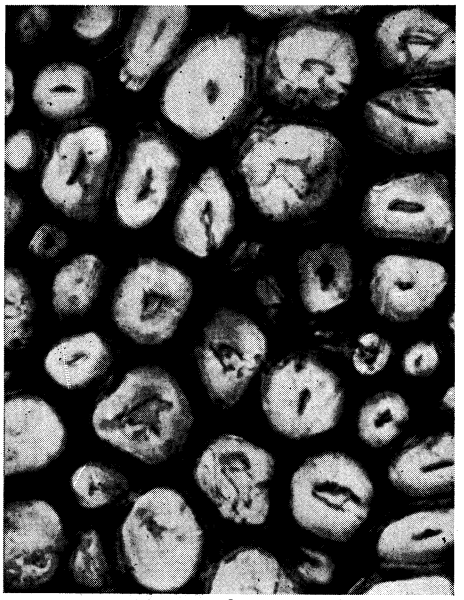

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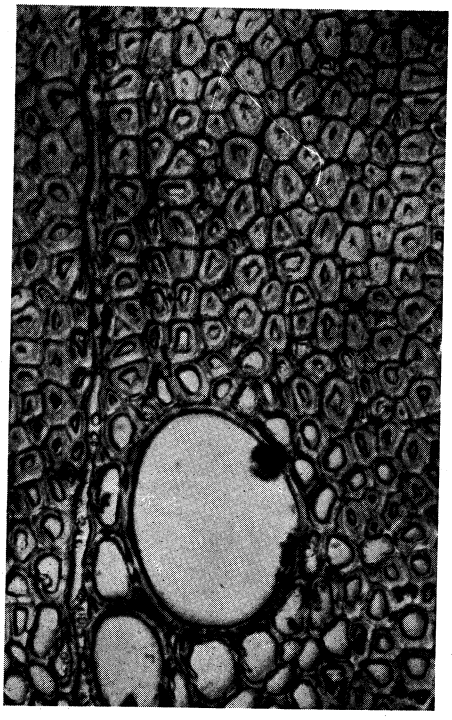
WARDROP and DADSWELL.—THE NATURE OF REACTION WOOD



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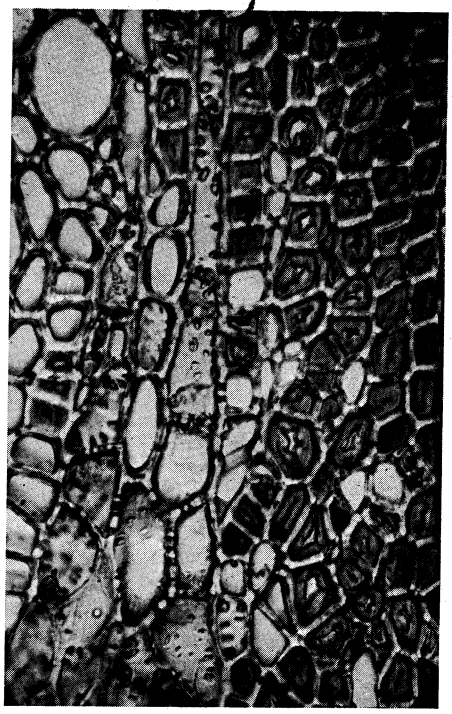

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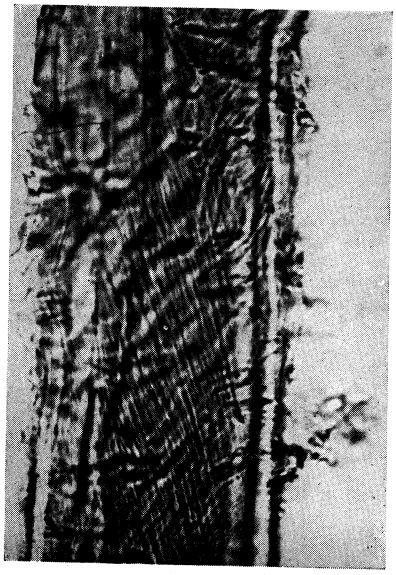

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WARDROP and DADSWELL.—THE NATURE OF REACTION WOOD

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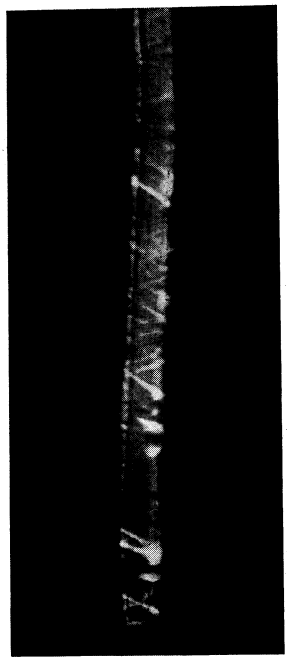

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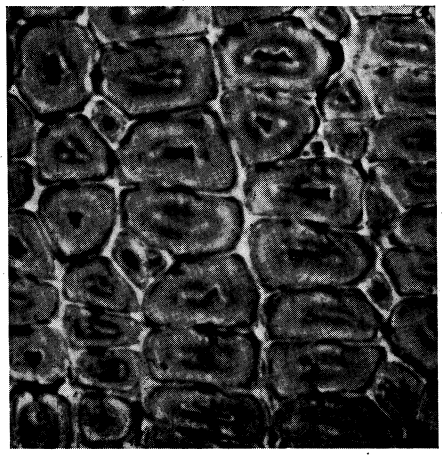

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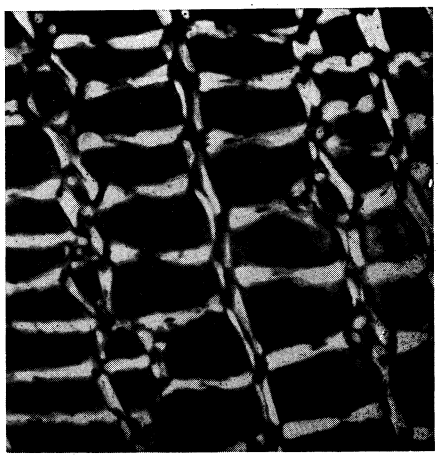

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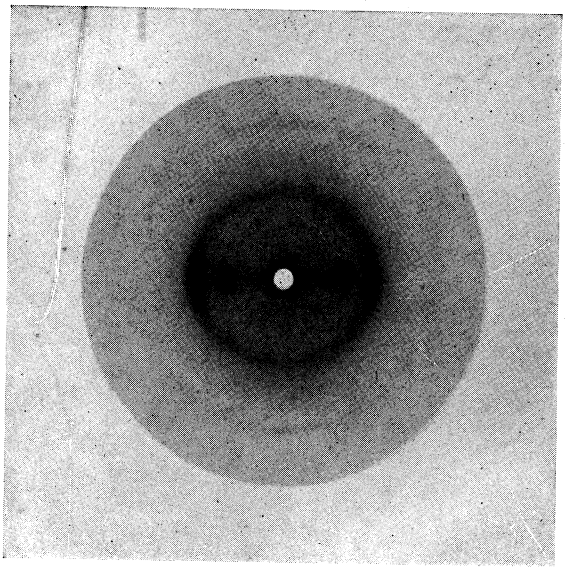
WARDROP and DADSWELL.— THE NATURE OF REACTION WOOD



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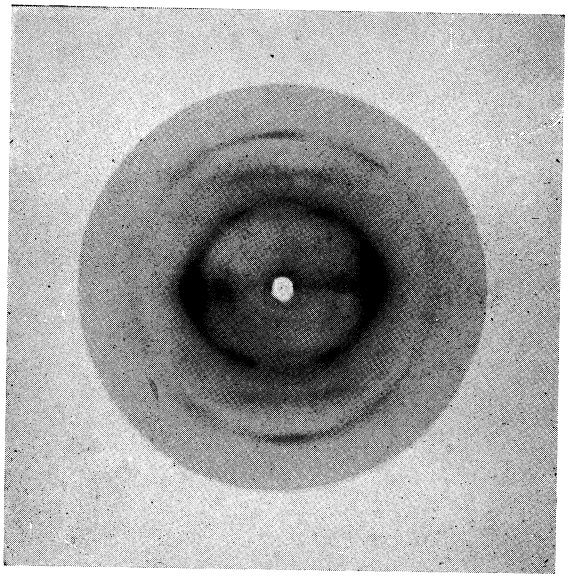

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WARDROP and DADSWELL.—THE NATURE OF REACTION WOOD