

THE NATURE OF REACTION WOOD

III. CELL DIVISION AND CELL WALL FORMATION IN CONIFER STEMS

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Summary

Cell division, the nature of extra-cambial readjustment, and the development of the secondary wall in the tracheids of conifer stems have been investigated in both compression wood and normal wood. It has been shown that the reduction in tracheid length, accompanying the development of compression wood and, in normal wood, increased radial growth after suppression, result from an increase in the number of anticlinal divisions in the cambium. From observations of bifurcated and otherwise distorted cell tips in mature tracheids, of small but distinct terminal canals connecting the lumen to the primary wall in the tips of mature tracheids, and of the presence of only primary wall at the tips of partly differentiated tracheids, and from the failure to observe remnants of the parent primary walls at the ends of differentiating tracheids, it has been concluded that extra-cambial readjustment of developing cells proceeds by tip or intrusive growth. It has been further concluded that the development of the secondary wall is progressive towards the cell tips, on the bases of direct observation of secondary wall formation in developing tracheids and of the increase found in the number of turns of the micellar helix per cell with increasing cell length. The significance of this in relation to the submicroscopic organization of the cell wall has been discussed. Results of X-ray examinations and of measurements of tracheid length in successive narrow tangential zones from the cambium into the xylem have indicated that secondary wall formation begins before the dimensional changes of differentiation are complete.

I. INTRODUCTION

The development of compression wood in conifer stems is characterized by a shorter average tracheid length, in comparison with that of previously formed normal wood, and by readily recognizable morphological features such as the rounded form of the tracheids, the intercellular spaces, and the helical checking in the secondary wall. In the second paper of this series (Wardrop and Dadswell 1950) it was suggested that the reduction in tracheid length resulted from an increase in the number of anticlinal divisions in the cambium associated with the rapid eccentric radial growth (periclinal divisions) that is usually associated with the development of compression wood.

In conifer stems generally the importance of anticlinal divisions in accommodating the increased girth of the stem was recognized by Bailey (1923) and by Priestley (1930). However, the recent work of Bannan and Whalley (1950) has demonstrated that the frequency of these divisions is very much greater than was previously supposed. From the changing pattern of the differentiating

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tracheids seen in longitudinal tangential sections, these investigators have concluded that increase in length of the daughter cells, following anticlinal divisions, results from tip growth. The development of the secondary wall is known to begin first in the region of the pits, but whether it continues to develop simultaneously over the entire inner surface of the primary wall does not appear to be known. Compression wood is particularly suitable for the further investigation of these problems. The rapid radial growth and the sudden reduction in tracheid length provide material in the formation of which, if the above assumption is correct, anticlinal divisions are frequent and the nature of the increase in length of the daughter cells of such divisions can be observed.

It has been shown previously (see Wardrop and Dadswell 1950) that the secondary wall of compression wood tracheids consists of two layers, the outer layer in which the micellar angle is large ($78-90^\circ$) in relation to the longitudinal cell axis and the inner wider layer in which the micellar angle is smaller ($30-45^\circ$). The helical checks peculiar to the inner layer provide a basis for analysing the relation between fine structure and cell wall development more exactly than can be done with normal wood cells. Preston (1934, 1948) showed that cell length in conifer stems was linearly related to the cotangent of the angle between the direction of the cellulose micelles in the helically organized middle layer of the secondary wall and the longitudinal cell axis. This relation has been shown to apply to all layers of the secondary wall of normal tracheids (Preston and Wardrop 1949; Wardrop 1952a) and implies that the number of turns of the micellar helix per cell is constant. However, in a study of the orientation of helical thickenings in the tracheids of *Pseudotsuga* and *Taxus*, where the inclination to the cell axis also decreases with increasing cell length, it was shown (Wardrop and Dadswell 1951a) that the number of turns of the helical thickening increased with increasing cell length. It was considered that this might indicate a directed synthesis of cellulose in the thickenings but, before such a consideration can be accepted for cell wall development generally, it is necessary to obtain cells in which the number of turns of the micellar helix can be measured. Such cells are provided by compression wood, in which the length-micellar angle relationship of Preston is known to hold (Wardrop and Dadswell 1950).

In the present investigations consideration has been given to the frequency of anticlinal divisions in the cambium, to the nature of the readjustment of the daughter cells, and to the development of the secondary wall during differentiation of compression wood tracheids. Because of the general implications of these questions parallel studies have, as far as possible, been carried out with normal wood tracheids.

II. EXPERIMENTAL

(a) Cell Division in the Cambium

Two specimens of *Pinus pinaster* Sol. were selected for examination. In specimen I, of unknown age, both normal wood and severe compression wood were

present and growth rings were not discernible in the compression wood zone. The formation of compression wood in the specimen had involved a rapid in-

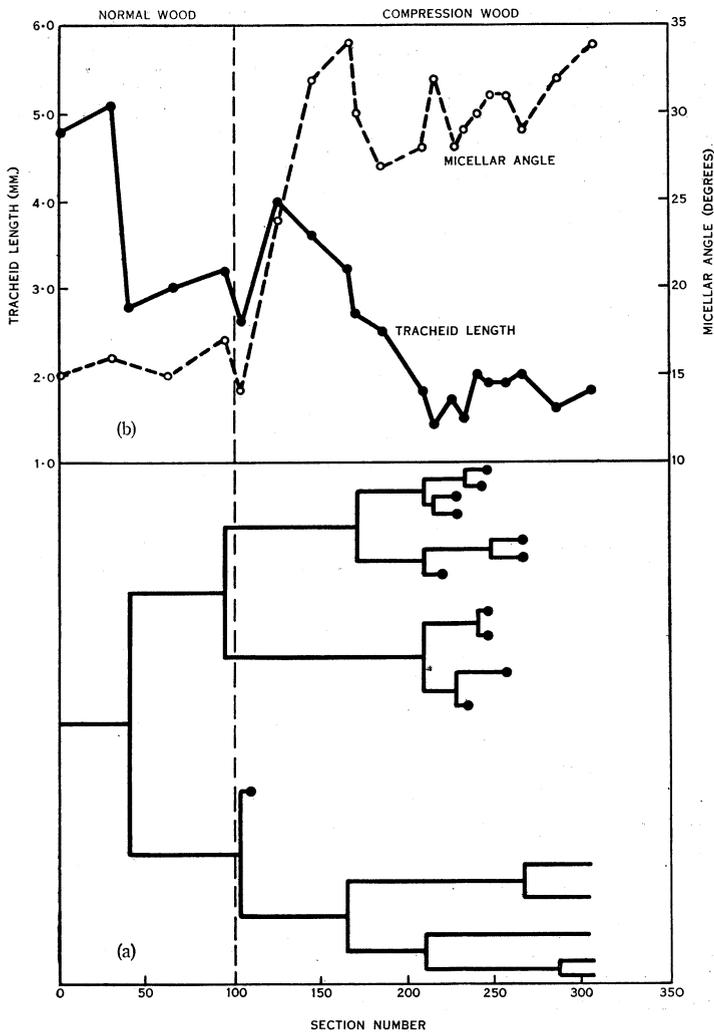


Fig. 1.—(a) Sequence of anticlinal divisions in a single radial file of tracheids as observed in successive tangential sections extending through a zone of developing compression wood. The black dots represent the elimination of a file of tracheids. The scale of the abscissa is the section number from the initial point of observation. The vertical broken line indicates the point at which features of incipient compression wood were first observed. (b) Tracheid length (mm.) and micellar angle ($^{\circ}$) as measured in the series of tangential sections depicted in (a).

crease in radial growth rate and was accompanied by considerable decrease in tracheid length. Specimen 2 was taken from a concentric stem showing 31

growth rings. The growth of the tree had been retarded and had responded to treatment with superphosphate resulting in a considerable increase in radial growth rate after the 14th ring, with decrease in tracheid length, but without the formation of compression wood. Serial longitudinal tangential sections, $30\ \mu$ thick, were cut from specimen 1 over the region of initial compression wood formation and from specimen 2 over growth rings 14 and 15, where there was the sudden increase in radial growth rate. Each section, as cut, was numbered according to the growth ring and its position in the ring, or, where no growth rings were evident, according to its position in the specimen. All

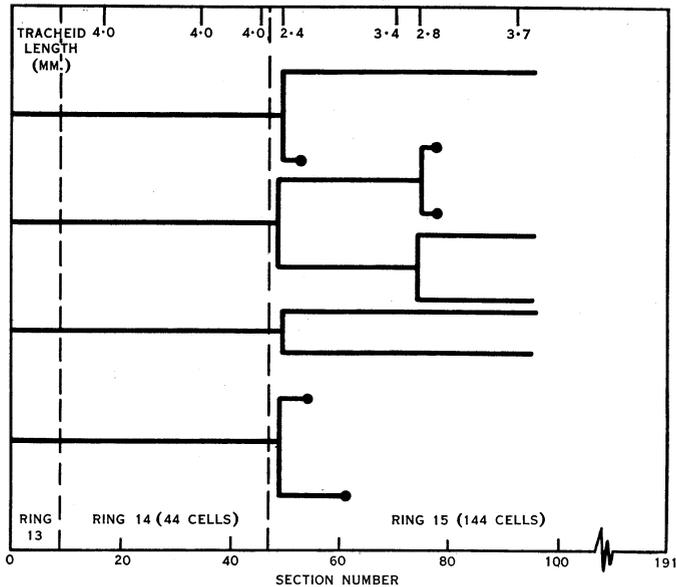


Fig. 2.—Sequence of anticlinal divisions in four radial files of tracheids followed through three growth rings of a specimen of *Pinus pinaster*. The scale on the abscissa as in Figure 1.

sections were examined microscopically to determine the sequence of anticlinal divisions according to the procedure adopted by Bannan and Whalley (1950). This method, used originally by Klinken (1914), involves a number of assumptions, among the most important of which are:

- (i) The arrangement and length of the tracheids approximately recapitulate the arrangement and length of the fusiform initials of the cambium at the time the tracheids were cut off;
- (ii) The appearance of two tracheids as seen in serial tangential sections, instead of one, has involved the occurrence of an anticlinal division; and
- (iii) The disappearance of a tracheid from a radial file has involved the disappearance of a fusiform initial from the cambium.

Some support for the first of these assumptions may be found in the observations of Bailey (1920) that tracheids of conifers are only 5-20 per cent. longer

than the cambium initials from which they are derived. The other assumptions, although justifiable, may be complicated by other factors such as the fact that cell division is not confined to a single initial or tangential row of initials—the cambium in Sanio's sense—but involves a radial zone of cells as proposed by Raatz, Schoute (see Meeuse 1941), and Wight (1933).

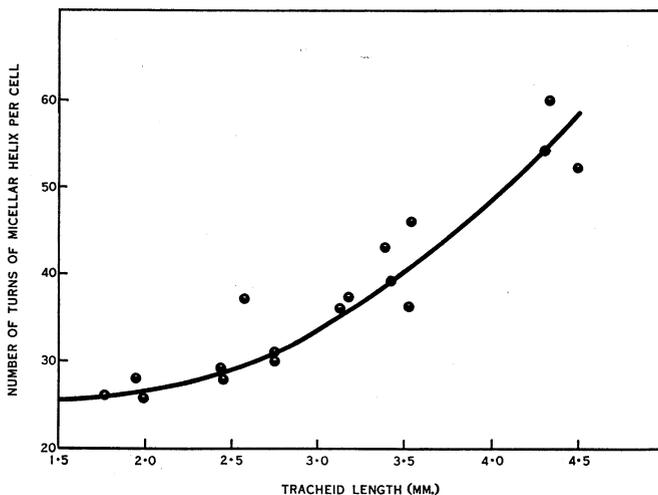


Fig. 3.—Variation in the number of turns of the micellar helix per tracheid with tracheid length in compression wood of *Pinus pinaster*.

The results obtained in the present investigation, on the sequence of divisions for selected radial files of cells, are shown in Figure 1 for specimen 1, and in Figure 2 for specimen 2. The position in the specimen is indicated by the section numbers. In specimen 1 one original radial file was followed through 306 sections, and it will be noted from Figure 1 that two anticlinal divisions occurred in the 100 sections before compression wood formation, three in the next 100 sections, and 11 in the remaining 106 sections. Of the total of 17 daughter cells only five survived. In specimen 2, in which no compression wood was present but in which a wide growth ring (No. 15) followed a narrow growth ring (No. 14), the presence of a large number of resin canals prevented examination over as large a radial distance as in specimen 1. However, from Figure 2, it will be seen that, in the four selected radial files, no anticlinal divisions occurred in the narrow ring (44 cells wide) but there were six anticlinal divisions in the first 50 sections of the following wide ring (144 cells wide), five of the daughter cells persisting.

An attempt was made to determine the influence of the anticlinal divisions on tracheid length and micellar angle by measuring the changes that occurred in the serial tangential sections after each division (for results see Figs. 1 and 2). It should be appreciated that in Figure 1, for example, the results given are for one tracheid before the anticlinal division and for two tracheids after. Because of the few cells involved and the difficulty of determining length and angle in sections the values plotted must be considered only as trends.

(b) Observations on Parent Cell Walls

Parent cell walls surrounding radial files of tracheids were observed traversing the intercellular spaces in cross sections of compression wood as shown in Plate 1, Figures 1 and 2. Similar membranes have been demonstrated in cross sections of normal wood after careful delignification (Wardrop 1952*b*). With ordinary methods of maceration the demonstration of the parent wall was extremely difficult because in mature tissue this wall is not continuous around a number of cells in a radial file and any slight agitation was sufficient to cause the cells to separate. Parent walls were not observed at the tips of the tracheids even after most careful delignification.

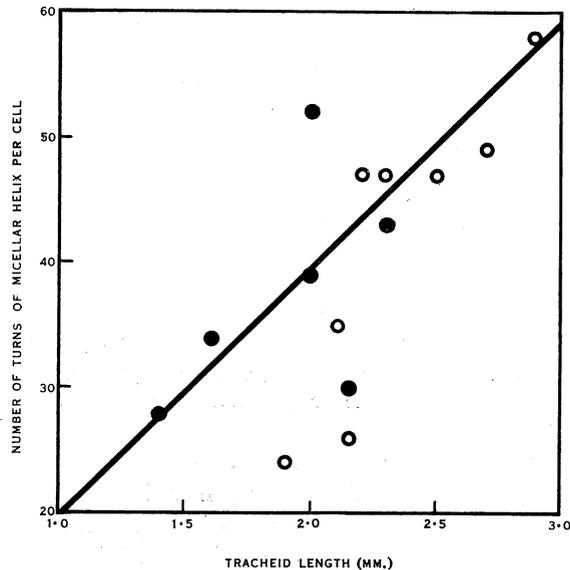


Fig. 4.—Variation in the number of turns of the micellar helix per tracheid with tracheid length in compression wood of *Cupressus macrocarpa*. ● Ring 4. ○ Ring 24.

(c) Micellar Orientation in Compression Wood Tracheids

In order to obtain further information on the helical organization of the cell walls of compression wood tracheids the number of turns of the micellar helix per cell was determined. This was done from photomicrographs of isolated cells at a magnification of 270. On the prints continuous lines were drawn parallel to the helical cracks (examples of such cracks are shown in Plate 1, Figs. 3-6) so that the total number of turns per cell could be counted. The length of each cell used for this purpose was determined from the photomicrographs. Such determinations were carried out on macerated material from the compression wood band in specimen 1, and from compression wood taken from the fourth and 24th growth rings on the lower side of a branch of *Cupressus macrocarpa* Gordon. An increase in the number of turns with increasing tracheid length was observed in both cases, the results being shown in Figures

3 and 4. Within individual tracheids the micellar angle showed some variation, becoming greater towards the tips.

(d) *Development of the Secondary Wall*

For certain of the observations on cell wall formation macerated material from both normal and compression wood in specimen 1 and from slow-grown and fast-grown material in specimen 2, was examined. Many examples of bifurcated and deformed tracheid tips, suggestive of tip growth, were observed. Some of these are illustrated in Plate 1, Figures 3-6, and Plate 2, Figures 1-5. Not all of these examples were from compression wood, some were from the region of rapid growth in specimen 2. In both compression wood and normal wood tracheids from specimens 1 and 2, and in partly differentiated tracheids of *Pseudotsuga taxifolia* (Poir.) Britt., it was also observed that thickening of the cell wall was often less at the tips than in the middle (see Plate 2, Figs. 6-13) and further that where the thickening was well developed at the tips the cell lumen was connected to the primary wall by a narrow terminal canal (Plate 3, Figs. 3-8).

Secondary wall formation was also studied in branches of *Pinus radiata* D. Don, where developing compression wood tracheids in all stages of differentiation from the cambium could be observed on the lower side of the specimens (Plate 3, Fig. 9; Plate 4, Fig. 1). It can be seen from these photomicrographs that thickening of the secondary wall was incomplete for at least six to eight cells from the cambium and, further, that the rounded form of the tracheids and the intercellular spaces appeared before the development of the inner of the two layers of the secondary wall. The progress of cell wall thickening could be followed in the X-ray diffraction diagrams of serial longitudinal tangential sections 40 μ thick cut from the cambium into the xylem. The first section, containing cambium and differentiated cells in which the outer wall only was present, gave two meridional arcs on a diffuse background (Plate 4, Fig. 2). The subsequent sections which included cells with both layers of the secondary wall present gave a similar diagram but with a typical four-point diagram superimposed (Plate 4, Figure 3). These results indicate the presence of transversely oriented micelles in the outer layer and helically oriented micelles at an angle of 38° in the inner layer, thus confirming the structure of compression wood previously put forward (Wardrop and Dadswell 1950).

After X-ray examination the 40- μ sections were separately macerated and the average length of 50 tracheids determined for each consecutive section. The results obtained are set out in Table 1.

A similar procedure was carried out with specimens taken from just under the bark of normal stems of *Pseudotsuga taxifolia* collected at monthly intervals during the 1951-52 growing season. The specimens were fixed immediately after removal from the tree. Variations in cell length from the cambial zone into the xylem are again shown in Table 1. As previously observed by Wight (1933) the number of partly differentiated cells rapidly decreased as the formation of late wood began.

III. DISCUSSION

The results obtained (see Figs. 1 and 2) show that the development of compression wood involves an increase in the number of anticlinal divisions which, in turn, is reflected in a decrease in the average tracheid length of the tissue. In addition, in a second specimen in which there was a considerable increase in radial growth rate but no compression wood, an increased number of anticlinal divisions is also involved, together with a resultant decrease in tracheid length. It is further apparent from Figure 1 that, in compression wood, the decrease in tracheid length was accompanied by an increase in micellar angle. This result, therefore, is in agreement with our earlier suggestion (Wardrop and Dadswell 1950) that the reduction in tracheid length and the increase in micellar angle associated with the development of compression wood reflect the occurrence of an increased number of anticlinal divisions in the cambium occasioned by the increased radial growth rate. They are not necessarily associated with the development of the characteristic morphological features of that tissue.

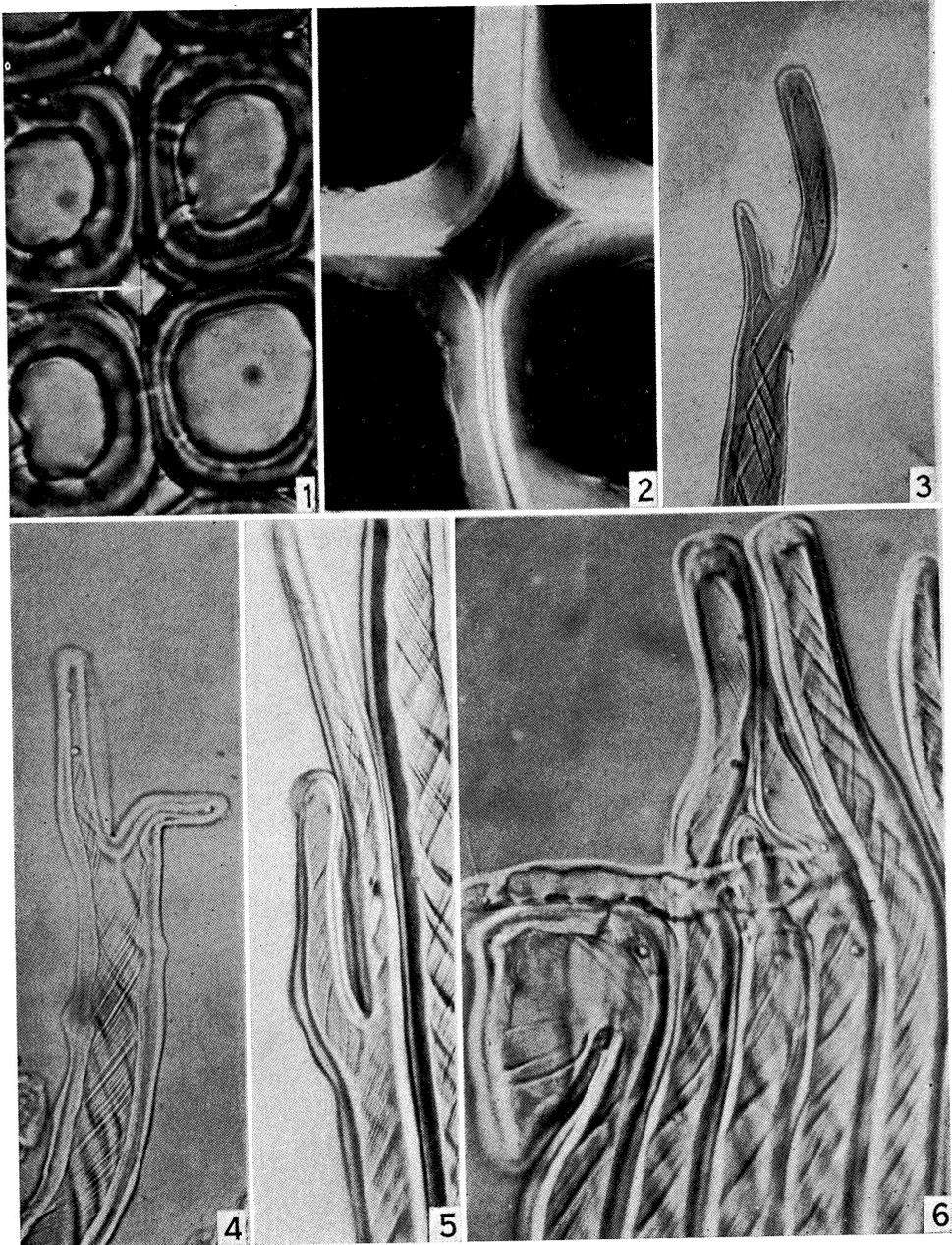
TABLE 1
VARIATION OF AVERAGE TRACHEID LENGTH IN SUCCESSIVE ZONES (40 μ THICK) FROM THE CAMBIUM INTO THE XYLEM

Specimen	Average Tracheid Length* (mm.)				
	Sect. 1 (Cambium)	2	3	4	5
<i>Pinus radiata</i> D. Don., A	1.40	1.47	1.63	1.74	1.87
<i>Pinus radiata</i> D. Don., B	1.41	1.45	1.51	1.55	—
<i>Pseudotsuga taxifolia</i> (Poir.) Britt. from Macedon, Vic., taken Nov. 1951	2.83	2.94	2.55	2.91	—
<i>Pseudotsuga taxifolia</i> from Macedon, Vic., taken Dec. 1951	2.43	2.53	2.63	2.59	—

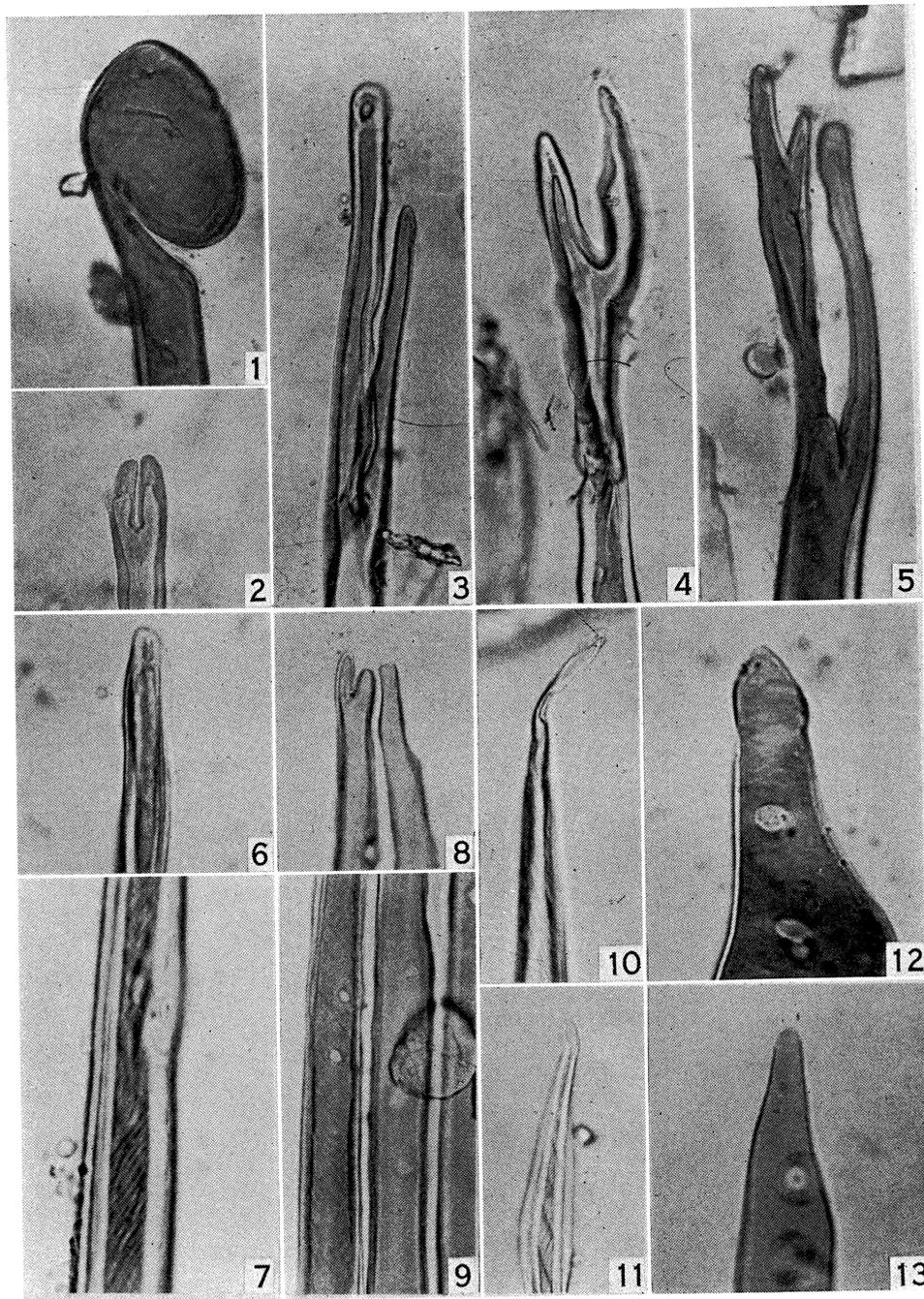
* Averages of 50 measurements.

The rapid sequence of anticlinal divisions and the subsequent elimination of many of the daughter cells of these divisions, illustrated in Figures 1 and 2, effect a considerable change in the pattern made by the cambial initials on the tangential face of the developing stem. The results of the present investigation add confirmation to those given in a series of papers by Bannan and Whalley (Bannan and Whalley 1950; Whalley 1950; Bannan 1950, 1951), who have concluded that readjustment of the daughter cells following anticlinal divisions involves tip growth of the cells rather than the relatively slow symplastic readjustment proposed by Priestley (1930) and subsequently supported by Meeuse (1941).

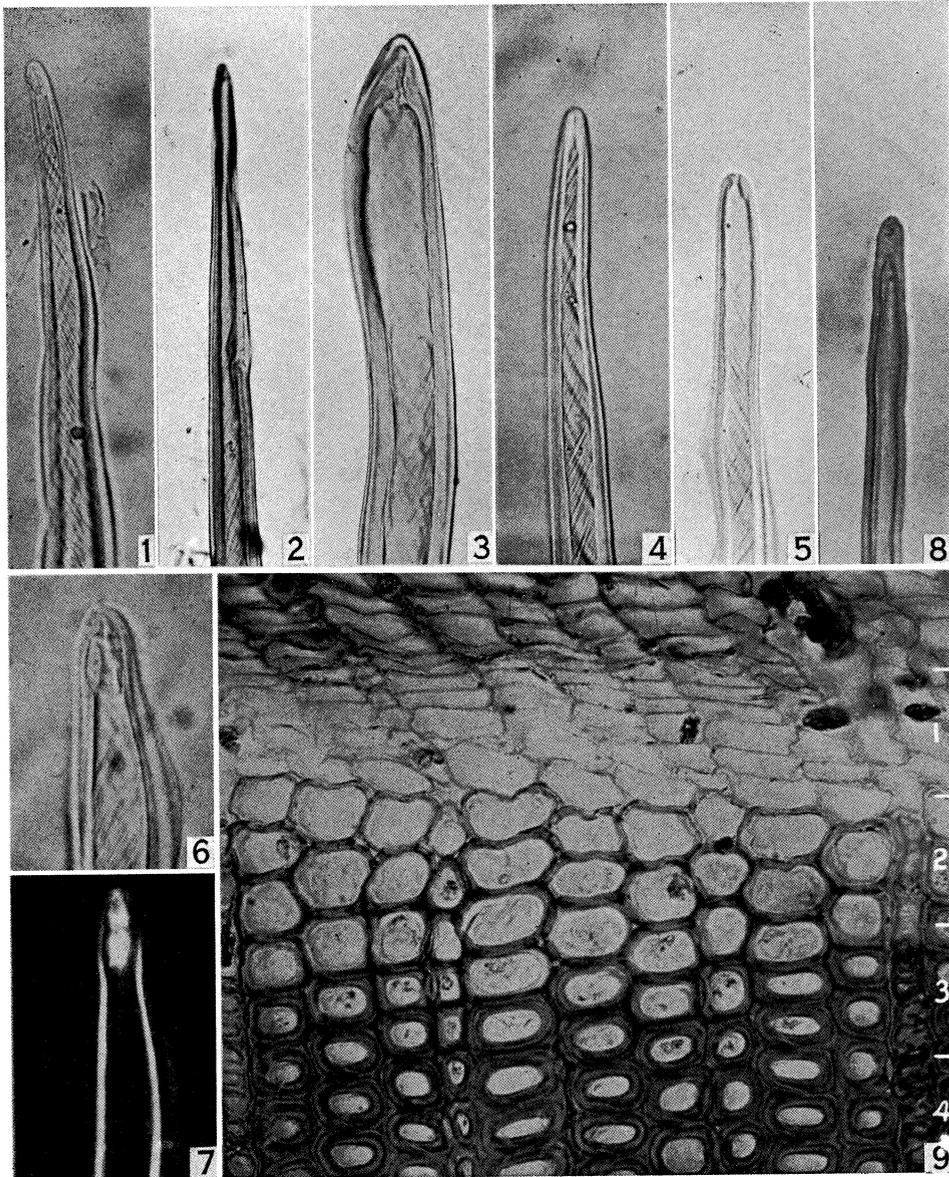
THE NATURE OF REACTION WOOD. III



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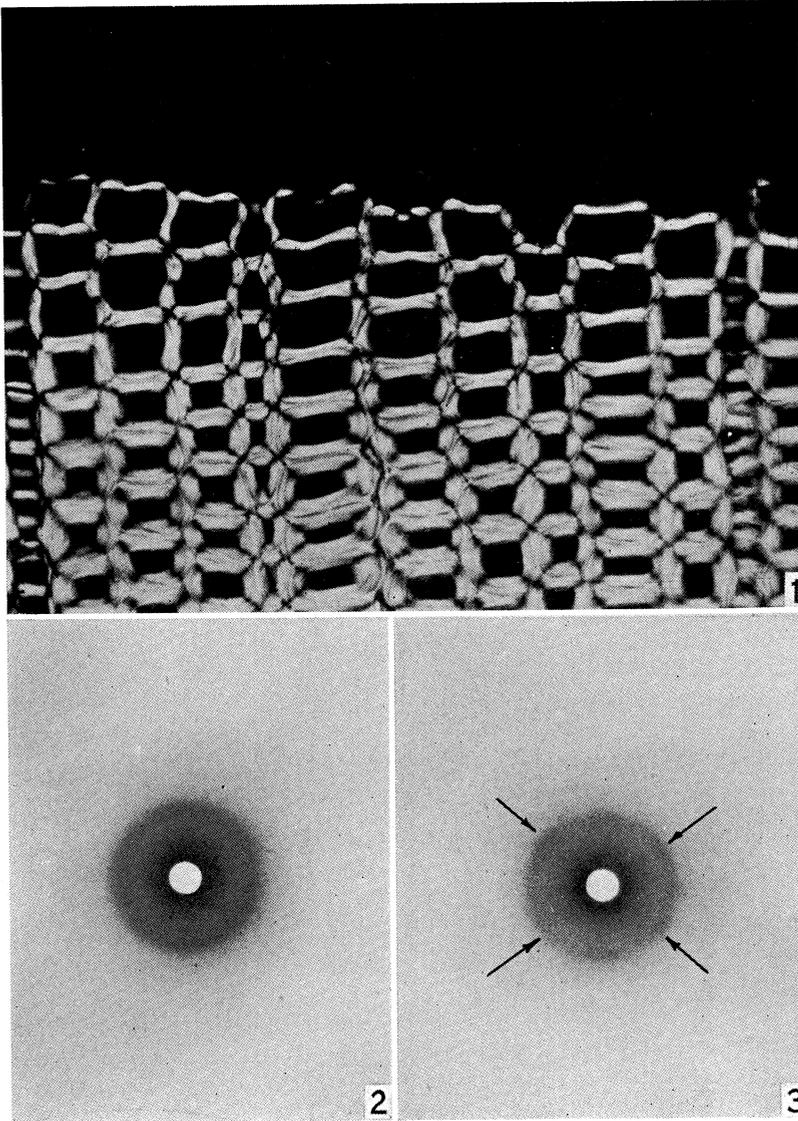


THE NATURE OF REACTION WOOD. III





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In cells in which sliding or intrusive growth* is known to occur the tips frequently show evidence of having grown against obstructions, being moulded into abnormal forms or even bifurcated (Schoch-Bodmer and Huber 1946, 1949, 1951). Impressive examples of this were found in compression wood tracheids (Plate 1, Figs. 3-6; Plate 2, Fig. 1). The frequency of occurrence of these features depended largely on the severity of the compression wood, but the fact that they were also observed in tracheids from the wide growth rings of specimen 2 in which no compression wood was present indicates that they are not a feature associated solely with the development of this tissue. Numerous examples of such bifurcated and deformed tips have since been observed in macerated material from various conifer stems. These observations thus contradict the statement of Meeuse (1941) made in support of the concept of symplastic readjustment, that in wood such as that of conifers, in which but little extra-cambial elongation takes place, no bifurcated tips are observed.

A second line of evidence supporting the concept of tip growth in conifer tracheids arises from the initial observation of Giltay (1882), subsequently supported by Priestley and Scott (1939), and by Elliot (1951), that at cell division each daughter protoplast secretes a new cell wall about itself so that the parent wall or fragments of it remain enveloping the daughter cells. The occurrence of fragments of the parent walls in the intercellular spaces of compression wood has been referred to above (Plate 1, Figs. 1 and 2) and Wardrop (1952*b*) has also demonstrated their presence in normal wood from conifers and in the ray parenchyma of angiosperms. In no instance have parent walls been observed near the tips of tracheids, suggesting that in these regions extension of the cells had ruptured them. This evidence is admittedly of a negative character, but it is consistent with the other evidence presented.

Furthermore, if tip growth occurs it is reasonable to expect that some evidence of this should be found in the anatomy of tracheid tips. Two sets of observations provide such evidence. Firstly, in partly differentiated tracheids of normal wood of *Pseudotsuga taxifolia* cell wall thickening takes place last at the cell tips so that the cytoplasm remains in contact with the extending primary wall in these regions for the greatest time (see Plate 2, Figs. 12 and 13). Secondly, in mature tracheids from both compression wood and normal wood of *Pinus pinaster* the lumen was observed to remain in contact with the primary wall at the extreme cell tip by means of a minute terminal canal (see Plate 3, Figs. 1-8), suggesting that growth, at least in the last stages of extension, was confined to the cell tips. These observations agree with those of Aldaba (1923) on the structure of the cell tips in *Linum* and *Boehmeria*, in which a similar terminal canal was observed and in which sliding growth is known to occur.

The close association of the growing cell wall and the cytoplasm is suggested in the literature by such evidence as the difficulty of plasmolysis of meristematic cells and by the fact that, although in the growing terminal cells of

* Sliding growth involves the slipping of the wall of one cell over that of a contiguous cell so that entirely new areas of contact with adjacent cells are produced. Intrusive growth involves the localized expansion of the cell wall with the newly formed parts penetrating between adjacent cells (see Eames and McDaniels 1947).

algae and fungi the cytoplasm retracts from the cell wall in regions of the filament removed from the apex, in the actual regions of growth it adheres firmly to the wall.

Thus, the rapidly changing pattern of the cambial initials, as seen in tangential section, the occurrence of bifurcated and otherwise distorted cell tips, the absence of the parent wall at the tips of tracheids, and the existence of structural features suggesting a close association between the cytoplasm and the primary wall at the tracheid tips are all points of evidence that support the concept that cell extension during differentiation proceeds by intrusive or tip growth of the cells.

Dimensional changes in the differentiation of tracheids from the cambium are closely followed by, or proceed in part simultaneously with, secondary wall formation, the completion of which constitutes the final phase of differentiation. Although it has long been recognized (Sachs 1882) that secondary thickening begins in conifer tracheids in the region of the pits, there appears to be no evidence whether thickening begins before the extra-cambial dimensional changes of differentiation are complete or whether thickening proceeds simultaneously over the whole cell length or takes place progressively. In the specimen of *Pinus radiata* with developing compression wood, relatively few cells could be seen that had undergone radial extension without formation of the outer layer of the secondary wall (cf. Plate 3, Fig. 9 and Plate 4, Fig. 1). It can be seen from Table 1 that in this and other specimens the tracheid length tended to increase in successive sections from the cambium. This clearly indicates that cell wall thickening has commenced, in these at least, before the dimensional changes of differentiation are complete. In partly differentiated tissue of *Pseudotsuga taxifolia*, tracheids were observed in which secondary thickening had obviously commenced over the major portion of the walls but not at the tips (Plate 2, Figs. 12 and 13). This also supports the view that thickening begins before the dimensional changes of differentiation are complete. In mature tracheids thickening often appeared to be less at the tips (Plate 2, Figs. 6-9) and in some specimens was quite obviously so (Plate 2, Figs. 10 and 11). Furthermore, the radial checks in the inner walls of compression wood tracheids were much less pronounced towards the cell tips, probably because of a decrease in wall thickness (see Plate 3, Figs. 1 and 2).

These radial checks, which in surface view give the appearance of pronounced striations, are parallel to the direction of micellar orientation in the inner layer and thus provide a reliable index of such orientation. By means of the method outlined above it has been shown that, in the specimens examined, the number of turns of the micellar helix per cell increases with cell length (see Figs. 3 and 4). This result at first sight appears to conflict with the relation between length and angle, used by Preston (1934) and applied by the writers to compression wood tracheids, implying a constant number of turns of the helix per cell. However, examination of individual tracheids has shown that the micellar angle varies over the cell length, usually increasing towards the tips. Phillips (1941) also has recorded variation near the flattened or irregular tracheid ends. Thus, although on the average the micellar angle

is less in longer cells, leading to the conclusion that the number of turns is constant, such a conclusion does not, in fact, hold for individual cells.

The increase in the number of turns in cells of increasing length suggests that there is a directed synthesis of cellulose in the cell wall, i.e. the synthesis is in the same direction as the orientation of the cellulose already formed. This conclusion was reached previously (Wardrop and Dadswell 1951*a*) from a study of the helical thickenings of *Pseudotsuga taxifolia* and *Taxus baccata* L., in which an increase in the number of turns of the thickenings with increasing cell length was observed. In the same way as the cell wall thickening often does not extend to the cell tips, so also the helical thickenings do not always reach the ends of the cells (Brown, Panshin, and Forsaith 1949). This evidence suggesting the progressive development of the cell wall is of interest in relation to the discussion by Thompson (1942) on the possible origin of helical structure from rectilinear growth on the surface of a cylindrical object. Furthermore, if rectilinear growth proceeds on the surface of a cone, towards its apex, the angle of inclination of the turns of the helix will tend to increase with respect to the cone axis (E. J. Williams, personal communication 1952). The similarity of this behaviour to that actually observed near the tips of tracheids is obvious. Progressive cell wall thickening is known to arise in other plant cells such as sporangiophores of *Phycomyces* and the seed hairs of cotton (Balls 1915), and of *Epilobium* (Clegg quoted by Denham 1923). In terms of sub-microscopic cell wall structure the suggestion implies that the microfibrils constituting the cell wall grow in the direction of their length. This is important in relation to the possible mechanism of development of the structural units (Wardrop and Dadswell 1951*b*) and is consistent with the tendency of microfibrils to interweave in *Valonia* (Preston and Kuyper 1951) and with the observation in *Phycomyces* of microfibrils apparently attached by only one end to the cell wall (Roelofsen 1951). It is possible that helically directed synthesis of cellulose as indicated by the above observations may be involved in the so-called spiral growth of some plant cells.

In relation specifically to the formation of compression wood, the following conclusions may be drawn:

- (i) The reduction in tracheid length that accompanies compression wood formation results from an increase in the number of anticlinal divisions in the cambium;
- (ii) The daughter cells of these divisions do not all persist;
- (iii) The subsequent extra-cambial extension of the daughter cells results from the intrusive growth between adjacent cells and the zone of growth in each cell appears to be confined to the extreme cell tips;
- (iv) Secondary wall formation apparently commences before the completion of any extra-cambial readjustment, and secondary thickening proceeds progressively towards the cell tips; and
- (v) At all times the cytoplasm of the lumen is in contact with the growing cell tips.

Although the observations account for the reduction in tracheid length that accompanies compression wood formation, the fact that a similar reduction can occur with changes of growth rate without the development of the particular morphological features characteristic of compression wood suggests that these features are a result of some additional influence in the stems associated with functional change. Thus, in view of the recent paper by Sinnott (1952), the development of compression wood cannot be regarded as being a purely gravitational response, but should be regarded as functional in character. Indeed, the location of compression wood in conifer stems and of tension wood in angiosperms offers an excellent example of new structural norms developed in respect to stimulus, in terms of the general principle proposed by Russel (1945) in relation to the behaviour of animals, "If . . . normal structural and functional relations, either external or internal, are disturbed, activities will usually be set in train that are directive toward restoring structural and functional norms or establishing new norms which are adapted to the altered circumstances."

The recognition of the principle governing the development of compression wood in conifer stems does not, however, offer any explanation of those factors involved in the development of the characteristic morphology of its tracheids, which must await further, perhaps physiological, investigations.

The mechanism of cell division, the subsequent spatial readjustment of the daughter cells, and the nature of cell wall formation are all processes of general botanical interest and it is thus advantageous to consider to what extent the results obtained for compression wood are generally applicable. As there exist, in all stems in which compression wood is found, gradations from compression wood to normal wood, and as there was no evidence in the present investigation, covering both types of wood, of any differences in the mechanism of cell division, in the readjustment of the daughter cells, or in the progressive development of the cell wall, it would seem justified to assume that, in these respects, the difference between compression wood and normal wood is one of degree only. It may therefore be concluded that these processes are similar for both normal and compression wood tracheids in spite of the obvious morphological differences. Arber (1950) has discussed the considerations involved in extending to normal tissue the conclusions reached from the study of apparently abnormal tissue.

Further investigations into the causes of the morphological differences between normal wood and compression wood are planned.

IV. ACKNOWLEDGMENTS

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EXPLANATION OF PLATES 1-4

PLATE 1

- Fig. 1.—*Pinus pinaster*. Transverse section of compression wood, showing parts of a parent wall traversing an intercellular space. x430.
- Fig. 2.—*Pinus pinaster*. Transverse section of compression wood photographed between crossed nicols, showing part of a birefringent parent wall traversing an intercellular space. x980.
- Figs. 3-5.—*Pinus pinaster*. Isolated tracheids from compression wood, showing bifurcated tips. x430.
- Fig. 6.—*Pinus pinaster*. A group of tracheids isolated by maceration, showing distortion of a tracheid tip in contact with a ray cell. x430.

PLATE 2

- Fig. 1.—*Pinus pinaster*. The distorted tip of an isolated tracheid from normal wood. x430.
- Figs. 2-5.—*Pinus pinaster*. Bifurcated tips in normal wood tracheids. In Figure 5 a triple bifurcation is present. x430.
- Figs. 6 and 7.—*Pinus pinaster*. The tip and middle part of a mature compression wood tracheid respectively, showing less thickening and absence of striations near the tip (Fig. 6). x430.
- Figs. 8 and 9.—*Pinus pinaster*. As for Figures 6 and 7. x430.
- Figs. 10 and 11.—*Pinus pinaster*. Examples of very slight secondary thickening near the tips of isolated tracheids. x430.
- Figs. 12 and 13.—*Pseudotsuga taxifolia*. Semi-differentiated tracheids of normal wood, showing only the primary wall present at the cell tips. Figure 12 x980; Figure 13 x430.

PLATE 3

- Figs. 1 and 2.—*Pinus pinaster*. Compression wood tracheids, showing the decrease in intensity of striations towards the cell tips. x430.
- Figs. 3-8.—*Pinus pinaster*. Compression wood tracheids, showing the terminal canal. Figure 7 photographed between crossed nicols. Figures 4, 5, and 8. x430. Figures 3, 6, and 7. x980.
- Fig. 9.—*Pinus radiata*. A transverse section through the cambium and region of xylem differentiation. x430.

PLATE 4

- Fig. 1.—*Pinus radiata*. As Plate 3, Figure 9, photographed between crossed nicols. x430.
- Fig. 2.—*Pinus radiata*. X-ray diffraction photograph of a 40- μ section including the cambium (zone 1, Plate 3, Fig. 9). NiK α radiation. Specimen-film distance = 2.1 cm.
- Fig. 3.—*Pinus radiata*. X-ray diffraction photograph of zone 4, Plate 3, Figure 9. NiK α radiation. Specimen-film distance = 2.1 cm.