# THE FINE STRUCTURE OF THE WALL OF THE CONIFER TRACHEID

## III. DIMENSIONAL RELATIONSHIPS IN THE CENTRAL LAYER OF THE SECONDARY WALL

by

R. D. PRESTON

*Department of Botany, University of Leeds (England)*

### INTRODUCTION

In the previous papers of this series (Preston, 1946, 1947) it has been shown that the primary layer in the walls of conifer tracheids (*i.e.*, the layer which alone surrounded each cell during its growth) is the only layer in which the molecular chains of cellulose lie approximately transversely to the cell length — in other layers the orientation is along fairly steep spirals — and as a result of X-ray examination of blocks of wood and study of dissected wall fragments under the polarising microscope it was decided at that time that the whole secondary layer, as far as the physical evidence went, was to all intents and purposes homogeneous in chain direction. Since then, re-examination of the birefringence of tracheids in transverse section has indicated that there is, in fact, in the secondary layer a narrow outer lamella in which the cellulose chains lie along a spiral ffatter than in the bulk of the wall within; and that failure to interpret correctly the features of this layer in the earlier work was due largely to the very considerable angular dispersion in this outer layer. A preliminary account of this later work has already been given (Wardrop and Preston, 1947) and it is intended to give a fuller account and a more detailed discussion later in this series. The present investigation concerns the organisation of the cellulose in the central lamella of the secondary wall, in an attempt to redefine the factors underlying the length relationships of spiral organisation first revealed many years ago (Preston, 1934). Briefly this relationship is as follows.

If the major extinction position (m.e.p.) of the walls of a number of tracheids in any one annual ring of a conifer is determined, and the average cotangent is calculated of the angles they make with the length of the cell, then this average cotangent is related to the average length by a relation approximately of the form

$$L = K \cot \vartheta, \qquad K \text{ being constant,}$$

over a considerable number of annual rings. The major extinction position defines approximately the orientation of the cellulose chains in the central layer under consideration here (Preston, 1947), so that the relation may be taken to imply a connection between cell length and chain orientation. This is clearly of the type connecting the length of a spiral spring to the angle the winding makes with the axis of the spiral if the spiral is extended at constant girth. Now since in conifers the cambial initials continue to elongate for about the first 60 years in the life of a tree, cutting off "replicas" of themselves (the tracheids) throughout each growing season, it was considered reasonable that this relation arose because (a) each primary (extending) wall consisted of cellulose chains oriented in a direction similar to that of the secondary wall later deposited upon it, and (b) the cambial cell, with its primary wall was, in effect, elongating at constant girth — in spite of some difficulty in precise interpretation due to the radial extension of the radial wall after each longitudinal division in the cambial cell, both in the daughter cell which remained meristematic and in the other which became a tracheid. Now, however, that the primary wall in the tracheid is known to possess cellulose chains which always lie more or less transversely — and this has been shown also for the cambial cells themselves (PRESTON AND WARDROP, 1948) — irrespective, apparently, of the history of the cell as regards dimensional changes, this type of explanation is ruled out. Indeed, it now seems that any explanation based simply on mechanical extension must be discarded, since the secondary layer is deposited after the bulk, at least, of the change in cell dimensions is over.

In seeking an explanation along new lines, it is tempting to recall that in the algae *Valonia* (PRESTON AND ASTBURY, 1937), marine *Cladophora* (ASTBURY AND PRESTON, 1940) and *Chaetomorpha* (NICOLAI AND FREY-WYSSLING, 1938) (and, as we now know, in freshwater *Cladophora* and in *Rhizoclonium* [PRESTON AND NICOLAI, 1948]) wall layers are laid down quite regularly in which the cellulose chains are oriented at an angle somewhat less than a right angle to those in the lamella last deposited. Similarly, in tracheids the primary layer is built of cellulose chains which are almost transverse, while in the secondary lamella under consideration here they are steeply inclined. This type of connection is particularly attractive since it throws the responsibility for the orientation back where it must belong — to the cytoplasm and almost certainly the cytoplasmic surface. At the moment, however, it seems undesirable to put much emphasis on this similarity between species of widely different types. For, firstly, there is interposed, between the primary wall and this central layer, a secondary lamella whose chain orientation is different from that in both these layers; and secondly the variability from cell to cell of the orientation in the primary wall is nothing like sufficient to account for the variability in the secondary lamella if the chains in the latter are to be oriented at a constant angle to those in the former (PRESTON, 1947). There remain, however, two lines along which an explanation of the length/spiral angle relationsnip is to be sought. It may be that the change in spiral angle from inner to outer annual rings arises in virtue of some "ageing" effect in the cambium so that the length/angle relationship is in a sense fortuitous; or it may be that knowledge of the increasing *average* tracheid length from one annual ring to the next has led to a misinterpretation of the phenomenon and that, in fact, a similar relation holds among the individual cells — of widely varied length — even within one annual ring.

It is the purpose of this paper to consider both these possibilities. It may be said now that it appears that the latter explanation is the correct one, and while this only takes us forward a small step, it does lead to some interesting speculations. During the course of the investigation a paper by MEEUSE (1938) was noticed in which a qualitative connection was reported between cell length and spiral angle in some monocotyledonous fibres and this has been recently confirmed for bamboo (PRESTON AND SINGH, 1948): and after the investigation was completed an article appeared by MEREDITH (1946) in which a length/spiral angle relationship was derivable for cotton hairs. It may well be, therefore, that the correlations to be described here are very general in plant cells and thus may carry implications of a very fundamental nature.

## MATERIALS AND METHODS

In order to explore the first of the two possibilities mentioned above — that change in spiral angle is associated with an "ageing" effect in the meristem — it was thought necessary and sufficient to determine the angles in several annual rings at one level in the leader of a softwood tree and to compare these with the corresponding regions at other levels. If the meristems were in fact ageing, then one might expect a progressive change in the spiral angle in, say, the second annual ring from the pith as the point of observation is raised in the tree. This could have been done roughly, but not accurately (PRESTON, 1947), by determining the m. e. p. 's of say 50 tracheids at each point, or directly and more accurately by noting under the ordinary microscope the orientation of the striations in the wall which clearly belong, in those species showing them, to this central layer. This would have involved, however, a tedious examination of some thousands of tracheids, so that it was decided to use an X-ray method. This yields figures for the average spiral angle at each point which are admittedly rather rough, but nevertheless sufficiently accurate for our purpose. The experimental material was a 15-year-old tree of *Pinus sylvestris* provided by the Forestry Commission at Thornton-le-Dale, Yorkshire, and from this a number of blocks of wood were prepared with two faces truly longitudinal tangential and 1 mm thick in the radial direction. Attention was confined to the late wood only and on this account the outer rings could not be used since the layer of late wood was too thin. The X-ray beam, collimated by a slit 0.5 mm diameter, was directed through the specimen in the radial direction so that the experimental material consisted of a cylinder of wood 0.5 mm in diameter and 1 mm long, including therefore parts of about 1000 tracheids. From the resulting X-ray diagrams, which refer almost exclusively to the central layer (PRESTON, 1946, WARDROP AND PRESTON, 1947, 1948) the average spiral angle could roughly be calculated (PRESTON, 1946).

In attempting to investigate the second possibility it was clearly essential to use a microscopical technique, since examination of small parts of individual tracheids by X-ray methods, while readily possible, again would have occupied far too much time. Determination of the m.e.p. was impossible since the lengths of the cells were also needed, and this left therefore only the microscopical observation of striations. In point of fact, however, by no means all the tracheids available showed striations with clarity sufficient for accurate determination, so that recourse had sometimes to be made to the run of the mouths of slit pits. In those cells which did show clear striations it was obvious that the "tails" at each end of the mouth of the slit pits gave better correspondence with striation direction than did the slit mouths themselves, so that these were invariably used in default of striations. Two species were investigated, *Picea sitchensis* (2nd, 3rd, 4th and 10th annual rings) and *Abies nobilis* (3rd and 10th annual rings), the former showing a rapid, and the latter a slow, change in average spiral angle from inner to outer rings. Late wood only was used, and was macerated by alternate treatments with chlorine and hot sodium sulphite.

Plate 1. All the figures in this plate are X-ray diagrams of the late wood at various regions in a specimen of *Pinus sylvestris*. In all the diagrams the specimen is 1 mm thick and the X-ray beam is directed radially through the wood. The grain (and therefore also tracheid length) lies parallel to the longer edge of the page in all cases.

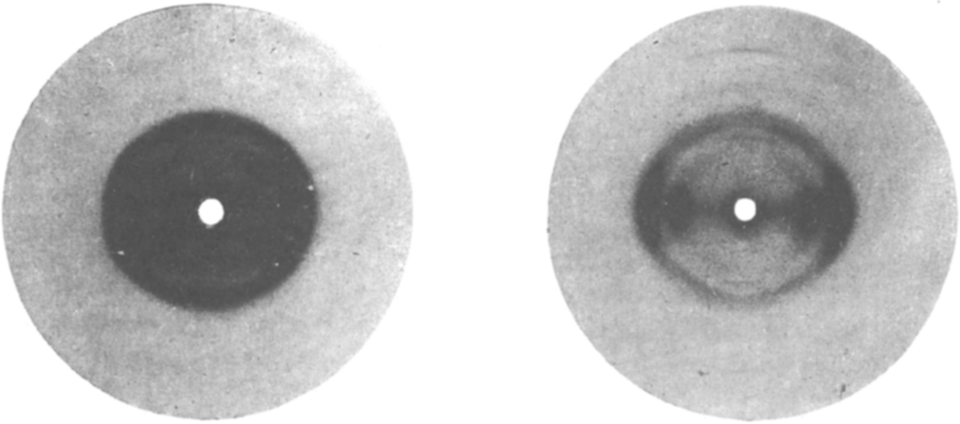

Fig. 1 a and b. Diagrams at the 280 cm level

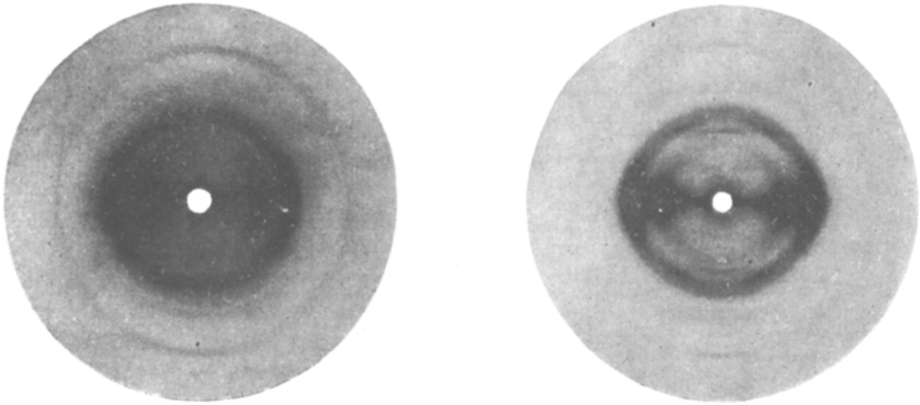

Fig. 2 a and b. Diagrams at the 247 cm level

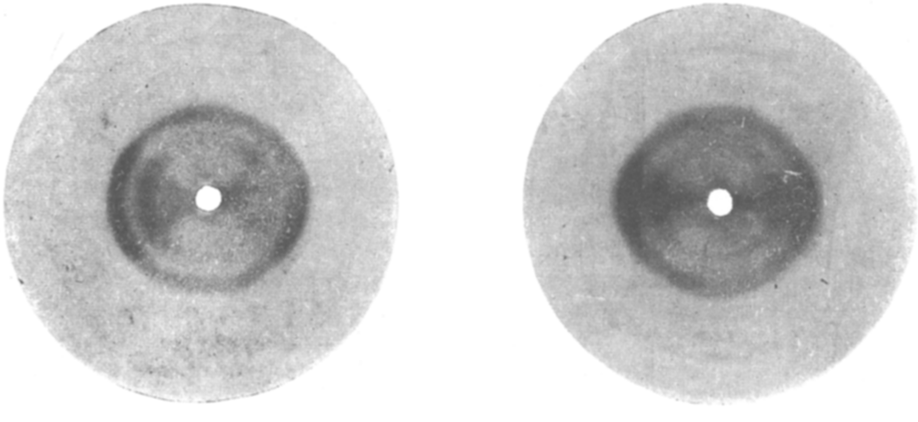

Fig. 3 a and b. Diagrams at the 180 cm level

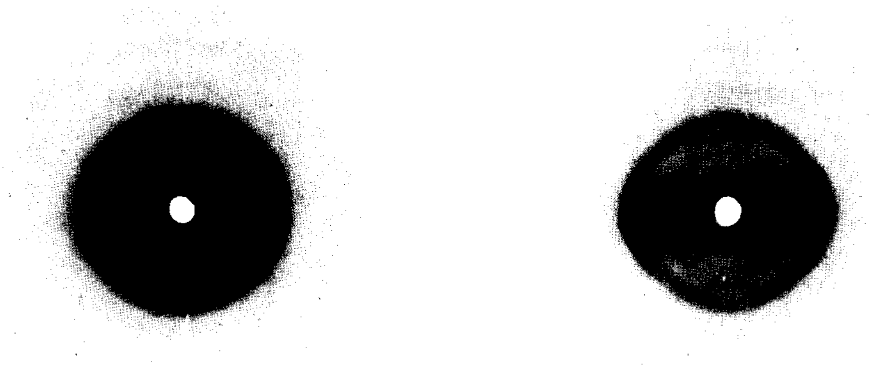

Fig. 4 a and b. Diagrams at the 95 cm level

Figs 1–4. The diagrams in the left hand column are of wood from the second annual ring from the pith, and in right hand column from the fifth annual ring.

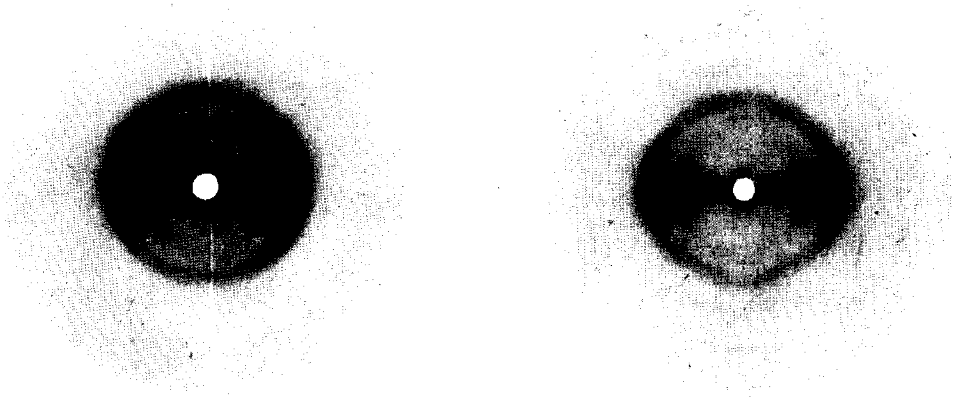

Fig. 5 a. Second annual ring

Fig. 5 b. Fifth annual ring.

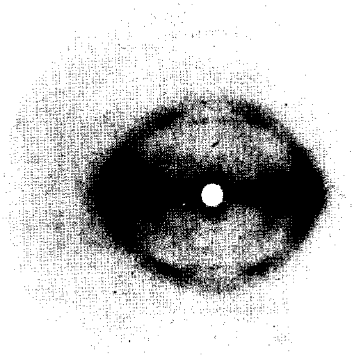

Fig. 5 c. Tenth annual ring.

Fig. 5. Diagrams of wood 14 cm from the base of the tree

## RESULTS

The values of the spiral angles, determined by an X-ray method, at various points in the specimen of *Pinus sylvestris* are presented in Table I and some of the relevant X-ray diagrams are reproduced in Plate I, Figs 1–5 in corroboration. From these results it is clear that the cellulose chains in the central layer of tracheids do in fact become more nearly parallel to cell length in passing from inner to outer rings at any one level*. This confirms the earlier statement (PRESTON, 1934) in which, however, a small correction must be made since the angles given in this early paper referred to the m. e. p.'s of the whole wall thickness (PRESTON, 1947). Similarly, as one might expect, the spirals also become steeper on passing from top to bottom of the tree in any annual cylinder laid down during one year (*e.g.*, ring 3 at level 390 cm; to 4 at 360, 5 at 280, etc.) There is, however, no general trend noticeable if the same annual ring is observed at each level (vertical columns) so that the present data supply no evidence of any ageing effect of the meristem on spiral angle; all changes in this angle could be readily understandable in terms of a length/angle relationship.

TABLE I

THE AVERAGE ANGLE BETWEEN THE CELLULOSE WINDING AND CELL LENGTH IN TRACHEIDS FROM VARIOUS ANNUAL RINGS AT DIFFERENT LEVELS IN THE LEADER OF A 15-YEAR-OLD TREE OF *Pinus Sylvestris*. LATE WOOD

| Height above ground level (cm) | Number of annual rings | Average angle (degrees) in annual ring number | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| 390 | 3 | — | 35 | | | | | | | |
| 360 | 4 | 34.0 | 27.5 | 32.5 | | | | | | |
| 280 | 5 | 37.5 | 30.0 | — | 26.0 | | | | | |
| 247 | 6 | 35.0 | — | — | 25.0 | — | | | | |
| 215 | 7 | 38.0 | 30.0 | — | 30.0 | — | — | | | |
| 180 | 8 | — | 35.0 | 29.0 | — | — | — | 25.0 | | |
| 140 | 9 | — | 25.0 | — | 27.5 | — | 27.5 | — | — | |
| 95 | 10 | 39.0 | — | 29.0 | — | — | — | 19.0 | — | — |
| 55 | 11 | — | 30.0 | — | 25.0 | — | — | — | 14.0 | |
| 14 | 12 | 34.0 | — | — | 27.5 | — | — | 14.0 | 14.0 | 14.0 |
| | Avge | 36.2 | 31.8 | 30.1 | 26.7 | — | 27.5 | 19.3 | 14.0 | 14.0 |

Turning now therefore to the second possibility — that the length/angle relationship refers to individual cells and not merely to whole annual rings — the first problem to be solved is that of assigning to one tracheid one characteristic spiral angle. This necessity arises by virtue of the fact that the spiral angle varies along a tracheid as the breadth of the tracheid varies. This is made clear in Table II, where a series of determinations are presented, chosen at random from a large sample, of the spiral angle $\vartheta$ at various points of measured cell breadth $b$ in individual tracheids. It is fortunate therefore that, as also shown in the Table, the spiral tends to become flatter as $b$ increases, in such a way that $\sin \vartheta$ is proportional to $b$. Hence for each tracheid a hypothetical spiral angle $\vartheta_{1.00}$ can be calculated corresponding to a breadth of 1 unit, and

---

* This has also been demonstrated by an X-ray method in *Pseudotsuga* (PRESTON, 1946) and in *Pinus insignis* and *Picea sitchensis* (unpublished).

TABLE II

DERIVATION OF STANDARD ANGLE $\vartheta_{1.00}$ FROM OBSERVED ANGLES

| Species | Tracheid | Breadth (b) (1 unit = 24 $\mu$) | Spiral angle ($\vartheta$) (degrees) | b/sin $\vartheta$ | $\vartheta_{1.00}$ (degrees) |
|---|---|---|---|---|---|
| *Pinus insignis* . . | 1 | $2.03_1$ | 25.4 | 4.73 | 11.4 |
| | | $1.83_2$ | 21.8 | 4.93 | |
| | | $1.57_8$ | 17.4 | 5.28 | |
| | | $1.39_3$ | 15.6 | 5.19 | |
| | | $1.32_9$ | 14.8 | 5.20 | |
| *Picea sitchensis* . . | 1 | $1.12_6$ | 19.2 | 3.41 | 17.0 |
| | | $1.12_0$ | 18.5 | 3.53 | |
| | | $1.20_2$ | 20.8 | 3.40 | |
| | | $1.01_6$ | 17.5 | 3.40 | |
| | 2 | $1.35_6$ | 21.0 | 3.78 | 19.3 |
| | | $1.16_2$ | 19.1 | 3.55 | |
| | | $1.78_2$ | 27.6 | 3.83 | |
| | | $0.80_8$ | 12.4 | 3.76 | |
| | 3 | $1.01_8$ | 19.2 | 3.09 | 19.3 |
| | | $1.15_8$ | 23.0 | 2.96 | |
| | | $1.21_8$ | 23.2 | 3.09 | |
| *Abies nobilis* . . . | 1 | $1.39_3$ | 43.5 | 2.02 | 28.5 |
| | | $1.60_0$ | 53.5 | 2.00 | |
| | | $1.56_6$ | 44.0 | 2.25 | |
| | 2 | $1.33_4$ | 44.0 | 1.92 | 31.2 |
| | | $1.25_0$ | 41.0 | 1.90 | |
| | | $0.90_8$ | 27.3 | 1.98 | |

this has been done in the Table. This constitutes a sample of the procedure adopted here with a number of observations too large (some 600 each of b and $\vartheta$) to be presented individually in this way. In Table III therefore is given only a summary of the bulk of the results, showing the relation between cell length and the standard angle $\vartheta_{1.00}$. In order to facilitate inspection of the results the figures are listed in order of increasing cell length, though the determinations were not of course made in that order. The averages of the real angles actually observed are also included for comparison. Measurements also made of lumen width at the same points are not included here, since much the better correlation was found between external width and $\sin\vartheta$. Incidentally, no correlation could be detected between wall thickness and cell width.

These results are also given graphically in Figs 6, 7 and 8, where the lengths are plotted, however, against $\cot\vartheta_{1.00}$. It cannot be claimed that this presentation has any theoretical merit except that it retains the general type of relation previously suggested in discussing *averages* in various annual rings (PRESTON, 1934). The justification is that, of the various possible *simple* functions of $\vartheta$ ($\cot\vartheta$, $\cot^2\vartheta$, $\cos\vartheta$, $\cos^2\vartheta$) which might be used, $\cot\vartheta$ is the only one giving an approximately linear relation.

## DISCUSSION

It is evident in Fig. 6, which presents the data for the uncorrected spiral angle in

TABLE III

THE STANDARD ANGLE $\vartheta_{1.00}$ FOR TRACHEIDS OF KNOWN LENGTH (THE UNIT OF BREADTH IS AS IN TABLE II, AND FOR LENGTH 1 UNIT = 74 $\mu$)

| Species | a | b | c | d | e | a | b | c | d | e |
|---|---|---|---|---|---|---|---|---|---|---|
| *Picea sitchensis* | 2 | 11.7 | 1.25 | 34.6 | 37.7 | 2 | 22.2 | 1.21 | 16.2 | 19.4 |
| | 4 | 13.6 | 0.66 | 38.6 | 22.8 | 3 | 22.3 | 1.15 | 18.6 | 20.1 |
| | 4 | 14.3 | 0.70 | 27.5 | 19.0 | 4 | 22.8 | 1.00 | 15.7 | 15.0 |
| | 4 | 14.6 | 0.80 | 27.6 | 21.0 | 10 | 23.1 | 1.70 | 16.6 | 19.8 |
| | 3 | 14.7 | 0.95 | 23.2 | 19.0 | 2 | 23.2 | 1.14 | 18.3 | 21.0 |
| | 3 | 15.2 | 0.96 | 26.2 | 21.6 | 3 | 23.5 | 1.36 | 11.0 | 17.0 |
| | 3 | 15.2 | 1.60 | 24.2 | 33.5 | 4 | 23.6 | 1.23 | 14.0 | 16.1 |
| | 4 | 16.0 | 1.12 | 22.0 | 24.0 | 4 | 24.0 | 1.34 | 10.8 | 12.5 |
| | 4 | 16.2 | 1.08 | 19.0 | 18.7 | 3 | 24.2 | 1.40 | 15.5 | 21.3 |
| | 3 | 16.4 | 1.01 | 22.9 | 22.7 | 4 | 24.2 | 1.18 | 12.5 | 13.8 |
| | 3 | 16.6 | 1.39 | 20.5 | 26.9 | 10 | 24.3 | 1.79 | 13.6 | 25.0 |
| | 2 | 17.2 | 1.20 | 17.0 | 19.5 | 2 | 24.6 | 1.89 | 15.1 | 23.7 |
| | 10 | 17.2 | 1.05 | 18.2 | 19.0 | 4 | 25.0 | 0.96 | 13.5 | 11.4 |
| | 3 | 17.3 | 1.46 | 17.9 | 23.4 | 3 | 25.2 | 0.97 | 13.4 | 13.0 |
| | 2 | 17.5 | 1.67 | 20.5 | 33.1 | 3 | 25.6 | 1.07 | 12.8 | 13.3 |
| | 10 | 17.6 | 1.14 | 18.2 | 21.0 | 3 | 25.8 | 1.26 | 18.0 | 18.0 |
| | 4 | 17.9 | 1.05 | 17.0 | 16.7 | 10 | 26.1 | 1.66 | 11.6 | 17.6 |
| | 2 | 19.1 | 1.29 | 16.1 | 20.0 | 2 | 26.2 | 1.16 | 14.5 | 15.9 |
| | 2 | 19.2 | 1.09 | 13.5 | 16.6 | 3 | 26.3 | 1.07 | 14.0 | 14.8 |
| | 3 | 19.2 | 1.72 | 17.4 | 28.0 | 10 | 26.4 | 1.31 | 12.7 | 12.3 |
| | 2 | 19.3 | 1.43 | 14.7 | 24.4 | 4 | 26.6 | 1.24 | 9.1 | 11.9 |
| | 2 | 19.5 | 1.35 | 17.3 | 24.0 | 10 | 27.6 | 1.46 | 12.3 | 16.4 |
| | 10 | 19.6 | 1.48 | 18.1 | 23.2 | 2 | 27.8 | 1.43 | 14.4 | 18.3 |
| | 4 | 19.8 | 1.37 | 17.4 | 24.3 | 4 | 28.0 | 1.04 | 10.7 | 10.7 |
| | 10 | 19.8 | 1.57 | 12.7 | 17.6 | 10 | 28.3 | 1.07 | 11.2 | 11.5 |
| | 2 | 20.0 | 1.20 | 19.9 | 21.7 | 4 | 28.4 | 1.07 | 13.7 | 13.7 |
| | 2 | 20.2 | 0.98 | 15.6 | 15.8 | 3 | 28.5 | 1.22 | 12.2 | 14.5 |
| | 4 | 20.2 | 1.08 | 16.5 | 17.5 | 2 | 28.7 | 1.40 | 12.0 | 15.8 |
| | 3 | 20.6 | 1.15 | 22.5 | 23.1 | 2 | 28.8 | 0.90 | 15.4 | 11.9 |
| | 10 | 20.7 | 1.46 | 16.7 | 22.5 | 3 | 29.0 | 1.20 | 10.0 | 9.6 |
| | 4 | 20.8 | 1.26 | 11.2 | 12.9 | 10 | 29.2 | 1.33 | 11.7 | 12.4 |
| | 10 | 20.8 | 1.22 | 19.3 | 21.8 | 3 | 29.5 | 1.00 | 12.5 | 16.2 |
| | 3 | 21.6 | 1.06 | 18.1 | 17.6 | 3 | 29.8 | 1.00 | 12.5 | 12.0 |
| | 4 | 21.8 | 1.04 | 14.1 | 14.4 | 4 | 30.0 | 1.41 | 10.1 | 11.8 |
| | 2 | 21.9 | 1.25 | 16.2 | 19.1 | 10 | 35.9 | 1.18 | 8.8 | 10.3 |
| | 2 | 22.0 | 1.19 | 15.4 | 15.7 | 10 | 37.8 | 1.43 | 8.4 | 10.6 |
| | 4 | 22.0 | 1.78 | 15.5 | 20.0 | | | | | |
| *Abies nobilis* | 3 | 13.0 | 1.44 | 36.5 | 58.8 | 3 | 24.0 | 1.90 | 19.5 | 31.5 |
| | 3 | 13.7 | 1.38 | 44.5 | 71.7 | 3 | 25.0 | 1.20 | 19.1 | 22.8 |
| | 3 | 14.0 | 1.14 | 37.3 | 43.2 | 3 | 25.0 | 1.24 | 19.0 | 23.0 |
| | 3 | 14.4 | 1.33 | 31.2 | 37.4 | 10 | 25.2 | 1.01 | 22.3 | 18.5 |
| | 3 | 15.2 | 1.61 | 28.5 | 47.0 | 3 | 26.2 | 0.82 | 23.8 | 18.2 |
| | 3 | 15.5 | 1.55 | 30.0 | 54.3 | 3 | 26.6 | 1.12 | 16.6 | 18.0 |
| | 3 | 16.1 | 1.34 | 33.2 | 47.0 | 3 | 26.6 | 1.72 | 20.5 | 37.0 |
| | 3 | 18.4 | 1.92 | 23.2 | 49.2 | 10 | 27.0 | 1.48 | 14.2 | 19.7 |
| | 3 | 18.6 | 0.92 | 35.6 | 29.8 | 10 | 27.5 | 1.17 | 19.4 | 22.9 |
| | 3 | 19.5 | 1.60 | 32.4 | 58.2 | 10 | 29.6 | 1.06 | 12.6 | 13.1 |
| | 3 | 19.9 | 1.61 | 25.1 | 38.9 | 10 | 29.6 | 1.13 | 19.9 | 17.8 |
| | 3 | 20.2 | 1.51 | 24.6 | 39.0 | 10 | 37.4 | 1.80 | 12.8 | 23.6 |
| | 3 | 21.3 | 1.03 | 23.8 | 21.5 | 10 | 41.0 | 1.63 | 13.1 | 19.4 |
| | 3 | 23.8 | 1.69 | 21.0 | 42.0 | | | | | |

a = annual ring from which tracheid is chosen  b = length of tracheid  c = breadth of tracheid  
d = $\vartheta_{1.00}$  e = average $\vartheta$

*Picea*, that there is a marked tendency for $\vartheta$ to decrease as L increases, *i.e.*, the molecular spiral is steeper the greater its length. This relation is much improved when $\vartheta$ is corrected to standard breadth (Figs 7 and 8), and there can remain little doubt but that the dimensions of a tracheid and the molecular configuration of its wall are closely related, roughly in the form $L = A + B \cot \vartheta_{1.00}$. The regression lines drawn in Figs 7 and 8 correspond to the relations:

$$\textit{Picea}\ L = 7.57 + 3.91 \cot \vartheta_{1.00}$$
$$\textit{Abies}\ L = 6.66 + 8.94 \cot \vartheta_{1.00}$$

where L is in scale units, or

$$\textit{Picea}\ L = 568 + 293 \cot \vartheta_{1.00}$$
$$\textit{Abies}\ L = 500 + 670 \cot \vartheta_{1.00}$$

where L is in $\mu$. The standard errors of the factors in the two $\cot \vartheta$ terms are ± 20 and ± 58 respectively, so that the difference is fully significant. The constants 568 and 500 are not significantly different for these samples, but it remains uncertain whether a difference could be established if the results for *Abies* were more numerous.

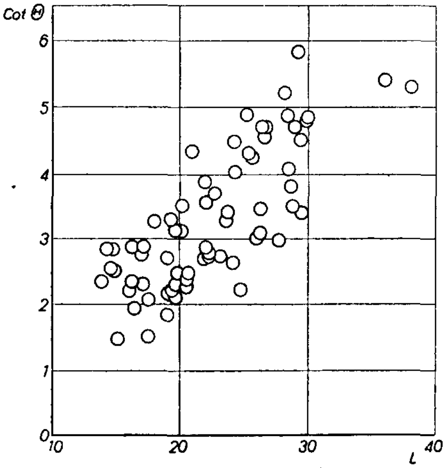

Fig. 6. *Picea*. Correlation between tracheid length and the cotangent of the average inclination $\vartheta$.

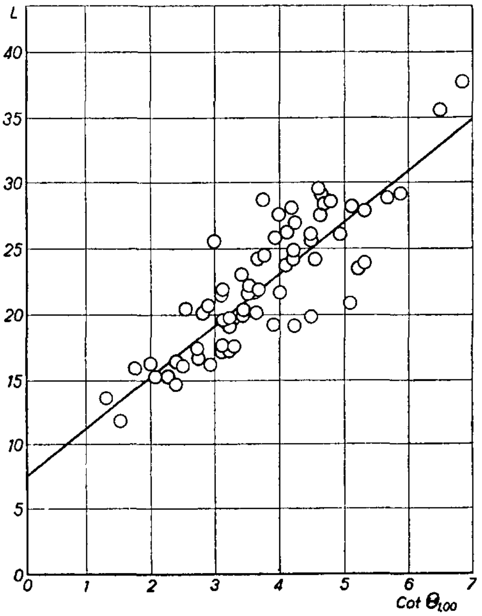

Fig. 7. *Picea*. Correlation between tracheid length and the cotangent of the standard angle $\vartheta_{1.00}$.

It is essential to note that these relations imply a statistical trend only and that other factors are also concerned which modify these simple relations and of which as yet we know nothing: it is not at all implied thereby that any *individual* shorter cell will have necessarily a slower spiral than any *individual* longer cell. Nevertheless the results demonstrate a relation as nearly rigid physically as may perhaps be expected in biology when, of necessity, comparatively few individuals come under consideration. The physical meaning of the constants A and B is obscure, as is common in numerical relations in biology. Formally, A represents the maximum tracheid length at which

$\vartheta_{1.00} = 90°$, but it seems certain that tracheids of length 500 μ would not in fact have transverse cellulose chains. The dimensions 500 μ × 24 μ (the standard width used here) are indeed very different from those of vessels where the orientation of the cellulose chains is still not transverse (PRESTON, 1938). B represents the increment in L above this limit for each decrement in $\vartheta_{1.00}$ causing unit increment in cot $\vartheta_{1.00}$. The complete relation between L and b is clearly

$$L = A + B\sqrt{(b)^2 \operatorname{cosec}^2 - 1}$$

In seeking an interpretation of these results we can, of course, no longer consider dimensional changes in the wall itself to be involved such as were used in the earlier (1934) paper; for firstly, the tracheid has completed its dimensional changes before this *secondary* layer is deposited and, secondly, during at least the greater part of the period when dimensional changes are occurring, the wall surrounding the cell is a *primary* wall with cellulose chains lying approximately transversely (PRESTON, 1947, PRESTON AND WARDROP, 1948). It is particularly to be stressed that since cot $\vartheta_{1.00}$ is related to the *whole* length L, then the small increase in length which occurs during the differentiation of a tracheid from the cambium is not in any case adequate to explain the effect. Two possible lines along which explanation is to be sought immediately suggest themselves. Both of these involve the assumption that orientation of cellulose chains is governed by some factor in the cytoplasm-wall interface, and are better understood if we adopt the simple picture that this factor is an orientation of protein chains in the surface forming, as it were, an "enzyme" which, with the aid no doubt of other accessory factors, as usual with enzymes, condense glucose (or cellobiose or some oligo-saccharide) to cellulose in such a way that the chains of cellulose lie parallel to those of the protein. This simple suggestion has some little support in the often quoted approximate equality of the length of the cellobiose unit in cellulose (10.3 Å) and the length in the extended polypeptide chain of three amino acids, together with the fact that, whether the proteins in protoplasm are globular or fibrillar, the surface may be expected to be covered with

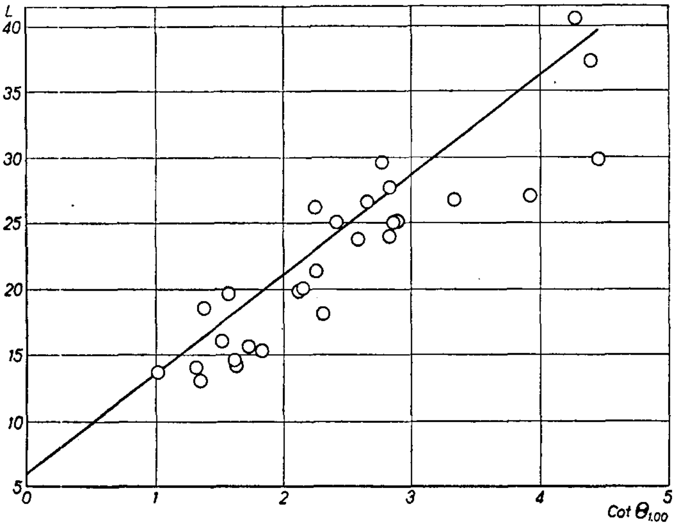

Fig. 8. *Abies*. Correlation between tracheid length and the cotangent of the standard angle $\vartheta_{1.00}$.

*References p. 383.*

a monolayer of polypeptide chains (HÖBER, 1943). The essence of the assumption is, in fact, that the whole surface of the cytoplasm constitutes an enzyme system similar to the phosphorylase involved in the condensation of $\alpha$-glucose to starch. Now the first, and less probable, explanation would be that this surface could replace the primary wall in the explanation previously given (PRESTON, 1934) *i.e.*, the surface could be considered as extending in such a way that the protein chains in the surface layer would be pulled into steeper spirals as the cell elongated and into flatter spirals as it increased in breadth. In support of this suggestion the observation could be quoted that in multilayers deposited on metal by repeated passage through protein monolayers the polypeptide chains tend to be oriented parallel to the direction of movement of the metal slip; for while the conditions in the two cases are different it is evident that the intermolecular forces in a monolayer are not sufficiently strong as to outweigh the effect of relatively slight external mechanical effects. Yet consideration of the detailed structure of the wall alone makes this suggestion rather improbable. Firstly, while the cambial initial is elongating, the wall surrounding it is a primary wall with cellulose chains which maintain approximately transverse orientation (PRESTON, 1947, PRESTON AND WARDROP, 1948): the layer we are considering now is not laid down until much later — in fact after a secondary layer has been deposited whose micellar spiral is relatively flat. The structure of the wall is therefore very complex and it is difficult to associate extension of the cytoplasmic surface with any *one* of these three layers. Secondly, the elongation is slow and amounts to only a few per cent increase per year while the cambial initial, in virtue of its repeated longitudinal tangential division, is increasing effectively in the radial direction by many hundreds per cent. It is therefore necessary to fall back on a second line of argument. It appears most likely that the structure of the layer examined here is determined by a mechanism which bears no direct relation to the previous history of the cell as regards dimensional changes, but rather to the actual dimensions attained at the time of deposition. This is in fact, as far as the wall itself is concerned, merely a restatement of the facts. Interpreting it in terms of the cytoplasmic mechanism suggested here would imply an orientation of polypeptide chains in the surface in a direction which depends, in a statistical sense, on cell dimensions. It is clearly not desirable to discuss this in any detail until the structure of the other cell layers has been reported upon, where a similar phenomenon has in fact been found. It will be clear even now that the detailed structures demand a change in the cytoplasmic membrane from time to time. A change of some kind is not in fact unlikely, for taking the view that the membrane is active in converting $\beta$-glucose to cellulose as it migrates outwards, this effective permeability of the membrane contrasts strongly with the known impermeability of the membrane to sugar in the adult cell.

## SUMMARY

A re-investigation has been attempted of the relation $L = K \cot \vartheta$ shown some years ago to connect the average length L of tracheids in an annual ring with the average cotangent of the angle $\vartheta$ which the cellulose chains make with the longitudinal cell axis. It is shown that the relation does not arise as a result of "ageing" in the meristem. New data suggest that the angle $\vartheta$ is related to cell breadth $b$ by the relation $b/\sin \vartheta = \text{constant}$, from which a standard angle $\vartheta_{1.00}$ can be calculated for unit cell breadth. It then appears that in *individual* tracheids there is a statistical relation between L and $\vartheta_{1.00}$ of the form

$$L = A + B \cot \vartheta_{1.00}$$

*References p. 383.*

The angle $\vartheta$ at any point in the wall is therefore related to the breadth of the cell at the point of observation and to the whole length of the cell. It is suggested that this might arise from structural peculiarities at the cytoplasmwall interface.

## RÉSUMÉ

Une nouvelle étude a été faite de l'expression $L = K \cot.\vartheta$ dont il a été montré, il y a quelques années, qu'elle relie la longueur moyenne L des trachéides dans une zone circulaire annuelle avec la cotangente moyenne de l'angle $\vartheta$ que la chaine cellulosique fait avec l'axe longitudinal de la cellule. On montre que cette expression ne résulte pas d'un vieillissement du méristème. De nouvelles données suggèrent que l'angle $\vartheta$ dépend de la largeur de la cellule $b$ selon l'expression $b/\sin\vartheta$ = constante, expression à partir de laquelle peut être calculé un angle type $\vartheta_{1.00}$ pour la largeur d'une cellule unité. Il apparait ainsi que dans les trachéides individuelles, il existe une relation statistique entre L et $\vartheta_{1.00}$ de la forme:

$$L = A + P \cot\vartheta_{1.00}$$

L'angle $\vartheta$ a tout point de la paroi: est ainsi fonction de la largeur de la cellule au point considéré et de la longueur totale de la cellule. Il est possible que cette dépendance provienne de particularités structurales à l'interface cytoplasme-paroi.

## ZUSAMMENFASSUNG

Eine Neuuntersuchung der Beziehung $L = K \cot\vartheta$, die, wie vor einigen Jahren gezeigt wurde, die Durchschnittslänge L der Tracheiden in einem Jahresring mit dem Durchschnittswert des cotangens des Winkels $\vartheta$, den die Zelluloseketten mit der longitudinalen Zellachse machen, in Zusammenhang bringt, wurde unternommen. Dabei wird gezeigt, dass diese Beziehung nicht als Resultat einer "Alterung" im Meristem auftritt. Neue Resultate führen zu der Annahme, dass der Winkel $\vartheta$ zu der Zellenbreite $b$ in Beziehung steht, und zwar dass $b/\sin\vartheta$ konstant ist. Hieraus kann ein Standardwinkel $\vartheta_{1.00}$ für die Einheit der Zellbreite berechnet werden. Hieraus folgt dann, dass für *individuelle* Tracheiden eine statistische Beziehung zwischen L und $\vartheta_{1.00}$ besteht, die die Form hat

$$L = A + B \cot\vartheta_{1.00}$$

Der Winkel $\vartheta$ an irgendeinem Punkt der Wand ist also abhängig von der Zellenbreite an dem Beobachtungspunkt und der gesamten Zellänge. Es wird angenommen, dass diese Beziehung durch strukturelle Besonderheiten der Zytoplasma-Wand-Grenzfläche verursacht sein könnte.

## REFERENCES

W. T. Astbury and R. D. Preston, *Proc. Roy. Soc.* London, B. 129 (1940) 54.
R. Höber, *The Physical Chemistry of cells and Tissues*, London 1943.
A. D. J. Meeuse, *Rec. trav. botan. néerland.*, 35 (1938) 288.
A. Meredith, *J. Textile Inst.*, 37 (1946) T 205.
E. Nicolai and A. Frey-Wyssling, *Protoplasma*, 30 (1938) 401.
R. D. Preston, *Phil. Trans.*, B. 224 (1934) 131.
R. D. Preston, *Ann. Botany*, N.S. III (1938) 507.
R. D. Preston, *Proc. Roy. Soc.* London, B. 133 (1946) 327.
R. D. Preston, *Proc. Roy. Soc.* London, B. 134 (1947) 202.
R. D. Preston and W. T. Astbury, *Proc. Roy. Soc.* London, B 127 (1937) 76.
R. D. Preston and E. Nicolai, *Unpublished* (1948).
R. D. Preston and K. Singh, *Unpublished* (1948).
R. D. Preston and A. B. Wardrop, *Unpublished* (1948).
A. B. Wardrop and R. D. Preston, *Nature*, 160 (1947) 911.
A. B. Wardrop and R. D. Preston, *Unpublished* (1948).

Received June 14th, 1948