

CELL WALL ORGANIZATION AND THE PROPERTIES OF THE XYLEM

I. CELL WALL ORGANIZATION AND THE VARIATION OF BREAKING LOAD IN TENSION OF THE XYLEM IN CONIFER STEMS

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Summary

The variation of breaking load in tension of tangential longitudinal sections of wood, taken from successive growth rings of each of six conifer stems, has been studied. An increase in this property was observed in successive growth rings from the stem centre of each specimen. This was paralleled by an increase in tracheid length, basic density, and cellulose content. The inclination to the longitudinal cell axis of the spiral micellar system of the cell wall decreased with increasing tracheid length. Because of this known relation between spiral angle and tracheid length, the latter was used as an index of the spiral organization of the cell wall. The breaking load in tension of single tracheids taken from successive growth rings of two stems was also measured and found to increase with increasing cell length.

Failure in tension occurred in the cell wall. In specimens of late wood the line of failure followed the direction of micellar orientation of the middle layer of the secondary wall. This was also observed for early wood specimens although the line of failure was often irregular. Within the cell wall separation between the outer and middle layers of the secondary wall, and the outer layer of the secondary wall and primary wall, usually occurred during failure. This has been attributed to the differences in micellar orientation and the relative extent of the micellar and intermicellar systems of the adjacent cell wall layers.

It has been concluded that the breaking load in tension of the wood sections was governed by the cell wall organization of the constituent cells and by the basic density of the specimens. The increase in the breaking load in tension which occurred upon drying was attributed primarily to changes in the intercellular layer (middle lamella), because the breaking load of isolated tracheids was less in the dry than in the water-saturated condition.

It was demonstrated that an increase in radial growth rate of the stem resulted in a decrease in the average tracheid length. This was paralleled by a decrease in the breaking load in tension of the wood. The possible applications of the investigations in forest practice are briefly discussed.

I. INTRODUCTION

In this series of papers it is proposed to discuss the cell wall organization of the main tissue elements of wood in relation to the variation of its properties. The investigations described are confined for the most part to the study of variations in properties within conifer stems.

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Following earlier controversy the cell wall organization of conifer tracheids has now been established (Wardrop and Preston 1947) as being similar to that proposed originally by Kerr and Bailey (1934). The mature cell wall consists of two structures: the primary cell wall and the secondary cell wall. In the primary wall the micelles are oriented almost transversely to the longitudinal axis of the cell, but are considerably dispersed about this direction (Preston 1947; Preston and Wardrop 1949a). The secondary wall consists of three layers. In the outer and inner layers the micelles are spirally arranged, making an angle of $45-90^\circ$ to the longitudinal axis of the cell. The central layer also possesses spiral organization but the spiral angle is smaller, the micelles making an angle of between 0° and 45° with the longitudinal axis of the cell (Bailey and Vestal 1937; Wardrop and Preston 1947). The central layer is higher in cellulose content, and in late wood is considerably thicker than the other secondary cell wall layers. The intercellular substance (middle lamella) is optically isotropic and consists mainly of lignin with smaller amounts of hemicelluloses (Kerr and Bailey 1934).

The nearly transverse orientation of the micelles in the primary wall of conifer tracheids is independent of the cell length (Preston 1947), and of its lateral dimensions (Preston and Wardrop 1949a). However, in the secondary wall the angle of the spiral micellar orientation becomes less (i.e. the spiral becomes steeper) with increasing tracheid length. This was demonstrated quantitatively by Preston (1934, 1948) for the middle layer of the secondary wall of conifer tracheids, and has since been shown to hold for the outer layer of the secondary wall (Preston and Wardrop 1949b). Thus it is probable that the spiral organization of the entire secondary wall is determined by the cell length. The dependence of spiral angle on cell length has also been shown to hold for the abnormal tracheids of compression wood (Wardrop and Dadswell 1950), for the fibres of *Eucalyptus gigantea* Hook. f. (author's unpublished data), as well as for cotton fibres (Meredith 1946), and for the fibres of *Sansaviera* (Meeuse 1938). It is reasonable to suppose that the known anisotropy of wood properties is a reflection of its structure. The dependence of anisotropy of properties upon fibre structure has been demonstrated for textile fibres. In wood, however, the matter is complicated in that it is extremely difficult to predict, from the behaviour of a single cell, that of a group of cells aggregated to form a tissue. In this connection it is obvious that the nature of the intercellular substance would be of importance, depending upon the extent to which it is involved in governing adhesion and movement between cells.

However, insofar as cell wall organization does influence the anisotropy of wood properties it will be clear from the above discussion that so long as comparison is made within a stem a relation may be expected to exist between either the micellar spiral angle and the anisotropy of properties, or, because the cell length determines the micellar spiral angle, between cell length and the anisotropy of properties. Thus in material of similar origin the cell length can be regarded as a factor to which the anisotropy of properties may be related. Furthermore since cell length in conifer stems is determined by growth

conditions, a study of variation of properties with variation in cell length offers a means of relating growth factors to properties. From this standpoint the variation of tracheid length in conifer stems is of importance.

In a cross section of a conifer stem the tracheid length increases rapidly in successive growth rings from the pith, attaining a more or less constant value after 10-50 growth rings, and, in any one growth ring, increases from the base of the tree till it reaches a maximum some distance up the stem (Sanio 1872; for numerous other references see Bisset and Dadswell 1949). At any arbitrary level in a stem the relation between tracheid length and growth ring number can be expressed in simple mathematical terms (Wardrop 1948). The possible relation between tracheid length and rate of the radial growth of the stem has been discussed by Priestley (1930) who pointed out that rapid radial growth is effected by rapid tangential longitudinal division of the cambial initials. If this increased rate of tangential division involves a postponement of transverse divisions in the cambium it was suggested by Priestley that a wider ring would be associated with longer tracheids. If, on the other hand, an increase in the number of tangential divisions is accompanied by an increase in the number of transverse divisions, then a wider ring might be expected to be associated with shorter tracheids. The latter alternative has been demonstrated for compression wood (Wardrop and Dadswell 1950). Evidence supporting this conclusion for normal wood formation is contained in the present paper (Fig. 5). The tracheid length in conifer stems can thus be related to both the age and the rate of division of the cambial initials.

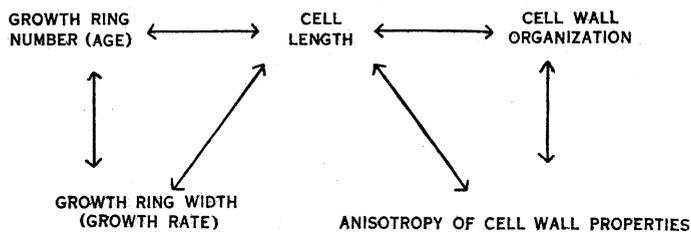


Fig. 1.—Some factors governing cell wall properties within a conifer stem.

The possible relations of the factors discussed above to the anisotropy of cell wall properties are illustrated in Figure 1. However, in specimens of wood, the magnitude of a property in a given direction will not depend solely upon the cell wall organization of the constituent cells, but may be modified or in some cases outweighed by other factors such as the basic density, gross anatomy of the specimen, or the nature of intercellular adhesion.

In the present series of investigations the influence of cell wall structure upon properties has been studied by following the variation in properties of small specimens of the xylem taken from comparable positions in successive growth rings from the pith, so that where possible in the one stem the influ-

ence of the gradual changes in cell dimensions and cell wall organization can be studied. This method possesses the advantage that genetically similar material is compared. In the first instance the investigations have been confined to gymnosperms because of their anatomical simplicity.

In the following investigation the variation of breaking load in tension has been studied, employing this general approach. The molecular factors involved in the rupture of fibres of cotton, flax, etc. have been extensively studied (see for example Hermans 1949) and it is reasonable to suppose that similar factors will also apply to conifer tracheids. Thus it is now generally agreed that failure in tension involves rupture of the primary valency chains rather than slipping between them, and that the degree of polymerization, chain length distribution, and the crystalline/non-crystalline ratio of the cellulose influence the properties (Mark 1943; Hermans 1949). Of major importance also is the angle of inclination of the micelles to the longitudinal axis of cells (Berkley and Woodyard 1938). Thus when a fibre with spiral micellar orientation is loaded in tension a compressive force is set up between adjacent regions of the micellar system. A shear force also acts between these regions, and the regions themselves are subjected to tensile forces acting parallel to the direction of orientation. Upon rupture of the cell in tension, separation of adjacent regions of the micellar system parallel to the direction of orientation occurs more readily when the inclination of the micelles to the longitudinal cell axis is large than when it is small. This is because the forces responsible for the lateral cohesion of the micellar system are considerably smaller than the primary valency forces responsible for the cohesion of the system parallel to its direction of molecular orientation.

The influence of these factors as well as the influence of basic density and various structural features upon the breaking load in tension are discussed in following sections of this paper.

II. MATERIALS

Cross sections from butt logs of the following plantation-grown conifers were used:

1. *Pinus radiata* D. Don—concentric, showing 18 growth rings—late wood of successive rings examined.
2. *Pinus radiata*—concentric, different from specimen 1, showing 18 growth rings—early wood of successive rings examined.
3. *Pseudotsuga taxifolia* (Poir.) Britt.—concentric, showing 18 growth rings—late wood of successive rings examined.
4. *Pinus radiata*—eccentric, showing 21 growth rings—early wood and late wood from the first 12 growth rings on the compression wood side examined and comparisons made with early wood and late wood from the same rings on the diametrically opposite side (rings 13-21 were rejected because of the presence of marked spiral grain).

5. *Pinus pinaster* Sol.—concentric, showing 31 growth rings—late wood of successive rings examined. The growth of the tree from which this section was taken had been greatly retarded but had responded remarkably to treatment with superphosphate. This was evident in the cross section, the first 15 growth rings being formed prior to the treatment.

6. *Pinus radiata*—concentric, showing 22 growth rings—late wood of successive rings examined. This tree had been suppressed and then released as a result of silvicultural treatment. The result was clearly marked in the cross section in which growth rings 10-16 from the pith were extremely narrow while growth rings 17-22 were very wide.

III. METHODS AND RESULTS

(a) Microscopic Examination of Tension Failures

Microscopic examination of the specimens in the region of failure was carried out after mounting the specimens in dilute glycerol. The main features of the tension failures from an early growth ring and from a later-formed growth ring of *Pinus radiata* are illustrated in Plates 1 and 2. Failures in both early wood and late wood specimens were examined.

In order to determine in what layers of the cell wall failure occurred, transverse sections ($20\ \mu$) were prepared from a standard tension specimen of *Pseudotsuga taxifolia* and examined between crossed nicols. The main features of failure can be seen in Plate 3, Figures 1, 2, and 3.

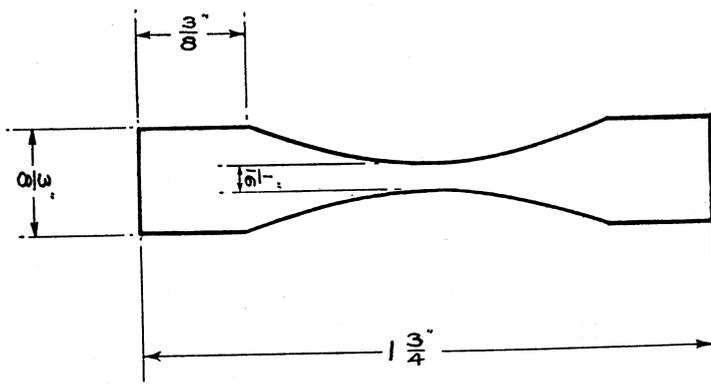


Fig. 2.—The lateral dimensions of the test sections of $80\ \mu$ in thickness used in the determination of breaking load in tension.

(b) Tension Tests on Longitudinal Tangential Sections

From each stem cross section a radial strip of wood was cut from the pith to the bark (in specimen 4 both on the compression wood side and the side diametrically opposite). Each strip was then shaped accurately on a

spindle moulder, so that the tangential faces appeared as indicated in Figure 2 with the dimensions shown. From the strips so prepared tangential longitudinal sections $80\ \mu$ in thickness were cut, using a sliding microtome, and kept wet until tested. By this means a number of serial sections could be obtained from early wood or late wood of successive growth rings as required for the various experiments.

TABLE 1
VARIATION OF TRACHEID LENGTH, BASIC DENSITY, MICELLAR SPIRAL ANGLE, AND
BREAKING LOAD IN TENSION OF $80\text{-}\mu$ SECTIONS IN SUCCESSIVE GROWTH RINGS OF
PINUS RADIATA D. DON.

Specimen	Growth Ring No.	Tracheid Length (mm.)	Micellar Spiral Angle (degrees)	Basic Density (g./cc.)	Breaking Load in Tension (g.)	No. of Specimens Tested for Breaking Load
<i>Pinus radiata</i> late wood, specimen 1	2	2.53	25	0.500	558	6
	4	3.00	19	0.515	616	6
	6	3.65	16	0.465	850	6
	8	3.80	13	0.545	1137	8
	10	3.83	12	0.532	924	6
	12	4.07	11	0.550	1303	7
	14	4.22	14	0.575	1019	6
	16	4.38	10	0.515	1442	8
	18	4.31	11	0.625	1283	6
<i>Pinus radiata</i> early wood, specimen 2	1	2.81	41	0.275	394	12
	2	3.03	30	0.286	387	12
	3	3.58	24	0.298	297	12
	4	—	14	0.303	—	—
	6	—	14	0.326	389	12
	7	4.57	13	0.346	397	12
	8	3.68	15	0.363	484	12
	9	—	13	0.411	594	12
	10	4.14	15	0.403	642	12
	11	—	—	0.374	510	12
	12	4.39	14	0.359	595	12
	13	4.37	—	0.377	697	12
	14	—	14	0.402	781	12
	15	5.60	—	0.374	681	12
	16	—	14	0.423	795	12
	17	—	—	0.381	845	12
	18	5.36	11	0.458	868	12

These sections were used for investigating the breaking load in tension using the testing equipment developed in this laboratory (Kloot 1950). The number of sections tested for each growth ring depended on the width of the early wood or late wood bands being investigated. The results for the various specimens are given in Tables 1-3. The values so obtained are listed as the breaking load in g. per section. As only relative values for sections from different growth rings of the same stem cross section were required, no attempt was made to compute the corresponding stress.

(c) Determination of Tracheid Length

Half the sections from each portion of the growth ring under test were macerated (using hydrogen peroxide and glacial acetic acid) and the average length of 50 tracheids taken at random was determined. Results are given in Tables 1-4.

TABLE 2
VARIATION OF TRACHEID LENGTH, BASIC DENSITY, MICELLAR SPIRAL ANGLE, AND
BREAKING LOAD IN TENSION OF 80- μ SECTIONS IN SUCCESSIVE GROWTH RINGS OF
PSEUDOTSUGA TAXIFOLIA

Specimen	Growth Ring No.	Tracheid Length (mm.)	Micellar Spiral Angle (degrees)	Basic Density (g./cc.)	Breaking Load in Tension (g.)	No. of Specimens Tested for Breaking Load
<i>Pseudotsuga</i>	1	2.04	35	—	330	11
<i>taxifolia</i>	2	2.27	28	0.448	745	16
late wood,	3	2.48	27	0.480	1199	11
specimen 3	4	2.74	23	0.445	1158	16
	5	2.75	25	0.519	1197	16
	6	2.71	27	0.530	1449	16
	7	3.02	22	0.550	1492	16
	8	3.15	23	0.585	1511	12
	9	3.12	20	0.581	1365	12
	10	3.17	18	0.519	1353	12
	11	3.46	19	0.545	1430	16
	12	3.33	14	0.520	1343	16
	13	3.61	13	0.529	1511	12
	14	3.42	10	0.510	1543	16
	15	—	—	0.635	1654	12
	16	3.87	9	0.551	1388	16
	17	—	—	0.538	1388	12
	18	3.80	9	0.570	1358	8

(d) Determination of Average Angle of Micellar Orientation in the Middle Layer of the Secondary Wall

X-ray diffraction diagrams were obtained either from the actual test specimens or from carefully matched material, and the micellar spiral angle was determined from the spread of the 002 diffraction arc. NiK α radiation was used with a specimen-film distance of 3 cm. Results are given in Tables 1-3.

(e) Basic Density

The basic density of the wood from each growth ring was determined, using early wood or late wood as required by the experiment. For this purpose the wood was isolated from a radial strip adjacent tangentially to that used for the test specimens. The water-saturated volume of each piece from each ring was determined by the water displacement method and the dry weight obtained after drying for 2½ hours at 105°C. The data obtained are presented in Tables 1-3.

(f) Radial Number of Cells per Growth Ring

In specimens 5 and 6 transverse sections were cut from the centre of the stem to the bark and from these the number of tracheids in a radial row was

TABLE 3
VARIATION IN TRACHEID LENGTH, BASIC DENSITY, MICELLAR SPIRAL ANGLE, AND THE BREAKING LOAD IN TENSION OF 80- μ SECTIONS IN THE SUCCESSIVE GROWTH RINGS OF *PINUS RADIATA* D.DON (SPECIMEN 4)

Growth Ring No.	Tracheid Length of Late Wood (mm.)	Micellar Spiral Angle of Late Wood (degrees)	Basic Density (g./cc.)		Breaking Load (g.)		No. of Sections Tested for Breaking Load	
			Early Wood	Late Wood	Early Wood	Late Wood	Early Wood	Late Wood
Compression Wood Side of Stem								
1	1.59	43	0.379	0.483	266	261	69	10
2	1.77	—	0.402	0.489	—	400	—	6
3	2.08	45	0.391	0.491	—	414	—	20
4*	2.18	42	0.437	0.531	300	340	47	24
5*	2.49	42	0.475	0.522	—	445	—	13
6*	2.48	—	0.374	0.568	—	552	—	19
7*	2.61	38	0.476	0.568	436	585	34	17
8*	2.90	—	0.458	0.617	—	780	—	15
9*	3.10	33	0.477	0.694	513	872	14	18
10*	3.24	—	0.588	0.633	918	1110	14	13
11*	3.41	35	0.457	0.606	657	1139	25	13
12*	3.32	34	0.550	0.712	—	1073	—	6
Normal Wood Side of Stem								
1	1.44	46	—	0.436	—	278	12	12
2	1.75	—	0.398	0.462	224	356	—	11
3	2.02	41	0.371	0.391	—	386	—	13
4	2.30	37	0.406	0.452	—	336	50	8
5	2.67	40	0.359	0.505	227	669	—	11
6	3.02	—	0.352	0.545	—	961	—	8
7	3.07	33	—	0.515	—	881	60	8
8	3.32	—	—	0.545	647	1065	—	8
9	3.36	30	—	0.630	—	1387	—	6
10	3.63	—	—	0.660	—	1615	12	8
11	3.58	22	0.406	0.600	820	1238	50	25
12	3.57	—	0.431	0.550	878	1075	—	14

* Compression wood present.

determined for each growth ring. The results for specimen 6 (*Pinus radiata*) are given in Table 4 and Figure 6 and for specimen 5 (*P. pinaster*) are illustrated in Figure 5.

(g) *Effect of Drying on Breaking Load in Tension*

This was investigated with sections from the early wood of *Pinus radiata*. Longitudinal tangential sections, 80 μ thick, were cut as indicated above from four growth rings (Nos. 3, 6, 10, and 19). Half of the sections were selected at random from each growth ring and kept in water before testing. The remaining sections were oven-dried for two hours at 105°C. and tested immediately after removal from the oven. Results obtained from both the dry and wet specimens are shown in Table 5.

TABLE 4
INFLUENCE OF SILVICULTURAL TREATMENT BY THINNING UPON GROWTH OF
PINUS RADIATA D.DON (SPECIMEN 6)

Growth Ring No.	Tracheid Length (mm.)	Radial Number of Cells per Growth Ring	Breaking Load of Late Wood 80- μ Sections (g.)
1	1.64	421	—
2	1.86	356	242
3	2.43	363	—
4	2.61	316	276
5	2.97	240	331
6	2.95	222	—
7	3.09	129	502
8	3.34	110	—
9	3.25	108	—
10	3.46	106	624
11	3.76	91	—
12	3.46	80	—
13	3.26	68	687
14	4.01	56	1207
15	3.98	50	1098
16	3.92	66	1107
17	3.20	169	618
18	3.16	278	808
19	2.86	360	—
20	3.14	288	—
21	3.76	274	1131
22	3.46	145	1353

(h) *Tension Tests on Isolated Tracheids*

Sections cut from the early wood of successive growth rings of *Pinus radiata* were macerated either by means of the hydrogen peroxide and glacial acetic acid method or by the method of Cohen and Dadswell (1939). In preliminary experiments it was shown that if the former treatment were not too prolonged the fibre strength was not adversely affected. The variation in breaking load in tension of isolated tracheids from successive growth rings was investigated by the use of a modified Westphal balance. To one arm of the

balance a pan was suspended, holding a 100 ml. beaker. The weight of the pan and beaker was counterbalanced on the other arm. The ends of a single tracheid were attached by means of dental cement to pieces of fine silk thread,

TABLE 5
COMPARISON OF THE BREAKING LOAD IN TENSION OF SECTIONS (80 μ) OF EARLY WOOD OF *PINUS RADIATA* D.DON, OVEN-DRY AND WATER-SATURATED

Growth Ring No.	Tracheid Length (mm.)	Breaking Load in Tension (g.)	
		Water-Saturated	Oven-Dry
3	2.45	300	596
6	3.16	473	1068
10	3.85	441	903
19	4.07	390	948

one of which was suspended from the balance arm holding the counterweight and the other attached to an adjustable metal rod set in a heavy base resting on the bench. By means of the adjustable rod the fibre and attached thread were drawn taut so that the balance arm was horizontal as indicated on the scale. Water was then allowed to flow into the beaker on the pan at a constant rate of 5.5 g. per minute until the tracheid failed. The water was then weighed.

TABLE 6
BREAKING LOAD IN TENSION OF EARLY WOOD TRACHEIDS ISOLATED FROM DIFFERENT GROWTH RINGS OF *PINUS RADIATA* D.DON

Growth Ring No.	Tracheid Length (mm.)	Breaking Load per Tracheid (g.)	Cell Wall Area per Tracheid (mm. ² $\times 10^{-4}$)	Breaking Load (kg./mm. ²)
1	2.33	2.40	3.07	7.8
3	3.17	3.73	3.80	9.8
6	4.11	5.34	4.42	12.1
10	4.67	6.27	5.40	11.6
13	4.83	7.09	6.42	11.0
17	5.13	5.96	4.57	13.0

By this means 20 tracheids from each growth ring were tested and results recorded when failure occurred in the centre of the tracheid away from the points of adhesion to the holding threads. An attempt was made to estimate the absolute value of the breaking load in tension by determining the average cross-sectional cell wall area per tracheid, from a cross section of the portions of the different growth rings from which the tracheids were isolated. The difficulty of obtaining accurate measurements in this manner was realized but it is of interest to consider the results obtained for different growth rings (see Table 6).

Using the above method the average breaking loads in tension of dry and wet tracheids from the same growth ring were determined. The results are given in Table 7.

TABLE 7
BREAKING LOAD IN TENSION OF CONIFER TRACHEIDS, WATER-SATURATED AND AIR-DRY

Specimen	Breaking Load per Tracheid (g.)		$\frac{BL_W}{BL_D}$
	Dry (BL_D)	Wet (BL_W)	
<i>Pinus radiata</i>			
early wood			
Ring 13	4.38	4.71	1.08
Ring 18	9.81	11.66	1.19

(i) Variation in Cellulose Content in Successive Growth Rings

The Cross and Bevan cellulose content was determined for early wood of successive growth rings in *Pinus radiata* (specimen 1) and for combined early wood and late wood of successive rings in *Pseudotsuga taxifolia* using the standard method of the Division of Forest Products. The values obtained were considered in relation to tracheid length and the angle of micellar spiral orientation of the middle layer of the secondary wall (θ). Results are shown in Table 8. The cellulose samples from the *P. radiata* growth rings were used in determining the moisture regain at 70°C. and 65 per cent. relative humidity.

TABLE 8
VARIATION OF CELLULOSE CONTENT OF WOOD FROM DIFFERENT RINGS OF CONIFER STEMS

Specimen	Growth Ring Number from Pith	Tracheid Length (mm.)	Micellar Spiral Angle (degrees)	Cross and Bevan Cellulose (%)	Moisture Regain (%)
<i>Pinus radiata</i> early wood	3	2.07	28	57.3	11.1
	4	2.69	21	58.7	11.2
	7	3.13	17	62.1	—
	10	3.51	12	62.5	10.8
	20	4.32	13	62.9	10.8
<i>Pseudotsuga taxifolia</i> early wood and late wood	2	1.6	31	58.0	—
	5	2.4	26	60.2	—
	10	2.9	15	62.5	—
	15	3.2	13	65.2	—
	20	3.5	12	65.3	—

IV. TREATMENT OF DATA

The variations in tracheid length, micellar spiral angle, breaking load, and basic density with successive rings from pith have been compared in Figure 3 for the late wood of *Pinus radiata* (specimen 1). The trends obtained are clearly shown. In Figure 4 the breaking load in tension has been plotted

against tracheid length, for the results obtained in the investigation of the successive growth rings of *P. radiata* (specimen 4, containing compression wood on one side).

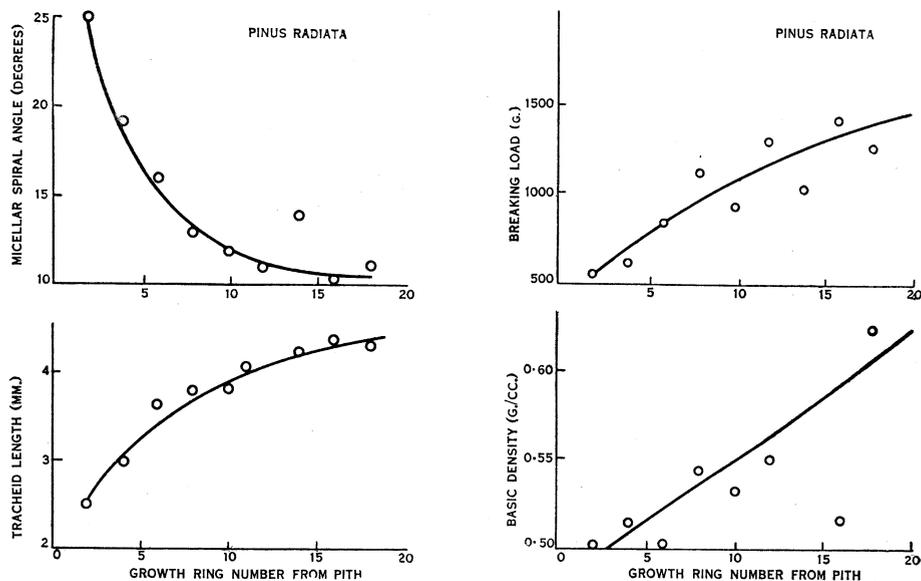


Fig. 3.—Variation of tracheid length, micellar spiral angle, basic density, and breaking load in tension in successive growth rings from the stem centre of *Pinus radiata* (specimen 1, late wood).

The results obtained with *Pinus pinaster* (specimen 5) and *P. radiata* (specimen 6), which were the two specimens showing the effect of suppression of radial growth and subsequent release, are shown in Figures 5 and 6. In Figure 5, tracheid length, micellar spiral angle, and number of cells per growth ring in the *P. pinaster* specimen have been plotted against growth ring number from the pith. Certain parallel and opposed relations may be noted. In Figure 6, tracheid length, number of cells per growth ring, and breaking load in tension for the *P. radiata* specimen have been plotted against growth ring number from the pith.

The relations obtained between breaking load in tension, BL_T (g. per section) and tracheid length, L (mm.) for the different specimens were as follows:

Specimen 1—*P. radiata* (late wood)

$$BL_T = 64.7 L^2 + 80 \quad (r = 0.914). \quad \dots \dots \dots (1)$$

This gave a somewhat better fit to the data obtained than the straight line

$$BL_T = 474 L - 755, \quad \dots \dots \dots (2)$$

although the improvement was not significant.

Specimen 2—*P. radiata* (early wood)

$$BL_T = 17.9 L^2 + 217 \quad (r = 0.757). \quad \dots \dots \dots (3)$$

This relation did not give a significantly better fit than the straight line

$$BL_T = 151 L - 90. \quad \dots \dots \dots (4)$$

Specimen 3—*Pseudotsuga taxifolia* (late wood)

$$BL_T = -4218 + 3360 L - 496 L^2 (R = 0.867). \quad \dots (5)$$

Specimen 4—*Pinus radiata* (late wood from stem containing compression wood). It was found that a curve could be fitted to the data for both the compression wood side and normal side of the stem, viz.

$$BL_T = 922 - 789 L + 254 L^2 (R = 0.961). \quad \dots \dots (6)$$

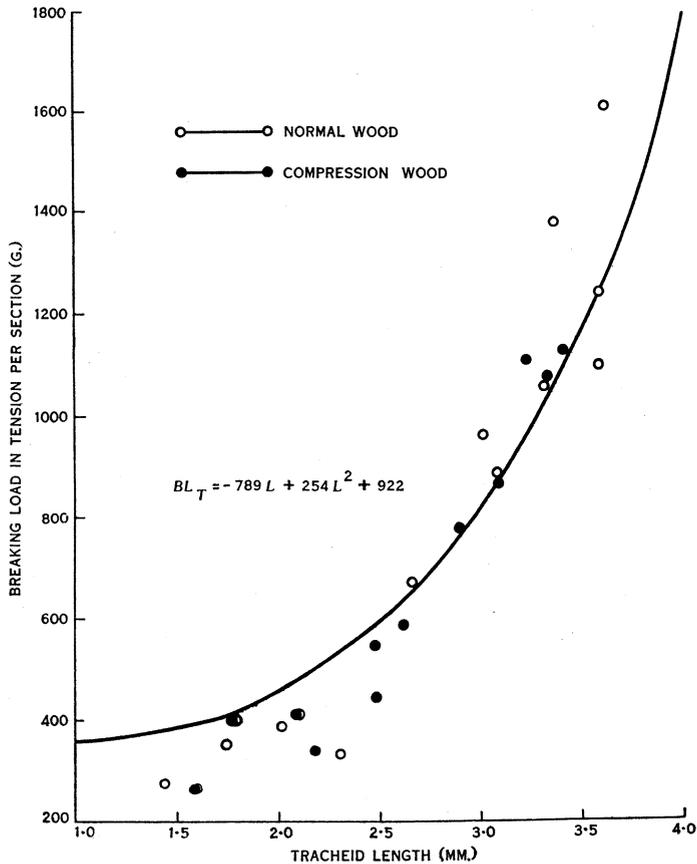


Fig. 4.—Relation between breaking load in tension (BL_T) and tracheid length (L) in *Pinus radiata* (specimen 4) containing both compression wood and normal wood.

From these relations it was apparent that the breaking load in tension and tracheid length were correlated (positively). However, from the specimens examined no conclusion could be drawn as to the form of the curves although, as will be pointed out below, a morphological interpretation of the trend of the values was possible in at least one case (specimen 3).

V. DISCUSSION

(a) *The Anatomy of Tension Failures in Conifer Tracheids*

With the exception of one doubtful case, in all the specimens examined during the present investigation, failure in tension of the wood sections involved rupture of the cell wall (Plate 1, Figs. 1-4; Plate 2, Figs. 1-6). That failure usually occurs within the cell wall has been reported elsewhere (Robinson 1921; Koehler 1933; Frey-Wyssling 1938; Garland 1939). This does not necessarily imply that the intercellular adhesion per unit area of contact surface between cells is greater than the strength of the tracheids, because the line of failure involved in the separation of cells is very much greater than that involved in the rupture of the cell walls.

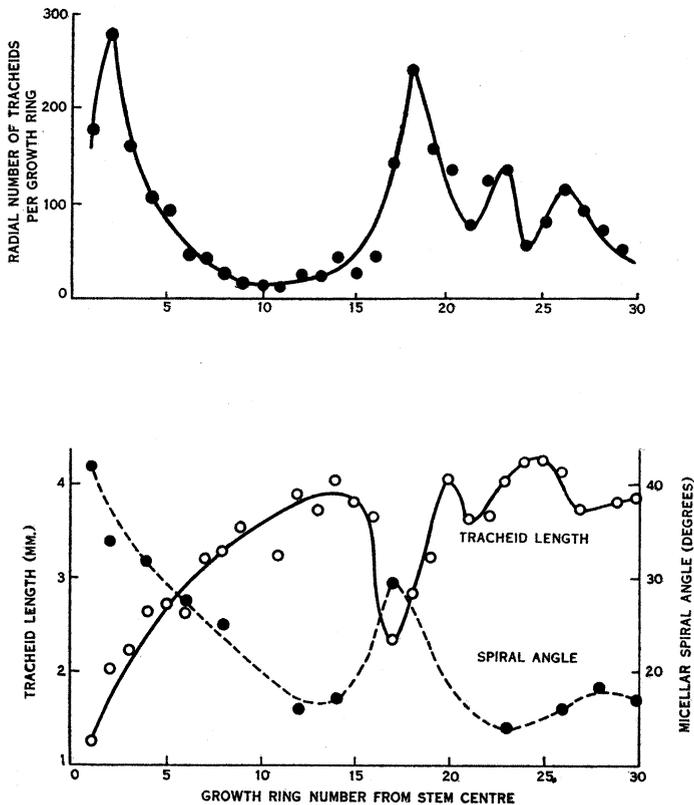


Fig. 5.—Variation of tracheid length, growth ring width, and micellar spiral angle in successive growth rings of *Pinus pinaster* (specimen 5).

Failure of the cell wall showed two features: (i) the rupture of the spiral micellar system in the different cell wall layers, and (ii) the separation of the different cell wall layers. In late wood the line of failure of the cell wall followed the direction of micellar orientation in the middle layer of the second-

dary wall. This is illustrated for a short tracheid in which the micellar spiral angle is relatively large in Plate 1, Figures 1 and 2, and in a long tracheid with a small micellar spiral angle in Plate 1, Figures 3 and 4. The fact that failure follows the direction of orientation in the central layer would indicate a relatively greater rigidity of this layer, which could arise from its greater thickness and higher cellulose content than the other cell wall layers. Parts of the primary wall can be seen adhering to the fractured tracheids in Plate 1, Figures

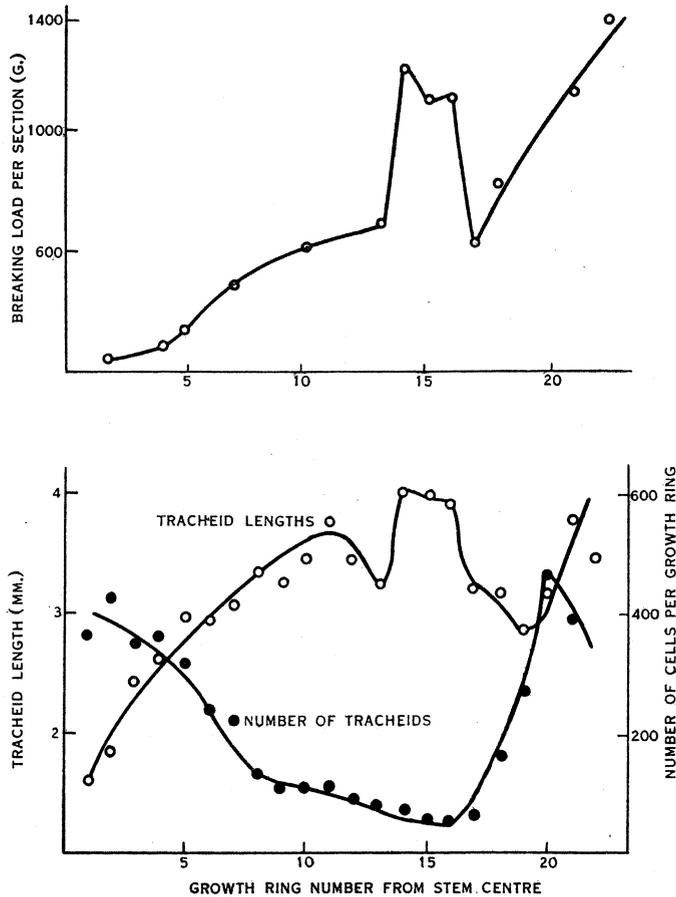


Fig. 6.—Variation of tracheid length, growth ring width, and breaking load in tension of the xylem from successive growth rings of *Pinus radiata* (specimen 6).

2 and 4. In early wood specimens the line of failure in the cell wall, as with the late wood, often followed the direction of micellar orientation in the middle layer (Plate 2, Figs. 1 and 2), but this was not always so and irregular failures were observed (Plate 2, Fig. 3). The irregular failure of early wood cells probably arises from the presence of a much thinner middle layer of the secondary wall, and the correspondingly greater influence of the outer and inner layers of the secondary wall and of the primary wall. Failure of the specimens was also frequently observed to occur in the rays (Plate 2, Fig. 4).

In tracheids of compression wood the line of failure also follows the direction of micellar orientation. In this case, however, unwinding of the micellar spiral system was easily observed (Plate 2, Fig. 5). This was due to the existence of radial discontinuities in the cell wall paralleling the direction of micellar orientation (Wardrop and Dadswell 1950). The same type of splintered failure perpendicular to the direction of spiral orientation was observed in all cases (Plate 1, Figs. 2 and 4; Plate 2, Fig. 6).

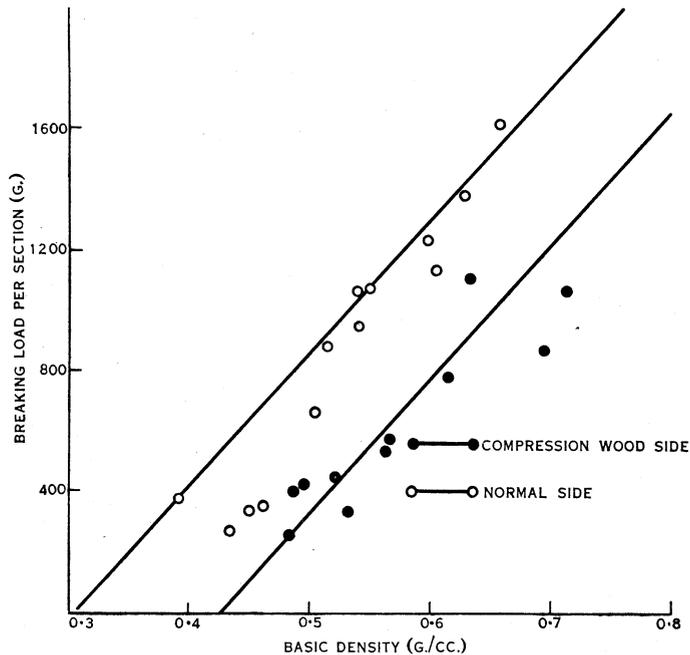


Fig. 7.—Relation between breaking load in tension and basic density of the xylem of *Pinus radiata* (specimen 4).

In the specimens examined in which separation of the cells was apparently involved it was often difficult to determine if true separation between cells was involved, or whether separation occurred between the different layers of the cell wall. In *Pinus radiata* failure between the primary and secondary wall was observed. This can be seen in Plate 1, Figure 5, in which fragments of the primary wall remained after separation of two tracheids. This was concluded to be the primary wall upon the basis of its extinction position (85° to the tracheid axis), birefringence, and dichroism after staining with congo red. In sections of *Pseudotsuga taxifolia* separation of tracheids appeared to have taken place (Plate 2, Figs. 7 and 8) although it was not possible to decide between which cell wall layers rupture occurred. This was examined further in transverse sections of a macro-tension specimen after failure had occurred. In Plate 3 separation of the primary wall and outer layer of the secondary wall (Fig. 3) and of the outer and central layers of the secondary wall (Figs. 2 and 3) can be seen. Consideration of the cell wall structure of conifer

tracheids suggests possible factors that may govern the adhesion between the different cell wall layers. Thus between the central and the outer and inner layers of the secondary wall there is a marked change in micellar orientation, as well as between the primary wall and outer layer of the secondary wall. In addition, the extent of the intermicellar system decreases enormously between the primary wall and the secondary cell wall, as well as between the outer and inner layers, and the central layer of the secondary wall. The great extent of the intermicellar system of the primary wall would tend to unify it with the intercellular layer so that failure might be expected to occur within the cell wall rather than between cells. Within the cell wall failure would, for similar reasons, be expected to occur more frequently between the outer and central layers of the cell wall than between the primary wall and outer layer of the secondary wall as well as because of the change in micellar orientation between these layers.

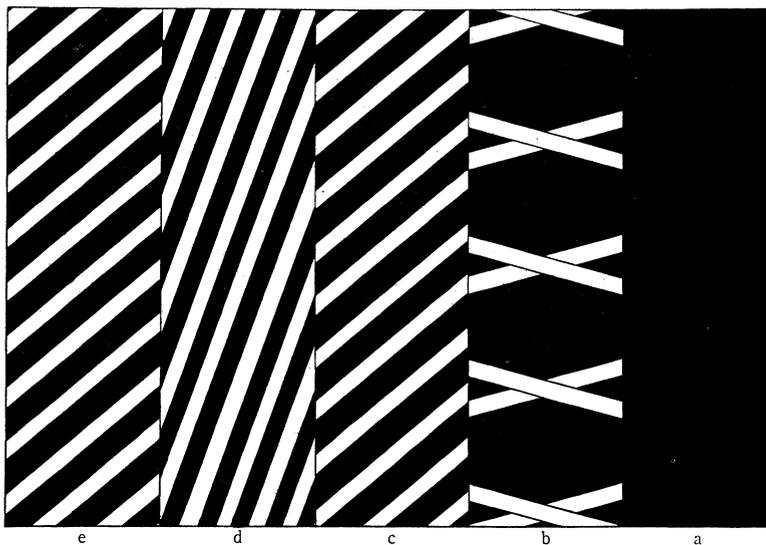


Fig. 8.—A diagrammatic representation of part of the cell wall of a conifer tracheid, in surface view with the cell axis parallel to the length of the page; illustrating the relative extents of the micellar and intermicellar systems (black). Successive layers of the cell wall are supposed to have been removed from right to left.

a, intercellular substance; *b*, primary wall; *c*, outer layer of the secondary wall; *d*, middle layer of the secondary wall; *e*, inner layer of the secondary wall.

An attempt to illustrate the relative extent of the micellar and intermicellar systems for the different regions of the cell wall is shown in Figure 8. The diagram was constructed assuming that the cellulose content of the outer layer of the secondary wall was approximately half that of the central layer (Lange 1949).

(b) Variation of Breaking Load in Tension of Wood within Conifer Stems

As pointed out in the Introduction of this paper, it was reasonable to expect that, upon the basis of their cell wall organization, the breaking load in tension of a short conifer tracheid in which the micellar spiral angle was large would be less than that of longer tracheids in which this angle was small. This was confirmed in the tests carried out upon single isolated tracheids from *Pinus radiata* (Table 6).

In determining the variation of the breaking load in tension of wood sections, measurements were attempted only in a direction parallel to the cell length, and because an accurate determination of the cross-sectional area of the specimens in the regions of failure was so laborious, attempts to calculate approximate values of the breaking stress were abandoned, although this was done for the tests involving single tracheids.

In view of these considerations, variations of the values of the breaking load in tension parallel to the tracheid length of the wood sections listed in Tables 1-4 and Figures 3, 4, and 6 could be attributed either to the changing orientation of the constituent tracheids or to changes in the density of the wood from which they were cut. For this reason the correlation coefficients between breaking load in tension and tracheid length, and between breaking load in tension and basic density, were determined. These values are listed in Table 9.

TABLE 9
LINEAR CORRELATION COEFFICIENTS BETWEEN BREAKING LOAD IN TENSION AND BASIC DENSITY, BREAKING LOAD IN TENSION AND TRACHEID LENGTH, AND TRACHEID LENGTH AND BASIC DENSITY

Specimen	Breaking Load and Tracheid Length	Breaking Load and Basic Density	Tracheid Length and Basic Density
<i>Pinus radiata</i> (specimen 1)	0.886**	0.631 (N.S.)	0.551 (N.S.)
<i>Pinus radiata</i> (specimen 2)	0.753**	0.902**	0.785**
<i>Pseudotsuga taxifolia</i> (specimen 3)	0.665**	0.715**	0.618*
<i>Pinus radiata</i> (specimen 4)			
Compression wood side	0.949**	0.859**	0.890**
Normal wood side	0.925**	0.920**	0.862**

N.S. = not significant.

** = significant at 1% level.

* = significant at 5% level.

In specimens 1 and 2, for which linear correlations between breaking load and tracheid length provide as good a fit for the data as curvilinear relations, it was found that the correlation coefficient between breaking load and basic

density was not significant for specimen 1 and in specimen 2 did not differ significantly from that for breaking load and tracheid length. In specimens 2, 3, and 4 there was a significant correlation between basic density and tracheid length (Table 9).*

Specimen 4, in which both normal wood and compression wood were present, provides further interesting information. Thus for both the normal wood side and the compression wood side of the stem, linear correlation coefficients between breaking load and basic density were found (Table 9) and the data could be represented by two linear relations (Fig. 7) as was found for specimens 2 and 3. However, comparing compression wood and normal wood it was found that, corresponding to any given value of the density (Fig. 7), there were two values of the breaking load significantly different from each other and the higher of which was that of the normal wood. Thus, although wood of higher basic density did possess a higher breaking load than wood of lower basic density for both the normal wood and compression wood sides of the stem, when comparison was made between these groups the density was no longer necessarily a criterion of breaking load.

In contrast to this, when the relation between breaking load in tension and tracheid length was examined it was found that a single relation (equation 6 above and Fig. 4) served to describe the data for both normal wood and compression wood. Thus both with the compression wood and normal wood groups, and between these groups, a small tracheid length served as a criterion of low breaking load and a larger tracheid length of a higher breaking load. These considerations confirm the previous general conclusion (Wardrop and Dadswell 1950) that comparison of the properties of compression wood in relation to normal wood should be made between compression wood and normal wood composed of tracheids of equal length (i.e. between cells of similar spiral cell wall organization) in order to eliminate the influence of structural differences between the constituent cells.

In the specimen of *Pseudotsuga taxifolia* examined (specimen 3) it will be noted (Table 2) that the breaking load in tension did not continue to increase after the eighth growth ring (tracheid length = 3.15 mm.) although the tracheid length did continue to increase. This was found to be due to failure occurring either between cells or between cell wall layers as discussed above (Plate 2, Figs. 7 and 8). Once the condition was reached that failure no longer occurred within the cell wall any further increase in the length of the constituent cells and corresponding decrease in their micellar spiral angle made no additional contribution to the strength of wood, although presumably the strength of the individual cells did increase.

Thus of the specimens examined, both the cell wall organization and the basic density of the specimens 2 and 3 appeared to have been of importance

* It may be noted further that in a recent investigation Kraemer (1950) found higher correlation coefficients between micellar spiral angle and the modulus of rupture and modulus of elasticity than between specific gravity and these properties in *Pinus resinosa*.

in influencing the value of the breaking load in tension observed. In specimens 1 and 4, however, the influence of cell wall organization appeared to predominate.

A further factor probably influencing the breaking load is tension in the cell wall composition. In Table 8 it can be seen that for both *Pinus radiata* and *Pseudotsuga taxifolia* the cellulose content of the xylem increased in successive rings from the pith and was apparently correlated with both tracheid length and micellar spiral angle. Although the increase in cellulose content was small it may have a significant effect upon the breaking load because relatively long cells with a higher cellulose content would have more cellulose chains potentially capable of taking an applied load in tension than shorter cells with a lower cellulose content. As the micellar spiral angle was smaller in the longer cells, not only were there more chains but they were more favourably oriented to take an applied load in tension. The possible influence of the cellulose content upon the intrinsic density of the cell wall substance would not be great because of the small variation in composition and the density of cellulose is but slightly higher than that of other cell wall constituents (Stamm and Hansen 1937).

It is possible that the correlation between cellulose content and spiral micellar organization as suggested by the data in Table 8 is of more general application. Thus within a single cell wall of a tracheid or fibre the cellulose content of the middle layer of the secondary wall is higher than that of the outer layer whereas the spiral angle is smaller. A similar correlation has been observed for different phloem fibres (Wardrop and Preston, unpublished data).

(c) *Change of Breaking Load in Tension with Moisture Content*

From Table 5 it can be seen that the breaking load in tension of the wood sections increased on oven-drying. This phenomenon is well known in wood (Forsaith 1944; Stamm 1936) and in phloem tissue (Haberlandt 1928). Stamm (1936) attributed the general increase in strength on drying to an increase in fibre strength in the following terms: "The strength of a swollen fibre in general increases upon drying. This is explained on the basis of the secondary valence forces between the micelles which in the swollen condition are partially satisfied by mobile water being brought together on drying thus satisfying each other."

If this explanation is correct it can be seen that the strength of individual tracheids of the wood should be greater in the dry than in the water-saturated condition. However, in a number of textile fibres the tensile strength has been observed to be greater in the wet than in the dry condition, and in the present study this has been demonstrated for conifer tracheids (Table 7). This increase in strength has been attributed to the water present in the intermicellar regions of the wet fibres permitting movement to occur between adjacent cellulose molecules so that a more uniform distribution of internal stress is achieved upon loading (Hermans 1949). In contrast to these results it has been reported by Klauditz, Marschall, and Ginzel (1947) that pulp fibres

possess a higher tensile strength in the dry condition, although it will be apparent that in this latter case considerable chemical breakdown had probably taken place.

If it is accepted that the tensile strength of single tracheids is greater in the wet condition, it is clear that the explanation by Stamm for wood quoted above cannot hold, and some other factor must be operative which results in a decrease in tensile strength of the wood with increasing moisture content predominating over the simultaneous increase in the tensile strength of the individual cells. It is suggested, therefore, that the two factors governing the strength of wood at any moisture content are the cell wall organization and the intercellular substance. In contrast to the behaviour of the tracheid the amorphous intercellular substances would be expected to weaken with increasing moisture content and consequent swelling, so that at least an increase in the plasticity of this layer could be expected. Thus in spite of any increase in strength of the tracheids, because of the influence of the intercellular substances, a decrease of the breaking load in tension could be expected with increasing moisture content.

This view receives some support from the observation that failure in tension of oven-dry specimens appears macroscopically regular and involves uniform rupture of the cell wall (Plate 3, Fig. 4), whereas tension failures in water-saturated specimens have a splintered appearance macroscopically, which results from failure taking place between cells in parts of the section, although fractures of many cell walls were still involved (Plate 3, Fig. 5). A similar observation has been made by Frey-Wyssling (1938) and by Garland (1939). Further support for the hypothesis presented above may be found in the observation of Kollman (1944) that a maximum tensile strength for wood exists at 8 per cent. moisture content, although apparently this maximum has not been observed in investigations of other static properties. However, if the breaking load in tension is determined by the interaction of the above factors, it is possible that if the intercellular layer weakens continuously with increasing moisture content, and the breaking load of the tracheids increases to a constant value as does cotton at 9 per cent. moisture content (Brown, Mann, and Peirce 1930), then a maximum might be expected to occur when the moisture content approached this value, which is close to that (8 per cent.) at which a maximum value of the breaking load in tension was observed by Kollman.

(d) Variation of Breaking Load in Tension with Radial Growth Rate

As pointed out in the Introduction, within any one stem a large radial growth rate (number of cells per growth ring) might be expected to involve the formation of short tracheids, and a small radial growth rate the formation of longer tracheids. This was found to be the case in the two specimens examined; in one, specimen 5, the growth rate was stimulated after the formation of 15 growth rings by the addition of superphosphate, in the other, specimen 6, after the formation of 16 growth rings by silvicultural treatment. In

both cases it is apparent from the results obtained (see Figs. 5 and 6) that the increase in radial growth rate arising from the treatments was accompanied by a decrease in tracheid length.

From an examination of Figure 6 a general parallelism of the trends observed for tracheid length and the breaking load in tension of wood from successive growth rings can be seen, the longer tracheids corresponding to higher values of breaking load as observed in other specimens examined. These results, although of only a preliminary nature, thus serve to give some indication of the way in which the breaking load in tension could be expected to change with varying radial growth rate and suggest an advantage that would be gained by maintaining an even radial growth rate of the stem.

It has also been observed (Wardrop 1948) in the examination of different trees of the same species from the same locality, that in a specimen in which the tracheid length of the first growth ring was large, the tracheid length continued to be greater in subsequent growth rings than in a specimen in which the tracheid length of the first growth ring was small. This observation suggests that if, by suitable nursery treatment or selection, seedlings could be obtained with initially long tracheids, then all the subsequently formed wood would consist of long tracheids. Insofar as a large value of tracheid length can be correlated with a large value of breaking load in tension (and preliminary experiments have shown similar correlations for other properties), it can be seen that the development of stems of high initial tracheid length may offer a means of effecting an improvement in the quality of the wood subsequently formed. Such an increase in tracheid length would also be advantageous in timber used for pulping.

It is fully realized that the latter conclusions are based on limited evidence, but they are presented here with a view to providing a starting point from which the implications of the present studies, in relation to the conditions governing development of conifer stems, may be further investigated.

VI. ACKNOWLEDGMENTS

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EXPLANATION OF PLATES 1-3

PLATE 1

- Fig. 1.—*Pinus radiata*. A late wood tracheid, from the third growth ring from the stem centre, broken in tension. Note the flat spiral fracture ($\theta = 50^\circ$). $\times 430$.
- Fig. 2.—The same tracheid as in Figure 1 in different focus, showing the serrated failure perpendicular to the direction of spiral fracture. $\times 430$.
- Fig. 3.—*P. radiata*. A late wood tracheid from the eighteenth growth ring from the centre of the same stem as that in Figure 1, showing failure at a slip plane. $\times 430$.
- Fig. 4.—*P. radiata*. A late wood tracheid similar to that in Figure 3, showing the type of failure accompanying very steep spiral orientation (cf. Figs. 1 and 2). $\times 430$.
- Fig. 5.—*P. radiata*. A late wood tracheid showing portion of the primary wall of an adjacent cell which had separated during failure in tension. $\times 430$.

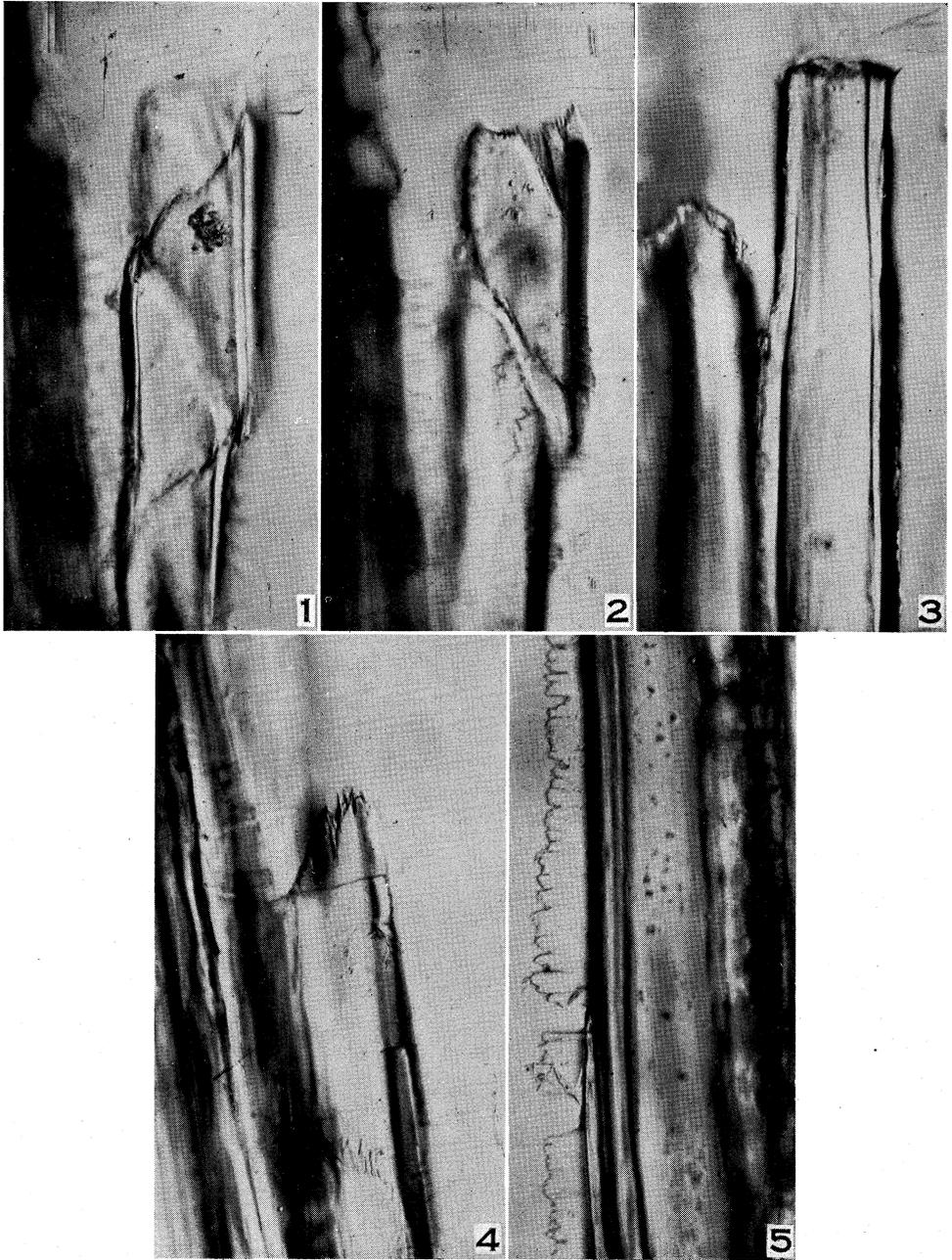
PLATE 2

- Fig. 1.—*Pinus radiata*. Early wood tracheids after failure in tension in which the failure paralleled the micellar orientation of the middle layer of the secondary wall. x430.
- Fig. 2.—Similar to Figure 1 except that separation between cells has also occurred. x430.
- Fig. 3.—Similar to Figures 1 and 2 but failure in the cell wall is here irregular. x430.
- Fig. 4.—Similar to Figures 1-3, and illustrating failure at a wood ray. x430.
- Fig. 5.—*Pinus radiata*. A compression wood tracheid after failure in tension, illustrating the unwinding of the spiral structure due to the presence of radial discontinuities in the cell wall. x430.
- Fig. 6.—Similar to Figure 5, illustrating the serrated failure perpendicular to the direction of micellar orientation. x980.
- Fig. 7.—*Pseudotsuga taxifolia*. A group of tracheids separated during failure in tension apparently without involving rupture of the cell wall. x100.
- Fig. 8.—The tip of the terminal cell of Figure 7. x430.

PLATE 3

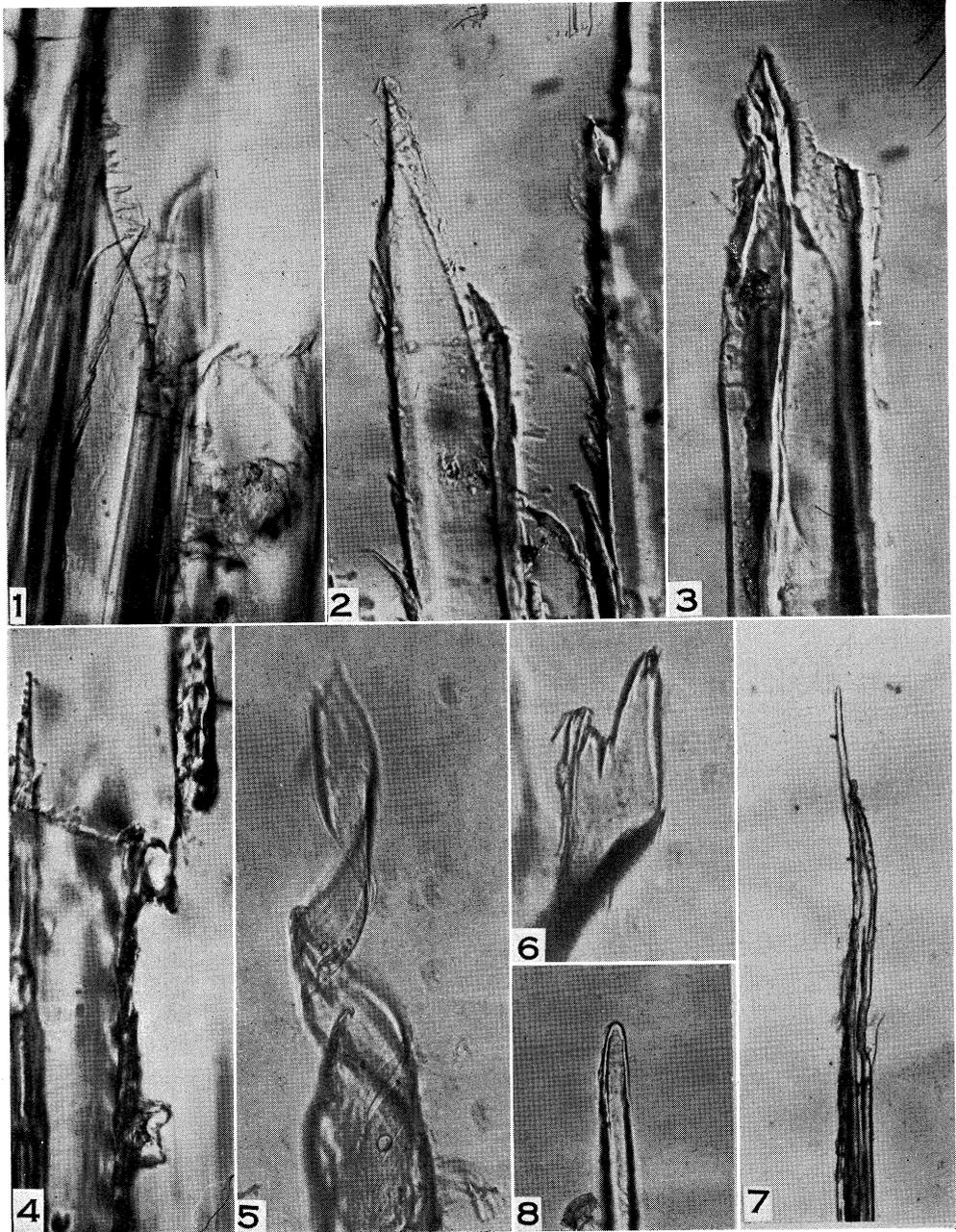
- Fig. 1.—*Pseudotsuga taxifolia*. Transverse section of the xylem extending over a region of failure in tension. Photographed between crossed nicols. x430.
- Fig. 2.—Similar to Figure 1, illustrating failure between the cell wall layers. Crossed nicols. x430.
- Fig. 3.—Similar to Figures 1 and 2 illustrating failure along a radial file of tracheids. Crossed nicols. x430.
- Fig. 4.—*Pinus radiata*. A tension failure in a section of early wood (80 μ) after drying. x100.
- Fig. 5.—*P. radiata*. A tension failure in a water-saturated section of early wood (80 μ). x100.

CELL WALL ORGANIZATION AND XYLEM PROPERTIES. I





CELL WALL ORGANIZATION AND XYLEM PROPERTIES. I





CELL WALL ORGANIZATION AND XYLEM PROPERTIES. I

