TANGENTIAL WALL THICKENINGS IN CONIFER TRACHEIDS AT RAY-CONTACT AREAS

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ABSTRACT

Measurements made on transverse and longitudinal sections of mature wood of red pine and white cedar established that the greater thickness of tangential tracheid walls at the areas where tracheids are in contact with uniseriate rays is proportional to the reduction in tangential width of tracheids at these areas and to the tangential width of the uniseriate rays. It is concluded that "ray thickenings" do not comprise an additional deposition of cell-wall material but arise from changes in the configuration of existing wall material at the ray contact areas.

Additional keywords: *Pinus resinosa, Thuja occidentalis*, wood structure, cell walls, earlywood, latewood, ray cells, tracheids.

INTRODUCTION

Thickening of tangential tracheid walls at ray-contact areas appears to be a general characteristic of coniferous wood. In spite of its widespread occurrence, however, this feature has apparently been discussed in only one technical paper (Ladell 1967) and it is not mentioned in the anatomical description of coniferous wood provided in any of the standard textbooks on wood technology. The name "ray thickenings" was proposed by Ladell for these features and when one becomes conscious of their presence, it seems difficult to understand why more attention has not been given to them in the past. This point is illustrated in Figs. 1–3, which show typical examples of ray thickenings in radial longitudinal sections of mature red pine wood (*Pinus resinosa*).

The publication of Ladell's paper on ray thickenings in 1967 was of immediate interest to me because at that time I had been observing these features in radial sections of white spruce (*Picea glauca*) and was attempting to determine what relationship they might bear to the initiation of microscopic compression failures at the ray-contact areas. Beyond Ladell's description of the general nature and distribution of ray thickenings, however, there arises some difficulty in accepting his interpretation that they comprise an addition of cell-wall material deposited on the tangential walls of tracheids at the ray-contact areas.

Observation of tangential longitudinal sections of coniferous wood (Fig. 4) has always conveyed to me the impression that the rays are intruding among the prosenchyma tissue and that they are accommodated spatially by constricting each of the two neighboring tracheids tangentially by approximately one-half of the width of the ray. Considering the central untapered portion of a tracheid, if tangential wall material is deposited so as to form walls of uniform thickness, a tangential constriction of the tracheid at ray-contact areas could logically result in a radial expansion (thickening) of the tangential walls accompanied by a reduction in the radial width of the lumen. This seemed to constitute a reasonable basis for the "ray thickening" phenomenon.

This explanation differs from that offered by Ladell in that it does not involve any deposition of additional cell-wall material. Furthermore, it is based on a reduction in tangential tracheid diameter at the ray contact areas which Ladell indicated did not occur. Results of a small study investigating these points are presented here.

MATERIALS AND METHODS

In accordance with the proposal that "ray thickenings" are due to the intruding effect

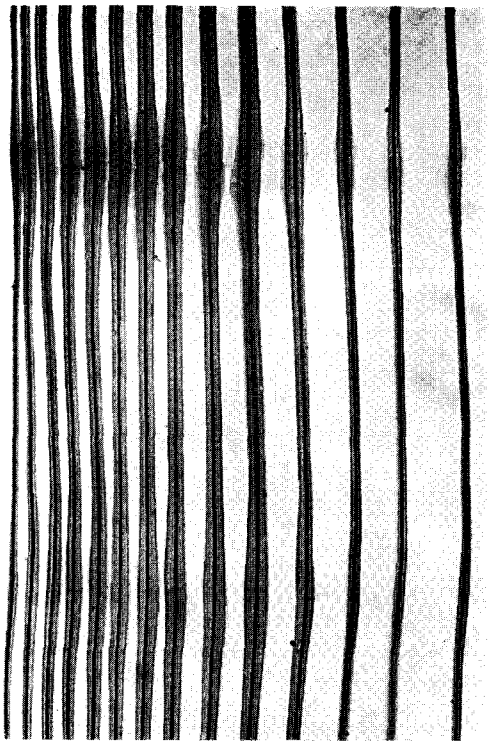

FIG. 1. Tangential walls of red pine tracheids with thickenings at two locations corresponding to ray contact areas. Radial section ×150.

of the rays, the thickenings should be approximately proportional in magnitude to the width of the rays. With this relationship in mind, I elected to study wood of red pine (*Pinus resinosa* Ait.) and white cedar (*Thuja occidentalis* L.) since the uniseriate rays in these species are among the widest (red pine) and the narrowest (white cedar) of the eastern conifers. A fresh stem section about 7 cm long of each species was obtained from the Petawawa Forest Experiment Station near Chalk River, Ontario. The material was carefully examined in the laboratory and fifteen sample blocks (approx. 2-cm cubes) for microtoming were selected from the mature region of the stems located between the 70th and 80th growth rings from the pith.

The sample material was kept moist throughout processing, and microtome sections were mounted on glass slides in a water-miscible resin. Transverse sections (two per block) were cut 15–20 μm thick from ten blocks of each species. The remaining five blocks of each species were sectioned tangentially—two sections in latewood and two sections in earlywood from the outermost growth ring on each block.

Measurements on tangential sections

On each microscope slide, the better of the two mounted sections was selected for measurement purposes. The section was scanned in a systematic pattern, and measurements were made at 20 suitable ray locations distributed throughout the section. In total, for each species, measurements were made at 100 ray locations (20 locations on each of five blocks) for earlywood and 100 ray locations for latewood.

A typical ray location is illustrated in Fig.

TABLE 1. *Average reduction in tangential width and increases in wall thickness of tracheids at ray contact areas*

	Tracheid Width				Ray Width (μm)	Double Tangential Wall Thickness			
	Control (μm)	Ray Contact (μm)	Reduction (μm)	Reduction (%)		Control (μm)	Ray Contact (μm)	Increase (μm)	Increase (%)
Number of Observations	400	200	—	—	100	200	200	—	—
Red Pine									
Earlywood	31.9	24.0	7.9	24.8	16.5	5.3	6.6	1.3	24.5
Latewood	30.8	24.2	6.6	21.4	17.1	7.8	9.9	2.1	26.9
White Cedar									
Earlywood	25.7	23.1	2.6	10.1	7.2	3.4	3.7	0.3	9.8
Latewood	26.2	23.6	2.6	10.1	7.8	7.2	7.7	0.5	7.1

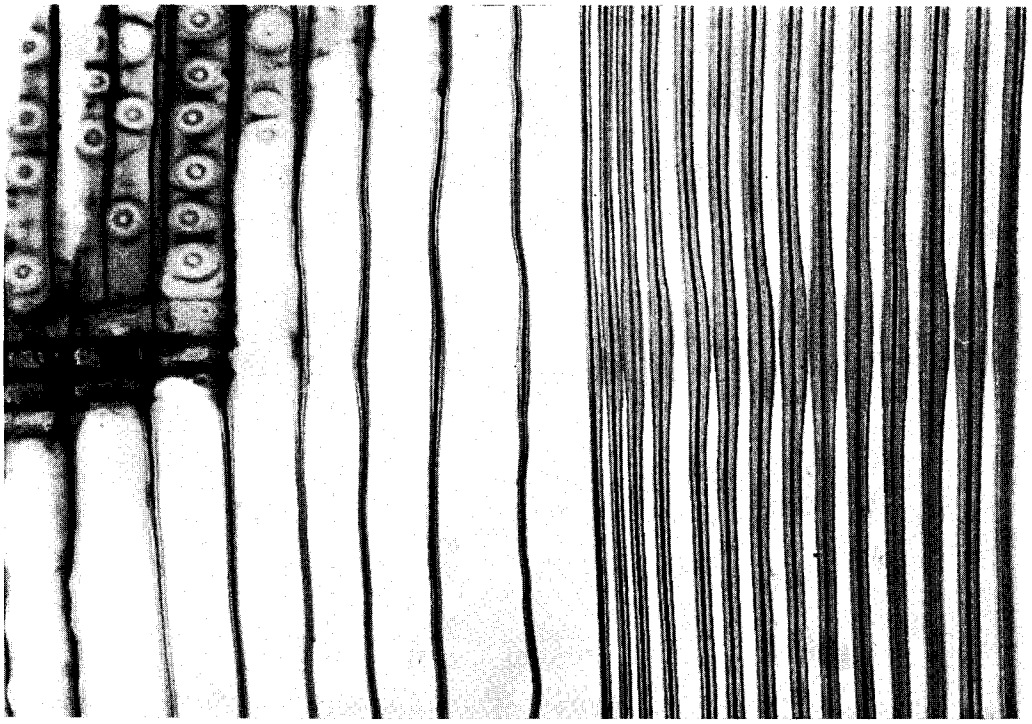

FIG. 2. Radial section of red pine showing the association between the tangential wall thickenings (right) and a ray (left). Mag. ×200.

5, which also shows the seven individual measurements taken at each location. These included the tangential width of each of the two bordering tracheids just above and just below the ray-contact area, the tangential width of each tracheid near the middle of the ray-contact area, and finally the tangential width of the ray near the midpoint.

Measurement on transverse sections

As above, the better of the two sections mounted on each slide was selected for the measurements. These were made at 10 ray locations for latewood and 10 for earlywood, distributed through each section. As illustrated in Fig. 6, four measurements were made at each ray location. These consisted

TABLE 2. *Statistical analysis of differences in tangential cell width and wall thickness between control and ray contact areas*

	Cell Width (μm) (Reductions)				Double Wall Thickness (μm) (Increases)			
	Red Pine		White Cedar		Red Pine		White Cedar	
	Earlywood	Latewood	Earlywood	Latewood	Earlywood	Latewood	Earlywood	Latewood
Number of Differences Observed	200	200	200	200	86	95	100	100
Mean of Differences	7.98	6.66	2.66	2.78	1.22	2.16	0.38	0.58
Standard Deviation ±	2.59	2.79	1.35	1.54	1.17	1.49	0.82	0.83
Standard Error ±	0.18	0.20	0.10	0.11	0.13	0.15	0.08	0.08
t	43.61**	33.78**	27.99**	25.51**	9.71**	14.12**	4.60**	6.99**

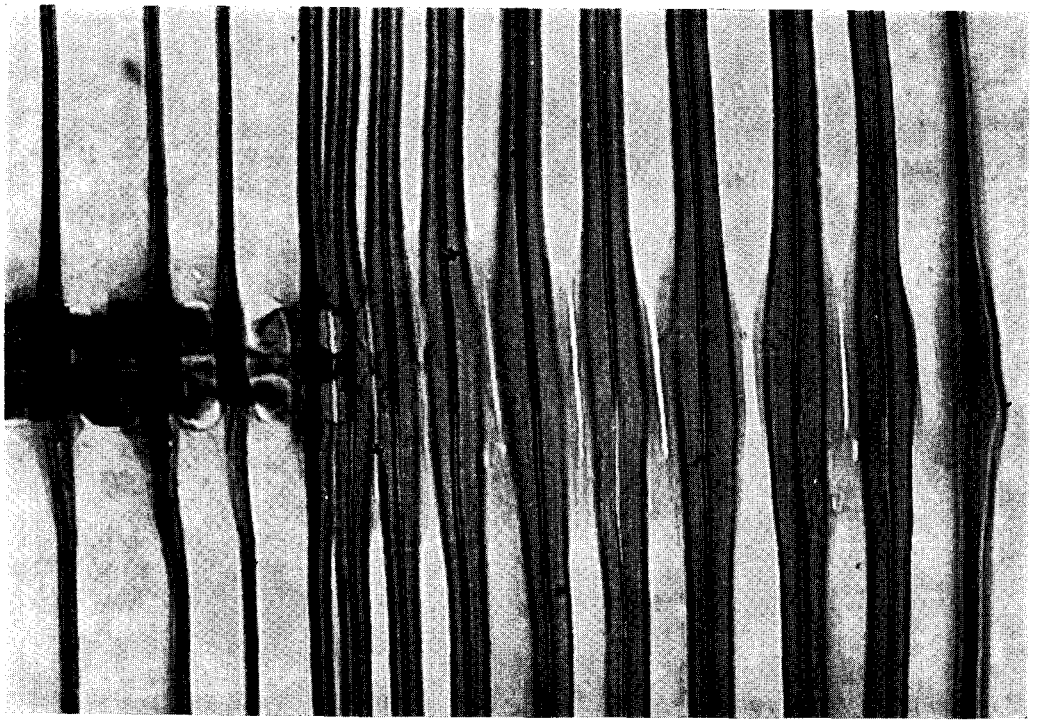

FIG. 3. Close-up view of a ray-contact area showing the thickened tangential walls. Radial section × 350.

of double tangential wall thickness (measured in the radial direction) in pairs of cells adjacent to a ray (ray files) and in pairs of cells not adjacent to a ray (control files) in the plane of section. The control files were normally taken to be the files next but one to the ray files. In some instances, however, it was necessary to take a control measure from the file of tracheids immediately next to the ray file in order to avoid unusual circumstances such as close proximity to the cell tips (Fig. 6).

All measurements on both tangential and transverse sections were made with a Reichert Visopan at a magnification of 800× on the viewing screen. At the time of making the double tangential wall thickness measurements on the transverse sections, an attempt was made to get comparative figures for the area occupied by cell-wall material and by lumen space in the ray and control cell files. This was done by putting a piece of draughtsman's parchment paper on the viewing screen of the Visopan and making tracings of each of the four pairs of cells selected for double tangential wall thickness measurements. Later, cell-wall and cell-lumen portions were cut out from these tracings. These were sorted and eventually weighed in a room controlled at constant temperature and relative humidity.

RESULTS AND DISCUSSION

Tangential width of longitudinal tracheids and of rays

Average widths of tracheids at ray contact and control areas are shown in Table 1. Also shown in the table are the average width of rays and the differences in average tracheid width at ray contact as compared with control areas. Table 2 deals with the width differences in individual tracheids and shows that the mean differences in width between ray contact and control areas are highly significant. Furthermore, the data in Table 1 indicate that the reductions in tracheid width at the ray contact areas

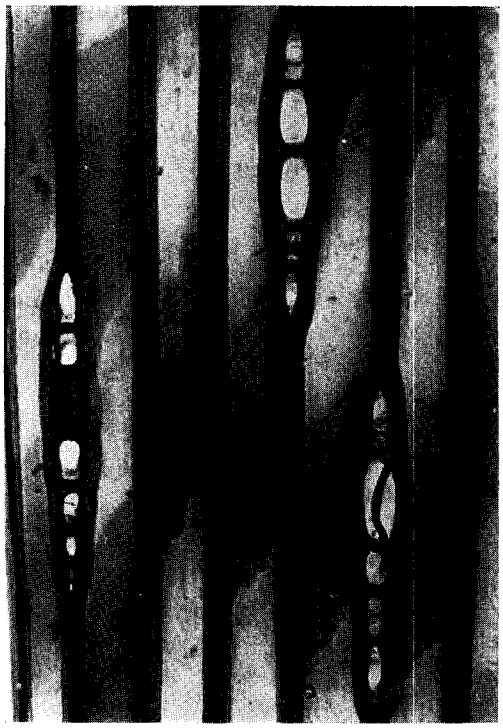

FIG. 4. Structure of red pine wood in the tangential plane showing the accommodation of uniseriate wood rays among the prosenchyma cells. Mag. ×325.

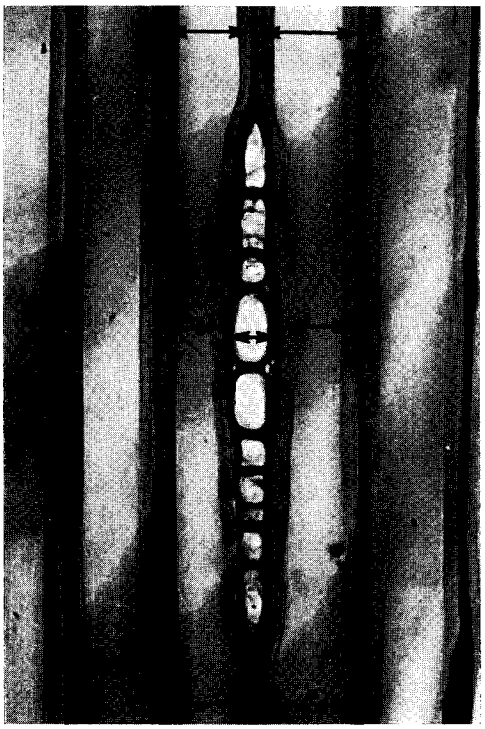

FIG. 5. Typical locations for measurements of tangential tracheid width and ray width in red pine. Tangential section ×350.

(about 10% for cedar and a little over 20% for the pine) are proportional to the width of the rays in these two species.

The average reductions in tracheid width at the ray-contact areas (2.6 μm for cedar and 7.2 μm for pine) are a little less than half the average ray-widths (7.5 μm for cedar and 16.8 μm for pine) observed. This indicates that the influence that rays exert on tracheid configuration is almost, but not entirely, limited to the two tracheid files bordering the ray. This point is demonstrated to an exaggerated extent by fusiform rays which, because of their width, tend to influence the shape of the tracheids in several adjacent cell files (Fig. 7).

Differences between earlywood and latewood with respect to the factors being observed in the present study did not appear to be great. In both species, the average ray width was slightly greater in latewood than in earlywood. The average reduction in tracheid width at the ray-contact area was found to be the same (10.1%) for both earlywood and latewood of white cedar. For red pine, however, the earlywood reduction (24.8%) was greater than that in the latewood (21.4%).

Ladell's interpretation of ray thickenings as deposits of additional cell-wall material at the ray-contact areas assumes that there is no reduction in tangential cell diameter at these points. He appears to have reached this conclusion on the basis of some measurements made on transverse sections. One of the problems associated with making measurements of this kind on transverse sections arises from the fact that the tracheids are not uniform in width but taper over extensive portions of their length toward pointed tips. Since there tends to be a random longitudinal distribution of cell tips among the cell files, any given transverse section provides a variety of tracheid sizes determined by the location of the plane of

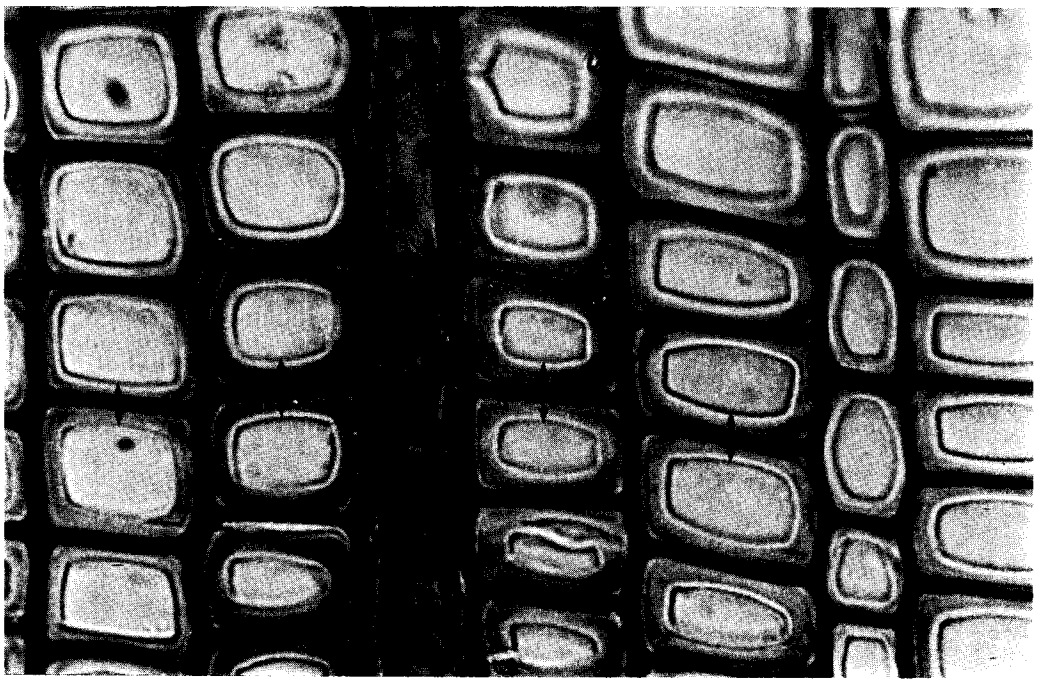

FIG. 6. Transverse section of red pine showing the greater thickness of double tangential walls at ray contact as compared with control areas. In this instance, control measurements were obtained from the tracheid files immediately adjacent to the ray files because the next tracheid file on the right side of the ray is close to the cell-tip region. Mag. ×750.

section along the longitudinal axes of the fibers (Fig. 6). The presence of this substantial source of variation in cell width greatly increases the difficulty of detecting a possible difference associated with ray contact.

Another problem with the use of transverse sections is that they do not allow one to measure the same cell or cells both at ray-contact areas and at non-ray-contact areas. The comparability of ray-contact data from one group of cells to control data from another group of cells becomes a statistical problem requiring adequate sampling. By using tangential sections, it was possible to avoid the tapering regions of tracheids and to make direct measurements to detect any change in cell width at the areas bordering rays.

Thickness of tangential tracheid walls

Results of the measurements of double tangential wall thickness made on transverse sections are summarized in Tables 1 and 2. It is apparent that cells in contact with rays displayed significantly thicker tangential walls than cells not in contact with rays.

The percentage difference in wall thickness between ray-contact areas and control areas in red pine was somewhat more than double that in cedar (a little over 20% as compared to a little under 10%). In cedar, the difference was slightly greater in earlywood whereas in pine, it was slightly greater in latewood. The very substantial increases in wall thickness associated with the ray-contact areas in red pine are consistent with the observations reported by Ladell. His values for red pine went as high as 31% and were, on the average, higher than for any of the other species which he studied.

It is of interest to examine the data on changes in wall thickness in cedar versus pine and to compare these with the data on tracheid and ray width described previ-

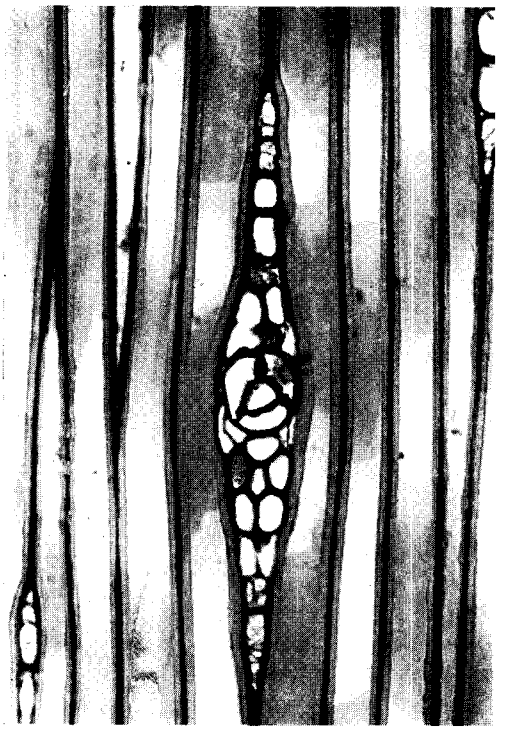

FIG. 7. Because of their greater width, fusiform rays may disrupt cell dimensions in several adjacent cell files. Tangential section ×270.

ously. As already mentioned, these two species were selected for study because they represent extremes among native conifers with respect to width of uniseriate rays. With a tangential breadth of about 7.5 μm, the rays in cedar average somewhat less than half the width of those in red pine. In my opinion, it is an unlikely coincidence that both the average increase in tangential wall thickness and the average decrease in tangential tracheid width at the ray-contact areas are somewhat below half the magnitude in cedar that they are in pine.

Cross-sectional area of cell walls and lumens

On the basis of observations of wood structure in the longitudinal planes, it is clear that the cell lumens are significantly constricted at the ray contact regions in both the radial (Figs. 1–3) and the tangential (Figs. 4 and 5) directions. In the transverse plane, therefore, tracheids sectioned at ray-contact areas should have smaller lumens than those sectioned at non-ray-contact (control) areas. On the basis of the observed reductions in tangential width of cells and the increase in tangential wall thickness, reductions in lumen area were expected to be about 30% in cedar and about 50% in pine. Unfortunately, no reliable information on this point was obtained from the present study. The data obtained on cross-sectional areas of cell walls and cell lumens were variable and inconsistent, reflecting excessive error arising from the imprecision of experimental measurement as well as the variation inherent in sampling on the transverse surface discussed previously. New approaches to this problem are currently being examined.

CONCLUSIONS

1. In coniferous wood, rays appear to be accommodated among the prosenchyma tissue by constricting the tangential breadth of tracheids with which they come in contact.
2. The influence of uniseriate rays scarcely extends tangentially beyond the tracheids immediately bordering them. This establishes the magnitude of the ray-contact constrictions in tracheid width at approximately one-half the ray width.
3. The greater thickness of the tangential tracheid walls at ray-contact areas, quite prominently visible in radial longitudinal sections, can be substantiated by measurements on transverse sections.
4. The increase in thickness of the tangential wall is proportional to the reduction in tangential width of the cell and to the tangential width of the ray.
5. These results indicate that "ray thickenings" are attributable to changes in tracheid configuration at the ray-contact areas rather than to additional deposits of cell-wall material on tracheids otherwise unaltered at these points.

REFERENCE

LADELL, J. L. 1967. Ray thickenings in the walls of conifer tracheids. Nature 213:470–473.