

DEVELOPMENT AND COMPOSITION OF THE WARTY LAYER IN BALSAM FIR. I. DEVELOPMENT¹

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ABSTRACT

The deposition and ultrastructure of the warty layer in developing tracheids of balsam fir [*Abies balsamea* (L.) Mill.] were studied by means of transmission electron microscopy. The wart structure gradually was developed external to the plasma membrane after secondary wall deposition and the greater part of lignification were complete. Warts were synthesized first in the cell corners and pit cavities and then on the remainder of the cell walls. No cytoplasmic organelle was found to be associated specifically with wart formation. After the warty layer was elaborated, the cytoplasm disappeared from the cell, leaving no discernible trace of disorganized residue. The bulk of the wart structure exhibited staining properties similar to those of lignin. However, the basal portions of individual warts were sometimes less darkly stained than the outer portions, indicating possible heterogeneous composition.

Additional keywords: *Abies balsamea*, warts, tracheids, softwoods, electron microscopy, cell structure, secondary walls, bordered pits, lignification, staining, cell wall.

INTRODUCTION

The warty layer (Figs. 1, 2) lines the internal surfaces of mature longitudinal tracheids of many softwoods and the vessel elements and sometimes fibers of a few hardwood species. Although its ultrastructure has been examined, its origin in the developing wood cell continues to be a subject of controversy. Liese (1965) reported that it consisted solely of dead protoplasmic material deposited on the lumen surface at the completion of cell differentiation. According to this view, the warty layer is comprised of two protoplasmic membrane residues, the plasmalemma and vacuole tonoplast, with fragments of cytoplasmic debris trapped between to form the warts. Wardrop and Davies (1962), on the other

hand, found evidence in developing cells that wartlike protrusions were formed as part of, and continuous with, the last-deposited secondary wall layer, S3. These authors contended that at cell death the cytoplasmic membranes retracted and ultimately dried onto the internal fiber surface, enclosing the remaining organelles which formed spherical bodies on top of the wartlike, cell-wall protrusions. Thus, according to this latter view, the complete wart structure consists of localized cell-wall thickenings with a covering of residual cytoplasmic components.

Several workers have suggested explanations for the origin of the warty layer based on wart morphology in mature wood cells, but without examination of developing tissue. According to Jurbergs (1965), who studied four pine species, the nonuniformity in distribution of warts and their preferential accumulation at certain sites were evidence that these structures are not produced by the still-organized cell protoplast. His interpretation of these observations was that wart deposition was a random process, perhaps resulting from sedimentation of decomposed protoplasts during translocation from the mature cell. In contrast,

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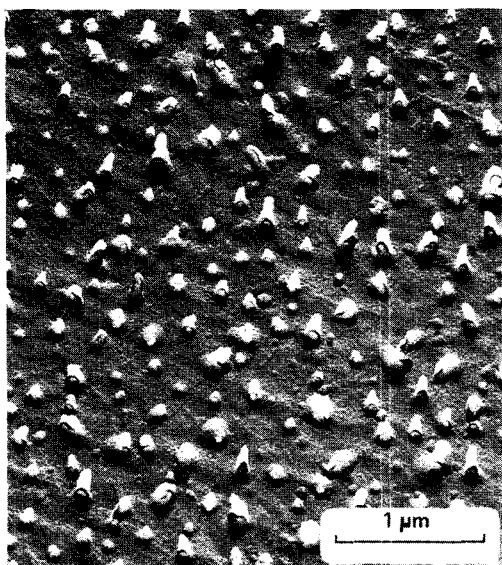


FIG. 1. Warty layer on the inner cell-wall surface of a mature tracheid in earlywood of balsam fir. Direct-carbon replica.

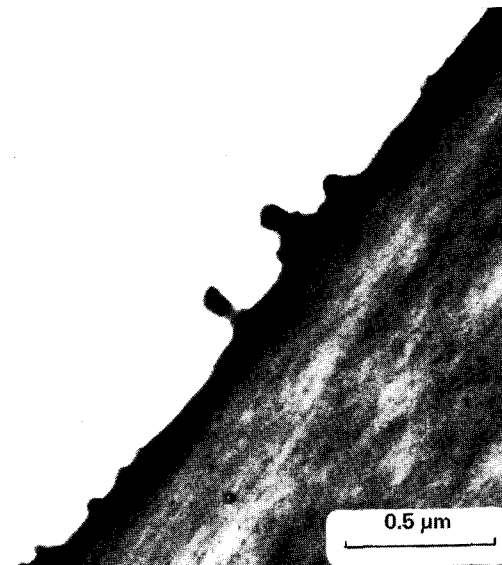


FIG. 2. Transverse section of the mature warty layer in balsam fir. KMnO_4 -stained ultrathin section.

Frey-Wyssling and Mühlethaler (1965) concluded that a morphogenic factor was active during wart formation, in addition to passive degradation of the cell contents. Their conclusion was based on the taxonomic relationship that exists between warts and dentate ray tracheids in pine (Frey-Wyssling et al. 1956) and between warts and vested pits in some hardwood species (Côté and Day 1962).

Cronshaw (1965) could not accept a cytoplasmic debris theory for origin of any part of the warty layer, explaining that this view was difficult to reconcile with the fact that conifer tracheids do not "dry out" until heartwood formation, many years after formation of the warty layer. He also cited the taxonomic trends of the wart structure (mentioned above) as additional evidence against a debris theory. Upon detailed study of pine cambium tissue, Cronshaw found that the wart structure was actually developed external to the plasma membrane during the final stages of cell differentiation. It formed the innermost layer of the cell wall and was distinct from the S3 layer. He suggested that after wart formation the cell contents were depolymerized and eluted

out of the cell by the transpiration stream as tracheids became functional for water conduction. This proposal is fortified by the results of Grozdits and Ifju (1973) who observed that there was a sharp decrease in nitrogen content (attributable to cytoplasm or residue of the same) within the last-formed growth increment of several woody species and that samples taken from other annual increments had remarkably low nitrogen contents. Therefore, according to Cronshaw, the warty layer is neither cytoplasmic remains nor part of the S3 layer. Rather, it is a structure elaborated by living cytoplasm in its final role before disintegration.

Kutscha (1968), supporting Cronshaw's contention, also found that the warty layer was deposited external to the plasmalemma following secondary wall formation in both normal and compression wood of balsam fir. Furthermore, he observed continuity between the tips of conelike warts and some membrane-bound vesicles or dark-staining particles in the cytoplasm.

Scurfield and Silva (1969), in considering the origin of the warty layer, speculated that warts constitute a replica of invagina-

tions of the plasma membrane through which wall materials were being actively secreted at the time of cell death. Warts might then be regarded as consisting of something less than completely elaborated wall constituents plus products released during protoplast autolysis. The latter were reported by Scurfield (1972) to be largely phenolic substances.

The object of the present work was to attempt to resolve some of the uncertainties concerning the nature and origin of the warty layer by following its development in differentiating tracheids of balsam fir and also by noting its relationship to the deposition of other cell-wall components.

EXPERIMENTAL

Cambial tissue was harvested in June from an erect balsam fir [*Abies balsamea* (L.) Mill.], 30-cm dbh, growing in central Wisconsin. Both 1-cm cubes and 1-mm radial slices that included the cambial zone were taken by the procedure described by Parham and Baird (1973). Radial slices were fixed with 2% KMnO_4 for 2 h at about 25 C and then dehydrated via ethanol and propylene oxide before embedding in Spurr's (1969) "hard" formulation epoxy. Ultrathin transverse sections were stained with lead citrate and KMnO_4 in sequence. The cube-size cambial samples were dehydrated by an ethanol-ether sequence, embedded in collodion (Johansen 1940), and then sectioned radially at about 100 μm with a sliding microtome. The collodion was dissolved with ether:ethanol (1:1), and the sections were air-dried from ether. Surface replicas were prepared by a direct-carbon method (Côté et al. 1964) using the procedure and apparatus described by Dunning (1968). Radial sections were shadowed with platinum at a 45° angle along the fiber axis. Both ultrathin sections and replicas were examined with an RCA model EMU-3F TEM at 50 kV.

RESULTS AND DISCUSSION

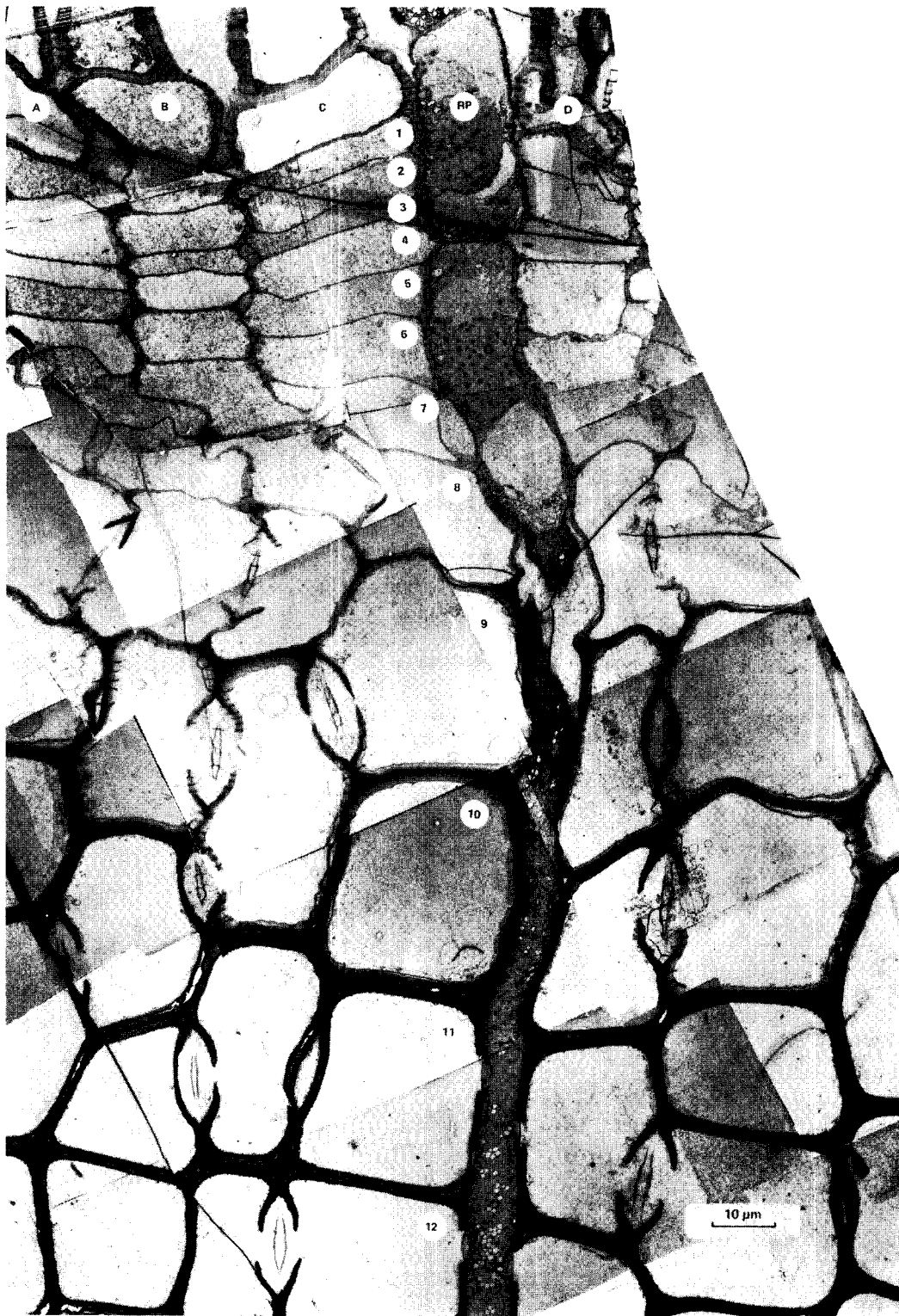
Cell-wall development and lignification

Figure 3 is a composite micrograph of the cambial zone and differentiating cells of balsam fir during earlywood formation. Radial files of developing tracheids are designated A–D. The cells in file C are numbered sequentially toward the mature wood from the fusiform initial, the latter cell being determined according to the reasoning of Mahmood (1968). Preservation of cytoplasm in the ray cells was generally better compared to that in developing tracheids, probably because the former were less vacuolated.

The cambial zone is seen in Fig. 3 as a band of radially narrow, thin-walled cells. Toward the top of the composite is maturing phloem with maturing xylem toward the bottom of the figure. Secondary wall deposition is occurring in cells 7–11 of file C. The concentration of organelles along a cell wall as secondary deposition nears completion is illustrated in Fig. 4. Golgi bodies, mitochondria, endoplasmic reticulum profiles, and associated vesicles can be seen along the developing tangential wall between the plasmalemma and vacuole tonoplast.

The major phase of wood lignification occurred after secondary wall deposition was completed and before wart formation. The lignification process here was monitored by staining ultrathin wood sections with potassium permanganate (Hepler et al. 1970; Bland et al. 1971; Schwarzmunn 1973). The sequential stages are illustrated in each tracheid file in Fig. 3. After the intercellular region was lignified, wall lignification began in the cell corners just inside the primary wall and then proceeded centripetally through the wall to the cell lumen. Schwarzmunn (1973) reported that lignification first extends along the tangential wall farthest from the cambium, then proceeds

FIG. 3. Composite micrograph of the cambial zone and differentiating cells of balsam fir during earlywood formation. Radial files of developing tracheids are designated A–D. File C is numbered sequentially from the cambial initial; RP-ray parenchyma.



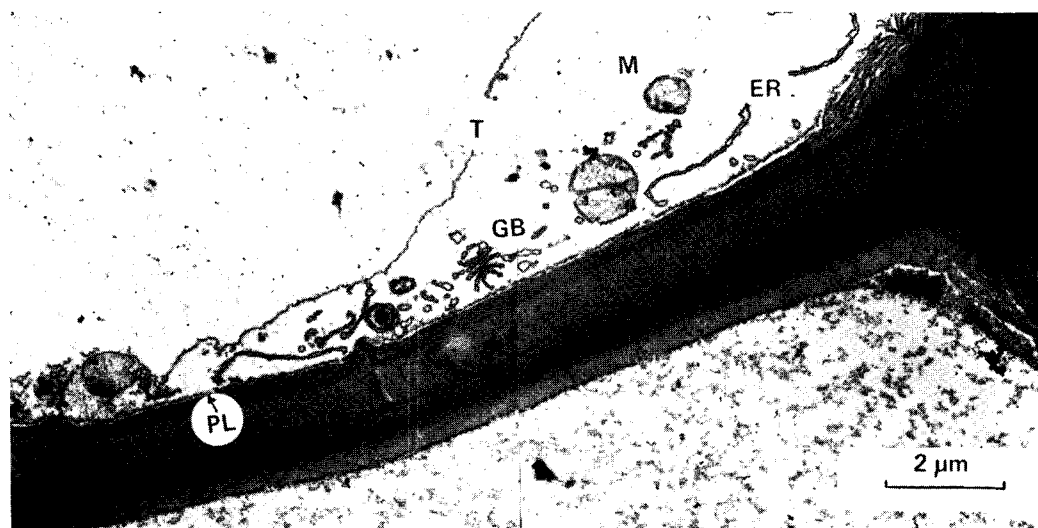


FIG. 4. Cytoplasmic organelles along a developing tangential wall; PL-plasmalemma, GB-Golgi body, M-mitochondrion, ER-endoplasmic reticulum, T-tonoplast.

along the radial walls and finally along the tangential wall nearest to the cambium. Wardrop (1971), however, reported that both tangential walls are lignified somewhat before the adjacent radial walls. As observed here, lignification began in the cell corners but then proceeded in all the

walls nearly simultaneously. Mature tracheids stained darkly throughout the wall, indicating complete lignification.

Figure 5 shows a double tangential wall between adjacent cells in radial file A of Fig. 3. The wall of the cell farther from the cambium is more completely lignified, as shown by the darker permanganate staining. Since both polymeric lignin and its monomeric precursors would presumably be stained with permanganate (Bland et al. 1971), this micrograph could be interpreted as evidence that the introduction of lignin precursors to the wall is directed by the individual cell. However, the influence of precursor concentration on stainability and the receptiveness of individual cells to lignification would have to be ascertained before such speculation could acquire credibility.

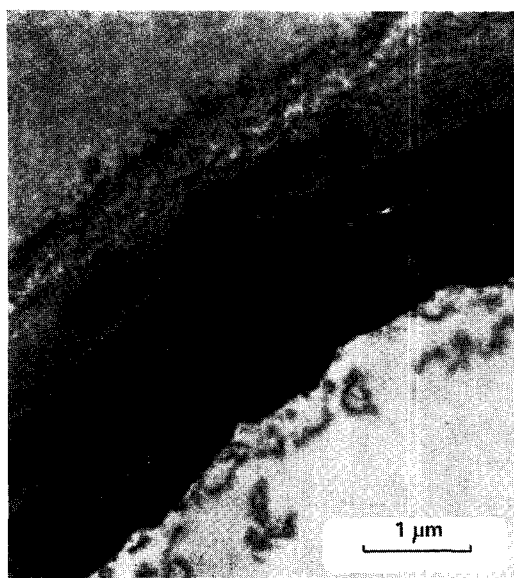


FIG. 5. Double tangential wall between two tracheids at different stages of lignification.

Wart development

Warts first developed at about the time cell-wall lignification was nearing completion. Schwarzmann (1973) has shown that wart formation may occur before the entire S3 layer is lignified; however, in the present study wart formation was observed only after S3 lignification was complete. In file C of Fig. 3, warts first occurred in cell 11.

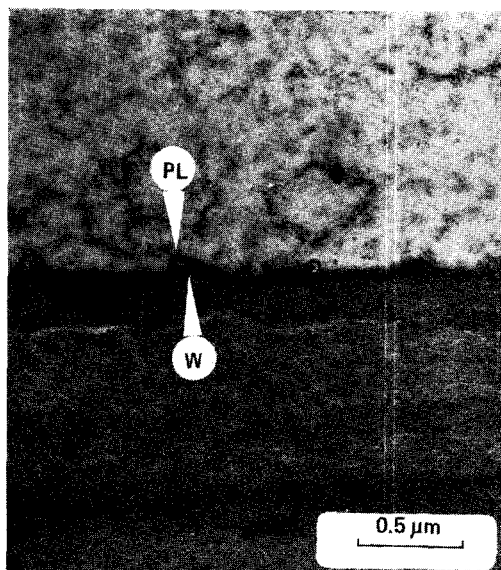


FIG. 6. The beginning of wart formation on the cell-wall exterior to the plasmalemma. The latter is seen here as a unit membrane; PL-plasmalemma, W-wart.

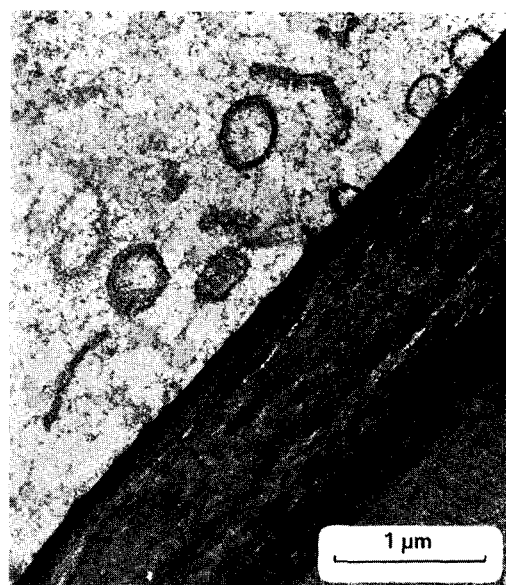


FIG. 7. A recently developed but mature warty layer in a living earlywood tracheid.

Analogous to the lignin depositional pattern, warts developed first in cell corners and then on the radial and tangential walls nearly simultaneously. Warts formed in pit cavities at about the same time that they were forming in cell corners of the same tracheid. Interestingly, the distribution of warts on the surface of the inner pit border corresponded to the extension of lignified areas within the pit border (Baird 1974).

Warts seem to appear first as small mounds that stain slightly darker with permanganate than the rest of the secondary wall (Fig. 6), implying that wart formation and lignification proceed concomitantly. They continue to protrude into the cell lumen and when mature, they, along with an associated amorphous layer, stain much more intensely than the subjacent wall. This observation is consistent with earlier illustrations in the literature (e.g., Wardrop and Davies 1962) as pointed out by Scurfield (1972).

In agreement with earlier reports (Cronshaw 1965 and Kutscha 1968), warts were observed to form exterior to the plasma-

lemma before cytoplasm degeneration and disappearance (see Figs. 6 and 7). The warty layer, therefore, cannot consist of desiccated cytoplasmic membranes with organelles trapped between to form the protrusions.

No organelle was found to be associated specifically with wart formation. Occasionally the plasmalemma did appear to retract slightly from the wart structure (Fig. 6), but this situation could have been due to partial plasmolysis in an imperfectly fixed cell, or possibly it represented the plasmalemma invaginations discussed by Scurfield and Silva (1969). There was no unique feature observed within the cell wall beneath a forming wart.

In mature tracheids, warts were more numerous and larger in the corners than along the walls. In some cases, an interior, basal portion of the warts along the cell wall stained less darkly with permanganate than the rest of the wart structure (Baird 1974). This may indicate a heterogeneous composition of the warty layer, a subject that is discussed more extensively in Part II of this paper (Baird et al. 1974).

Figure 8 shows the internal surfaces of

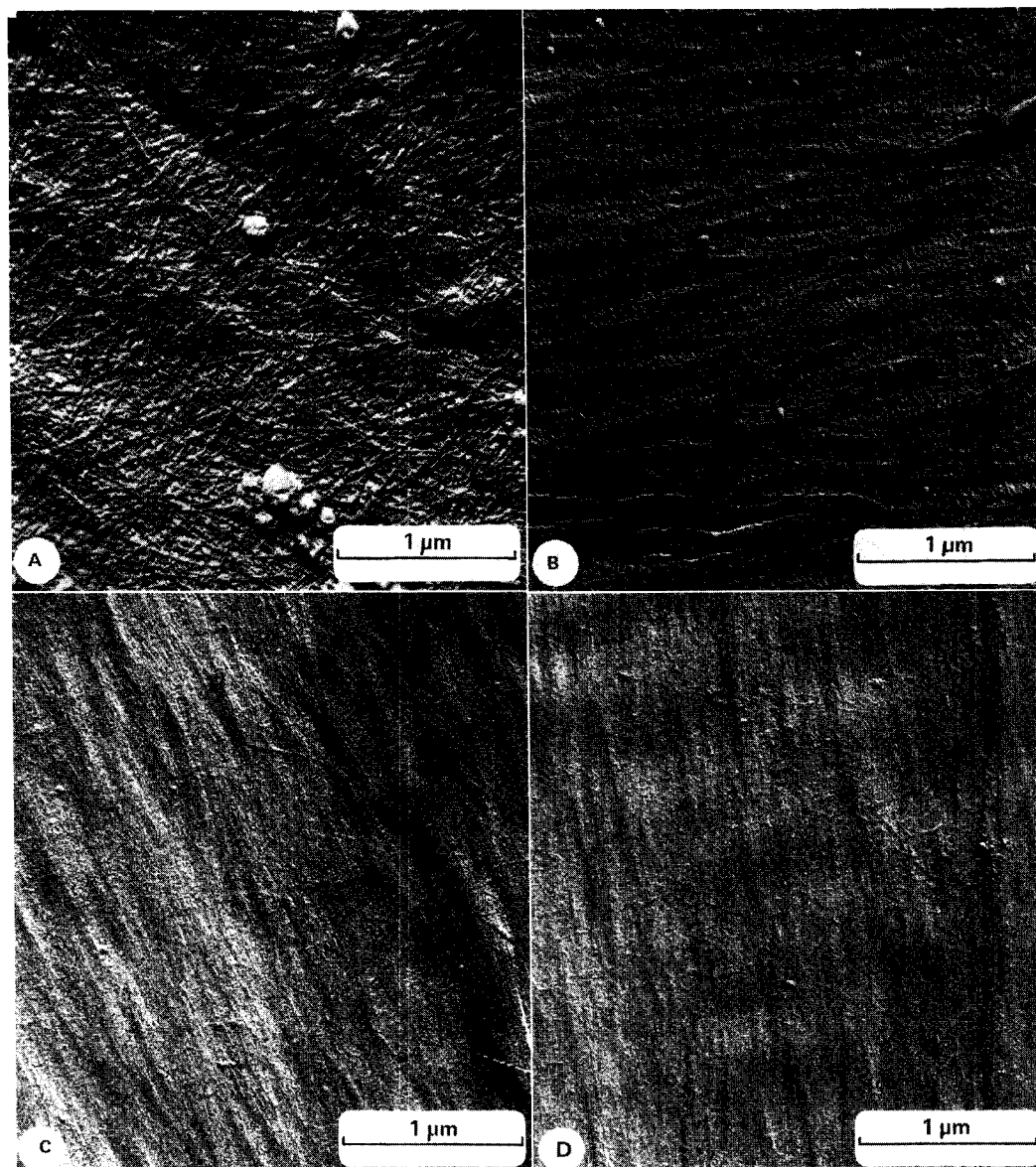


FIG. 8. Inner surface of 7 developing tracheids in a radial file moving inward from the cambium: A. Primary wall; B. S1 layer; C. Exterior region of S2 layer; D. Interior region of S2 layer; E. S3 layer; F. Immature warty layer; G. Nearly mature warty layer; H. Mature warty layer. Tracheid axis is vertical.

tracheids as they develop in a radial file moving inward from the cambium as observed in radial sections of unfixed, collodion-embedded samples. The entire series corresponds to cells 5 or 6 through 12 in file C of Fig. 3 and is illustrative of the

sequential cell-wall layers deposited on a single tracheid as it develops.

In Fig. 8A is shown the irregular orientation of microfibrils on the inner surface of the primary wall deposited after cell division in the cambial zone. Figure 8B illus-

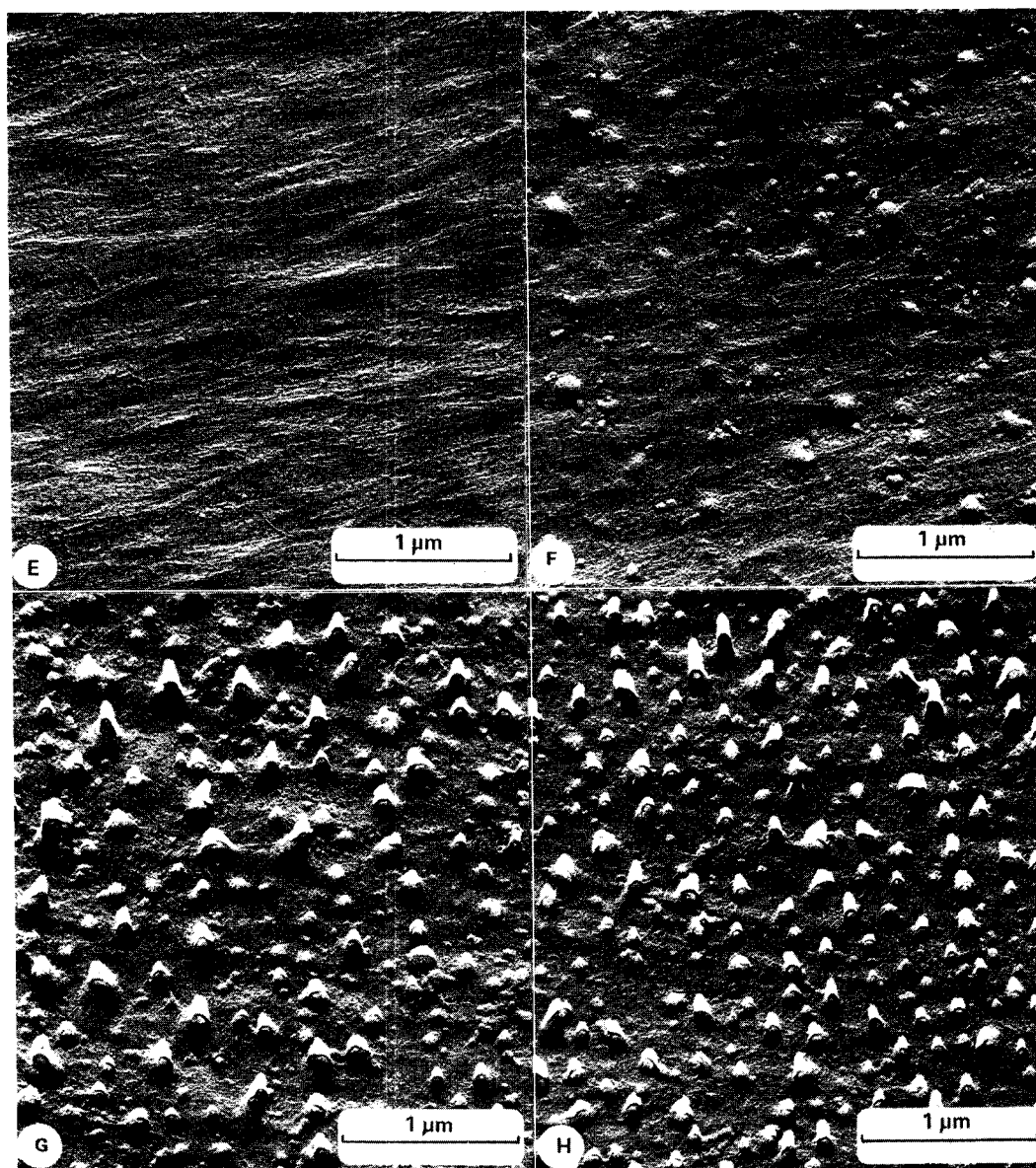


FIG. 8. Continued.

trates a lamella of S1 layer microfibrils oriented almost normal to the tracheid axis. The microfibrils in the S2 layer (Fig. 8C) display a steep helical pattern oriented only 10–20° to the fiber axis. Figure 8D reveals a more interior portion of the S2 layer with microfibrils oriented nearly the same as in the preceding micrograph. In Fig. 8E microfibrils of the S3 layer are displayed at a

70° angle to the fiber axis and form a relatively flat helix around the cell.

Figure 8F shows a partially encrusted S3, but the characteristic S3 orientation is still evident. This micrograph is a surface view of the warts in an early stage of formation. Warts in the corner of this same tracheid (not shown here) protruded farther into the lumen, illustrating the typical situa-

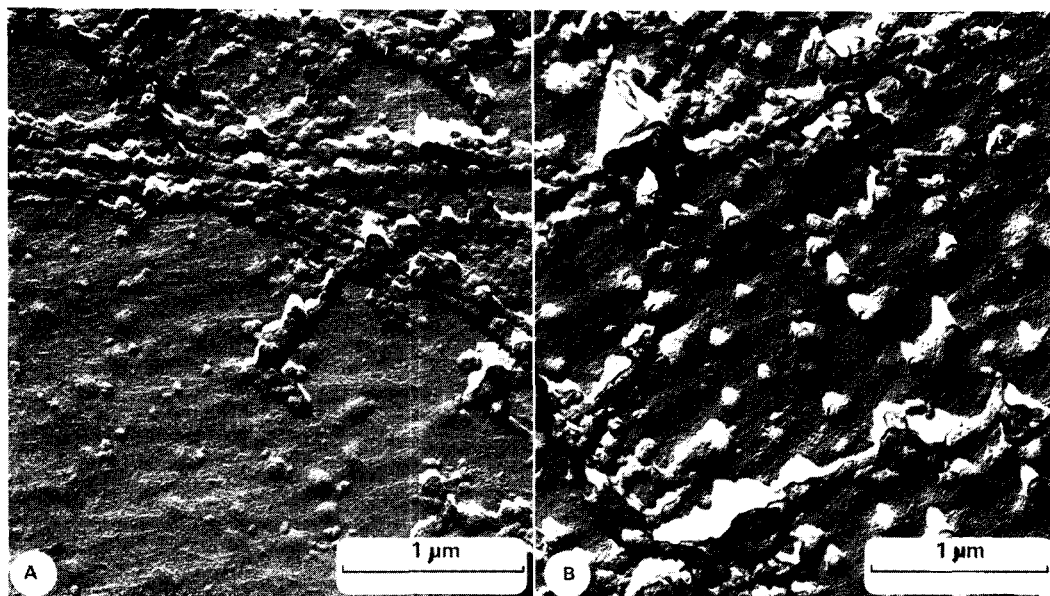


FIG. 9. Cytoplasmic residue on developing warty layers: A. Immature warts; B. Mature warts.

tion in which warts develop earlier in cell corners. A nearly mature warty layer on a radial cell wall is depicted in Fig. 8G. Here the microfibrillar orientation of the underlying S3 layer is totally obscured. These two micrographs, Fig. 8F and 8G, confirm that mature warts are developed gradually over a period of time and do not appear suddenly as suggested by Wardrop et al. (1959). The numerous mature warts of a completely differentiated tracheid were typified earlier in Fig. 1.

The electron micrographs in Fig. 8 were purposely taken of wall surface areas not obscured by desiccated cytoplasm. Figures 9A and 9B, however, show dried cytoplasm over a developing warty layer and mature warty layer, respectively, and provide further confirmation that the cell is still living when the warty layer forms.

Desiccated cytoplasmic material often appeared as strands aligned perpendicular to the fiber axis in the more completely developed tracheids. This alignment was nearly parallel to the orientation of the last-deposited S3 microfibrils. Such observations may indicate a relationship between some organization in the cytoplasm and the orien-

tation of the deposited microfibrils. In cells beyond the differentiation zone, there was no evidence of cytoplasmic residue anywhere on the cell wall. By this time all the cytoplasm with associated organelles and membranes apparently had been degraded and left the cell.

On the origin of warts

Three alternative hypotheses are offered to explain the formation of the warty layer in the tracheids of balsam fir:

(1) Warts are vestiges of sites of material transport from the cytoplasm to the developing cell wall. When wall formation is complete, excess material deposition (see below) at these locations leads to the formation of warts.

(2) Warts are formed by deposition of autolysis products of the moribund cell exterior to the plasmalemma and with no relationship to sites of previous deposition of cell-wall components.

(3) The wart structure is due to an eruption of material from the cell wall into the lumen caused by localized areas of high osmotic potential. As water was drawn into these areas, which might be pockets of lig-

neous or hemicellulosic substances exterior to the plasmalemma, pressure could develop and cause local inward distension and eruption of the plasmalemma.

The third hypothesis is intriguing and should not be discounted, but it is least satisfying of the three. Seemingly, any areas of high osmotic potential could be dissipated throughout the cell wall or at least evenly along the cell wall/plasmalemma interface, eliminating any localized eruption.

Of the first two hypotheses, there is little evidence to present from this work that would favor one over the other. However, it is perhaps worth while to consider some recent observations concerning the morphology and possible taxonomic significance of the warty layer. It has been noted that warts are typically larger in latewood of coniferous woods (Ohtani and Fujikawa 1971) and in hardwoods are found preferentially in the latewood (Ohtani and Ishida 1973; Parham and Baird 1974). With respect to the mechanism of latewood formation, it is the favored opinion that the increase in cell-wall thickness reflects primarily an increase in the net availability of tree photosynthates (Larson 1969). Thus, drawing from hypothesis (1), and judging from the relationship already described between wart structure and latewood cells, it seems reasonable to propose that the same biochemical apparatus that causes additional wall substance to be laid down in latewood may also be responsible in some way for the stronger association of warts with the same tissue. But, whether the warts actually represent excess wall substance produced during a period of high photosynthetic activity and ensuing wood lignification, or whether they are, according to hypothesis (2), phenolic compounds expelled near or during cell autolysis, is impossible to interpret from the present data. Furthermore, it is conceivable that some combination of these processes may operate to produce the total wart structure as suggested by Scurfield (1972, with Silva 1969). The complete lack of a warty layer in some wood species might be explained by the

proposal of Parham and Baird (1974) that warts seem to be associated evolutionarily with the degree of phylogenetic advancement of the species and type of xylem element.

It was of interest to note in the present experiments that in all developing tracheids situated on the TEM grids such that examination of most of their inner surfaces was possible, the microfibrillar orientation of the last-deposited wall lamellae was relatively constant over their entire visible length. Radial wood sections were usually cut only slightly oblique to the fiber axis, which prevented scrutiny of only the very tips of such tracheids. These observations are somewhat at odds with the concept of progressive, longitudinal deposition of the secondary wall from the center of the fiber toward the ends as put forth by Wardrop (1964), Wardrop and Harada (1965), and later endorsed by Robards and Kidwai (1972). Further work is in progress to determine the significance of this observation.

SUMMARY AND CONCLUSIONS

The warty layer in balsam fir was developed during the final stages of tracheid differentiation exterior to the plasmalemma and before cell autolysis. After the microfibrils of the S3 layer had been deposited, the internal cell-wall surface became slightly encrusted with an amorphous material and low mounds appeared. The warty layer (consisting of both the mounds and amorphous covering) continued to develop until the S3 layer was completely covered with encrustant and the warts protruded into the lumen as blunt cones.

Most of the cell-wall lignification process preceded wart formation. However, judging from the permanganate staining reaction, when developing warts were still in their initial stage as low mounds, they already appeared slightly more lignified (or ligninlike) than any portion of the adjoining secondary wall. In the final stage when warts protruded noticeably into the lumen, they appeared much richer in lignin (or ligninlike material) than the secondary wall.

In a few cases, a heterogeneous nature of the warty layer was indicated where the outer portion was very darkly stained in comparison to the basal region. Warts developed first at tracheid corners and on the inner surface of bordered pits and then on all walls over the entire length of the cell nearly simultaneously. The pattern of wart formation was analogous to that of cell-wall lignification.

No organelle or membrane system other than the plasmalemma was found to have a specific association with wart formation, though this is not to say that no such relationship may exist. After warts were formed, the living cell contents degenerated and disappeared from the tracheid, leaving no disorganized residue on the inner surface of the cell wall.

Three hypotheses were offered to explain the origin of warts in tracheids of balsam fir.

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Technology and Weyerhaeuser
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Products R&D; Technical Service R&D; Technical Support; and Facilities Planning and Engineering. Not all research and development personnel will be centralized. Some will require on-site locations at selected regional facilities, primarily major pilot operations and regional forestry activities at Centralia, Washington; Southern Forestry at Hot Springs, Arkansas; and Tropical Forestry in Indonesia.

The building comprises three areas: (1) a two-story integrated laboratory and office complex; (2) a central support area housing reception lobbies, audio-visual complex, library, cafeteria, and blocks of conference rooms opening onto landscaped courts; and (3) a two-story structure housing development and warehouse areas in a clear height portion, and work areas in a double

story portion. Greenhouse and nursery space are also provided.

The new corporate research building thus embodies on one hand and symbolizes on the other the Weyerhaeuser Company's commitment to technology. R&D staff will be increased dramatically and allocation of corporate resources to research and technological development doubled over the next five years. The commitment is perhaps best summed up in President George H. Weyerhaeuser's statement, "An acceleration in research and technology emphasis is needed in the forest products industry today and we expect to lead this increased effort as we have led in forestry and forest management research."

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