ANATOMICAL FEATURES AFFECTING LIQUID PENETRABILITY IN THREE HARDWOOD SPECIES[1]

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ABSTRACT

Variation in liquid penetrability of hickory, sweetgum, and blackgum is related to differences in tyloses, gum depositions, encrustations, pit membrane structure, volume of the various cell types present, and types of cells connected by pits. In hickory, blockage of the intervessel pits, isolation of vessels from fibers, parenchyma, tyloses, and low vessel volume resulted in liquid flow along heartwood fibers. Tyloses and heavily incrusted pit membranes in both vessels and fibers of sweetgum heartwood effectively halt liquid flow. Blackgum heartwood is easily penetrated as it lacks tyloses and contains a relatively small amount of incrusting materials.

Additional keywords: *Carya tomentosa, Nyssa sylvatica, Liquidambar styraciflua,* heartwood, tyloses, pit membranes, liquid penetrability, encrustations, permeability.

INTRODUCTION

During a recent study concerned with characterizing the ultrastructure of three hardwoods, anatomical features that influence liquid penetrability were noted. Although species selection was not based on liquid penetrability, by chance a diverse range of penetrability was obtained. The species studied and their classification with respect to heartwood penetrability (MacLean 1935) were blackgum (*Nyssa sylvatica*), easily penetrated; hickory (*Carya tomentosa*), moderately difficult to penetrate; and sweetgum (*Liquidambar styraciflua*), very difficult to penetrate.

Since the structure of vessels facilitates longitudinal liquid flow in the living tree, it is not surprising that vessels play a primary role in liquid penetrability. However, their effectiveness is dependent upon size, number, and distribution and even more importantly upon the extent of extraneous materials and tyloses present as well as upon the character of pitting that leads to contiguous cells. The factors emphasized in this study were extraneous materials, tyloses, and pitting to adjacent cells.

Although fibers often constitute the bulk of woody tissues, in general they are not considered to be as important as vessels in initial liquid penetration. However, their permeability may have a decided influence on the subsequent spread of liquid from vessels. Compared to vessels, fibers with their thick cell walls and irregular distribu-

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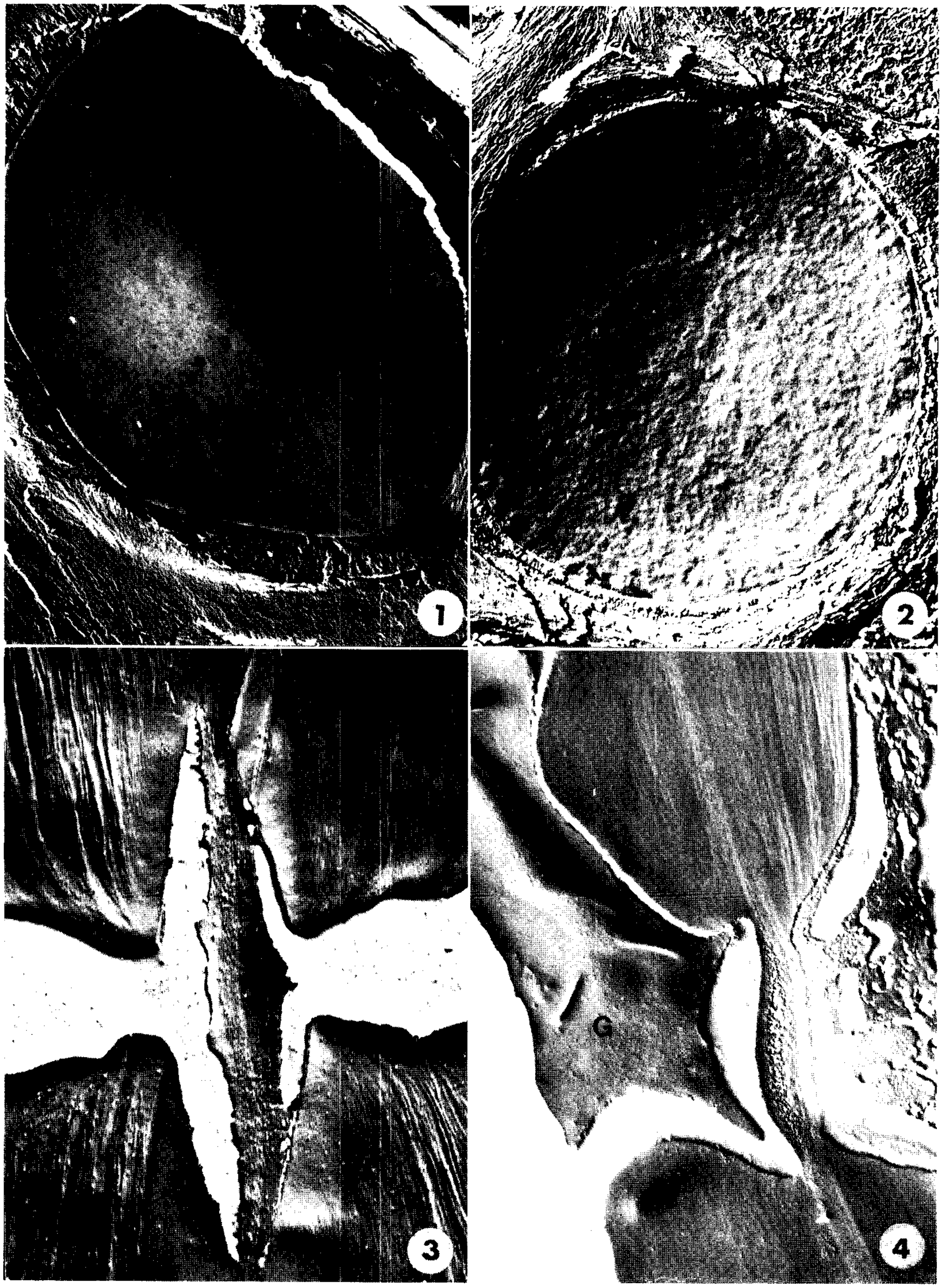
FIG. 1. Typical heavily incrusted intervessel pit membrane found in the sapwood of mockernut hickory. 10,500×. FIG. 2. Intervessel pit membrane from the heartwood of mockernut hickory depicting the high degree of encrustations. 10,500×. FIG. 3. Cross-sectional view of portion of an intervessel pit-pair from the sapwood of mockernut hickory. Note the incrusted and thick pit membrane. 13,700×. FIG. 4. Vessel to parenchyma pit-pair from hickory sapwood showing a deposit of gum (G) in the vessel. Note also the fingerlike projections of the protective layer on the parenchyma side of the pit membrane. Gum was displaced from the pit membrane as a result of cutting stresses. 9,900×.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tion of relatively small pits do not appear especially adapted for liquid conduction. Since liquid flow between fibers is dependent primarily upon pits, these structures were also examined.

The objectice of this paper is to describe the ultrastructural features that apparently control the heartwood penetrability of three hardwood species.

MATERIALS AND TECHNIQUES

From four trees of each species, a cross-sectional disc was cut at a point four feet above the ground. From each disc, samples were selected from the outermost sapwood, inner sapwood, outermost heartwood, and inner heartwood.

Specimens were either air-dried or embedded green in a mixture of n-butyl and methyl-methacrylate (75:25) for sectioning. Specimens were oriented to provide sections from the cross-sectional, tangential, and radial planes.

Ultrathin sections cut with a diamond knife were picked up with carbon-coated, celloidin-filmed grids. The methacrylate was removed with xylene prior to shadowing with platinum at an angle of approximately 20° in a high vacuum evaporator.

Direct-carbon replicas were prepared following the technique described by Côté et al. (1964). Replicas were made of split radial and tangential surfaces as well as 200-μm sections cut from the radial and tangential planes.

RESULTS AND DISCUSSION

Hickory

Solitary vessels in hickory have as contigous cells either ray or longitudinal parenchyma elements. Longitudinal parenchyma border the tangential wall, whereas either ray or longitudinal parenchyma are adjacent to the radial wall. Since vessels do not end in isolation, individual vessel elements occasionally border the tangential walls of other vessel elements. Individual vessels, as well as vessels in radial rows of two or three, are also completely surrounded by parenchyma. Therefore vessels, whether they are solitary or in radial rows of two or three, are

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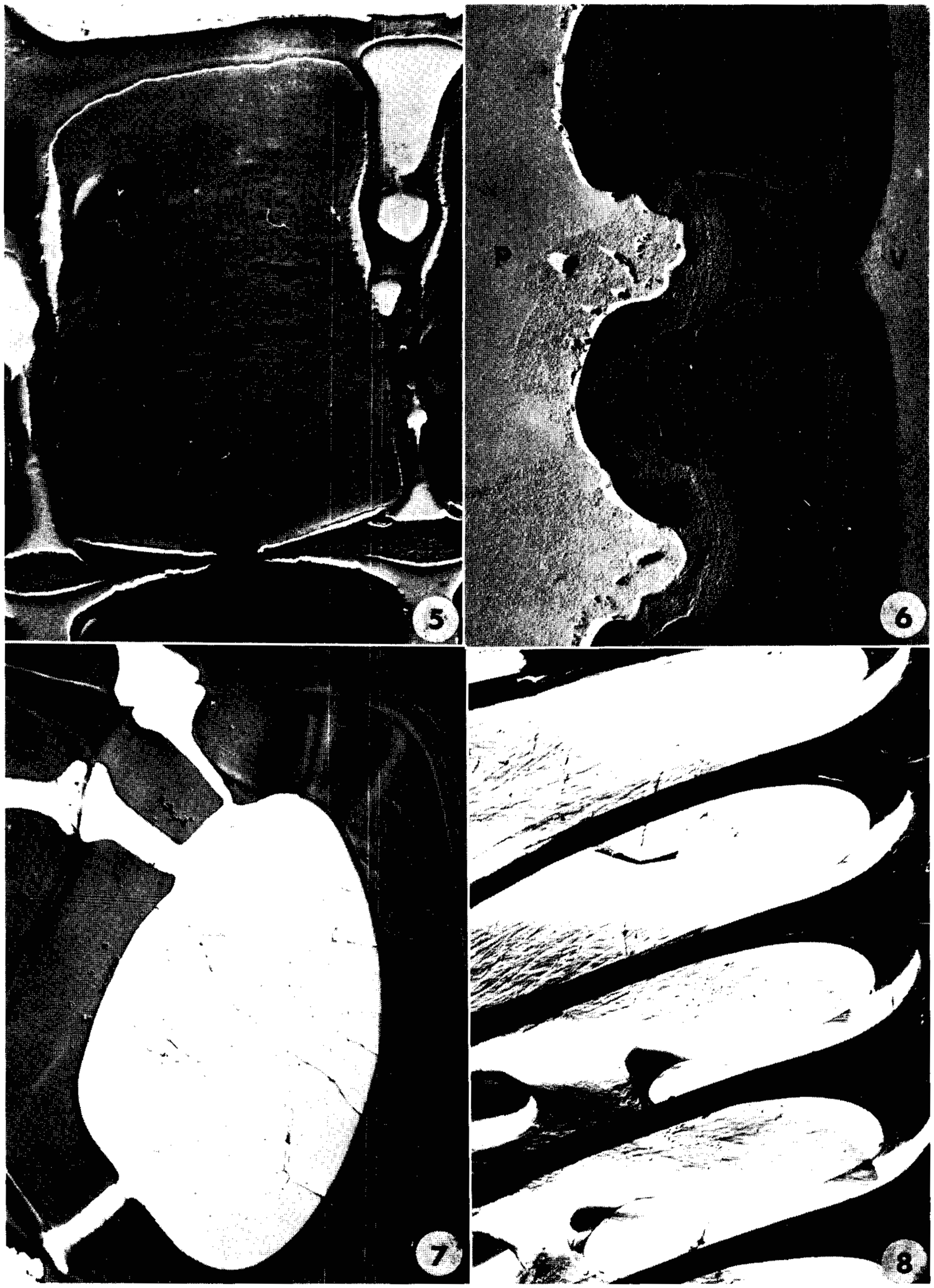
FIG. 5. Portion of intervessel pits from hickory sapwood showing blockage of the pit canal by gum secretions (arrow) from parenchyma cells. Note also the gum lining the thick vessel wall. 6,700×. FIG. 6. Vessel (V) to longitudinal parenchyma (P) pit-pairs from hickory heartwood. The pit chamber (arrow) in the vessel wall is completely filled with gum and tyloses (T) completely obstruct the pit apertures. 7,900×. FIG. 7. Cross-sectional view of a fiber tracheid from hickory sapwood showing cell-wall layering, fiber tracheid pit-pairs, and a fiber tracheid to longitudinal parenchyma pit-pair (lower left corner). Note the thin pit membrane in one of the fiber-tracheid pit-pairs and its absence in the other pit-pair. 5,300×. FIG. 8. Part of a scalariform perforation plate from sweetgum sapwood. Revealed through the open perforations are vessel to ray parenchyma pits in the back wall of the vessel. 3,400×.

FIG. 9. Segment of scalariform perforation plate from sweetgum heartwood with the perforations completely sealed by tyloses. 5,300×. FIG. 10. Cross-sectional view of part of a scalariform perforation plate from sweetgum heartwood showing blockage of the perforations by tyloses. The tyloses completely surround the perforation plate bars and extend across the openings. 14,700×. FIG. 11. Pit membrane of an interfiber pit-pair from sweetgum sapwood. Notice the lack of encrustations. 18,400×. FIG. 12. Interfiber pit from sweetgum heartwood with typical heavy encrustations coating the pit membrane. 18,400×.

FIG. 13. Cross-sectional view of an interfiber pit-pair from sweetgum sapwood. 18,400×. FIG. 14. Cross-sectional view of an incrusted interfiber pit membrane from sweetgum heartwood. Note the substantial increase in pit membrane thickness as a result of encrustations. The original pit membrane can be detected (arrows). 51,500×. FIG. 15. View of a segment of a scalariform perforation plate from blackgum heartwood showing encrustations deposited on perforation plate bars. 2,700×. FIG. 16. Cross-sectional view of perforation plate bars from blackgum heartwood. Notice the high degree of encrustations around the bars but not completely sealing the opening as in sweetgum heartwood. 9,200×.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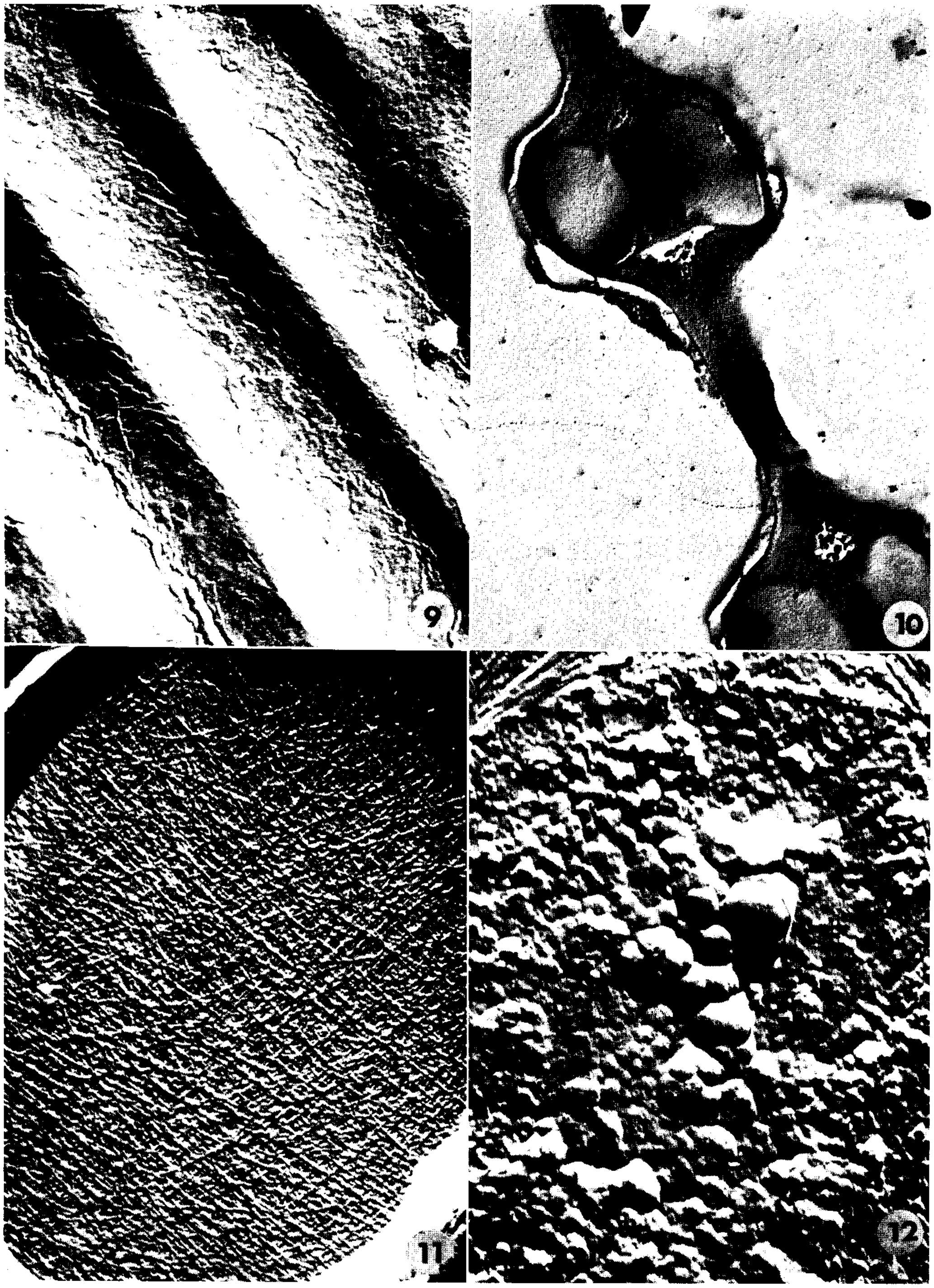
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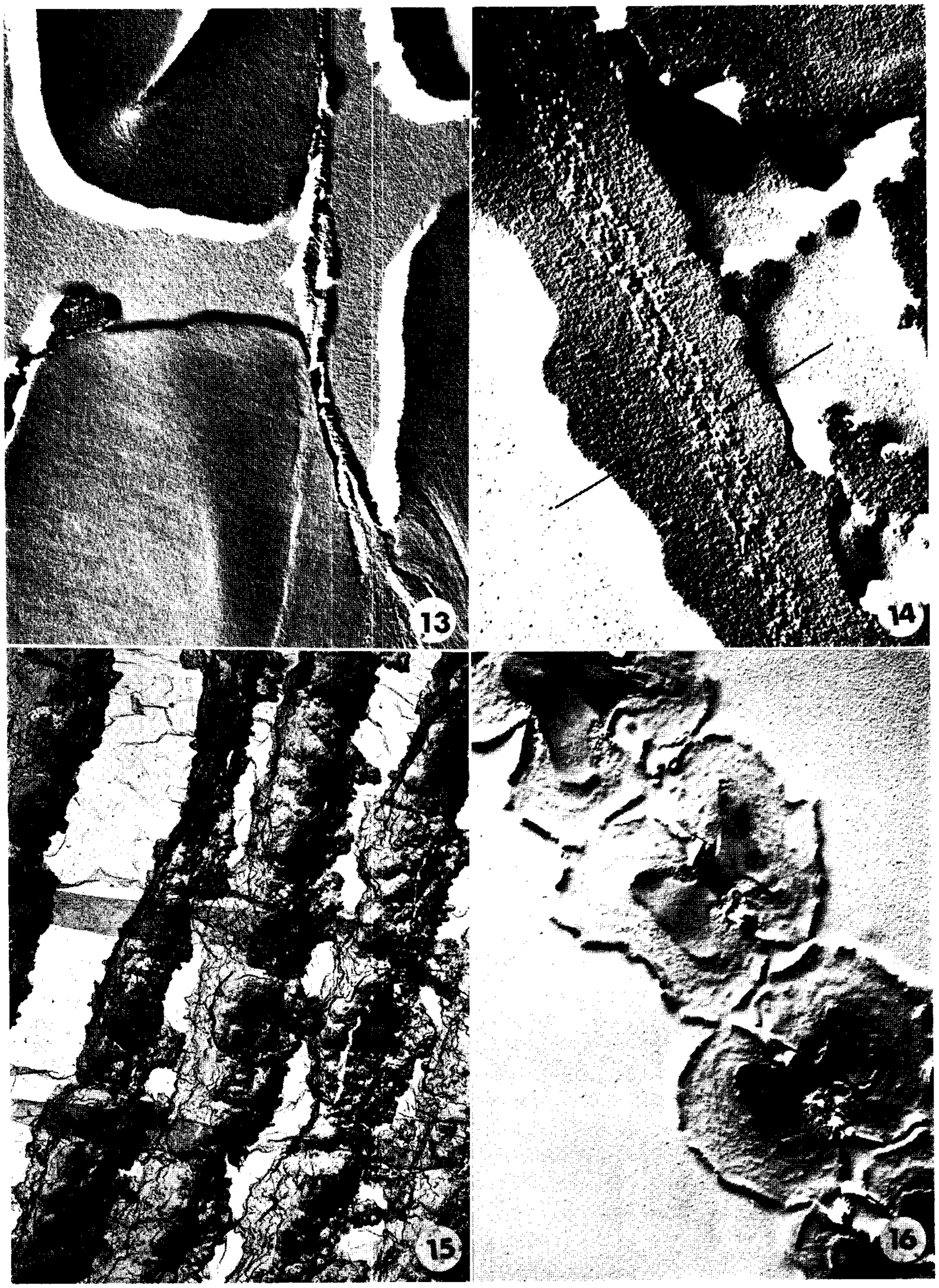
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isolated from fibers. As a result, pits in vessels lead either to other vessels or parenchyma cells.

The intervessel pit membranes from both the sapwood and heartwood zones were heavily incrusted (Figs. 1 and 2). As a result pit membranes showing the microfibril component were not observed unless treated with sodium chlorite. An illustration of the relatively thick and incrusted sapwood pit membranes is revealed in the cross-sectional view shown in Fig. 3. Not only is the membrane thicker, but it does not present the loose and porous arrangement of microfibrils found in the sapwood of many hardwood species (compare Figs. 3 and 13). Obviously, the efficiency of sapwood and heartwood intervessel pit-pairs with regard to conduction is considerably reduced as a result of the large amount of encrustations that completely overlay the intervessel pit membranes.

Pit membranes connecting vessels to parenchyma cells consist of the primary walls of both cell types separated by a middle lamella. Also, material termed the protective layer is found on the parenchyma side of the membrane. In addition to the above, the vessel side of the hickory vessel-parenchyma pit-pairs in the sapwood contains encrustations apparently secreted by the parenchyma cells (Fig. 4). Chattaway (1949) grouped all parenchyma cell exudates together and termed them "gum." Often the gum material lined the vessel wall and filled the intervessel pit canals, thus hindering the flow pathway from vessel to vessel (Fig. 5).

The lumens of hickory heartwood vessels contain many tyloses. Not only do the tyloses fill and thus block the lumen, but they also line the vessel lumen walls and obstruct the pit apertures. For example, Fig. 6 reveals heartwood vessel to parenchyma pit-pairs with the vessel pit chambers completely filled with gum and the pit apertures overlaid with tyloses. As a result of these structural alterations, vessel-parenchyma and intervessel pit-pairs are virtually eliminated as conducting passageways.

Fiber tracheids, which constitute over one-half of the wood volume of hickory, are relatively thick-walled fibrous cells with pointed ends and bordered pits, Since fibers are not contiguous to vessels, only pit-pairs interconnecting fiber tracheids and fiber tracheids to parenchyma are present. The pit-pairs connecting fiber tracheids are bordered and possess a deep pit canal (Fig. 7). The pit membrane is relatively thin as compared to intervessel pit membranes and is often disrupted or missing. The possibility exists that the disrupted or missing pit membranes are an artifact caused by methacrylate swelling. However, if this is the case, the fact that intervessel or fiber-to-parenchyma pit membranes remained intact illustrates the tenuous nature of the interfiber pit membranes and the likelihood that they provide the liquid flow pathway. The above description of interfiber pits characterizes both the heartwood and sapwood zones as encrustations are not deposited on the heartwood pit membranes. The pit-pairs between fibers and adjacent parenchyma contain a thick membrane and, as in the case of pitting between parenchymatous and prosenchymatous elements, do not appear conducive to liquid flow.

Although the vessels of hickory constitute a very small percentage of the wood volume and their pits are occluded with tyloses and gum deposits, hickory is only moderately difficult to penetrate. This is largely due to the fact that longitudinal flow occurs along the fibers (Gerry 1914; Teesdale and MacLean 1918). The lack of encrustations on the heartwood pit membranes and the relatively thin pit membranes account for the important conduction role of fibers in hickory.

Sweetgum

Despite the fact that vessels occupy slightly over half of the wood volume, sweetgum heartwood is classified as very difficult to penetrate. In the sapwood, uninterrupted flow occurs between vessel elements, and thus along the vessel, through scalariform perforation plates. Perforation plates consist of a number of openings arranged parallel to one another separated by cell-wall material termed bars (Fig. 8). In the heartwood region, the perforation plate openings are completely obstructed by tyloses (Fig. 9). Ultra-thin sections revealed the growth of the tyloses around the bars and across the openings, thus completely blocking free liquid flow along the vessel (Fig. 10). Tyloses were for the most part confined to the vessel wall and only occasionally were they detected crossing the lumen. Thus, in addition to obstructing the perforation plates, the tyloses also block the pits leading from vessels to adjacent cells. Also, further hindrance to liquid flow results from the large amount of encrustations present on the heartwood intervessel pit membranes.

Pit-pairs interconnecting sapwood fibers possess a membrane with clearly visible microfibrils (Fig. 11). Although openings were not detectable in replica views, ultra-thin sections showed a rather thin membrane (Fig. 13). However, in the heartwood region the encrustations deposited on the pit membranes are so heavy that the microfibrils are obscured (compare Figs. 11 and 12), and a substantial increase in pit membrane thickness is apparent (Fig. 14).

Thus structural alterations, which occur as sweetgum heartwood is formed, obstruct the liquid flow paths and are responsible for the extreme resistance to liquid penetration.

Blackgum

Although extractives are also deposited in the heartwood of blackgum, the amount is such that complete blockage of the flow path does not occur. Figures 15 and 16 depict scalariform perforation plates with depositions which only partially block the openings. This material, the identity of which is not known, was also found in the vicinity of intervessel pits partly obstructing the pit apertures, canals, and chambers. The interfiber pits contained relatively thick membranes without detectable openings and many fibers contained depositions along the lumen wall.

Since vessels constitute about one-half of the total volume and lack tyloses or depositions that completely block the liquid flow pathways, the wood is easily penetrated with liquids.

CONCLUSIONS

The minor role played by vessels in liquid penetration of hickory was found to be due to the deposition of gum and formation of tyloses, which obstructed the liquid flow path. In addition, the fact that all vessels were completely surrounded by parenchyma therefore were not in direct communication with longitudinal fiber elements also limited their conduction function. This is especially true in hickory since substantial liquid flow occurs along the fibers because of the presence of thin, nonincrusted fiber-to-fiber pit membranes.

The high resistance to liquid penetrability of sweetgum heartwood was the result of thick and heavily incrusted interfiber pit membranes and tyloses which block both perforation plates and intervessel pits.

Although the blackgum heartwood contained encrustations, they did not completely block the perforation plates or pits. This and the absence of tyloses allow the heartwood vessels to play a major role in conduction, thus permitting easy liquid penetration of the wood.

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