# ULTRASTRUCTURAL CHARACTERISTICS OF MATURE WOOD OF SOUTHERN RED OAK (*QUERCUS FALCATA* MICHX.) AND WHITE OAK (*QUERCUS ALBA* L.)

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## ABSTRACT

The fine structure of mature wood of white oak and southern red oak was studied using ultrathin sections and direct carbon replicas. In most details, the fine structure of the wood of these two species is similar. Differences detected include a slightly coarser appearance of intertracheary pit membranes and fewer vessel-ray parenchyma pit contacts in southern red oak. Intervessel pitting was not found in either species, implying that flow between vessels occurs via vasicentric tracheids as vessel-vasicentric tracheid and vasicentric tracheid-vasicentric tracheid pitting is abundant. The appearance of the pit membranes differs in pits interconnecting different types of cells, e.g. vessel-vasicentric tracheid pit membranes were thicker than vasicentric tracheid-vasicentric tracheid pit membranes. Differences in the orientation of the pit aperture in the bordered pits of various cell types appeared to correlate with differing $S_2$ orientations. Vessel-vasicentric tracheid and vasicentric tracheid-vasicentric tracheid pit membranes in the outer conducting sapwood and inner nonconducting sapwood appeared similar with randomly arranged microfibrils and no visible openings. In the outer and inner heartwood, these membranes were coated and infiltrated by extractives. The low permeability of multiseriate rays compared with uniseriate rays may be accounted for by the scarcity of lateral wall pitting and direct vessel-ray parenchyma cell contact in the interior of the multiseriate ray.

*Keywords:* Oak, wood anatomy, pit membranes, ultrastructure.

## INTRODUCTION

More than a decade ago, Schmid (1965) commented that pit ultrastructure in hardwoods had received considerably less attention than pit ultrastructure in softwoods, and she attributed this difference to the greater complexity of hardwood anatomy. This statement still applies to ultrastructural studies of hardwoods, as fewer than ten species of hardwoods have been examined in any detail with the transmission electron microscope. Most studies of hardwood ultrastructure have examined details of a single feature, such as intervessel pitting (Bonner and Thomas 1972), tyloses development (Meyer 1967a, 1967b), or characteristics of parenchyma cells (Fengel 1966a) and have used either ultrathin sections (Fengel 1966a), or direct carbon replicas (Bonner and Thomas 1972), but not both. Much valuable information has accrued from these investigations, but additional information on hardwood ultrastructure is still needed.

This paper describes the ultrastructure of wood of southern red oak, *Quercus falcata* Michx., and white oak, *Quercus alba* L., as seen in both ultrathin sections and direct carbon replicas. Although the emphasis of this paper is on those details observable with the transmission electron microscope, these observations are complemented by ones made with the light microscope. The wood of these two oak species was examined as part of a continuing study whose purpose is to characterize the ultrastructure of nine southeastern United States hardwoods,

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and when possible, to relate their anatomy to their physical properties. In the first phase of this study, Thomas (1976) described those features that account for the differing heartwood penetrability of mockernut hickory (*Carya tomentosa* Nutt.), blackgum (*Nyssa sylvatica* Marsh.), and sweetgum (*Liquidambar styraciflua* L.).

Oak wood is of considerable commercial value, yet a comprehensive description of the ultrastructure of any one of the numerous oak species is not available. Meyer (1967a), coincidental to a study of tyloses formation in white oak (*Q. alba*), and Murmanis (1976), as part of a study of the protective layer in northern red oak (*Q. rubra*), described some additional ultrastructural features of those species. To our knowledge, southern red oak anatomy has not previously been examined with the transmission electron microscope.

Williams (1939, 1942a, 1942b) and Panshin and deZeeuw (1980) described the light microscope anatomy of the oaks native to the United States and the features useful in distinguishing the wood of the red and white oaks. Both species have ring-porous wood that has vessel elements with simple perforation plates; vasicentric tracheids characterized by an irregular shape and abundant pitting on both radial and tangential walls; fibers with infrequent small bordered pits that are more common on the radial walls; longitudinal parenchyma that is in narrow, short apotracheal bands as well as in contact with vessels; and rays of two distinct sizes, a single cell or many cells wide.

According to Huber (1935) and Braun (1970), water conduction in the ring-porous European oaks takes place in the vessels and vasicentric tracheids in the outermost growth ring and portions of the preceding year's growth ring. The anatomy of the ring-porous American oaks is similar to the anatomy of the ring-porous European oaks, and so it is likely that water conduction in the American oaks also occurs in the outermost rings (Zimmermann and Brown 1971).

Cell-wall organization and pit structure in the various cell types of oak were examined in this study. As pits are important in liquid movement in wood, particular attention was paid to their structure. The surface appearance of the pit membranes in conducting and nonconducting sapwood of southern red oak and white oak was compared. The appearance of the pit membranes in the sapwood and heartwood was also compared. Although the heartwood of very few species has been examined to determine radial variation in extractive content and durability, the generalization has been made that heartwood extractive content and durability decrease from the pith to the bark. In this study, we examined the surface appearance of pit membranes in inner and outer heartwood to see if there was any difference in the appearance of extractive deposits in these two regions.

## MATERIALS AND METHODS

Wood samples were cut at diameter breast height from mature trees of southern red oak (*Quercus falcata* Michx.) and white oak (*Quercus alba* L.). Direct carbon replicas (Côté et al. 1964) of tangential and radial surfaces of the outermost two growth rings, the growth ring two rings out from the sapwood-heartwood boundary, heartwood just to the inside of the sapwood-heartwood boundary and inner heartwood approximately one inch from the pith were prepared from air-dried wood.

Ultrathin sections of the outermost growth rings and inner heartwood were cut from both never-dried or air-dried wood embedded in a mixture of n-butyl and metyl-metacrylate (75:25). These sections were shadowed with platinum at an angle of approximately 20° in a high vacuum evaporator.

Cross-sections of both species stained with safranin were examined with the light microscope.

## RESULTS AND DISCUSSION

### *Vessels and vasicentric tracheids*

Despite intensive searching using the light microscope, intervessel pitting was not observed in samples cut for this study or in twelve different herbarium-vouchered samples from the wood collection housed at North Carolina State University. Ultrathin sections of regions where earlywood vessels appeared contiguous as viewed with the dissecting microscope did not reveal intervessel pitting. Examination with the transmission electron microscope showed that there were no pits in what appeared to be a common wall or there was an intervening vasicentric tracheid or longitudinal parenchyma cell. Metcalfe and Chalk (1950) and Williams (1942a) have indicated that intervessel pitting in oak is exceedingly rare because of the solitary vessels and they did not present direct evidence of the existence of intervessel pits.

Vessels consist of a series of vessel elements stacked one on top of the other, and they are of finite length. Earlywood vessels of ring-porous woods such as oak are long (Huber 1935; Zimmermann and Brown 1971); in northern red oak (*Quercus rubra* L.) vessels up to eight meters long have been found (Zimmermann 1968); vessels practically never end in isolation. Overlapping ends of individual vessels provide, through bordered pit pairs, for the passage of water laterally from one vessel to a continuing vessel.

There are two possible explanations for this apparent absence of intervessel pitting in white oak and southern red oak. It is possible that there are no areas of vessel overlap and consequently, no intervessel pitting. Flow between nearby vessels could occur via vasicentric tracheids as pitting between vessels and vasicentric tracheids is abundant. Alternatively, the great length of the solitary earlywood vessels of oak results in few areas of vessel overlap. Therefore, the probability of making a section at the site of intervessel pitting is small.

In replicas, the different types of pits on the vessel walls can be readily distinguished as they have different shapes. Vessel-vasicentric tracheid pits are round in outline; vessel-longitudinal parenchyma pits are smaller than vessel-tracheid pits and not as rounded in outline; vessel-ray parenchyma pits are distinctive as they are elongated and irregular in outline; vessel-fiber pits, if they exist at all, are apparently extremely rare, as vessels are rarely adjacent to fibers (Williams 1942b).

Vasicentric tracheids have numerous pits. In replicas, it is difficult to determine what type of cell the vasicentric tracheid pits interconnect with unless a pit membrane is torn away to reveal the pit border in the contiguous cell. The long axis of the bordered pit aperture in a vessel element is nearly perpendicular to the longitudinal wall, while the long axis of the bordered pit aperture in a vasicentric tracheid is inclined 20°–35° from the longitudinal wall.

In both species, the surface appearance of vessel-vasicentric tracheids and vasicentric tracheid-vasicentric tracheid pit membranes is similar. Pit membranes from the earlywood and latewood of the outermost growth rings exhibit distinct microfibrils that are randomly arranged and lack visible openings. Their appearance in the inner nonconducting sapwood is similar. The texture of the southern red oak pit membranes (Fig. 1) in all regions of the sapwood is slightly coarser than that of the white oak (Fig. 2).

The intervessel pit membranes in hardwoods, at least in the early stages of differentiation, consist of the middle lamella and the primary walls of adjacent cells. Schmid and Machado (1968) have detected layering in the pit membranes of some woods of the Leguminosae in both sections and direct carbon replicas. Figure 3 shows a split vessel-vasicentric tracheid pit membrane from the outermost growth ring of red oak with an "amorphous layer" under the layer of distinct microfibrils; Schmid and Machado (1968) also observed an amorphous layer.

The pit membranes in both the outer and inner heartwood are heavily encrusted with extractives; either the microfibrils look quite coarse-textured or are completely obscured by a coating of extractives (Fig. 4). At times, these deposits have a disk-like appearance and give the impression there has been infilling of the pit chamber (Fig. 5). Apparently, no significant differences in the surface appearance of pit membranes from the outer and inner heartwood exist.

Ultrathin sections show some variation in the appearance of the pit membrane. In the earlywood of the outermost ring, both the vessel-vasicentric tracheid and vasicentric tracheid-vasicentric tracheid pit membranes are loose-textured (Fig. 6). The membranes in the preceding year's wood generally appear not as loose-textured (Fig. 7). In most of the sections, the vessel-vasicentric tracheid pit membranes are thicker than the vasicentric tracheid-vasicentric tracheid pit membranes (Figs. 6, 7). In heartwood, pit membranes no longer have any signs of porosity, there is no obvious difference in electron density and texture between them and the compound middle lamella, and they appear to be permeated with extractives. The coating of extractives on the pit membranes appears continuous with the coating on the pit border and cell wall (Fig. 8).

Yang (1978) reported a difference between the structure of earlywood and latewood intervessel pit membranes of birch, a diffuse-porous wood; the latewood vessel elements had distinctly denser pit membranes. We found no such difference between earlywood and latewood pit membranes in conducting cells of white oak and southern red oak, although there is a pronounced difference in earlywood and latewood vessel element morphology in ring-porous woods such as oak. The earlywood intervessel pit membranes figured in Yang's paper are from the sapwood; the latewood intervessel pit membranes figured are from the heartwood. Thus, it is unclear whether the difference in density of earlywood and latewood intervessel pit membranes in birch that Yang reported is based on a comparison of membranes from the same region of the tree.

### *Half-bordered pits*

Pits connecting vessels to parenchyma also occur. The details of vessel-ray parenchyma pits and the role of the protective layer in tyloses formation in white oak have been studied previously (Meyer 1967a, 1967b; Meyer and Côté 1968). The features we observed match those reported earlier, the membrane of half-

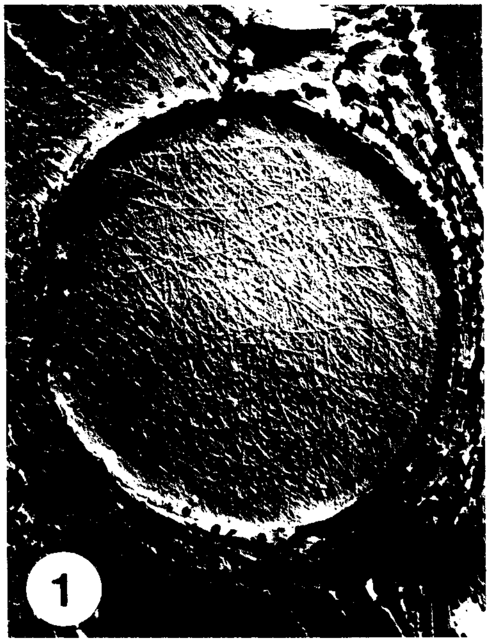
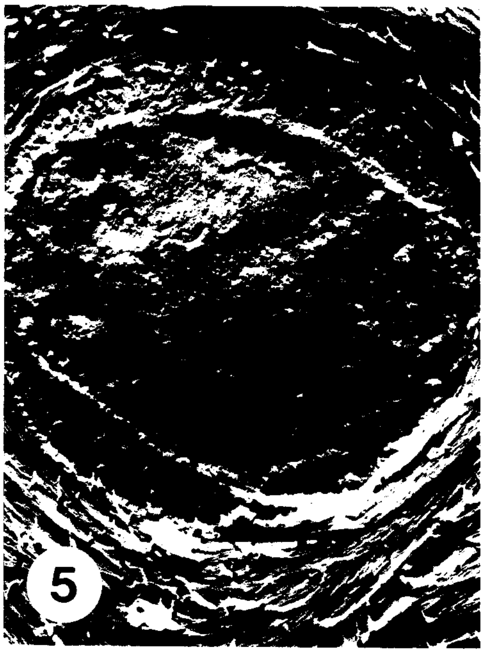


FIG. 1. Typical vessel-vasicentric tracheid pit membrane found in outer sapwood of southern red oak. 9,000×.

FIG. 2. Vasicentric tracheid pit membrane in the outer sapwood of white oak. 13,000×.

FIG. 3. Layering in a vessel-vasicentric tracheid pit membrane in the outer sapwood of southern red oak. 16,000×.

FIG. 4. Vasicentric pit membrane with extractives obscuring the microfibrils, inner heartwood of southern red oak. 12,500×.



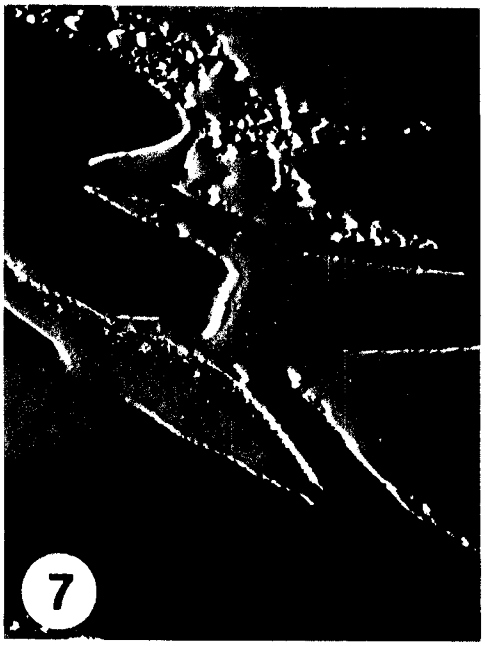


FIG. 5. A heavily incrusted vessel-vasicentric tracheid from the inner heartwood of southern red oak. 13,000×.

FIG. 6. Cross-section of the outermost ring of white oak showing a vessel (V)-vasicentric tracheid (T) pit, a vasicentric tracheid-vasicentric tracheid pit, and a vasicentric tracheid-longitudinal parenchyma (P) pit. 7,700×.

FIG. 7. Pits between a vessel (V) and a vasicentric tracheid (T) and between two vasicentric tracheids in the second sapwood ring of white oak. 7,700×.

FIG. 8. Vasicentric tracheid-vasicentric tracheid pit-pair from the heartwood of southern red oak. 12,900×.

bordered pits being relatively thick without any visible openings and with a supplementary protective layer on the parenchyma side of these pits (Fig. 6). Murmanis (1976) described the structure and formation of the protective layer in northern red oak (*Quercus rubra* L.). According to her work, the protective layer is present only in parenchyma cells that form pit-pairs with vessel members and fibers. In white oak and southern red oak, well-developed protective layers also occur in parenchyma cells that form pit-pairs with vasicentric tracheids. Figure 9 shows, from the lumen side of a vessel element, a vessel-ray parenchyma pit membrane in southern red oak; microfibrils cannot be discerned and what may be the beginning of tyloses formation or gum deposition is visible in the lower half of the micrograph. Note that the layer obscuring the microfibrils in this membrane also covers the vessel wall. Figure 10 is also a radial view of a vessel-ray parenchyma pit membrane in southern red oak; however, the wood was treated with sodium chlorite prior to replication and microfibrils are now obvious in the pit membrane and the vessel element wall.

Tyloses generally are abundant in the earlywood vessels of white oak heartwood and rare in the earlywood vessels of red oak heartwood (Williams 1942a; Panshin and deZeeuw 1980). The difference in the abundance of tyloses formation between the groups may very likely be related to physiological differences that would not be reflected in the mature wood structure. However, when preparing samples for ultrathin sections, fewer vessel-ray parenchyma contacts were observed in the earlywood of southern red oak than in the earlywood of white oak. Subsequent light microscopic examination of cross sections revealed that southern red oak has a lower percentage of earlywood vessels with ray contact than white oak (9% compared to 16%). Red oak also has a lower percentage of earlywood vessels with ray contact on both sides than white oak (23% compared to 44%). Although direct evidence for attributing the more common occurrence of tyloses in white oak to the larger number of vessel-ray parenchyma contacts is lacking, the correlation between these features seems noteworthy.

No one has noted any differences between the structure of the protective layer adjacent to earlywood and latewood vessels of oaks. However, in white oak the latewood vessels rarely have tyloses, while the earlywood vessels commonly do (Williams 1942a). Tyloses are believed to be the result of gas embolism (Klein 1923; Zimmermann and Brown 1971), and embolisms are much more likely to occur in large diameter vessels. Perhaps the small diameter latewood vessels of white oak remain water-filled and so do not develop tyloses. Also, the greater frequency of tyloses in latewood vessels of red oak as compared to white oak (Williams 1942a) may be related to their larger diameter.

### *Fibers*

Oaks are reported to have both libriform fibers with simple pits and fiber tracheids with bordered pits, but all fibrous elements have bordered pits when viewed with the electron microscope. Fiber pits are smaller and less numerous than vasicentric pits. The interior of the fiber pit border has a coarse texture and the long axis of the slit-like apertures is more vertically oriented (approximately 20° from the longitudinal wall) than in the vasicentric tracheids, presumably correlating with a steeper $S_2$ microfibril angle in fibers. Only a small number of intact pit membranes were found in fibers. In the sapwood, these membranes appear

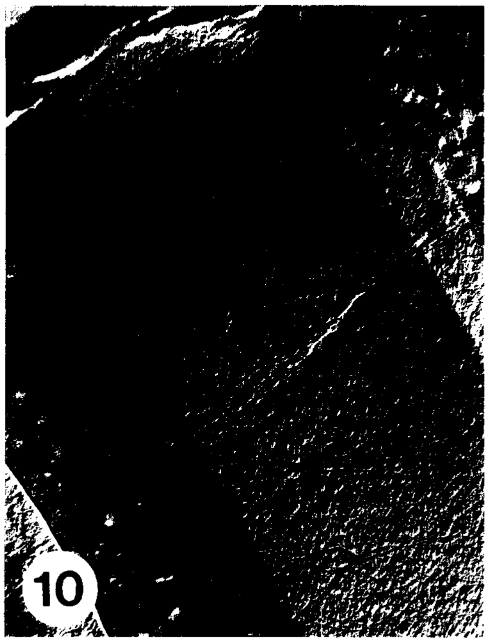


FIG. 9. Vessel-ray parenchyma pit as viewed from the lumen side of the vessel element, southern red oak. 15,500×.

FIG. 10. Sodium chlorite treated southern red oak wood. This treatment makes apparent the difference in texture of the vessel-ray parenchyma pit membrane and the vessel wall, southern red oak. 10,300×.

FIG. 11. Pit membrane in a fiber of southern red oak sapwood. 11,000×.

FIG. 12. Tangential section of southern red oak sapwood showing simple pit-pairs between ray parenchyma (R) and longitudinal parenchyma (L). 9,700×.

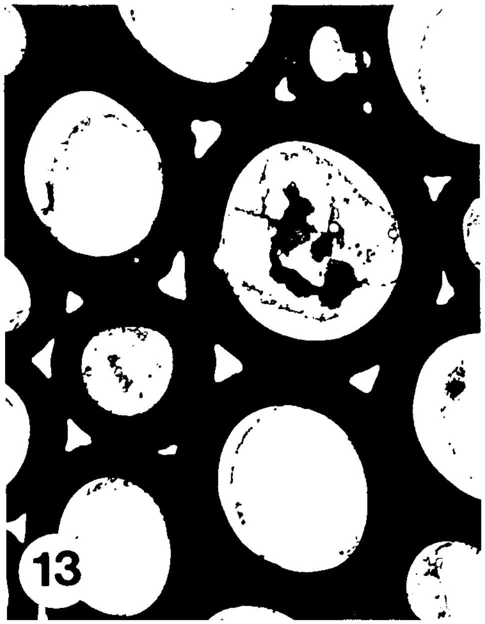


FIG. 13. Interior cells of a multiseriate ray of white oak sapwood. Note the numerous intercellular spaces and scarcity of interparenchymatous pits. 1,700×.

FIG. 14. Intercellular space (I) and two "blind" pits in a ray in southern red oak sapwood. 18,000×.

FIG. 15. Cross-sectional view of vasicentric tracheid (T)-fiber (F) and vasicentric tracheid-vasicentric tracheid pit-pairs in southern red oak heartwood. The $S_1$ (1) does not form a major part of the pit border. 11,800×.

relatively thick and nonporous with large amounts of amorphous materials between the microfibrils (Fig. 11); in the heartwood, the membranes are even coarser textured and appear to have a coating of extractives. The difference between the surface texture of sapwood and heartwood pit membranes is not as pronounced in fibers as it is in vessels and vasicentric tracheids.

### *Parenchyma*

Both southern red oak and white oak have rays of two distinct sizes and considerable longitudinal parenchyma. According to Myer (1922), the average ray volume of white oak is 27.9%; he did not give a figure for the ray volume of southern red oak, but in other red oak wood it exceeds 20%.

Simple pit-pairs occur between contiguous parenchyma cells. The membranes in these pits have the same thickness and electron density as the compound middle lamella, but are traversed by channels where plasmodesmata existed (arrows in Fig. 12); these channels are also detectable in surface views of parenchyma-parenchyma pits.

Ray parenchyma-ray parenchyma pit-pairs are common in the end walls (walls in the tangential plane) and rare in the lateral walls. This is particularly evident in the interior of large multiseriate rays (Fig. 13). Côté (1963) stated that the uniseriate rays of oak are more permeable than the broad rays and Behr et al. (1969) microscopically examined pressure-treated red oak heartwood and found oil common in the uniseriate ray cells, but rare in the multiseriate ray cells. These results correlate with the anatomy of oak. The cells of the uniseriate rays of oak have more direct contact with the vessels and other longitudinal elements than the bulk of the cells in the multiseriate rays and so uniseriate rays would be expected to be more permeable.

Intercellular spaces are frequently associated with both longitudinal and ray parenchyma cells. Pits between the ray cells and intercellular spaces occur (Fig. 14). An obvious protective layer is not developed in the parenchyma cells that formed these blind-pits, although Schmid (1965) stated that protective layers were formed in the vicinity of blind-pits to intercellular spaces. The primary wall of the parenchyma cell is obvious in these regions and what appear to be cytoplasmic debris and gums are generally present in the pit canal (Fig. 14). However, the appearance of these extraneous substances does not appear significantly different from those present in the vicinity of simple pit-pairs between parenchyma cells or adjacent to the cell wall (compare Figs. 12 and 14). The function suggested for the protective layer is that of protecting the contents of living parenchyma cells from the deleterious environment of contiguous dead cells. The protective layer develops after the contiguous cell dies (Schmid 1965; Murmanis 1976). Bolton et al. (1975), in their review of literature on interstitial spaces, point out that most authors assume the interstitial space system in wood serves as a gas canal system for respiring tissues. If this assumption is true, we suggest that the intercellular space system could not be considered a deleterious environment and a "protective layer" would be unnecessary.

### *Correlations of anatomy with some physical properties*

Southern red oak was one of several species utilized by Behr et al. (1969) in studying the permeability of some woods to oil-borne preservatives. They found that vessels and vasicentric tracheids of southern red oak were easily treated, while longitudinal parenchyma was especially resistant to penetration. These results correlate with the structural features observed in southern red oak. Earlywood vessels are not clogged with tyloses and so offer an unimpeded pathway for liquid flow and vasicentric tracheids have many pits that interconnect with vessels and other vasicentric tracheids. Longitudinal parenchyma cells are short, and although longitudinal parenchyma-vessel or vasicentric pitting occurs, it is not common and the pit membranes of these pit-pairs are relatively thick.

As discussed in the section on parenchyma, the low penetrability of the multiseriate rays of oak relative to the uniseriate rays (Côté 1963; Behr et al. 1969) is probably attributable to the smaller number of pits per ray cell and the lack of direct vessel-ray parenchyma cell contact in the interior of the ray.

### *Cell-wall organization*

The inclination of the pit apertures in vessel elements, vasicentric tracheids, and fibers relative to the longitudinal axis is 90°, 20–35°, and 20° respectively. Longitudinal splits of vasicentric tracheid and fiber walls show that in these cells the inclination of the pit aperture follows the inclination of the $S_2$ microfibrils. Splits showing cell-wall layering in vessel element walls were rarely obtained and we were unable to detect a wall layer with the "typical" longitudinal $S_2$ microfibril orientation. The orientation of the pit apertures in vessel elements has been suggested to be the same as the $S_3$ microfibril orientation (Harada 1965, for beech; Côté in Panshin and deZeeuw 1980, for basswood). This would make the vessel element unique, as in other cell types the orientation of the aperture apparently parallels the $S_2$ microfibril orientation (Harada 1965). Although vessel elements are perforate, making them different from other cell types, it seems phylogenetically unlikely that they would differ in the construction of the pit border, a feature found in the other cell types. Where there are many pits in the cell wall as in oak vessel elements, the microfibril arrangement is complex, and interpretation of the microfibril orientation of the $S_1$, $S_2$, and $S_3$ is consequently difficult.

There is believed to be an inverse relationship between cell elongation and microfibril angle, i.e. the longer the cell, the smaller the $S_2$ microfibril angle (Panshin and deZeeuw 1980). Vasicentric tracheids are shorter than fibers, and the $S_2$ microfibril angle and angle of pit aperture alignment of the fibers are smaller. Vessel elements in oak are shorter than the other elements and the earlywood vessel elements are 50 to 125 $\mu$m shorter, on the average, than the latewood elements (Williams 1942b). During differentiation, vessel elements do not elongate much. This is especially true of the earlywood vessel elements of ring-porous woods which greatly increase their diameter during differentiation. Consequently, one could expect the $S_2$ microfibril angle of earlywood vessel elements to be relatively large. The orientation of the pit aperture in vessel elements may indicate a large $S_2$ angle, rather than reflect a parallel alignment with the $S_3$. Butterfield and Meylan (1973) generalized that the $S_2$ microfibrils in vessel elements are aligned at an angle of approximately 70–80°.

There may be a fundamental difference in the structure of pit borders in softwoods and hardwoods. Yang (1978) observed that the pit borders of birch fiber-tracheids and vessel elements lack the $S_1$ in the overarching portion of the pit border. There is still controversy over the construction of the conifer pit border, but some investigators, e.g. Harada and Côté (1967), suggest the $S_1$ is part of the border. In sections of oak (Fig. 15) and published micrographs of beech pits (Fengel 1966b; Harada 1963), the $S_1$ does not appear to form a significant portion of the pit border.

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