

Relationships between wood density (oven-dry weight/green volume) and various wood structure characteristics tested for the materials investigated. Linear regressions, correlation coefficients and standard errors of estimate.

Wood or fibre charact.	regression equatation	correla- tion coeffic.	standard error of estimate
p	$d_b=0.10253+0.05872 p$	0.844*	0.03835=10.4%
l	$d_b=0.69595-0.01134 l$	-0.634*	0.05590=15.2%
2p/l	$d_b=0.14073+0.71164 2p/l$	0.929*	0.02709= 7.4%
$V_f \times 2p/l$	$d_b=0.13028+0.01285 V_f \times 2p/l$	0.919*	0.02844= 7.7%
p,l	$d_b=0.36246+0.05088 p-0.00774 l$	0.945*	0.02437= 6.6%
2p/l, V_f	$d_b=0.16580+0.70262 2p/l-0.00038 V_f$	0.927*	0.02778= 7.6%
p, l, V_f	$d_b=0.28830+0.05003 p-0.00924 l+0.00208 V_f$	0.937*	0.02513= 6.8%

p=fibre-wall thickness; l=fibre width; 2p/l=ratio fibre-wall thickness to fibre radius (=relative wall thickness); V_f =percentage volume of fibres; d_b =wood density; * = level of significance 0.01.

BOOK REVIEW

LINDEMAN, J.C. and MENNEGA, A.M.W. : Bomenboek voor Suriname

Mededeling van het Botanish Museum en Herbarium, Rijksuniversiteit Utrecht No. 200. Edit. Kemink en Zoon, Utrecht 1963. 312 pages text, 16 pages photographs of trees, 96 plates and 96 photomicrographs.

This is a wonderful book. It includes 370 trees species, 120 of which are shown by excellent line-drawings of their leaves, flowers and fruit. Beautiful photographs of trees with a characteristic appearance are included. The wood of species used as timbers is fully described and explained by photomicrographs of cross-sections. - The description of the plants is arranged in alphabetical order of the families and of the genera within a family. Two dichotomous identification keys allow of finding the name of a given tree. These have been drawn up with the help of punched cards prepared by the authors. The first makes use of vegetative characters (leaves, twigs, bark) disregarding flowers and fruit used in floras. The second key is based on the anatomy of the wood as disclosed by a hand-lens. A taxonomic survey of the families involved indicates not only the numbers of the described genera and tree species, but also includes the numbers of all the other woody plants (shrubs and vines) in Surinam. A bibliography and alphabetical lists of the scientific and local tree names conclude the book. - In a way it is a pity that this standard monograph is written in the Dutch language. For scientists who master this language it possesses a special flavour and excites admiration for the Dutch scientific achievements in the East Indies. The unfamiliarity of many Anglo-Saxons with continental languages may, however, prevent this valuable "Book of Trees in Surinam" from obtaining the international recognition it so highly deserves. Fortunately there are short introductions in English and Spanish which explain the use of the identification keys, and the Dutch terms involved are illustrated by line-drawings.

F.W.

News Bulletin

ZÜRICH 1964/2

Editor: A. Frey-Wyssling, Secretary-Treasurer

N. K. K.

EDITORIAL

Applied Wood Anatomy

Wood anatomy is not only a pure science, but it covers also numerous fields of applied branches in botany, forestry and technology. The main concern of the botanist centres on compared anatomy, phylogeny, systematics and taxonomy of woody plants, as well as on ontogeny, differentiation and physiology of secondary tissues. The theoretical knowledge gathered may be used for wood identification and tree-ring research (cf. News Bulletin 1960/1, p. 11), the activity of the wood anatomists shifting over to the application of their science to problems of archeology, quaternary geology, ecology, technology etc.

Among the foresters whose task is to produce wood, the anatomist is even more involved in applied problems. In tree physiology, wood and phloem formation are investigated with the aim of elucidating and enhancing cambial growth, and in ecology, studies on the phenotypical fluctuations of the width in growth rings serve the same purpose.

The technologist finally considers wood as a raw material, the application of which has to be improved, so that practical views predominate for its anatomy. On the other hand, if the properties of different pulps are compared, fibre qualities considered or if the relation of anatomical pattern to the technical behaviour of various wood species is elucidated, there is a genuine scientific interest as well. In such cases it is difficult to decide which wood anatomist performs essentially basic research, which practices creative application and which is merely bound to routine work, because there are sliding boundaries between these different activities in wood anatomy.

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Under the article "Membership" our constitution reads: "Members shall be scientists who are actively engaged in the study of wood anatomy". Based on this definition, a motion was presented to our general meeting in Edinburgh aiming at creating a special type of membership for candidates who have not published papers on wood anatomy. This would mean that many foresters and technologists who have a keen interest in the application of anatomy for wood identification, wood testing and wood pulping could not be admitted to our Association as full members. This question has been amply discussed by the plenary session, which then un-animously voted against such a restriction. The Council was invited to stipulate an admission scheme more liberal than our constitution indicates when it will be revised in the near future. Your Secretary-Treasurer welcomes this proposal, because it seems to be the only possibility to improve our financial situation. It certainly must be considered unsatisfactory that, after ten years of economising, the Association could pay only for 35 % of the expenses of our "Multilingual Glossary of Terms used in Wood Anatomy", whilst for 65 %, i.e. sfrs. 7000.--, we had to go begging money from other institutions.

The plenary session also voted for an improvement of our News Bulletin in the direction of a real scientific periodical comparable to the vanished "Tropical Woods"; but only an Association with a sufficiently large membership can handle such an assignment. As our general meeting in Edinburgh was attended by a relatively restricted number of members, I request any colleague who has constructive ideas concerning the problems mentioned here to write to the Secretary-Treasurer.

A. Frey-Wyssling

ULTRASTRUCTURE OF TYLOSES AND A THEORY OF THEIR GROWTH MECHANISM*

by Zoltán Kórán and Wilfred A. Côté, Jr.

Manuscript received on August 1964

A. A theory of the mechanism of tylosis growth

The development, structure and composition of tyloses have been of interest to physiologists, anatomists and chemists for many decades. The references listed have been selected from among a large number to illustrate the range and diversity of interests in these fascinating structures (1-13). There have been suggestions or implications that the development of a tylosis originates entirely from protoplasmic material of ray or longitudinal parenchyma adjoining prosenchyma (1,5,6,7,13). However, the more widely accepted theory has been that the membrane of the half-bordered pit pair is ballooned or stretched into the vessel by pressure in the parenchyma cell and becomes the limiting wall of the mature tylosis. The probability of localized growth of the pit membrane on the parenchyma side has been put forth (3,5) and growth by intussusception suggested (13).

Although tylosis buds arising from ray parenchyma cells and bulging into vessels have been shown in photomicrographs by a number of investigators (2,3,5,8), the details of the pit membrane stretched or arched into the vessel segment have never been resolved well enough to be convincing evidence. The sac-like growths shown in drawings also fall short of providing clear proof of the true nature of a tylosis.

In this study, electron microscopy was employed to overcome this shortcoming. Though many hundreds of serial sections, 1/40th micron in thickness, were prepared and examined in the electron microscope, in no case was a pit membrane ever observed to arch into a vessel as a tylosis. It would seem unlikely that such a situation could be found since a pit membrane, lignified on one side, would need to undergo much stretching or a large amount of

* This study was made possible by a grant from the U.S. National Science Foundation (GB-1050).

surface growth. Actual measurements and subsequent calculations indicate that a pit membrane in black locust, *Robinia pseudoacacia* L., with an average diameter of 7.8 microns would have to stretch at least 400 times its original surface area and at the same time increase 3.7 times its normal thickness (0.17 μ average) to form a spherical tylosis measuring 78 microns in diameter.

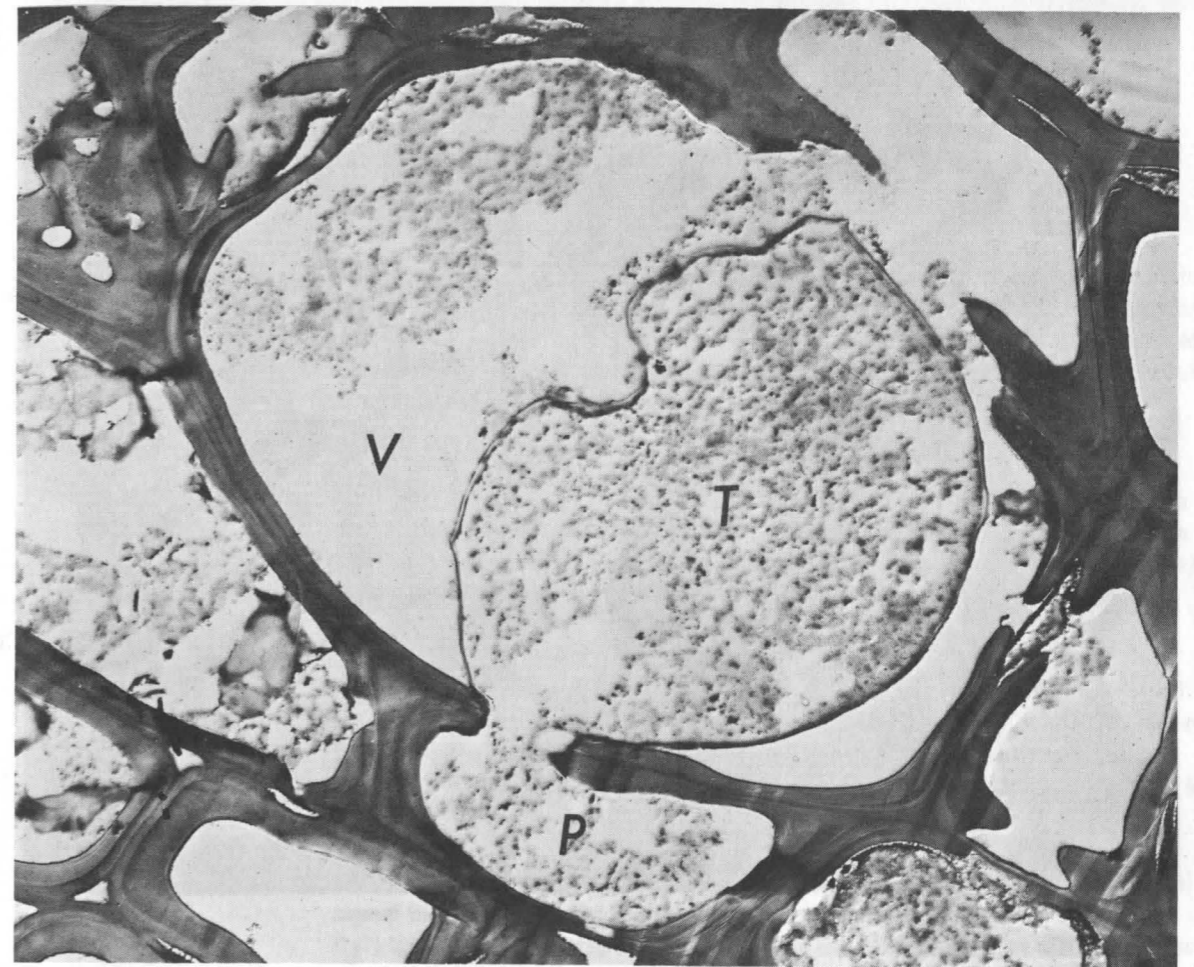
The mechanism of tylosis formation was studied on the basis of artificially induced growth in black locust, white oak, *Quercus alba* L., and osage-orange, *Maclura pomifera* (Raf.) Schneid., sapwood with the hope of observing a tylosis in its early and later stages of development. The study yielded no evidence of ballooned pit membranes, but considerable other evidence on tylosis formation and structure was found.

Briefly, sections of living trees were cut, placed under what is believed to be suitable growth conditions, and the development of tyloses was studied periodically by means of light and electron microscopy. A brief summary of this procedure is presented below.

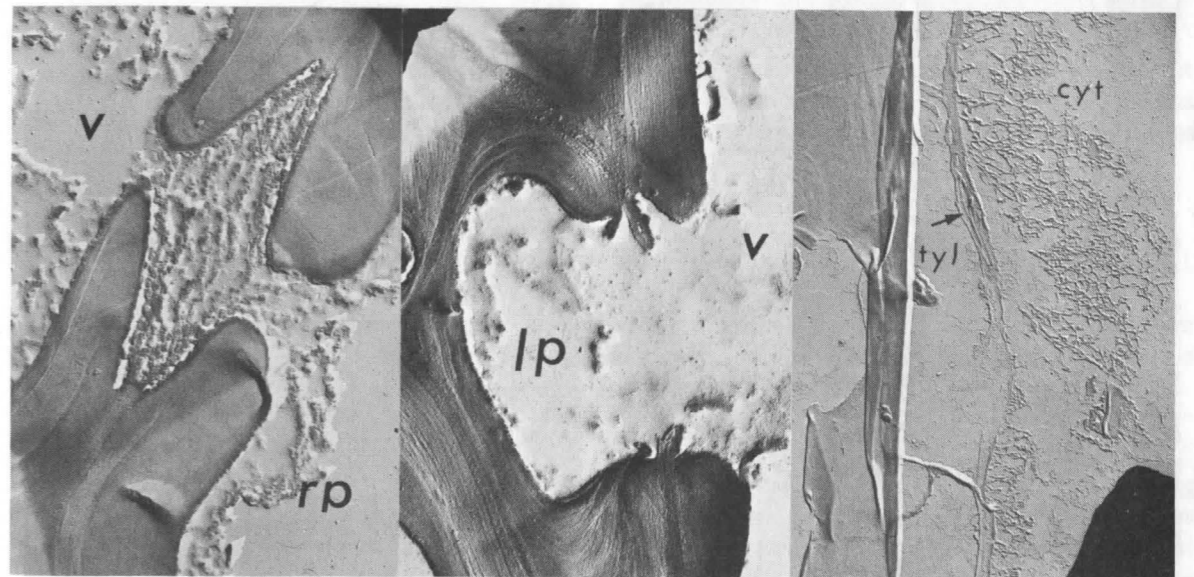
After a tree is felled and a section is taken of it, the negative pressure in the conducting vessels, e.g. in vessel V of Figure 1, is changed to a value approaching atmospheric pressure. This instantaneous relief of the negative pressure within the water column of vessel V causes a decrease in its diffusion pressure deficit. The latter in turn, perhaps with some action of auxin induced by wounding, is believed to cause an intense osmosis of water from vessel V into parenchyma cell P through the membrane of the half-bordered pit-pair. As the osmotic pressure increases in the parenchyma cell, as a result of water influx and increased protoplasmic activity, the protoplasm is believed to be forced against the pit membrane which in turn may be stretched, softened, loosened (Fig. 2), partially dissolved, ruptured, or completely disintegrated (Fig. 3) by some dissolving action of the protoplasm. After the pit membrane is ruptured, part of the protoplasm contained in parenchyma cell P, but still enclosed by the ectoplasmic membrane, bulges into vessel V, through the newly developed rupture, whereby it is inflated into a spherical bud.

In many cases, however, the pathway for protoplasmic transfer could not be readily traced to a visible rupture in the pit membrane. An example of this can be seen in Figure 5. While there are a number of protoplasmic buds lying on the vessel side of the half-bordered pit-pairs, the pathways through which protoplasmic transfer occurred are not clear due to the level of cut through

¹ For a more detailed discussion, reference is made to the original work (Kórán, 1964).



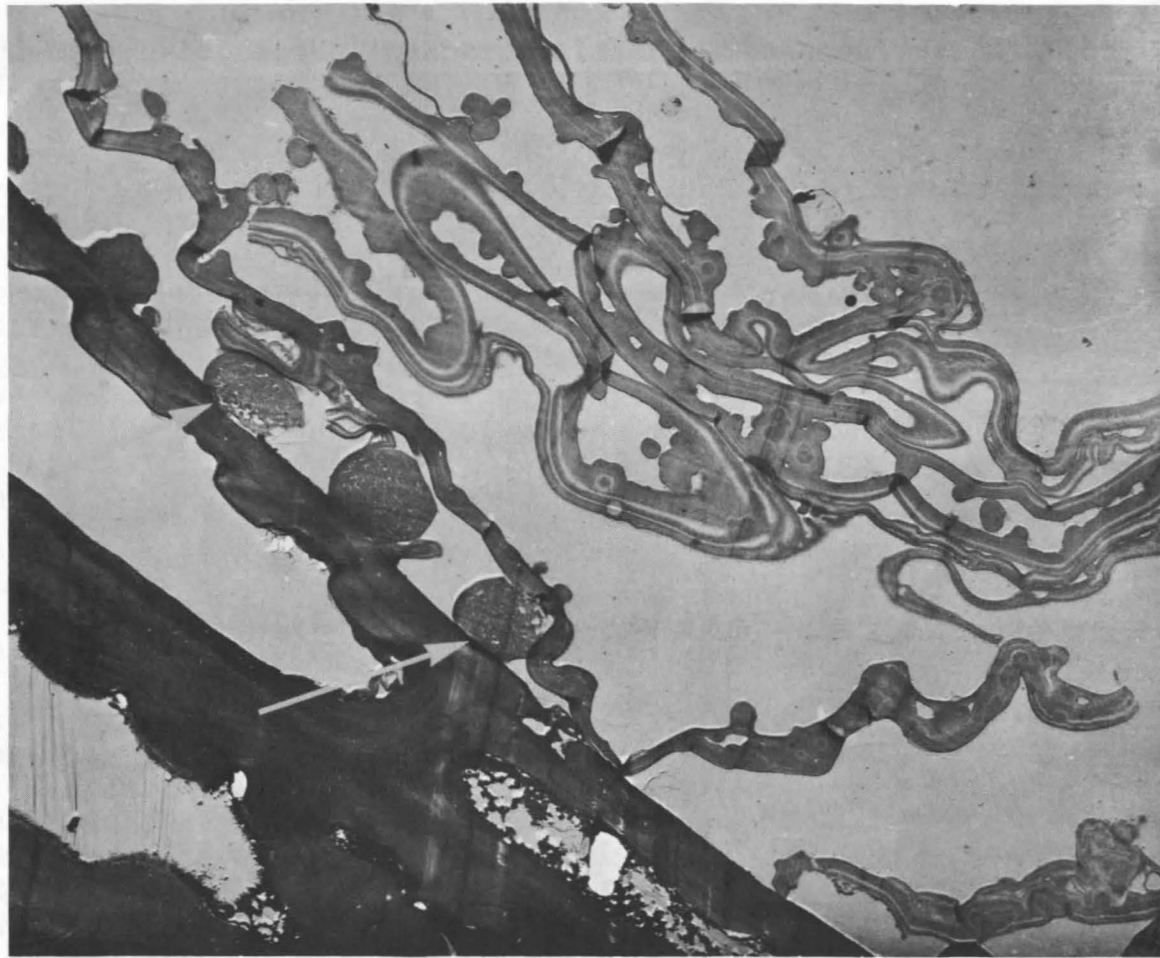
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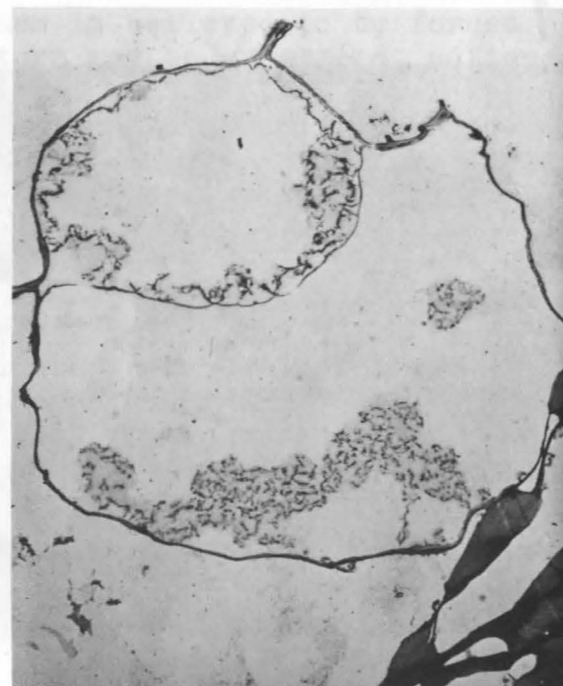
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- Figure 1. A cross-section of white oak (*Quercus alba* L.) sapwood. The electron micrograph shows that the 54-hour old tylosis, developing in summerwood vessel V, originates from longitudinal parenchyma cell P. The once-existing pit membrane between P and V is believed to have disintegrated under the dissolving action of the turgescent protoplasm of parenchyma cell P prior to the bulging of protoplasmic material. Specimen freeze-dried before embedding. 3200x.
- Figure 2. A pit pair separating a summerwood vessel segment (v) and a ray parenchyma cell (rp) in white oak (*Quercus alba* L.) sapwood. The pit membrane became swollen during methylmethacrylate embedding which indicates its unstable and weak structure. This initial weakening is believed to be due to a dissolving action of the adjacent protoplasm. Cr shadowed. 7500x.
- Figure 3. A portion of a springwood vessel segment (v) adjacent to a longitudinal parenchyma cell (lp) in white oak (*Quercus alba* L.) sapwood. It is believed that the membrane of the half-bordered pit-pair was ruptured under the combined action of protoplasmic dissolving and osmotic stretching of the turgescent protoplast contained in the parenchyma cell. Cr shadowed. 6400x.
- Figure 4. A portion of a developing tylosis wall with protoplasmic material in a springwood vessel segment of black locust (*Robinia pseudoacacia* L.) sapwood. The developing tylosis wall (tyl) appears to be an integral part of the cytoplasm. It appears to be a stage of deposition of wall building units by the cytoplasm (cyt) into the inner surface of this developing tylosis wall in forms of thin lamellae. Cr shadowed. 3800x.
- Figure 5. Tyloses displaying highly irregular shapes and structures in a springwood vessel segment of white ash (*Fraxinus americana* L.). The round structures lying on the inner vessel wall (arrows) are believed to be tylosic buds, possible centers of tylosis growth. Cr shadowed. 3700x.
- Figure 6. A 28-hour old tylosis bud in a springwood vessel of black locust (*Robinia pseudoacacia* L.) sapwood. The tylosis wall (tyl) in this early stage of development is very thin. It probably represents the initial form of a developing primary wall. Contents of the tylosis bud include starch (light density, round structures) and protoplasmic material. Fixed in osmium tetroxide, methacrylate matrix removed. 1600x.
- Figure 7. A 54-hour old tylosis in a springwood vessel segment of black locust (*Robinia pseudoacacia* L.) sapwood. The protoplasm lying loosely on the inner surface of the smaller tylosis bud was probably in closer contact with the inner tylosis wall when alive and active. The tylosis bud has little remaining protoplasmic content, but possesses a well-differentiated tylosis wall. Specimens freeze-dried. 1600x.

the pit. Plasmodesmic openings observed in the pit membranes of ray parenchyma cells could be a possible pathway, but these are extremely small. Other possibilities may include the passage of protoplasmic material through small perforations in the pit membrane, or its diffusion through the fibrillar meshwork of the pit membrane after its partial dissolution. The former was evidently implied in the 1933 version of the International Association of Wood Anatomists' "Glossary of terms used in describing woods" (1). The latter would appear possible if the openings created were large enough to allow the protoplasmic organelles to move through the membrane.

Tylosis growth is believed to start at the time the protoplasm enters the vessel and halts upon the death of the protoplast of the tylosis. This period can arbitrarily be divided into two phases, the phase of dimensional enlargement, and the phase of wall thickening. The former includes all activities starting from the time the protoplasmic material enters a vessel to the point when the tylosis has reached its mature size, while the latter consists of secondary thickening.

After part of the protoplasm of a parenchyma cell enters an adjacent vessel, it is inflated into a spherical bud, most probably under the mutual action of osmotic pressure and turgor pressure. These spherical buds are then transformed into tyloses by protoplasmic growth. In tylosis growth, the development of tylosis wall, the differentiation of intertylosic pit fields, the rate of tylosis growth and the change in protoplasmic content are important considerations.

Figure 6 shows a tylosis in its early stage of development. The tylosis wall appears very thin which probably represents the initial form of a developing "middle lamella" and a primary wall. On the other hand, the 54-hour-old tyloses of Figures 1 and 7 possess well-differentiated tylosis walls. The actual development of a tylosis wall can best be explained on the basis of Figure 4. The electron micrograph suggests that the wall of the 150-hour-old tylosis is not only in contact with the cytoplasm, but appears to be an integral part of it. In fact, the entire tylosis wall is probably penetrated by the cytoplasm. As new microfibrils are synthesized within the protoplast, they are presumably deposited in the older layers of the developing tylosis wall. It is believed that in the phase of dimensional enlargement these newly formed and deposited microfibrils do not become firmly fixed in the wall so that as the enlargement of the tylosis wall occurs, they can still slide along and over one another. Portions of fully developed tyloses can be seen in Figure 8. Note that Figures 4, 6, 7, and 8 represent various stages of tylosis wall development in black locust.

An increase in tylosis dimension was not accompanied by a corresponding increase in its protoplasmic content. It was observed that the 8-hour-old tyloses were completely packed with protoplasmic material, while tyloses near the end phase of their dimensional enlargement appeared highly transparent and their protoplasmic content was much reduced.

In the last annual ring (next to the cambium) of white oak sapwood the first tylosic buds appeared 8 hours after the trees were felled. By the 40th hour, approximately half of the vessels contained tyloses. After about 60 hours of growth, tyloses displayed the differentiation of intertylosic pit fields. The existence of the primary pit fields shows that a tylosis in this stage of development possesses a well-differentiated primary wall. Ninety-six hours from felling, all but a few vessels contained tyloses. At the conclusion of one hundred hours of growth, tyloses developing from different sides of a vessel came in contact with one another and thus the vessels became occluded with tyloses. This represented the end of the phase of dimensional enlargement. From this point on, only growth in thickness occurred, namely, secondary thickening.

B. Ultrastructure and properties of tyloses

The study of the ultrastructure and properties of tyloses includes a number of features, such as shape, contact between tylosis wall and vessel wall, intertylosic pitting, layering and chemical composition.

Fully developed tyloses in the vessels of black locust and osage-orange heartwood may be moderately or highly compact, round to angular in shape and cellular in appearance. Tyloses in American beech, *Fagus grandifolia* Ehrh., occur as more or less horizontally oriented partitions across the vessels and appear ladder-like on longitudinal sections. Figure 10, for example, shows a portion of a double cell wall (vessel plus parenchyma) with a double tylosis wall attached to it perpendicularly. This double tylosis wall runs horizontally across the vessel cavity and joins the other side of the vessel wall in the same manner. Tyloses in white ash, *Fraxinus americana* L., exhibit highly irregular shapes and variable sizes. In many cases they appear collapsed, wrinkled and curved in all directions (Fig. 5).

While tyloses in white ash may lie loosely on the inner vessel wall, those in American beech, white oak, osage-orange and black

locust appear to adhere or grow to it (Figs. 8 and 10). At the junction where two tyloses and the inner vessel wall meet, the triangular space may be filled with substances possessing both the electron density and the appearance of a normal middle lamella (Figs. 8 and 10) or alternatively, an intertylosic space may be formed. Tyloses lying on the inner surfaces of vessel walls were observed to arch over the borders of pit-pairs, thus acting as dividing walls between contiguous pit and vessel cavities (Fig. 8). The enclosed space between a tylosis and pit membrane may be filled in with substances which appear highly amorphous in nature or they may remain empty (Fig. 8). When two tyloses come in contact with one another, they invariably grow together and form a double tylosis wall.

The wall of a single tylosis may be extremely thin and delicate, as in white ash (the thinnest recorded was 0.05μ), or it may be of medium thickness, as in black locust, (average thickness = 0.63μ), or in some species, such as white oak, it may become thick walled (average thickness = 2.98μ).

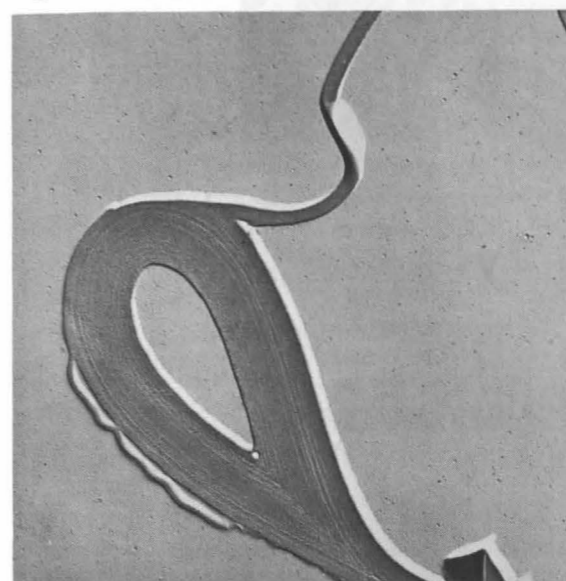
Electron microscopic evidence reveals the presence of intertylosic pitting in the tyloses of white oak, osage-orange, and black locust species. In black locust, intertylosic pit-pairs were observed to be simple, rather than bordered. Their pit membranes appear to be similar to those of regular hardwood pit-pairs. On the average, pit membranes in black locust tyloses measure 0.1 micron in thickness and 1.5 microns in diameter. After some of their incrusting materials are removed by a mild treatment in sodium chlorite, the intertylosic pit membranes display randomly oriented fibrillar structure (Fig. 13) which is a characteristic feature of hardwood pit membrane.

Electron micrographs of ultrathin sections reveal three distinct layers in a double tylosis wall of black locust, osage-orange and American beech heartwood. These are the compound middle lamella and the two secondary walls. (Figs. 8 and 10). The intercellular substance in the compound middle lamella of adjacent tyloses possesses apparently the same electron density and texture and it is degraded, upon ozone treatment to the same extent as the intercellular substance between adjacent fibers. On this basis, such a binding layer in the middle portion of a double tylosis wall could be classified as analogous to a regular middle lamella.

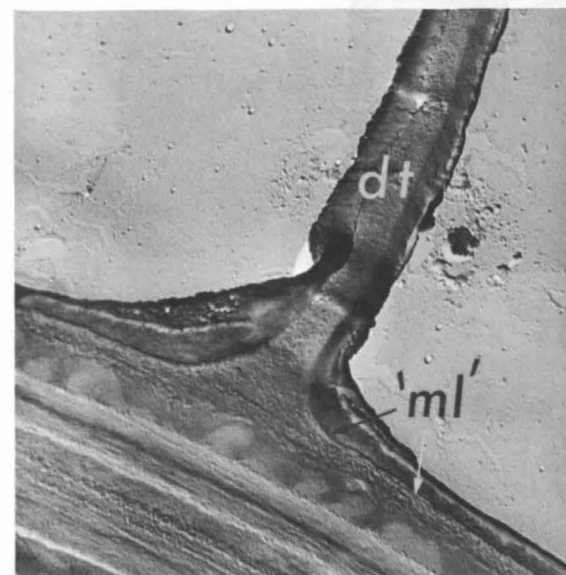
Although the two primary walls are not resolved on ultrathin, cross-sectional views of tyloses, their presence in the compound middle lamella is suggested by the randomly oriented fibrillar structure found in replicas of tylosis surfaces (Figs. 11 and 13).



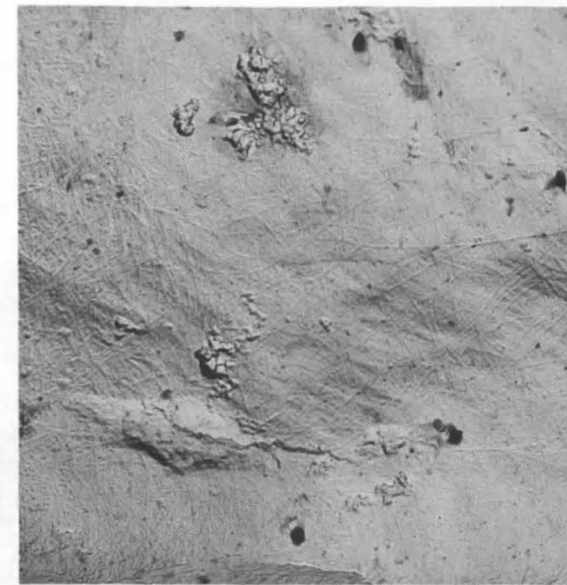
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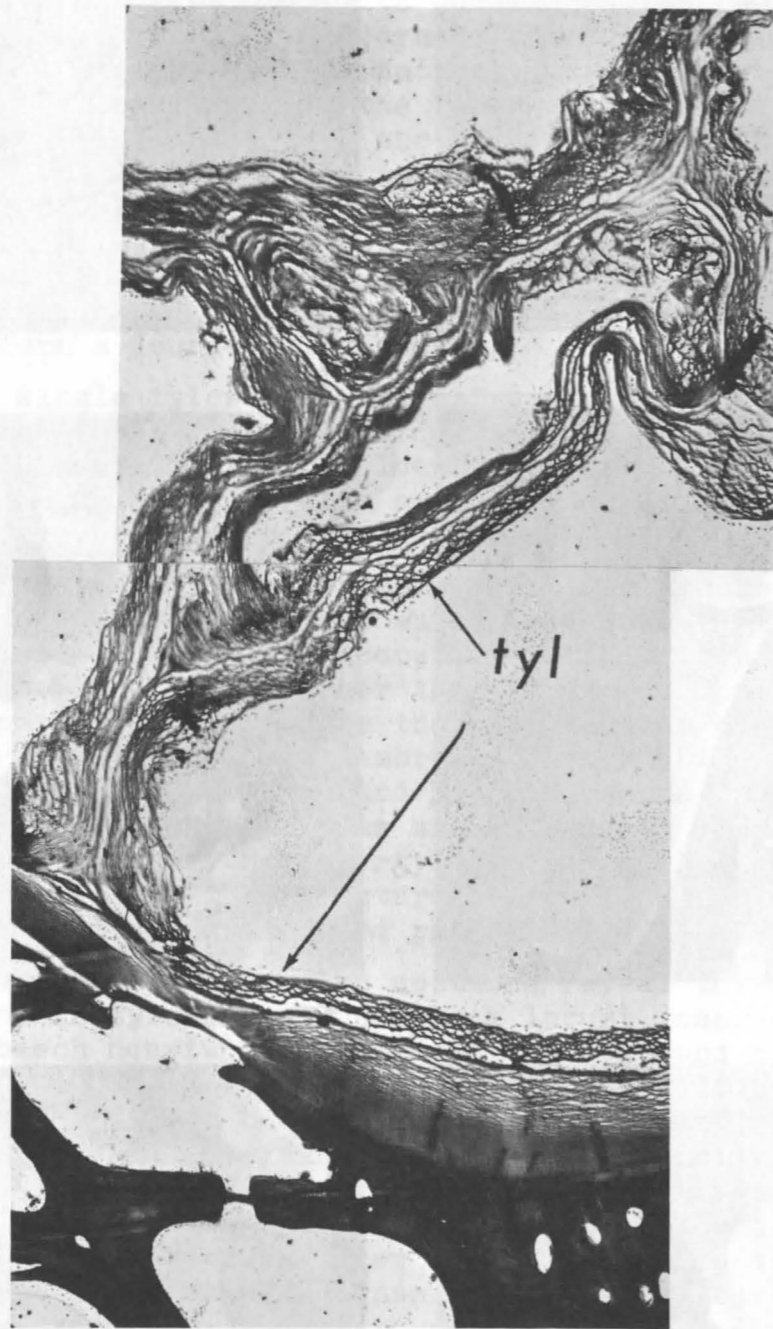
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- Figure 8. Portions of tylosis walls (t) in a springwood vessel segment of black locust (*Robinia pseudoacacia* L.) heartwood. The single tylosis walls are joined together and to the inner vessel wall by a middle-lamella type ("ml") of layer. The tylosis at the right bridges over the borders of the intervessel pit and forms an enclosed cavity. Cr shadowed. 14,000x.
- Figure 9. A portion of a tylosis in a springwood vessel segment of white ash (*Fraxinus americana* L.) heartwood. The tylosis wall displays a multilayered structure. The individual layers appear to be assembled into a composite tylosis, are fairly uniform in thickness and highly parallel to one another. Cr shadowed. 9000x.
- Figure 10. A portion of a double tylosis wall (dt) joined to the inner wall of a springwood vessel segment in American beech (*Fagus grandifolia* L.) heartwood. The double tylosis wall consists of a compound middle lamella and two secondary walls. The "compound middle lamella" resembles that of a normal cell wall. A middle-lamella type of layer ("ml") joins the individual tyloses to the inner vessel wall. Cr shadowed. 4200x.
- Figure 11. Randomly oriented fibrillar structure in a tylosis of white oak (*Quercus alba* L.) heartwood. Tyloses were treated with a dilute solution of sodium chlorite for a 20-hour period. Cr shadowed. 18,000x.
- Figure 12. A direct carbon replica showing the inner surface of a tylosis with intertylosic pitting in black locust (*Robinia pseudoacacia* L.) heartwood. The parallelly aligned fibrillar structure and the presence of fully developed intertylosic pitting indicate the existence of a secondary wall in black locust tylosis. Tyloses were treated with a dilute solution of sodium chlorite for a 20-hour period. Cr shadowed. 12,000x.
- Figure 13. A direct replica of intertylosic pitting in black locust (*Robinia pseudoacacia* L.) heartwood. The pit membranes (p) show randomly oriented fibrillar structure. Specimens were treated with a dilute solution of sodium chlorite at 75° C. for a 20-hour period. Cr shadowed. 16,000x.
- Figure 14. Tyloses in a springwood vessel segment of osage-orange, *Maclura pomifera* (Raf) Schneid., heartwood following a 30-hour ozonization. The individual tylosis walls (tyl) are degraded to a fairly uniform degree. The binding layer between individual tyloses and between a single tylosis and the inner vessel wall appear to be degraded to a similar degree as the middle lamella of adjacent fibers. This fact suggests a chemical similarity between a regular middle lamella and a "middle lamella" of adjacent tyloses. Cr shadowed. 2500 x.

The identity of the two outer layers with the secondary walls is indicated by their more or less parallelly oriented fibrillar structure (Fig. 12) and by their fully developed intertylosic pitting (Figs. 12 and 13), both revealed in surface replicas. Although the presence of the secondary wall in a double tylosis wall appears to be well-established, no definite layering within the secondary wall could be resolved. Whether the secondary wall of a tylosis wall contains the three layers of a normal secondary cell wall, viz., the S₁, S₂, and S₃ layers, is not known.

Tyloses in white ash occur in the form of very thin membranes, a few of which are shown in Figure 5, or as a so-called "composite tylosis" laminated from individual tyloses (Fig. 9). The number of individual layers in a composite tylosis appears to vary in the different tyloses. Although the lamination of individual tyloses may result in structures of highly variable sizes and shapes (Fig. 5), the individual layers in a composite tylosis appear to be highly parallel to one another (Fig. 9). In this study, all electron microscopic evidence points to the fact that white ash tyloses possess no layering comparable to that of a normal cell wall.

A method of exposing wood blocks to ozone gas for a period of 30 hours, followed by ultrathin sectioning and electron microscopic observation, was employed to provide some information about the chemical composition of the different layers of tyloses. Electron micrographs (Fig. 14) show that the binding layer between two tyloses, two fibers, or between a single tylosis and the inner surface of a vessel wall was degraded by ozone to the greatest degree in all of the three sites. This evidence, plus the similarity in electron density, texture, and general appearance suggest that the bond between individual tyloses is similar to that of the middle lamella found between ordinary cells. On the same basis, the primary and secondary wall of tyloses do not appear to differ from those in the ordinary cell wall.

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Changes in cell wall structure and cytoplasmic organization
during differentiation of xylem*.

by A.B. Wardrop, Tasmania

A study of these aspects of xylem differentiation in *Pinus radiata* and *Eucalyptus regnans* has been made. The most conspicuous change in cytoplasmic organization involves the development of a large single vacuole in cells in which secondary wall formation is in progress from a dispersed vacuolar system existing in the cambium and in xylem mother cells. In this process the cytoplasmic organelles become confined between the tonoplast and plasmalemma, to a degree which may involve a change in their form, or, in the case of the Golgi apparatus, its disorganization. During the differentiation of the second layer of the secondary wall of the reaction xylem of gymnosperms, the plasmalemma appears to become discontinuous and the vacuolar system changes. At this stage there is some evidence of vesicular secretion into the wall. During the formation of the first layer of the secondary wall, these effects were not observed.

Further evidence of the operation of the multinet mechanism of surface growth of the primary wall in the fibres, tracheids, vessels and parenchyma of *Papuodendron lepidotum* has been obtained by mapping the microfibril orientation over the surface of the mature cells. In each case, as required by the multinet hypothesis, the microfibril orientation reflected the extent and polarity of growth which had occurred. Thus, in the fibres, the localization of growth at the cell tips was not associated with a localization of cellulosic synthesis. The above observations are reviewed in relation to previous optical and electronmicroscopic studies in this field.

* Abstract of a paper presented at the Tenth International Botanical Congress in Edinburgh, August 1964