Excretion and Heartwood Formation in Living Trees

The death of many cells in secondary tissues seems to result from the accumulation of waste metabolites.

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All higher living organisms utilize nutrients derived from photosynthesizing cells. After extracting the required substances from the nutrient supply, the organisms often eliminate from their bodies the unused nutrients and always excrete, in some fashion, the waste metabolic products, in amounts which vary considerably according to the quantity and quality of the initial nutrients and according to other factors.

Individual cells and whole tissues must possess suitable means of excretion during their active life. Normally, the waste products of metabolism are eliminated in aqueous solution from living cells; these materials are then transported through special cells which seem to function chiefly for purposes of translocation or storage (either temporary or permanent) of nutritive or excretory substances. Animals have well-developed systems for eliminating unnecessary materials from their bodies, whereas land-based plants, in general, must make use of suitable space within their tissues for the accumulation of most of the solid and liquid excretory products (*1*, *2*).

The higher vascular plants have evolved, during a period of several hundred million years, from simple marine plants which were able to excrete waste metabolites into the aqueous substrate. In order to survive in their environment on land, the vascular plants have developed methods of translocating and storing those metabolic products which tend to inhibit the normal functioning of living cells. The arrangement of cells in the stem cross section of an advanced tree species is shown in Fig. 1.

During the growth of a tree, the cambium becomes circumferentially continuous a short distance below the growing tip of a stem or branch. Thereafter, as a result of successive tangential divisions of the cambium cells, the cells of the secondary xylem (wood) and phloem (bark) are produced in a radial array to the inside and outside, respectively, of the cambium. The newly formed cells then differentiate into the various cell members of the secondary tissues (see Fig. 1). The prosenchyma cells (*3*) die within a millimeter or so of the cambium, whereas the parenchyma cells (vertical and ray) are alive at much greater distances from the cambium. The fibrous members (libriform fibers and fiber-tracheids in angiosperms; tracheids in gymnosperms) of the prosenchyma cells, especially those of the xylem, seem to provide the main structural strength of the stem.

The growth rings result from differences in the rates of cambium cell division during various seasons of the year. The lines of discontinuity between late (summer and autumn) and early (spring) woods are clearly visible in Fig. 1, and are formed as a result of a period of dormancy in winter when the cambium cells undergo few, if any, tangential divisions.

Ray and vertical parenchyma are the only living cells in most of the outer, central, and inner sapwood. Heartwood formation occurs by the death of these cells in a zone of transition between sapwood and heartwood. Heartwood, which thus consists entirely of dead cells, is usually distinguishable from sapwood by its darker color (see Fig. 2). It is formed at a distance of a few to many growth rings from the cambium in most tree species. In a few species, heartwood is never formed—that is, the parenchyma cells remain alive right in to the pith.

The majority of the nutrients required for secondary growth are synthesized in the leaves and represent the photosynthates produced in excess of the requirements of the photosynthesizing and neighboring cells. These excess assimilates (chiefly nonreducing sugars) are translocated to all living parts of the tree through the sieve members of the inner phloem (Fig. 1). The water and solutes of the transpiration stream are translocated from the roots to the crown within the vessels (in angiosperms) and tracheids (in gymnosperms) of the outer xylem. The rays provide radial translocation channels between the sieve members and the vessels (or tracheids)—that is, channels across the region of differentiating cells. The ray parenchyma cells of the sapwood and of the phloem also appear to serve as translocation channels from the differentiating cells near the cambium to the nonfunctioning tissues of the heartwood and outer bark. Furthermore, the ray and vertical parenchyma cells are involved in the storage of reserve and, probably, of excretory substances.

This article deals mainly with the probable fate of the waste products produced during the various biochemical reactions involved in the differentiation of fibrous and other prosenchyma cells and in the normal functioning of parenchyma cells, especially the ray cells.

Carbon dioxide, the main gaseous excretory product of respiration, is probably dissolved in the cell liquid and then translocated, by way of the rays and the transpiration stream, to the crown of the tree, where it is utilized again in photosynthetic reactions during periods of daylight and where it is released to the atmosphere by the leaves during periods of darkness.

The roots and various other portions of a plant are known to excrete certain substances outside the plant's body (*4*). For example, the roots excrete, to the surrounding soil, organic substances such as amino and other acids, sugars, nucleotides, and polyphenols. Some of these excreted metabolites, apart from sometimes preventing the germination of seeds (*4*), may be of importance to the metabolism of those soil or nodule microorganisms which are symbiotically associated with the

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plant in the production of vital nitrogenous substances.

In certain tree species, the dead outer bark (or rhytidome) and the extraneous materials contained within it are shed periodically. Again, extraneous substances produced within the leaves of deciduous trees are deposited outside the tree during autumnal leaf fall. The shedding of some leaves (probably the overmature ones) by evergreen trees may represent a means of excreting extraneous materials contained within the leaves.

In general, the extraneous substances (except, perhaps, for some lignin precursors) seem to possess no important biological functions in normal living tissues, and they usually tend to accumulate in cells which become nonfunctional soon after a high concentration of these substances develops within them. Many of the extraneous materials are known to possess toxic or inhibitory properties, or both, with respect to living cells; for example, Jacquiot (*5*) has shown that cambial cells will not proliferate in media containing more than trace amounts of tannins.

Because of the great variations in their quantity and composition, it seems probable that many of the soluble extraneous materials (extractives) are excretory molecules which must be either (i) detoxicated or accumulated in the vicinity of the site of their formation or (ii) translocated away from regions of active growth. One may assume that the two processes may be combined; that is, if the excreta are highly toxic to living cells, they may be detoxicated prior to translocatory excretion through living cells such as the ray cells, which must be the chief channels for horizontal translocation in the tissues of the xylem and of the phloem (*1*).

During secondary growth the most effective means of translocatory excretion is via the rays, away from the regions of intense metabolic activity. That is, excreta from the differentiating cells of the xylem and of the phloem would tend to travel along the rays in the respective directions of the center of the tree and of the outer bark. This contention has received some support from the work of Stewart, Amos, and Harvey (*6*), who have shown that tannins occur in minimum concentrations in the cambial zone (*7*) and increase, on both sides of the cambium, to maximum values in the nonfunctioning tissues of the heartwood and outer bark.

Utilization of Nutrients during Secondary Growth

The nutrients for secondary growth are generally composed, to the extent of 90 percent or more, of carbohydrates—usually sucrose and sometimes raffinose, stachyose, and verbascose as well (*8*). These nutrient sugars seem to be translocated, via the rays, from the sieve members to the differentiating cells of the xylem and of the phloem. For example, Hasegawa and Shiroya (*9*) have shown that radioactive sucrose, applied to the cambial zone of living trees, is translocated in decreasing concentration along the rays toward the heartwood. Moreover, they found that the concentration of radioactive ether solubles (polyphenols and so on) was low in the central sapwood and increased in the inner sapwood of the transition zone between sapwood and heartwood.

The major portion of the nutrients is utilized for the formation of cells, for the thickening of their walls, and for respiration during periods of active growth. During the summertime period, when the supply of nutrients is ample and cambial subdivision occurs at a lower rate, a portion of the nutrients is translocated along the rays and is converted to reserve substances —such as starch, which is stored in amyloplasts which may be located well in toward the sapwood-heartwood boundary.

During the period of vernal resurgence in the growth of trees in temperate climates, mobile carbohydrate nutrients may be regenerated by enzy-

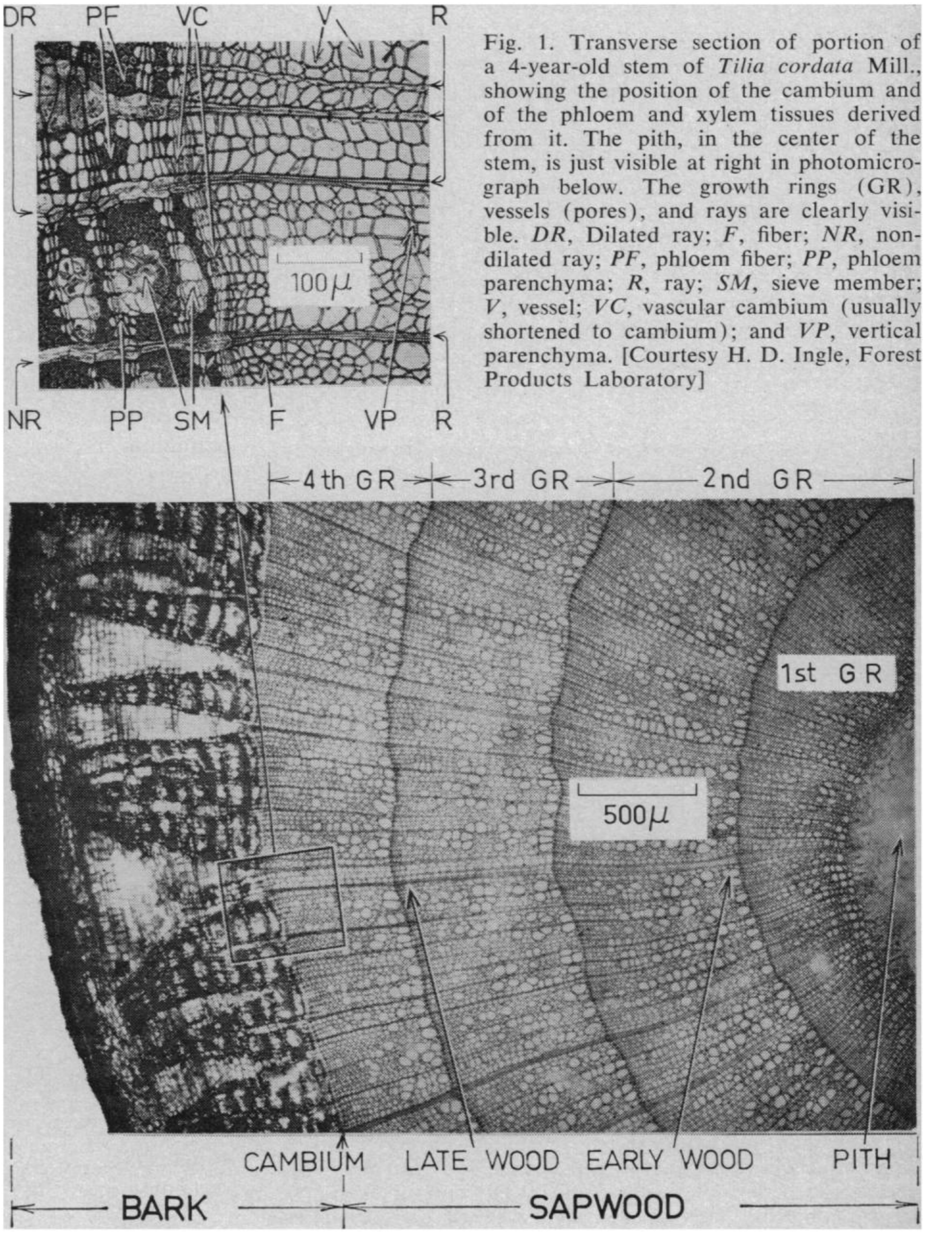

Fig. 1. Transverse section of portion of a 4-year-old stem of *Tilia cordata* Mill., showing the position of the cambium and of the phloem and xylem tissues derived from it. The pith, in the center of the stem, is just visible at right in photomicrograph below. The growth rings (GR), vessels (pores), and rays are clearly visible. *DR*, Dilated ray; *F*, fiber; *NR*, nondilated ray; *PF*, phloem fiber; *PP*, phloem parenchyma; *R*, ray; *SM*, sieve member; *V*, vessel; *VC*, vascular cambium (usually shortened to cambium); and *VP*, vertical parenchyma. [Courtesy H. D. Ingle, Forest Products Laboratory]

mic hydrolysis of reserve starch, with probable concomitant formation of by-product polyphenols (*10*). The regenerated nutrients may travel back along the rays to the sieve members and then ascend to provide nutrients for the developing leaves in deciduous trees (*11*). When the leaves become self-sufficient with respect to nutrients, they export any excesses, and basipetal translocation of sugars recommences and continues during the summer and autumn, the assimilates being utilized for secondary growth and for the formation of reserve nutrients such as starch, protein, and lipid (*11*).

What is likely to happen to the nutrients in the neighborhood of the cambial zone? The cells of the cambium must use the nitrogenous and carbohydrate nutrients for the development of the protoplast, which then controls the biochemical utilization of the carbohydrates and other nutrients within each differentiating cell.

The formation of the primary wall involves chiefly the biosynthesis of polysaccharides; these comprise a little cellulose [say up to 20 percent, by weight, of the wall (*6*)] and large quantities of noncellulosic polysaccharides composed mainly of uronic acid, galactose, mannose, rhamnose, arabinose, and xylose units (*12*).

The sugar nutrients consist mainly of glucose and fructose units, with galactose units as well when the raffinose family of nonreducing oligosaccharides is present. The glucose and galactose units of the nutrients may be transferred, directly or indirectly, following the action of hydrolases and phosphotransferases or nucleotidyl transferases, whereas the fructose units are probably transferred subsequent to the action of isomerases or, perhaps, are utilized mainly for the processes associated with respiration. The other monosaccharide residues (that is, units of mannose, rhamnose, arabinose, xylose, and uronic acids) of the polysaccharides of the primary wall must become incorporated into the wall after enzymic degradation or rearrangements of the hexose-based units of the carbohydrate nutrient pool.

Without doubt, many of the processes outlined above result in the production of by-products which may be regarded as superfluous, and sometimes harmful, to the protoplasts of living cells. During the cytoplasmic stages of the direct and indirect reactions involved in the synthesis of the cell-wall polysaccharides, a portion of the various "intermediates" formed may participate in aminohydrolase, aminotransferase, and other reactions with aromatic amino acids to produce hydroxyaromatic by-products of the substituted *n*-phenylpropane and other types; the by-products may then be converted to phenolic glycosides, to esters such as chlorogenic acid, to lignans, and so on, probably as a means of detoxication prior to either transport through, or storage in, living cells (*13*).

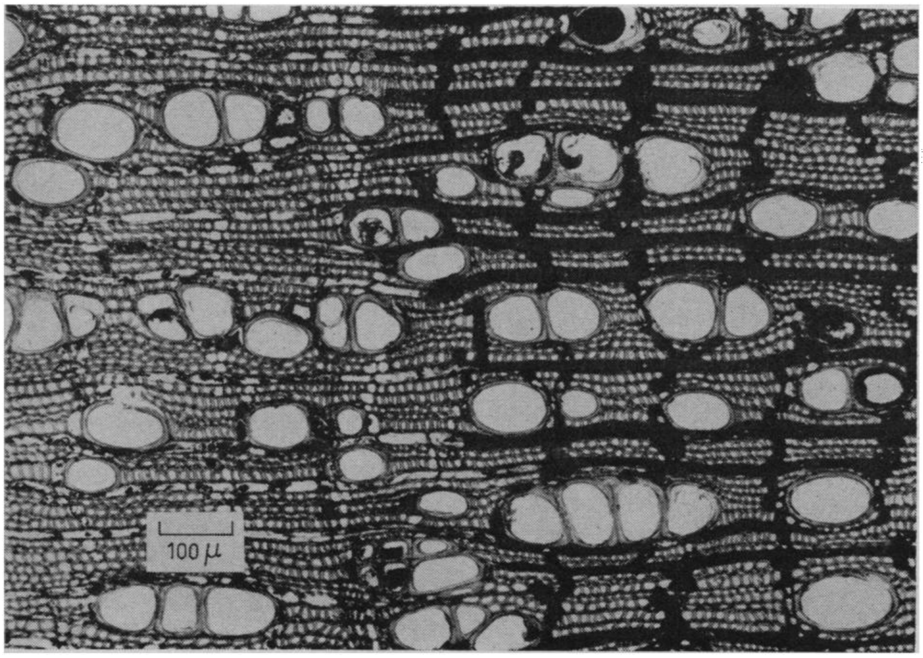

Fig. 2. Transverse section of the wood of *Excoecaria parsifolia* Muell-Arg., showing an apparently sharp demarcation between sapwood and heartwood. Large amounts of polyphenols occur in the rays, vertical parenchyma, and some of the vessels of heartwood. [Courtesy R. K. Bamber, Division of Wood Technology, Forestry Commission of New South Wales, Sydney]

Excretion of Metabolic By-products

The aromatic and other substances of the excretory pool may leave the active cytoplasm of a cell by at least three possible routes (*13*).

1) They may be excreted into the cell vacuole for storage during the active life of the cell; while their concentrations are low, this may be the sole means of excretion.

2) They may be excreted through pits from prosenchyma cells into adjacent ray cells, where they may be either stored in the vacuoles or translocated along the rays, in low concentrations, away from the differentiating tissues. Energy provided by respiration reactions is probably used to drive the excretory products from the more active to the less active ray cells—that is, from a region of low concentration of excreta to one of higher concentration. The movement of certain solutes in the direction of the inner sapwood may be aided by the deposition of extraneous substances in the ray cells of the sapwood-heartwood transition zone.

3) The metabolic by-products, contained perhaps in vesicles, may be excreted through the plasmalemma into the nonliving cell-wall regions. The phenolic aglycons or glycosides may then be subjected to the action of extracellular enzymes such as glycoside glycohydrolases or oxidoreductases (laccase or peroxidases) to produce lignin, according to Freudenberg's mechanism for lignification (*14*).

After most of the cellulose of the secondary wall of the libriform fiber (*15*) and of other prosenchyma cells has been deposited, the protoplast enters its senescent stages, which culminate in its final breakdown. During the senescent activities, which may be triggered either by a decreasing concentration of carbohydrate nutrients or, more probably, by an increasing concentration of toxic substances (or by both), the breakdown of the cytoplasmic membranes would result in a blending of the vacuolar components with components of the general cytoplasm. Additional lignin precursors and extraneous materials may result from the action of transferases and other still-active enzymes on the admixed molecules in the dead cell; these reactions may continue either until the enzymes become inactivated by toxic substances such as polyphenols or until substrates become exhausted. The excretory constituents may then diffuse through the cell wall or remain in the lumen.

The final phases of fiber senescence and the post-mortem enzymic reactions are probably responsible for providing more than 50 percent of the total lignin after most of the cellulose has been laid down in the cell wall. Evidence of this sequence of deposition has been obtained from chemical analyses of differentiating xylary tissues (*6, 13, 16*) and by specific work on lignification by Wardrop and Bland (*17*) and by other workers.

The above example of what is essentially nontranslocatory "excretion"—or, better, detoxication (lignification in this instance)—of phenolic substances is of great importance to present-day trees. According to Neish (*18*), the initial production of phenolic compounds may have been the result of a mutation early in the evolutionary history of the plant; a new enzyme with the ability to deaminate phenylalanine may have been formed as a result of the mutation. The cinnamic acid produced could have been acted upon by other enzymes of broad substrate specificity which were already present for other purposes, and thus several simple secondary metabolites (various esters or glycosides) may have accumulated; hence, due to the alleviation of toxicity of cinnamic acid, the mutant may have acquired some extra survival value.

Eventually (*18*) another mutation may have resulted in the production of an enzyme which could act on one or more of the secondary metabolites, formed as a result of the first mutation, and in time a complex biosynthetic sequence could have arisen, leading to the formation of lignins, flavonoids, and so on. Other examples of what are probably cases of nontranslocatory excretion have been reported (*1*).

Translocatory Excretion and Heartwood Formation

All cells of sapwood, except for the differentiating ones within about 1 millimeter of the cambium and the parenchyma cells (including septate fibers in some species) of the sapwood, are physiologically dead; that is, their protoplasts, and perhaps many of the associated enzymes, have ceased to function in a normal vital manner. All cells of heartwood are dead, the vertical and ray parenchyma cells having died at the sapwood-heartwood boundary.

The death of parenchyma cells at the inner limits of the sapwood may be explained by means of a simple mechanism. It is probable that not only do the prosenchyma cells excrete extraneous materials into the horizontal translocatory channels of the xylem but that the ray cells themselves contribute substantial quantities of excretory substances during their differentiation, during respiratory processes, and during the biosynthesis and the enzymic hydrolytic degradation of reserve starch. Those materials which do not accumulate in the vacuoles of ray cells are probably transported, in concentrations below toxicity limits, along the rays in the direction of the pith. In the region of the pith the toxic and other materials will accumulate until the concentration of toxic substances reaches a lethal level. The innermost parenchyma cells will then die, forming the first cylinder of heartwood.

The outermost heartwood cells will then provide a reasonably effective barrier to the inwardly moving excreta; hence the continuous accumulation of toxic molecules and the consequent death of parenchyma cells will cause the sapwood-heartwood boundary to move outward as the diameter of the tree increases. Heartwood, moreover, will form only in those trees in which the concentration of toxic materials reaches a lethal level.

The above mechanism of heartwood formation is consistent with experimental observations made by various workers. For example, Frey-Wyssling and Bosshard (*19*) have shown, from the results of a cytological study of the ray cells of species of *Pinus, Larix, Taxus, Pseudotsuga, Sequoia, Robinia, Picea, Abies, Carpinus, Tilia, Fagus,* and *Fraxinus*, that a gradual degradation of the cell nucleus and inhibition of mitochondrial activity occur in a direction from the outside of the sapwood toward the transition zone between sapwood and heartwood. At the sapwood-heartwood boundary the activity of all mitochondria seems to be completely inhibited and all cell nuclei have disintegrated. Thus there is little evidence for a great burst of metabolic activity such as that which might be imagined to be associated with the formation in living cells of large quantities of extraneous materials at the sapwood-heartwood boundary.

Hulme and Jones (*20*) have reinforced the foregoing contention by showing that polyphenols inhibit the activity of plant mitochondria. In general, with leucoanthocyanins and the more polymerized phenolic compounds, the degree of inhibition increases with the degree of polymerization, and Roux (*21*) and Roux and Evelyn (*22*) have shown that the degree of polymerization of hardwood extractives increases from the outer sapwood to the inner heartwood. Cole (*23*) has suggested that the inhibition of mitochrondrial activity by polyphenols is of the nature of the direct tanning action.

Hillis and Carle (*24*) have found differences in the chemical structure of polyphenols which may be extracted from cambial tissues, from sapwood, and from heartwood of eucalypts, and they have concluded that, because of such differences, the polyphenols of heartwood must be formed *in situ* from excess starch and other carbohydrates at the sapwood-heartwood boundary. This conclusion is not necessarily correct, since differences in chemical structure may be expected because of changes which are known to occur in the metabolism of a cell at successive stages of its differentiation.

Therefore, if extraneous materials are regarded as metabolic by-products, differences in their structure may be expected during the formation of the primary wall, during the formation of the secondary wall, and during the final phases of lignification of prosenchyma cells. Only the *excess* aromatic and other extraneous substances will reach the ray cells for excretory transport toward the inner xylem; the majority of such substances in, say, the cambial cells may be retained in the differentiating cells and eventually become incorporated in the cell wall during the final phases of lignification. However, extraction of cambial cells by the method of Hillis and Carle would yield all or most of the extraneous materials contained within the cells regardless of their ultimate destination (*13*).

One may assume, therefore, on the basis of existing evidence, that much of the extraneous material which accumulates in the innermost living ray cells of the sapwood is translocated from the outer, more active ray cells, and that the accumulated toxic excreta are responsible for the death of the ray cells and thus for the formation of heartwood.

However, it is possible that signifi-

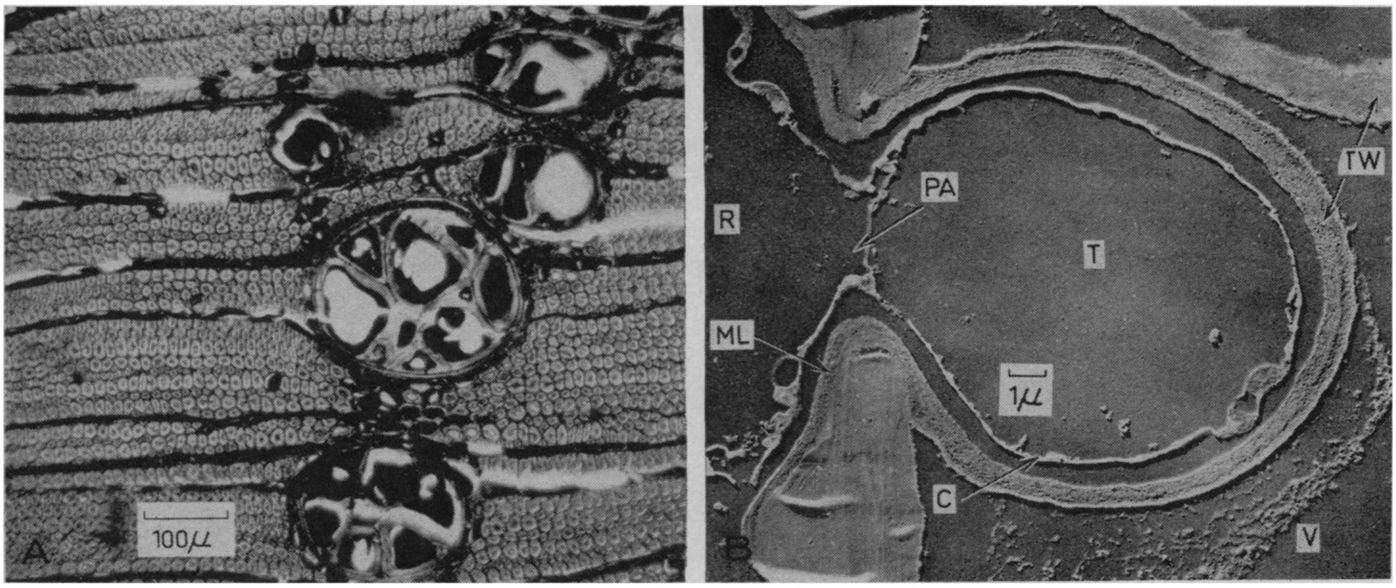

Fig. 3. Transverse sections of tyloses in wood. (A) Portion of the heartwood of *Eucalyptus miniata* A. Cunn. ex Schau., showing vessels full of sclerosed tyloses. The ray cells and tyloses contain much polyphenolic material. (B) Electron micrograph of an ultrathin section of the sapwood of *Eucalyptus obliqua* L'Herit., showing a tylosis, *T*, in the early stages of its development. The ray cell *R* produces a special microfibrillar layer *ML*, which grows out through the pit aperture, *PA*, into the lumen of a vessel, *V*, to form the tylosis. The tylosis wall *TW* is lined with a thin layer of cytoplasm, *C*, which is continuous with that of the parent ray cell. [Courtesy R. C. Foster, Forest Products Laboratory]

cant amounts of extraneous substances may result from the action of transferases and other still-active enzymes on the mixture of vacuolar and cytoplasmic materials formed when the parenchyma cell dies. Such reactions are "abnormal" in that they may take place in the absence of vital control. As mentioned earlier in connection with a similar phenomenon in prosenchyma cells, the reactions may continue either until the enzymes become inactivated or until suitable substrates become exhausted.

Frey-Wyssling and Bosshard (*19*) have observed that all residual starch in the ray cells of the transition zone seems to be utilized before the heartwood forms; its utilization may be associated with the following processes: (i) the supply of carbohydrate nutrients to the outer sapwood; (ii) the synthesis of the cell walls of tyloses in certain species (see *25*); and (iii) the formation of polysaccharides, polyphenols, and so on during senescent or post-mortem reactions, or both, in the innermost ray cells of the sapwood.

The quantity of excretory materials produced in the areas of secondary growth is probably related, directly or indirectly, to the difference between the amount of nutrients supplied and the amount of nutrients consumed in the essential processes of cell-wall formation, respiration, build-up of storage starch, and so on. Thus, fast and slow rates of secondary growth should tend to produce, respectively, minimum and maximum quantities of excretory substances.

Tylosis Formation

The ray parenchyma cells of many tree species often develop outgrowths which enter, through pit apertures, either the lumen of a contiguous dead cell (tracheid, vessel) or an adjacent intercellular space (Fig. 3B). Such outgrowths, which are contained within microfibrillar walls (Fig. 3B) and which may be so numerous that they completely fill the neighboring lumen (Figs. 3A and 4A) or intercellular space, are termed tyloses. Analogous structures, called tylosoids, do not grow through pits but occur as the result of protrusive growth of the walls of living cells into a neighboring space. For example, tylosoids are sometimes observed as enlargements of epithelial cells which tend to fill the duct of a resin canal in gymnospermous tissues.

If the proposed mechanism for the formation of heartwood is accepted, one may envisage the production of tyloses as a related process. Thus their formation may be regarded as a controlled reaction against the increase in concentration of toxic excreta within a ray cell. Therefore the production of tyloses may represent a means of increasing the size of the ray cell with a concomitant decrease in the concentrations of toxic substances as a result of their dilution by water withdrawn, via the outer ray cells, from either the outer sapwood or the transpiration stream. The combined ray cell and tylosis may then continue to live until the concentration of toxic molecules rises to a lethal level.

In general, the lumina of vessels of angiosperms lose most of their free water and tend to become filled with air in the outer sapwood. Therefore, if tylosis formation is associated with the entry of air into vessels (*26*), one would expect to find large numbers of tyloses in the outer sapwood. Under normal conditions of growth, the frequency of occurrence of tyloses increases from the outer to the inner sapwood. This distribution of tyloses is consistent with their suggested function as receptacles for the accumulation of extraneous excretory substances.

Chattaway (*26*) has observed that the formation of tyloses occurs only in species which contain ray parenchyma cells with pit apertures whose width exceeds approximately 10 microns. When the width of the pit apertures is less than 10 microns, "gum" is secreted in the vessels of species such as *Acacia*, *Albizzia*, and *Melia* (see Fig. 4B). Thus, in these species, it is apparent that protrusion of portions of the ray cell wall is prevented by the narrowness of the pit apertures. The secretion of "gum" may represent another way of excreting polyphenols and other waste metabolic products from ray cells into adjacent dead cells, and thus of decreasing the concentration of toxic substances within the living cells.

Water Content of Wood

The outermost vessels of angiosperms are involved in the transport of large quantities of water and dissolved solutes from the roots to the crown of the tree. The inner vessels of the outer sapwood seem to lose much of their liquid water as a result of the combined effects of active transpiration tension and the presence of gases within the transpiration stream (*27*). Hence in most angiospermous species the moisture content of the wood decreases from the cambium toward the central sapwood (*28*); the decrease is quite marked across the fully differentiated tissues and, therefore, is not due to the replacement of water by the deposition of cell-wall components in the regions of developing cells (see *6*). The wood of gymnosperms shows a marked decrease in water content during its change from sapwood to heartwood. Most angiospermous woods exhibit an analogous but less marked decrease in water content (*29*).

Peck (*30*) has demonstrated that, in some hardwood species, the moisture content of heartwood is greater than that of sapwood. Several workers (*28*) at the Forest Products Laboratory, Commonwealth Scientific and Industrial Research Organization, have observed that, in several species of eucalypt (for example, *Eucalyptus regnans*), an increase in moisture content occurs from the central sapwood across the inner sapwood to the heartwood.

It is probable that the observed increase in moisture content is due mainly to the uptake of water during the formation of tyloses and the consequent tendency of those vessels and neighboring cells which had lost or partially lost their free water in the inner tissues of the outer sapwood to refill with aqueous solution (*13*).

The more normal decrease in moisture content, which is associated with the change of sapwood into heartwood in most tree species, may be attributed to three main causes.

1) The deposition of water-insoluble excreta in the transition zone tends to dehydrate the tissue.

2) The dying parenchyma cells of the transition zone tend to lose the ability to control their water content.

3) The tension in the direction of the transpiration stream tends to withdraw water from the tissue.

Thus the normal situation, with respect to these three causes, would be for the more active outer ray cells to acquire water from the inner ones, especially if the inner ones contain only small amounts of water-soluble materials capable of exerting an osmotic pressure.

During tylosis formation a suction pressure of direction opposite to that developed by the transpiration tension must be responsible for the increase in moisture content of the inner sapwood. Such a suction pressure may be provided by an increase in osmotic pressure due to the accumulation of water-soluble excretory substances. If sufficient accumulation of water-soluble substances occurs in the parenchyma cells of the inner sapwood, it is conceivable that an increase in the moisture content of the sapwood may take place even in the absence of tylosis formation.

Various workers have suggested that heartwood formation is related to the water content of wood, and that partial desiccation of living cells in the inner sapwood is likely to be responsible for the transformation of sapwood into heartwood. Undoubtedly a general decrease in the water content of the inner sapwood would result in an increase in the concentrations of toxic and other substances and hence would hasten the senescence and eventual death of the inner ray cells. However, because the moisture content in some species increases toward the sapwood-heartwood transition zone, it is improbable that physiological drought in this zone is the basic cause of heartwood formation.

An attempt has been made to ex-

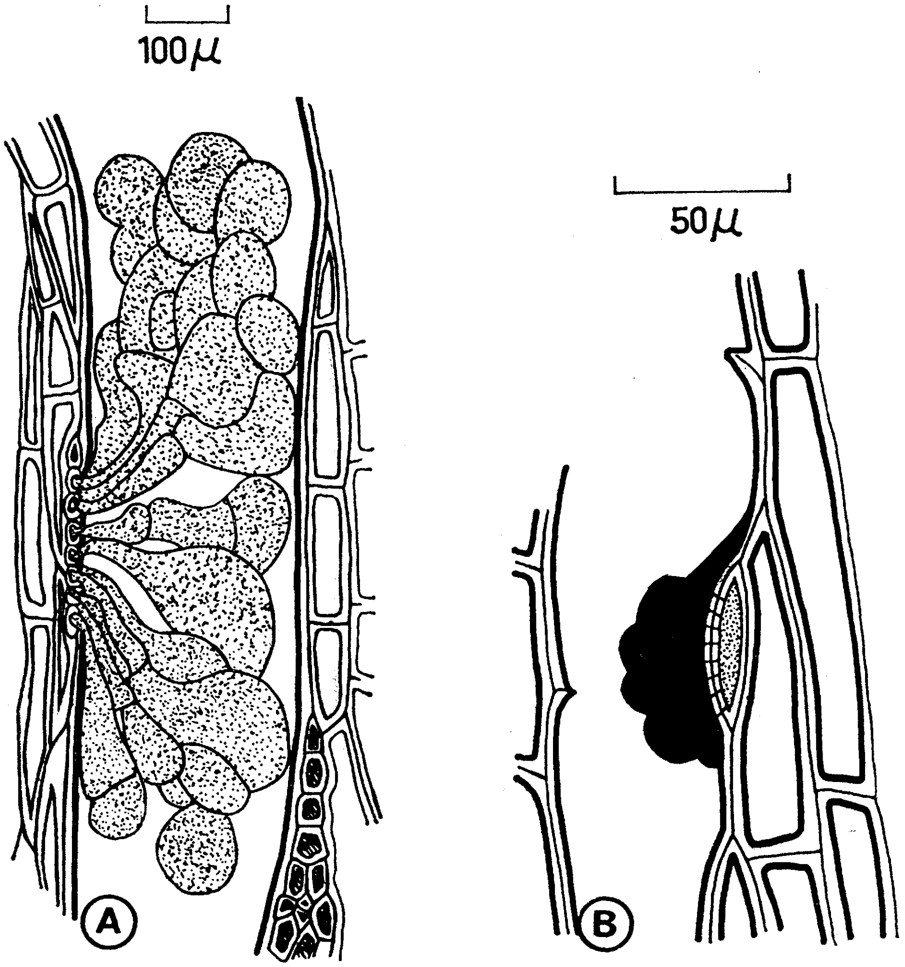

Fig. 4. Extrusions of materials from ray cells into contiguous vessels (reconstructions from actual photographs). (A) Longitudinal section of a portion of wood from *Anisoptera marginata* Korth., showing tyloses arising from every cell of a uniseriate ray and filling the whole of the vessel cavity. (B) Longitudinal section of a portion of wood from *Furea macnaughtoni* Phillips., showing secretion of "gum" from a uniseriate ray which is only one cell high. [Redrawn from Chattaway (*26*)]

plain the enigma of the mechanism of heartwood formation in living trees on the basis of a simple generalized process of excretion. Many excretory products have toxic or inhibitive properties with respect to the protoplasts of living cells and seem to be translocated along the rays away from the regions of secondary growth; that is, in the xylem they are translocated toward the center of the stem or branches.

Initially the xylem is composed entirely of sapwood, but in the region of the pith the concentration of toxic substances increases, and eventually the continued accumulation of excreta results in the death of all living xylary parenchyma cells near the pith, and so the first cylinder of heartwood is formed. The continuation of the process of translocatory excretion results in the outward movement of the sapwood-heartwood boundary.

The formation of tyloses and certain changes in moisture content within the sapwood seem to be associated with the formation heartwood in living trees.

References and Notes

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Distribution of Wild Wheats and Barley

The present distribution of wild forms may provide clues to the regions of early cereal domestication.

Jack R. Harlan and Daniel Zohary

The last decade has witnessed a major breakthrough in our understanding of the start of agriculture in the Old World. Archeologists, anthropologists, prehistorians, and historians have teamed with botanists, zoologists, and geologists in a concerted effort to discover when, where, and under what circumstances early domestication of cereals came about. Recent excavations that have yielded critical information include Ali Kosh, Tepe Sabz, and Tepe Sarab in Iran, Jarmo and Jawi Chemi Shanidar in Iraq, Çatal Hüyük, Hacilar, and Çayönü Tepesi in Turkey, Ramad in Syria, and Beidha in Jordan (*1*). Some of these sites have yielded abundant archeobotanical material, much of which has been critically examined by Hans Helbaek of the Danish National Museum (*2, 3*).

It is clear from these studies that, by 7000 B.C., more or less permanently occupied farming villages had been established over a wide arc from Khuzistan in southwest Iran, through the hilly country of the Zagros and Taurus mountains of Iran, Iraq, and Turkey, into central and western Anatolia and southward into Palestine. The permanence of these villages was made possible by cereal domestication that had taken place at some time preceding 7000 B.C. The first plant domesticates of major importance throughout the region were (i) two-rowed barley, (ii) emmer wheat, and (iii) einkorn wheat. Various leguminous crops and flax were also common at this time, but they were never as important in the diet as the early cereals. It is largely on the energy supplied by the wheats and barley that the first civilizations subsequently emerged in the Near East, and it was wheat and barley that made it possible for man to move from hunting and food collecting to farming in that region.

The present distributions of the wild forms of the three cereals could provide important information on the place or places of origin of Neolithic agriculture, provided they are properly interpreted. Any interpretation of mod-

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