Biological Processes in the Formation of Wood[1]

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DURING THE PAST CENTURY AND A HALF, data regarding the anatomical structure, the physical properties, the chemical composition, and the physiological functioning of wood have accumulated in ever-increasing volume. In recent years, owing to the rapid diversification of science in narrowing fields of intensive specialization, it is difficult for a single individual to become thoroughly familiar with all these data and to visualize their true significance in a broadening front of research. It is essential, however, that evidence obtained by new techniques be interpreted in harmony with summations of previously acquired knowledge. Much of the confusion and controversy during the past two decades regarding both the microscopic and the submicroscopic structure of wood could have been avoided, and more rapid progress could have been made, by broadened syntheses of available information and by closer integration of the researches of investigators in different scientific disciplines.

In view of such facts as these, it is advisable to summarize a number of salient generalizations that can be made at present regarding the development and the structural composition of wood. Extensive surveys of the plant kingdom, covering both living and fossil forms, indicate that fundamentally significant structural and physiological changes occurred when plants passed from an essentially aquatic to a truly terrestrial habitat. In the case of the so-called land plants—where photosynthesis occurs in parts elevated above the water level, where carbon dioxide is obtained directly from the atmosphere, and where water containing nitrogen and various essential minerals is moved upward from the soil to the transpiring green parts—tissues for facilitating rapid movement of sap and of enhanced mechanical strength are essential. Thus, all the land plants characteristically form tracheary cells, which serve to differentiate these plants, the Tracheophyta, from algae, fungi, and other lower forms.

Tracheary cells, the ubiquitous constituents of xylem or wood, serve as channels for a relatively rapid movement of water from the subterranean, absorbing rootlets to the aerial, transpiring leaves, and simultaneously impart a varying degree of rigidity and strength to parts of the plant in which they occur.

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It is highly significant in this connection, however, that the two functions are to a considerable degree mutually antagonistic, because certain structural features that enhance rapid conduction tend to weaken the cells and, conversely, others that strengthen them retard the movement of sap from cell to cell.

Primitive forms of tracheary cells are more or less extensively elongated and lose their living contents at functional maturity—two morphological features that enhance longitudinal movement of water in the woody tissue. Strength and rigidity are provided by a lignified secondary wall, formed internal to the original, delicate, primary wall, which alone is present throughout the earlier stages of cellular differentiation. The secondary wall inhibits a rapid movement of water from cell to cell and, therefore, must have holes or pits to facilitate such movement. The pit pairs of adjacent tracheary cells, in contrast to those of other forms of strengthening cells, are of a distinctive bordered form and are essentially an adaptation for exposing maximal areas of tenuous, unlignified, and relatively permeable primary wall without unduly enlarging the holes in the secondary wall. They have attracted much attention in botanical literature and are particularly significant in the preservative treatment of timber.

It is evident, accordingly, that conduction is enhanced in primitive forms of wood by increasing the number of bordered pits in the walls of the tracheary cells, but that the breaking strength of these elements is inversely proportional to the number of such pits per unit area.

The volume of wood in early land plants is relatively low in most cases, but the bordered pits in the secondary walls of the tracheids are very numerous and closely crowded. The woody tissue is thus efficient in conduction but is comparatively weak. With increasing height of land plants, the problem of attaining an adequate equilibrium between water lost by the leaves and water supplied by the roots without losing mechanical strength in the stems became a critical one. The solutions of this problem attained by evolutionary experimentation during the development of the vast array of modern land plants are highly diversified and are significant from both theoretical and practical points of view.

One means of strengthening the stem without reducing conduction in the wood is by the formation of cells with thick secondary walls in other tissues—e.g., in the bast or the cortex. Since such additional strengthening elements are not actively concerned in the conduction of sap, their secondary walls may become very thick, and pits may be held to a minimum both as regards size and number. Among the flowering plants, bast fibers (closely associated with tracheary tissue in numerous independent strands) are particularly significant as strengthening elements in the monocotyledons—i.e., palms, yuccas, grasses, sedges, bamboos, etc.—and provide a source of much industrially important material.

In the case of the gymnosperms, particularly the so-called evergreen or cone-bearing trees, an equilibrium between transpiration, conduction, and strength is attained in a fundamentally different manner. Conduction and strength in the stems and roots are simultaneously enhanced by progressively increasing the volume of wood as the trees grow larger. This is accomplished through the activity of a jacketing layer of meristematic tissue, the cambium, which forms new increments of wood each growing season. The tracheary cells of the laterally enlarging cylinder of wood vary more or less markedly in length, in cross-sectional area, in thickness of their secondary walls, and in the number, size, and arrangement of the bordered pits in their radial surfaces. Certain of these structural differences are evidently correlated with variations in the equilibrium between transpiration, conduction, and strength during the successive stages of enlargement of the tree. The most striking structural contrasts occur where cambial activity is intermittent —i.e., where the cambium is inactive during the winter or during a prolonged dry season. In such coniferous species, the tracheids formed during the early part of the growing season have a larger cross-sectional area and have thinner walls with larger and more numerous bordered pits, in contrast to the tracheary cells formed later in the growing season, which have smaller diameters, much thicker secondary walls, and a few rudimentary pits only. The weakness of the permeable early wood is obviously compensated by the markedly increased density and strength of the late wood.

It is in the arborescent dicotyledons, or so-called broad-leaved trees, however, that division of labor among tracheary cells attains its highest level of specialization. These are flowering plants, but, like the coniferous trees, they also have cambial activity. Because of their broader leaves, they have comparatively high transpiration, and there is a complete series of successive evolutionary stages in the development of vessels—long, open, tubelike conducting passageways —from vertical series of apically contiguous tracheids, the essential structural change being the dissolution at functional maturity of the primary walls in the bordered pit pairs of the contiguous tracheary cells. Closely paralleling the development of these channels of accelerated conduction within the wood are concomitant structural changes in the general residue of imperforate tracheids, leading to progressive accentuation of their mechanical function and to elimination of their role in conduction. The end products of this trend of specialization have reduced diameters, thick secondary walls, and small pits without borders. They resemble bast fibers rather than tracheary cells. In many cases, these so-called libriform fibers of the wood retain their living contents at maturity and assume a storage function in addition to a mechanical one.

The wood formed by the cambium in gymnosperms and dicotyledons is not composed solely of tracheary cells but contains varying proportions of parenchymatous elements, which retain their living contents for many years in the mature sapwood. These living cells differ fundamentally in size, form, and structure from the tracheary ones. They may have a primary wall only, of varying thickness and degree of lignification, as in the cedars, cypresses, redwood, etc.; or they may have an additional lignified secondary wall, as in the spruces, larches, firs, and a majority of the broad-leaved trees. They function in the synthesis and storage of starch, fat, and many other organic substances. Those of the rays facilitate radial movements of water, sugars, and various elaborated compounds forward and backward between the bast and the wood.

At this point, I anticipate considerable skepticism regarding the significance of such biological data in a symposium on the chemistry of wood. It is essential, however, that the biochemist and the biophysicist be fully cognizant of the variables in the material that they are attempting to analyze. Wood, particularly that formed in industrially significant quantity by cambial activity, is exceedingly complex and highly variable, as I have indicated, not only in different groups of land plants, but also within different parts of a single tree. Therefore, generalizations regarding the chemical composition or the physical structure of wood, or of its constituent cells, must be verified by the study of a wide range of material, to be valid and of general utility. Gross chemical analyses of wood have yielded information of great economic value, but it is becoming increasingly desirable to determine from what part of the wood each organic residue is obtained, its form and relationships when *in situ,* and the changes that it undergoes during removal.

Fourteen years ago, in a symposium of this division held at Chapel Hill, North Carolina, I summarized evidence that had accumulated regarding the microscopic, and certain phases of the submicroscopic, composition of the walls of plant cells. I shall not attempt at this time to review this evidence, since it has already been published in detail (*1*), but shall merely reemphasize certain generalizations that were formulated at that time.

In dealing with tracheary cells, as with bast and cortical fibers, stone cells, and the hairs of the cotton plant, one is concerned with two fundamentally different types of cell walls. The cells of the cambium, as of the apical meristems and such of their derivatives as retain a capacity for growth and for increase in volume, are characterized by having a wall that is capable of increasing in surface area and of undergoing reversible changes in thickness. Tracheary cells and fibers that undergo various irreversible changes during their maturation and thus lose their potentialities for growth and enlargement retain this original primary wall in a more or less modified condition, but form in addition a secondary wall of a supplementary strengthening character. The cellulosic matrix of both types of walls is composed, not of discrete particles, such as have frequently been hypothesized in the earlier literature, but of a coherent, continuous system of microfibrils. In the case of the secondary wall, where these fibrillar aggregates of chain molecules commonly are less than 500 A units in diameter, it is possible to make them visible under an ordinary microscope by carefully controlled swelling techniques and to study their configurations with considerable clarity of detail. It is no longer possible to brush them casually aside as artifacts, for their significance is now being verified by the electron microscope.

In the secondary wall, in contrast to the tenuous primary one, the microfibrils are relatively compactly arranged parallel to one another in strongly preferred orientations. The tracheids formed by the cambium in both coniferous and dicotyledonous trees commonly have a three-layered secondary wall, the fibrils of the inner and outer layers—except in the borders of the pits—being transversely oriented or in helices of relatively low pitch, whereas those of the central layer are arranged longitudinally or in helices of comparatively steep pitch. The inner and outer layers are tenuous, and fluctuations in the thickness of the secondary wall are due primarily to variations in the width of the central layer. Deviations from this typical three-ply structure occur, however, in certain modified types of tracheary cells—e.g., in the tracheids of the so-called compression wood of conifers, in the members of highly specialized forms of vessels, and in the more fiberlike elements of certain dicotyledonous woods. Such deviations may consist of multiple layering resulting from repeatedly changing preferred orientations, or from one or more discontinuities in the cellulosic matrix that are due to the deposition of noncellulosic layers.

Within the secondary wall the microfibrils of anisotropic cellulose are not uniformly distributed throughout, but in the broader central layer, at least, they are aggregated in patterns of varying density or porosity —at times, in concentric lamellae resembling the diurnal ones of the cotton hair and, at others, in radial configurations of varying complexity. The interstices between the microfibrils form a continuous system of elongated microcapillaries oriented parallel to the microfibrils. Lignin is deposited within these microcapillaries and, where it is abundant, forms a continuous system of anastomosing strands that persists as a coherent residue after chemical removal of the cellulose. Thus, the secondary wall of heavily lignified tracheary cells consists at maturity of two continuous interpenetrating systems of remarkably similar configuration, one of cellulose and the other of lignin.

The intensity of lignification varies not only in different groups and species of the land plants, but also in different cells of the same sample of wood and in different parts of the same cell. In general, the tracheids of coniferous woods and the vessel members of dicotyledonous ones—cells in which the conducting function is strongly emphasized—are heavily lignified, the tenuous primary wall, except in the membranes of the bordered pits, and the thin inner and outer layers of the secondary wall commonly being more intensely lignified than the central layer of the secondary wall. In contrast, the fiber tracheids and libriform fibers of dicotyledonous woods—cells in which the mechanical function is dominant—usually, but not invariably, are less intensely lignified, the difference being due largely to lighter lignification of the broad central layer of the secondary walls of these cells. It should be emphasized in passing that these diversified, internal fluctuations in the lignification of wood are particularly significant in the extraction of organic constituents by standardized chemical procedures and in the degradation of wood through the activity of fungi and bacteria. It should be mentioned that recent investigations (*2*) of wood, where the hydrolysis of cellulose is gradual and without conspicuous swelling of the material, provide data of considerable significance in any summation of evidence regarding structure and chemical behavior.

Although we are gradually acquiring reliable information regarding the form and distribution of cellulose and lignin in wood, less progress is being made with other organic constituents, particularly the pectic compounds and hemicelluloses of various kinds. The unlignified primary walls of cells that are capable of growth and enlargement, such as the cambial initials and their tracheary derivatives during the earlier stages of their maturation, certainly contain, in addition to cellulose, galactose, galacturonic acid, arabinose, and usually if not invariably, a relatively large proportion of protopectin. The intercellular substance between the primary walls of adjacent cells is composed, it is generally believed, of calcium pectate. There is considerable cumulative evidence that indicates that the polyuronides of the primary wall and of the intercellular substance are not replaced by lignin during the later stages of the development of wood, but persist in the mature tissue. It should be recognized in this connection that the volume of primary walls and of the intercellular substance in mature wood is so slight in comparison with that of the secondary wall that, unless the latter wall contains pectic substances, the proportion of such substances obtainable in gross analyses must be very low. Small yields of pectin can be obtained by careful analyses, at least from dicotyledonous woods.

There is no conclusive evidence, except possibly in certain aberrant types of tracheary cells, of the physiological utilization of the series galactose, galacturonic acid, and arabinose during the formation of the secondary wall. In many dicotyledonous woods there is, on the contrary, a physiological state involving glucose, glucuronic acid, and xylose.

Cumulative evidence tends to indicate that the polyuronide hemicelluloses of the secondary wall are deposited in the microcapillaries in close association with lignin; that certain polyoses of Norman's terminology may occur at times in the cavities of cells, rather than in their walls, and that the cellulosans are intimately associated in some manner with the cellulosic matrix; but the exact configurations of these substances, when *in situ,* are relatively obscure.

In conclusion, I should comment upon the unsatisfactory state of available information regarding the biochemical reactions that occur in the cambium and during successive stages in the development of fully matured wood.

There are six significant regions in the development of the woody cylinder of a tree. As seen in a cross section of a stem, these are in centripetal succession: (1) the cambial zone or region of cell multiplication, of the synthesis of protoplasm, and the formation of primary walls; (2) a zone of cell enlargement and increase in surface area of the primary walls; (3) a zone of maturation, involving in tracheary cells the formation and lignification of a secondary wall and culminating in the dissolution of their living contents; (4) a zone of fully matured sapwood containing, in addition to tracheary cells, living parenchymatous elements that function in the formation of many complex substances and in the storage of starch, fat, and other potential sources of food; (5) a zone of transformation of sapwood into heartwood, where diversified substances formed by the expiring parenchymatous cells saturate the wood; and (6) an inner core of heartwood, which contains no living cells and is chemically inert.

Owing to strong industrial stimulation, chemical research has been focused largely upon the heartwood and upon sapwood, the living cells of which have died subsequent to the felling of the tree. Furthermore, there has been a tendency to concentrate upon the study of tracheary and fiberlike cells, and to overlook the significance of parenchymatous cells as sources of certain fractions of the organic substances obtained in chemical analyses of wood as a whole. Plant physiologists, in investigating the complex biochemical processes in living cells, have naturally been inclined to deal primarily with plants of relatively small size that can be more easily grown and studied under controlled experimental conditions. Thus, there is a serious dearth of reliable information regarding the diversified biochemical reactions that occur in the living cells of the cambium, of the two succeeding zones of tissue differentiation, and of the mature sapwood. It should be recognized, in addition, that there are inherent difficulties, owing to spatial relations and cellular configurations, in studying the biochemical activities in these parts of a tree.

Under normal conditions, organic substances essential for cambial activity and the development of wood are formed in the leaves and move downward in the bast. The mechanism of rapid movement in the phloem is obscure, and the subject has been the source of much recent controversy. That photosynthesis is not indispensable in the development of wood is indicated by the demonstrated possibility of growing plants in the dark, if they are provided with an adequate supply of sucrose (*3*). Tall, etiolated sunflower plants grown under these conditions form a relatively wide zone of lignified wood. There is a summation of evidence, however, which indicates that in trees of northern environments cambial activity is activated in the spring by a downward flow of auxin from the expanding buds. It should be possible by suitable modifications of experiments with etiolated plants—supported by comparable experimentation with green ones—to determine what substances can be formed by the cambium and its living derivatives, and which ones, if any, must be obtained at all times from other parts of the plant.

Although much can be learned by such methodologies as these concerning substances essential in the development of wood, the complexities of their biochemical utilization—for example, in the formation of cell walls—must ultimately be studied in the living cells themselves. It is in this connection that the spatial relations and cellular configurations referred to in a preceding paragraph become so significant. The cells of the cambium commonly fluctuate between 4 and 8 microns in radial diameter. In slowly growing trees, the cambium consists of a single circumferential row of initials; i.e., it has a radial thickness of one cell, whereas in rapidly enlarging stems there may be two to three rows of actively dividing cells. In any case, the cambium of our common coniferous and broad-leaved trees usually does not exceed 24 microns in thickness. The zone of cell enlargement and the succeeding stages in the maturation of the sapwood may at times be considerably broader than this, but still are of relatively microscopic thickness. It is evident, accordingly, that there are inherent difficulties in removing part of any one of the successive layers and of studying it dissociated from adjacent layers. Thus, analyses of the cambium that have been reported in the literature actually are based upon a complex of cells, only a minor fraction of which are truly cambial. Similarly, so-called tissue cultures of the cambium are derived from complexes of living cells, which include, in addition to cambial initials, tissue cells that are known to be capable of dedifferentiation and of subsequent division. Furthermore, when parts of the cambium are removed from a tree and are grown in tissue cultures, the initials cease to function normally and become involved in the formation of callus, such as is formed in nature in the healing of injuries, in graft unions, and in the rooting of cuttings.

Such illustrations as these serve to emphasize the complexities and difficulties involved in studying the vital biochemical reactions that occur during successive stages in the development of wood. Thus far, progress in elucidating them has been disappointingly slow, owing in considerable part to a concentration of effort in studying their end products in fully matured wood, rather than the developmental processes themselves. However, the growth of forests on nonagricultural lands is so significant to the future welfare of man as potential sources of diversified organic substances and of stored solar energy that a sustained and comprehensive effort should now be made toward a better understanding of developmental processes in the formation of wood. To be successful such an effort must involve a much closer and broader integration of research in different scientific disciplines.

References

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News and Notes

Seminar on Social Processes in the Pacific

THE Australian National University sponsored a Jubilee Seminar on Social Processes in the Pacific August 27–29 in Canberra, with the Research School of Pacific Studies as host. Following the formal opening of the seminar by Douglas Copland, Raymond Firth, of the University of London, outlined the aims of the conference. It was not intended for the presentation of papers on original work or the discussion or formulation of research plans as such. Rather it was designed to discuss and define problems of social process in the Pacific and to formulate hypotheses for further research.

Four keynote papers were presented as points of departure for discussions. The first of these was given by Margaret Mead on "The Changing Structure of the Family and Higher Kin Units." Dr. Mead noted that in the past anthropologists have focused their attention on the unique character of island groups and have tended to lose sight of the larger regularities, which transcend differences among culture areas such as Polynesia, Melanesia, etc. She suggested that a subject requiring study is the social organization of detribalized and deculturated natives. She further indicated that an investigation of native workers may reveal new forms of social organization based on kin patterns. The central question, Dr. Mead felt, was "How are old kin relationship patterns being used in newly created situations?" Future work in the Research School will involve the study of individual cultures under contact conditions. Dr. Mead concluded by pointing out that the Pacific is becoming an arena for clashing ideologies:

> It is possible that if adequate attention is given to the formal kinship patterns, in contrast to whatever new patterns of organization and allegiance are to be introduced, considerably greater integration of native character might be maintained, and some of the destructive accompaniments of culture contact prevented—for example, the extreme growth of *anomie,* and proletarianization and detribalization.

A. P. Elkin, University of Sydney, explored the concepts of social process in the Pacific. In the process of adaptation to changing environment, the task is to determine and isolate the factors involved. Elements concerned in the process are receptiveness toward outside influences and inventiveness within the group; hostility, which strengthens the cohesion of a community; isolationism in language, customs, values; the family, which is not strongly integrated within itself; larger kin groups. Examples of fatal attacks on the structure of society were cited in the usurpation of the aborigines' land and, in Melanesia, absence for long periods at work of marriageable men. Contact and clash in the Pacific have resulted in a double life—on one side the natives express need for European benefits, whereas on the other there are conflict and hostility toward European influence.

W. E. H. Stanner, Australian National University, described "The Economic Development of Pacific Peasant Peoples against their Social Background." He listed six important basic factors affecting development in the South Pacific: relative poverty of physical resources; small and usually ill-distributed populations; high incidence of disease, malnutrition, and illiteracy; primitive technological attainment; a prevalent traditionalist ethos; social structures of fairly simple differentiation. At the more immediate level one has to deal with the factors of low average production per head, low real or monetary income per head, low rate of capital investment per head, and a high maldistribution of income. All Pacific territories also share in what Dr. Stanner termed "typical" disabilities of the "colonial" type of economy. Pacific economic prospects are not promising. Some island situations are clearly antipathetic toward development, some are anomalous and thus make prediction difficult if not impossible, and a few show some developmental coherence. The developmental problem is to change the elements that have dominated the traditional island economic systems so that expanding systems can replace the characteristic island stationary systems.

> Unfortunately, the rate of population expansion over the next twenty years will probably be so high that the rate and scale of capital investment needed to maintain