Reprinted from
ANNUAL REVIEW OF PHYTOPATHOLOGY
Vol. 11, 1973

HEARTWOOD, DISCOLORED WOOD, AND MICROORGANISMS IN LIVING TREES

Alex L. Shigo and W. E. Hillis
Northeastern Forest Experiment Station, U.S.D.A. Forest Service, Durham, New Hampshire, and Forest Products Laboratory, Division of Applied Chemistry, Commonwealth Scientific and Industrial Research Organization, South Melbourne, Victoria, Australia

The state of our knowledge of plant pathology is reflected by the terms we use (120). Consider some of the terms used to describe wood altered by processes associated with aging and injury of living trees: heartwood, wound heartwood, pathological heartwood, traumatic heartwood, false heartwood, precocious heartwood, blackheart, brownheart, red heart, blue butt, mineral streak, mineral stain, woundwood, discolored wood, wound-initiated discolored wood, wetwood, ripewood, reaction zone, protection wood, and even true wood. Indeed, there is confusion!

The main visible change observed in wood of trees is change of color. This can be the result of processes associated with aging (heartwood), injury (discolored wood), or both. However there are more important characteristics than color for the sapwood altered by these processes. The factors that initiate the formation of heartwood, discolored wood, and extractives (which are largely responsible for color) are different.

This is the major reason for the confusion in understanding a situation when color alone is the basis for distinguishing the type of tissue under study. When injury-altered tissues are considered as age-altered tissues, and the role of microorganisms in the processes are not considered, it is impossible to interpret the situation accurately. The confusion is further compounded when the injury processes occur in tissues already altered by aging. Clarification of these processes obviously is needed.

We will discuss in this review those processes in living trees that are associated with colored wood, in the hope of clarifying them so that future research will be more accurately oriented and the opportunity to bring these changes under our control will be improved. We will consider and contrast two types of wood, which we will refer to as "heartwood" and "discolored wood."

remain viable for many years. In *Tamarix aphylla* sapwood, however, the fibers retain their living protoplasts for the same period as the parenchyma and ray cells (36). The shape of the nuclei of living ray parenchyma cells in the sapwood of several species of Gymnosperms and Angiosperms changes and they eventually disintegrate (45, 64). They lose organelles (36), their vitality (115), nitrogen-containing compounds (106), starch (69), and their ability to consume oxygen (65) as their distance from the cambial region increases. The amount of sugars and biotin and pyridoxine can decrease abruptly at the heartwood boundary (27, 181).

The sapwood vessels in Angiosperms occasionally contain tyloses; but as heartwood and discolored wood form, they usually appear in much greater numbers in many species, so that movement of liquids and perhaps microorganisms is blocked. Aspiration of the pits in conifer tracheids as heartwood forms has a similar effect on liquid movement.

To meet different physiological needs throughout the year, primary metabolites are stored in the sapwood in the form of starch or fats, according to the type of tree (68). The amounts vary according to prior needs and current demands, and are not uniform across the sapwood. The distribution of photosynthates within a tree can be considered a system of competing metabolic sinks, which are constantly changing in size according to the needs of a particular zone at a particular time. There is little information about the dynamic translocation of carbohydrate through the rays of the sapwood.

Formation of Heartwood

The sapwood of the trunk, branches, and roots of many—but not all—uninjured trees changes abruptly in appearance and function after a certain age. This interior core is "heartwood," of which one definition is: "The inner layers of wood which, in the growing tree, have ceased to contain living cells and in which the reserve materials (e.g. starch) have been removed or converted into heartwood substances. It is generally darker in color than sapwood, though not always clearly differentiated" (84).

The proportion, and even the existence, of heartwood in a mature tree varies within the family, genus, and even species (25, 76). Within a species, under normal circumstances, the amount and rate of heartwood formation varies to a lesser extent with tree age (66), growth rate, environment, and silviculture practice (154). In some genera (such as *Eucalyptus*) and in some species, the age of the sapwood transformed to heartwood is remarkably constant (25), and possibly is mainly genetically determined. It has been observed with some species that heartwood formation commences at some distance above ground level (25, 166) and that the proportion of heartwood in some species remains greatest at this level. Sometimes, however, heartwood may never form, as in *Alstonia scholaris* (19). Living cells 115 years old have been found in *Acer saccharum* (50).

shown an increase in vitality in the parenchymous cells (80), and in respiration (180) at the heartwood periphery. Extractives are formed mainly in the radial parenchyma, but the longitudinal parenchyma can also form them. Peroxidase activity increased markedly at the periphery of the heartwood (27, 95, 172), as did the activities of amylase (78), phenol oxidases, malate dehydrogenase, etc. (182). Recent studies showed that tyloses form before extractives in *Eucalyptus* and *Nothofagus* species (V. Nečesaný, unpublished), and that calcium oxalate crystals are not found in the cells containing polyphenols (G. Scurfield, unpublished). The chemical reactivity of cellulose in Douglas-fir trees, as shown by the accessibility of hydroxyl groups, revealed a marked maximum at the sapwood-heartwood boundary. The carbonyl index, moisture content, and extractives content also showed maxima at the same point, indicating increased biochemical activity in this region (20).

The transformation of sapwood to heartwood is accompanied by necrosis of the xylem parenchyma, although some enzymic activity may be found in the heartwood. Phenol-oxidizing enzymes have been reported in the heartwood of *Pinus lambertiana* (159), and the two found in *P. radiata* heartwood were probably of host origin (137). Other major differences from sapwood can include aspiration of the pits in Gymnosperms (53), formation of tyloses in Angiosperms, or gum when the pit aperture is less than 10μ (18). Although starch is absent from heartwood, small amounts of free sugar may be found (74). The nitrogen content is lower (106), and the pH higher than in sapwood (74). Fatty and resinous materials that are stored in sapwood of some trees instead of starch, are changed in composition as heartwood forms (62, 109). The most noticeable change is the formation of nonstructural material, (extractives), sometimes in amounts exceeding 30% of the total wood, which increases the density, color, durability, and many other properties of the wood (68, 74, 76).

Extractives accumulate in the lumen, or occlude or encrust pits and walls (7, 38, 91, 92). In some species, phenolic substances can diffuse from the ray parenchyma cells into the cell walls and into fiber lumens (38). The capillaries of the cell wall are wide enough to accommodate the molecules of some extractives (75). There is a good deal of indirect evidence for the presence of extractives in cell walls of the heartwood of different species (162, 170) (W. E. Hillis, unpublished data). New techniques, such as the use of gas-liquid chromatography and microspectrophotometry, make it possible for very small amounts of most extractives to be estimated or detected in small parts of tissues. These and other techniques will enable the relative amounts of extractives in the cell wall and lumen to be determined (10, 92). Toxic components probably convey greater durability if present in the cell wall than in the lumen.

The amounts of polyphenols formed in cultures of *Juniperus eommunis* (23), rose (26), and tea (40) were dependent on the sugar concentration.

point the narrow transition zone (when present) or the heartwood periphery as dynamic zones in the living tree. Chattaway (19) suggested that heartwood formation must be preceded by a period of increased metabolic activity. Other workers suggested that both the Krebs cycle and pentose shunt enzymes were affected (66, 70, 72, 74, 182).

Although some direct evidence of increased metabolic activity has been found at the heartwood periphery (95, 105, 180), most studies have been unsuccessful in this regard. Hirai (77) produced evidence that heartwood formation takes place mainly when cambial growth ceases, so that the frequently reported lack of evidence of activity at the heartwood periphery could be due to collection of samples at inappropriate periods. The recent work of L. Shain & J. F. G. Mackay (unpublished data) has shown that increases in respiration and the activity of malate and glucose-6-phosphate dehydrogenases in the transition zone of *P. radiata* are seasonal, maximum amounts occurring in the dormant period of tree growth. The factor that initiates these increases in activity requires consideration.

Many studies have shown that ethylene acts as a regulatory hormone (14, 119) in a variety of physiological changes occurring at many stages in the ontogeny of plants. It can play an important role in the regulation of cellular metabolism, which is related not only to morphological changes, but also to basic cell processes. Very small amounts (1–5 ppm and smaller) of ethylene effectively trigger a wide range of events according to the tissue involved (12, 14, 119). Because of the ready production of ethylene on injury of many tissues and their sensitivity to it, experimental work in this area is fraught with difficulties (119). The considerable data collected on ethylene in studies of vegetative tissues point to a probable pattern of events that lead to heartwood and extractives formation.

Ethylene is produced by the transition zone surrounding the heartwood of *Pinus radiata* (the peak of production taking place in the dormant period) and in larger amounts than the adjacent sapwood (L. Shain & W. E. Hillis, unpublished data). In *P. radiata,* the transition zone contains very small amounts of polyphenols and a lower moisture content than the heartwood. The transition zone of *Eucalyptus tereticornis* also produces more ethylene than the sapwood, but in this species the transition zone contains more polyphenols than the sapwood, and has a moisture content similar to that of sapwood and heartwood (W. E. Hillis, unpublished data). Cell suspension or callus cultures of different plants, including sycamore, also release ethylene; and a very sharp peak of production occurs in the latter after 10–14 days of culture (113) or toward the end of the growing phase of cell cultures (96).

The factor initiating ethylene production by injured, diseased, or senescing plant tissues has not been established (119). There is an absolute need for oxygen (102) and, at low oxygen concentration, sensitivity of the tissue to ethylene is decreased. Once the threshold value is exceeded, the system can produce ethylene autocatalytically. However, the system does not seem to be

overall effect of auxin in heartwood formation requires further study. A very high concentration of carbon dioxide has also been reported to be conducive to the formation of heartwood polyphenols in *Acacia mearnsii* (15).

Although the most detailed studies on ethylene were concerned with the production of polyphenols, it is well established that ethylene promotes an increased production of rubber in *Hevea braziliensis* (2) and carbohydrate gum in *Prunus* spp. (W. E. Hillis, unpublished data).

In summary, evidence indicates that ethylene plays a key role in the formation of extractives, which are largely responsible for the color of heartwood. Whether the initiation of ethylene formation is triggered by water stress, which has been suggested as a key factor in heartwood formation (129, 183), remains to be determined. Heartwood extractives are formed at the heartwood periphery or in the transition zone during the dormant season, from translocated or stored carbohydrate. Peroxidase, whose activity increases at the heartwood periphery (95, 172), and the phenol oxidases in the heartwood (27, 89), can cause darkening of the tissues after exposure to air.

The role played by ethylene in the formation of discolored wood requires determination. It is notable that different trees of *P. radiata* respond differently to *Sirex-Amylostereum* damage in the formation of ethylene, polyphenols, and discolored wood. The ethylene appears to result from host-parasite interaction. It is known that some fungi produce ethylene; and whether these produce discolored wood—in contrast to those that do not form ethylene—requires further study. It should be noted, however, that discolored wood can have a different composition from that of heartwood in the same tree.

Formation of Discolored Wood

The major conditions in heartwood formation—cell death, depletion of nutrients, deposits in cells with darkening of tissues—also occur in formation of discolored wood, but there are other processes too.

Though discoloration is a condition of the wood, the color is a poor indicator of the changes that have occurred (144). Attention should be focussed on the events that follow wounding, rather than on one minor condition—discoloration—of these important events. Although this minor condition has served as the focus for so many studies, it will be treated here within the broad context of the events that follow wounding.

The many events that occur from wounding to total decomposition of tissues are continuous over time, and actually it is not possible to separate them. But, for the sake of clarifying the events that follow wounding and putting discoloration and decay in proper perspective, the sequence of events in a model system are separated into three major stages (143) (See Table 1).

Stage I includes all processes associated with host response to wounding, in which both the tree and the environment are considered. Slight discoloration may occur in the xylem as a result of chemical processes, including those involving formation of phenols and other components, and oxidation resulting from exposure to air (37, 47, 90, 98, 160).

similar tissues. Most branch wounds heal and prevent exposure of the trunk to air and microorganisms, but healing may be complete only after some of the trunk tissues have been altered. One of the minor conditions of the altered tissues in Stage I is discoloration. More discoloration is associated with branch wounds than with any other type of wound, and it is usually in the center of the tree.

The severity of the wound and the vigor of the host affect the rate and effectiveness of the tree's response to the wound (116, 161). Wounds that break the bark, but injure the cambium and xylem only slightly, usually heal rapidly (21, 143), although it has been found that the "wound heartwood" of *Pinus sylvestris* forms with the beginning of cambial activity and terminates in winter (100). The processes can stop in Stage I, and some discoloration may be associated with the wound.

It is noteworthy that when the sapwood is deeply penetrated by a wound, a pale-colored transition zone (similar to that around heartwood) surrounds the discolored wood in a number of species (133, 144). A similar zone has been observed around the discolored wood of lesions resulting from attack on *P. radiata* by the *Sirex-Amylostereum* complex (136), and on *Picea abies* by *Fomes annosus* (134). Thus, with some species at least, there is a visual similarity between the formation of discolored wood and heartwood, and further examination may show the existence of the transition zone to be more widespread.

HOST RESPONSE TO WOUNDING The response to wounding in herbaceous and woody plants is similar in principle: a chemical protective response occurs, and tissues darken (127). Most woody plants survive after wounding because the protective response is effective most of the time. However, in some cases, the tree may be so low in vigor, or the conditions for invasion by microorganisms may be so favorable because of inoculum quantity, environmental conditions, and severity of wound, that invasion occurs rapidly. Between the extremes of no invasion and rapid invasion are all degrees of effectiveness of host protection and aggressiveness of microorganisms. Also, between the extremes there are all degrees and gradations of color changes in the wood.

In general, the living sapwood cells show a dynamic response, and discolored wood containing extractives is formed in a zone several millimeters wide around the area containing microorganisms (133). Heartwood shows a passive response. When the protection processes in Stage I function effectively, the xylem altered by host response to wounding is indeed a protective wood that resists invasion by microorganisms, and "protection wood" (43, 63, 87) is an accurate term for these tissues.

The extractives formed in "protection wood" or "reaction zone," as in the lesions from *Fomes annosus* (133, 135), *Sirex noctilio-Amylostereum areolatum* (73), etc., can be different from those of the heartwood and even those of lesions in different trees of the same species. The extractives can play a

that have a colored core of age-altered wood, the columns of discoloration and decay advance most rapidly above and below the wound along the sapwood-heartwood boundary that was present at the time of wounding (146). When severe wounds occur, however, the entire column of wood present at the time of wounding may discolor and decay (64).

SUCCESSION OF MICROORGANISMS Microorganisms that inhabit wood in living trees have the greatest survival advantage when they attack wounds in a sequential manner. Each invading microorganism exerts its specific force against the dynamic protective barriers formed by the wounded tree. The pioneer microorganisms first alter the substrate to their advantage and then digest the cell contents. As the pioneers advance, the substrate is altered further to the advantage of other organisms that follow—a *succession* (5, 6, 31, 34, 51, 97, 101, 107, 140, 163).

A good account of microorganisms associated with heartwood in *Thuja plicata* was given by Eades & Alexander (28) and by Findlay & Pettifor (39). Dark and light heartwood occur in this species; the dark heartwood contained nondecay fungi, but no organisms were found in the light heartwood. Findlay & Pettifor concluded that the fungi were responsible for the dark heartwood and its reduced strength and specific gravity. The toxicity of dark heartwood is also low (48). Consequently it would be more correctly defined as discolored wood. The hyphae they observed in the cells was shown by Roff (126) to be due to nonhymenomycetous fungi, and thus the conclusion of Findlay & Pettifor was supported that the fungus in the "dark heartwood" probably was not a decay fungus.

Findlay & Pettifor also reported (39) results from laboratory tests showing that test blocks of dark heartwood were susceptible to attack by certain hymenomycetous fungi such as *Coniophora cerebella,* whereas it was with great difficulty that fungi could be induced to grow at all over the light-colored heartwood. The results indicated that the pioneer nonhymenomycetous fungi altered the wood to the advantage of *C. cerebella.* Similar results with *Acer saccharum* suggested that the pioneer microorganisms attack wood altered as a result of host response to injury, and the alterations are to the advantage of hymenomycetes (142). Tissues in Stage I may have evolved as effective deterents to invasion by hymenomycetes. The bacteria and nonhymenomycetous fungi then probably adapted to the new substrate.

COMPARTMENTALIZATION As resistant as the tissues may be in Stage I, under certain conditions some microorganisms are able to surmount the chemical protective barriers and invade. At this time the tree forms a second line of defense and restricts the path of the invaders.

One of the first mechanical barriers to form in tissues after wounding is plugged vessels (124, 138). In those species capable of doing so, tyloses are formed; and in the other species the vessels are plugged with a gummy material (138, 160). These plugs begin to form in *Acer rubrum* a few days after

cesses, growth of microorganisms (112, 147, 171), etc. Shakes are associated with wounds, but not all wounds form shakes (147).

If part of the cambium of eucalypts and some other trees containing heartwood is killed, the region between that part and the heartwood remains as "included sapwood" when the adjacent sapwood is converted to heartwood during subsequent growth of the tree (68). These areas can subsequently discolor and decay. Included sapwood is frequently seen in trees that have been scarred by fire (146).

Differences Between Heartwood and Discolored Wood, and Means of Recognition

When living sapwood cells encounter different stimuli, they usually respond differently when forming colored wood. The latter can be heartwood when the oldest tissues are affected first, or different types of discolored wood when often the youngest tissues are affected first. The differences between sapwood-heartwood and sapwood-discolored wood are mainly in the amount and distribution of inorganic elements, the pH, the amount and composition of extractives, and moisture content.

EXTRACTIVES Normal heartwood has a similar color throughout the cross-section of a log, and a chemical composition that is in almost all cases constant for a particular species. In injured and discolored wood, the amount of extractives is higher than in the sapwood, amorphous deposits of melanistic substances are more abundant than in heartwood (55), and the extractable materials in these tissues frequently differ qualitatively from each other (74, 76, 135). Discolored woods of the same species, and apparently resulting from the same cause, can contain different ratios of components (73).

Components in discolored wood can be different from those found in heartwood, as in *Prunus* species affected by *Trametes versicolor* (60) and *Stereum purpureum* (67). The cellular inclusions in histological examinations have been defined as tannins, deposits, etc.—in most cases without consideration of their variable composition, which can be different even a few cells apart (92). Aside from the confusion caused by the theories regarding their biogenesis, such loose terminology overlooks their difference in properties to invading organisms, either by presenting physical barriers such as gums or by forming toxic components. Certain types of wounds in certain species show a stimulation of the synthesis and accumulation of materials inhibitory to decay fungi; in other species the discolored wood surrounding the wounds is no more decay-resistant than the sapwood of that particular species (57). The age of the sapwood that has given rise to discolored wood may also influence the ability of the latter to resist decay fungi. It should be noted, however, that the ability of the sapwood to form discolored wood containing toxic components may be linked with an ability to produce heartwood resistant to decay fungi (57).

in the surrounding tissue. Discolored wood of sugar maple had 6 times more ash than normal sapwood; however, there was a 9-fold increase in calcium but a 56% reduction in potassium (E. L. Ellis, unpublished data). There can also be an increase in manganese with this species (148). The differences in these three aspects in shagbark hickory are much greater (29).

The situation can be more complex. Hart (55) found in the discolored wood of *Robinia pseudoacacia* a 136% increase in ash as compared with normal sapwood, when potassium increased 61%, calcium 100%, and magnesium 168%, but phosphorus decreased 35%. A similar pattern was observed with *Maclura pomifera.* The minerals in the stained wood of *Acer saccharum* are not removed by water, and this behavior may be due to combination with the polyphenols (N. Levitin, unpublished). It is interesting that, whereas the accumulation of calcium salts in aging cells of plants is well documented (167), the increase observed in discolored wood has not so far been observed in heartwood.

The discolored woods of *Quercus alba, Maclura pomifera, Robinia pseudoacacia, Juglans nigra,* and *Acer saccharum* had higher pH, moisture, and ash contents than uninjured sapwood (56). The deeper the stain of discolored wood of *A. saccharum,* the higher the pH and mineral content (50; N. Levitin, unpublished). As the wound that resulted in the surrounding discolored wood of sugar maple is approached, there is a general increase in moisture (144), pH, and ash (144, 163, 164). The pH of the discolored wood of *Picea abies* (134) and *Quercus rubra* (130, 142, 171) is also higher near the wound. The pH of discolored wood of many species is above 6, even as high as 9 (50, 144), whereas that of sapwood and, in particular, heartwood in the same stem is below the pH of discolored wood, usually below pH 5.5.

Valuable use has recently been made of the content of inorganic materials and of developments in electrical techniques to detect discoloration and decay in living trees. The technique enables a quantitative and objective assessment of discolored wood and heartwood.

The changes in concentration of ions in wood are in direct relation to resistance to a pulsed electric current (153, 165). As tissues die, discolor, and decay, the resistance to a pulsed electric current decreases, as long as the moisture content of the wood being measured remains above the fiber saturation point (165). The decrease in resistance is related to the increase in mobile ions (such as potassium) in dying tissues, leading to discolored wood (165). Resistance to a pulsed electric current throughout unaltered and uninfected heartwood in *Quercus* spp. is higher than that of sapwood (165). The electrical apparatus indicates the differences between age-altered high-resistance (12–60 thousand ohms) tissues and injury-altered low-resistance (1–20 thousand ohms) tissues. The measurements indicate accurately the degree of degradation of injury-altered tissues (153, 165) in living trees. With this method, numbers can be put on the model system to show that, as the tissues go from Stages I to II to III, the resistance to a pulsed electric current decreases steadily.

Literature Cited

1. Abeles, F. B., Leather, G. R. 1971. Control of cellulase secretion by ethylene. *Planta* 97: 87–91
2. Abraham, P. D., Wycherley, P. R., Pakianathan, S. W. 1968. Stimulation of latex flow in *Hevea brasiliensis* by 4-amino-3,5,6-trichloropicolinic acid and 2-chloroethane-phosphoric acid. *J. Rubber Res. Inst. Malaya* 20:291–305
3. Anderson, A. B., Scheffer, T. C., Duncan, C. G. 1963. The chemistry of decay resistance and its decrease with heartwood aging in incense cedar (*Libocedrus decurrens*). *Holzforschung* 17:1–5
4. Bakshi, B. K., Singh, S. 1970. Heart rots in trees. *Int. Rev. Forest. Res.* 3:197–251
5. Basham, J. T. 1958. Decay of trembling aspen. *Can. J. Bot.* 36: 491–505
6. Basham, J. T. 1966. Heart rot of jack pine in Ontario. *Can. J. Bot.* 44:275–95
7. Bauch, J., Liese, W., Scholz, F. 1968. Über die Entwicklung und staffliche Zusammensetzung der Hoftüpfelmembranen von Längatracheiden im Coniferen. *Holzforschung* 22:144–53
8. Berlin, J., Barz, W. 1971. Metabolism of isoflavones and coumestanes in cell and callus suspension cultures of *Phaseolus aureus*. *Planta* 98:300–14
9. Berlyn, G. P. 1969. Microspectrophotometric investigation of free space in plant cell walls. *Am. J. Bot.* 56:498–506
10. Bland, D. E., Hillis, W. E. 1969. Microspectrophotometric investigation of lignin and polyphenol distribution in wood sections. *Appita* 23:204–10
11. Brooks, F. T., Moore, W. C. 1926. Silver leaf disease—V. *J. Pomol. Hort. Sci.* 5:61–97
12. Burg, S. P., Burg, E. A. 1965. Ethylene action and the ripening of fruits. *Science* 148:1190–96
13. Burg, S. P., Burg, E. A. 1967. Molecular requirements for the biological activity of ethylene. *Plant Physiol.* 42:144–52
14. Burg, S. P. 1968. Ethylene, plant senescence and abscission. *Plant Physiol.* 43:1503–11
15. Carrodus, B. B. 1970. Carbon dioxide and the formation of heartwood. *New Phytol.* 70:939–43
16. Carter, J. C. 1945. Wetwood of elms. *Ill. Nat. Hist. Surv. Bull.* 23:407–48
17. Chalutz, E., De Vay, J. E., Maxie, E. C. 1969. Ethylene-induced isocoumarin formation in carrot root tissue. *Plant Physiol.* 44:235–41
18. Chattaway, M. M. 1949. The development of tyloses and secretion of gum in heartwood formation. *Aust. J. Biol. Sci.* 2B:227–40
19. Chattaway, M. M. 1952. The sapwood-heartwood transition. *Aust. Forest.* 16:25–34
20. Chow, S.-Z. 1972. Hydroxyl accessibility, moisture content, and biochemical activity in cell walls of Douglas-fir trees. *Tappi* 55: 539–44
21. Chudnoff, M. 1971. Tissue regeneration of debarked eucalypts. *Forest Sci.* 17:300–05
22. Clark, J., Gibbs, R. D. 1957. Studies in tree physiology. Part IV. *Can. J. Bot.* 35:219–53
23. Constabel, F. 1968. Gerbstoffproduktion der Calluskulturen von *Juniperus communis*. *Planta* 79: 58–64
24. Cosenza, B. J., McCreary, M., Buck, J. D., Shigo, A. L. 1970. Bacteria associated with discolored and decayed tissues in beech, birch and maple. *Phytopathology* 60:1547–51
25. Dadswell, H. E., Hillis, W. E. 1962. Wood. In: *Wood extractives and their significance to the pulp and paper industry*. Ed. W. E. Hillis 3–55 New York: Academic 513 p.
26. Davies, M. E. 1972. Effects of auxin on polyphenol accumulation and the development of phenylalanine ammonia-lyase activity in darkgrown suspension cultures of Paul's scarlet rose. *Planta* 104: 66–77
27. Dietrichs, H. H. 1964. Chemisch-physiologische Untersuchungen über die Split-Kern-Umwandlung

significance in decay. *Can. J. Bot.* 40:615–24
52. Harris, J. M. 1954. Heartwood formation in *Pinus radiata. New Zealand Forest Serv. Forest Res. Inst. Tech. Pap. 1*
53. Harris, J. M. 1954. Heartwood formation in *Pinus radiata. New Phytol.* 53:517–24
54. Hart, J. H. 1965. Formation of discolored sapwood in three species of hardwoods. *Mich. Agr. Exp. Sta. Quart. Bull.* 48:101–16. East Lansing
55. Hart, J. H. 1968. Morphological and chemical differences between sapwood, discolored sapwood and heartwood in black locust and osage orange. *Forest Sci.* 24:334–38
56. Hart, J. H., Wardell, J. F., Johnson, K. C. 1969. Abstr. *XI Int. Bot. Congr. 11:* Seattle
57. Hart, J. H., Johnson, K. C. 1970. Production of decay-resistant sapwood in response to injury. *Wood Sci. Technol.* 4:267–72
58. Hart, J. H., Hillis, W. E. 1972. Inhibition of wood-rotting fungi by ellagitannins in the heartwood of *Quercus alba. Phytopathology* 62: 620–26
59. Hartley, C., Davidson, R. W., Crandall, B. S. 1961. Wetwood, bacteria, and increased pH in trees. *U. S. Dept. Agr. Forest Serv. Forest Prod. Lab. Rept.* 2215. 34 p.
60. Hasegawa, M., Shirato, T. 1959. Abnormal constituents of *Prunus* wood. Isoolivil from *P. jamasakura* wood. *J. Jap. Forest. Soc.* 41:1–4
61. Hemingway, R. W., Hillis, W. E. 1970. Heartwood formation in living stumps of Douglas-fir. *Wood Sci. Technol.* 4:246–54
62. Hemingway, R. W., Hillis, W. E. 1971. Changes in fats and resins of *Pinus radiata* associated with heartwood formation. *Appita* 24: 439–43
63. Hepting, G. H., Blaisdell, D. J. 1936. A protective zone in red gum fire scars. *Phytopathology* 26:62–67
64. Hepting, G. H., Shigo, A. L. 1972. Difference in decay rate following fire between oaks in North Carolina and Maine. *Plant Dis. Reptr.* 56:406–07
65. Higuchi, T., Fukazawa, K., Shimada, M. 1967. Biochemical studies on the heartwood formation. *Hokkaido Univ. Coll. Exp. Forest. Res. Bull.* 25:167–94
66. Higuchi, T., Shimada, M., Watanabe, K. 1967. Studies on the mechanism of heartwood formation. Pt V. *J. Jap. Wood Res. Soc.* 13:269–73
67. Hillis, W. E., Swain, T. 1959. Phenolic constituents of *Prunus domestica.* III. *J. Sci. Food Agr.* 10: 533–37
68. Hillis, W. E. 1962. The distribution and formation of polyphenols within the tree. In: *Wood Extractives and their Significance to the Pulp anl Paper Industry:* 59–131 Ed. W. E. Hillis, Academic: New York. 513 pp.
69. Hillis, W. E., Humphreys, F. R., Bamber, R. K., Carle, A. 1962. Factors influencing the formation of phloem and heartwood polyphenols. *Holzforschung* 16:114–21
70. Hillis, W. E. 1964. The formation of polyphenols in trees. II. The polyphenols of *Eucalyptus sieberiana* kino. *Biochem. J.* 92:516–21
71. Hillis, W. E. 1966. Variation in polyphenol composition within species of *Eucalyptus. Phytochemistry* 5:541–56
72. Hillis, W. E., Inoue, T. 1966. The formation of polyphenols in trees. III. The effect of enzyme inhibitors. *Phytochemistry* 5:483–90
73. Hillis, W. E., Inoue, T. 1968. The formation of polyphenols in trees. IV. The polyphenols formed in *Pinus radiata* after *Sirex* attack. *Phytochemistry* 7:13–22
74. Hillis, W. E. 1968. Chemical aspects of heartwood formation. *Wood Sci. Technol.* 2:241–59
75. Hillis, W. E. 1969. The contribution of polyphenolic wood extractives to pulp colour. *Appita* 23: 89–101
76. Hillis, W. E. 1971. Distribution, properties and formation of some wood extractives. *Wood Sci. Technol.* 5:272–89
77. Hirai, S. 1951. Study on the pro-

protein in developing fig fruits. *Plant Physiol.* 48:806–08
105. Matsukuma, N., Kawano, H., Shibata, Y., Kondo, T. 1965. Studies on the intermediate zone of sugi wood, some physiological activities of the xylem tissue. *J. Jap. Wood Res. Soc.* 11:227–31
106. Merrill, W., Cowling, E. B. 1966. Role of nitrogen in wood deterioration: Amounts and distribution of nitrogen in tree stems. *Can. J. Bot.* 44:1555–80
107. Merrill, W. 1970. Spore germination and host penetration by heart-rotting hymenomycetes. *Ann. Rev. Phytopathol.* 8:281–300
108. Miller, C. O. 1969. Control of deoxyisoflavone synthesis in soy bean. *Planta* 87:26–35
109. Mutton, D. B. 1962. Wood resin. In: *Wood Extractives and their Significance to the Pulp and Paper Industry:* 337–63. Ed. W. E. Hillis, Academic: New York. 513 pp.
110. MacDougal, D. T. 1927. *Composition of gases in trunks of trees.* Carnegie Inst. Wash. 26:162–63
111. MacDougal, D. T., Overton, J. B., Smith, G. M. 1929. *The hydrostatic-pneumatic system of certain trees.* Carnegie Inst. Wash. 1–98
112. McGinnes, E. A., Jr., Chang, C. I. J., Wu, K. Y. T. 1971. Ring-shake in some hardwood species: The individual tree approach. *J. Polymer Sci.* 36:153–76
113. MacKenzie, I. A., Street, H. E. 1970. Studies on the growth in culture of plant cells. VIII. The production of ethylene by suspension cultures of *Acer pseudoplatanus. J. Exp. Bot.* 21:824–34
114. McMichael, B. L., Jordan, W. R., Powell, R. D. 1972. An effect of water stress on ethylene production by intact cotton petioles. *Plant Physiol.* 49:658–60
115. Nečesaný, V. 1966. Die Vitälitarsveranderung der Parenchymzellen als physiologische Grundlage der Kernholzbildung. *Holzforschung Holzverwert.* 18:61–65
116. Neely, D. 1970. Healing of wounds on trees. *J. Am. Hort. Sci.* 95:536–40
117. Nelson, N. D., Maeglin, R. R., Wahlgren, H. E. 1969. Relationship of black walnut wood color to soil properties and site. *Wood & Fiber* 1:29–37
118. Nobuchi, T., Harada, H. 1968. Electron microscopy of the cytological structure of the ray parenchyma cells associated with heartwood formation of sugi (*Cryptomeria japonica*). *Jap. Wood Res. Soc.* 14:197–202
119. Pratt, H. K. Goeschl, J. D. 1969. Physiological roles of ethylene in plants. *Ann. Rev. Plant Physiol.* 20:541–84
120. Pringle, R. B., Scheffer, R. P. 1964. Host-specific plant toxins. *Ann. Rev. Phytopathol.* 2:133–56
121. Reid, M. S., Pratt, H. K. 1972. Effects of ethylene on potato tuber respiration. *Plant Physiol.* 49: 252–55
122. Rhodes, M. J. C., Wooltorton, L. S. C. 1971. The effect of ethylene on the respiration and on the effect of phenylalanine ammonia lyase in swede and parsnip root tissue. *Phytochemistry* 10:1989–97
123. Ridge, I., Osborne, D. J. 1970. Regulation of peroxidase activity by ethylene in *Pisum sativum. J. Exp. Bot.* 21:720–24
124. Rier, J. P., Shigo, A. L. 1972. Some changes in red maple, *Acer rubrum,* tissues within 34 days after wounding in July. *Can. J. Bot.* 50:1783–84
125. Rishbeth, J. 1951. Observations on the biology of *Fomes annosus,* with particular reference to East Anglian pine plantations. *Ann. Bot.* 15:1–21
126. Roff, J. W. 1964. Hyphal characteristics of certain fungi in wood. *Mycologia* 56:799–804
127. Rubin, B. A., Artsikhovskaya, E. V. 1964. Biochemistry of pathological darkening of plant tissues. *Ann. Rev. Phytopathol.* 2:159–78
128. Rudman, P. 1965. The causes of variations in the natural durability of wood: Inherent factors and ageing and their effects on resistance to biological attack. *Holz u. Organismen* 1:151–62 Ed. G. Becker, W. Liese. Duncker & Humblot: Berlin
129. Rudman, P. 1966. Heartwood formation in trees, *Nature* (London) 210:608–10

Stain and decay around carpenterworm galleries in southern hardwood trees. *U. S. Dept. Agr. Forest Serv. S. Forest Exp. Sta.* Res. Note. 4 pp.
156. Stahmann, M. A., Clare, B. G., Woodbury, W. 1966. Increased disease resistance and enzyme activity induced by ethylene production by black rot infected sweet potato tissue. *Plant Physiol.* 41: 1505–12
157. Stankewich, J. P., Cosenza, B. J., Shigo, A. L. 1971. *Clostridium quercicolum* sp. n. isolated from discolored tissues in living oak trees. *Anton. van Leeuwenhoek* 37:299–302
158. Stewart, C. M. 1966. Excretion and heartwood formation in living trees. *Science* 153:1068–74
159. Stutz, R. E. 1959. Control of brown stain in sugar pine with sodium azide. *Forest Prod. J.* 9: 459–63
160. Sucoff, E., Ratsch, H. Hook, D. 1967. Early development of wound-initiated discoloration in *Populus tremuloides* Michx. *Can. J. Bot.* 45:649–56
161. Swarbrick, T. 1926. The healing of wounds in woody stems. *J. Pomol. Hort. Sci.* 5:98–114
162. Tarkow, H., Krueger, J. 1961. Distribution of hot-water soluble material in cell walls and cavities of redwood. *Forest Prod. J.* 11: 228–29
163. Tattar, T. A., Shortle, W. C., Rich, A. E. 1971. Sequence of microorganisms and changes in constituents associated with discoloration and decay of sugar maples infected with *Fomes connatus. Phytopathology* 61:556–58
164. Tattar, R. A., Rich, A. E. 1973. Extractable phenols in clear, discolored, and decayed wood tissues and bark of sugar maple. *Phytopathology* 63: (in press)
165. Tattar, T. A., Shigo, A. L., Chase, T. 1972. Relationship between the degree of resistance to pulsed electric current and wood in progressive stages of discoloration and decay in living trees. *Can. J. Forest. Res.* 2:236–43
166. Trendelenburg, R., Mayer-Wegelin, H. 1955. In: *Das Holz als Rohstoff:* 245–62. Hanser Verlag: Munich
167. Varner, J. E. 1961. Biochemistry of senescence. *Ann. Rev. Plant Physiol.* 12:245–64
168. Wallin, W. B. 1954. Wetwood in balsam poplar. *Minn. Forest Note* 28, 2 pp.
169. Wallis, G. W., Reynolds, G. 1965. The initiation and spread of *Poria weirii* root rot of Douglas fir. *Can. J. Bot.* 43:1–9
170. Wangaard, F. F., Granados, L. A. 1967. The effect of extractives on water-vapor sorption by wood. *Wood Sci. Technol.* 1:253–77
171. Ward, J. C., Hann, R. A., Baltes, R. C., Bulgrin, E. H. 1972. Honeycomb and ring failure in bacterially infected red oak lumber after kiln drying. *U. S. Dept. Agr. Forest Serv. Res. Paper FPL-165.* 36 pp.
172. Wardrop, A. B., Cronshaw, J. 1962. Formation of phenolic substances in the ray parenchyma of angiosperms. *Nature* (London) 193:90–92
173. Whitney, R. D. 1961. Root wounds and associated root rots of white spruce. *Forest. Chron.* 37:401–11
174. Wilcox, W. W. 1968. Some physical and mechanical properties of wetwood in white fir. *Forest Prod. J.* 18:27–31
175. Wilson, C. L. 1959. The Columbian timber beetle and associated fungi in white oak. *Forest Sci.* 5: 114–27
176. Wright, E. 1938. Further investigations of brown-staining fungi associated with engraver beetle (*Scolytus*) in white fir. *J. Agr. Res.* 57:759–73
177. Yazawa, K., Ishida, S., Miyajima, H. 1965. On the wet-heartwood of some broad-leaved trees grown in Japan. I. *J. Jap. Wood Res. Soc.* 11:71–76
178. Yazawa, K., Ishida, S. 1965. On the wet-heartwood of some broad-leaved trees grown in Japan. II. *J. Fac. Agr. Hokkaido Univ.* 54: 123–36
179. Yazawa, K., Ishida, S. 1965. On the existence of the intermediate wood in some broad-leaved trees

- FORMATION OF Wood
- FORMATION OF HEARTWOOD
- MECHANISM OF FORMATION OF HEARTWOOD & EXTRACTIVES
- FORMATION OF DISCOLORED WOOD
  - Types of wounds
  - Host Response to Wounding
  - Infection and Invasion Processes
  - Decay Processes
    - Secession of Microorganisms
    - Compartmentalization
- DIFFERES BETWEEN HEARTWOOD & DISCOLORED WOOD
  - Extractives
  - Inorganic Elements

~~Commercial Impor~~

- COMMERCIAL IMPORTANCE OF DISTINGUISHING BETWEEN HEARTWOOD & DISCOLORED WOOD

Formation of Wood

Formation of Heartwood

Sapwood —internal processes (amount of ethylene?)→ heartwood

Sapwood	Heartwood
	less H_2O
	formed during dormant period
	radial & axial parenchyma form extractives
starch	no starch
N higher	N lower
pH higher	pH lower
	extractives phenols

extractives decrease ← heartwood extractives → extractives increase → pit

heartwood
cell death → depletion of nutrients ⇒ deposits & cell darkening

Mechanism of the Formation of Heartwood & Extractives

DNA-coded aging effect (some environmental effect also)

Sapwood	Heartwood
Peroxidase ↑	Phenol oxidases

Formation of Discolored Wood

Stage 1 / 2 / 3 /

discolored wood
cell death
wounding, host response, invasion, infection, depleted nutrients, decomposition
discoloration

- Types of wounds
- Infection and Invasion Processes
- Decay processes
- Succession of microorganisms
- Compartalization

Stage I — Wounding & Host Response

Stage II — Invasion & Infection by pioneers — discoloration
bacteria, yeast, non-hymenomycetes

Stage III — Decay — hymenomycetes

Host Response

1. plugged vessels - tyloses — reaction zone at margin of response
at wounding

2) cambial barrier formation after wounding

Sapwood

Discolored Wood
& different,
more extractives transpired
melanistic deposits
higher inorganic materials
< 5.5 pH — higher pH >6
high MC

Heartwood
consistent color
& chemistry for spp.

cell death — discoloration — decay — cell decomposition ↑
resistance to pulse electrical current ↓
(@ fiber saturation point)

Heartwood vs Discolored Wood

Inorganic elements

Commercial Importance of Distinguishing Between Heartwood & Discolored

Sapwood

Live parenchyma

Non-Sapwood

no live parenchyma

Heartwood — genetics

Discolored wood — open wounds

Wet Wood — bacteria

Fake Heartwood - bruise

Case hardened wood — environment stress