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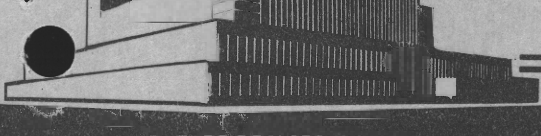

FOREST PRODUCTS LABORATORY
MADISON 5, WISCONSIN

UNITED STATES DEPARTMENT OF AGRICULTURE
FOREST SERVICE
In Cooperation with the University of Wisconsin

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WETWOOD, BACTERIA, AND INCREASED pH IN TREES

By

Carl Hartley,[1] Ross W. Davidson,[2] and Bowen S. Crandall[3]

Summary

The knowledge of the differences between sapwood and heartwood and the transition from one to the other leaves much to be desired. The common assumption has been that heartwood formation coincides with the natural death of the parenchyma due to its age, or as in oak to its distance from the cambium. In the pines, Douglas-fir, oaks, and some other common trees, heartwood is more acid than sapwood, and in the pines and Douglas-fir, it is lower in moisture. Both heartwood and sapwood of healthy trees are thought of as ordinarily free from micro-organisms except for the heart-rotting Hymenomycetes or local infections near wounds. For the most important commercial genera, there is little reason to challenge this view.

In many tree species, the picture is quite different from the foregoing. Particularly in elms, willows, and the true poplars most trees have interior wood that is obviously wetter than the adjacent sapwood. The wetwood is usually in the outermost heartwood, but in young trees may occupy the entire center. In cottonwood, wetwood is commonly found in 2-year-old seedlings. The wet zone is usually less acid than the sapwood and, in a number of species, it is distinctly alkaline. Wood so affected is referred to as "wetwood." In the species most studied, the Truog acidity indicator is a convenient aid in detecting or locating the limits of wetwood on a cut surface. Unpleasant fermentation odors are often encountered in the wet zones in elm and poplar, and positive gas pressures up to 60 pounds per square inch have been reported, especially during the latter part of the summer. Analyses have shown the gas to be about half methane.

In the true firs, a similar wet zone is common, but the associated peculiarities are less marked. In several other genera including birch, maple, and yellow-poplar, interior zones with somewhat similar though less pronounced high moisture or pH, or both, have been found. Wetwood, when seen in oaks, has been usually but not always limited to localized areas in the inner sapwood.

In the species in which wetwood has been most studied, bacteria have been the organisms most often obtained in cultures made from it. In birch and maple, fungi, mainly <u>Torula ligniperda</u>, have been obtained in the majority of the trees cultured, but in paper birch, the only species intensively studied, an inconspicuous and difficult-to-cultivate bacterium is frequently found. The evidence for bacteria as the cause of the wetwood condition is weakened somewhat by the reports of bacteria in normal-appearing sapwood of representatives of four genera. Inoculations with bacteria from wetwood have been reported as causing wetwood in elm and aspen. Bacteria from less typical wetwood have killed seedlings or shoots of plane trees and willows. Wetwood has also been induced in outer sapwood of maple and cacao by inoculation with <u>Phytophthora</u> spp. No reports have been encountered of phycomycetes in wood except in connection with bark diseases. Neither high moisture nor high pH have been associated with wood infections by ascomycetes or hymenomycetes.

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[1]Formerly Pathologist-in-Charge, Forest Disease Laboratory, U.S. Forest Service, Beltsville, Md., retired.

[2]Pathologist-in-Charge, Forest Disease Laboratory, U.S. Forest Service, Beltsville, Md.

[3]Formerly Pathologist, Division of Forest Pathology, B.P.I.S.A.E., U.S. Department of Agriculture, now Food and Agriculture Officer, ICA, Honduras.

Early opinion that the water in internal wet zones is a useful reserve for the tree is no longer held; the indication is that it cannot be drawn on readily for transpiration needs, and in some cases is toxic.

Wetwood in the outer growth rings is closely associated with the nearly universal early dying of Lombardy poplar in the District of Columbia and the decline and death of many elms as well as of some varieties of willow. It may be concerned also in some otherwise unexplained dying of balsam fir and European white fir. Wetwood has been found frequently as an advance zone ahead of heart-rots caused by white-rot fungi.

Mechanical wounds, frost cracks, and branch stubs are apparently common ports of entry. Wetwood has been found following winter killing of sapwood, but this is not common. The familiar brown slime flux at pruning wounds usually originates from wetwood previously established in the tree, rather than from the effects of organisms working at the surface of the wound from which the flow issues as had been supposed by most early writers. The frequent association with shake and frost cracks may also mean that the wetwood is a factor in the initiation or extension of these conditions.

The wetwood condition also contributes to difficulties in transportation, seasoning, and use of forest products. In various species, it has resulted in degrade or rejection for particular uses. The excess weight of logs or pulpwood with wetwood can cause sinkage during water storage or river driving of some species. Excessive checking or collapse in wetwood has been a problem particularly in aspen and balsa. Uneven drying of veneer containing wetwood zones has caused gluing difficulties. The lower permeability of wetwood in some species may be a factor in preservative treatment. In some species, high pH in wetwood zones persists after seasoning, and presence of carbonates can be demonstrated. In aspen, the toughness of wetwood has been reported low.

The inference that seems most consistent with the available information is that most of the properties peculiar to wetwood are due to saprophytic or weakly parasitic bacteria in the standing tree. At least it is evident in studies of living trees that no conclusions can be safely drawn on the amount and movement of moisture in the wood, the composition and pressure of gases, the change from sapwood to heartwood or ripewood, the progress of heart-rots, or the decline or other obscure health disturbances of several tree species, without considering the possible effect of nondecay infections in the wood.

In studies of wood properties and of their relation to utilization of wood, particularly with respect to colorations, acidity, mineral content, toughness, seasoning defects, treatability, and natural decay resistance, the past history of the wood as to nondecay infections in the standing tree cannot safely be ignored.

Suggestions are offered for different phases of the subject that could profitably be made subjects of study.

Introduction

The first study of water-soaked wood and associated factors in living trees, using modern techniques, appears to have been by Fujioka and Takahashi (38)[4] on Cryptomeria japonica. The next were by Day (25) in 1924 on the watermark disease of the cricket-bat willow, and by Eades and Alexander (32) in 1934 on western redcedar. Lagerberg in 1935 (64) coined the term "wetwood" for two types of water-soaked central wood in pine in Sweden. One, in which he detected no infection, was in the upper bole and directly connected with wounds that trap rainwater. The other, with which decay was associated, was limited to the butt. The present writers, at the same time (49), noted the association of bacteria and water-soaked wood with a serious wilt disease of Lombardy poplar, and later (50) adopted Lagerberg's convenient term for any internal zone of undecayed wood that appears

[4]Underlined numbers in parentheses refer to the literature cited at the end of this report.

wetter than the inner sapwood and called attention to its widespread occurrence and usually increased pH especially in broadleaved species. Later studies in individual species, including those by Campbell and Davidson (12), Crandall (22), Carter (15,16,17), Seliskar (94,95), Clausen et al (19,20), Wallin (105), Kemp (63), and Hossfeld et al (57), have much increased the knowledge of the condition and its relation both to the health of the tree and to certain properties of the wood, but so many kinds of trees, organisms, and effects are involved that the information on the subject as a whole must still be classed as fragmentary. Enough has been learned to cause revision of the concept of wood in the standing tree as sterile except near wounds or when invaded by heart-rot, and of the idea that moisture and gas content differences are always due to physiological processes of the tree itself. The attempt in this paper is to assemble the diverse and widely scattered observations and evidence, both published and unpublished, for such stimulus and aid as it may give to more intensive study.

Detection of Wetwood

Wetwood is not only wetter than the inner sapwood, but usually has a somewhat darker color, a higher pH, and often a fermentation odor. In Lombardy poplar, the outer edge of the wet zone sometimes turns orange on exposure to air.

Most of the writers' examination of trees for wetwood has been by inspection of cores taken with an increment borer. In elms, willows, and true poplars, inspection of a fresh core taken while the tree is in leaf is usually sufficient to determine whether it contains wetwood; for the poplars and willows, the greater translucence of the water-soaked parts of the cores makes its recognition easy, while in the elm, the surface of the core is usually obviously wet.

In some woods, it is not easy to distinguish the drier and wetter parts of the core by inspection. In balsam fir, all parts of a fresh core may be very translucent. In species so dense that there is no translucence at any moisture content, it is sometimes helpful to float the core sections in water. The drier portion of the core commonly floats and the wetwood sinks. In dense species, it may be necessary to dissolve sugar or a salt in the water to get any part of a fresh core to float. Sinking in some cases might, of course, be the result of original density difference and is thus not a very reliable wetwood index. Wetness is not easy to detect on a sawed end; this is a probable reason for the small amount of attention it has received. An increment core or, particularly in fir, a fresh axe cut is much easier to diagnose. On a fresh cut, a wet surface can be distinguished by the conspicuous mark an indelible pencil leaves on it. It is frequently possible to force free water out onto the surface of an axe cut by pressing it with the point of a knife. A resistance-type moisture meter with a scale reading well above fiber saturation point, while inaccurate in the upper range, nevertheless quickly distinguishes between adjacent parts of the same section that differ materially in moisture content. Acidity indicators are helpful both on cores and cut surfaces, and often detect wetwood zones in specimens that have dried too far to show original wetness, though high pH alone is not sufficient evidence of previous wetwood. Details of their use are considered under the heading of acidity.

Species Affected

Broadleaves With Typical Wetwood

In boardleaf trees, "typical wetwood" will be used to designate wood, usually inward from the sapwood, that is obviously wetter than the adjacent bright sapwood and shows a higher pH when an indicator is applied to it.

Numerous white elms (Ulmus americana) in the Mississippi Valley and Eastern States and smaller numbers of slippery elm (U. fulva), Siberian elm (U. pumila), Chinese elm

(U. parvifolia), and European elm (U. sp.) have shown wetwood in every tree bored. Curtis May and other workers at the former elm disease laboratory at Morristown, N. J. (personal communications) reported similar uniform occurrence. In winged elm (U. alata), apparent wetwood was found but in a less distinctive form. Carter (16) indicates that some elms have normal heartwood. The thickness of the normal-appearing sapwood of white elm varies from 1/2 to 6 inches or more in different individuals. The remainder of the trunk is visibly wet on freshly cut surfaces, with an odor sometimes suggesting ammonia or pig manure. The apparent absence of wetwood in the few trees examined of the related hackberries (Celtis reticulata) is of some interest.

In cottonwood (Populus deltoides or its segregates) and Lombardy poplar (P. nigra italica), widely sampled, and in P. alba, P. alba bolleana, P. trichocarpa, and P. balsamifera sampled at single localities only, all trees examined by the writers showed wetwood, though cottonwood in the South is said to be less universally affected at least in trees up to 18 inches in diameter (personal communications from Roy Chapman, Ira Hatfield, and Howard Lamb). Wetness in P. trichocarpa is also reported in Canada (103). Wallin (105) reports typical wetwood common in P. balsamifera in Minnesota, and Hale (46) mentions water-soaked zones in its heartwood in Canada. Samuel Grober (personal communication) found the discoloration characteristic of wetwood to be regularly present in a pistillate clone of P. alba planted widely in the United States, but rare in the staminate clone of the closely related P. canescens in this country. In the aspens, P. tremuloides and P. grandidentata, some of the trees examined in Arizona, Colorado, and elsewhere had reached large size without recognizable wetwood in increment cores taken at breast height; in Colorado, some entire study plots were nearly free from it (24). Clausen et al (20) report some logs free from it in Minnesota. The European aspen (P. tremula) has been reported (6) to be almost universally affected by the age of 10 years with a nondecay discoloration that was presumably wetwood. Fermentation odors are usually encountered in the poplars but are somewhat less noticeable than in elm.

In both erect and weeping varieties of Salix babylonica and S. cinerea (identifications by C. R. Ball) and in unidentified native streambank willows in Virginia and Nebraska, wetwood was found in nearly all of the considerable number of trees examined, and its frequency in willow is confirmed by Seliskar (94).

In elms and poplars, the wetwood is ordinarily classed as heartwood, and after drying retains a definite brown color in the elms and usually a light gray in the poplars. In some willows, there is practically no difference in appearance between sapwood and wetwood after both become dry. Most of the papers on the watermark disease of Salix alba and S. caerulea in England and Holland (25,28,29,66,67,75,76) describe it as a wilt due to bacterial infection in the outer 2 or 3 rings, but central stem discoloration with a fecal odor was reported in S. caerulea by one of the investigators of watermark disease in Holland, and dark centers are shown in some of the illustrations. In Russian aspen, red, brown, and green discolorations are reported from the wet zones (6).

Typical wetwood has been found insufficiently in individual trees of other species studied to permit conclusions as to frequency. These included basswood (Tilia americana) and hickory (Hicoria sp.). In plane tree (Platanus occidentalis or P. acerifolia), the center is often reddish and moist, but typical alkaline foul-smelling wetwood has been seen infrequently. The wetwood in young planes following a spring freeze described by Crandall (22) is a special case, to be considered later. Apple, listed with elm (33) as a tree having wet heartwood, was found to have a definitely water-soaked and foul-smelling center in only one of several mature trees examined. A wide, dark-brown zone with a pH of 7 or above was found preceding white heart-rot in the related mountain ash (Sorbus sp.). Mulberry (Morus sp.), in which a number of cases of apparently moist and fermented centers have been observed, will be considered further in sections entitled "Moisture content" and "Acidity." Wilting cuttings of Elaeagnus sp. in a Carolina nursery showed central water-soaked discoloration. Djaparidge (26) reports what appears to be wetwood islands in the outer ripewood of Cornus Mas and C. australis, though his description is not entirely clear. Among the legumes, fairly typical wetwood has been observed in mesquite (Prosopis juliflora) that showed slime flux, and in redbud (Cercis sp.), but does not appear to be common. In oaks, typical wetwood occurs infrequently; obviously wet zones or islands have been seen in the inner sapwood on cross sections of white oak (Quercus alba), chestnut oak (Q. montana), black oak (Q. velutina), and red oak (Q. borealis) and can be readily demonstrated with an increment borer above or below fluxing wounds. In red and chestnut oak and in pin oak (Q. palustris) (Curtis May, personal communication), large parts of the trunk or the entire central portion have been found involved only in single localities. In balsa, wetwood has been described as frequent in Ecuador (43,44). Experience to date indicates that broadleaved trees of any kind that show the common brown slime flux will be found on examination to have typical wetwood in the trunk.

Broadleaves With Less Typical Wetwood

In birches and maples, wetwood is less obvious than in elms and poplars. In paper birch, the species most carefully studied (12), the redheart commonly encountered is regarded as a fairly typical wetwood. In most of the relatively few trees examined of other species, Seliskar (95) reports wetwood common in maples. In sugar maple, Wakefield (104) describes brown heart as appearing in only part of the trees and being more pronounced at its outer margin. As in aspen, some sugar maples become large, up to a 24-inch diameter at breast height in stands in Vermont (J. R. Hansbrough, personal communication) without any indication of heartwood, a degree of variation indicative of wetwood rather than of absence of true heartwood formation. Strong odors and gas production have not been noted in them. Moisture content and pH will be considered further under those respective headings.

Typical wetwood was found in yellow-poplar at the center of one small tree, associated with frost crack and slime flux, which were reported to be frequent in the Virginia locality from which the specimen came. The bizarre colors commonly encountered in decay-free wood of this species (54) and the possibly-overlapping classifications of mineral stain, pathological heartwood, and figure in sweetgum (90), and redheart or pathological heart in beech (10) are not typical wetwood, but their irregularity of outline as described by Putnam (84) for gum and Büsgen et al (10) for beech suggest a relationship to it. Of these, only the "blue butt" of yellow poplar has been reported as commonly water soaked.

Conifers

No wetwood has been observed by the writers in pine, spruce, or Douglas-fir. However, wetwood was recognized on increment cores from 2 percent of lodgepole pine (Pinus contorta and alpine fir (Abies lasiocarpa) by Hornibrook (56) and in logs from an overmature stand of western white pine (P. monticola) in Oregon (unpublished report by J. L. Bedwell). A remarkably vivid salmon color is seen occasionally in eastern white pine, in irregular islands up to 4 or more centimeters in diameter on transverse surfaces. The tint is in close agreement with the color so commonly seen in lumber of Paraña pine (Araucaria angustifolia) which the British Timber Development Association classifies as mineral stain (4). In the white pine examined, these islands were scattered through the heartwood at varying distances from its periphery, and while presumably due to infection do not appear related either to wetwood or to decay. Linzon (69) has described wet zones, mainly around imbedded branches; wet pith in white pine stems; and wetwood rings between heartwood and sapwood, reported as sterile and resembling somewhat the original description of wetwood in Scotch pine (64).

In balsam fir (Abies balsamea), visibly water-soaked wood (fig. 1), sometimes with slightly elevated pH, is common in localities visited in both Minnesota and New England. No odor is noticeable over the strong normal fragrance of the trunk. F. C. Craighead (oral communication) reports a sour or salty taste as characteristic of the wetwood in this species in Canada, where he observed wetwood in over 50 percent of the trees, and in some localities in 90 percent. At a Wisconsin locality (personal communication from F. W. Stearns) wetwood is common in hemlock. Both hemlocks and true firs on the Pacific coast often show wetwood, though apparently less regularly than A. balsamea (observations by one of the writers, reports by Eades (31) and Englerth-Hansbrough (35), and unpublished information from E. P. Meinecke, F. C. Craighead, W. W. Wagener, T. W. Childs, Ernest Wright, G. H. Englerth, and J. L. Bedwell). Some trees of both genera are reported to have an unpleasant odor. Hale (46) reports irregularly distributed wet areas in heart of hemlock and balsam fir in Canada. In white fir in Poland, wetwood in the outer heartwood has been described by Janiczek (61) in stands in which winter injury had occurred, but the wet condition described was apparently much like that found regularly in normal A. balsamea. Neger (82) reports foul-smelling wetwood in declining white fir.

The dark water-soaked alkaline zone reported for Cryptomeria in Japan (38) is the only report known to the writers of typical wetwood in the cedar-cypress group. The relatively high moisture of the rather light-colored outer heart of western redcedar (Thuja plicata) described by Eades and Alexander (32) may be related to the more typical wetwoods of other species.

Initiation and Distribution of Wetwood in the Tree

In very young trees or the upper parts of older ones, wetwood ordinarily occupies the center of the stem. For example, in a balsam fir showing only six annual rings at breast height, the inner three rings were obviously wet. In older cross sections, wetness and high pH are usually limited to the outer heartwood or to the transition zone between heartwood and sapwood. The reasonable supposition in such cases is that the central wood, though usually more acid and less wet than the sapwood, was wetwood at an earlier stage. Whether the central wood in wetwood species is called heartwood apparently depends mainly on how much discoloration remains after the wood dries. Persistence of high moisture and pH in central wood is more marked in elm and some poplars and less in willows, maples, and balsam fir.

In sugar maple, T. C. Scheffer (personal communication), in northern Michigan, found water-soaked cores in many sugar maples less than an inch in diameter. In Lombardy poplar in the District of Columbia, wetwood has been found not only present but regularly well developed before the trees reach the age of 3 years. In cottonwood, Kenneth F. Baker (personal communication) found it occasionally in injured first-year seedlings and very common before the end of the second year in natural reproduction at five localities in North Dakota, Nebraska, and Oklahoma. The wetwood streaks found in trees less than 2 years old he traced to insect, especially beetle, injuries near the soil surface or to dead tips of shoots. In aspen in Colorado (24), association with wounds and especially wood borer tunnels was noted. Ankudinov (6) reports for European aspen that the discoloration apparently connected with wetwood is associated more often with wounds than with branch stubs. Lindejer (67) obtained indications in willow that a beetle was carrying the causal organism from tree to tree, and British observations (1,42) throw suspicion on a wasp. In paper birch, the smaller wetwood zones can often be traced to recent wounds (12). In oak and Lombardy poplar, isolated streaks of wetwood running longitudinally through normal sapwood have been traced directly to recent wounds. J. C. Carter states that he has never found wetwood in elms under 5 years of age (personal communication). He mentions indications that in elm, wetwood appears to be sometimes distributed discontinuously in sapwood, suggesting multiple infections.

Wetwood in older balsam firs is often connected with small wounds and, in the experience of F. C. Craighead, commonly with Pissodes dubis punctures (fig. 1), but may have spread outward to these injuries in most cases rather than inward from them. Hornibrook (56) relates wetwood in alpine fir to wounds. In Cryptomeria, origin is regularly at wounds (38). In elm (16), cricketbat willow (25), and Lombardy poplar, the wetwood may occur within one or two rings of the cambium by spread of new infections from recent wounds.

Wetwood in the species most observed by the writers extends throughout the bole and into the larger branches, thus differing from that reported by Lagerberg in pine (64). Root examination in cottonwood and American and Siberian elms showed wetwood below the soil surface, but in the first two species it was much less extensive than in the parts above ground; in American elm, the condition has been seen to extend into an occasional root as small as 1 inch in diameter. Carter (16) found little extension of wetwood into elm roots. Watermark of willow is described (25,66) as spreading more rapidly down than up, promptly invading the roots of small trees as well as branches and twigs.

Moisture Content

Quantitative information on the moisture in apparent wetwood has been mainly limited to scattered observations, reinforced by the more intensive determinations by Seliskar (94) on elm and by Wallin (105) and Clausen et al (20) on aspen and balsam poplar. Moisture percentages were also shown for *Cryptomeria* wetwood in Japan (38), which may be on the basis of green wood rather than dry wood as is also possible for the cedar heartwood moisture values of Eades and Alexander (32). The fragmentary data available are presented in table 1. Percentages not otherwise indicated are presumably on the dry weight basis. While this basis is the familiar one and the easiest to compute, the values shown by Michels (77) for percentage of pore space occupied by liquid are more meaningful when considering moisture contents of green material. At high moisture contents, electrometric values are subject to large errors, but are considered useful for ranking as to wetness of different zones in the same tree and are so easily obtained with two-point contacters in narrow wood zones and in large numbers of trees on active felling operations that they should be very useful in any extensive field study of wetwood occurrence. In dealing with material showing a high degree of variation, greater reliability is obtained by rough measurements of a large sample than by precise measurements on a small sample. It is interesting to note that Moses and Scheffer (80) found that in green oak their meter readings showed better correlation with the moisture content expressed as percentage of the wood volume than they did with the moisture as percentage of the dry weight.

It might be noted that gravimetric comparisons of wetwood or heartwood with sapwood may also fail to represent precisely the relative moisture content of the wood as it was before the tree was cut. A transverse cut in a trunk at least during the growing season is likely to result in instantaneous pulling away of some of the water from the cut both upward and downward, due to the negative pressure in the conducting zones. Such movement has been demonstrated by investigators of the U.S. "Dutch" Elm Disease Laboratory. This should lead to a decrease in the moisture content of the outer rings in specimens taken at or very close to the cut, which would not occur in the wetwood. This is not too important, since in most of the data encountered the high moisture content of the most rapidly conducting part of the wood has not been obscured. It is correspondingly probable that wood taken from the outer rings somewhat farther from a first cut may have more than its original moisture due to the pulling back into the log of moisture originally nearer the end. This should not affect materially the large differences generally encountered in a wetwood study, especially since it is the less sap-conductive inner sapwood with which the moisture content of the wetwood zone is most logically compared. Moisture content of specimens taken from trees that have been cut or broken for some days with the crowns still attached is more likely to show abnormally low contents for the outer rings, and any sapwood data from them must be used cautiously. Even for laboratory specimens, Kemp (63) reports evaporation loss, after 22 hours, nearly twice as large for aspen sapwood as for wetwood, so all comparisons involving sapwood should be made promptly after cutting.

Despite the inadequacy of the available figures as shown in table 1, taken together they confirm the high moisture content of the water-soaked zones in the species tested. Seliskar (94) points out that visible wetness of the surface on a fresh cut, and even flow of sap, may be deceptive due to the fact that the positive gas pressures often occurring in wetwood tend to push interior water out on the surfaces, making the differences appear large when they really are small, as shown by his results in elm. But there can be no doubt of the high moisture content shown by the translucence of increment cores from the wetwood zones of true poplars.

Table 1.--Wood Moisture Content Percentages in Different Zones

Tree species	Source of data	Moisture: Sapwood	Moisture: Wetwood	Moisture: Heartwood	Remarks
		Percent	Percent	Percent	
True poplars (Populus spp.):					
Lombardy	Present authors	120	182		Mean difference between sapwood and wetwood at 10 different heights in the tree 62 $\pm$ 9 percent. $P < 0.001$.
Balsam (P. balsamifera)	Wallin (105)	122	186	150	Mean for 18 trees.
Quaking aspen (P. tremuloides)	Gibbs	Summer 140 Winter 80		All year 65-85	116 in some blocks with supposed decay infection.
	Clausen et al (20)	91	113	80	
	Max Pillow (pers. comm.)	100	127	107	Wetwood > 200 at some points.
	Kemp (63)	53-150	112-215	54-162	
European aspen (P. tremula)	Ankudinov (6)	[1]54	See Remarks column		Discolored wood that yielded bacteria, 124; fungi, 113; no organism, 88.
Yellow poplar (Liriodendron)	F. F. Lombard (pers. comm.)	42	194		A small severely wounded tree, with the only fully typical wetwood seen in this species.
Paper birch (Betula papyrifera)	Gibbs (41)	Outer > 80 Inner > 90			Redheart much wetter than sapwood.
Silver maple (Acer saccharinum)	Authors	[2,3]55-85	[2,3]80-120		Wetwood sample from outer part of blackheart.
Boxelder (Acer negundo)	........do........	[2,3]50	[2,3]80-100		Wetwood sample from outer part of pink stain.
Mulberry (Morus rubra)	........do........	90-94 [2]65		105-122 86 outer [2]75 central	Read with moisture meter calibrated for plaster; all percentages probably too low.
American elm (Ulmus americana)	Seliskar (94)	5 trees: 79 89 90 94 104 mean 91	5 trees: 96 100 107 111 105 mean 104		Each value the mean of 40 specimens. The sapwood blocks were mostly from the outer rings. Blocks from the inner sapwood would probably have differed more from the wetwood.
Slippery elm (Ulmus fulva)		3 trees: 97 98 103 mean 99	3 trees: 93 111 106 mean 103		
Both species of elm		mean 94	mean 104		$P < 0.02$
Pinus banksiana and Picea canadensis	Gibbs (41)	>100		<50	Both summer and winter.
Balsam fir (Abies balsamea)	Gibbs (41)	136-271	to 287	as low as 32	
1 tree, d.b.h. 3 inches	Authors	Outer high [2]Inner lower	No wet zone	No heartwood	
1 tree, d.b.h. 6 inches	........do........	[2]Inner lower	[2]High		
2 trees, d.b.h. 7 inches	........do........	Outer 87-98 [2]Inner 35-65	[2]80		One tree with heart-rot in which moisture meter read 98.
European fir (Abies pectinata)	Michels (77)		See Remarks column		In some specimens 80 to 90 percent of pore space of heartwood filled with water.
Western hemlock (Tsuga sp.)	Eades (30)		Sometimes 300		Wetwood in brown streaks 4 to 14 rings wide.
Western redcedar (Thuja plicata)	Eades et al (31)			Outer 70 Inner 44	
Cryptomeria japonica	Fujioka et al (38)		[4]53-66	[4]40-50	

[1]Mean of only 2 specimens.

[2]Estimated with moisture meter.

[3]In trees that had been broken at the base by wind some days earlier, sapwood had presumably lost more moisture than had the wetwood.

[4]Percentage perhaps on green weight basis.

There are also included in table 1 some of the published measurements for interior wood reported simply as heartwood. A more extensive list of sapwood and heartwood moisture contents in green wood is found in table 40 of the U.S. Forest Products Laboratory Wood Handbook (5). Most of these reports made no distinction between the outer heart, where any typical wetwood is most likely to be found, and the wood nearer the center which, except in very young trees, has often decreased in moisture content. The need for more localized sampling and reporting before interpreting the findings is well illustrated by the moisture distributions shown in diagrams by Craib (21) for sycamore maple and by Michels (77) for European white fir. Even these diagrams, which show moisture contents separately for different concentric zones, fail to give the complete picture. Michels described wet islands distributed throughout the central portion of Abies pectinata trunks. Von Schrenk (97) described balsam fir in winter as showing "glassy" areas on a crosscut but not in continuous concentric zones. In these islands, the water content was so high that the wood was imbedded solidly in ice and cut smoothly in contrast to the rest of the wood in which the saw teeth picked out fibers or splinters to leave the usual rough saw cut. These especially wet islands in the wetwood zone in balsam fir can often be observed in summer condition on a fresh ax cut. There can thus be large variation within the same growth rings, so that means for separate concentric zones fail to show the full picture. F. H. Kaufert and C. C. Christenson (personal communication) found Minnesota balsam-fir specimens immediately adjacent either radially or longitudinally to differ by as much as 75 percent in moisture content, and Gibb's range of 32 to 287 percent in what he referred to as heartwood, in which both wetwood and older heartwood were presumably included, caps the climax. In healthy yellow birch in Nova Scotia, Greenidge (45) reported heartwood always wetter than either inner or outer sapwood. It has sometimes been assumed, for example by Craib (21), that high water contents found in interiors of trunks were storage supplies that could be used in time of water shortage. This is presumably true for free water in the inner sapwood, but is very doubtful for wetwood. In aspen, the low permeability of wetwood that Kemp (63) found delaying water loss argues against ready mobility of this excess water. High positive gas pressures in the wetwood could scarcely reach the degree reported for elm and Lombardy poplar if the excess water in the lumina of the vessels in the zone could be readily forced out into the conducting zone. Wilting of elm and Lombardy poplar (94) has been noted in trees in which the wetwood has most nearly approached the cambium, and the water from elm wetwood was found by Carter (16) to be toxic. Craib's (21) cross sectional diagrams of maple trees cut at monthly intervals were interpreted as evidence of seasonal radial movement. In absence of replicates, it would seem equally reasonable to attribute them to individual differences between trees. His report of failure of this excess water to move longitudinally across a graft union is of some interest.

It is of course common for the inner sapwood rings to contain less water than do the outermost. Frequently there appears to be a further and very striking drop in moisture content in a narrow light-colored opaque zone between wetwood and sapwood that can be seen on a smooth surface--an ax cut rather than a saw cut. This zone is commonly only 2 to 4 millimeters wide. The driest and the wettest wood in the trunk are thus often only a few millimeters apart. This has been noted in balsam fir in this country by Gibbs (41) and one of the writers, and is described for silver fir in Europe (61,77). A similar zone has been seen in parts of the wetwood periphery in willow (Salix nigra altissima) and in apple. Such a zone is also reported by Wakefield (104) between the sapwood and the central brown stain of sugar maple, the outer part of which is apparently to be classed as wetwood. A zone similar in appearance has been noted just outside normal-appearing heartwood or mesquite. Berliner et al (8) reported a similarly located zone in elm, from 1/64 to 5/32 inch wide, which refused to take either dimethylolurea or the accompanying dye except in the large vessels despite treatment for an hour at 120° F. and 200 pounds of pressure. Craib's sycamore maple zones (21) include a narrow, pale, much drier zone between the outer and inner regions of maximum moisture, and his graphs show a striking drop of moisture content in a narrow intermediate zone in Populus trichocarpa and Taxus baccata, below the moisture level of the heartwood. This dry zone bounding wetwood makes it especially difficult to accept his belief in seasonal radial movement into the conducting area. In Gibb's better supported data on balsam fir (41), moisture content of the inner wood did not change with the seasonal change in the sapwood.

In cottonwood, Lombardy poplar, American elm (15), and some of the other elms examined, deep borer holes not only often yield an immediate flow of liquid but gas commonly bubbles out with it. When there is not enough flow to interfere with gas exit and cause visible bubbling at the mouth of the hole, a sound like boiling water inside the hole can often be heard. This phenomenon is relatively rare in willow. It occurs when trees are in full leaf and negative pressures are to be expected in sapwood. In Lombardy poplar, there may be vigorous and continuing gas emission at one hole when there is none at another hole 3 feet above or below it. Attempts to ignite some of the heavier gas flows from the poplars have failed, perhaps because of the large amount of water that comes out with them.

Seliskar (95) measured gas pressures in wetwood in Lombardy poplar as increasing at an approximately uniform rate from 8 pounds per square inch in late May to 35 pounds by the termination of the test in early August. Changes during the same day were small.

Beilman (7) in borer holes that passed through both sapwood and heartwood recorded pressure differences between trunk interior and the outside air never larger than 18 millimeters of water. His failure to find negative pressure was perhaps because he blocked the outer rings by the brass nipples by which he attached the manometers. The lack of positive pressures appears to have been due to his use of oak trees as subjects which presumably lacked wetwood. In trees which he does not identify, he found that glass covers fastened over freshly bored holes in the trunk were broken or blown off in 24 hours.

Carter (16) demonstrated gas pressures from zero in winter and up to 60 pounds per square inch in summer in an elm that had wetwood. He found a large difference in pressure between young trees in which he had produced wetwood by inoculation and an uninfected control tree. Carter, like Seliskar, found much more daily variation in elm than Seliskar (94) found in poplar. It also is interesting to note that the changes in pressure in a wetwood tree in the greenhouse during a day in which air temperatures did not exceed optimum for the bacteria followed closely the air temperature rise for the interior of the tree, but continued high for a time after the temperature started to drop. On the other hand, when rising air temperature surpassed the optimum, gas pressure began to decrease while the temperature was still high. The tiny pressures and pressure changes he recorded for the tree without wetwood showed close correlation with the air temperature. His results are consistent with the supposition that the effect of temperature was on gas production rather than on the pressure of gas already present.

In addition to the daily pressure fluctuations in the elm, Seliskar (94) found for the wood, from 3 to 7 inches deep in each of his five wetwood trees, a general upward trend from May 27 to the end of July. This contrasted with absence of perceptible trend in internal trunk temperature in the same trees. Two control trees with sapwood zones over 6 inches thick were bored to, but not into, the heartwood. No measurable pressures were found.

Chase's analyses of gas from the trunk of elm and cottonwood (18) show, for these wetwood species, a much greater summer reduction in oxygen content than occurred in his probably uninfected oaks. This difference, which he related to difference between the species in growth rate, may well be due instead to bacterial activity in the two wetwood species, though the rather low summer oxygen content he found also in white pine is not so easily explained. He also failed to get gas from the heartwood of these species in winter. In cottonwood for the five times during August and early September for which he had comparable data, sapwood gas averaged 6.1 percent carbon dioxide and 12.6 percent oxygen, while the heartwood values were 19.8 and 0.33 percent respectively. The ratio of carbon dioxide to oxygen was thus only 0.5 in sapwood and 60 in heartwood. In his two early spring determinations, the ratio was 0.1 in sapwood and 15.0 in the heartwood. He found that the carbon dioxide percentage was the highest when the total gas content was low and the water content presumably high. In trees with high gas pressure, discharge of water at fluxing wounds or into a borer hole was especially abundant.

Bushong (11) also analyzed gas from cottonwood. He bored deep holes and from them obtained gas containing 1.2 percent oxygen, 7.2 percent carbon dioxide, 51 percent methane, and 30 percent nitrogen.

Carter (17) reported finding 5 percent oxygen, 14 percent carbon dioxide, and 46 percent methane in gas from wetwood elm, together with 34 percent nitrogen but no carbon monoxide or illuminants.

The very low oxygen content of the heartwood makes it easier to understand the production of a reduction product such as methane. It seems evident, in tree physiology studies involving either moisture or gas contents of the interiors of trunks, that wetwood and heart-rot trees should be distinguished from trees free from infection, and that gas at different depths in the trunk should be studied separately.

Acidity of Wetwood

The Truog-Triplex wide-range soil acidity indicator, earlier used by Ernest Wright to test acidity of decayed wood, was found convenient for examining wetwood. Streaked across the surface, it gives colors which agree with those on the chart supplied with the indicator. The colors are visible on all but the darkest woods, as they often are not when the individual indicators are used at the concentrations commonly employed in soil testing. Even on very dark woods, the Triplex indicator can still be read in many cases by using a hand lens on the small slivers that project from a sawed surface or with the help of the inert white powder supplied with the indicator for use on dark soil suspensions.

On both conifers and broadleaved species, the indicator when applied to fresh sapwood has shown a color corresponding to a mild acidity between pH 5 and 6. Dried sapwood is more acid, with pH usually below 5 and frequently as low as 4. Normal uninfected heartwood is still more acid than sapwood, in both oak and Douglas-fir (3,30,87,100), enough so that it can be regularly distinguished from the sapwood by applying relatively strong solutions of low-range indicators. So far as known, uninfected wood, either heart or sap, always has a pH below 7.

The apparent pH of wood infected with decay fungi or with the few ascomycetes tested has generally been found as low as, or lower than, uninfected wood from the same source, except in occasional soft, wet-rot pockets. Freshly cut undecayed wetwood, on the other hand, has regularly shown a pH at least as high as the fresh sapwood, and in the outer wetwood in broadleaves, the pH is often above 7 and thus on the alkaline side. In elms, the wetwood zone commonly shows a pH near or above 8 and thus near the equilibrium point for calcium carbonate, though the central wood in some cases goes back down to pH 6 after the wetwood zone has moved outward.

In the poplars, the pH of the outer wetwood zone has usually been 7 to 8, while the inner and therefore older wetwood is ordinarily somewhat lower in pH but still above the sapwood. Wallin (105) reported balsam poplar sapwood slightly acid, the wetwood zone slightly basic, and the heartwood (which had earlier been wetwood) essentially neutral. The aspens not only show wetwood less regularly than other true poplars but pH observed has usually not been so high. On drying, the pH of some of the alkaline poplar wetwood goes down to 6 or below.

In fresh wetwood tested from willows, maples, boxelder, hickory, and birches, the outermost and wettest zone or sections of it have shown a relatively high pH, sometimes to 8, but the interior portions commonly reacted approximately the same as fresh sapwood. In what appeared to be normal heartwood of yellow birch in Maine and Pennsylvania, the outer portions showed higher pH than the sapwood, of particular interest in view of Greenidge's report of high moisture content previously cited (45). Twenty-nine woods-run, partly dry maple logs in northern Pennsylvania apparently free from decay showed higher pH in the heartwood than in the adjacent sapwood in 12 logs and lower in 3, while in the remaining 14 there was no difference.

In Ecuadorian balsa, old dried cross sections in two specimens seen at the University of Minnesota Forest School still showed pH of 7 or more to the very center, while the outer sapwood was approximately 4. The portions of the wet zone that have the highest pH are ordinarily those that have most recently become wet, where any hypothetical causal organisms should be, or most recently have been, active. The wet islands that have been tested in the inner sapwood of oak have been definitely alkaline. High pH was found by G. H. Hepting (personal communication) in a core from southern sour gum (Nyssa sp.). The highest wood pH report encountered is that by R. H. Farmer, British Forest Products Research Laboratory (personal communication), of values ranging from 8 to 10 in Cavanillesia platanifolia and Pterygota sp. No lasting high pH has been observed in wet or wet-appearing zones in the few mulberry and mesquite trees bored.

The true firs tested have had no definitely alkaline zones, but on fresh cuts the outer wetwood has shown pH as high or higher than the sapwood, occasionally as high as 7. In Abies nobilis lumber, the outer heart was about one unit higher than sapwood on end grain, a character which one of the writers found helpful in distinguishing lumber of this species from that of western hemlock in which difference was not evident on dried ends. However, the reversion of the former wetwood in the true firs generally to a lower pH as it changes to ordinary heartwood with the growth of the tree is so marked that Eades (30) includes the western fir species among the woods in which heartwood can be distinguished from sapwood by lower pH. In hemlock, both eastern and western, increases in pH, where found, have been small, even in eastern hemlock so wet that water oozed out of it under pressure of a knife blade.

The dark-brown wetwood of Cryptomeria japonica (38) was reported alkaline (litmus test), while sapwood and the normal red heartwood were acid. Its dark discoloration could be duplicated by adding alkali to the normal wood, and the darkening found in nature could be changed to nearly the normal red color by rather rapid drying or by the action of any acid, organic or inorganic. The restoration to normal color by the application of vinegar was described as established practice in Japan (38). Similar color changes by application of acid or alkali can be made in various species (50). T. C. Scheffer (personal communication) found that the colorations in black heart of maple could not be produced or changed in this way.

The changes that occur in the color of the indicator after application to the wood are reversible by the subsequent application of dilute acid or alkali to the wood. Transverse surfaces give sharper differences than longitudinal surfaces. No reason for this can be suggested. Application of an acidity indicator to a sawn face can give misleading results because the saw apparently drags over onto other areas, alkaline material from the wetwood zone. Application on sapwood should be to parts which were cut when the saw teeth were not also traversing wetwood. Increment borer cores are not ordinarily subject to this error.

While there may be question as to just what is being measured by the indicator, it is probably the approximate pH of the water in the wood. The interpretation of the slower method of testing leachate from the wood is also questioned by Campbell and Bryant (13). The advantage of the refinement involved in their equilibrium pH test method can be partly utilized in the direct application of indicator to wood if different batches of indicator are adjusted to different pH values and the final reading taken as a compromise between that given by the batch just above and that just below the apparent pH of the wood. For the rather rough estimates that are precise enough to help in detecting and delimiting wetwood in most of the broadleaved species studied, the Truog indicator adjusted to about pH 6 seems satisfactory.

Carter's electrometric tests (16) of sap from slime flux in elm and of leachate from elm wetwood resulted in values always above 7, though usually below 8, while his leachate from healthy wood ranged from 6.1 to 6.5. Seliskar (94) found, in leachate from sapwood outside the wetwood zone in 25 elms representing several localities, electrometric pH values between 5.9 and 6.4 in four-fifths of the trees, while the same proportion of the values for the wetwood zone in the same trees lay between 6.0 and 7.7. The coefficient of variation for the sapwood was 3 percent and for the wetwood, 10 percent. Means were

6.16 for sapwood and 6.77 for wetwood; the difference of 0.61 ± 0.136 is highly significant. There was no correlation between sapwood and wetwood pH in the same tree; computed from Seliskar's data was -0.06.

Seliskar also found leachate from Lombardy poplar wetwood in 24 trees in New York State to have electrometric pH from 7.4 to 8.4. The fresh flux from borer holes of the seven trees that showed gas pressure showed the same or slightly higher values than the leachate from the same trees.

Bailey Sleeth (personal communication) placed in distilled water shavings of sugar maple; after 48 hours the colorimetric pH of the water was 5.8 for normal sapwood, 6.4 for each of two samples he had classified as normal heartwood, and 7.2 and 7.4 for mineral streak and mass mineral stain, respectively.

Just as not all wetwood is notably high in pH, it would be unsafe to assume that all wood with high pH is or has been wetwood. But particularly in hardwoods, a pH in outer heartwood higher by as much as one unit than that of adjacent sapwood is believed to indicate wetwood, past or present.

Mineral Content

In broadleaved wetwood with the highest pH values, carbonates are often indicated by effervescence, visible under a hand lens and sometimes to the unaided eye, when dilute hydrochloric acid is applied to the wood; this also occurred in some "mineral streak" in sweetgum (90). No such effervescence has been found in adjacent bright sapwood. High lime contents were reported many years ago by Molisch (79) for various broadleaved species, in elm up to 44 percent of the dry weight; he described vessels so filled with the carbonate that after burning away the vessel walls, columns of the salt were left intact with the imprints of the wall thickenings still visible on them. Wise (106) cites a report of 4.3 percent of calcium carbonate in *Ulmus effusa*. Scheffer (89) reports persistently high pH and calcium carbonate in mineral stain of maple, which is reputed to cause the dulling of saws. Schorger (93) cites calcium carbonate contents up to 18 percent in *Hieronyma alchorneoides*. Record (85) lists 26 angiospermous families in which he found calcium carbonate in the wood of one or more species, usually in the vessels. He states that while it is especially common in certain species, it is too sporadic to be used in wood identification, a statement that is consistent with the hypothesis that it is the result of infection rather than of the normal activity of the tree.

Calcium carbonate deposits are reported in iroko (2) in the form of white concretions so hard and massive as to break saws and containing silica and oxides of iron and aluminum. Farmer and Campbell (36) cite five earlier papers on this phenomenon in iroko, in one of which calcium carbonate masses up to 50 kilograms in weight were reported. In their own study, organic crystals found to be a hydrate of calcium malate also occurred in a fissure, in one case in considerable quantity. These call to mind the floccosoids of western hemlock, reported from wet streaks (35) and apparently containing an organic calcium compound (40). The conspicuous deposits in iroko have been in pockets at what had probably been exposed surfaces where evaporation for a long period had produced unusually large accumulations of salts. Considerable deposits are frequently seen on large pruning wounds on shade trees which have had much slime flux from internal wetwood.

In view of the frequently observed carbonates in recent wetwood of broadleaves and lack of any other clue as to their source, it seems reasonable to suppose that they are ordinarily evidence of previous wetwood, in which the increased pH during the active period of the associated organisms had caused the precipitation of enough calcium salt to have caused the persistence of the high pH. The narrow mineral streaks, locally called "sand streaks," seen running from old woodpecker injuries in hickory in North Carolina, showed residual high pH in a number of cases and may well be the after effect of bacterial infection at the time of the injury. A particularly interesting phenomenon studied by the late W. G. Campbell was the deposit of a calcium phosphate ($2CaO \cdot P_2O_5 \cdot H_2O$) in tunnels of the bee-hole borer in teak and of basic aluminum succinate in beetle galleries in Qualea (personal communication from R. H. Farmer).

Micro-Organisms Associated With Wetwood

Phycomycetes and bacteria are frequently though by no means always associated with unusual wetness in plant tissue they invade. While this may be due mainly to their preference for soft tissues, one of the writers induced obvious water soaking to the depth of a centimeter in the outer wood of cacao trees in 10 days by inoculating the cambium with Phytophthora palmivora. The fungus sporulated profusely on the water-soaked wood after removal of the bark. Howard and Caroselli (58) cultivated a pythiaceous fungus later identified as Phytophthora cactorum from bleeding outer sapwood of maples. For most other fungi, there has been little indication of association with high moisture content in trunks. Caroselli (14) found no increase in moisture of sapwood inoculated with Verticillium. The white-rot fungus, Polyporus tabacinus, is apparently systemic in young wood of Tabernaemontana elaeagnifolia in middle Java but without causing wilt, decay, or obvious wetness. A number of ascomycetes are known in the outer wood causing wilt of various hosts, but no reports have been encountered of unusual wetness associated with them, and neither plant-inhabiting ascomycetes or hymenomycetes, so far as our experience goes, produce or thrive in high pH conditions. Wet heart-rot is sometimes found but is believed to be either associated with entry of rainwater or with the secondary bacterial infection frequently found with decay, rather than specifically with the decay fungi. The pink stain of boxelder, which Hubert (60) described as associated with a Fusarium, has proved in some trees examined in Wisconsin where he worked, and also in Minnesota, to coincide closely with high moisture content and high pH. Subsequent isolation attempts in Wisconsin by C. Audrey Richards and associates failed to confirm a regular Fusarium association. Lombardy poplar wood under two active bark lesions on which Fusarium was sporulating showed sharply lowered pH. According to Ankudinov (6), Borisov isolated a Fusarium from pink aspen wood but was unable to reproduce the pink color by inoculation of living wood.

Fritz (37) found Torula ligniperda in the outer zone of the wet redheart of paper birch in 25 of 28 trees examined. Her Torula inoculation on specimens in vitro resulted in discoloration but not in wetness. Campbell and Davidson (12) found T. ligniperda in 80 percent of the 643 outer zone samples cultured, but in most of the remaining 20 percent found very slow-growing bacteria which Fritz may have missed. They produced a discolored zone in agar around a sliver of infected wood but no readily recognizable growth. Microscopical examination of such zones revealed rods 0.6 to 0.8 by 2 to 7 microns, often in filaments up to 35 microns in length. Had they been present in the wood that yielded Torula, they would have been overgrown and failed of detection. It is, therefore, possible that they were primary and the Torula secondary.

Preliminary culture attempts with reduced oxygen supply did not result in increased growth. Similar organisms were obtained from wetwood in elm, yellow and paper birch, red and sugar maple, balsam fir, and from partly dried specimens (suspected to have been wet originally) of oak, hickory, beech, and basswood. After acquiring experience in recognizing these growths, they were found to be relatively common in cultures from wetwood samples from genera other than poplar and willow.

Lorenz (70) found discolorations spreading from borer holes made with aseptic precautions in birches, maple, and basswood. In 88 percent of his 600 isolation attempts on malt agar, bacteria or nondecay fungi, or both, were obtained. The fungi were somewhat more frequent than the bacteria. Positive isolations were as frequent for both fungi and bacteria in holes plugged with black locust dowels as in open holes. Similar discolorations spread into paper birch logs from the cut ends, but these organisms were not found if covers soaked in an organic mercury solution were promptly applied to the fresh cuts. He regarded the discolorations as results of oxidation.

Miller (78) early reported bacteria as commonly isolated from dying Lombardy poplar in western Tennessee. His cultures were taken from the cambium region at the dividing line between dying and healthy portions. Cultures from healthy tissue were clean.

Wakefield (104) found large parts of the central brown stain areas in sugar maple to be free from fungi microscopically and culturally.

The commonest organism noted by the writers in Lombardy poplar in the Washington, D.C., area was a thick, doubtfully-Gram-positive rod readily visible in unstained vessels in recent wetwood in which it appeared to measure 1-1/2 to 2 by 3 to 4 microns. It grew readily on the somewhat acid malt agar used for wood fungi and produced abundant gas, sometimes promptly pushing part of the agar to the top of the tube. A similar organism was found also in willow and mulberry wetwood and in discolored wood from a wilted wild plum, the original moisture condition of which was unknown. Cultures of this type from these four host genera were compared by John C. Dunegan with several canker and leaf-spot bacteria he had obtained from stone and pome fruits and found (personal communication) to be more strongly acid-forming than his organisms; the poplar culture he reported as forming much acid and gas on various sugars but starting to change to alkaline within a week.

W. H. Burkholder is quoted by Seliskar (94,95) to have isolated from Lombardy poplar a small Gram-positive nongas-producing bacterium which (letter to G. H. Hepting from Burkholder) made little or no growth on potato dextrose or beef-extract peptone. Seliskar at first obtained no consistent organism from wetwood in Lombardy poplars in several localities in New York, but by adding 1 percent dextrose to his nutrient agar, he obtained from about half of his trees a small, curved, slow-growing bacterium 0.4 to 0.7 by 0.7 to 2.8 microns, mostly 0.5 by 1.5 microns. Similar short rods were the commonest organisms also in smears from the sap obtained from borer holes in 32 of the poplars. He described this organism under the name Corynebacterium humiferum n. sp. Acid production was observed in culture but no gas production. In some other respects, as in the small amount of fermentation odor in the wetwood and the more gradual character of the decline of dying trees, the clinical description differed somewhat from that in the Washington, D.C., area, so a significant difference in the microflora would not be too surprising. Wallin (105) made 270 isolation attempts from each of the sapwood, heartwood, and the intermediate wetwood zone of balsam poplar. Bacteria appeared in 93 percent of the wetwood cultures but also in 54 percent of the sapwood and 68 percent of the heartwood cultures. Fungi appeared in 2 percent of the sapwood and wetwood cultures and 10 percent of those from heartwood.

From the 2- to 4-year-old cottonwoods in which K. F. Baker reported wetwood (personal communication), his 75 isolation attempts representing 5 localities in the Great Plains yielded bacteria from 36, various fungi from 10, and no growth from 27. Except from a single tree, the bacteria appeared identical, white and gas forming.

A. J. Riker and L. F. Roth (personal communication) cultured increment borer cores from 65 cottonwood trees in Wisconsin, all but one of which yielded bacteria. They commonly found white Gram-positive bacteria, which were powerful gas producers, blowing agar shake cultures to pieces.

It is not clear from the descriptions whether the European bacterial canker and dieback of poplar (34,88,102) are limited to the bark or involved wetwood symptoms. The bulk of the work on bacteria in willow has been on the watermark disease. The emphasis in papers from England and Holland (25,67) has been on infection in the last two wood rings, with no record of intensive study of the older wood. In this apparently parasitic infection, there has been difference in opinion if not in fact as to the organism that is primary in different localities.

Riker and Roth obtained bacteria less consistently from elm than from cottonwood, finding them in 60 percent of the 57 trees bored. Carter obtained bacteria from the heartwood in 28 of 30 Illinois elm trees cultured. The bacteria found in elm show considerable diversity, the five of his isolates which Carter studied intensively differing among themselves and from those earlier reported in elm in Holland in several respects (16), and lacking the yellow pigment frequently seen in bacteria cultivated from elm wetwood by Eugene Holst and others at the Dutch Elm Disease Laboratory and in some of those obtained by the writers, but agreeing with others found by the writers in their poor growth on malt agar. Carter found that all of his five isolates grew better deep in agar shake cultures than near the surface, as might be expected in view of the much reduced oxygen contents of trunks generally and wetwood species in particular.

There are other unpublished American records of bacteria in tree trunks for which no descriptive data are available. L. W. R. Jackson found bacteria in wet and fermented outer sapwood of wilting trees of Lombardy poplar and a single wilted red oak (Quercus borealis), from both of which he was unable to obtain fungi. Thomas and Podmore (103) found bacteria so abundant in the water-soaked zone in black cottonwood as to cause abandonment of the attempt at cultural identification of the heart-rot fungi. In conifers, Linzon (69) reported no infection in the wet zones he found in white pine. Eades and Alexander (32) state that, except in western redcedar (Thuja plicata), it is universal experience in British Columbia commercial softwoods studied, that nondecay organisms, especially bacteria and yeasts, are plentiful in the outer heartwood or inner sapwood but not in the inner heartwood. In the cedar they found that a sapwood zone 2 inches wide and a straw-colored moist zone 8 inches wide, which they regarded as heartwood, were practically free from infection, while in the darker colored and drier central zone of apparently sound wood, they found a variety of fungi imperfecti together with bacteria and slime molds.

The fact that so much cultural study of wood had been made before the frequency of bacteria was recognized is reasonably explained in part by the general use of malt agar. When made with distilled water instead of the artificially alkalinized water supplied by most municipalities, this agar is definitely on the acid side, favorable to most decay fungi but less favorable to most bacteria. Most of the cultural work has been in connection with heart-rot studies, and bacteria when encountered were generally discarded as contaminations. Bacterial infections in wood are more difficult to detect than fungus hyphae. Wood cannot be safely passed as free from bacteria unless isolation substrata are tried differing from those ordinarily used for decay fungi and under reduced oxygen pressure. What appear to be sterile diffusion colorations in the agar around wood fragments should be examined microscopically before discarding.

The interpretation of the reported association of bacterial infection with wetwood is complicated by the considerable number of reports of bacteria in what was classified as normal sapwood. In the writers' cultures from Lombardy poplar and in those from paper birch, the bacteria were obtained only from obvious wetwood or redheart. In the large amount of isolation work at Beltsville in the study of heart-rot fungi in many timber species, bright sapwood in fresh material has regularly appeared sterile, and this was the experience in isolations made from elms at the Dutch Elm Disease Laboratory. Carter (16) reported bacterial growth from 79 percent of 232 isolation attempts from elm sapwood specimens, but these perhaps included streaks of wetwood in the outer rings due to recent infections. He described the most consistently obtained organism as Erwinia nimipressuralis n. sp. Seliskar (94) compared one of Carter's isolates with that which he invariably obtained from elms in New York, finding good agreement; he isolated other organisms frequently but not regularly. Clausen et al (20) report numerous isolations of bacteria from normal sapwood of the several species of poplar they examined, though (19) less frequently from aspen sapwood than from heartwood. E. R. Roth (86) reported isolation of bacteria from normal sapwood of yellow poplar as well as from the discolored zones in the trunk. A finding of a different type is that by Nellie Brown (communicated by Lee M. Hutchins) of bacteria commonly present in normal-appearing wood of peach-tree roots, equally in trees with the phony disease virus and those without. The possibility that boring tools carry infections into the wood despite attempts to disinfect the bark is raised by Ankudinov (6) as a possible explanation of some bacteria he found in normal-looking sapwood of Populus tremula. There is also the possibility that some of the bacterial isolations have resulted from bacteria drawn some distance into the wood in air that enters the sapwood vessels at the moment that a crosscut is made. The contradictions in both the negative and positive findings call for some careful checking of isolation technique before final conclusions can be drawn with confidence.

Nondecay infections, in need of study before wood discolorations are fully understood, are not limited to those associated with bacteria and fungi. The virus of the phony peach disease exists only in the wood. Psorosis, a virus disease of citrus trees, is reported to lead to striking zonate markings in the stem wood. The rubber-wood disease of apple in Europe is due to a virus that markedly affects the stiffness and microscopic anatomy of the wood. There are undoubtedly many unrecognized virus diseases in trees which probably contribute to the rather high variation in physical and mechanical properties of wood.

Disease Symptoms Associated With Wetwood

An early report from Sumatra includes teak as one of the many hosts of the well-known wilt organism, Bacterium solanacearum, which is associated with abundant slime production in the xylem of many herbaceous plants. The most striking association of general disease symptoms with bacterial wetwood is that earlier described by Day (25) and others as the watermark disease of the cricket-bat willow, a clonal variety of Salix coerulea. Lindeijer (66,67) describes the same disease in Holland, affecting also S. amygdalina and S. purpurea. The development of wetwood in the outermost wood rings, starting at wounds and full of bacteria, is followed by reddening of leaves and wilting and death of branches or twigs arising from the infected zones. Slime full of bacteria is forced out onto the surface of dying twigs. The wetwood spreads up and down but only slowly transversely, and general involvement of trees of any size perhaps requires multiple infections. Death of an entire tree is described as taking place commonly in 3 years. None of these papers has described the chronic infection and water soaking of the outermost heartwood with which the present paper is mainly concerned, probably because the work was largely with very young stems. One of the illustrations, however, shows a larger trunk section with a dark center that indicates that the more ordinary type of wetwood also occurred in the willows studied.

The most striking association of wetwood with disease in the United States is in Lombardy poplar (figs. 2 and 3). In eastern United States, the tree is notorious for premature mortality. More recently, similar conditions have been observed in Utah and California (personal communication, W. W. Wagener). In Washington, D.C., some trees die within 5 years after they are planted, and after making vigorous growth with annual rings in some cases nearly one-half inch wide up to the year of death. Few trees live to the age of 20. In the smaller trees, the entire crown may die at one, but usually only part of the crown dies in any single year. All or most of the top is usually dead by the end of the second summer after the first symptoms appear; farther west and north, the dying is apparently slower, some parts of the crown persisting after others are so long dead as to have lost their bark. An occasional tree shows bark lesions, from some of which a Fusarium was obtained, and at one locality in central Virginia, many bark lesions were found, but in most cases examined near Washington, the bark of trunk and roots and most branches showed no lesions at the time wilting occurred. Wilting occurs mainly in August and September, the season in which Seliskar found highest gas pressures. Less trouble was noted during a particularly moist summer and less in recent decades than in the relatively dry 1930's, but a considerable number of trees die each year. On branches that wilt near the end of the season, some of the leaves may revive and continue alive for several weeks or, if the wilting occurs in late fall, very small new leaves may appear on these branches the following spring; such branches usually die early in the season and all branches kept under observation have died in less than a year after the first wilting. In trees that have not yet shown foliar symptoms, bleeding sometimes occurs for a time from the unwounded trunk; examination at such points has shown narrow strips of dead bark with underlying wetwood. In young trees in which there has been recent simultaneous wilting of the entire crown, the wetwood has been found to occupy most of the lower part of the trunk, even including the inner portion of the current year's ring but not usually the cambium. In trees on which parts of the crown have wilted, the wetwood in the trunk is usually in or near the outer rings, approaching closer to the cambium in the trunk than in the affected branches. In one tree 10 inches in diameter, cut in the early stages of crown dying, the wetwood was so near the cambium that when the bark was removed, the affected wood could be seen as a dark shadow through the cambium over much of the periphery, though the cambium itself had been killed over not more than 1 percent of the area. In the wilting trees, layers or streaks of wetwood have sometimes been observed near the cambium, separated from the inner body of wetwood by apparently normal sapwood; in such cases, there is an approach to the situation described for the watermark disease of willow. In many Lombardy poplars that show wilting, the wet sectors in outer rings appear to be connected with the central wetwood.

In Lombardy poplar, the wetwood has not been observed in branches or twigs as small as those reported in the willow watermark disease. Another decided difference in symptoms between the Lombardy poplar wilt and the willow watermark disease is in the season of wilting; in the willow, Day states that wilting is rare after July while in Lombardy poplar wilting rarely appears until August, except of the dwarf-leaf branches that had shown wilt and death of parts of the leaf blades the preceding autumn. This is an added reason for suspecting that the poplar wilt is ordinarily at least in part due to spread outward of the central infection rather than to the multiple peripheral infections postulated for the watermark disease. On poplars whose tops have died, sprouts commonly arise from the lower stem or root collar. These sprouts sometimes live through two growing seasons. Carter reports in elms temporary wilting or leaf drop and in severe cases, the decline and death of the tree, which he attributes to wetwood (16,17). He says that wilting is mainly in trees less than 10 inches in diameter. In maple, small leaves and premature leaf fall have been linked by Howard and Caroselli (58) with the wet Phytophthora infection of the trunk.

Cottonwood evidently tolerates wetwood better than Lombardy poplar during the early part of its life, but the common loss of large branches of older trees in which wetwood was widespread has been observed, especially in the Great Plains. Cytospora bark lesions appeared too late to be a probably cause of death.

Wetwood of balsam fir is interesting. The location of the wetwood zone in the tree is extremely variable, often extending outward in some places nearly to the cambium, and reaching the cambium at places where it is dead or (personal communication, F. C. Craighead) at Pissodes feeding or oviposition punctures (fig. 1). One of the reasons for the economic inferiority of the species is said to be its unpredictable mortality, only part of which can be explained on the basis of age and other known factors. Similar statements are made for Abies pectinata in Poland (61) in connection with wetwood, but attributing it to an unconvincing history of abnormal winters. The possibility is suggested that in both species the outward spread of the generally present wetwood may be a factor in some of this mortality.

In gray willow, bacterially infected internal wetwood has been found connected with bark lesions, with subsequent dying of main branches or entire trees, following unusual winter warmth and March freeze. In 4-year-old London plane (Platanus acerifolia) in Maryland (22), a severe March freeze following an unprecedentedly warm February had killed some of the trees; a year later, in most of the survivors, all of the wood except that formed since the freeze was wet and infected with bacteria. The affected wood near wounds was rotted and yielded cultures of a hymenomycete resembling Polyporus versicolor. The wetwood extended little if at all during the immediately subsequent years. In this special case, the winter killing of the wood parenchyma is regarded as primary with the bacteria and wetwood secondary and the decay fungus tertiary; this despite the fact that bacteria taken from the wetwood killed green shoots of newly rooted London plane cuttings at needle-prick inoculations and entire cuttings at bark-wound inoculations.

In the 4-year-old London planes mentioned in the foregoing, cracks penetrating to the pith, and thus resembling frost cracks, were found after the winter that followed the one suspected of initiating the injury. They occurred in about half of the trees that showed the wetwood and in none of those that were free from wetwood. Frost cracks in stems so small are at least unusual. The hypothesis is advanced that they were caused by abnormal freezing stresses as a consequence of the water soaking. Frost cracks are frequently associated with slime flux in various species, but are also frequent in older trees without wetwood.

In the bark of Lombardy poplar, cottonwood, willow, and Siberian elm, longitudinal cracks which did not overlie cracks in the wood have been frequently noted. There was slime flux from some of them. In Siberian elms in Oklahoma, fluxing bark cracks were frequent in 5-year-old trees (information from Howard Lamb).

Brown slime flux, the most troublesome type, appears most commonly from pruning wounds, and from exposed heartwood rather than sapwood. It has long been a subject of speculation. The bacteria and other organisms found in the flux have been generally considered the result of local external infection, as part of them undoubtedly are. They were supposed by some writers to perpetuate the flow by the irritating action of the fermentation products produced at the discharging surface. The relation to internal wood fermentation was recognized by Ludwig (71) in 1888, but it was not until the 1930's that it came to be regarded as a symptom of pressures developed in internal wetwood and commonly present before the occurrence of the wound through which the flux issues (16,23,27,74). Commercial tree experts evidently reached this conclusion before the pathologists, judging from their practice of installing drain pipes in the trunks near the base of trees in which slime flux was troublesome. Ogilvie (83) reports for the spring white flux around wounds the expected acid reaction, while for the brown flux he gives the surprisingly high pH values of 9.0 to 9.5. Carter's values for the flow from wetwood, mostly between 7.3 and 8.3, are more in accordance with data by Large (65), and the authors' results with indicators on the wetwood itself.

The statement by Büsgen *et al* (10) that pathological heartwood on beech starts at wounds and his illustration indicating periodic advances of such heartwood into limited sectors of sapwood strongly suggest microbiologic cause. If either this or the wetwood of European fir were due to winter injury to the sapwood, as some investigators believe, it would seem necessary to assume that most affected trees of these species are subject to frequently repeated killing of zones of inner sapwood by cold, a supposition difficult to accept. Seliskar (94) found sugar and starch content of poplar wetwood only about a third as high as for normal sapwood at same position in trees having wider sapwood. Since normal heartwood would also be expected to be low in carbohydrates, the observed difference is difficult to interpret. Gaumann (39) accepts winter injury as the source of some cases of beech falseheart, but attributes most of it to an agency or stimulus spreading from wounds. This picture is easier to accept. In case of winter injury to the sapwood, it should affect the younger rings as it did in the plane trees, rather than a definitely limited zone just next to the heart in which it is said to appear.

Wetwood and Heart-rot

It is not uncommon to find water-soaked wood above or at the periphery of heart-rot infections. Hubert (59, p. 528), Eades (31), and Boyce (9, pp. 387, 392, and 400) call attention to this characteristic for a number of white rots. A somewhat similar condition has been noted with *Hydnum erinaceum* and with an unidentified white rot of sugar maple in which a dark-brown marginal wet zone about 5 millimeters wide was found just outside the decayed zone on the cross section. This brown zone was so wet that water could be pressed out of it with a knife point. It had a pH of 8.0 and was outlined by an outer orange zone also with high pH but not excessively wet. The bleached wood in the decayed zone was on the acid side and not visibly wet. The dark-brown zone that extended upward from the top of the rot as a broad column was all alkaline, though not so wet as the narrow brown zone around the decay. The association was similar to that described for redheart of paper birch (12) which is commonly a forerunner of decay, though the decay development may be much delayed. Similar narrow brown alkaline zones, though less obviously wet than in the maple, were noted in Wisconsin encircling central decay on cross sections of yellow birch with *Fomes igniarius* heart-rot, and of paper birch with *Poria obliqua* decay, both of them important white rots. The water soak reported by Stevens (101) as an important defect in old white oak was regarded as either the result of entry of water at wounds, or as a forerunner or possibly an early stage of decay.

In aspen, early studies by Schmitz and Jackson in Minnesota (92) showed that in trees with Fomes igniarius heart-rot, an outer zone, at first supposed to be incipient infection, but which usually failed to yield the fungus in the Minnesota study and in the writers' observations farther west, had instead the appearance of wetwood. Ankudinov describes what is likely the same situation in Russian aspen (6). He obtained no Fomes from the advance zone of F. igniarius decay in more than 200 attempts; bacteria alone appeared in 7 percent of his cultures and two species of Verticillium, Sclerotium sp., Torulospora sp., and other fungi in order of decreasing frequency appeared in 40 to 60 percent of his cultures. In half of these cultures, bacteria were present also. It is worth noting that Poria obliqua is reported by Manka (73) to make better growth on agar at pH 7 and 8 than at pH 6, an unusual preference for a wood decay fungus and perhaps an advantage in enabling it to invade readily a preceding wetwood zone. In general, the brown rots like (96) and make considerable acid, while white rots make little. Schmitz (91) determined experimentally that wood of two conifers and two broadleaves, inoculated with bacteria 6 to 8 weeks after inoculation with decay fungi, decayed faster than wood containing the fungi alone. The acceleration by the bacteria was much more marked for the white rot he employed than for his two brown-rot fungi.

Durability of Wetwood

The effect of the wetwood condition on subsequent decay is an interesting subject. The increased pH of wetwood in some species may make it less susceptible to acid-forming brown-rot fungi but offers no protection from white-rot fungi. The tree species in which wetwood is regularly found are generally classed as nondurable. Because of its high moisture content and slow drying rate, wetwood may favor decay in some situations by increasing the time required for air drying to a safe moisture content. However, its low permeability could be an advantage after it is once dried. Reports of apparent increase in resistance of wetwood come from Hossfeld et al (57) for aspen, and from Fujioka and Takahashi (38), who say that the alkaline wetwood of Cryptomeria is preferred to normal heartwood in uses in which it is exposed to decay. Seliskar (94) decayed specimens of outer wetwood and adjacent sapwood from 59 points in 3 American elms, using Poria incrassata as test fungus. Weight loss in the wetwood specimens averaged one-seventh larger than in the sapwood, a doubtfully significant difference.

Mechanical Properties of Wetwood

Both the wood in the zone that was wet at the time the tree was felled and the wood nearer the center of the tree that had previously been wet are considered and termed heartwood in the following discussion.

Mineral stains or streaks, probably resulting from wetwood infections, are said to dull tools. Scheffer (89) made tests on mineral stain specimens from sugar maple which showed 5.2 percent of ash, mainly calcium carbonate. The pressure required to imbed a ball in the wood to a depth equal to half its diameter, in 47 specimens, averaged only 3 percent greater than that required for matched controls from adjacent normal sapwood, but the difference was consistent enough to be significant at the 0.01 level.

Clausen and Kaufert (19) reported the heartwood of four poplar species containing wetwood to be inferior to the sapwood in the same logs by 3 to 11 percent in density, 10 to 37 percent in compression strength parallel to the grain, and 27 to 55 percent in toughness (percentages based on sapwood values). The regressions of the strength measurements on density in the two zones were found to differ significantly. Nevertheless, there can still be some question whether a similar difference might be found in density or in the relation of strength to density between uninfected wood formed in the first several years and the later wood. Their conclusion that the density deficiency was due to wetwood bacteria is particularly open to question, since both staining and decay fungi, where they have caused weight reduction equal to the reported deficiency in this case, generally (48) cause much larger toughness losses than occurred in the quaking aspen, the species in which Clausen and Kaufert had the best numerical basis.

Blue butt of yellow poplar, described as frequently water soaked, showed only an insignificant reduction in toughness (54). Of other hardwood discolorations which may be associated with wetwood, those in Honduran mahogany and Khaya showed no real loss (47). In sweetgum, both normal and figured or mineral-streak heartwood veneer were commonly less tough than sapwood veneer (90), but only by the usually unimportant amount of 5 to 15 percent. Wakefield (104) found no clearly defined difference between brown heart of sugar maple and white sapwood in cleavage, shear, or tension. The low toughness in Australian woods previously mentioned under the name of brittle heart is of interest as possibly of wetwood origin.

Seliskar (94) reported toughness tests on 500 small specimens from wetwood in 5 trees of American elm and 3 of slippery elm (Ulmus fulva) and an equal number of specimens from normal sapwood taken at the same heights. In five trees, specific gravity was 0.01 higher in the wetwood, in one it was 0.01 higher in the sapwood, and in the other two trees they were equal. There was no difference between the two species in the results obtained. In two of the trees that yielded a third of the specimens, the sapwood on the whole was tougher than the wetwood, while in the other six the wetwood proved the tougher. Most of the wetwood specimens came from just inside the boundary of the wetwood zone, but 78 were from somewhat deeper in the trunk. Of these latter, 44 were below the median toughness for all the specimens of their respective sections and sectors, a negligible departure from the 39 expected if the sapwood and wetwood were equally tough. His results pretty thoroughly removed any liklihood of strength differences of practical importance between wetwood and sapwood of elm.

Miscellaneous Properties of Wetwood

There is necessarily more tendency for logs containing appreciable volumes of wetwood to sink in water driving or storage, and it is said frequently to cause sinkage losses even in balsa in Ecuador (personal communication from L. V. Teesdale). Gibbs (41), on the basis of his moisture studies, concludes for logs of aspen, birch, and balsam fir that the moisture content of normal sapwood is much more important than wetwood as a cause of sinkage because of the larger volume of the sapwood zone. Heiskanen (52) recognizes wetwood in the heart as a factor in flotation of Scotch pine.

In maple and birch, the dark discolorations, at least part of which are believed to be the aftermath of a wetwood condition, are cause for degrade said for paper birch in the Northeast to have more effect on financial return from this species than does decay. Wakefield (104) describes brown heart in sugar maple as shrinking excessively in kiln drying. In figured sweetgum, should that condition prove related to wetwood, we would have an isolated case like Cryptomeria in which affected wood is increased in value. In aspen (51), wetwood is objectionable for pulp because of added bleaching costs and, in lumber, because of warping. In white poplar logs with figured grain, valued for veneer, wetwood is reported to cause rejection because of associated shake and loss of luster (Samuel Grober, personal communication).

In mineral stain of maple, there is sometimes excessive checking. The severe checking of wetwood in white fir on the Pacific coast has caused it to be heavily culled in some operations; similar discrimination against water-soaked white oak has been practiced in stave utilization in Kentucky and elsewhere. Some extreme internal checking has been seen in balsa wetwood and is reported by Teesdale to occur even in mild air seasoning. In aspen (20,63,98) and an earlier unpublished report by Max Pillow, this subject has received careful study. In aspen furniture core stock, kiln drying is reported to result in heavy checking or definite collapse in the currently wettest part of the wetwood zone. A board found by Pillow had been reduced in kiln drying to half of its original thickness in a band coinciding with the current location of the wetwood zone. The heartwood inward from the wetwood zone, which has previously been wetwood, showed little or no seasoning defect.

Spotty wetwood distribution in western hemlock has caused complaints of difficulty in bringing veneer to the uniform moisture context required for best results in gluing (F. H. Kaufert, personal communication). Eades (31) mentioned collapse in kiln drying as characteristic of western hemlock basal wetwood which he says Grondahl found associated with gelatinized fibers.

It has also been suggested that shake in standing trees, such as is shown in a photograph of Lombardy poplar published by Seliskar (95), may be favored by wetwood.

The low permeability of wetwood (63) is of interest in connection with preservative treatment. Kaufert (62) for aspen and Hopkins (55) for willow and cottonwood have described the great irregularity in the penetration of preservatives into these wetwood species, though in Hopkins' diagrams the zones of deficient penetration were not well correlated with the usual wetwood distribution pattern. McKnight (72) states that cottonwood and willow posts absorbed large quantities of preservatives in a hot-and-cold bath but distribution was patchy, allowing much decay, while the same treatments in a number of other species gave good protection.

Elm is sometimes described as slow-burning (53) except at high temperatures. If there was much elm wetwood approaching the 44 percent calcium carbonate content previously quoted from Molisch, some fire retardance might be expected, but most elm does not appear to be very high in carbonate; long-persistent high moisture content of the heartwood might explain part of such slow-burning reputation as it may deserve.

Causal Relations

In the foregoing, the attempt has been to record the phenomena associated with wetwood. There has been so little experimental work that interpreting the associations in terms of causal relation must be largely speculative.

The best material for such speculation is the wood in the outer heart of elms and true poplars, in which excessive wetness, high pH, fermentation odors, and high gas pressures have been found together. For the etiology of this syndrome, the following hypotheses are suggested:

A. The parenchymatous elements at the inner limit of sapwood die of old age or from impaired communication with the cambial zone. The consequent distinguishing symptoms result from action of the tree's own enzymes on the contents of the moribund cells.

B. As in hypothesis A, the parenchyma dies a natural death but the other changes noted in wetwood are due mainly to the action of saprophytic bacteria.

C. The death of the parenchyma is caused or hastened by weakly parasitic bacteria which may or may not have been present in small numbers in the nonliving elements of the sapwood but were unable to attack living cells and develop in quantity until the cells became senescent. The gas production and odor may depend largely on secondary bacteria.

Hypothesis A is immediately discredited for such species as aspen, since many individual trees live to relatively large size and high age without developing wetwood. This is still more evident in such species as apple in which wetwood is found only in part of the trees. The more uniform change from sapwood to heartwood in the pines, spruces, and oaks is the type of change that would be expected where the tree is the only organism involved. The numerous micro-organisms found in typical wetwood can scarcely have multiplied to the observed extent without causing changes in some of the properties that are characteristic of wetwood.

Hypothesis B also makes the death of the parenchyma a natural process, but admits micro-organisms as the cause of the increase in moisture and pH and associated changes. It cannot be ruled out generally on the basis of present knowledge. The indications in some trees of a narrow especially dry zone just outside the wetwood zone supports the idea that the sapwood was dying before wetwood developed. However, this low-moisture zone could conceivably result from premature weakening or loss of tone of parenchyma due to toxic materials produced by the organisms in the adjacent wetwood. The toxicity of wetwood sap to elm shoots demonstrated by Carter (16), and in some cases to bark at fluxing wounds, lends color to this speculation.

In special cases, there is some positive evidence for hypothesis C. Carter in elm and Seliskar in aspen produced wetwood in young trees by inoculation with bacteria cultured from wetwood, which they were then able to recover from the inoculated trees. Carter's inoculations resulted in gas pressure as well as the characteristic wetness and discoloration. The fact that, in both elm and Lombardy poplar, typical wetwood sometimes develops in new sapwood indicates strongly that the organisms involved in wetwood are not always limited to dead wood.

If hypothesis C is accepted for part or all of the elm and poplar wetwood, it is still quite possible that some of the wetwood characteristics are due to secondary saprophytic organisms. Mixtures of different kinds of bacteria have been reported in wetwood. The bacteria used in Seliskar's inoculations failed to produce in culture the gas that is so characteristic of many cases of wetwood in Lombardy poplar from which his cultures were obtained. As he suggests, they might be able to produce gas under the nearly anerobic conditions in the wetwood. However, it is possible that the gas production in the poplars is by a secondary and perhaps entirely nonparasitic organism. In the opinion of the writers, hypothesis C is the most probable for elms and poplars generally.

In willows, the general wetwood picture, based on observations in this country, is enough like that in the poplars to justify preference for hypothesis C for them also. In fact, it seems reasonable, pending more definite information, to regard hypothesis C as the most probable one in any tree in which the wetwood occurs much closer to the cambium than in the majority of trees of the species. Hypothesis C is especially indicated for those species in which some of the trees never form recognizable heartwood. For wetwood in conifers and in broadleaves in which pH differences are smaller and less commonly found and in which there has been little attention to micro-organisms, there is need for more factual evidence before any definite opinion on causal relations is justified. While there has been enough study to justify considering redheart of paper birch as an example of wetwood and to implicate micro-organisms in its etiology, there is much room for doubt as to whether the bacteria or the Torula found with it is the more likely cause.

Whether wetwood is the result of a natural process of the tree or induced by bacteria, no very plausible explanation occurs to the writers as to the source of the excess moisture in the wetwood. If water produced by the oxidation processes of micro-organisms were the answer, more water should be produced by decay fungi than by bacteria. However, accumulation of any water and gas produced could be explained in bacterial wetwood by its low permeability (63), and the lack of accumulation in decayed wood by the very high permeability that follows fungus infections (68).

The high pH in the most recently formed wetwood is presumed to result at least in part from ammonia release by the bacteria. The pH could conceivably be due to routine senile breakdown of protoplasm in the innermost sapwood by the trees own enzymes. The large variation in pH in the wetwood zone, in Seliskar's elms (94) three times as great as in the sapwood, is more reasonably explained as due to infection. The higher pH and gas pressures observed in wetwood in broadleaf than in evergreen species parallel the larger volume of living elements and the supposedly larger amount of food stored in the wood in deciduous species described by Busgen (10). A pH persistently above 7 in the mineral stain areas that are regarded as having been wetwood is taken as indication of calcium. Calcium carbonate precipitation from the bicarbonate in the wood and subsequent accumulation would presumably occur in zones in which pH has been raised by bacterial activity to approximately 8. Narrow streaks with high mineral content may date back to isolated early infections of narrow zones then located in the outer region where there was more movement of sap and thus larger amounts of calcium bicarbonate were subject to trapping in the streak.

The slight increase in hardness of the wood found in maple mineral stain is presumably due to the carbonate deposits. The indicated reduction in toughness of some wetwood is presumably due to slight chemical changes in some of the cell wall components rather than any real destruction of material. The cause of heavy checking or collapse of wetwood on rapid drying may be sought in the low permeability of the wetwood to gas entry, which likely leaves the cells from which the water is driven under strong negative pressure that would tend to cause some degree of collapse of the cells. The inner heartwood with less excess moisture has some air in the cells to start with and is therefore not subjected to as heavy pressures on drying.

Stamm (99) found that ammonia treatment could lead to collapse, but such ammonia as may be produced in the wetwood is presumably not sufficient to have such an effect.

Passing from the properties of the wood to the health of the tree, the etiology in general is even more obscure. Only in the watermark disease of the cricket-bat willow have leaf-wilt symptoms been reproduced experimentally by bacteria found associated with the trees in nature. These inoculations were in recent wood rings, giving no information as to whether the bacterial flora of the ordinary deeper wetwood zones was affecting the health of the crown.

It has been suggested that active wetwood infection may cause wilting by forcing the pressurized gas in the wetwood outward into the water-conducting rings, thus breaking the ascending water column. The narrow white opaque zone previously mentioned as frequently found just outside the wetwood in some species might be due to such gas movement, but no indication of similar effect has been seen in the outer sapwood rings in which most conduction occurs.

Some of the observations on Lombardy poplar by one of the writers indicate that the killing infections may resemble those described for the cricket-bat willow, as depending on recent entry from wounds or dead shoots into the second or third rings from the cambium. The pH distribution on trunk cross sections of wilting Lombardy poplars indicates continuity of infection at some points between the deeper wetwood zone and the infection in the outer rings (fig. 3). The possible error in interpreting the results of artificial inoculations that have killed seedlings or shoots, in terms of diseases of larger trees, is brought out by Crandall's killing of plane tree seedlings by wetwood bacteria, which in nature have given no indication of killing trees unless they hastened death in young trees in which the real cause of difficulty had been injury to the wood by a spring freeze.

The association between wetwood and frost crack is probably mainly because of the excellent infection ports provided by the cracks. It seems possible, however, that moisture saturation of a zone in the trunk might result in increased expansion of the wood in freezing, to either start new cracks or perpetuate old ones.

At least in such species as aspen, southern cottonwood, and American elm, in which the thickness of the sapwood zone varies greatly from tree to tree, it seems reasonable to suppose that the infection has hastened the death of the parenchyma in the inner and thus older part of the sapwood of the trees in which the sapwood zone is thinnest.

The temporary or permanent wilting associated with bacterial wetwood in elm, Lombardy poplar, and cricket-bat willow is most likely due to toxicants resulting from the bacterial action after the infection had spread outward into the younger conducting wood rings.

The high frequency of shake sometimes reported in heartwood of some species might be caused by wetwood infection, either by decreasing the toughness of the wood or by causing rigidity of wet zones when the wood is frozen and consequently greater stress in the plane of contact with less wet inner wood.

Suggestions for Further Study

Numerous observations of anomalous moisture distribution in trunks have been reported, but with relatively few measurements. In willow and cottonwood, for which no measurements are known, excessive moisture is so obvious as to need little confirmation. But even for these species, and certainly for maple, birch, yellow poplar, hemlock, larch, and the true firs, in all of which there is less visual evidence of water soaking, valuable additional information could be secured by using directly on increment cores or freshly cut trunks a high-range, resistance-type moisture meter and the Truog pH indicator, with occasional gravimetric moisture determination on fresh specimens to aid in interpreting meter readings. Within zones, the wettest appearing spots should be compared with the less wet. The mark made on a fresh axe cut by an indelible pencil, or the spread of the ink from a fountain pen, will often serve roughly to differentiate wetter wood from that less wet. Some southern oak species reputed to suffer collapse in drying, species showing an unusual amount of shake, persimmon dark heart which is said to check excessively, Philippine ebony in which the dark heart is said to develop in only part of the trees, and the numerous genera listed in Australian publications on brittle heart cited by Clausen and Kaufert (19) might well be examined for evidence of wetwood. Acidity indicators and moisture meter tests would be especially interesting in trunks with heart-rots to determine the frequency of a wetwood zone preceding infection with white-rot fungi.

For best understanding of the condition, a more intensive study should include application of dilute hydrochloric acid under a magnifier to detect carbon dioxide bubbling, examination of the wood for hyphae, and cultural isolations using not only ordinary malt agar but also substrata and technique better adapted to bacteria or to partially anerobic organisms. Such studies on the wood just ahead of white heart-rots might add materially to the understanding of the spread of some of the fungi. For any fungus that commonly is preceded by an alkaline wetwood zone, it would be desirable to determine the relation of its growth in agar to pH.

The seasonal factor should be investigated. The limitation of gas pressures to summer and their special prominence in late summer, together with the frequency of wilt in Lombardy poplar in August and September, suggest that sharpest differentiations may be obtained also in other characters, and in species in which the moisture and pH contrasts are less consistent if the comparisons are made mainly in late summer. If another series of moisture and pH observations were made by the same techniques in winter or very early spring, the comparison of the two series might be enlightening.

Study of moisture, pH, and micro-organisms of the discolored streaks spreading from fresh wounds (such as those described by Murphy (81) as regularly extending up and down from tapping holes in sugar maple) might throw more light on the origin of mineral streaks in maple and other species.

More inoculation trials with bacteria obtained from wetwood are, of course, badly needed, with reisolations and reidentification. The organisms encountered need to be more carefully separated and described than in most of the previous work. Both shallow and deep inoculations are needed to bring out differences in susceptibility of the outer and the inner, supposedly less-resistant, sapwood. Effect of exclusion of air on development of stain or infection may prove of interest in both artifically inoculated holes and those left exposed to natural infection. Lorenz (70) and Murphy (81) found nearly as much stain in plugged as in open holes but, if the plugs contained open pores, they may have admitted too much air to settle the question.

Not only the understanding of wetwood but also the understanding of the general subject of the change from sapwood to heartwood or ripewood could be improved by some microphysiological study. The development of tyloses at the time of wetwood formation and their part in the decrease of permeability noted by Kemp (63) deserves attention. If microsections somewhat thicker than a parenchyma cell were cut from the sapwood at different depths, treated with intravitem stains, and then given hypertonic salt treatment, the proportion of the cells that showed plasmolysis and the character of their response should give some information on the tone or senescence of the living elements in different aged zones.

To elucidate the effect of wetwood infection on the health of trees, toxicity tests such as Carter (16) made with wetwood leachate should be repeated, particularly with Lombardy poplar and cottonwood. Isolation and inoculation at superficial wounds or at the base of new shoots should be attempted in Lombardy poplar to determine whether the independent wetwood streaks that run from small wounds or dead shoots up through the outermost rings are more probable causes of branch killing than the old central bacterial infections.

It will be difficult by inoculation experiments to confirm the clinical evidence that the wetwood bacteria cause wilting or high early mortality of elm or Lombardy poplar, because all trees in the age range in which crowns show symptoms are usually naturally infected, and there is probably no way in which control trees can be kept free from infection. But even with trees all of which have central wetwood, inoculations in the second growth ring might cause wilting of branches in line with the inoculations which would be informative.

There is need to repeat the work on the toughness and other physical properties of wetwood in aspen and extend it to other species. Differences between sapwood, wetwood, and inner heartwood zones should be compared with zones in the same radial position in trees of comparable size and age in which neither wetwood nor recognizable heartwood had developed. Such trees can be readily found, at least in the aspen in western Colorado. Tests of relative permeability of wetwood in species other than aspen would be of interest.

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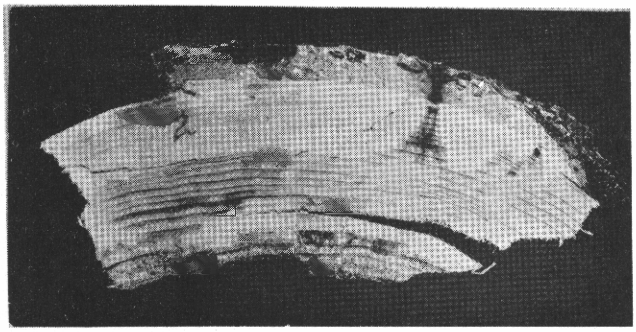

Figure 1. --Balsam fir (Abies balsamea) showing wetwood extending outward to within 10-12 annual rings from the cambium. Cones of wetwood extend to the cambium at Pissodes punctures as shown near the right end of the specimen.

Figure 2. --Lombardy poplar dying at age of 10 years, at Washington, D. C.

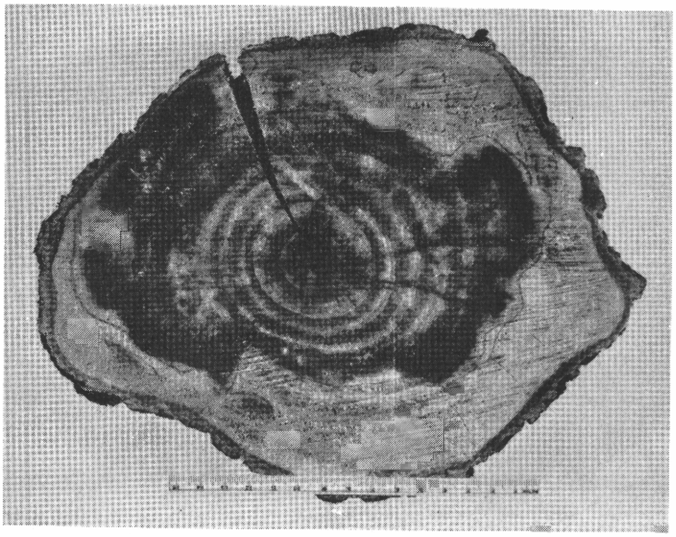

Figure 3. --Section from wilting Lombardy poplar showing much wetwood. Pencil lines indicate discoloration margins. The Truog indicator applied after drying turned yellow on the sapwood (pH 4-4.5) and dark blue on the advancing wetwood (pH near 8). The small isolated wetwood areas in the sapwood lost most of their high pH on drying, and the center of the section was lower in pH than the outermost wetwood.