12

# Biological Decomposition of Solid Wood

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*Decomposition of wood is an important part of the carbon cycle of nature. Decomposition is caused by fungi, insects, and marine borers that use the wood as food or shelter, or both. Lignin in wood provides a physical barrier to enzymatic decomposition of cellulose and hemicelluloses. This barrier is breached mechanically by insects and marine borers, biochemically by white- and soft-rot fungi, and possibly by small nonenzyme catalysts in the case* of *brown-rot fungi. Cellulose* is *degraded by* endo- *and* exo-*glucanases and* β-*glucosidases, hemicelluloses by* endo-*glycanases and glycosidases, lignin by nonspecific enzymes, and perhaps by nonenzymatic, oxidative agents. Rapid strength loss occurs with all decay fungi; but especially with brown-rot fungi. Strength loss due to insect attack is roughly proportional to the amount of wood removed. Fungal decomposition of wood can be prevented by keeping it below its fiber-saturation moisture content (approximately 27% of its dry weight) and by using the heartwood of naturally durable woods (species) or preservative-treated wood. Useful application of wood-decomposing fungi is limited currently to production of edible mushrooms. Potential applications include biological pulping, pretreatment for enzymatic conversion of wood to sugars, and waste treatment. Many aspects of wood biodecomposition have not been researched adequately.*

*Millions of tons of wood are produced every year in the forests of the world. Observation, however, tells us that the sum-total of wood upon the surface of the earth remains fairly constant from year to year and from century*

*to century. We must, therefore, conclude that there are destructive agencies at work by which millions of tons of wood are destroyed annually. Regarded in this light the problem of what these destructive agencies are, and how they act, becomes of general scientific and economic interest.*

A. H. R. Buller,
preeminent mycologist,
1906 *(1)*

BULLER RECOGNIZED THAT WOOD IS THE MOST ABUNDANT ORGANIC MATERIAL on earth. He also recognized that the trees that form wood through photosynthetic processes, and the fungi and other "destructive agencies" that destroy wood through respiratory processes are engaged in a never-ending cycle of biosynthetic and biodecompositional forces. These relationships are shown by the following simplified reaction for the predominant part of the carbon cycle of the earth:

Photosynthesis by trees and other plants

$$6nCO_2 + 5nH_2O + 677{,}000n \text{ calories} \rightleftarrows (C_6H_{10}O_5)_n + 6n0_2 \quad (1)$$

Respiration by fungi and other destructive organisms

Life as we know it would stagnate for lack of atmospheric carbon dioxide in about 20 years if wood destruction were to cease while photosynthesis continued unabated *(2)*. Thus, the biological decomposition of wood is both a great blessing and a serious limitation to the usefulness of wood.

Man has probably always recognized that wood disintegrates on the forest floor and in other moist environments. But it was only a century ago, in 1878, that wood decay was recognized as a biological process. The pioneering German forest pathologist Robert Hartig was the first to prove that fungi are the cause rather than the product of wood decay *(3)*. Forty years later Oshima *(4)* demonstrated that some insects digest the structural polymers of wood.

This chapter presents an overview of the biological decomposition of wood. It begins with a brief description of the major types of wood destruction and their causal agents, and it continues with a description of the progressive changes that take place in wood as it is decomposed. Special emphasis is given to the chemistry and bio-

chemistry involved. The chapter ends with a brief treatment of how wood in use can be protected from decomposition and some beneficial uses of wood-decomposing organisms.

We have used the terms *decomposition* and *degradation* to refer to the conversion of one or more of the structural polymers of wood to simpler molecules. *Degradation* can also be used to mean *deterioration,* i.e., to decrease the value of wood for some use; we have used only *deterioration* in this narrower sense. *Decay* and *rot* refer to the fungal decomposition of wood.

Hundreds of research papers on wood biodecomposition have been published since the pioneering works of Hartig *(3)* and Buller *(1)*. We aim to introduce the reader to the principles that those investigations have developed. With this in mind we have categorized and generalized, but we hope that we have not oversimplified. The biodecomposition processes are quite complex biologically, chemically, and biochemically. We have pointed to some of the unknowns in a field that retains many. In Table I we have listed a number of reviews that can be consulted for details.

### *Susceptibility and Resistance*

When wood is laid down by the cambium of a living tree, two major types of wood cells are formed-thick-walled fiber cells that make wood strong and thin-walled parenchyma cells in which reserve foods are stored. Wood fiber cells die a few days or weeks after they are formed and lose their cytoplasmic contents as soon as they become functional in water transport. Thus, mature wood fiber cells consist almost entirely of cell wall polymers-cellulose, hemicelluloses, and lignin. For this reason, wood fiber cells can be degraded only by organisms that have the ability to decompose these structurally complex high-polymeric materials.

**Table I. Some Reviews on the Biological Decomposition of Wood**

| *Subject* | *References* |
|---|---|
| General, historical | 5-10 |
| Insects, marine borers | 6, 11-14 |
| Chemical, physical changes during decomposition | 5, 6, 15-M |
| Cellulose and hemicellulose decomposition | 19-27 |
| Lignin decomposition | 28-33 |
| Control of biodecomposition | Chapter 11 this book, 34-40 |
| Uses and potential uses of biodecomposing organisms | 26, 41, 42 |

By contrast, wood-storage cells remain alive for many years and only lose their cytoplasmic contents when sapwood is transformed into heartwood. The sugars, starch, amino acids, and proteins in the wood-storage cells make sapwood highly susceptible to invasion by a large number of fungi and bacteria that can use the reserve food materials but cannot attack the more complicated cell wall polymers.

The heartwood of certain species of trees is moderately to highly resistant to decomposition even by organisms that can degrade the cell wall polymers. Highly resistant species include trees such as cypress, various cedars, and osage-orange; moderately resistant species include white oak, Douglas-fir, and certain pines. Resistance is caused by phenols, terpenes, alkaloids, and other substances that are deposited in heartwood and are toxic to wood-destroying fungi, bacteria, insects, and marine borers *(43)*. Because these toxic substances do not occur in sapwood, the dead sapwood of all tree species is highly susceptible to biological decomposition. It should be noted that the living sapwood in trees is resistant to decay by virtue of active defense mechanisms; the heartwood is actually more susceptible than the living sapwood.

Although numerous fungi and some insects can cause decomposition of the dead heartwood tissues inside living trees, these organisms rarely continue to cause decomposition of timber products after the trees are harvested. Despite much speculation about why this is so, no scientific explanation of this phenomenon has been provided to date *(44)*.

### *Types of Wood Deterioration*

Table II summarizes the major types of wood deterioration and the causal organisms. The following discussion deals with deterioration without cell wall decomposition; the bulk of the chapter deals with deterioration with decomposition of cell walls.

**Deterioration Without Decomposition.** When fresh-cut lumber or veneer is properly air-seasoned, the stored food materials in the sapwood are soon depleted by the respiratory processes of the wood parenchyma cells themselves. If drying is delayed, however, the fresh-cut wood can be invaded by so-called sap-stain fungi and algae, or by bacteria and molds that develop over the surface or penetrate deep into the sapwood by growing through the ray cells from one wood storage cell to another. These organisms use the contents of the wood storage cells as food and thus do not affect the strength of wood seriously; they primarily discolor the wood or alter its permeability.

When fresh-cut wood is kiln-dried immediately, the living cells of the sapwood are killed by the heat and the reserve foods are

**Table II. Types of Biological Deterioration of Wood and the Organisms Responsible**

| *Type of Deterioration* | *Organism(s)* |
|---|---|
| Deterioration without decomposition | |
| Loss of stored food reserves | Living wood cells in sapwood |
| Mechanical boring, pecking, cutting | Insects, birds, mammals |
| Stains | Fungi |
| Surface discoloration | Fungi, algae |
| Pit membrane destruction | Bacteria, fungi |
| Decomposition of structural polymers | |
| Mechanobiochemical | Insects, marine borers |
| Biochemical (decays) | Fungi |

retained in the wood storage cells. If kiln-dried wood becomes wet again, these stored foods can again become substrates for growth of discoloring fungi and bacteria.

When fresh-cut logs are converted quickly into large piles of chips, the living cells of the sapwood, together with the fungi and bacteria mentioned above, rapidly convert the stored food reserves into carbon dioxide ($CO_2$), water, and heat (*see* Reaction 1 for respiration) *(45)*. If this metabolic heat is not dissipated, the pile becomes hot, and under conditions of very poor ventilation can lead to spontaneous combustion *(46)*. For all of these reasons, fresh-cut sapwood must be considered to be alive and, therefore, must be handled as a perishable raw material.

The most common discoloring organisms are of two general types-surface molds with colored spores, and algae that grow on wood surfaces; and fungi with dark-colored hyphae that discolor the wood interior as they penetrate deep into sapwood. *Aspergillus* spp. and *Penicillium* spp. are among the most common surface molds. Discolorations caused by these fungi usually are so superficial that they can be removed by brushing, planing, or sanding. *Ceratocystis* spp. are among the most common deep-penetrating sapstain fungi *(47)*. These discolorations usually cannot be removed even by vigorous bleaching chemicals.

*Bacillus polymyxa* (Prazmowski) Mace and certain other bacteria *(48)*, as well as stain fungi and some molds such as *Trichoderma viride* Pers. ex Fr. *(49,50)*, degrade the pectin membranes in the bordered pits between wood cells. This degradation greatly increases the permeability of the wood to water and organic solvents. Increased per-

meability is a problem in wood finishing but can be a help in the penetration of pulping chemicals and preservatives into sapwood.

Mechanical disintegration of wood is caused by many species of insects, birds, and some mammals. In some cases this disintegration can be quite serious.

**Deterioration with Decomposition.** The susceptibility of the wood cell wall polymers to biological decomposition is determined largely by their accessibility to enzymes and other metabolites produced by wood-destroying fungi or, in the case of certain insects and marine borers, by microorganisms that live in the digestive tracts of these animals. Direct physical contact between the enzymes or other metabolites and the wood cell wall polymers is prerequisite to hydrolytic or oxidative degradation. Because the cellulose, hemicelluloses, and lignin are all water-insoluble polymers and are deposited in wood cell walls in intimate physical admixture with each other, this necessary physical contact can be achieved only by diffusion of the enzymes or other metabolites into this complex matrix or by fine grinding of the wood prior to digestion.

The crucial structural component of wood governing wood's biological decomposibility is lignin. In wood, the cellulose microfibrils are coated or overlayered by hemicelluloses which in turn are under a lignin sheath *(51)*. The lignin is covalently bonded to, and to some extent physically intermixed with, the hemicelluloses; the bonds between lignin and hemicelluloses are probably infrequent *(52)*. Whatever the exact relationship between the hemicelluloses and lignin, the lignin physically prevents enzyme access to both the hemicelluloses and cellulose. Digestibility of solid wood and other intact lignified tissues (lignocelluloses) is largely a function of lignin content (Figure 1).

Three biological mechanisms have evolved for overcoming the lignin barrier: (1) insects and marine borers physically disrupt the barrier by grinding the wood very finely; (2) some microorganisms, primarily higher fungi, decompose lignin and thus expose the polysaccharides; and (3) certain other higher fungi apparently secrete nonenzymatic cellulose-depolymerizing agents that are small enough to penetrate the-lignin sheath. Mechanism 1 permits *mechano-biochemical decomposition* of solid wood; Mechanisms 2 and 3 permit *biochemical decomposition*. We will discuss each mechanism in turn.

### *Mechanobiochemical Decomposition*

Circumventing the lignin barrier to enzymatic digestion of the polysaccharides occurs when wood is finely ground. Below a certain wood particle size, the polysaccharides (celluloses and hemicellu-

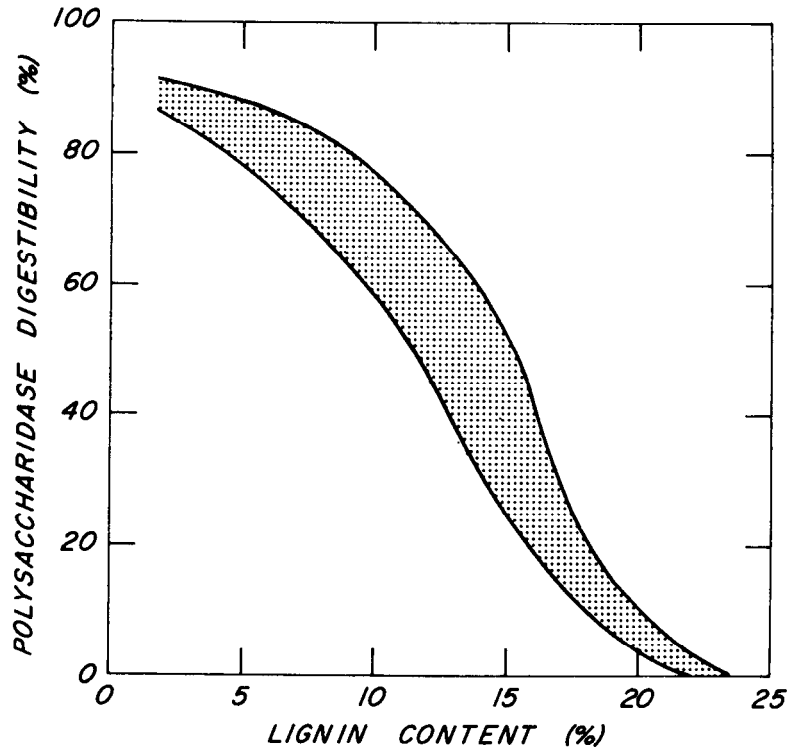



*Figure 1. Digestibility of wood by mixtures of cellulases and hemicellulases is largely a function of lignin content (adapted from Reference 53).*

loses) should become maximally digestible by enzymes. This size probably varies somewhat with lignin content and perhaps distribution, and hence wood species. Maximum digestibility has been achieved with some woods (sweetgum, red oak, aspen) by vibratory ball milling, but with other woods (red alder, conifers) this milling technique has other effects that adversely affect digestibility *(54).* The effect of particle size reduction on enzyme accessibility deserves further study with other milling procedures. Virtanen and coworkers (55) first demonstrated the effect of reducing particle size on digestibility by showing that cellulolytic bacteria unable to degrade intact wood are able to utilize fine sander dust. Pew *(56)* later demonstrated that fine milling makes wood susceptible to mixtures of cellulases and hemicellulases.

The effect of fine grinding had already been demonstrated by many insects and marine borers whose mouth parts, augmented in some cases by internal grinding organs, reduce wood to a digestible particle size. Cellulases and hemicellulases in the guts digest the exposed polysaccharides; excreta are enriched in lignin. Digestion in

many insects is incomplete, reflecting failure to grind the wood finely enough, absence of a full enzyme complement, insufficient residence time, or other factors. Certain wood-boring insects, including ambrosia beetles, lyctus beetles, carpenter ants, and carpenter bees do not digest the structural polymers of wood. Wood passes through the gut of the lyctus beetles, but only the easily digested nonstructural materials-primarily starch in parenchyma cells-are removed *(6, 11, 12)*. The ambrosia beetles, bees, and ants do not ingest wood.

Some insects, such as the Indian longhorn beetle, *Stromatium barbatum* Fabricius *(57)*, and the common marine borers *Limnoria tripunctata* Menzies (an isopod) *(58)* and *Bankia setacea* Tryon (a mollusk) *(59)*, are thought to have endogenous cellulases (and perhaps other polysaccharide hydrolases). Termites and most of the other wood-digesting insects rely on polysaccharolytic microbes in their guts. The beetle *Stromatium barbatum (57)* and the marine borer *Bankia setacea (60)* are thought to utilize both their own cellulases and those of gut microbes.

Wood-decomposing insects and the marine borers commonly digest only the cellulose and hemicelluloses. Reports of extensive decomposition of lignin *(6, 60)* deserve further study with modern techniques. Limited decomposition of lignin, however, probably does occur in some insects. One of the most convincing reports is that conversion of $^{14}C$ lignin to $^{14}CO_2$ in the gut of the termite *Nasutitermes exitiosus* (Hill) was demonstrated *(61)*. Because anaerobic decomposition of lignin has not been observed *(62, 63)* it is probable that some oxygen is present in the guts of *Nasutitermes (61)* and in those of certain other insects that reportedly digest lignin.

Table III lists representative wood-decomposing insects and marine borers and summarizes some features of their action on wood. Figure 2 shows the extensive damage caused by some of these wood-decomposing animals. Only a few detailed studies of the chemistry and biochemistry of wood degradation by the insects and marine borers have been made. Because the animals derive nourishment from the structural polymers of wood, the subject is of practical significance and deserves more research attention.

### *Biochemical Decomposition: The Wood Decays*

**Types of Decay.** As shown in Figure 3, wood decay fungi can be divided into three classes based on the type of decay they cause: white, brown, and soft rots. The white rots can be further separated into pocket rots and uniform rots (Figure 3). In North America, the white and brown rots are caused by about 1700 species of wood-decaying fungi in the class Basidiomycetes; over 90% of these cause the white rot type of decay *(67)*. Early reports of non-basidiomycete

white rots (e.g., decay by Xylaria spp.) may be incorrect *(26)*. White- and brown-rot fungi are closely related, which makes the evolutionary basis for their very different effects on wood most intriguing.

Soft rots are caused by fungi in the classes Ascomycetes and Fungi imperfecti. Most are normally found in the soil or in marine environments *(68)*. The list of soft-rot fungi is long and growing longer. A streptomycete has been shown to cause at least limited soft rot in beech *(69);* it is likely that other soil bacteria will be shown to cause soft rot. We have observed that certain litter-decomposing basidiomycetes, such as *Collybia butyrucea,* cause a slow decomposition that resembles soft rot macroscopically.

Macroscopic and microscopic characteristics of white, brown, and soft rots are summarized in Table IV

**Progressive Changes in Chemical Composition.** The chemical composition of wood begins to change as soon as it is colonized by the hyphae of wood-destroying fungi. Initial invasion of the ray cells and vessels *(70)* is primarily at the expense of soluble sugars, starch, and other carbohydrates. The hyphae then penetrate and become established in virtually every cell of the wood in which environmental and other factors are favorable. This attack results in a progressive depletion of all three structural polymers during white and soft rots, and in the polysaccharides during brown rot (Figure 4). Depletion of lignin roughly parallels loss of polysaccharides in white rot, lags behind polysaccharide depletion in soft rot, and is insignificant in brown rot. A slight initial increase in lignin is frequently seen during brown rot (see Figure 4). This increase is probably due to partial oxygenation of the lignin polymer *(31, 72)*.

Some variation in the relative rates of cellulose vs. hemicellulose depletion is observed among various fungi and woods. Marked selectivity for the hemicelluloses has been achieved through genetic manipulation of several white-rot fungi *(73)* and occurs naturally in some species, e.g., *Polyporus pargamenus* Fr. *(74)*. Selective removal of cellulose is not observed, a consequence of its location within the lignin-hemicellulose sheath. Selective removal of lignin does not occur, apparently because polysaccharides provide energy necessary for lignin decomposition *(28, 75–77)*.

**Progressive Changes in Strength Properties.** Decay of wood has profound effects on strength properties. Of the various measures of wood strength *(78),* toughness and the related property of work to maximum load are most sensitive to decay. Toughness, which is also called *impact bending strength,* is relatively easy to measure and has been the most widely studied.

All three types of decay cause losses in toughness and related properties that far exceed their losses in weight. Wood decayed to

**Table III. Decomposition of Wood by Some Insects and Marine Borers**

| *Classification (example)* | *Description of Damage* | *Notes and References* |
|---|---|---|
| | Insects | |
| Coleoptera, Anobiidae *[Xestobium rufovillosum* (De G.), "deathwatch beetle"] | Round, powder-filled galleries (<3 mm in diameter); wood becomes riddled (Figure 2) | "Powderpost" beetles; damage done primarily by larvae; limited digestion of cellulose and hemicelluloses *(6)* |
| Coleoptera, Cerambycidae *[Hyalotrupes bajulus* (L.) "old house borer"] | Oval-shaped galleries winding irregularly through the wood, galleries powder-filled (6-10 mm in diameter) (Figure 2) | Longhorn beetles; larvae ("round-headed borers") do damage; limited digestion of cellulose and hemicelluloses *(11)* |
| *[Stromatium burbutum* (Fabricius) "Indian longhorn beetle"] | As above | Larvae do the damage; extensive digestion of cellulose and hemicelluloses; lignin decomposition reported *(57)* |

| | | |
|---|---|---|
| Isoptera, Kalotermitidae *(Kulotermes flavicollis* Fabr.) | Galleries, chambers within wood; honeycombing; wood structure thoroughly destroyed (Figure 2) | "Drywood" termites; polysaccharides are extensively digested; lignin may be partly decomposed *(6, 64)* |
| Isoptera, Rhinotermitidae *(Reticulitermes* spp.) | First attack is on less dense part of wood, so that earlywood is removed preferentially; wood structure is thoroughly destroyed (Figure 2) | "Subterranean" termites; polysaccharides are extensively digested; lignin at least slightly altered *(65)* |
| Hymenoptera, Siricidae *(Sirex phantoma)* | Small (4-6 mm in diameter) round galleries tightly packed with frass | "Wood wasps"; some digestion of cellulose *(6)* |
| | Marine Borers | |
| Adapedonta, Teredinidae (bivalve mollusks) *(Bankia, Teredo* spp.) | Small entry holes on wood surface; interior riddled with much larger bore holes (Figure 2) | Digest cellulose extensively, and probably hemicelluloses, but not lignin; *Bankia* secretes own cellulase, and also has cellulolytic gut microbes *(59)* |
| Isopoda, Limnoridae *(Limnoria tripunctata* Menzies) | Maze of tunnels from surface inward, resulting in progressive erosion (Figure 2) | Preferentially digest cellulose (and probably hemicelluloses); lignin unaltered *(66);* thought to secrete own cellulases; gut is sterile *(58)* |

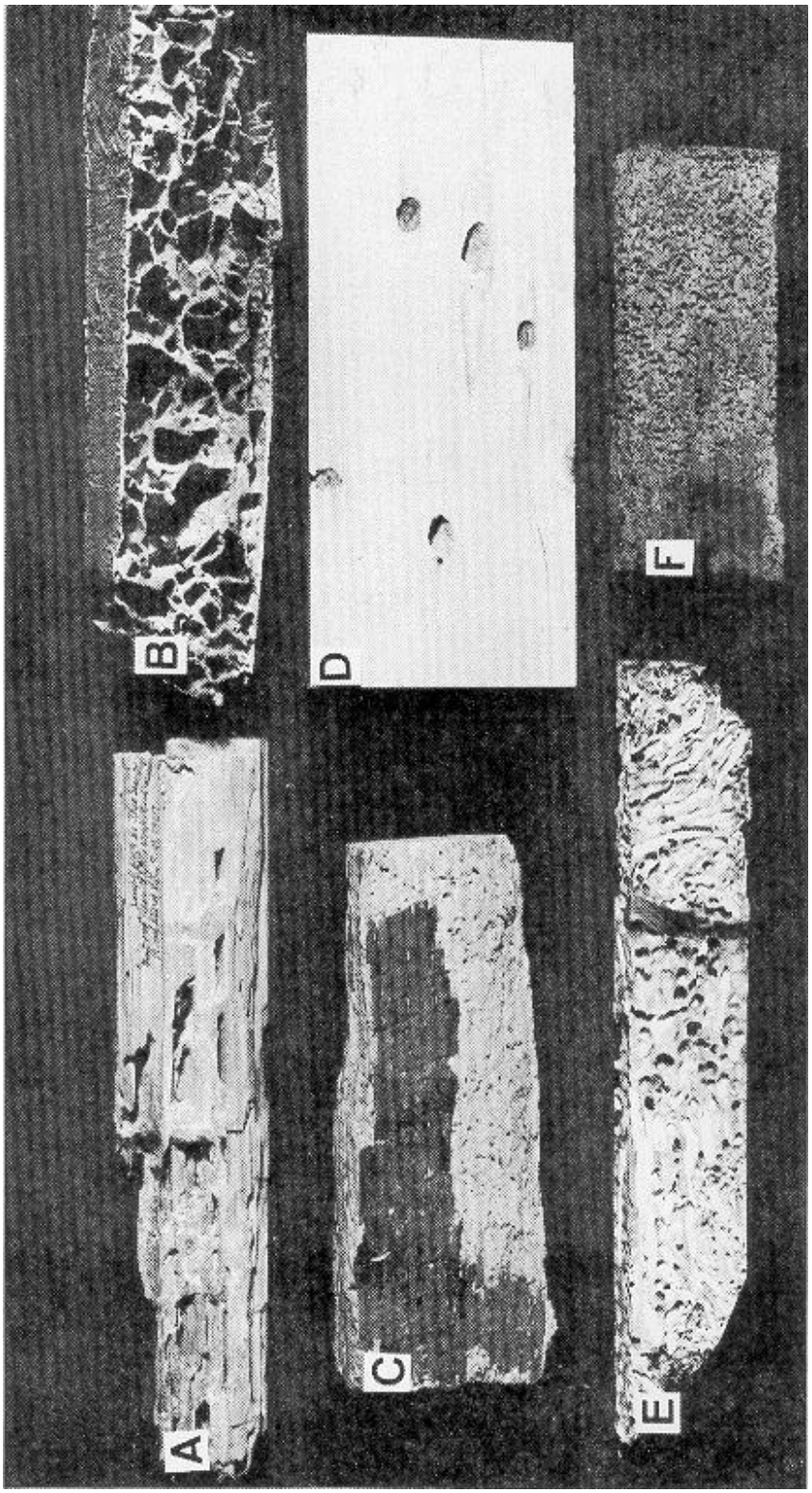



*Figure 2. Wood attacked by some insects and marine borers. Key: A, oak flooring by subterranean termites; B, cross section of albizzia board by drywood termites (chamber walls within board are unattacked wood); C, cuangare by anobiid beetle; D, white pine by a longhorn beetle; E, yellow pine by a bivalve marine borer (Teredo sp.); and F, Douglas-fir by an isopod marine borer (Limnoria sp.). Board A is 27 cm long.*

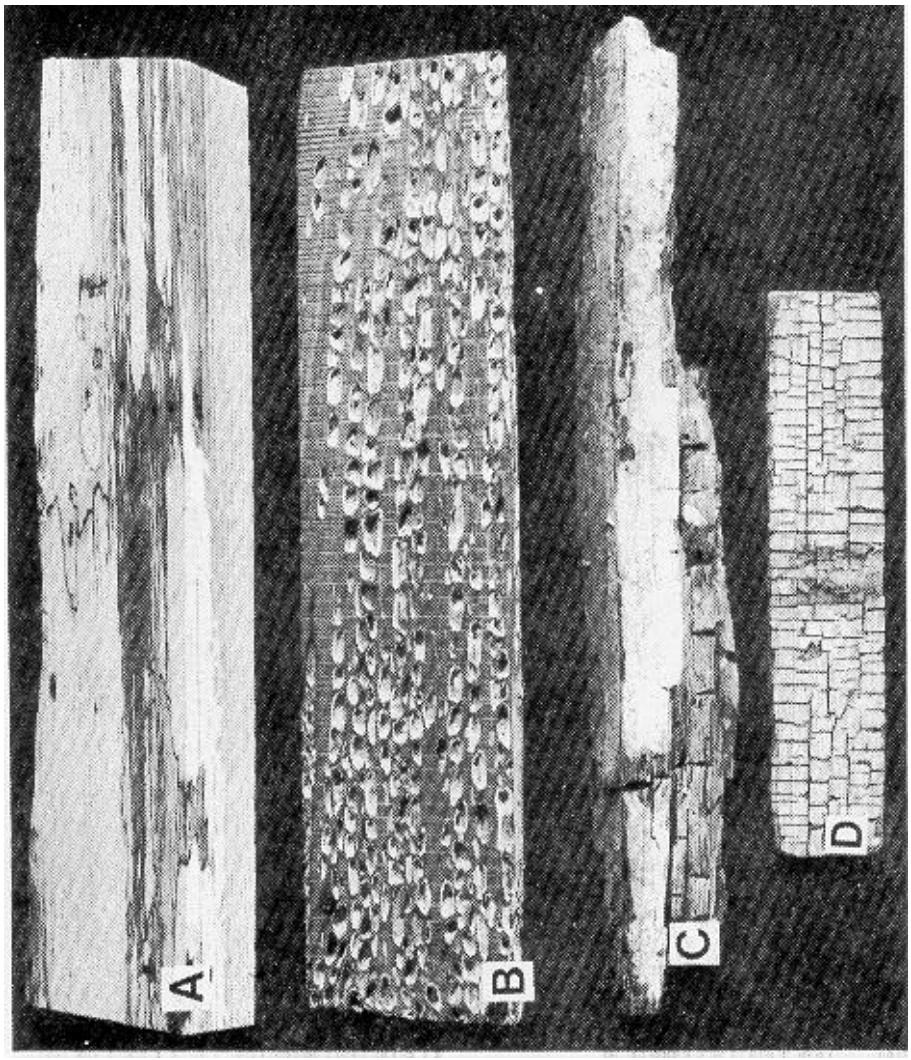



*Figure 3. Wood partially decomposed by fungi. Key: A, uniform-white rot in northern red oak: decay has permeated sapwood (broad, tangential-face), but is only slowly penetrating into heartwood (narrow, radial face); B, white oak heartwood decayed by a white-pocket rot fungus; C, western redcedar decayed by a brown-rot fungus (white mycelium is visible on surface); and D, yellow pine decayed by a soft-rot fungus. Board A is approximately 20 cm long.*

**Table IV. Macroscopic and Microscopic Features of White, Soft, and Brown Rots of Wood**

| *Type of Decay (representative causal organisms)* | *Macroscopic Features*[a] | *Microscopic Feutures*[b] |
|---|---|---|
| White rot<br>*[Coriolus versicolor* (L. ex Fr.) Quel., *Phanerochaete chrysosporium* Burds.] | Usually not discernible in early stages, wood later becomes bleached or discolored; mottling or flecking is common; some species form white pockets in wood; dark zone lines often observed in nature; wood retains size and shape | Hyphae colonize lumens of cells, penetrate first from cell to cell via pits, later directly via bore holes; progressive decay observed as thinning of cell walls; (in "pocket rots," decay is limited to the developing pockets) |
| Soft rot<br>*(Chaetomium globosum* Kunze, *Paecilomyces* spp., *Allescheria* | Only water-soaked wood attacked; decay even in early stages characterized by softening and | Hyphae grow longitudinally within the secondary walls; characteristic catenate, spindle-, or dia- |

| | | |
|---|---|---|
| *terrestris* Apinis) | minute checking of surfaces; dull gray to brown color. Decay progresses gradually from the surface inward | mond-shaped cavities, oriented with cellulose microfibrils |
| Brown rot<br>*[Gloeophyllum trabeum* (Pers. ex Fr.) Murr., *Poria plaenta* (Fr.) Cke., *Merulius lacrymans* (Wulf.) Fr.] | Often not discernible during early stages, but wood rapidly becomes brash; later, wood becomes discolored, finally brown and soft; drying causes extensive checking across the grain, giving a cubical pattern; mycelial fans may be present on surfaces or within the checks | Hyphae colonize lumens of cells, penetrate from cell to cell via pits and often directly via bore holes. As decay progresses, cell walls may shrink and collapse |

[a] See Figure 3 *and* References 7 and 8.
[b] See Reference 70.

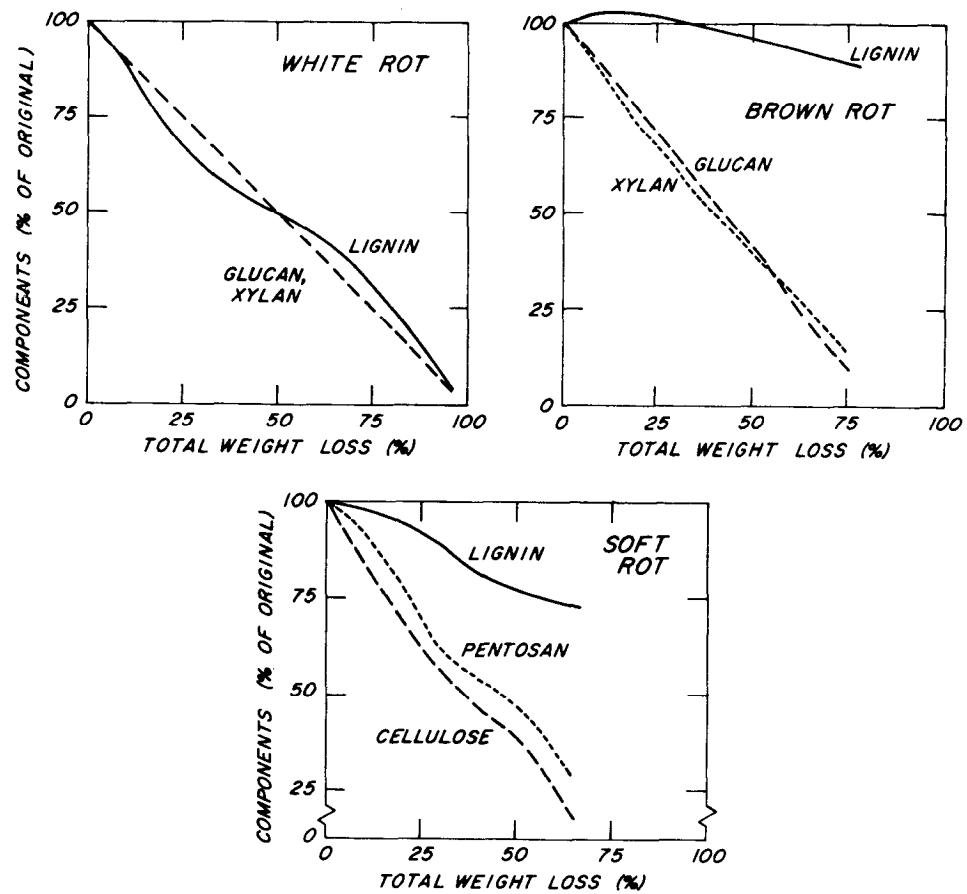



*Figure 4. Cellulose (glucan) and hemicelluloses (xylan, pentosan) are depleted during decay by white-, brown-, and soft-rot fungi; lignin is decompose efficiently only by white-rot fungi. Key: white rot, sweetgum by* Coriolus versicolor *(L. ex Fr.) Quel.* (15); *brown rot, sweetgum by* Poria placenta *(Fr.) Cke.* (15); *and soft rot, beech by* Chaetomium globosum *Kunze* (71).

weight losses of less than 3% by white-, soft-, or brown-rot fungi frequently has lost over 50% of its strength measured as toughness *(18, 79-85)*. Microscopic observations reveal that this loss is not due to a localized destruction of part of the test piece, but rather to a general decomposition.

It is not known why toughness is so sensitive to decay by all three groups of fungi. Campbell *(5)* concluded that the reduction is due to a "shortening of the cellulose chain molecules in wood." This is reasonable for brown rot, but unlikely for white rot or soft rot. Cowling *(15)* demonstrated that the brown-rot fungus *Poria monticola* Murr. [now *Poria placenta* (Fr.) Cke.] causes a sharp reduction in the degree of polymerization (DP) of cellulose during decay of sweetgum wood (Figure 5). In contrast, the white-rot fungus *Polyporus versicolor* L. ex Fr. [now *Corioius versicolor* (L. ex Fr.) Quel.] only gradually reduces cellulose DP (Figure 5). Levi and Preston *(71)* showed that the residual cellulose in beech wood is also only gradually decreased in DP during decay by the soft-rot fungus *Chaetomium globosum* Kunze. Thus the basis for toughness loss in white and soft rots lies elsewhere and deserves further research.

The effect of brown-rot fungi on other wood strength properties is much more pronounced than that of white-rot fungi (see Reference 18), and reflects cellulose depolymerization. Interestingly, wood species vary substantially in strength loss at a given weight loss by brown-rot fungi *(18)*. The basis for this variation is not known and deserves additional research.

Mechanisms of Wood Decay. Microscopy indicates that the enzymes or other agents that degrade the wood cell wall polymers diffuse away from the hyphae, and that they are secreted by the laterals as well as by the growing tips *(70, 86, 87)*. Gelatinous sheaths encase both hyphae and substrate when brown- or white-rot fungi attack isolated cellulose *(88)*. The nature and actual importance of such sheaths in the decay of solid wood need further investigation. The sheaths might provide an optimum environment for enzyme action and might also help prevent loss of enzymes with their precious nitrogen. Because the nitrogen content of wood is quite low, this important element is limiting in the nutrition of wood-decomposing organisms. Its importance in wood decay has been discussed *(89)*.

Studies of the biochemical mechanism of wood decay have, with very few exceptions, been conducted with isolated cellulose, hemicelluloses or lignin, or with appropriate model compounds, rather than with solid wood. The few studies with enzymes produced during growth on or in wood have revealed no peculiarities that would bring into question the results of studies with the isolated components.

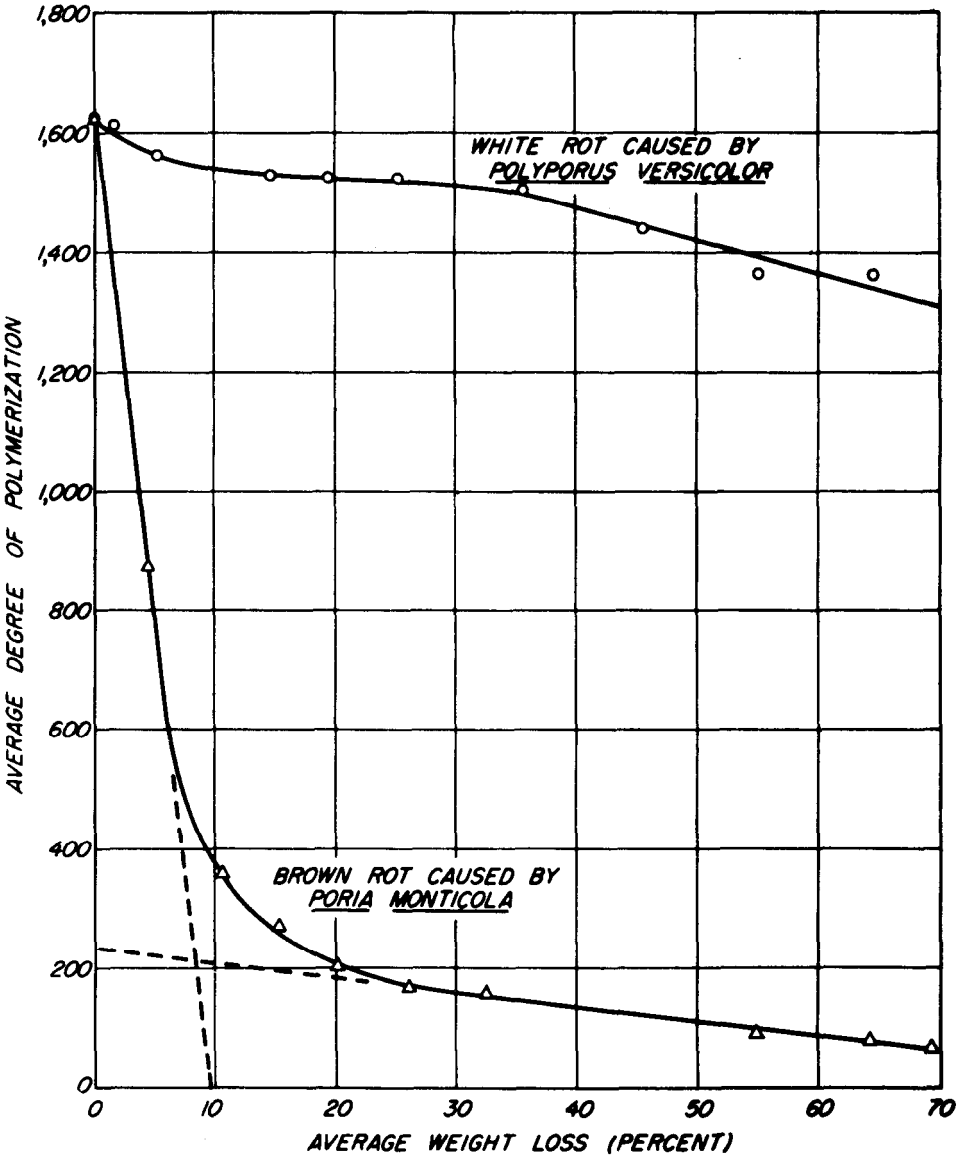



*Figure 5. Cellulose in wood is depolymerized early during brown rot, but only gradually during white rot. The data are for sweetgum sapwood decayed by the brown-rot fungus* Poria placenta *(Fr.) Cke. (formerly* P. monticola *Murr.) and for the white-rot fungus* Coriolus versicolor *(L. ex Fr.) Quel. (formerly* Polyporus versicolor *L. ex Fr.)* (15).

Isolated cellulose was not degraded by the brown-rot fungus *Poria placenta* unless the fungus was in contact with whole wood *(90)*. Further study indicated, however, that the wood could be replaced with simple sugars, i.e., that nutrients in the wood were simply serving as starter carbon/energy sources *(90)*.

In the following discussion, we have assumed that wood decay is due to the concerted action of the individual enzyme systems responsible for cellulose, hemicellulose, and lignin decomposition.

**CELLULOSE DECOMPOSITION.** Decomposition of crystalline cellulose by white-rot fungi and various soil fungi (including the soft-rot fungi), results from the synergistic action of three types of hydrolytic enzymes: *endo*-1,4-β-glucanases, *exo*-1,4-β-glucanases, and β-glucosidases. Presumably, bacterial and animal cellulases are similar. Brown-rot fungi also decompose crystalline cellulose, but most possess no *exo*-glucanase; their unique mechanism of cellulose degradation is discussed later.

The mechanism of cellulose degradation by fungi has been the subject of extensive research *(19–21, 23–25)*, primarily with the mold *Trichoderma viride* and the white-rot fungus *Sporotrichum pulverulentum* Novo. (now *Phanerochaete chrysosporium* Burds.). Results indicate that the *endo*-1,4-β-glucanases ($C_x$ enzymes) act randomly over the exposed surfaces of cellulose microfibrils. Nonreducing termini generated by this action are then hydrolyzed by *exo*-1,4-β-glucanases (cellobiohydrolases, $C_1$ enzymes), releasing cellobiose. Cellobiose may be cleaved by a β-glucosidase to yield glucose, or in white rot and perhaps other fungi it may be oxidized to cellobionic acid and then cleaved. The *endo*- and *exo*-glucanases act synergistically, perhaps as a loose complex *(91)*. Generally, the *endo*-glucanases and probably the *exo*-glucanases are repressed by high concentrations of monosaccharides *(23)*. Both types of glucanases have molecular weights ranging up to about 75,000 *(92, 93)*, whereas the β-glucosidases are considerably larger *(94)*.

In addition, oxidizing enzymes probably are involved in cellulose decomposition by certain white-rot fungi. *Phanerochaete chrysosporium* possesses cellobiose oxidase, which converts cellobiose to cellobiono-δ-lactone, with $O_2$ serving as electron acceptor *(23)*. This enzyme is responsible for the more rapid hydrolysis of cellulose under aerobic conditions than under anaerobic conditions, presumably because it removes cellobiose and prevents the transglycosylation reactions and the inhibition of *endo*-glucanase activity that occurs when cellobiose accumulates *(23, 73)*. Similar oxidizing activity is not found in the species of Fungi Imperfecti examined *(91)*. Another enzyme, cellobiose:quinone oxidoreductase, has the same action, but requires quinones as electron acceptors *(23)*. A glucose oxidase also has been implicated in the overall process *(23);* it oxidizes glucose to gluconolactone with $O_2$ or quinones as electron acceptors. Presumably, these oxidizing activities regulate the amounts of glucose and cellobiose, ultimately coordinating the rates of cellulose hydrolysis and the metabolism of end products. Phenols, which are inter-

mediates in lignin decomposition, also affect the amounts of endoglucanase activity in white-rot fungi *(23)*. Figure 6 summarizes the interconversions and regulatory interactions in cellulose hydrolysis by white-rot fungi *(23)*.

Cellulose decomposition by brown-rot fungi is an unusual process. In the early stages of their decay of wood, and in contrast to decay by white-rot fungi, the cellulose is severely depolymerized (see Figure 5). This discovery *(15)* explained the highly destructive effects of these fungi on wood, as described in the section entitled "Progressive Changes in Strength Properties" (page 463), but it presented an enigma because only a very small percentage of the cellulose in wood is accessible to cellulolytic enzymes. *Enzymatic* degradation must cause a gradual loss in cellulose integrity, as seen in white rot *(15)*.

Because the depolymerizing agent of the brown-rot fungi completely penetrates the crystalline microfibrils, only very small molecules can be responsible *(15)*. In discussing this, Cowling and Brown *(92)* noted that G. Halliwell *(95)* had described experiments on the depolymerization of cellulose under physiological conditions with Fenton's reagent ($H_2O_2$ and ferrous salts). Subsequent studies demonstrated that brown-rot fungi secrete $H_2O_2$ and that wood contains enough iron for a possible involvement of an Fe–$H_2O_2$ system in cellulose depolymerization *(96)*. Cellulose is in fact oxidized during attack by the brown-rot fungus *Poria placenta (90)*. Oxalic acid, which is secreted by brown-rot fungi, can reduce the $Fe^{3+}$ normally present in wood to $Fe^{2+}$, the active form in Fenton's reagent *(97, 98)*. Figure 7 shows the proposed mechanism for the depolymerization of cellulose. Nicholas et al. (personal communication) demonstrated degradation of $^{14}$C-cellulose by *Gloeophyllum trabeum* (Pers. ex Fr.) Murr. through a membrane with a nominal molecular weight limit of 1000.

This initial oxidative depolymerization of cellulose evidently opens up the wood cell wall structure so that cellulolytic and hemicellulolytic enzymes can reach their substrates despite the presence of lignin. Solubility of wood in 1% NaOH increases markedly on brown-rot attack *(15)* and reflects cellulose depolymerization and the opening up of the wood structure.

Interestingly, enzyme preparations from most brown-rot fungi possess *endo*- but not *exo*-1,4-β-glucanase activity *(99–101)*. These fungi differ from other cellulolytic organisms, too, in that *endo*-glucanase production is not repressed by monosaccharides *(102)*. Still another unusual feature is a large enzyme complex that hydrolyzes carboxymethyl cellulose, xylans, glucomannans, and various glycosides *(103)*.

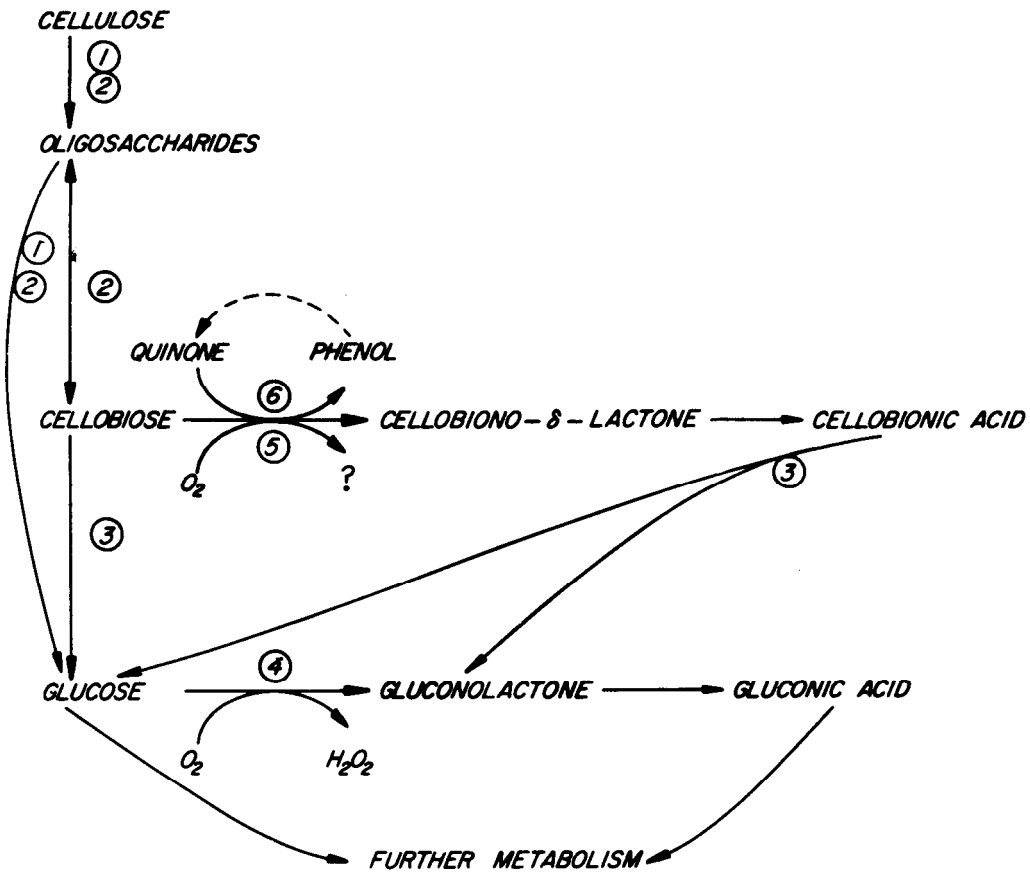



*Figure 6. Both hydrolytic and oxidative enzymes participate in cellulose decomposition by the white-rot fungus* Phanerochaete chrysosporium *Burds. Hydrolytic enzymes: 1,* endo-*1,4*-β-*glucanases; 2,* exo-*1,4*-β-*glucanase; and 3,* β-*glucosidase. Oxidative enzymes: 4, glucose oxidase, 5, cellobiose oxidase; and 6, cellobiose:quinone oxidoreductase. Adapted from Reference 23.*

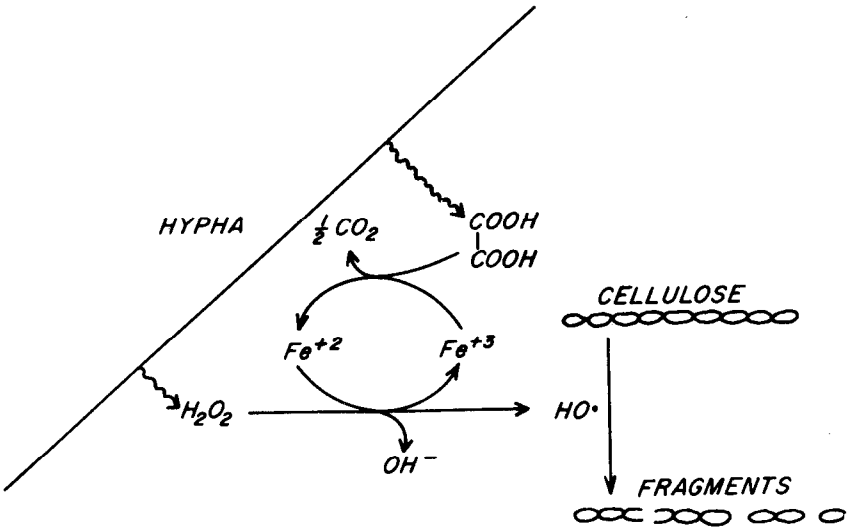



*Figure 7. Depolymerization of cellulose in wood by brown-rot fungi might involve* $Fe^{2+}$ *and* $H_2O_2$ (92, 96, 97).

Although white-rot fungi also secrete $H_2O_2$ *(104),* they have not been found to depolymerize cellulose oxidatively. One reason might be that they possess oxalate decarboxylase, which decomposes oxalate, whereas brown-rot fungi apparently do not *(98).* This problem deserves further investigation.

The cellulolytic system of soft-rot fungi has received relatively little attention. It is probably similar to that of the closely related Ascomycetes and Fungi Imperfecti *(19-25, 27),* which apparently differs little from that of white-rot fungi, except perhaps in the absence of oxidizing enzymes.

HEMICELLULOSE DECOMPOSITION. Dekker and Richards have reviewed the microbial hemicellulases *(22).* Wood-rotting fungi produce enzymes capable of hydrolyzing a variety of β-(1 → 4)-linked glycan (mannan and xylan) substrates, as well as various glycosides *(94, 101, 105-8)* Judging from the relatively little research done, corresponding enzymes from the three groups of decay organisms appear to be similar, and are also similar to those from other microbes *(22, 106).* To our knowledge, the enzymes responsible for *complete* depolymerization of a wood hemicellulose have not been described in any microbe. This is another subject that needs additional study. *endo*-Glycanases from white-, brown-, and soft-rot fungi apparently all act randomly and produce dimeric and higher oligomeric products *(22, 108-11).* Uronic acid-substituted oligosaccharides are produced from glucuronoxylan substrates *(107-9, 111)* but enzymes catalyzing

hydrolysis of the xylose–uranic acid linkage have not been reported. A mannanase purified from a brown-rot fungus hydrolyzed both mannose-(1 → 4)-glucose and glucose-(1 → 4)-mannose linkages *(110)*. Glycosidases active on hemicellulose-derived disaccharides also are produced by the wood-rotting fungi *(94)*, but *exo*-hydrolases degrading hemicellulose oligosaccharides have not been reported in these organisms.

The enzyme complex with multiple glycan and glycoside hydrolase activity in the brown-rot fungus *Poria placenta*, mentioned above *(103)*, has a molecular weight of $1.85 \times 10^5$; other hemicellulases (*endo*-glycanases) of wood-rotting fungi have molecular weights of $3 \times 10^4$–$6 \times 10^4$ *(94)*.

Information regarding regulation of the synthesis of the hemicellulases is somewhat contradictory *(22)*. Regulation in wood-decomposing fungi, however, has not been the subject of the detailed study that it deserves. Multiple hemicellulase activity is found in culture filtrates of both white- and brown-rot fungi after growth on a variety of substrates *(107)*. Hemicellulase production by the two types of fungi is different, however, in that brown-rot fungi exhibit good hemicellulase (as well as cellulase) activities during growth on simple sugars, whereas white-rot fungi do not *(107, 112)*. Production of the enzymes on simple sugars might be induced in response to hyphal wall constituents following substrate depletion, as is an *endo*-xylanase in the white-rot fungus *Stereum sanguinolentum* Fr. *(94)*. Hemicellulases in the soft-rot fungus *Chaetomium globosum* are induced specifically by their substrates *(108)*.

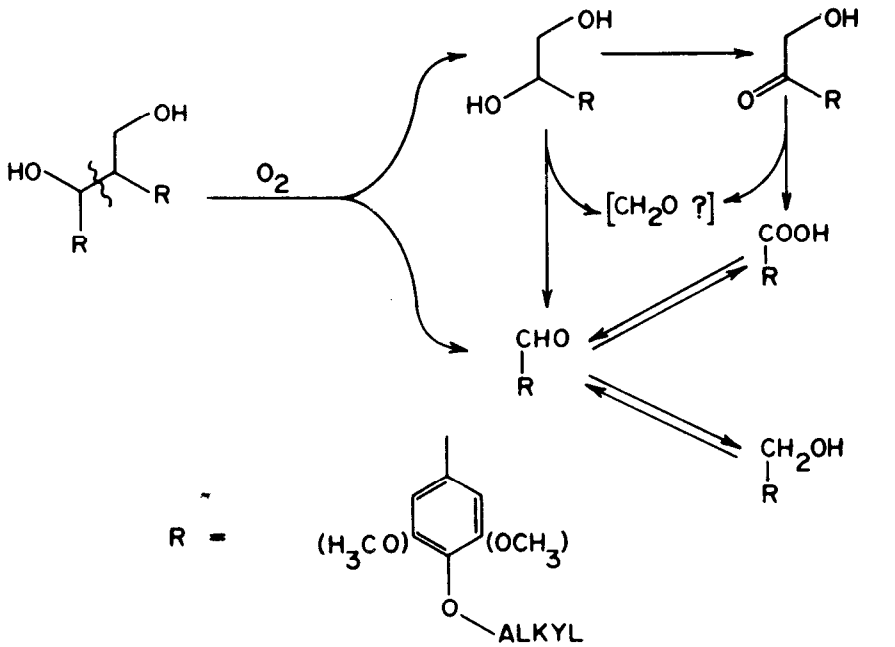
LIGNIN DECOMPOSITION. Research on the fungal decomposition of lignin has accelerated greatly in recent years. Some of the reactions comprising degradation have been elucidated, and the unusual biochemical and physiological features are being described. Several reviews *(28-33)* provide specific literature references.

Research with the white-rot fungi has shown that the process is oxidative, that the ligninolytic system is nonspecific, that its rate-limiting component is not induced by lignin, and that depolymerization may not be an obligatory first step. Lignin degradation, therefore, is distinct from cellulose and hemicellulose degradation; indeed, it differs from the biodegradation of all other biopolymers studied. Prominent reactions of lignin polymer degradation are oxidations and oxidative cleavages in the propyl side chains, demethylations of methoxyl groups, and even cleavages in aromatic rings. The chemistry of degradation is being investigated both by characterization of the partially degraded polymer and of low molecular weight degradation products, and through studies of the metabolism of low molecular weight dirneric model compounds representing substructures in the

polymer. With the model compounds, the specific reactions that comprise degradation are rapidly being described; for example, Scheme 1 shows the fate of the nonphenolic diarylpropane-type of substructure model in cultures of the white-rot fungus *Phanerochaete chrysosporium (113-15)*. Models representing other important substructures have been studied similarly.

Many past studies on the enzymes of lignin decomposition focused on phenol-oxidizing enzymes, such as lactase and peroxidase, produced by white-rot fungi. It is unlikely, however, that this type of activity is important in structural decomposition *(33)*, although the enzymes may have some other role in lignin decomposition *(28)*.

Because the lignin polymer is attacked by extracellular nonspecific oxidizing agents, it is possible that enzymes may not be involved directly, just as cellulose apparently is nonenzymatically oxidized by brown-rot fungi. Hall (116) suggested that diffusible species such as super-oxide ($O_2^-$), derived from molecular oxygen, may participate in lignin decomposition. Research has since indicated that activated oxygen species apparently are commonly produced by the lignin-degrading fungi. Singlet oxygen, an excited state of $O_2$ reportedly in-




*Scheme 1. Model compounds are being used to elucidate the specific reactions of lignin decomposition by white-rot fungi. The fate of a nonphenolic diarylpropane-type of model in ligninolytic cultures of* Phanerochaete chrysosporium *Burds is shown (115–15).*

volved in other biological reactions, was implicated in lignin biodegradation *(117)*, but was later shown not to be involved *(118)*. Hydroxyl radical (•OH) has now been implicated *(119-21)*, but not proven to be involved. Whether it is or not, good evidence has been gained for participation by its immediate precursor, $H_2O_2$ *(119, 121, 144)*. Hydroxyl radical is formed by metal reduction of $H_2O_2$ (see Figure 7).

Findings in this very active research area indicate that enzymes are directly involved. An extracellular enzyme in ligninolytic cultures of *P. chrysosporium* has been discovered *(122)*. It requires $H_2O_2$ for activity and catalyzes the cleavage of nonphenolic model compounds of both the diarylpropane and the arylglycerol-β-aryl ether types. In the former type of model, the degradative reaction is the initial cleavage shown in Scheme 1. The new enzyme catalyzes the partial depolymerization of lignin. It is not the same as earlier reported "lignin-degrading enzymes" *(123-26)*.

Further metabolism of low molecular weight products of the initial degradation of lignin, however it occurs, is probably via classical modes. Vanillic acid, a prominent product of the fungal degradation of lignin *(127)*, is degraded by substrate-inducible enzymes in *P. chrysosporium (128, 129)*.

Although brown-rot fungi are poor degraders of lignin (see Figure 4) they do apparently possess the basic machinery. The main effect they have on lignin is demethylation of arylmethoxyl groups *(130)*, although oxidative changes occur, including some cleavage of aromatic rings *(72)*. Indeed, limited oxidation of aromatic and propyl side chain carbon as well as methoxyl carbon to $CO_2$ has been demonstrated *(131, 132)*. Extensive depolymerization apparently does not occur *(133, 134)*, and it seems unlikely that the limited degradation of lignin by brown-rot fungi is sufficient to open up the wood structure to polysaccharidases. The nonenzymatic oxidative depolymerization of cellulose, discussed in the section entitled "Cellulose Decomposition" (page 473), is evidently what opens up the structure.

Analyses of soft-rotted wood have revealed limited depletion of lignin *(71, 135)*. That these fungi can oxidize lignin to $CO_2$ was shown by using $^{14}C$-lignins *(132)*. Rates did not approach those seen with white-rot fungi, but optimization studies have not yet been conducted. Clearly, the wood-decomposing machinery of the soft-rot fungi has received too little attention.

### *Control and Uses of Wood-Decomposing Organisms*

**Control.** When used properly, wood will retain its strength and other desirable properties for many centuries. When wood is used

improperly, however, it can be decomposed by various organisms, as discussed in this chapter.

The cardinal rules for proper use of wood can be stated simply: keep wood dry, and, if you can't keep it dry, use naturally durable or preservative-treated wood. The first rule is based on a simple biological principle: liquid water is needed in wood cells to provide a medium for diffusion of the enzymes or other metabolites by which wood-decomposing organisms digest the wood substance. If there is no liquid water present inside the wood cells, there will be no medium for diffusion, and therefore no biological decomposition except for certain insects of relatively minor importance. Thus, as long as wood is kept below its fiber-saturation point (about 27% of its dry weight), it will never decay.

A few brown-rot fungi, notably *Serpula incrassata* (Berk. and Curt.) Dank. and *Merulius lucrymans* (Wulf.) Fr. have the unusual ability to conduct liquid water from moist soil or other sources of moisture into dry wood *(36)*. Similarly, subterranean termites can attack very dry wood and, if they have access to water, can transport it through the tubes they construct between moist soil and wood. But chemical soil treatments around wood buildings can prevent attack by even these organisms. Construction practices that thwart both fungal decay and insect attack have been described *(36, 38)*.

The second cardinal rule is based on an equally simple biological principle: some chemicals inhibit living organisms. When wood must be used in moist environments, use of naturally durable or preservative-treated timber will provide long-lasting protection against biological decomposition. Although the heartwood of many tree species is naturally durable *(36, 43, 136, 137)*, sapwood of all tree species is highly susceptible to decomposition. Most construction timbers of temperate regions are sapwood and require preservative treatment for use in moist environments.

The chemicals that have found wide use and acceptance as wood preservatives, primarily creosote, pentachlorophenol, chromated copper arsenate, and ammoniacal copper arsenate, are broad-spectrum pesticides. To achieve greater specificity, advantage could be taken of the unique physiological features of the causal organisms. One such feature is digestion of wood. Treatments that make wood a nonsubstrate (Chapter 4), or chemicals that interfere with the synthesis, secretion, or activity of the wood-decomposing enzymes can be envisioned. A chemical that prevents the synthesis of chitin, which is an essential component of both insects and fungi, is a goal of current research *(138)*. Many other possibilities for more specific interference with the growth or activity of the wood-decomposing organisms could result from a better understanding of the physiology and biochem-

istry of the decomposition processes and of the organisms responsible.

**Uses and Potential Uses *(26, 139).*** Although wood partly degraded by fungi or attacked by insects sometimes has increased aesthetic appeal for use in decorative paneling, wooden bowls, or other household items, a decrease in attractiveness and usefulness is more often the case. Thus biological decomposition usually leads to a decrease rather than an increase in the value of wood.

However, deliberate conversion of solid wood by the agents of biodecomposition is done commercially and has considerable additional potential. The world's second most important commercial mushroom, comprising 20% of world sales *(140-42)*, is shiitake *(Lentinus edodes)* (Figure 8). Cultivated in Asia, primarily on oak logs, shiitake is a major food in Japan and that nation's largest agricultural export. Several other commercial mushrooms are also grown on solid wood (Table V). These mushrooms have much potential in the West where they are currently of minor importance.

Most, and perhaps all, of these edible mushroom-forming fungi cause the white-rot type of wood decomposition. *Lentinus edodes* and some of the others increase the ruminant digestibility of wood-sometimes to over 60% *(26)*–because they remove the lignin and hemicelluloses before the cellulose. Thus, they have potential for direct conversion of wastewood into feed for ruminants. Although the residue from shiitake production is sometimes fed to cattle in Japan, a process aimed at converting wood to cattle feed by this fungus or other fungi apparently has not been developed.

The possibility of using brown-rot fungi to open up the wood structure for ruminants or for conversion via enzymatic hydrolysis or direct fermentation has received virtually no research attention.

Another potential use of white-rot fungi that has received some research attention is in biomechanical pulping. Treatment of wood to a weight loss of less than 3% can lower the energy requirements for subsequent mechanical pulping by more than 20% *(139)*. Mechanical pulps make up a growing share-now about 10%—of U.S. pulp production. Energy consumption is high and makes any treatment attractive that decreases energy demand. We are struck by the similarity in the rapid loss in toughness (see the "Progressive Changes in Strength Properties" section) and the rapid decrease in energy requirements for mechanical pulping during white rot. The physical-chemical basis for this decrease should be investigated; it might actually have little to do with lignin degradation, which has been assumed to be the basis *(139)*. Biomechanical pulping deserves additional investigation.

Production of microbial chemical products during growth on

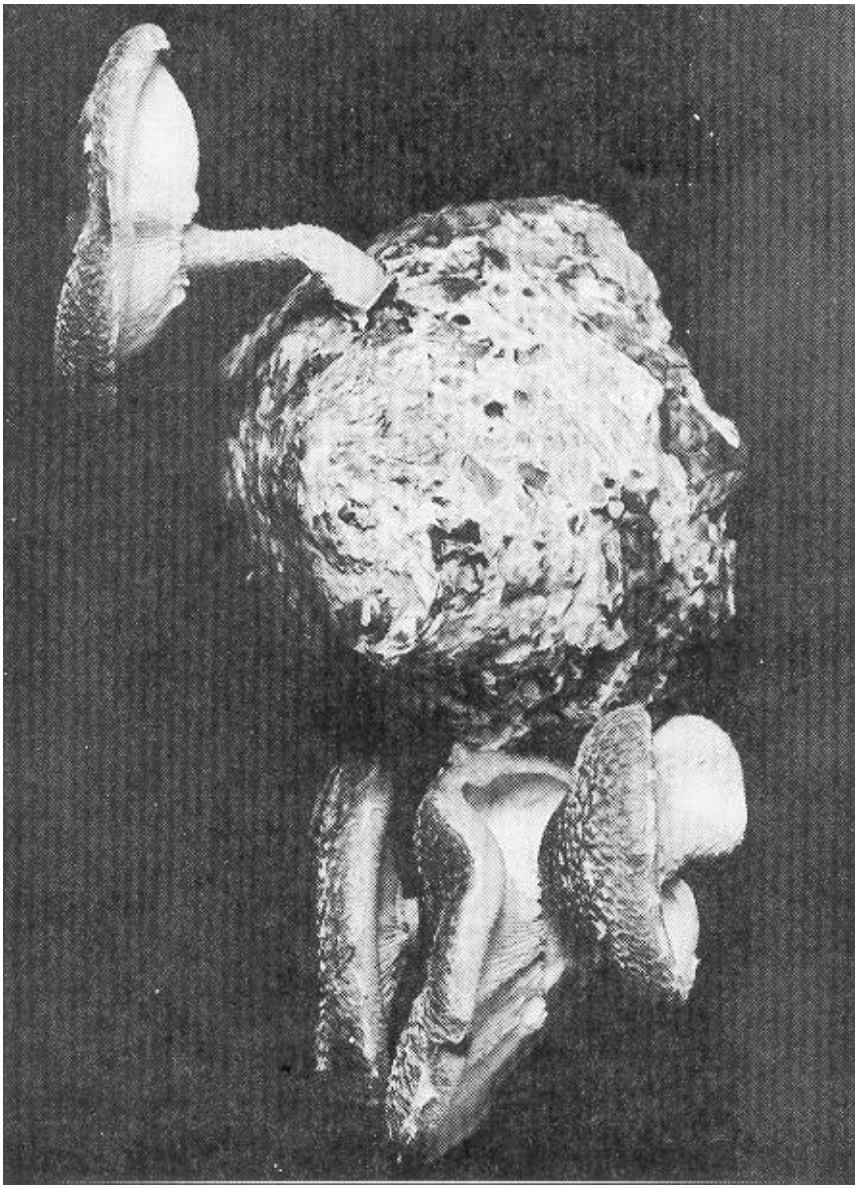


*Figure 8. Shiitake* (Lentinus edodes *(Berk.) Sing.), the Japanese forest mushroom, is grown commercially on oak logs in Asia but can be grown on shredded wood-bark mixtures as shown (average cap diameter here is approximately 10 cm). The world's second most important commercial mushroom, shiitake is Japan's largest agricultural export* (142).

*(Courtesy of G. F. Leatham, unpublished data.)*

**Table V. Some Commercial Mushrooms Cultivated on Solid Wood *(140, 143)***

| *Species* | *Substrates* |
|---|---|
| *Auricularia* spp. | Hardwood logs |
| *Flamulina velutipes* (Fr.) Sing. | Sawdust |
| *Pholiota nameko* (T. Ito) S. Ito et Imai | Hardwood logs |
| *Pleurotus* spp. | Hardwood logs, sawdust |
| *Tremella fuciformis* Berk. | Hardwood logs |
| *Lentinus edodes* (Berk.) Sing. | Hardwood logs, sawdust |

NOTE: Adapted from References 140 and 143.

solid wood, although possible, seems unlikely to become important, because of the availability of more practical substrates.

Altering the properties of wood components for particular uses is another possible use of wood-decomposing microbes. As an example, in their attack on solid wood, brown-rot fungi leave a lignin residue that is enriched in phenolic hydroxyl groups *(72, 130);* such lignin might serve well in phenolic adhesives.

One additional potential application of wood-decomposing fungi is in waste treatment. Although not directed at solid wood, such applications may be possible simply because the fungi have evolved the capacity to degrade such a complex solid substrate. The potential use of the lignin-decomposing system of white-rot fungi to decolorize lignin-derived wastes from pulp bleaching has been investigated with promising results *(139).* The lack of specificity of the oxidative ligninolytic system suggests a broader applicability than just to wood-derived wastes.

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