TREE DECAY

An Expanded Concept

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This publication is the final one in a series on tree decay developed in cooperation with Harold G. Marx, Research Application Staff Assistant, U.S. Department of Agriculture, Forest Service, Washington, D.C.

The purpose of this publication is to clarify further the tree decay concept that expands the classical concept to include the orderly response of the tree to wounding and infection—compartmentalization—and the orderly infection of wounds by many microorganisms—successions. The heartrot concept must be abandoned because it deals only with decay-causing fungi and it states that these fungi grow unrestricted through heartwood after infection of fresh wounds. The heartrot concept emphasizes descriptions of decay-causing fungi and types of decayed wood. It describes disordered wood and events that occurred in the past. The expanded decay concept emphasizes the order of a compartmented tree, the order of compartmentalization, and the order of successions. Regulation of discoloration and decay depends on understanding compartmentalization and successions.
Tree Decay Can Be Beneficial . . .

Recycling dead organic matter essential for life of new trees; providing food and shelter for wildlife and many other microorganisms; decreasing the potential for fire. (fig. 2)

Or Destructive . . .

Reducing the strength and value of trees and wood products; decreasing the attractiveness of trees. (fig. 3)
Decay Is a Natural Recycling Process...

Cell walls are digested; strength of wood is reduced. (fig. 4) Decayed wood is the RESULT of the process. (fig. 5) Tree decay involves interactions among trees, which are the tallest, greatest in mass, and longest-lived organisms ever to inhabit the earth, and microorganisms—(fig. 6) primarily bacteria and fungi—which are some of the smallest organisms on earth.
To Understand the Decay Process it is Necessary to Understand Size Relationships.

For example, if a large wood-inhabiting bacterium—almost 3 microns long—were enlarged to the size of a 6-foot man, (fig. 7) the man enlarged proportionally would be over 700 miles tall! (fig. 8)

And a giant redwood enlarged to the same proportions would be over 40,000 miles tall, (fig. 9) five times the diameter of the earth! We must keep these size relationships in mind when we consider ways to deal with the wood-inhabiting microorganisms.

Figure 7

Figure 8
Microscopic, wood-inhabiting organisms and the long-lived, gigantic trees interact intimately in a long and intense struggle for survival. This struggle starts with a wound and can end with total decomposition of the wood. Many biotic and abiotic factors are involved in the decay processes. It is difficult to determine where one event or process starts and another ends.

The events and processes overlap and mingle like the colors in a large spectrum or rainbow. Where does one color stop and another start? The natural process of decay is even more complicated and it might be more accurately likened to a multidimensional spectrum that is constantly changing over time. When we get too close to some processes, they are changed because of our methods of study and measurements. This is why we must consider the PATTERNS of events rather than specific events. (fig. 10)
Then, what CAN and CANNOT be done about the decay processes? The more we learn about the processes the better are our chances for REGULATING them.

WE CANNOT:

* Stop the processes. We cannot stop our ultimate death either, but that does not mean we cannot live a long, healthy, and productive life.

WE CAN:

* Prevent decay—temporarily.
* Decrease the rate.
* Increase the rate.
* Detect it.
* Predict its rate.
* Predict its ultimate configuration.
* Minimize its volume.

How effectively we can do the above depends on how well we understand the decay processes. The decay processes are not so overwhelming that they defy regulation.

SURVIVAL of any organism depends on its ability to compete effectively with other organisms for space and an energy source. To survive, organisms must live long enough to complete a life cycle. They must compete for food and space under constantly changing environmental conditions. They must respond rapidly and effectively to injury caused by abiotic and biotic factors. The response must be such that it enables the organisms to continue to survive.

Figure 11

MICROORGANISMS:
1) Spores of fungi,
2) Cladosporium,
3) Trichoderma,
4) Aspergillus,
5) Pithophora,
6) Bacteria,
7) Yeasts,
8) Fusarium,
9) Penicillium,
10) Alternaria,
11) Pseudallescheria,
12) Cytospora.
The Major Reason Why Wood-inhabiting Microorganisms Survive is that They Become Established in Succession.

THE TREE DECAY PROCESSES START WITH A WOUND—a break in the protective bark that exposes the xylem. New space and nutrients become immediately available to a wide variety of organisms—bacteria, nondecay fungi, decay-causing fungi, algae, mosses, lichens, insects, slugs, spiders, and small animals. The competition is intense. Many organisms compete, but as time passes, fewer and fewer are successful. Environmental factors—rain, ice, snow, wind, heat, cold—affect their survival. And, while the wound surface battle rages, those living wood cells that are behind the wound are REACTING to the injury and infection. The normal physiological processes give way to new protective processes. Shifts in metabolism occur. Materials that are poisonous to some organisms are formed in the tree cells. In a sense, the tree begins to form a protective chemical shield around and immediately behind the wound. (fig. 11)
As time passes, fewer species of organisms survive on the wound surface. The concentration of any one group of organisms on the wound surface may fluctuate greatly if there are temperature extremes in the seasons. But now most of the action is inside the tree. A look into the tree after a year shows that a few microorganisms surmounted the chemical barriers formed by the tree. The microorganisms either used the protective materials in the barrier as nutrients or altered these materials in such a way that they were no longer toxic. The protective materials are mostly phenolic compounds in angiosperms and terpenes in gymnosperms. Oxidation and polymerization of these materials take place after wounding. Usually, but definitely not always, the microorganisms that are the first to infect are bacteria and non-decay fungi. In some cases, decay-causing fungi are first. The microorganisms that are the first to infect are called PIONEERS. Which microorganisms become the pioneers is affected greatly by many factors—time of year of wounding; type, position, and severity of wound. The pioneers in turn affect greatly the species of microorganisms that follow in the succession. And, the species that follow will affect greatly the rate and type of wood alteration. Successions are orderly, but complex. (fig. 12)
After 4 years fewer microorganisms are active behind the wound. Sporophores of decay fungi may begin to develop. The first few years after wounding are the most important for the tree and the microorganisms. Within this time, the rate and much of the extent or limits of the infection will be set. One group or species of organisms follows another until all the wood is decomposed—a succession. But all wounds do not follow such a pattern of infection to decomposition. Most of the time the tree is effective in blocking or limiting the infection. The wound may close. The final stages of the succession may not occur. But, after the tree dies, many OTHER groups of microorganisms will begin to digest the wood. And when this happens, another succession occurs. In summary MANY species of microorganisms are involved in the decay processes. The microorganisms become established in successions. (fig. 13)

**MICROORGANISMS:**
1) Hyphae of Hymenomycetes,
2) Fusarium,
3) Phialophora,
4) Trichoderma,
5) Bacteria.
6) Sporophores of Hymenomycetes.
Trees Survive Wounds and Infection Because They Are Highly Compartmented Plants That Compartmentalize the Injured and Infected Tissues.

Trees have evolved over a period of 200 to 400 million years while being under the constant stress of wounding. Even with this stress, they still have evolved to be the largest and longest lived organisms ever to inhabit the earth. And yet trees have NO WOUND HEALING PROCESS—healing in a sense of REPLACING or REPAIRING injured tissues. HEAL means to restore to a previous healthy state. It is impossible to HEAL injured and infected xylem. Trees have evolved as highly ordered, COMPARTMENTED plants, that instead of healing, COMPARTMENTALIZE in an orderly way the injured and infected tissues. A coded MODEL SYSTEM for explaining how a tree is compartmented and how it compartmentalizes infected and injured wood has been developed. It is called CODIT, an acronym for COMPARTMENTALIZATION OF DECAY IN TREES. Terms such as “walls” and “plugs” are used in the model only to help present a mental image of the compartments. These terms are not meant as technical terms. (Fig. 14)
Wall 1. After being wounded, the tree responds in a dynamic way by plugging the vertical vascular system above and below the wound. The conducting elements—vessels in angiosperms and tracheids in gymnosperms—are plugged in various ways: tyloses, gum deposits, pit asperations, etc. The plugged elements complete the transverse top and bottom walls of the compartments. Wall 1 is the weakest wall.

Wall 2. The last cells to form in each growth ring make up the tangential walls of the compartments. These walls are CONTINUOUS around each growth ring—except where sheets of ray cells pass through. Wall 2 is the second weakest wall.

Wall 3. Sheets of ray cells make up the radial walls. They are DISCONTINUOUS walls because they vary greatly in length, thickness, and height. Walls 3 are the strongest walls in the tree at the time of wounding.

Wall 4. After a tree is wounded, the cambium begins to form a new protective wall. The wall is both an anatomical and a chemical wall. This wall separates the tissue present at the time of wounding from tissue that forms after. It is the strongest of the four walls. [fig. 15]

For additional information about CODIT see Agriculture Information Bulletin Number 405.
A More Detailed Look Shows That, in a Diagrammatic Way,
a Tree Is Made Up of Many Rooms or Compartments. (fig. 16)

Figure 16

In a sense, a tree is a multiple perennial plant. Every growth ring
can be thought of as an individual tree. Every new “tree” envelopes all
the older trees. (fig. 17)

Figure 17
Each growth ring is subdivided into compartments that have sheets of ray cells as radial walls (Walls 3) and the cells that are the last to form in each growth ring are the tangential walls (Walls 2). Within these walls there are fibers, vessels, and axial parenchyma in angiosperms, and longitudinal parenchyma and longitudinal tracheids in gymnosperms. The vessels and the pits between the longitudinal tracheids keep the tops and bottoms of the compartments partially open. This is essential to maintain the vertical flow of liquids. (fig. 18)

BUT AFTER WOUNDING, THE TREE REACTS.

The vertical conducting elements begin to plug in various ways. This completes the transverse walls (Walls 1). (fig. 19)
Another close look at Walls 2 and 3 gives the impression of subdivided three-dimensional wheels. (Fig. 20)

There is great variation in the dimensions of Walls 3. (Fig. 21)
To the invading microorganisms, Walls 3 present a maze of obstacles. Each sheet of ray cells in sapwood contains living parenchyma cells that present a chemical as well as an anatomical barrier. The chemicals in the living ray cells are altered after a tree is wounded. The altered chemicals may be poisonous to some microorganisms. (fig. 22)

Within the compartments are the elements—vessels, tracheids—that conduct liquids vertically. (fig. 23)
In angiosperms, one typical arrangement for the vessels is a uniform distribution of similar-sized vessels throughout each compartment. This is typical for diffuse-porous trees such as maples and birches. (fig. 24)

In other angiosperms, most of the larger diameter vessels may be clustered more towards the beginning of each growth ring or compartment, while much smaller diameter ones are found at the end of each growth ring or compartment. This ring-porous arrangement is typical for oak, cherry, and locust. Many trees have variations on these basic arrangements. (fig. 25)
In gymnosperms, the compartments are filled with longitudinal tracheids that are the vertical conducting elements. In conifers, there are also parenchyma cell arrangements that form resin ducts or canals in the rays. Their position is usually near the end of each growth ring or compartment. (Shown here in green.) There may also be radial resin ducts in the rays; however, none are shown in the drawing. (fig. 26)

Figure 26

After wounding has occurred, the conducting elements may be plugged by a wide variety of materials that come from living cells that surround the elements—often contact parenchyma in angiosperms. Or the pits between the tracheids may close. (fig. 27)

Figure 27
The Classical Concept of Tree Decay

ROBERT HARTIG developed the concept of tree decay almost a century ago. At that time, decay was well recognized as a serious economical problem. In tune with the theory of spontaneous generation, scientists believed that

Decay Caused Fungi.

Robert Hartig, in tune with the germ theory that emerged after 1845, said that

Fungi Caused Decay.

This simple reversal of two words set the stage for the decay concept and, in some ways, for the beginning of the science of FOREST PATHOLOGY.

The Classical Concept of Tree Decay has Three Major Parts:

1) WOUNDS started the processes (below left). (fig. 28)

2) DECAY FUNGI (Hymenomycetes) (below, upper right) (fig. 29) infected the heartwood through fresh wounds. (Robert Hartig showed that the sporophores on the wound surface (opposite page) (fig. 31) and the hyphae associated with the wood decay (below, upper right) were the same fungus.)

3) DECAYED WOOD resulted (below, lower right). (fig. 30)

Figure 29  Hyphae of Phellinus tremulae.

Figure 28  Wound on yellow birch.

Figure 30  Decayed wood associated with Phellinus tremulae.
Figure 31

Phellinus tremulae on Populus tremuroides.
The Expanded Concept of Tree Decay

The expanded concept of tree decay has four major parts:

1) WOUNDS start the PROCESSES (below left). (fig. 32)

2) MANY ORGANISMS are associated in the processes (below right). SUCCESSIONS of organisms are involved in the infection of the wood. (fig. 33)

3) The tree REACTS to the wound. The living cells behind the wound react immediately (opposite page, upper left). (fig. 34)

4) DISCOLORED and DECAYED wood results, but this wood is COMPARTMENTALIZED by WALLS 1, 2, 3, and 4 (opposite page, lower). (fig. 36)

Figure 32

Figure 33

22
Figure 35

Brown—decayed wood
Green—discolored wood
Red—tree chemical protective zone
Orange—barrier zone—Wall 4
Blue—Wall 3

Figure 34

Figure 36
Here Are Some Basic Patterns of COMPARTMENTALIZATION and SUCCESSIONS After One Wounding Period.

COLOR CODES
Red—Tree response (chemical protective reactions).
Green—Position of pioneer microorganisms (can be bacteria, decay fungi, or nondecay fungi). Wood in this area is usually discolored; its cell contents are altered.
Brown—Position of decayed wood; cell walls are digested.

Five branch stubs. Strong compartmentalization. The wound closure is complete. (fig. 37)

Four large open stubs. Diameter of the tree at time of branch death is the diameter of the column of decayed wood. Discolored wood surrounds the decay. Pioneer organisms are in green zone. (fig. 38)
Closed minor wound after 5 years. Invasion is well compartmentalized. (fig. 39)

Two large open wounds after 10 years. Column of discolored and decayed wood is diameter of tree when wounded. This pattern will be the same in trees that have heartwood. INJURED AND INFECTED TISSUES IN HEARTWOOD ARE ALSO COMPARTMENTALIZED. (fig. 40)

One severe wound after 10 years. The discolored and decayed wood is confined to one side of the tree.

Although the red zone is shown on the side opposite the wound, no anatomical changes will be seen. All the wood within the entire cylinder present at the time of wounding will be slightly altered; in most cases, this will be too subtle to be visible. (fig. 41)
WOUNDS start the processes that could lead to discolored and decayed wood. The classical concept and the expanded concept both recognize wounds as the starting point for the processes. Trunk wounds can be caused by a variety of agents: insects, birds, small and large animals, wind, ice, snow, temperature extremes, chemicals, and people and some of their activities. Often the wound is seen but not the agent that inflicted it, such as the porcupine wound in this pine. (fig. 42)

And the black bear wound on the western hemlock. Wall 4 forms as a cylinder and the decay develops as a cone within the cylinder as Walls 1, 2, and 3 give way to microorganisms. (fig. 43)
Root and butt decay associated with wounds are also compartmentalized in gymnosperms (fig. 44) and angiosperms. (fig. 45)
WOUNDS are of two major types:

1) BRANCH—The branch wounds expose all tissues, from the new outer tissues to that of the older tissues in the center of the tree. (fig. 46)

In a vertical plane, each growth ring ("tree") will have its own column of discolored and decayed wood. The response of the "older trees" or innermost rings is slower and weaker than that of the "younger trees." (fig. 49)

2) OUTER CORE—The outer core wounds usually expose only the most recently formed tissue. This depends, of course, on the depth of the wound. (fig. 47)

When microorganisms infect, they grow from compartment to compartment. The column of discolored or decayed wood that is seen macroscopically will be a composite of many columns as seen in these radial sections through drill wounds. (fig. 48)

The "holding strength" of Wall 1 decreases as the injury goes inward. The older "trees" have a weaker response. This action determines the shape of the column, shown here from a radial view. (fig. 50) In a sense, the wounds set the stage. The DISCOLORATION PROCESSES begin immediately after wounding when the tree reacts—both by chemical reaction and by plugging. When the pioneer microorganisms invade, the discoloration processes may intensify. The DECAY PROCESSES begin when microorganisms begin to digest cell walls. Many factors affect the rate of the discoloration and decay processes—severity of the wound, position, size, time of year of wounding, wounding agents that import materials into the wound, and the types of microorganisms that infect.
A branch wound will usually have this shape of column. Of course, there are many variations to this shape. (fig. 51)
Ring rot is one configuration associated with branch infections.
(fig. 52)
When many branches die at about the same time, the entire central column of the trunk may be decayed. The diameter of the column will be the diameter of the tree when the branches died. Although the death of the branches determines the diameter of the internal column, the fungi associated with the decay in the column may have entered the branch and trunk after a long growth period in the dying branch. Some fungi, such as *Echinodontium tinctorium* and possibly *Fomes pini* and others, first infect minute branchlet stubs on the living branch and therefore usually do not infect the large, freshly exposed branch stubs. (fig. 53)

Branches are often decayed by a wide variety of microorganisms that do not enter the trunk. Branch decay of this type is very beneficial as the tree is pruned when the branches fall. (fig. 54)
An outer core wound will usually have this shape, but again, many variations exist. In nonheartwood-forming trees, the column will be as shown. In heartwood-forming trees, the column will extend farther along the heartwood-sapwood boundary that was present at the time of wounding.

Also, concentrations of pigments and oxidized protective materials will usually be greater along the side of the column closest to the cambium. The column stays to the pith side of Wall 4. (fig. 55)
Some Typical Patterns of Discolored and Decayed Wood Associated with Wounds

Near the wound, the individual columns within each growth ring will be clustered. Some of the various shapes of discolored and decayed wood will be seen as on transverse wedge-shaped sections in the next series of diagrams. (fig. 56)

The eye sees a macroscopic view like this. (fig. 57)

But the mind’s eye SHOULD see a diagrammatic view like this. Keep this in mind while viewing the following diagrams. (fig. 58)

Walls 2, 3, and 4 are pointed out by arrows in this drawing. These walls will be present in other diagrams, but no arrows will be shown. (fig. 59)

CODES FOR ALL DIAGRAMS

Green—Discolored wood

Brown—Decayed wood

Orange—Wall 4
Six-Year-Old Severe Type Wound
The discolored wood forms the typical triangular pattern into the pith. (Fig. 60)

Four-Year-Old Moderate Type Wound
The compartments directly beneath the wound were the only ones affected. (Fig. 61)

Multiple Wounds: A central 10-year-old wound associated with a central column of discolored wood. A later 4-year-old wound with a triangular column of discolored wood that developed to the boundary of the inner barrier zone surrounding the 10-year-old wound. (Fig. 62)

Multiple Wounds: A central 10-year-old wound with a central column of discolored wood. A 2-year-old wound with a small column of discolored wood did not spread into the older, more central column. (Fig. 63)
A Deep Drill Wound: The tissues between the end of the drill wound and the inner column of discolored wood will discolor slightly. The radial walls (Walls 3) limit the lateral spread of the discolored wood. (fig. 64)

When the drill hole is shallow, the compartments between the inner column and the tip of the drill hole may remain healthy or nondiscolored. This is the case when shallow injection wounds are inflicted. (fig. 65)

A slanted drill hole usually gives this type of pattern. Note that the discolored compartment between the central column of discolored wood and the tip of the drill hole follow the ray pattern inward (Wall 3). The column beyond the end of the drill hole does not continue in the same direction as the hole. Often the side of the hole closest to the cambium will be darker from an accumulation of phenols. (fig. 66)
A series of seven sections from above a wound similar to that shown on page 39 figure 56. Each section is approximately 20 centimeters above the other. Note the pattern of discolored and decayed wood and the position of the barrier zone. (figs. 67-73)
Four sections showing the pattern of discolored and decayed wood associated with multiple wounds on four trees. A multitude of specific multiple patterns is possible depending on the wounds inflicted, their severity, position, and time between woundings. (Figs. 74-77)
Some Variations and Exceptions

Canker rots have yet another pattern of decay. After the canker rot fungus becomes established, it forms a pressure pad that kills the cambium, thus enlarging the wound. The tree responds by compartmentalizing each new wound. These fungi may kill a tree by girdling. [Figs. 78-79]

*Figure 78*  
Innotus obliquus on white birch.
Figure 79
Fomes
chrysoloma
on white fir.
Some decay-causing fungi can attack and kill roots that have not been wounded. But, these fungi may be compartmentalized as they grow from the roots upward into the trunk. The trees attacked by these fungi are often stressed or weakened by other factors first. (figs. 80-81)
1. Fruit body
2. Rhizomorphs

Figure 81

*Armillariella mellea* on red oak.
Other species of decay-causing fungi usually attack wood after the tree has been made into a product. In some cases the patterns of decays in the product will still follow the patterns set while the tree was alive. (Figs. 82, 83)

1. Hot spot for decay in poles. 6 inches above and 18 inches below ground.
2. Typical patterns of internal decay in poles: A, shell; B, wedge; C, in-between; D, central; E, complete.
3. Typical patterns of external decay in poles: A, surface rot; B, soft rot.

Figure 82
2. Color change associated with stub.
3. Ring shake associated with wound.
4. Decay starting above and below stub—typical in-between pattern common in southern yellow pine.

Figure 83
Some Additional Details on the Expanded Concept of Tree Decay
Decayed Wood
The Breakdown of Ordered Wood Results in Disordered Material.

DISCOLORATION is a process. DECAY is a process. DISCOLORED and DECAYED wood represent the DISORDERED PRODUCT of an ORDERED material.

DISCOLORED WOOD results from an alteration of cell contents. There is only slight or no loss of strength. The tree AND the microorganisms are involved in the processes that result in discolored wood.

DECAYED wood is a result of a breakdown of cell walls. There is a great loss of strength.

Many microorganisms are involved in the processes that result in decayed wood. The wood cells have been killed and the decay-causing microorganisms compete among themselves for the dead matter. Many factors affect the rate of decay. The TREE has the greatest influence in the LIMITS of the decay column. Most of the events in the decay process are ORDERED. The classical concept of decay deals mostly with disordered events. It is impossible to regulate disorder.

The expanded concept of decay deals primarily with ORDERED events. The ordered system of trees and microorganisms is constantly impacted by many types of ordered and disordered events: Temperature extremes for short periods, moisture extremes for short periods, changing soil elements, storms, fires, logging operations, soil compaction, flooding, earthquakes, soil grade changes, pollution, chemicals, gas leakage, human-caused epidemics, or diseases and insects.

These factors alone or in combinations greatly affect the MICROORGANISMS and the TREE. The factors may alter the rate of the decay processes but not the patterns of successions and compartmentalization, which are ordered events.

For example,

1) SUCCESIONS, an ORDERED process, often determine RATE. Upset the normal successions and the process will be stalled (not stopped). This can be done by purposely infecting wounds with microorganisms that normally occur late in the succession, such as with species of Trichoderma. The decay process will be stalled.

2) COMPARTMENTALIZATION represents order. Some trees have a stronger wound response than others; they can compartmentalize invaded tissues more effectively than other trees of the same species. The differences are shown in the next three illustrations.
When drill holes are inflicted in strong compartmentalizers, a pattern like this results—very short vertical columns and little to no lateral extension. (fig. 84)

When drill holes are inflicted into moderate compartmentalizers, a pattern like this results—long vertical columns and some lateral extension of discolored wood. (fig. 85)

When drill holes are inflicted in weak compartmentalizers, columns that look like this are seen—long vertical columns and complete lateral extension of discolored wood. (fig. 86)

The tree’s response in the compartmentalization of discolored wood appears to be under strong genetic control.
Wood Is Altered by Microorganisms in Five Basic Ways.

There are, of course, many variations to the five basic themes.

**Discolored wood.** Color of the wood is changed when cell contents are altered.

Bacteria—anaerobic, aerobic, and facultative forms—and nondecay fungi usually are involved in these processes, but decay fungi can also be involved.

Some genera of fungi commonly associated with discolored wood are: *Ceratocystis, Fusarium, Trichocladium, Hypoxylon, Graphium, Phialophora, Leptographium, Alternaria, Pullularia, Torula*, and *Rhinocladia*. Also associated are species of *Fomes* and *Polyporus*. Plugging in vessels can impart a color change, a vertical type of discoloration, but most color changes result from alteration of cell contents in ray parenchyma (radial discoloration). Some slight discolorations can result from the reaction of the tree alone to a wound, but intense discoloration usually involves the interaction of microorganisms with living and dying cells in the tree.

Blue stain fungi in white pine—tangential section through discolored rays. Bacteria are clustered near pits. (fig. 87)

Blue stain fungi in white pine—radial section through discolored rays. Bacteria are clustered in the ray cells. (fig. 88)
Figure 89
Transverse section through discolored wood surrounding decayed wood in *Populus tremuloides* (see page 22, fig. 30).

Figure 90
Radial section of discolored rays in red maple.

Figure 91
Magnified section of above showing vessel plugs.
White rot.

The cellulose and lignin are digested at about equal rates. The digestion usually starts from the cell lumens and proceeds towards the middle lamella. Hymenomycetes are involved mostly, although species in the Xylariaceae also are associated with white rot (genera—Hypoxylon, Xylaria, Daldinia). There are many types of white rot (fleck, stringy, ring, pocket, etc.). These terms describe their macroscopic appearance. White rots occur also in wood products such as utility poles. Some of the most damaging fungi associated with white rots are Phellinus pini, Armillariella mellea, Fomitopsis annosa, Ganoderma applanatum, Oxyporus populinus, Phellinus igniarius, Imnotus glomeratus, I. obliquus, and Echinodontium tinctorium. (figs. 92-94)
Figure 94

*Ganoderma lucidum* on eastern hemlock.
Brown rot.

The cellulose is digested preferentially, and the lignin is only altered slightly in this type of rot. Brown rots have a shrunken cubical appearance. Brown rot occurs mostly in gymnosperms and in wood products. Some common fungi associated with brown rots are *Phaeolus schweinitzii*, *Poria monticola*, *Lentinus lepideus*, and *Polyporus betulinus*. *Polyporus sulphureus* and *Fomes pinicola* are examples of fungi that cause the less common brown rot in angiosperms.

(figs. 95-96)
**Soft rots.**

The $S_1$ layer of the middle cell wall is digested by some microorganisms. Several patterns of digestion occur: Rhomboid cavities, long spindle-shaped cavities, and a general breakdown of the $S_1$ layer. Many variations occur. The causal fungi are usually non-hyphomycetes—*Phialophora, Penicillum, Chaetomium*, etc. Soft rots occur mostly in moisture-saturated angiosperm wood products. Little is known about soft rots in living trees.

**Bacterial alteration.**

Little is known yet about the effects of bacteria alone on wood. In ponded logs, bacteria do invade pits—mostly the microfibrils of the pit margins. Under some conditions, bacteria have been known to digest some cell wall constituents. Some bacteria genera commonly associated with this type of wood alteration are *Pseudomonas, Bacillus, and Clostridium*. Bacteria are often intimately associated with fungi in the decay process. Many bacteria are facultative forms.
Wetwood.

Bacteria are the major organisms associated with a wood condition called wetwood. The infected wood may or may not be darkly discolored. The infected wood may have a bleached or glassy appearance. (Figs 100-101)

Figure 100  Wetwood associated with small stubs in white fir.

Figure 101  Wetwood zones in white fir.
Slash Deterioration

Dead wood on the forest floor is inhabited by a wide variety of microorganisms that continue their activities until the wood is completely decomposed. The microorganisms compete among themselves under constantly changing environmental conditions. (fig. 102)
The Following Series of Paintings are Designed to Move the Mind's Eye Into a Tree Through a Wound.

Reference is made again to size relationships because as large as trees are, the decomposition processes are developing at the microscopic level with the microorganisms and the tree cells.

A large fresh basal wound on a mature sugar maple. (fig. 103)

Figure 103
The bark has been torn and the wood is injured deep into the trunk. (fig. 104)

The crushed wood at the surface of the wound contains debris and broken pieces of mosses, lichens, and other plants. Small droplets of moisture begin to ooze from the tree. (The red block shows the section magnified in the next painting.) (fig. 105)
Each minute droplet of moisture is like an enormous ocean to the microorganisms. Each minute crack is like several grand canyons in width to the microorganisms. The wound surface is made up of thousands of microsites for growth of microorganisms. (fig. 106)

The minute droplets, too small to be seen by the human eye, are sites for groups of microorganisms to begin growth on the wound. Each droplet is a storehouse of nutrients. The microscopic wood splinters are excellent places for propagules of microorganisms brought in by wind, rain, and insects. The broken tangential faces of the ray sheets begin to show. The broken and crushed ray cells make INFECTION easy for the microorganisms. (fig. 107)
The minute droplets now appear as gigantic globes. After several weeks, many bacteria and fungi begin to grow into the broken wood cells—this is infection. Here a vessel is being infected by nonhymenomycetous fungi and groups of rod-shaped bacteria. Some fungi are also growing into the broken wood cells. Competition for this new space and for the abundance of nutrients is intense. The tree exerts little or no protective force here because the cells have been injured severely or killed by the wound.

( fig. 108)
A large basal wound after a few weeks on a pine. (fig. 109)
A copious flow of resinous material is obvious on the wound surface. (fig. 110)
The torn wood, debris, and droplets of moisture and resin become visible at this magnification. (fig. 111)

Here the droplets act as prisms that reflect the light like minute rainbows. The minute wood splinters now appear as gigantic spears coated with multicolored resin. (fig. 112)
Droplets and torn wood not visible to the human eye now become visible. This is the view small insects have of the wound. (fig. 113)

Here the tangential ends of the rays begin to show. The minute splinters appear as gigantic branches that trap the minute droplets of moisture and resin. Each droplet supports many colonies of competing microorganisms. (fig. 114)
Several weeks later, the fungi and bacteria have begun to infect the wood. A diagrammatic view shows the ray cells infected, and a resin pocket forming as the walls of the surrounding cells begin to dissolve. (fig. 115)
A blue-stain fungus and many bacteria in ray cells. The bacteria are clustered near the pits. The microorganisms begin to digest the cell contents, and blue stain results. (fig 110)
Broken and dying branches are some of the most common infection courts for microorganisms. Large branch stubs on trees (that have heartwood) expose heartwood. (fig. 117)
A closer view of a branch stub on an old oak. (fig. 118)

When the stub surface is sawn smooth, this is the view of the old branch with central heartwood. (fig. 119)
A closer view of the heartwood near the branch center shows the vessels plugged with tyloses. (fig. 120)

A closer view of the sapwood shows the open vessels oozing moisture. (fig. 121)
The vessels appear as large tunnels or caves at this magnification (fig. 122)
The ordered pattern of fibers surrounding the vessels is shown here. Each microscopic droplet of moisture could be the site or battleground for intense competition by many groups of different microorganisms. (fig. 123)

After several weeks, the fungi and bacteria invade. The small dots are the bacteria. The cells have been injured or killed, so invasion is an easy matter for the microorganisms. They reproduce rapidly and begin to interact with the tree. (fig. 124)

Figure 123

Figure 124
In the end, trees will continue to grow, die, and decay; and grow, die, and decay; and grow, die, and decay. (fig. 125)

COMPARTMENTALIZATION extends the time a tree will grow under the constant stress of wounds.

SUCCESSIONS make it possible for microorganisms to survive against the protective forces of a tree.

AN UNDERSTANDING OF THE EXPANDED CONCEPT OF DECAY GIVES US BETTER OPPORTUNITIES TO REGULATE TREE DECAY.