LESSON 2 Decay

LESSON OVERVIEW

CONTENT

This lesson deals with decay, both in living and dead trees, and, to a minor extent, in wood that is in the form of lumber (i.e., "in service").

The study of decay is also a good way of starting a course dealing with tree pathogens, because decay fungi are largely restricted to dead wood tissues (either dead trees or the heartwood of living trees), and represent one of the simplest disease situations that you will encounter.

Decay fungi play an important role in ecosystems. They recycle the carbon and mineral nutrients tied up in wood, and they create special habitats that are required for a number of organisms, from birds to nitrogen-fixing bacteria. Decay also causes great losses in value in standing timber, and it greatly limits the time that dead standing timber can be salvaged.

The content of this lesson is developed through discussion of the following six topics:

- Enzymatic degradation of wood
- Types of decay
- Ecological considerations
- Infection
- Rate of decay
- Decay and forest management

OBJECTIVES

When you have completed this lesson, you will be able:

1. to summarize the requirements for growth and reproduction of decay fungi, and to describe the manner in which various groups of decay fungi digest wood;
2. to outline the infection process, and to list the special infection pathways required by decay fungi;
3. to predict how fast decay can be expected to develop once a tree has been infected, and to identify which phenomena control the rate of decay;
4. to summarize the role of decay in natural ecosystems;
5. to predict, based on information about decay in natural ecosystems, where decay is likely to be a problem;
6. to apply the principles that underlie decay estimation techniques; and
7. to appraise how various silvicultural operations and management decisions can either promote or retard decay.

LESSON STUDY INSTRUCTIONS AND ASSIGNMENT

Start this lesson by reading Chapter 14 in Manion (1991). Then study the commentary below and the papers in the reading section at the end of this lesson, which include Etheridge and Craig (1976), Shain (1979), Shortle (1979) and Merrill and Shigo (1979). The commentary includes notes to direct you to certain readings at appropriate times. In addition, study Pest Leaflets Numbers 55 and 62 (supplied with the course manual package).

At the end of the lesson, do the self-testing/review questions. These questions will help you test your understanding of the material covered in this lesson, and will also provide a good review when you are studying for the final exam.

After you have answered the self-testing/review questions, complete Assignment #1 (in Appendix A) and submit it to your tutor for marking. Remember to include a comment sheet for your tutor's use. Check your course schedule for the due date.

COMMENTARY

ENZYMATIC DEGRADATION OF WOOD

Wood consists of cellulose, hemicellulose, lignin and various extractives. Cellulose consists of long chains of sugar units strung end to end, and these chains give wood its strength. Lignin is a more complex material of indefinite structure. The conifer tracheid cell wall may be compared to reinforced concrete, with cellulose bundles representing the steel and lignin the concrete. The formation of celluloses is mediated by enzymes, and the first steps of degradation are almost the reverse of the last step of formation. This is not true for lignin, since the last step of lignin formation, the condensation of the various phenyl propane units into the complex, three-dimensional lignin polymer, involving many different kinds of chemical bonds (see Manion Figure 14-3), is apparently not mediated by specific enzymes, and cannot be reversed by enzymatic action. Hence lignin is much more resistant than cellulose to enzymatic breakdown.

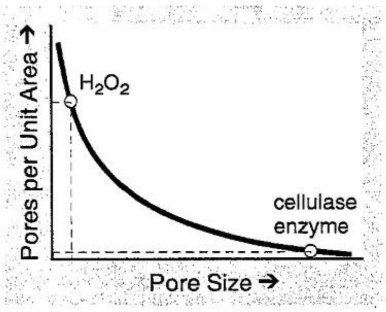


FIGURE 2.1
Distribution of pore size in lignin matrix compared to a cellulase enzyme molecule and a molecule of hydrogen peroxide.

The cellulose is at least partly protected from enzymatic degradation by the lignin in which it is embedded. The pores in the lignin matrix are too small for large, protein enzyme molecules (see Fig. 2.1). There are many fungal species that can survive and grow with pure cellulose as their only carbon source, but only a small subset of these have the peculiar ability to utilize cellulose in wood efficiently, and these are the decay fungi. Decay fungi deal with lignin in two ways. The white rots, which can digest both lignin and cellulose, slowly degrade cell walls from the inside, beginning their attack in the S3 layer of the tracheid cell wall. As the lignin is degraded and dissolved, the cellulose is exposed to enzymatic degradation. Brown rots on the other hand, do not produce enzymes that can degrade lignin. Instead, they produce hydrogen peroxide (H_2O_2), and Fe^{+++}. These small molecules can enter the pores in the lignin, and together they react with the cellulose to break the long cellulose chains into shorter segments. Once this has happened, the lignin matrix relaxes, and the pores become large enough to admit enzymes.

In white rots, the breakdown of cellulose proceeds as two related, enzyme-mediated processes. Enzymes can be named according to the substrate on which they act. Thus **cellulases** are cellulose-digesting enzymes. **Exocellulases** are enzymes that attack the ends of the cellulose chains and release soluble sugar units by hydrolysis. There are two exocellulases, since the two ends of a cellulose chain are chemically different. Since the chains are very long, there are few sites available that exocellulases can act on, and by themselves they would lead to very slow digestion of cellulose. However, white rots produce another enzyme, **endocellulase**, which breaks the long cellulose chains into smaller fragments, thus creating sites at which the exocellulases can operate (see Fig. 2.2). In brown rots the function of endocellulase is achieved by the action of hydrogen peroxide and iron.

All these enzymatic processes occur outside the living fungal cell. The enzymes involved are therefore all **extra-cellular** enzymes, produced by the fungus and released into their immediate aquatic environment. If

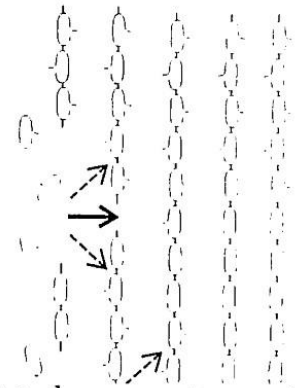


FIGURE 2.2
Long cellulose chains are broken into smaller fragments by endo-cellulases (solid arrows), creating sites where exo-cellulases can operate (broken arrows).

there is no liquid water on the cell wall surface, decay cannot proceed since there is no medium in which the enzymes can act.

The half-life of enzymes, particularly extra-cellular enzymes such as the cellulases, is quite brief. The fungus therefore controls the rate of the process through controlling the rate at which enzymes are formed and released. High sugar concentrations inhibit the production and release of endocellulase, resulting in a decrease in the number of sites at which exocellulases can operate.

TYPES OF DECAY

Decay fungi can be divided into three major groups, namely the soft-rots, the white-rots and the brown-rots, according to the type of decay they produce.

Soft-Rot

Soft-rots are Ascomycetes whose hyphae grow within the cell wall or sometimes on the inner surface of cell walls. Deterioration of the wall occurs only in the immediate vicinity of the hyphae; the enzymes apparently remain attached to the hyphal wall. Those that grow within the cell wall produce small, regularly shaped cavities within the wall. Those that grow on wall surfaces produce characteristic grooves. Soft-rot is almost wholly restricted to wood in service and is common in wet wood. There is little or no soft-rot in living trees. As the name indicates, soft-rots produce soft, spongy decayed wood.

White- and Brown-Rots

The white- and brown-rots, on the other hand, produce free extra-cellular enzymes that attack the wood material some small distance from the hyphae. The two groups are distinguished by the types of enzymes they produce, although the distinction isnít absolute; there is some gradation from one group to the other. Both groups digest cellulose and use the resulting sugar as a major energy source. In addition, the white-rot fungi produce enzymes that digest the lignin at least partially, while the brown-rots don't. Thus when white-rots decay a piece of wood, there is almost nothing left when the decay is complete; in contrast, when the brown-rots are finished, the lignin remains as a brown, crumbly material.

There are a number of ways in which the behaviour of white- and brown-rots differ, and these are mostly related to the basic difference in the enzymes they produce and the manner in which they deal with lignin. White-rot hyphae travel from cell to cell by dissolving bore holes in tracheid walls; brown-rot hyphae can pass from cell to cell only through pits. Hardwoods are most commonly decayed by white-rots; both types of rot occur in conifers.

The initial attack of white-rots in conifers is unevenly distributed in wood. Typically advanced decay develops as small elliptical pockets (about 1 mm by 2 mm in size). This leads to a stringy or laminar decay, but, at an early stage of decay, the wood retains considerable strength. Kraft pulp yield (measured as weight of pulp produced per unit weight of wood) is also not greatly affected. Severely decayed wood is lost as fines in the chipping and screening process. Parts of the decaying wood that are at an early stage of decay, and still strong enough to withstand the chipping process without breaking into small pieces, give a nearly normal yield of pulp.

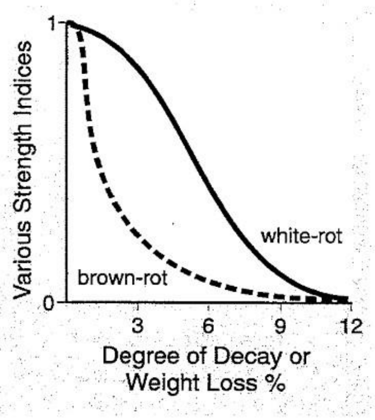


FIGURE 2.3
Comparison of loss of strength in wood infected with white-rot or with brown-rot.

Brown-rots, on the other hand, develop evenly throughout the infected wood. At a very early stage the long cellulose chains are broken into short fragments. As soon as that has happened, the strength is gone. The decaying wood is usually dark in colour and the first cracks develop across the grain, leading, in the typical case, to a cubical rot. Strength loss at early stages of decay is very rapid and pulp yield of partially decayed wood is very low (refer to Fig. 2.3).

ECOLOGICAL CONSIDERATIONS

Carbon Cycling

Decay of wood is virtually the only way in which wood is destroyed in natural ecosystems. Fire and insects kill trees but do not destroy much wood. After the tree is dead, decay fungi move in and eventually reduce the wood to carbon dioxide and water. It follows that over large natural areas (e.g., the province of B.C. a century ago) decay equals growth. The two processes are balanced, and the average amount of carbon per hectare that is tied up in wood and other organic materials is constant.

The total carbon tied up as wood in a single stand rises with stand age to some maximum and then declines to an equilibrium level in the climax forest. At the same time, the total carbon tied up as organic material in the forest floor may continue to rise with stand age, although it too may reach an equilibrium level in the climax forest. Switching from natural forests to managed forests involves a decrease in the average amount of carbon tied up as biomass in the ecosystem, particularly in those cases where the natural forests tend to be quite old at stand renewal, and under cool climatic conditions which are more prevalent on the coast than in the interior (refer to Fig. 2.4).

The rate of carbon dioxide assimilation by immature stands can be quite fast. Such stands can assimilate an amount of carbon dioxide equal to that present in the column of air above them to the limit of the atmosphere in about one year.

Currently, we cut and use wood before it decays naturally. Wood and wood products in service have a fairly short half-life, and so the return

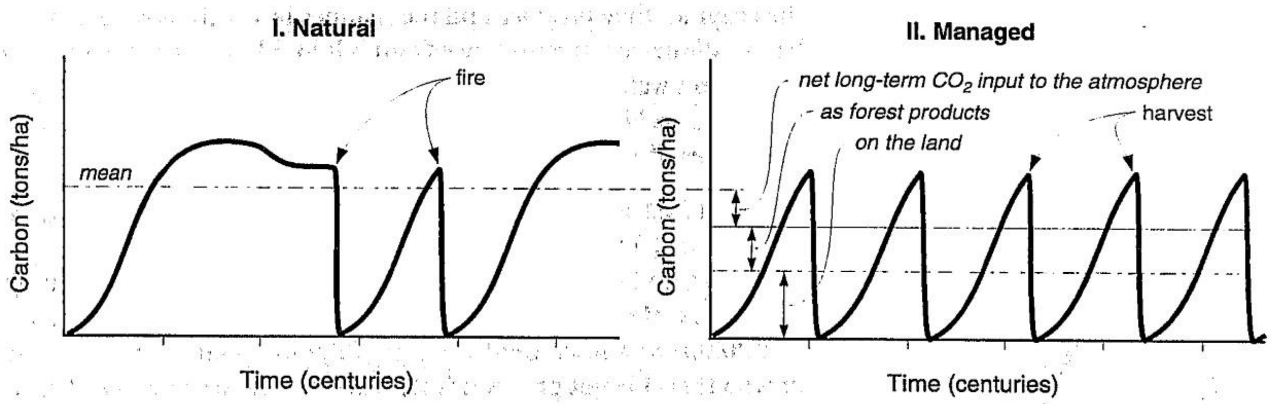


FIGURE 2.4
Comparison of amount of carbon tied up as wood in natural and in managed forests.

to the atmosphere of carbon tied up in wood that is harvested and used (for lumber, pulp, and other products) is somewhat faster than if the trees had been left in the forest to die and decay naturally. In addition, a great deal of biomass other than wood is rapidly returned to the atmosphere following logging. The overall effect of harvest therefore is to increase atmospheric carbon dioxide. Eventually a new stable equilibrium will be reached. In a fully regulated forest, carbon uptake by photosynthesis and total carbon release (largely by decay in the forest, deterioration of wood and other forest products in service, and release during manufacturing) will be in balance for all practical purposes (Fig. 2.4 illustrates these concepts). The graph labeled "I. Natural" depicts a natural forest over many centuries in which stand renewal events occur at irregular intervals; the graph labeled "II. Managed" illustrates events in a managed forest in which the rotation age is a little over one hundred years. The dotted horizontal lines represent the average amount of carbon tied up as wood in these two cases. In the case of the managed forest, one must also consider that some carbon is stored in the form of wood or wood products in service, shown by the solid horizontal line. The difference between the solid line in the managed forest graph and the dotted line represents the amount of carbon that is permanently released when such natural forests are brought under management. The magnitude of that difference varies a great deal, depending on the ecological zone and ecosystem being considered, and may even be negative (i.e., managed forests tie up more wood than natural forests) for some zones.

Habitat Creation

Partially decayed wood provides a special habitat that is required by many organisms. Cavity-nesting birds need snags or living trees with decay in which they can excavate their nesting cavities. Some small mammals also use such cavities. Decaying stumps and logs (Coarse Woody Debris) can act as nurse logs, and sometimes these are the only places where regeneration can become established. Such wood also provides essential habitat for various amphibians. Finally, decaying wood commonly harbours nitrogen-fixing bacteria. Their action can represent a significant nitrogen input into the local ecosystem.

There may well be other significant roles of decaying wood. The difficulty is that most studies of decay have been wholly focused on the damage and loss of wood to the forest industry. Little thought has been given to possibly beneficial roles. Yet if we don't understand and appreciate these roles, our prescriptions for management may well miss the mark!

INFECTION

Spore Production

Most decay fungi belong to the Basidiomycetes, but a few are Ascomycetes. Many Basidiomycetes produce large numbers of sexual basidiospores and sometimes asexual conidia. Figure 2.5 shows how a fruiting body (conk) is constructed. The typical fruiting body has a dark, weathered upper surface, while the lower surface consists of layers of pores. Each year, or sometimes twice a year if there are distinct warm, moist seasons, the fungus grows another layer of pores and abandons the old one. The pores are lined with a layer of basidia (see Lesson 1), the layer being called the **hymenium**. When the basidiospores mature, they are shot off with a speed just enough to carry them to the center of the

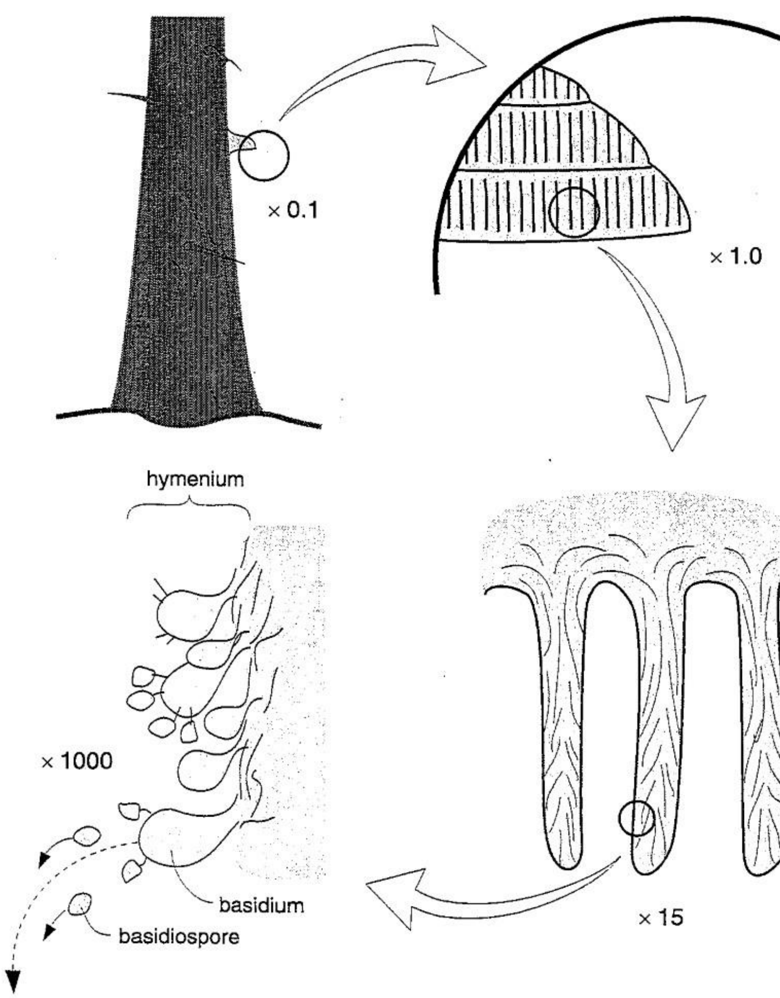


FIGURE 2.5
Progressively greater magnified views of a conk.

pore, and then they drop out of the pore under the force of gravity, and are carried away by wind. A single large fruiting body can produce tens of millions of spores per hour! So, it is not surprising that spores of decay fungi are in the air virtually year round, except during very cold or dry weather. All exposed plant surfaces receive a constant rain of decay spores. Every time you go for a walk in the forest on a warm day, you inhale several live decay spores with each breath!

Penetration of Decay Fungi

Living plant tissues (phloem and sapwood) are immune to decay (with some exceptions in the genus *Phellinus*). Thus, in living trees, only the heartwood decays. How then do decay fungi get in? Branch stubs (knots) do not function as entry courts, or, if they do, the process is very slow. Knot wood is very resistant to decay, but pruning of large-diameter, live branches can create an entry pathway, especially if some stem bark is damaged. Decay fungi can be divided roughly into three groups depending on their mode of entry: the true heartrots, wound entry heartrots, and saprot fungi.

the true heartrots

The few species in the group of true heartrots can apparently enter unwounded trees. The pathway is not always known. Good examples in B.C. are *Echinodontium tinctorium* on hemlock, and true firs; *Phellinus pini* on Douglas-fir, pine, and spruce; and *Phellinus tremulae* on aspen. Because all individuals of a host species are susceptible, decay is found in many trees in affected stands. Usually there is a critical age at which the true heartrots first appear. That age, which varies from place to place and species to species, becomes a critical age with respect to several forest management considerations.

Echinodontium Tinctorium

The case of *E. tinctorium* on hemlock is perhaps best understood. When small, tertiary branchlets close to the main stem die, they become infected with *E. tinctorium.* The fungus forms a small colony, no more than a few cubic millimeters in size, and then remains dormant. Eventually the tree bole grows around branches containing such colonies, and once the fungus finds itself well within the bole, it begins to colonize the heartwood. It is evident that all trees are susceptible, and that decay will begin to appear at a certain age or size.

reading

At this point, you should read the paper by Etheridge and Craig included at the end of this lesson on pages 55–74. This rather long paper has become a classic in work on decay infection pathways. It is included in this course material not only for its own sake, but also because it gives you a taste of the painstaking work required to establish what, in retrospect, appear to be fairly straightforward events. Moreover, you should notice that the evidence for the last stage of development of *Echinodontium* decay in hemlock, the activation of small latent branch infections, is rather scanty and circumstantial. That is typical of descriptions of many processes in forest pathology, because in most cases definitive research that establishes explanations beyond doubt has not yet been done.

Etheridge uses the term "medullary tissues" to refer to what is commonly known as the pith. You will also come across references to the fungus

Ascocoryne sarcoides, a non-decay fungus that can inhibit decay (see p. 46 under the heading "Antagonism" for a description).

wound entry heartrots

Wound entry heartrots include many species. All require wounds of some sort (scars, cracks, broken tops, or patches of dead bark killed by other parasites or sunscald, etc.) in order to gain entry to the heartwood. This group can be divided into two subgroups — primary and secondary wound heartrots. The primary wound heartrots require fresh wounds that expose virtually sterile wood in order to germinate and penetrate. *Heterobasidion annosum* is a good example. Decay fungi belonging to this group usually develop quickly once they gain entry. Wounds remain suitable for entry by this group for only a few days or weeks. Once the wound surface is colonized by micro-organisms other than decay fungi, the primary wound-invading heartrots are excluded. Secondary wound-invading heartrots continue to invade wounds for a much longer time, often following other staining fungi and bacteria. These situations are best understood as a form of succession. Various micro-organisms invade in turn, each changing the nature of the substrate (the wood) to make it suitable for the next one. The final stage will always be decay, but the length of time between wounding and the establishment of decay varies from months to decades.

Even large wounds heal over eventually, and such healing may slow the rate of decay development, possibly due to low oxygen levels. A host reaction in the sapwood may restrict decay in the case of small wounds (see below).

A special case of a wound-invading decay fungus is that of a *Amylostereum chailletii,* the spores of which are injected into wood of trees by a *Sirex* woodwasp together with its eggs. The larvae feed on the decaying wood, apparently relying on the fungal enzymes to digest the wood for them. Balsam fir and radiata pine are commonly attacked in this way. The woodwasp is initially attracted to the tree host by small wounds.

saprot fungi

The final group of decay fungi is restricted to dead trees, which include logs and slash. Once a tree dies, the sapwood becomes very susceptible to decay. Some very specific associations develop. Thus the sapwood of dead standing hemlock in south coastal forests is almost always invaded by *Trichaptum abietinum,* while the heartwood of such trees is destroyed by *Fomitopsis pinicola.* T. *abietinum* produces large numbers of small, purple to white fruiting bodies on the bark within two or three years of tree death, while *F. pinicola* produces its larger, perennial fruiting bodies some years later. *Cryptoporus volvatus,* closely associated with bark beetle galleries in various conifers, decays the recently killed sapwood. Other species are commonly found on slash.

RATE OF DECAY

Even if decay fungi manage to gain entry into the heartwood of living trees, it does not necessarily mean a great deal of decay. The rate at which decay fungi develop in heartwood columns varies widely. Maximum rates of invasion, measured longitudinally, can exceed one meter per year, but may be as little as one centimeter per year. Radial and tangential movement is always slower than longitudinal movement, but these vary just as much. The rate becomes an important determinant of the eventual loss.

Physical and chemical factors have some effect on the rate of decay. Thus the rate is controlled in part by temperature, moisture content, mineral nutrient content of the wood (wood is particularly low in nitrogen), pH, and the presence of natural toxins. The effect of such factors has been well studied in wood test blocks *in vitro* (literally "in glass" - meaning in the lab away from living trees), but predictions based on such studies do not match well with observed rates of decay in living trees. For instance, western redcedar heartwood contains several potent toxins such as the thujaplicins and a complex set of water soluble phenolics, and redcedar wood is widely promoted as having considerable decay resistance. Nevertheless, the total volume of accumulated decay in living trees is greater for redcedar than for any other conifer in B.C. This is only partially attributable to the greater average age of redcedar. Anomalies such as these abound.

Other mechanisms play an important role. They include the factors discussed below, although more may be discovered as the biology of decay is studied in greater detail.

Antagonism

Old undecayed heartwood is seldom sterile. One can usually find various species of non-decay fungi, bacteria, and yeasts. These organisms live on some of the extractives and perhaps some hemicellulose. Attempts to inoculate living trees with decay fungi through holes drilled in the trunk usually result in the stimulation of these non-decay fungi, and only seldom lead to decay. Sometimes the organisms living in wood are antagonistic to decay fungi, meaning that they inhibit or prevent the invasion by decay fungi. A good example is certain strains of *Ascocoryne sarcoides.* This fungus is occasionally found in the heartwood of *Abies, Tsuga* and *Picea.* Some strains provide very good protection against decay, even after the tree dies, as long as the heartwood remains moist. Little is known about such antagonistic fungi. It is not sure how they get into trees, or why some trees in a stand are protected from decay by their presence, while they are absent in others.

There is a potential use of fungi such as these to provide decay resistance to wood in service (e.g., in wooden utility poles). The current chemical treatments provide protection, but among the chemicals commonly used to treat wood, some (such as chromium and arsenic) are environmentally dangerous. Some of these toxic chemicals always leach out of treated wood, and when the wood eventually decays, the remainder is released. The problem so far for using these fungi has been to get a consistent response. To be useful, a treatment must be nearly 100 percent reliable. That has not been achieved so far by treatment with biologicals. A similar situation obtains in the development of anti-stain treatments in lumber.

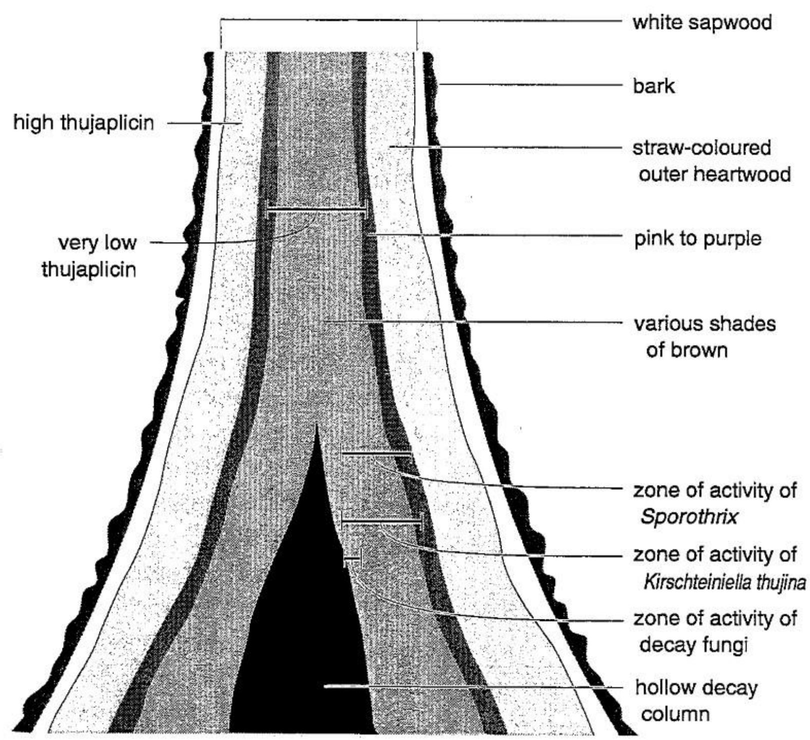
Destruction of Toxins

The heartwood of many tree species contains toxins that inhibit or stop the development of decay. Western redcedar heartwood is well known for its high decay resistance, attributable to thujaplicins and water soluble phenolics. In the case of this species, the heartwood of living trees is commonly invaded from the base and center of the trunk outwards by a succession of fungi (see Fig. 2.6). The first one to invade, a species of *Sporothrix*, converts the thujaplicins into a non-toxic dimer (a molecule derived from two thujaplicin molecules joined at their active end). In the process it turns the normal straw-coloured heartwood a pink or red to purple colour. Once this has happened, a second fungus, *Kirschteiniella thujina,* follows, and possibly together with *Sporothrix* detoxifies the water soluble phenolics. Then yet more species appear, and the wood turns various shades of brown. Finally the decay fungus shows up. It is found in a narrow zone (about 1 cm wide) along the edge of a central decay column. Within the decay column, the decay fungus can no longer be found. In turn it is replaced by a complex microbial community resembling that found in forest floors. The whole process can be regarded as a form of succession in which each succeeding sere changes the environment (heartwood chemistry) to prepare it for invasion by the next. The process is so effective that it largely negates the supposed durability of redcedar heartwood.

Anaerobic Conditions

All decay fungi require oxygen. In some tree species, notably western black cottonwood, normal heartwood is completely replaced by wetwood. Wetwood is nearly saturated wood occupied by a complex community of bacteria which may include nitrogen-fixing species. It has a high pH.

FIGURE 2.6
A vertical section through a large old western redcedar.



Sometimes it is under pressure and it may contain considerable amounts of methane. It is also essentially anaerobic (i.e., without oxygen), and it is this property that stops decay. As long as the tree trunk is free of large scars, the bacterial community uses the little oxygen that diffuses in from the sapwood, and the wood remains free of decay. Once a large, deep scar or crack is formed, too much oxygen is admitted, and the anaerobic condition is lost. Then the tree becomes very susceptible to decay. Wetwood is found in several species of hardwoods, such as aspen and elms and willows, and also occurs in hemlock and true firs, although seldom in large columns that occupy the heartwood completely. In all such cases, some decay resistance is imparted. Wetwooleads to problems in lumber drying during the manufacturing process, and for that reason is considered to be detrimental for some purposes.

Nitrogen Fixation

Nitrogen concentration of heartwood is very low and nitrogen is often a limiting factor for the rate of decay. Decay fungi require nitrogen not only for regular protein formation, but also to build their chitin cell walls. Decay fungi have special adaptations for growth in a low-nitrogen environment. Among other things, they can digest their own old hyphae and recycle the nitrogen that would otherwise be tied up in them. Enriching wood with nitrogen usually increases the rate of decay. Some decay fungi produce within their columns of partially decayed wood a set of conditions in which nitrogen-fixing bacteria can flourish. The nitrogen so produced is thought to be partly absorbed and translocated by the decay fungi to the sites of decay activity, thus presumably increasing the rate of decay. Eventually, of course, that nitrogen enters the nutrient cycle and is used by all the living organisms in the ecosystem.

Host Reactions

There is no direct host reaction to decay of heartwood, apart from some evidence for increased radial growth (appearing as butt swell) to compensate for loss of strength of the bole. However, trees react to wounding, and that reaction can have a major influence on the development of decay caused by agents entering through wounds. Two major types of barrier protection occur:

sapwood wounds

If sapwood is wounded, the tree reacts by forming a barrier between the wounded sapwood and the remaining functional sapwood. That barrier forms only during the growing season. When fully formed, usually within a few weeks of wounding, it is impervious to gases and liquids, and also serves to block the advance of decay and stain. The precise chemical and physical structure of that barrier has not yet been determined. In small, shallow wounds, the barrier may surround the wound completely and block the entry of decay fungi into the heartwood. In subsequent years, the wound heals by formation of a callus. That callus is initiated by the cambium at the point at which the barrier meets the cambium. In such cases little or no decay results. In larger or deeper wounds, the barrier still forms. but now it forms a ring around the wound extending from the cambium to the heartwood-sapwood boundary, and decay can enter the heartwood. Thus, small, shallow wounds do not usually lead to decay, whereas large (large in this context is greater than 5–10 cm tangentially, while longitudinal extent matters little) or deep ones often do. This mechanism of barrier formation occurs in both conifers and hardwoods.

CODIT

In hardwoods, a second phenomenon known as Compartmentilization Of Decay In Trees (CODIT) occurs. In the case of large wounds, the tree forms an unusual annual ring that extends throughout the whole tree (roots, bole, and branches) in the year of wounding. The unusual ring consists of a dense layer of wood impregnated with tannins and other materials. As the tree grows, the ring becomes embedded in the sapwood and eventually heartwood. Decay fungi are unable to penetrate the ring. Thus any fungi entering through the wound are restricted to wood that was laid down before the time of wounding; they cannot penetrate the ring and invade wood formed later. After many years, the tree in question may develop a column of decay that has the exact shape of the tree at the time of wounding, with a very sharp boundary between decay and normal wood. A similar ring is formed in conifers, but it does not extend more than a couple of decimeters from the wound edge, and may not even continue around the tree.

These various phenomena, and possibly many more, determine to a great extend how rapidly decay is going to develop. Whether or not they influence the process depends on the tree species, the age, and the ecological position of the tree, as well as on such random events as scarring and frost cracks. It is not surprising, then, that the amount of decay in mature and overmature stands varies a great deal.

reading

At this point, you should read the three papers included at the end of this lesson, beginning on page 75. These papers are taken from a symposium on decay published in the journal *Phytopathology* (a U.S.A. journal devoted to the science of plant pathology). These papers were chosen because they give a good indication of the state of affairs in the study of decay. It isn't difficult to show that all sorts of things are going on in living trees invaded by decay fungi; there are physical and chemical changes in the wood, as well as changes in the microbial populations active in wood. The precise nature of these changes, however, often depends on the host species and the identity of the decay fungus involved. Also, contradictory results are not uncommon. A major research goal is to arrange the very large body of data (observations of all kinds from many places around the world, and under a variety of circumstances and conditions) into a coherent system in which cause and effect can be shown.

In their paper, Merrill and Shigo point out, quite correctly, that simple models that are concerned only with dead wood and a single decay fungus (typical of the classical model of study) are inappropriate. I have made a similar argument above, showing that *in vitro* studies do not provide the required predictive ability. Both the Shortle and the Shain papers, by proposing broad, generalizable concepts, attempt to help us identify the significant underlying processes. Such an approach is essential: it cannot be said that we have an understanding of the processes unless we can arrange all the observations into reasonable patterns that make sense biologically and that identify chains of causes and effects. In fact, the essence of science is just such an activity; mere observation and recording of what's going on in particular instances is only the starting point!

You will notice, however, that both Shain and Shortle leave a lot of loose ends — many parts of their proposals need further refinement. Don't let that disturb you, because it's the usual state of affairs. Scientists attempt to explain events in the simplest terms possible, but must continuously "fine-tune" these generalities to account for all observations.

Next time you have a chance to observe a set of decayed logs, take some time to examine the various patterns of stained and decayed wood and the apparent barriers that seem to limit decay. Notice how commonly there are islands of stained but sound wood within decay columns. Ask yourself what has gone on. It's a necessary but humbling experience.

Decay and Forest Management

Estimating the Volume of Decay

The only effective way of measuring the amount of decay in standing trees is by destructive examination. Every year new instruments come on the market that are supposed to be able to measure decay in living trees without boring into them or cutting them down. Some are based on differences in sound transmission through normal and decayed wood; some on electrical resistance; and some on deflection under mechanical forces. You may be told that the latest version of the instrument will do the job faultlessly, but be cynical — perhaps some day such an instrument will be developed, but those currently available are at best reliable only in very limited situations. Normal variation in moisture content, wood density, ring width, defects such as knots and cracks, and islands of stain often confuse the situation and lead to faulty readings. Also, all such instruments tell you only about the state of the tree at or below DBH (unless you climb the tree with the instrument).

Estimates of decay volume are made by using **cull factors**. Cull factors are derived by making the following observations:

- All trees in representative small plots are examined for signs (fruiting bodies), or indicators (large scars, broken tops, cracks, etc.) of decay.
- They are then divided into two groups: "suspect" (bearing such signs or indicators) and "residual" (without visible signs of decay). The former group may be subdivided depending on the kind of indicators that are present and their height.
- All trees are then felled and bucked into small sections, and the volume of decay determined.
- From this information, cull factors are calculated for each group.

Each tree in a timber cruise is examined for signs and symptoms of decay, and an appropriate cull factor is applied. Cull factors vary widely depending on species, age and geographic location.

Cull factors give an estimate of the actual volume of decay, but the losses may be much greater because the lumber recovery from logs with a central decay column is greatly reduced. In fact, logs in which more than half of the volume is decayed are usually regarded as cull and left in the woods even though there is some sound wood, because it is uneconomic to produce lumber from these logs.

Age of Tree and Decay

Significant decay usually does not develop until a particular age that is characteristic for the species and site. The decay fungus involved is usually a true heartrot. That age determines the length of time that timber volumes can be "saved on the stump" without significant deterioration; however, insects must also be considered. Some rough critical ages are: 150–175 years for interior spruce; 100 years or less for interior subalpine fir; about 150 years for lodgepole pine; 200 or more years for coastal hemlock but less than 100 years for interior hemlock and cedar; 300 or more years for coastal Douglas-fir; less than 50 years for aspen in much of the interior. These are only rough estimates and they vary somewhat from place to place.

When an overall timber supply area harvesting plan is developed, this kind of information can be very useful because it tells the planner which stands are likely to deteriorate rapidly, and which will retain their value for a considerable time. Thus the likelihood of decay can be an important determinant of the sequence in which various forest types and age classes should be harvested.

Following are two examples that illustrate the importance of decay in management decisions. In the early 1960s several pulp mills and sawmills were built near Prince George, and the rate of harvesting increased rapidly. East of Prince George were large areas of old, valuable spruce; to the west were mostly smaller and younger pine. The spruce was about 150 years old and could not be expected to get much older without significant decay developing. For that reason, the decision was made to concentrate logging in the spruce forests. Later, outbreaks of spruce bark beetle speeded the logging in that area even more. The alternative, namely, to harvest both the spruce and the pine at sustainable rates was (quite rightly) rejected because it would have led to significant losses in value of spruce before it could be harvested.

The second example concerns interior hemlock, which is known to develop significant decay at an early age. Until very recently, it was not acceptable as regeneration in much of the interior cedar hemlock ecological zone. Recent studies, however, suggest that decay is minimal before about age 90. It thus appears that hemlock can produce an acceptable crop after all, leading to a major change in silviculture in the zone. For now, the use of advanced regeneration remains uncertain, and, without further studies, it should probably not be accepted. Interior western redcedar appears to be a similar situation, although we do not have enough data for a thorough assessment.

Decay in Immature Stands

Decay will become less common as our forests come under management. Nevertheless some decay will continue. Scarring caused by various forestry operations is an important factor. Much of the damage can be prevented by reasonable care and appropriate timing (e.g., by avoiding operations in early summer when the cambium is very succulent). A great deal also depends on the tree species. Douglas-fir and lodgepole pine can withstand considerable scarring when young and develop little decay. Other species such as hemlock and true firs are more easily infected. Again this also varies from region to region, and local experience is the best guide.

Decay of Dead Standing Timber

Stands killed by fire or insects can be salvaged. The rate of deterioration depends on temperature, moisture, species, and the wood-utilizing insect population. On the coast, small trees (i.e., DBH less than 25 cm) can deteriorate within a few years, but for larger trees a rough rule of thumb is a loss of 2–4 cm radially each year. In the interior and at high elevations, decay of dead standing timber can be much slower.

Decay in Parks and Recreation Areas

Old decayed trees add to the variety of habitats available in ecosystems, and thus are often desirable in parks. However, public safety needs to be considered and high use areas such as parking lots, picnic areas and campsites should be checked for dangerous trees. On the coast a fungus of particular concern is *Phellinus tsugina* on hemlock and true fir. This species is able to invade and decay sections of sapwood in living trees. Where that happens, typical fruiting bodies are often produced. Such trees are very weak and commonly break at the decay. Wherever *P. tsugina* is spotted in high use areas, the affected tree should be removed.

Decay in Wooden Structures

The single effective rule is: "Keep it dry" (i.e., keep moisture content below the fiber saturation point), and this is achieved by appropriate design of wooden structures. If exposure to moisture cannot be prevented, treated wood should be used. Another approach is to exclude oxygen, which happens when using wooden pilings in wet soils. Notice that prevention of decay usually involves creating a set of conditions in the wood that do not allow decay fungi to grow (i.e., conditions are too dry, too toxic, no oxygen, etc.). It is not feasible to prevent spores of decay fungi from landing on wood because such spores are present everywhere in the air. Various types of paints and coatings seldom serve a useful purpose. Sooner or later they crack or peel, and decay enters.

All of the processes discussed above can be illustrated with the example of a telephone pole. The base of the pole, buried at least two meters below ground, is always water saturated. It remains sound because the rate of diffusion of oxygen in water-soaked wood is very slow, so that the wood at the base of the pole is essentially anaerobic. The top of the pole is generally too dry for decay fungi. There are of course periods when the whole pole is wet, but during periods of extreme drying, decay fungi cannot survive. Between these two regions, at ground level, conditions are just great for decay. Enough water wicks up from the soil to keep the pole moist year round. If a telephone pole decays, it always happens at ground level.

Since all this is well known, poles are always pressure treated with a wood preservative. Various preservatives have been used over time. The earliest was creosote. This was replaced in the 1950s and 60s with pentachlorophenol. More recently the preservative of choice is copper-chrome-arsenic (CCA), which gives the pole a green colour. These preservatives can be forced into the wood to a depth of about 3–6 cm depending on species and the amount of sapwood left on the outside of the pole. The preservative-treated zone remains sound for many decades. However, as the pole dries, radial cracks appear, and these extend into the untreated interior of the pole. Such cracks form entry pathways for the spores of decay fungi, and decay begins in the interior of the pole. Thus, 10–20 years after installation, poles typically will look sound on the outside, but a good proportion of them will have some internal decay, some of them extensively.

SECTION ASSIGNMENT

SELF-TESTING/REVIEW QUESTIONS

Test your understanding of the material in this lesson by attempting to answer these questions. Do not proceed to the next section until you are satisfied with your proficiency in this section.

Do *not* send your answers to the tutor for marking. If you continue to have difficulty with a question after you review the relevant material, you may wish to discuss it with your tutor.

After you answer the questions in this part, proceed to Appendix A and complete Assignment #1 for submission to your tutor for marking.

1. What special feature distinguishes decay fungi from all other fungi that digest cellulose?
2. What enzymatic features differ between white and brown-rots?
3. List two major roles that decay fungi play in natural ecosystems.
4. What are the minimum requirements of decay fungi for growth and reproduction?
5. How do living trees become infected with decay?
6. List and describe at least five ways in which the spread of decay in the heartwood of living trees may be either retarded or promoted.
7. How do trees react to decay of their heartwood?
8. How do trees react to wounding of the bark in a way that influences decay development?
9. Examine and describe at least two decay fungus fruiting bodies found on living or dead conifers in your area. Specify colour, size, shape. location, features of the lower surface, and type of decay produced.
10. Which species of conifer is thought to have the greatest amount of decay in your area?
11. What are cull factors, and how are they derived?
12. What are the basic rules for prevention of decay in wooden structures?