Dying Trees and Parasitic Plants

CHAPTER 11

Trees live longer than any other form of life, sometimes for 2,000 years or more. In many places, trees serve as memorials to historic events long after the people who participated in the event have died. They remain standing in one place, unable to move, while lightning, insects, fungi, bacteria, and human beings and other animals feed on or invade their tissues. Yet they may be able to withstand this dangerous onslaught and continue to grow for hundreds of years.

The survival of trees in a hostile environment is mainly due to two important features: the protective woody bark and a mechanism for continuous growth despite damage. To understand how trees protect themselves, one must first examine the transition from the soft and relatively vulnerable green stem of a young tree to the woody, bark-enclosed twigs, branches, and trunk of a mature tree.

Transition to Bark and Wood

The young stem of a woody plant is composed of the same kinds of cells as those in the stems of herbaceous plants. The outer epidermal layer encloses a cortex of parenchyma cells. The center of the stem is also composed of parenchyma cells. The vascular tissue is arranged in a cylinder, with xylem (water- and mineral-conducting) cells toward the inside of the stem and phloem (food-conducting) cells toward the outside of the stem. Often, there are also bundles of thick-walled supporting cells called sclerenchyma.

As the stem matures, two important meristems begin to function. Apical meristems, at the growing tips both above and below the ground, were already mentioned in previous chapters. The new meristems, important for the lateral growth of woody plants, are the vascular cambium, which provides xylem and phloem cells for the developing woody tissue, and the cork cambium, which contributes cells to the developing corky bark. Sometimes the cork cambium develops gradually in patches, initiating a bark layer on some parts of the stem while other parts of the stem remain temporarily green. Eventually, the entire stem is covered with bark. The cork cambium continues to produce cork cells, sometimes for many years, to replace bark sloughed away due to weather or wounds. As the girth of the trunk increases, new cork cambia begin to originate from parenchyma cells deeper in the bark to maintain coverage of the expanding circumference of the tree. Similar changes occur belowground as roots develop bark and secondary vascular tissues.

The vascular cambium produces secondary xylem and secondary phloem.
The layer of active secondary phloem remains relatively thin as the older phloem becomes compressed by the expanding trunk. Secondary xylem layers are commonly referred to as wood. These layers are produced each year, and, unlike the secondary phloem, are preserved for the life of the tree. In many trees, the cells of the secondary xylem produced in the spring are larger than those produced in the summer. The resulting seasonal variation in cell size creates a pattern in which each year's growth can be discerned. These are called annual rings. Where rainfall and temperature are uniform and less “seasonal,” as in parts of the humid tropics, annual rings may not be as apparent. In many climates, annual rings record the growing conditions in each year of the tree’s life. Historical studies of drought periods and other environmental variations have been made by studying the annual rings of ancient trees that have fallen or been cut down or through the study of sample cores taken from living trees.

The chief functions of the secondary xylem are water conduction and support. Secondary xylem is composed of several types of cells. Tracheids are elongated, nonliving, conducting cells that consist only of cell walls. Besides having a primary cell wall, tracheids are endowed with a secondary cell wall that adds support. The tracheid wall contains numerous pits where only the primary cell wall, not the secondary cell wall, is present. Where the ends of the tracheids overlap, water and minerals pass from one tracheid to the next through the primary cell wall. Tracheids are the only conducting tissue in conifers, and they also play a conductive role in hardwoods. Hardwood trees, like oaks and maples, also produce larger conducting tubes called vessels. The formation of thickened secondary walls and the dissolution of end walls occurs in young living cells, but the last part of the xylem fibers, a third kind of nonliving cell that adds support to the wood.

In conifers, tracheids and living parenchyma cells are found in radial layers only one cell thick. In hardwoods, radial layers are composed of tracheids, vessels, and parenchyma cells that vary in thickness. These radial layers are called rays and may be visible in the wood pattern. Living parenchyma cells are also present in the vertical plane of the secondary xylem. The role of these living cells is explained later in this chapter. In cross section, the secondary xylem of older trees is often composed of a darker inner cylinder known as heartwood and an outer, lighter-colored layer known as sapwood. The sapwood remains approximately the same thickness throughout the life of the tree and actively functions in conduction. Each year, new sapwood is produced from the vascular cambium, and the oldest part of the sapwood becomes part of the heartwood. The heartwood is often darker because it has undergone chemical changes that help protect it from decay and increase its strength. Many trees that are entirely hollow, due to decay of the heartwood, continue to function and grow because the sapwood conducts water and minerals for the tree.

Unlike the secondary xylem, which consists mainly of nonliving cells, the secondary phloem is composed of living cells, including parenchyma.
cells and sieve elements, which transport the products of photosynthesis from the leaves to the rest of the plant. This relatively narrow band is vital to the health of the tree because it carries food to the roots. If a tree is "girdled" by having its bark stripped away, the layer of separation is usually the vascular cambium. Technically, bark includes all tissues outside the vascular cambium. When the bark is peeled away, the secondary phloem is often removed as well. The tree may remain alive temporarily using food stored in the roots while the secondary xylem continues to carry water to the leaves, but eventually the tree dies due to a lack of food. The phloem is also very vulnerable to damage when cuts are made in tree bark due to human mischief or accidents.

The protective part of bark is composed of cork cells. Cork is nonliving tissue that helps make the tree trunk impervious to water loss and helps prevent physical damage. The continual production of cork cells is necessary since bark is constantly subject to weathering and other damage. Commercial cork is peeled from the extra thick bark of the cork oak, Quercus suber, which grows in the Mediterranean region. In the thin bark of some trees, such as birch and cherry, lenticels may be particularly visible. These are lens-shaped structures composed of loosely packed cells that help in the exchange of air for the living tissues within the woody tissues. Lenticels can be vulnerable to invasion by pathogens and insect pests.

Leaves are the most vulnerable aboveground parts of a tree. The woody trunk and twigs are generally well protected from invasion by microorganisms and insect pests. Deciduous trees lose their leaves and replace them with new ones each year, shedding not only leaf tissue but many insects and parasites as well. A recommended sanitary practice is to clean up and compost, burn, or dispose of diseased leaves in autumn to help prevent spores from reinfecting the new leaves in spring. Anthracnose fungi sometimes invade woody twigs from infected leaves, especially in stressed trees or during particularly wet years, but generally these diseases do not cause severe damage.

The most devastating tree diseases are those caused by microorganisms imported from foreign lands. Because tree populations are not likely to have natural resistance to an imported pathogen, initial disease outbreaks are often severe. Generally, indigenous pathogens cause little trouble on native trees in the countries of origin because those trees have reached a genetic balance with their attackers over long periods of coexistence.

Fig. 11-2. The American elm. Top, healthy tree with characteristic shape; bottom, street sign suggesting that elms have been important shade trees, although none exist at this location today.

Fig. 11-3. Dutch elm disease, caused by Ophiostoma ulmi.
Dutch Elm Disease

A particularly sad example of the effect of an imported pathogen has been the demise of the American elm, *Ulmus americana*, an important shade tree in most parts of the United States. Dutch elm disease, named for the country where many of the important early scientific studies were done, was introduced into the United States on elm logs from Europe on at least three occasions. Its presence was first confirmed in Ohio in 1930. The disease had already caused losses of elm trees in Europe, starting at the time of World War I. Two Dutch plant pathologists, Christine Buisman and Bea Schwarz, played key roles in the discovery of the cause of Dutch elm disease. It is suspected that the fungus originated in Asia, because Japanese and Chinese elms are generally resistant to the disease. In the late 1960s, a renewed epidemic of Dutch elm disease plagued Great Britain and Europe, killing many elms that had survived the initial outbreaks, apparently due to the introduction of a more aggressive strain of the fungus imported from North America. It has been estimated that more than 40 million urban elms have died of Dutch elm disease in the United States alone but that perhaps 136 million landscape elms with a diameter of more than four inches (about 10 centimeters) still exist, primarily in Europe, Asia, and North America.

Fig. 11-4. American elms and the effect of Dutch elm disease. *Left*, American elms were popular because of their overarching growth that provided shade over the streets. This planting pattern increased the demise of the elm due to Dutch elm disease because *Ophiostoma ulmi* moves through xylem connections in root grafts between neighboring trees. Photo taken in 1975 at Longwood Gardens, PA. *Right*, American elm that has died of Dutch elm disease.

Dutch elm disease is a vascular wilt disease in which the fungus, unlike *Verticillium* species and *Fusarium oxysporum*, never lives a life independent of its host. The fungus, *Ophiostoma ulmi* (formerly *Ceratocystis ulmi*), produces several spore stages that help this clever parasite complete its life cycle. The fungus is an Ascomycete, but the sexual stage is relatively rare in the United States because the second mating type necessary for sexual reproduction is not common. The fungus produces two conidial (asexual) stages.

As with other vascular wilts, the primary disease symptom is one of water stress. The invading fungus may produce toxic substances that increase tylose production by parenchyma cells lining the xylem vessels. Tyloses are overgrowths of the parenchyma cell protoplasts; these push through the pits in the xylem walls and contribute to vessel blockage. In addition, the fungus produces enzymes that degrade the cellulose, pectin, and other components of the vessel cell walls. The cell walls begin to break down and collapse, which greatly restricts the movement of water in the xylem. In addition, the mycelium and budding conidia of the fungus contribute to vessel blockage. The small, white, oval conidia help spread the fungus throughout the xylem after the fungus is introduced into the tree.

After the tree has died, the fungus becomes saprophytic and grows throughout the trunk of the dying tree. A second kind of conidium is produced in a sticky mass on the tip of a stalk of fused hyphae under the bark of an elm tree that has recently died. These reproductive structures, called *synnemata* or *coremia*, are produced in tiny tunnels carved out beneath the bark by female elm bark beetles. The tunnels are maternal *galleries*.

Fig. 11-5. Damage by *Ophiostoma ulmi*, a vascular wilt pathogen. A symptom of the disease is discoloration of the active xylem tissue.
about an inch (two to three centimeters) long, in which the beetles lay their eggs. After the eggs hatch, the larvae feed under the bark, each one making its own side gallery perpendicular to the egg gallery. After a short pupation or resting stage, the new adult beetles emerge through the bark and fly to a healthy elm tree, carrying on their bodies the sticky conidia of *O. ulmi*. The beetles feed on twigs and branches of healthy elm trees and, in the process, deposit the conidia in the xylem of the tree, thus completing the disease cycle.

Two species of elm bark beetles are vectors of the Dutch elm disease in North America: *Hylurgopinus rufipes*, a native elm bark beetle, and *Scolytus multistriatus*, a European elm bark beetle that was inadvertently introduced from Europe. The European beetle is more numerous, because it can complete two generations in many parts of the United States, and is an important vector of Dutch elm disease. Beetle galleries are visible on the trunks of dead elm trees when the bark is removed. The European elm bark beetle creates its egg gallery parallel to the wood grain, while the native beetle galleries are more or less perpendicular to the grain. An additional European elm bark beetle exists but, luckily, has not yet been introduced into the United States.

Since fungus transmission by European elm bark beetles is to young twigs in the crown of a healthy tree, the earliest symptom of Dutch elm disease is the flagging or wilting of small branches. Because the xylem fluid moves upward, the initial invasion is fairly slow. Careful inspection of elm trees and pruning out of infected branches at an early stage of disease can sometimes save a tree.

A second means of transmission is more difficult to control. It occurs on the elm-lined streets in many towns and cities in Europe and North America. When trees of the same species are grown close together, roots may graft together underground. Vascular connections may form in the grafts, allowing the passage of the fungus from one tree to the next. The fungus, moving upward in the xylem fluid, may then colonize a tree very quickly. This has led to the death of trees one after another along streets. Monoculture, whether in a wheat field or on a city street, leaves plants vulnerable to diseases. Nearly every town has an Elm Street, but now few elms remain to be seen over much of the United States. Too often, they have been replaced by monocultures of maple, honey locust, or oak that are equally vulnerable to other diseases.

A disease similar to Dutch elm disease and caused by a related fungus is striking oak trees in the Midwest, Michigan, Pennsylvania, Maryland, and West Virginia. Red and black oaks are most susceptible, but all oaks can become infected by *Ceratocystis fagacearum*. This fungus, like *O. ulmi*,
causes a vascular wilt disease. Under the bark of dying trees, the oak wilt fungus produces pads of mycelium and conidia that are attractive to insects. Many kinds of insects are attracted by a fermenting odor, and, after leaving the oak, they may move on to another oak and feed in such a way that the fungus is introduced into the xylem, commonly through pruning wounds or bark. Because the vector relationship is not as efficient and specific as in Dutch elm disease, the spread of oak wilt has been slower. However, along tree-lined streets, root graft transmission may increase the rate of infection and death of oak trees.

Control of both Dutch elm disease and oak wilt is difficult. An important sanitary practice is to burn or remove dying and dead trees. In many places, it is illegal to store bark-covered elm logs in wood piles. When Dutch elm disease was first discovered in the United States, intensive insecticide spraying was attempted to reduce the spread of the fungus by elm bark beetles. On tree-lined streets, trenching or herbicides were used to break root grafts between trees to try to prevent the fungus from spreading. Today, most remaining elm trees in the United States exist as individuals. These trees can be maintained if carefully watched and pruned when flagging twigs appear. Some trees receive fungicide injections as well. Unfortunately, such injections are relatively expensive and must be repeated every one to three years. Many studies have been made to discover microorganisms that could be injected for biological control of the disease, but so far results have either not been successful or are not yet approved by the U.S. Environmental Protection Agency.

The future of the American elm probably lies in the prolific seed production of the species. Each seed is genetically unique. As young trees grow, many become infected and die, but the introduction of a foreign parasite has never been known to eliminate a species. Over hundreds or perhaps thousands of generations, the species will finally come into balance with its parasite, and mature elms may once again grace the landscape. Tree breeders hope to shorten this time through deliberate crossing and selection for genetic resistance. They have had some success. The earliest resistant trees were selected in Europe and named for the Dutch scientists who participated in the initial studies of the disease. Named Buisman, Schwarz, and Groeneveld, they were, unfortunately, not resistant to all strains of the fungus and also lacked the cold-hardiness of the American elm. Today plant pathologists and breeders continue to search for an elm cultivar that will resist O. ulmi and also have the same graceful shape and hardiness that have made the American elm such a popular shade tree. Resistant elms have been released by the U.S. Department of Agriculture and the University of Wisconsin. In North America, breeding programs must take into consideration an additional fatal disease that is threatening elms. It is called elm phloem necrosis or elm yellows and is caused by a bacterium-like pathogen that is described in Chapter 12.

Some beautiful specimens of mature elms still exist, but they require care and protection if they are to survive. The Dutch elm disease story is yet another example of the importance of quarantines for protection of native plants from foreign pests, pathogens, and vectors, but it is not only a historical example. It is a threat today in Australia and New Zealand. Perhaps half a million susceptible elm trees are providing shade and beauty on the Australian continent. An elm bark beetle has found its way to Australia, but, so far, quarantines have successfully barred O. ulmi. New Zealand has not been so lucky. Dutch elm disease was discovered in late 1989, and eradication programs have been initiated. It is too soon to know if they will be successful.

**Chestnut Blight**

The loss of a major shade tree species leaves whole neighborhoods with a bare and blighted look. Earlier in the 20th century, a major forest tree

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**Fig. 11-8.** Oak wilt disease, caused by *Ceratocystis fagacearum.* Top, water stress symptoms in leaves of an infected oak tree; bottom, fungus pads attractive to insects are produced under the bark of dying and dead oak trees.
species was nearly destroyed. Chestnut blight was, with citrus canker and white pine blister rust, one of the diseases that triggered the first U.S. quarantine legislation in 1912. Before the blight struck, the American chestnut, *Castanea dentata*, was a major tree species throughout the eastern forests from Maine to Georgia. In the early 1900s, perhaps as many as every fourth tree in the Appalachian forests was a chestnut. The straight, rot-resistant trunks were important for lumber, fence posts, and poles, and the nuts were an important human food crop as well as a major food for a number of wild animals. The dark tannins in the bark were important in the tanning industry.

Chestnut blight is caused by a fungus previously known as *Endothia parasitica* but recently renamed *Cryphonectria parasitica*. Unlike *O. ulmi*, which causes a vascular wilt, chestnut blight is a canker disease. The fungus invades the bark of twigs through small wounds, such as insect feeding sites, and begins to invade the vulnerable vascular cambium of the growing twig. Slowly the mycelium spreads outward until eventually the entire twig is girdled and dies. As the fungus continues growing, it may reach the main trunk, and the mature tree may eventually be killed.

Control of this disease is theoretically possible in a single tree if infected twigs and branches are pruned and destroyed. Fungicide applications are useless, and, of course, pruning trees in forests is not practical. By 1923, the disease had invaded 80% of the chestnut’s range, and by the 1950s, 80% of the chestnut trees had died. The fungus, apparently introduced on chestnut seedlings brought to the New York Botanic Garden by a collector, produces sticky conidia and ascospores that are carried to American chestnut trees by birds and insects. The rapid and devastating spread of the disease caused tremendous economic and ecological disruption throughout the Appalachian forests.

The tragedy did not end in North America but spread on to Europe, probably by the export of chestnut wood about 1917. Many European chestnut groves were destroyed following the initial invasion. However,

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**Fig. 11-9.** Chestnut trees. *Left*, forest chestnuts in the Appalachian range before the blight; *right*, chestnut trees in Fairmount Park, Philadelphia, in 1878 and people harvesting the nuts with ladders.

**Fig. 11-10.** Nuts of the American chestnut, *Castanea dentata*. *Top*, burr with nuts; *bottom*, harvest from a chestnut plantation in the United States before chestnut blight became widespread.
chestnut trees have a growth habit that keeps the species alive despite the presence of the virulent fungus. From the base of the dead tree trunks, the extensive root system stores enough food reserves to send up new shoots, or "suckers," from the base of the trunk. Year after year, these young shoots allow renewed growth, but eventually they too succumb to the fungus once it has invaded their tissues. Some young trees are able to grow to a sufficient size to allow fruit production, and new chestnuts sprout. Eventually, there is hope that, as with the elm, the chestnut will be able to coexist with *C. parasitica* as a minor parasite. Most people do not expect to live long enough to see this happen.

The continued production of suckers from the base of the dying chestnut trees inspired some to think that perhaps, somehow, the trees could overcome the effects of the deadly parasite. Robert Frost, the famous American poet, even discussed this possibility in his poem "Evil Tendencies Cancel":

Will the blight end the chestnut?
The farmers rather guess not.
It keeps smoldering at the roots
And sending up new shoots
Till another parasite
Shall come to end the blight.

There is now scientific evidence that this scenario may be happening. In Italy, in the 1950s, some orchard chestnuts were found to be surviving despite the presence of extensive cankers. Studies of the *C. parasitica* isolates from these cankers suggested that new strains of the fungus had arisen that were much weaker than the common strains. Such strains have been designated hypovirulent. Not only are they weaker but, when they come into contact with virulent strains, the hyphae may fuse (a process called anastomosis), and the factor that causes hypovirulence spreads to the virulent strain and weakens it. The phenomenon of hypovirulence seems to be a disease of the fungus. An extra piece of double-stranded RNA in the mycelium of the hypovirulent strains replicates and spreads into the mycelium of virulent strains, weakening them.

While this is not completely understood, the existence of hypovirulent strains has provided a practical biological control to "cure" existing cankers. In Europe, the application of hypovirulent strains of *C. parasitica* to active chestnut blight cankers is now used to stop canker activity. In the United States, there is hope that perhaps this naturally occurring biological control can somehow be used to help reestablish the chestnut in eastern forests.

The practical application of this procedure faces some complications. The hypovirulent strains usually grow more slowly and produce fewer spores, which reduces their ability to spread in nature. The procedure is helpful in stopping the growth of an active canker, but so far no way has been found to prevent the disease in the first place. Also, the parasite has numerous genetic strains. Spread of the hypovirulence factor is possible only if the virulent strains present in a tree are genetically compatible with the hypo-

![Fig. 11-11. An old photograph of dying chestnuts during the initial outbreaks of the blight caused by *Cryphonectria parasitica.*](image-url)

![Fig. 11-12. Natural range of the American chestnut.](image-url)
virulent ones so that anastomosis will occur. In the United States, cankers may contain 10 or more different genetic strains, so biological control may require application of hypovirulent strains that are genetically compatible with all the virulent strains present.

Scientists are optimistic that this method may eventually provide useful results. In the meantime, they are greatly interested in the general phenomenon of hypovirulence. Hypovirulent strains associated with double-stranded RNAs have been found in other fungi, and scientists believe that more knowledge about this interesting phenomenon may lead to a better understanding of how plants and parasites come into genetic balance.

Other Canker Diseases of Trees

Tree species remain the most vulnerable to destruction by introduced pathogens due to the long time needed to replace mature trees. Potential economic and ecological losses make their protection a high priority. The American beech (Fagus grandifolia), an important tree in mature eastern forests, is being destroyed by an introduced canker fungus, Nectria coccinea var. faginata and a native fungus N. galligena. By themselves, the fungi cannot penetrate bark, but they can enter through tiny wounds made by the beech scale, Cryptococcus fagisuga, a tiny sucking insect. As in chestnut blight, the vascular cambium is killed by the invading fungus. The future of an infected tree depends on the growing conditions and age of the tree. Older trees seem more susceptible to rapid killing, whereas younger trees, although more likely to survive, become defective as timber trees. Following infection, the bright red fruiting bodies of these Ascomycetes erupt through the bark of infected trees. The fungi produce both conidia and ascospores that can be disseminated by air, water, and vectors such as insects, birds, and small mammals.

Control of these canker diseases in forest situations is very difficult and lies mainly in forestry management practices that provide greater species diversity and the culling of infected trees. Beech trees in yards and parks can be protected by pruning infected branches and reduction of scale infestations. Scale insects are usually well protected by a waxy coating, but insecticides can be used to kill them in their crawler stage. Scrubbing of beech bark with a detergent will also help remove the scales. The relatively sedentary life style of the scales reduces the spread of this canker disease. It made very slow progress from the site of its initial introduction in Nova Scotia, Canada, on European beeches in 1890 and did not arrive in the Adirondack Mountains of New York until 1978.

Numerous canker fungi threaten woody plants, including many ornamental trees and shrubs. In some cases, native fungi are an important threat to imported plants. For example, the popularity of the Colorado blue spruce in the eastern United States has increased losses due to Cytospora canker. Colorado blue spruces are adapted to the dry, cold winters of the western

Fig. 11-13. Living chestnut trees planted outside the natural range in Michigan where they have, so far, escaped infection.

Fig. 11-14. Cankers on chestnut trees. a, Lethal canker of Cryphoneectria parasitica. b, Blighted but recovering chestnut tree. Hypovirulent strains of the pathogen have been isolated from the cankers. c, A healing canker in which hypovirulent strains of the pathogen have been found.
Rocky Mountain states and become infected by canker fungi in the moist climates in the eastern United States. Many canker diseases are dependent on host plants being concentrated in a small area. For instance, black knot of _Prunus_ species is a serious canker disease in uncared-for cherry and plum orchards but is usually a minor problem on wild cherry trees growing in genetically diverse and species-diverse natural ecosystems.

The damage that a canker fungus causes often depends on the vigor of the tree. Healthy trees may be able to produce callus and new vascular cambium at a rate that will keep the canker fungus from girdling the branch or trunk. In such cases, a canker may show annual rings of callus growth as the tree attempts to contain the growth of the invading fungus. Such a biological defense depends on the vigor of the host, so trees stressed by other environmental factors such as drought or air pollution may not be successful in containing the pathogen. Many canker-forming fungi are "opportunists" and can only attack woody plants stressed by drought, extremes in temperature, other diseases, or a reduced root area.

Woody plants in landscapes and orchards should be pruned to remove canker infections while they are still limited to small branches. Since most canker fungi enter woody plants through wounds, dormant-season pruning is safest because the air is dry and fungi are not active. Pruning wounds are not as likely to be invaded by other canker and decay fungi and bacteria from fall to late winter.

**Wood Decay Fungi**

A specialized group of fungi is capable of wood decay. Most of these fungi are Basidiomycetes, and many produce relatively large fruiting bodies commonly seen on the trunks and branches of infected trees. To penetrate the normally protected woody tissues, wood decay fungi require wounds that expose the wood. Wounds may be produced by birds, insects, animals, wind or winter, lightning, and many human abuses from lawn mowers and automobiles.

The fruiting bodies of wood decay fungi exist in an amazing array of sizes, shapes, and colors. They may be fleshy or dry, annual or perennial.
some tree maintenance practices. For instance, some tree surgeons no longer "clean out" decayed areas of hard, darkened wood but leave it as a protective layer. Tree branches should be cut without damaging the branch collar rather than flush with the trunk. This allows the tree to compartmentalize the branch stub more successfully. Also, many tree specialists no longer "paint" a tree wound after pruning because compartmentalization processes should normally protect the tree from invasion.

It is now clear that trees that react quickly to a wound may be able to isolate the tissue before invading microorganisms can cause further damage. The success with which the tree can compartmentalize and prevent infection depends on several factors. The size, depth, and location of wounds are physical factors that affect successful compartmentalization. In addition, because the process is biological, the health and vigor of the tree affects the rate and strength of the chemical and biological reactions of the healing process. Trees subjected to other stresses are less likely to be successful.

![Diagram of tree with compartments and wound]

**Fig. 11-18.** Natural compartments in trees help reduce the spread of decay. **Left,** compartments in a mature tree. **Right,** branch stubs may or may not cause further decay in a tree trunk. A properly pruned branch (A) does not disturb the branch collar, allowing the branch stub to compartmentalize. Improper pruning (B) cuts open larger areas of the trunk to potential decay. Broken branches (C) may encourage the growth of decay fungi that can overcome compartmentalization of the branch stub.
Besides avoiding wounds and using proper pruning techniques, the best way to assure the long life of a tree is to keep it healthy and vigorous through fertilization, watering, spacing, and site selection, so it will be able to compartmentalize successfully.

**Mushrooms and Trees**

It is relatively common to find mushrooms beneath many kinds of trees. An important parasite that causes root rot of many tree species is *Armillaria mellea*. It is an aggressive parasite of conifers in the western United States and a parasite of stressed hardwoods in the eastern United States. In autumn, clumps of the spore-producing mushrooms can often be found at the base of infected trees. *A. mellea* commonly infects tree stumps and then spreads to neighboring healthy trees with stringlike masses of mycelium called rhizomorphs, giving it the common name "shoe string" fungus.

Other types of mushrooms are commonly found in forests. While some are saprophytes important for the decay of dead and dying trees, many have an intimate **mutualistic** relationship with a nearby tree. Such fungi are called mycorrhizae. The word **mutualistic** means that both organisms benefit from the relationship. The fungus obtains nutrients from the tree, and the tree receives protection from root pathogens as well as increased surface area for absorption of water and certain minerals, especially phosphorus. Nearly all plants, woody and herbaceous, have mycorrhizae associated with their roots. Some, like orchids and maples, host endomycorrhizae that grow into the root cortical cells. Many trees, such as pines and oaks, commonly host ectomycorrhizae that form a thick outer layer of mycelium and grow around the cortical cells, forming a layer called the **Hartig net**. Early attempts to plant trees in treeless regions, such as the U.S. Great Plains, Southern Africa, and parts of Australia, were not very successful because the proper mycorrhizal fungi were missing. The seedling trees were grown in sterile soil, and many died when transplanted outdoors without their mycorrhizae. Modern forest plantings include inoculation of sterilized soil and tree seedlings with mycorrhizae.

Mycophiles (mushroom lovers) and mycophagists (mushroom eaters) quickly learn to search for their favorite fungi under the appropriate tree hosts. Flushes of mushrooms are especially profuse under dead and dying trees as the mycorrhizal fungi move on to new host trees via airborne spores. As in other Basidiomycetes, each basidiospore of a mushroom is usually haploid and of a single mating type. The primary mycelium produced from the basidiospore must then fuse with the primary mycelium of a

![Fig. 11-19](image) **Fig. 11-19.** Reproduction of a wood decay fungus. **a**, A fruiting body is produced on an infected tree trunk. **b**, The lower surface of the fructifying body is composed of numerous tiny pores, each lined with spore-producing cells (basidia). **c**, Karyogamy and meiosis take place in each basidium, resulting in the production of four haploid basidiospores. **d**, Basidiospores are forcibly discharged to be wind-dispersed.

![Fig. 11-20](image) **Fig. 11-20.** Root rot caused by *Armillaria mellea*. **Top,** mycelial fans beneath the bark of an infected tree; **bottom,** mushrooms produced at the base of an infected tree.
basidiospore of the other mating type to form a dikaryotic mycelium capable of continued growth and reproduction. Karyogamy and meiosis take place in specialized cells, the **basidia**, from which the **basidiospores** are produced. Each basidiospore forms on a tiny projection, from which it is forcibly discharged. Some related Basidiomycetes use a more passive dispersal mechanism such as puffballs, which produce millions of basidiospores in a powdery mass that is dispersed by raindrops or other bumbs.

**Parasitic Higher Plants**

Another kind of parasite may infect many kinds of trees. This type of pathogen is much larger than the others discussed so far. More than 2,500 species of flowering plants that parasitize other plants are found among many botanical families. Most are not of economic importance but are interesting curiosities. The largest known flower is that of the parasitic plant **Rafflesia arnoldii**, which grows only in a few areas of Indonesia and Malaysia. The dark red, mottled flowers can be more than three feet (more than one meter) across, can weigh 15 pounds (six kilograms), and smell like rotten flesh to attract flies that assist in pollination. The species is **dioecious**, which means that individual plants produce either male or female flowers. The plants produce no photosynthetic tissue but rely totally on a tropical vine for all water and food. In North America, beech-drops (**Epiphyllum virginianum**) and squaw-root (**Conopholis americana**) are common parasites of beech and oaks, respectively.

Many trees host various species of parasitic mistletoes. True mistletoes are large evergreen plants that invade the xylem of hardwoods trees, absorbing water and minerals through haustoria. In North America, true mistletoes, **Phoradendron** species, exist mostly in the South. The name comes from the Greek for "tree thief." In Europe, true mistletoes are classified in the genus **Viscum**. Like **Rafflesia**, all mistletoes are dioecious. Female mistletoe plants produce white berries that attract birds, which aid in seed dispersal.

Mistletoes have fascinated people for many centuries. Their ability to stay green in winter and their seemingly magical ability to live without roots on trees, never touching the ground, led ancient people to believe they were divine gifts, perhaps created by thunderbolts. Mistletoe had an important place in many ancient religious rituals among tree worshippers of western Europe, including the Celtic Druids and early Scandinavians and Germans. Ceremonies of both the summer and winter solstice holidays frequently involved the harvest of mistletoes. Druid priests cut the mistletoe with a golden sickle onto a white cloth to prevent the plant from touching the ground. Mistletoe harvest was also part of Norse ceremonies involving Balder, the son of Odin. Because of its role as a parasite of the all-powerful oak, mistletoe became a symbolic source of protective and medicinal powers. The burning of oak logs, human sacrifice, and the harvest of mistletoe were intertwining solstice ceremonies. Mistletoe was brought into houses for protection, and enemies would hug beneath the mistletoe to make a truce. The Christmas custom of hanging mistletoe and kissing under it probably originated in these ancient practices.

![Mistletoe Diagram](image_url)

**Fig. 11-22.** Mistletoes, dioecious plant parasites. **Left**, true mistletoes, **Phoradendron** species, infect hardwood trees and are found in the southern half of the United States. **Right**, dwarf mistletoes, **Arceuthobium** species, infect conifers and are found in the range indicated on the map, primarily the western states, the Great Lakes region, and northern New England.
Another type of mistletoe is an important parasite of conifers. The dwarf mistletoes, *Arceuthobium* species, grow up to several inches tall and invade both the xylem and phloem of host trees. They produce tiny sticky seeds that are shot from mature fruits, landing on the needles and twigs of host trees. They germinate there and penetrate, then grow deep into the woody tissues. Conifers heavily infected by dwarf mistletoes become distorted and stunted, resulting in poor-quality timber. Infected trees often develop clusters of branches known as *witches' brooms*. Many modern forestry practices, in particular improved fire control and the reduction of "clear cutting" of timber lands to help prevent soil erosion, have, unfortunately, increased problems due to mistletoes. Fires reduce many parasites and insect pests. Selective cutting and replanting over a period of time provide trees of many ages in the same areas and allow the parasites to flourish. Control of these parasites is very difficult.

Some parasitic plants cause problems in agronomic crops as well. *Dodders*, *Cuscuta* species, parasitize many crops, including clovers, alfalfa, and cranberries. Their common names include strangleweed, pull-down, and devil's hair. Dodder seeds germinate to form rootless shoots that grow upward in search of a host. Once a host plant is contacted, dodder plants sink haustoria into the plant tissue to form both xylem and phloem connections. The tangled yellow strands of dodder reduce the growth of host plants and can make harvest extremely difficult.

A major agricultural pest in many parts of Africa and Asia is witchweed (*Striga* species). These plants get their name because they are root parasites. The aboveground green shoots produce beautiful yellow and red flowers that deceptively mask the deadly parasitism below the ground. Witchweed parasitizes important food crops, including corn, sugarcane, rice, and sorghum. It is a particularly difficult parasite to control because a single plant can produce over 50,000 tiny seeds that can remain viable in soil for up to 20 years. The seeds will not germinate until they detect a chemical

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**Fig. 11-23.** Spruce tree with distorted growth resulting from infection by dwarf mistletoe in northern Michigan.

**Fig. 11-24.** Dodder (*Cuscuta* species) parasitizing cranberries.

**Fig. 11-25.** Diagrammatic view of dodder on a host plant (a). Dodder winds around the host stem as it grows (b), invading with haustoria to absorb water and nutrients from the vascular tissue of the host (c).
stimulus from root exudates of host plants. In recent years, the return of rain to many drought-ridden areas of Africa resulted in the germination of many *Striga* seeds along with those of the food crops. Badly infested fields can lose 90% of the crop to witchweed, which has led to the abandonment of farmlands in areas of the world that can least afford the loss.

Witchweed was accidentally introduced into the United States in 1956. It is under strict quarantine in North and South Carolina, where eradication programs are in progress. The potential ecological range of this important weed parasite includes most of the eastern half of the United States. The most effective means of control involves stimulation of seed germination without allowing the plants to mature and produce new seed. In some cases, sacrificial "trap crops" have been planted to stimulate witchweed seed germination and then plowed under to destroy the parasites before they set seed. Ethylene, the growth hormone that aids in fruit ripening, can be applied to soils to stimulate witchweed seed germination before crops are planted. In the United States, the hope remains that witchweed can be eradicated. In Africa and Asia, it remains a serious agricultural pest for the world’s poorest farmers.

**Selected Readings**


