INTRODUCTION

Many diseases occur on the foliage of trees and include needle casts of conifers and leaf spots, blights, and mildews on hardwoods (Tainter and Baker 1996). Some diseases occur both on the foliage and branches such as anthracnose and rusts. Although rust fungi cause foliage diseases, we will consider them under the separate category of rust diseases in this chapter. Rust fungi can infect the foliage, stems, and branches of trees.

FOLIAGE DISEASES

Foliage diseases of trees are caused primarily by Ascomycetes or Fungi Imperfecti. Injuries to foliage also are caused by abiotic agents such as low and high temperatures and air pollutants, and other biotic agents like viruses, phytoplasmas, bacteria, insects, mites, and nematodes (Agrios 1997). Foliage diseases caused by Oomycetes are almost unknown in temperate forests, and no foliage diseases are caused by Basidiomycetes, except those caused by rust fungi (Manion 1991). Excellent descriptions and photographs of foliage diseases are given in Funk (1985), Sinclair et al. (1987), Skelly et al. (1987), Scharpf (1993), Allen et al. (1996), and Hansen and Lewis (1997).

Fungi growing in or on leaf surfaces are of concern because they reduce plant photosynthesis and growth, and reduce plant vigor making them more susceptible to attack by insects and other fungi. Foliar pathogens are considered to be weak parasites and generally do not kill trees, but can do so under extreme circumstances (Agrios 1997). Foliage diseases on conifers are thought to be more serious than those on hardwoods, although anthracnose diseases result in considerable damage. Damage to conifers is more serious because conifers cannot refoliate like hardwoods, and if they lose several years of foliage, growth can almost cease. The most damaging situations for conifers occur when trees are planted (1) “off site” (wrong...
type of site for species or out of its native range, e.g., radiata pine in New Zealand, Ecuador, or Chile) and (2) in pure, dense stands. Most damage occurs in stands less than 30 years old and in Christmas tree plantations.

Fungi are common on leaf surfaces (the phylloplane). Many are not pathogens, but rather are saprophytes living on leaf exudates and other substances on the leaf surface. There are hundreds of foliage diseases, but most do not cause serious damage (Tainter and Baker 1996). A list of the most serious foliage diseases of hardwoods and conifers is shown in Table 13.1, along with the causal fungi and host species. These diseases have the most potential for defoliation. Some of the fungi involved are very host specific; whereas others have a broad host range. You will note that the disease common names are very descriptive of typical symptoms you see on leaves and needles—for example, leaf and tar spots, shot-holes, blights, anthracnose, needle casts, downy mildews, and sooty molds. A leaf spot is a small lesion on a leaf. Tar spots are similar, but usually larger and dark in color due to the color of the fungi involved, thus resembling tar. Shot-holes occur when small diseased leaf fragments fall out, leaving small holes. A blight is a disease characterized by general and rapid killing of leaves and stems; anthracnose is a term coined in 1876 to describe numerous plant diseases characterized by ugly dark sunken lesions and blisters. Needle casts are characterized by premature shedding of conifer needles. In downy mildews the fungus appears as a downy growth on the lower surface of leaves and stems. A sooty mold involves a sooty coating formed by the dark hyphae of fungi growing on the secretions of leaf-sucking insects (honeydew), such as scale insects and aphids, and is managed by controlling the insects.

Most foliar pathogens parasitize leaves by extracting carbon and nutrients through intracellular haustoria or by the direct penetration of mesophyll and parenchyma cells (Agrios 1997). Haustoria are specialized hyphae of fungi that enter host cells and absorb food. Fungi producing haustoria usually do not kill host cells immediately, whereas those that directly penetrate cells usually cause rapid cell death. The host typically reacts to both types of infections by producing defensive chemicals.

Typical Symptoms

Symptoms vary markedly from simple localized necrotic spots on leaves to total necrosis and shriveling of leaves (Sinclair et al. 1987). Very heavy infections may cause premature defoliation of deciduous hardwoods and production of a second crop in the same growing season. New shoots and foliage may be produced from adventitious buds and sometimes witches’-brooms are formed. Terminal growth reduction and tip dieback may occur. Anthracnose fungi invade the stem as well as the leaves, causing twig death. In conifers premature defoliation and a thin crown are typical symptoms of heavy infection. Fungal fruiting bodies usually are common in necrotic areas and are typically pycnidia. If the leafspot is sharply delimited, dry, and necrotic, it may tend to fall out, causing “shot-holes.” Typical symptoms and signs of hardwood and conifer foliage diseases are shown in Figures 13.1 and 13.2, respectively.
### Table 13.1: Serious Foliage Diseases of Hardwoods and Conifers

<table>
<thead>
<tr>
<th>Common name</th>
<th>Fungal species</th>
<th>Main hosts</th>
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<tbody>
<tr>
<td><strong>Hardwoods</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Septoria leaf spot and canker</td>
<td><em>Septoria musiva</em></td>
<td>Eastern cottonwood, black cottonwood/black poplar hybrids</td>
</tr>
<tr>
<td>Phyllosticta leaf spot</td>
<td><em>Phyllosticta negundinis</em></td>
<td>Maple</td>
</tr>
<tr>
<td></td>
<td><em>P. hamamelidis</em></td>
<td>Witch hazel</td>
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<tr>
<td></td>
<td><em>P. cornicola</em></td>
<td>Dogwood</td>
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<tr>
<td></td>
<td><em>P. platani</em></td>
<td>Sycamore</td>
</tr>
<tr>
<td>Anthracnose</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sycamore</td>
<td><em>Apignomonia venata</em></td>
<td>Sycamore</td>
</tr>
<tr>
<td>Oak</td>
<td><em>A. guercina</em></td>
<td>Oak</td>
</tr>
<tr>
<td>Ash</td>
<td><em>A. errabunda</em></td>
<td>Ash</td>
</tr>
<tr>
<td>Dogwood</td>
<td><em>Discula destructiva</em></td>
<td>Dogwood</td>
</tr>
<tr>
<td>Leaf blister</td>
<td><em>Taphrina caerulescens</em></td>
<td>Red oak</td>
</tr>
<tr>
<td>Powdery mildew</td>
<td><em>Sphaerotheca spp.</em></td>
<td>Oaks, and many other hardwoods</td>
</tr>
<tr>
<td></td>
<td><em>Erysyphe spp.</em></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Podosphaeria spp.</em></td>
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<td></td>
<td><em>Microsphaera spp.</em></td>
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<td></td>
<td><em>Uncinula spp.</em></td>
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<tr>
<td></td>
<td><em>Phyllactina spp.</em></td>
<td></td>
</tr>
<tr>
<td>Sooty molds</td>
<td></td>
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<tr>
<td>Tar spot of maples</td>
<td></td>
<td></td>
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<tr>
<td>Large tar spot</td>
<td><em>Rhytisma acerinum</em></td>
<td>Maples</td>
</tr>
<tr>
<td>Small tar spot</td>
<td><em>R. punctatum</em></td>
<td>Maples</td>
</tr>
<tr>
<td><strong>Conifers</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Brown spot needle blight</td>
<td><em>Mycosphaerella dearnessii</em></td>
<td><em>Pinus echinata</em> and 25 other species</td>
</tr>
<tr>
<td>Elytroderma needle blight</td>
<td><em>Elytroderma deformans</em></td>
<td>Ponderosa and Jeffrey pines</td>
</tr>
<tr>
<td>Larch needle blight</td>
<td><em>Hypodermella laricis</em></td>
<td>Western larch</td>
</tr>
<tr>
<td>Larch needle cast</td>
<td><em>Meria laricis</em></td>
<td>Western and alpine larch, tamarack</td>
</tr>
<tr>
<td>Lophodermium needle cast</td>
<td><em>Lophodermium seditiosum</em></td>
<td><em>Pines</em></td>
</tr>
<tr>
<td>Diplodia tip blight</td>
<td><em>Sphaeropsis sapinea</em></td>
<td>Pines, Douglas-fir rarely</td>
</tr>
<tr>
<td>Dothistroma needle blight (red band needle blight)</td>
<td><em>Mycosphaerella pini</em></td>
<td>Pines (30 species, especially <em>P. radiata</em> and <em>P. nigra</em>), hybrids or varieties</td>
</tr>
<tr>
<td>Rhabdocline needle cast of Douglas-fir</td>
<td><em>Rhabdocline pseudotsugae</em></td>
<td>Douglas-fir</td>
</tr>
<tr>
<td>Swiss needle cast of Douglas-fir</td>
<td><em>Phaeocryptopus gaeumanii</em></td>
<td>Douglas-fir</td>
</tr>
<tr>
<td>Snow blight</td>
<td><em>Phacidium abietis</em></td>
<td>True firs and Douglas-fir</td>
</tr>
<tr>
<td>Snow molds and brown felt blights</td>
<td><em>Herpotrichia coulteri</em></td>
<td>Pines</td>
</tr>
<tr>
<td>Sphaeropsis tip blight</td>
<td><em>H. juniperi</em></td>
<td>Other conifers</td>
</tr>
<tr>
<td>Sphaeropsis tip blight</td>
<td><em>Sphaeropsis sapinea</em></td>
<td>Pines</td>
</tr>
<tr>
<td>Cedar leaf blight</td>
<td><em>Didymascella thujina</em></td>
<td>Cedars and incense-cedars</td>
</tr>
</tbody>
</table>
Foliage diseases caused by fungi can be confused with foliage damage caused by viruses, bacteria, insects, mites, and abiotic causes. Observations on patterns of necrotic tissue usually enables one to tell the cause. Symptoms produced by fungi usually are located randomly on the leaf or in the crown, whereas frost or air pollution injuries are more uniform and the transition from healthy to damaged tissue is more abrupt. Saprophytic fungi may fruit on dead areas resulting from abiotic damage, and this can sometimes confuse the issue. Natural phenomena such as fall coloration and conifer needle drop, especially cedar flagging, are

Figure 13.1
Typical hardwood foliage disease; Phyllosticta leaf spot on red maple.
(Source: From Skelly et al. 1987.)

Figure 13.2
Typical signs and symptoms of a conifer foliage disease caused by Hypodermella laricis on western larch.
sometimes confused with foliage diseases caused by biotic agents (Manion 1991, Tainter and Baker 1996). Insect problems usually are easily identified by distinctive feeding patterns, and the presence of insects, particularly larvae and frass. Mites can cause distinctive morphological and color changes, such as needle curling and chlorosis. Viruses may cause flecking or ring spots and phytoplasmas may induce chlorosis and witches'-brooms. Bacteria may cause leaf spots and blights, such as fire blight of cherry caused by *Erwinia*, and can be isolated on agar media.

The Life Cycle of Foliage Pathogens

The life cycle of many Ascomycete foliage pathogens is remarkably similar (Figure 13.3). Production of ascospores usually occurs in the spring about the time that new foliage is emerging (Agrios 1997). A few fungi produce ascospores in late summer and early fall and the fungi involved infect buds. Conidiospores are produced during the summer growing season; they usually are produced in large numbers and can rapidly spread a new pathogenic strain. Spores alighting on a leaf or needle surface germinate if the environment is favorable and the hyphae either directly penetrate the cuticle and epidermal cells by enzymatic action or physical force or they go through stomates. Many fungi are host specific because the structure and chemical composition of the leaf surface layers varies from host to host, preventing penetration by all but a few fungi.

Foliar pathogens typically overwinter as mycelium in diseased leaves or needles that remain on trees or in dead foliage on the forest floor. Some overwinter as mycelium in infected shoots or buds. Most foliage diseases have both a parasitic and saprophytic phase to their life cycle. In contrast, the mildew fungi are obligate parasites and survive as cleistothecia rather than hyphae in dead host material (Agrios 1997).

Weather conditions are particularly important in the development of foliage diseases, and moist conditions usually are necessary. Moisture is required for ascospore or conidia release as well as for spore germination and infection. Thus foliage diseases are most serious in cool, moist years.

There is some confusion in the naming of foliar pathogens, which sometimes leads to difficulty when teaching students the names of these organisms. Some produce the sexual phase infrequently and are commonly recognized by their conidial stage. Thus they are better known by their anamorph names rather than their teleomorph names. This means the fungus has two names, and classification has been further complicated by the fact that mycologists have changed many of these names over the years. On the other hand, some rarely produce asexual spores and are known only by their sexual or Ascomycete name.

Specific Hardwood Foliage Diseases

**Anthracnose of Sycamores, Oaks, and Other Hardwoods**  
Sycamore anthracnose, caused by *Apiognomonia veneta*, Ascomycota (Pyrenomycetes) or *Discula platani*, Fungi Imperfecti, occurs widely in the United States in forest, park, and street trees (Tainter and Baker 1996). American, Arizona and California sycamores are susceptible; London plane has some resistance, and Oriental and European
Planes are resistant. Typical symptoms include leaf, bud, shoot, and twig blight, defoliation (Figure 13.4), and cankers. Severe infections weaken trees and predispose them to borers and winter injury, resulting in mortality. Oak anthracnose is caused by a different fungus, but symptoms are similar. Black and white oaks are severely infected.

The life cycle of the fungus causing sycamore anthracnose is as follows. Anthracnose is initiated in the spring by ascospores in perithecia and conidia in pycnidia that are produced from overwintering mycelium in infected twigs on the
Mycelium in infected buds will also infect emerging leaves. Secondary infection by conidia also occurs in the summer. The conidial state (acervuli), however, looks different in leaves than cankers. Sycamore anthracnose is very severe in cool-wet weather. If temperatures are above 16° C, shoot blight is slight, but if temperatures for a 2-week period after leaf emergence are below 10° C, shoot blight is severe. The shoot blight stage is not affected by rain, but the leaf blight stage and secondary cycles are favored by moisture since spores are dispersed by both wind and rain.

No control is practiced for forest trees, although wide spacing is recommended in plantations to reduce leaf moisture. Pure stands of sycamore should be avoided. Chemicals are commonly used for control on ornamental and shade trees. Fungicides are applied during bud break and 14 days later. Pruning infected twigs also reduces inoculum, but removal of fallen leaves does little because infection usually is initiated from diseased tissues on the tree. Fertilization to promote shoot growth appears to reduce infection. Resistant trees such as London and Oriental plane or hybrids should be selected for planting in parks and as street trees.

**Dogwood Anthracnose**  Dogwood anthracnose is an important disease of both forest and ornamental species in North America (Tainter and Baker 1996). It was first reported in the 1970s in New England and in the western United States now is widespread (Daughtrey et al. 1996). It increased dramatically in the southeastern
United States from 0.2 million ha in 1988 to 5.1 million ha in 1992, and dogwoods have been eliminated from the understory in some areas. Its origin is unknown, but it was probably introduced on *Cornus kousa*. The major hosts are flowering dogwood (*Cornus florida*) in eastern North America and Pacific dogwood (*Cornus nuttallii*) in western North America, including British Columbia.

The Ascomycete fungus *Discula destructiva* is responsible. There appears to be two types (Type 1 and Type 2). Type 2 may be a different species of *Discula*. Symptoms are similar to sycamore anthracnose with infections first developing on leaves in spring due to spore infection. Bracts also may be infected. The fungus then progresses down the petioles into shoots in winter and eventually produce cankers. A proliferation of epicormic shoots may form on large branches and the stem. Infection of these shoots allows direct entry to the main stem. Twig and branch death is a common symptom.

Again cool, moist conditions favor infection. In the eastern United States, high-hazard sites are close to water, on north-facing slopes, and above 1,000 m in elevation where foggy conditions are common. Control in forest stands usually involves thinning stands to lower the risk of infection. Ornamental dogwoods respond well to cultural treatment including pruning of dead twigs and branches, removal of infected leaves in the fall, mulching, watering (without wetting foliage), and fertilization. Fungicide sprays also can be used as well as resistant species and varieties. *Cornus kousa* is more resistant than *C. florida*.

**Powdery Mildews of Oaks and Other Hardwoods**

Infection by powdery mildew fungi results in a powdery whitish material on the foliage, shoots, flowers, and fruits (Agrios 1997). The mycelium is almost entirely superficial, except for the haustoria in the epidermal cells. Powdery mildews are widely distributed throughout the world and are common and obvious on foliage. They occur on thousands of species of plants and cause considerable economic damage on grapes, cereals, apples, and roses. However, they usually cause little damage on trees except on young sprouts and seedlings in nurseries. Deciduous hardwoods and at least 30 species of oaks are susceptible, but conifers are not susceptible (Tainter and Baker 1996).

Seven genera of fungi are involved—*Erisyphe*, *Phyllactina*, *Microsphaera*, *Podosphaera*, *Sphaerotheca*, *Cystotheca*, and *Uncinula*. All are Pyrenomycetes, and are obligate parasites that form cleistothecia, usually in the late summer and early fall, overwinter and discharge airborne ascospores in the spring. In summer they produce conidia in chains on short conidiophores. Powdery mildew fungi are somewhat less dependent on wet conditions than many other foliage pathogens and are very host specific; one species is narrowly restricted to the female catkins of alder.

*Microsphaera penicillata* and *Cystotheca lanestris* are the most common species on oak. The disease is initiated in spring by ascospores formed in overwintering black cleistothecia on fallen leaves, or by conidia from overwintering mycelium. Hyphae then penetrate the leaf surface and form haustoria in the epidermal and subepidermal cells. Superficial mycelium covers the plant surface,
giving the powdery white or tan appearance. Leaf surfaces may be blistered and distorted. Secondary spread is by conidia in the summer, and high relative humidity and temperatures favor infections. Thus this problem typically is prevalent in greenhouses and nurseries. No control is necessary in forests, but wide spacing helps reduce incidence of powdery mildews. Fungicide dusts and sprays are used on nursery and ornamental trees, and the disease can be successfully controlled even after it is established because of its superficial nature.

**Sooty Molds**  Like powdery mildews, sooty molds are superficial on leaf and bark surfaces and cause little damage to trees, although they are unsightly (Hughes 1976, Tainter and Baker 1996). The associated sap-sucking scale insects and aphids, however, may cause damage and can retard growth and kill small trees. The disease is widespread in North America and commonly occurs mostly on hardwoods and shrubs such as *Camelia*. It also can occur on conifers. A number of genera of Ascomycetes and Fungi Imperfecti are involved (e.g., *Capnodium*, *Leptothyphium*, *Fumago*, *Auerobasidium*, and *Cladosporium*). *Dimerosporidium* and *Adelopus* spp. occur on grand fir; *Dimeriella* and *Capnodium* spp. occur on Douglas-fir and eastern white pine, respectively.

Most sooty mold fungi are saprobes and have black mycelium growing on excrement from aphids and scale insects called *honeydew*. Spores also are usually dark colored. Plant exudates may be the substrate in some cases. Sooty mold fungi appear to be most abundant in mild, moist climates. No control is necessary in the forest, and insecticides are commonly used against aphids or scale insects in ornamental or nursery plants which indirectly controls the fungus.

**Tar Spots of Maples**  Although tar spots are common on maples, they are of little economic importance. *Rhytisma acerinum* causes large tar spot (Figure 13.1); *R. punctatum* causes small tar spot (Sinclair et al. 1987, Tainter and Baker 1996). This disease, when severe, can result in defoliation and is unsightly on shade ornamental and nursery trees. Large tar spot is common on red and silver maples and also occurs on Norway, sycamore, sugar, and bigleaf maples. Small tar spot also occurs on many maples and box elder. Tar spots also occur in madrone, yellow poplar, and willow. No control is practiced in forests. Sanitation, particularly raking of leaves and burning or removal of leaves in the fall, is a good method of control for ornamental trees because the fungus is an obligate parasite and does not produce conidia for secondary infection cycles.

**Leaf Blisters and Other Diseases Caused by Taphrina spp.**  *Taphrina* spp. are obligate parasites and cause hypertrophy in the host (i.e., overgrowth in infected areas), leading to blistering, puckering, and curling (Sinclair et al. 1987). Ascospores are produced in naked asci (no ascoma) on the leaf surface, and because ascospores keep dividing, the asci usually have more than the typical eight spores. Peach leaf curl is an important disease in orchards caused by *Taphrina deformans*. There is a curious disease caused by *Taphrina* on the female catkins of alder, causing the bracts to grow much longer than normal.
Specific Conifer Foliage Diseases

Needle casts or blights are general terms to describe situations where needles are lost, or cast, prematurely (Sinclair et al. 1987, Hansen and Lewis 1997). However, there are some strange situations where needles are kept longer than normal (e.g., on larch). At least 40 species of Ascomycete fungi cause needle casts and blights in North America. They produce apothecia on needle surfaces that are often dark and glossy. If fruiting bodies are elongated, they are called hysterothecia and have special “lip cells” that respond to wet conditions by opening a slit to expose the asci. When the weather is dry, they close again. Some produce pseudothecia in which the asci are formed directly in cavities, such as stomates. Pycnidia are produced by some needle cast fungi. Pines, spruces, firs, larches, cedars, and Douglas-fir all suffer from needle casts. Descriptions of the most common needle cast diseases follow.

Rhabdocline Needle Cast of Douglas-Fir

Rhabdocline needle cast is a problem in Christmas trees and young plantations (Hansen and Lewis 1997). It has severely affected the success of Douglas-fir plantations in Western Europe and occurs wherever exotic plantations of Douglas-fir occur in North America. It is caused by Rhabdocline pseudotsugae, which has subspecies epiphylla, and Rhabdocline weirii, which has subspecies oblonga and ovata. Conidial stages are unknown. Ascospores produced in apothecia are released in spring and infect newly emerging needles. First symptoms occur in autumn as yellow spots or bands. By late winter the yellowing has changed to purple-brown mottling. Rupturing of the epidermis by maturing apothecia then occurs followed by defoliation. Symptoms are shown in Figure 13.5. No control usually is necessary in plantations, but Christmas trees are commonly sprayed with fungicides beginning at budbreak and repeated at 2 to 3-week intervals until shoots and foliage are fully grown.

Swiss Needle Cast of Douglas-Fir

Like Rhabdocline needle cast, Swiss needle cast is a problem in Christmas trees and young plantations (Hansen and Lewis 1997). It was discovered in Switzerland in 1925, giving it the name. It occurs throughout the natural range of Douglas-fir, and wherever it has been planted in

Figure 13.5

Rhabdocline needle cast symptoms caused by Rhabdocline pseudotsugae.
(Source: From Skelly et al. 1987.)
Western Europe, including Scandinavia, in Japan and in New Zealand. It is currently causing extreme defoliation, growth loss, and mortality in young Douglas-fir plantations in north coastal Oregon, where it appears to have increased in recent years for reasons unknown. The disease is caused by *Phaeocryptopus gaeumannii* and only the sexual stage is known. Ascospores are released from stomatal pseudothecia in late spring that infect the newly emerging needles. Cool, wet springs favor development of Swiss needle cast. Appearance of slight yellow-green discoloration at needle tips is the first symptom in the fall, and ventral sootlike bands of stomatal perithecia begin to develop as early as November (Figure 13.6). The time between infection and defoliation is variable.

Forest plantations usually are not treated for this disease, although chemical sprays have been applied in cases of severe defoliation. Losses in Christmas tree plantations are minimized by early detection and fungicide spraying. The first application is typically carried out when new shoots are 1 to 5 cm long. A second spray 2 to 3 weeks later usually is needed and in wet years a third spray may be needed.

**Lophodermium Needle Cast** Lophodermium needle cast has been a problem in pines in Europe for a century, but has been a problem in nurseries in North America only since the mid-1960s (Tainter and Baker 1996, Hansen and Lewis 1997). It has been reported from 27 states in the United States as well as British Columbia, Nova Scotia, and Ontario. The most common mode of long-distance spread is by infected seedlings, and it is a particular problem for the Christmas tree industry. The greatest injury is to red pine and the short-needled varieties of Scots pine, but as many as 26 species and varieties of pines are known to be susceptible.
The perfect stage is *Lophodermium pinastri* and the pycnidial stage is *Leptostroma pinastri*. Ascospores are released from hysterothecia in late summer, but foliage spots are not observed until the following spring. Needles yellow then brown and defoliation results. Other *Lophodermium* spp. attack a variety of other conifers (i.e., true firs, spruces, and cedars).

Cultural methods for management usually are sufficient, but occasionally fungicidal sprays are needed during the spore dispersal period (July–September). Long-leafed varieties of Scots pine should be favored over the more susceptible short-leafed varieties.

**Elytroderma Needle Cast** The major hosts of this disease are ponderosa and Jeffrey pines, but jack, lodgepole, and shortleaf pines also are susceptible (Scharpf 1993). The disease occurs from California to British Columbia and in Arizona and New Mexico with isolated examples in Colorado and Ontario. The fungus involved is *Elytroderma deformans*, and although it produces conidia in pycnidia, this stage has not been named. Airborne ascospores produced in hysterothecia (Figure 13.7) are dispersed in late spring and early summer and infect the new needles. The fungus colonizes the phloem of needles and twigs and infects needles in buds. In May and June pycnidia develop as blisters and during wet weather conidia are exuded in tendrils. As well as causing defoliation, brooming and shoot deformation are common symptoms, and the fungus is unique in that it can persist in tree tissues (Hansen and Lewis 1997). The combined effects of premature defoliation and perennial branch dieback lead to drastic growth reduction and sometimes death, especially when associated with attack by bark beetles. The disease tends to be worse at high elevations and is favored by high stand density. Trees of all ages can be attacked.

Elytroderma needle cast can be managed using silvicultural techniques. Damage can be reduced by maintaining healthy stands through thinning and removal of trees with high crown flagging.

**Dothistroma Needle Blight** This disease, also known as red band needle blight, is a major problem in exotic pine plantations in the northern and southern hemispheres (Hansen and Lewis 1997). In the southern hemisphere it is a major problem in radiata pine plantations, particularly in New Zealand, Chile, and Ecuador. It also occurs in Australia. In the northern hemisphere it is mostly a problem in...
ornamental and Christmas tree plantations, particularly with Austrian pines. About 30 species of two-, three- and five-needle pines have been recorded as hosts (Tainter and Baker 1996), and the fungus was recently reported to be causing mortality of limber pine in Montana (Taylor and Schwandt 1998).

The fungus involved is *Dothistroma septospora*, which is the asexual stage. The perfect stage (*Mycosphaerella pini*) is rarely found. Conidia are produced in acervuli from late spring to early fall and are dispersed by rain splash. Both old and new foliage are susceptible, and dark green bands that develop into brown/reddish bands commonly appear first in early fall. The banding is due to the production of the toxin dothistromin. Distal necrosis of the needles usually is followed by defoliation. Infection is typically most severe in the lower canopy, but the whole crown can be involved. Symptoms are shown in Figure 13.8. In New Zealand young radiata pine plantations are commonly sprayed by crop-dusting aircraft using copper fungicides. Selection of blight-resistant provenances also holds promise in New Zealand.

**Diplodia Tip Blight** This disease, like Dothistroma needle blight, is mostly a problem in exotic plantations of radiata pine and other exotic pines in New Zealand, Australia, South Africa, and Swaziland (Hansen and Lewis 1997). In Swaziland this pathogen causes a root stain disease of stressed loblolly and slash pines. It typically occurs in the northern and southern hemispheres between 40 and 50° north and south latitude, although it has not been reported from Asia. Thirty-three species of pines are known to be hosts and in the northern hemisphere Austrian, ponderosa, red, Scots, and mugo pines are the most important hosts.
The causal fungus is *Sphaeropsis sapinea* (formerly *Diplodia pinea*) the conidial stage. The perfect stage is unknown. Spores are produced in pycnidia in dead shoots or stunted needles from late spring to the end of the growing season and are dispersed primarily in wet weather. Infection occurs through stomates, on developing shoots, and on umbos of second-year cones. New growth is mostly affected, and infected branches can be killed back to the main stem and successive attacks result in dieback of branches and tops. Tip blight usually increases with time and injury tends to be most severe in plantations as they approach 30 years. Wounds are not necessary for entry, but wounding created by hail and spittle bugs favors infections. In New Zealand the fungus enters radiata pine trees through pruning wounds. Fungicidal protection of new shoots during a critical 2-week period after bud break is the principal control. Two applications of protectant or systemic fungicide at 1-week intervals has proven effective. Avoidance of wounds immediately before and during the growing season reduces infection. This is particularly important with Christmas tree shearing.

**Brown Spot Needle Blight** This is the most serious disease of grass-stage longleaf pine in the southeastern United States (Hansen and Lewis 1997). Twenty-five other species of pine in the eastern and midwestern United States, however, are known to be susceptible, and the disease can be important on Christmas trees or in nurseries. It also has been reported from the western United States and Canada.

The pathogen is *Mycosphaerella dearnessii* (*Schirrhia acicola*) and the conidial stage is *Lecanosticta acicola*. Ascospores are wind dispersed from pseudothecia. Conidia are produced from acervuli on dead fallen needles and have rain-splash dispersal. Hyphae from germinating spores penetrate through stomates. In warm areas both types of spores are produced throughout the year during wet periods. Peak sporulation is in late summer in cooler climates. The first symptoms are yellow spots on needles that change to brown bands and distal necrosis. Toward the end of the growing season defoliation begins.

This disease can be controlled in grass-stage plantations of longleaf pine by prescribed winter burning. Fungicidal sprays can be used in nurseries at 10- to 13-day intervals, depending on rain frequency, and root-dip treatment with benomyl before outplanting also gives excellent control. There is also potential for genetic resistance.

**Larch Needle Diseases** Larch needle blight is caused by *Hypodermella laricis*, and it occurs on western and alpine larch as well as tamarack (Hansen and Lewis 1997). Infected needles turn yellow and then red-brown in spring and early summer. Elliptical black spots (hysterothecia) form soon after the needles are killed (Figure 13.2). Diseased needles are retained in the fall after normal needle drop. This is in contrast to larch needle cast (caused by *Meria laricis*) where needles also turn prematurely yellow, but are shed soon after they turn brown. *Meria laricis* appears to attack only western larch. Neither of these diseases kill large trees, but repeated infections can result in growth reductions. Infected nursery seedlings can be killed by *Meria laricis*. The rapid onset of symptoms may resemble frost damage, but no fruiting bodies are formed in frost-damaged trees.
Snow Molds  Snow molds are sometimes called *brown felt blights* (Tainter and Baker 1996). They grow under snow in the spring and cover the needles of seedlings and lower branches of larger trees with a thick brown or black mycelium that can impede photosynthesis. In North America the fungi causing them are *Herpotrichia coulteri* on pines and *H. juniperi* on other conifers. Since these two fungi develop only under snow, they are only in the snow belt at higher elevations. Once foliage extends above the snowpack, snow molds do not develop.

RUSTS

Rusts occur on both hardwood and conifer trees (Ziller 1974, Tainter and Baker 1996). The name “rust” arises because of the rust-colored appearance of one of the spore stages (uredinial stage) in rusts that attack cereal crops, particularly wheat. On a worldwide basis the damage and economic losses caused by cereal rusts are immense and have resulted in the development of an international breeding program to produce crop strains that are rust resistant (Agrios 1997). The name rust now applies to any fungus in the Urediniales of the Basidiomycota.

Not only do rusts cause cankers on the branches and stems of trees, they also occur on leaves and needles and cones. Because of this they are discussed as a separate group of diseases rather than being classed as foliage, canker, or gall diseases. They also are unique in that they are obligate parasites and have an extremely complex life cycle not found in other fungi. The life cycle often involves five spore stages and two different plant hosts. A list of common North America rusts is shown in Table 13.2 including alternate hosts. There are hundreds of species, but only a few cause serious economic damage. The two most damaging rusts in North America are white pine blister rust on five-needle pines (Figure 13.9) and fusiform rust on southern pines (Tainter and Baker 1996) (Figure 13.10). Poplar rust, caused by several species of *Melampsora* (Figure 13.11), has become economically important on hybrid poplars, which now are grown for paper pulp. Another rust of some importance is western gall rust on lodgepole pine in western North America (Figure 13.12).

White pine blister rust was introduced from Europe into eastern North America. It was known to be in the northeastern United States in 1898, but it wasn’t until 1909 that it was first reported on eastern white pine. It was introduced into Vancouver, British Columbia, in 1921 on a shipment of eastern white pine transplants from France. The fungus is native to Asia and now has invaded the range of five-needle pines in North America and is still spreading. The alternate hosts are *Ribes* spp. (currants and gooseberries). This rust is so devastating because there is little resistance in North American five-needle pine populations. It is widespread in the northeastern United States, but it is not as severe as it is in western North America, perhaps because conditions are not moist enough in late summer and fall in the Northeast to promote basidiospore infection. In western North America *C. ribicola* has spread throughout the North Rocky Mountains, the Cascade Range, and the Sierras. There are isolated populations in New Mexico, Nevada, and Utah and it has recently been reported from Colorado.
<table>
<thead>
<tr>
<th>Disease</th>
<th>Pathogen</th>
<th>Aecial host</th>
<th>Telial host</th>
<th>Features</th>
</tr>
</thead>
<tbody>
<tr>
<td>White pine blister rust</td>
<td>Cronartium ribicola</td>
<td>5-needle pines; Ribes spp.</td>
<td></td>
<td>Blisters on branches and stems</td>
</tr>
<tr>
<td>Fusiform rust</td>
<td>Cronartium quercuum f. sp. fusiforme</td>
<td>Pinus elliottii, P. taeda, and other pines</td>
<td>Quercus spp.</td>
<td>Spindle-shaped (fusiform) cankers</td>
</tr>
<tr>
<td>Stalactiform rust</td>
<td>Cronartium coleosporoides</td>
<td>Pinus contorta, other 2- and 3-needle pines</td>
<td>Scrophulariaceae, e.g., Indian paintbrush (west), cow wheat (east)</td>
<td>Cankers long; length/width = 3</td>
</tr>
<tr>
<td>Comandra blister rust</td>
<td>Cronartium comandrae</td>
<td>Pinus ponderosa, P. jeffreyi, P. contorta, P. attenuata</td>
<td>Comandra spp.</td>
<td>In western states; in east length/width = 2–3</td>
</tr>
<tr>
<td>Western gall rust</td>
<td>Endocronartium harknessii</td>
<td>2- and 3-needles pines; Pinus radiata, P. contorta, P. ponderosa</td>
<td>Probably none</td>
<td>Globose galls, yellow/orange</td>
</tr>
<tr>
<td>Eastern gall rust, pine-oak gall rust</td>
<td>Cronartium quercuum f. sp. banksiana and other f. sp.</td>
<td>Pinus banksiana, P. echinata, P. virginiana, and other pines</td>
<td>Many oaks (bur, chestnut, pin, red)</td>
<td>Galls like western gall rust</td>
</tr>
<tr>
<td>Pine needle rust</td>
<td>Coleosporium solidagine</td>
<td>2- and 3-needle pines (P. resinosa, P. banksiana, P. sylvestris)</td>
<td>Goldenrod or aster</td>
<td>Overwinters in needles where it can survive 2–3 years</td>
</tr>
<tr>
<td>Cedar-apple rust</td>
<td>Gymnosprangium juniperi-virginianiae</td>
<td>Apple</td>
<td>Junipers, especially eastern red cedar</td>
<td>No uredinial host; conifer is telial host</td>
</tr>
<tr>
<td>Leaf rust of poplar</td>
<td>Melampsora medusae</td>
<td>Conifers</td>
<td>Poplars</td>
<td>Poplars particularly susceptible; little damage to conifers</td>
</tr>
</tbody>
</table>

*Introduced.
In contrast to *Cronartium ribicola*, *Cronartium quercuum* f. sp. *fusiforme*, the cause of fusiform rust, is a native pathogen, with oak species as alternative hosts (Tainter and Baker 1996). Interestingly, it had little impact before 1930, but is now the most important disease in the southeastern United States. So what happened to make it so important in a region where the fungus had evolved with the hosts? There are a number of reasons related to forest management including (1) fire control—oaks are more sensitive to fire than pine, so fire control has increased the abundance
Figure 13.11
Uredial and telial stages of *Melampsora medusae* on poplar leaves.
(Source: From Skelly et al. 1987.)

Figure 13.12
Galls on lodgepole pine caused by *Endocronartium harknessii*, the cause of western gall rust.
(Source: From Allen et al. 1996.)
of oaks; (2) off-site planting of slash and loblolly pine in areas where resistant longleaf pine used to grow; (3) thinning and fertilization increased growth of southern pines, but made them more susceptible to rust infection; (4) genetically superior trees were selected only for growth, not for rust resistance; (5) seeds from infected trees were used for early plantings; and (6) infected seedlings from nurseries were widely planted.

Poplar rusts also have increased recently due to plantings of fast-growing susceptible hybrid poplars (Populus trichocarpa × P. deltoides) in Oregon, Washington, and British Columbia. The most important species involved are Melampsora medusae f. sp. deltoidae, which is native to eastern North America, and M. laricipopulina, the cause of Eurasian poplar rust, which had not been reported in North America before 1991 (Newcombe and Chastagner 1993). Some hybrid clones are very susceptible and whole plantation blocks have been killed by these fungi. Melampsora medusae f. sp. deltoidae has now spread to southwestern Europe, Australia, New Zealand, Africa, and South America.

Western gall rust, a native disease caused by Endocronartium harknessii, has generally not been a problem in the past. However, with recent intensive management of lodgepole pines, where large areas of young trees are regenerating in inland western North America, young trees have become severely infected. Gall formation severely distorts growth (Figure 13.12), kills branches, and can even kill trees. This disease also can be a problem in forest nurseries (Sutherland et al. 1989).

**Rust Life Cycles**

Rust fungi are obligate parasites (Agrios 1997). They can be long-cycle heteroeous rusts (with two hosts) or short-cycle rusts with only one host (autoecious). White pine blister rust is a typical heteroeous rust, and the life cycle of the causal fungus is illustrated in Figure 13.13. The spore stages are shown in Box 13.1.

Alternate hosts for white pine blister rust are Ribes spp. (currants and gooseberries) (Tainter and Baker 1996). Haploid (1N) basidiospores are produced on a septate basidium on the underside of Ribes spp. leaves. The basidium arises from dikaryotic (N+N) teliospores also on the Ribes leaves. These teliospores function like the hymenium of the Hymenomycetes and do not disperse. Airborne

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**Box 13.1**

**Rust Spores Stages**

<table>
<thead>
<tr>
<th>Spore type</th>
<th>Fruiting structure</th>
<th>Hosts</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spermatia</td>
<td>Spermogonium</td>
<td>Five-needle pines</td>
</tr>
<tr>
<td>Aeciospores</td>
<td>Aecium</td>
<td>Five-needle pines</td>
</tr>
<tr>
<td>Urediniospores</td>
<td>Uredium</td>
<td>Ribes spp.</td>
</tr>
<tr>
<td>Teliospores</td>
<td>Telium</td>
<td>Ribes spp.</td>
</tr>
<tr>
<td>Basidiospores</td>
<td>Basidium</td>
<td>Ribes spp.</td>
</tr>
</tbody>
</table>
Basidiospores are dispersed at night in late summer or early fall and travel only short distances, usually less than a few kilometers, before they land on their pine hosts. The hyaline basidiospores are very sensitive to UV radiation and do not survive during the day. If basidiospores land on the needles of five-needle pines (e.g., *P. albicaulis*, *P. flexilis*, *P. lambertiana*, *P. monticola*, and *P. strobus*), they...
germinate if the local environment is favorable (cool temperatures and high needle surface moisture), and penetrate the needle surface through stomates. A small yellow or orange fleck develops at the infection site within a few weeks. The hyphae then move down the needle to the branch or stem by the following spring. In the cambium region, hyphae penetrate between the cells of the host and derive nutrients through haustoria.

Cankers begin to develop on infected branches or stems and in 1 year spermogonia (pycnia) are produced. In the spermogonia haploid spores known as spermia are produced in a sweet liquid and moved about by insects. They do not infect plant tissue, but function to exchange genetic material. Insects attracted by the sweet exudate move spermia from one spermogonium to another. Compatible spermia fuse with specialized hyphae in the spermogonium and transfer a nucleus so that the fungus thallus then has dikaryotic \((N+N)\) nuclei. One year later in the spring aeciospores formed in aecia are produced from the dikaryotic hyphae where the spermogonia were. They become airborne and can travel as far as 1,300 km to infect Ribes leaves. These spores germinate and then produce urediniospores from uredinia that form on the undersurface of Ribes leaves. Urediniospores generally travel only short distances. In the fall telial columns and basidiospores are formed once again. Depending on location and weather conditions, it can take 2 to 3 years to go through the cycle.

*Cronartium quercuum* f. sp. *fusiforme* on southern pines has a similar life cycle, but the alternate hosts are oaks and the life cycle usually is 1 year or less, because of the warmer environment (Tainter and Baker 1996). Telia are produced on oak leaves in spring not long after infection by aeciospores. They can produce basidiospores and go back to pines before June. Thus uredinia play a smaller role in the life cycle than they do for white pine blister rust, since there is little buildup of inoculum on oak before telia are produced. The life cycle of the poplar rust fungus (Figure 13.14) is interesting because the telial hosts are poplars, and conifers, such as larch and Douglas-fir, are the aecial hosts. A typical short cycle rust is western gall rust caused by *Endocronartium harknessii* (Tainter and Baker 1996). There appears to be no telial host and aeciospores can infect pines directly. It forms globose galls on two- and three-needle pines, especially on lodgepole pine.

The complexity of the rust life cycle must have required a long evolutionary process. Neither the fungus nor the host could gain a strong advantage over the other for any length of time, so that the relationship is for the most part in balance. Why then do rusts cause some of the major forest diseases? The balance is tipped in favor of the fungus when (1) the fungus is introduced into an area where host plants have not evolved a genetic tolerance, (2) cultural practices in forestry and agriculture reduce genetic diversity, and (3) intensive forestry practices increase the incidence of native rust diseases by upsetting ecological balances.

Management of Rust Diseases
A number of strategies can be used to manage rust diseases, including (1) quarantine, (2) genetic resistance, (3) identification of high-hazard areas, (4) correct nursery practices, (5) management of the alternate host, (6) thinning and pruning,
and (7) fungicides (Tainter and Baker 1996, Maloy 1997). Had quarantine been practiced in the early 1900s, white pine blister rust probably would not have spread so easily. The important quarantine principle now is to ensure that seedlings infected with rusts are not transported to the field. Genetic resistance has shown a lot of promise and has been used successfully for fusiform rust in southern pines, where resistance genes have been incorporated without losing growth gains (Wilcox et al. 1996). Resistant western white pine seedlings now can be purchased, but resistant seedlings of eastern white pine are still not available. The use of resistant clones is particularly important with poplar rusts. However, it must be recognized that breeding programs tend to reduce genetic diversity, a value that is important in modern-day forestry.

Understanding the life cycle and spread mechanisms of *Cornartium ribicola* has been important in implementing silvicultural management strategies. Knowledge of overstory conditions, site characteristics, and topography are particularly

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**Figure 13.14**

Life cycle of *Melampsora medusae*, cause of poplar rust.
important in eastern North America. Early work in the Lake states identified high-

hazard areas on the landscape where planting of white pine should be avoided. Air-

borne basidiospores from *Ribes* plants reach and infect pine needles only near the
tops of hills between lakes because of local airflow circulations on cool nights in

autumn. Basidiospores released from understory *Ribes* plants are embedded in
downslope cold airflows that rise once they reach the lake surface and return to the

land at higher elevations where they are impacted on pine needles (VanArsdel 1967).

Infection of seedlings in nurseries also can be reduced by removing the alternate

hosts near nurseries to prevent spread of basidiospores. This works well with

fusiform rusts and oaks because spread from oak to oak by urediniospores is rel-

atively small. However, it is more difficult to accomplish with white pine blister

rust and *Ribes*. The decades spent from the 1930s to the 1960s trying to “grub”

out or chemically control *Ribes* in the western states generally failed. However,

there is evidence of success of *Ribes* removal in the eastern states. It also is impos-

sible to remove all the larch, Douglas-fir, and hemlock in coastal western North

America to protect poplars from rust.

Thinning and pruning can be used effectively for rust control. Thinning

removes infected trees and creates conditions that may be less favorable for

basidiospore infection. Pruning of infected lower branches to manage white pine

blister rust has been effective in western Washington and Idaho. Fungicides are
generally not very effective and are usually restricted. However, benlate can be

used, particularly in high-value urban areas, and there is potential for fungicide

control in nurseries.

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