serious threat in pine forests in European countries, because Scots pine (*P. sylvestris*) and maritime pine (*P. pinaster*) are very susceptible to it.

See also: **Pathology**: Insect Associated Tree Diseases; Vascular Wilt Diseases.

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Leaf and Needle Diseases

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Overview of Foliage Diseases

Foliage diseases of forest trees can be caused by a variety of biotic agents: fungi, bacteria, algae, phytoplasmas, and viruses, as well as abiotic agents such as air pollutants, chemical deposition (e.g., salt injury, acid precipitation), thermal injury, and nutritional deficiencies, both individually and in combinations. Recognition of the primary cause of diseased plants is often a difficult puzzle for the diagnostician, who must consider interactions between host plant, pathogens, environmental conditions, and management history to determine accurately the underlying cause of a foliar disorder. Often, unhealthy-looking foliage may actually indicate a root or stem disease problem.

Foliage diseases affect trees in nurseries and greenhouses, forest plantations, and urban and natural forests worldwide. Foliage pathogens, like their hosts, can occur either as natural components of a forest ecosystem or as exotics introduced through human activity. Exotic pathogens on endemic hosts, and endemic pathogens on exotic hosts, are often more destructive because host plants have no coevolved resistance to the pathogens. Diseases affecting trees in managed situations, such as nurseries and plantations, tend to be more uniformly distributed than in natural forests. Uniform host populations (with respect to species, clone, and age), i.e., monocultures, are more prone to damaging epidemics than plantations and forests managed for genetic diversity.

The inventory of pathogens that pose a threat to forest health is constantly expanding. The lists of forest foliage pests given below are a necessarily selective attempt to enumerate the most common and important foliage pathogens and their current known distributions, recognizing that forest pathogens and pests are constantly changing. New pest organisms are continually being discovered and described. Probably fewer than 20% of the pathogens that pose a threat to forest health have been recognized. Very little information is available on foliage diseases of several important forest trees such as dipterocarps, *Metrosideros*, and *Nothofagus*. Biological evolution continues to shape the interactions between plants and pathogens, as evidenced by development of pesticide resistance and the emergence of aggressive strains and races in pathogen species. Interspecific hybridization and resultant changes in host range have been documented for *Melampsora* and *Phytophthora* pathogens affecting forest trees. Despite international phytosanitary regulation, international trade involving plant and forest products continues to provide an avenue for introduction of insects and pathogens to new hosts and environments. The changing state of scientific knowledge also affects our understanding of pathogen distribution and importance. As increasingly powerful methods of population genetic analysis are applied to the study of forest pathogens, a more detailed picture of the dynamics in pathogen populations and species is revealed.

Diseases Caused by Fungi (Including Oomycetes)

Fungi are eukaryotic, heterotrophic microbes in the kingdom Fungi that occur either as single-celled (yeast) or filamentous forms. The filamentous fungi have evolved a variety of structural adaptations to penetrate directly and colonize plant tissues and cells to establish parasitic relationships. Fungal pathogens can also invade host tissue through wounds caused by breakage, insect feeding and freezing injury. Symptoms caused by fungal foliar pathogens can vary in severity from severe defoliation to inconspicuous leaf spots. Many have prolonged (1 year or more) incubation periods during which infected foliage remains symptomless. Symptoms of fungal foliage diseases include leaf spots, leaf blotch, scorch, anthracnose, needle blights, and needle casts. Typically, the presence of a fungal pathogen is indicated by minute fruiting structures characteristic of the pathogen species or taxonomic group.

Fungal foliage diseases rarely cause death of mature trees, although they can be responsible for serious economic losses due to decreased growth yield. Chronic fungal foliage diseases can weaken or stress trees so that affected hosts are outcompeted by other species, or are predisposed to attack by secondary agents such as bark beetles or opportunistic root diseases. Control of fungal diseases in forest plantations by protectant fungicides is feasible for certain pathogens and hosts. Successful control depends on timing of applications to coincide with optimum periods of pathogen sporulation and host susceptibility. Specific recommendations for control depend on approved materials, pathogen, tree crop, and local conditions, and are available from local pest management agencies. Judicious selection of planting stock and careful sanitation, where practicable, are often effective means of controlling fungal foliage diseases. The greatest diversity of fungal foliar pathogens of woody hosts are ascomycetes (phylum Ascomycota) and basidiomycetous rusts (Uredinales) (*see* **Pathology**: Rust Diseases).

Oomycetes

Because of their filamentous habit, parasitic oomycetes (kingdom Stramenopila) traditionally have been considered together with fungal pathogens, although they are more closely related to chrysophyte algae. Relatively few oomycetes are associated with foliage diseases of trees; those that cause tree diseases mainly attack roots. However, recent discoveries of foliage-inhabiting *Phytophthora* species, several as yet unnamed, suggest that foliar *Phytophthora* of woody hosts may be much more widespread than previously thought. *Phytophthora ramorum*, the causal agent of sudden oak death in the western USA, also infects foliage of species of *Acer*, *Lithocarpus*, *Quercus*, *Umbellularia*, and several other unrelated hosts, such as *Pseudotsuga*, and causes symptoms ranging from leaf spots and marginal necrosis to shoot blight and dieback. Other *Phytophthora* foliage pathogens include *P. palmivora*, which causes bud rot of coconut palm (*Cocos nucifera*) and other hosts throughout the tropics and subtropics. Littleleaf disease, caused by a suite of factors including the oomycete pathogen *P. cinnamomi*, affects short-leaf pine (*Pinus echinata*) in the southern Appalachians of eastern North America. Although *Phytophthora cinnamomi* infects rootlets, the primary symptoms are initially chlorotic, stunted foliage, and a progressively thinning crown.

Diseases of Conifers

Needle casts Foliage diseases of coniferous trees are usually categorized either as needle cast diseases, where affected needles are prematurely abscised, or needle blights, where needles are abruptly killed and typically remain attached. Needle cast pathogens generally have longer periods of development than those causing needle blights. Typical needle cast pathogens infect newly emerging foliage and complete their development to produce infective ascospores the following spring. An exception is the larch needle cast pathogen *Meria laricis*, which infects needles and sporulates in the same growing season. Needle blights typically attack and kill foliage and sporulate in a period of a few weeks. Important needle cast diseases are *Lophodermella*, *Cyclaneusma* and *Elytroderma* needle casts of pine, *Rhabdocline* and Swiss needle casts of Douglas-fir (*Pseudotsuga menziesii*), *Lirula* needle cast of spruce (*Picea* spp.), and *Meria* needle cast of larch (*Larix* spp.).

Pinus radiata is planted widely in forest plantations and hence *Cyclaneusma* needle cast is probably one of the most significant needle cast diseases worldwide. *Cyclaneusma minus* causes severe damage to *P. patula*, *P. ponderosa* and *P. radiata*, and *C. niveum* affects *P. nigra* and *P. pinaster* plantations in Europe, North America, South America, New Zealand, and southern Africa. *Elytroderma* needle cast of pines is unique in that the pathogen invades shoot tissue, causing hypertrophy and deformation, often killing branches. Although most damaging to young trees, *Elytroderma* needle cast can cause severe growth losses in medium-aged and mature stands, and can predispose mature trees to attack by insects and root diseases. *Elytroderma deformans* is a serious pathogen of *P. ponderosa* in western North America, and *E. torres-juanii* affects *P. brutia* in Greece, *P. halapensis* and *P. uncinata* in Spain, and *P. pinea* in Portugal.

Swiss needle cast of Douglas-fir, caused by *Phaeocryptopus gaeumannii*, is ubiquitous wherever Douglas-fir is grown worldwide, but generally is more destructive on trees grown outside their native range of western North America, and is more damaging on the interior (var. *glauca*) variety of Douglas-fir. The pathogen was first noticed on diseased Douglas-fir in plantations in Switzerland but later shown to be widespread throughout the natural range of Douglas-fir in western North America, where it is presumed native. Serious outbreaks of Swiss needle cast have occurred in Europe, New Zealand, and coastal Oregon; however in most of western North America the disease has negligible effects. *Rhabdocline* needle cast, caused by *R. pseudotsugae* and *R. weirii*, can cause severe defoliation of Douglas-fir, particularly on the interior form (*Pseudotsuga menziesii* var. *glauca*) in the Rocky Mountain region of western North America and in other regions where it has been planted as an exotic. The related asexual fungus *Meria laricis* is the cause of larch needle cast in western North America, northern Europe, and Siberia.

Lophodermella needle casts caused by *L. concolor* and *L. montivaga* affect *Pinus attenuata*, *P. contorta*, and *P. banksiana* in North America. In severe years entire hillsides of affected stands can aquire a reddish color due to the effect of these pathogens. Repeated years of severe defoliation can weaken trees, leading to mortality through attack by bark beetles and root pathogens. Tar spot needle cast is the most common needle cast of soft pines, mainly *P. strobus*, in northeastern North America. It is readily identified by the shiny black raised ascomata on the undersides of necrotic needles. *Ploioderma lethale* is the most damaging needle cast of hard pines (mainly *Pinus clausa*, *P. echinata*, and *P. elliottii*) in the southeastern USA.

The small (2–3 mm) but conspicuous gray to black, raised, elliptical fruiting bodies of several species of *Lophodermium* are very common on fallen needles of many species of pines, but most are considered harmless. One species however, *L. seditiosum*, is considered a serious pathogen causing *Lophodermium* needle cast. *Lophodermium* needle cast affects several species of pines, especially *P. sylvestris* in Europe and *P. resinosa* in North America. Attack by *L. seditiosum* kills young needles, and in nurseries and on young trees defoliation by this pathogen can be fatal.

Needle blights Important needle blights of conifers include *Dothistroma*, *Diplodia*, and brown spot needle blights of pine. *Dothistroma* blight, caused by *Mycosphaerella pini* (anamorph *D. septospora*), affects several important pine species, including *P. contorta*, *P. nigra*, *P. ponderosa*, and *P. radiata*, and has been especially damaging in *P. radiata* plantations in South America, southern Africa, and New Zealand. The disease has also recently caused severe losses in lodgepole pine (*P. contorta*) in northwestern British Columbia. Often a reddish band appears between the killed tips of needles and the green base and this is diagnostic for *M. pini*. *Sphaeropsis sapinea* (=*Diplodia pinea*) causes a needle blight and shoot dieback of many species of pine worldwide, notably *P. nigra*, *P. pinea*, *P. sylvestris* in Europe; *P. patula*, *P. pinaster*, *P. radiata* in southern Africa, where it has mainly been associated with hail damage; *P. nigra*, *P. palustris*, *P. ponderosa,* and several other pine species in New Zealand; *P. greggii*, *P. elliotii*, and *P. patula*, in Brazil; *P. canariensis*, *P. radiata*, and *P. sylvestris* in Argentina; several pine species in North America including *P. nigra*, *P. ponderosa*, *P. resinosa*, and *P. strobus*; *P. canariensis*, *P. elliotii*, *P. pinaster*, and *P. roxburghii*, in Australia; and *P. luchuensis* in Taiwan. Other hosts affected by *S. sapinea* include *Abies*, *Cedrus*, *Chamaecyparis*, *Juniperus* and *Pseudotsuga*. In addition to the needle blight and shoot dieback, *S. sapinea* also causes stem cankers and root disease in several pine species.

Other significant foliage blights include *Gleosporidina cryptomeriae* and *Cercospora sequioiae* which cause twig blight of *Cryptomeria japonica* in plantations in Japan and Brazil. Brown needle disease of pines, caused by *Cercoseptoria pini-densiflorae*, affects several species of pines including *P. pinaster* and *P. radiata* and can be particularly destructive to nursery stock. Young plantations and seedlings in nurseries are most severely affected. *Hypodermella laricis* causes a severe needle blight of larch and is distributed throughout the northern hemisphere. Tip blight and shoot dieback caused by *Kabatina juniperi* affect several Cupressaceae in North America and Europe.

Bud blights of conifers are caused by several pathogens. *Gemmamyces piceae* kills buds and causes abnormally twisted shoots of *Abies alba*, *Picea abies*, and *P. pungens* in Europe. In North America, severe bud and shoot blights of *P. englemanii*, *P. glauca*, *P. sitchensis* and *Pseudotsuga menziesii*, are caused by *Dichomera gemmicola* and buds of *Abies lasiocarpa*, and *P. glauca* by *Camarosporium strobilinum*. *Sirococcus conigenus* also causes shoot dieback of several conifer species, including *Picea sitchensis*, *Pinus resinosa*, *Pseudotsuga menziesii*, and *Tsuga heterophylla*, and can be particularly damaging to seedlings in nurseries. Shoot dieback of several conifer species, especially Douglas-fir, caused by *Botrytis cinerea* is most commonly associated with succulent young shoots damaged by late spring frost.

Felt blights and snow molds are diseases of alpine and boreal conifer foliage that is covered by snow for extended periods, typically affecting young trees and the lower branches of mature trees. The pathogens in the genera *Herpotrichia* and *Neopeckia* rapidly colonize snow-covered foliage in a distinctive wooly felt that binds needles together, initially gray and becoming brown as the foliage is exposed. The masses of brown felt mycelia are persistent and can survive summer desiccation, resuming growth when snow cover returns to cause a perennial blight. *Neopeckia coulteri* affects pines; *Herpotrichia juniperi* and *H. parasitica* affect various Pinaceae and Cupressaceae in North America and Europe, respectively. Snow molds (snow blights) similarly attack snow-covered foliage, but mycelia of these pathogens are evanescent, not persisting as felt mats after snowmelt. Several genetic variants of *Phacidium infestans* are recognized; var. *infestans* occurs on species of *Abies*, *Juniperus*, *Picea* and *Pinus*, throughout boreal Eurasia, mainly attacking *Pinus sylvestris*; a southern race mainly affects *P. cembra* in the Alps. Several different snow blight fungi attack conifers in North America. *Phacidium abietis* and *Sarcotrochila balsameae* are snow blight pathogens affecting *Abies* in western North America, *Hemiphacidium planum* attacks pines in the southern Rocky Mountains, and *S. piniperda* spruce, mainly in northeastern North America. Symptoms of snow blight are a progressive discoloration, eventually becoming gray-brown, with the dead needles remaining attached until the following year.

Diseases of Broadleaved Hosts

There is a bewildering diversity of foliage parasites of broadleaved woody hosts worldwide, the majority of which are ascomycetes or asexual states. Many occur as inconspicuous leaf spots and cause negligible injury to their hosts. Other than rusts, there are very few basidiomycetous foliar pathogens. One exception is *Chondrostereum purpureum*, which is primarily a sapwood rot, but basidiospores from nearby sporocarps are able to infect leaves of several broadleaved trees, causing a typical 'silver leaf' symptom due to the formation of air spaces between epidermal and palisade tissues. Silver leaf disease can be damaging to fruit orchards, but also occurs on maple, birch, willow, and *Eucalyptus* species.

Powdery mildew diseases are caused by fungi in the Erysiphaceae, which are specialized, host-specific ectoparasites of foliage of many plants, including broadleaved woody hosts. The mycelia of powdery mildews grow over the leaf surface, often appearing cottony, with intermittent penetration of epidermal cells by haustoria, specialized feeding structures by which nutrients are translocated from the host leaf to the superficial mycelia. The name derives from the masses of asexual spores (conidia) which can give the appearance of dusty patches on leaves. Important powdery mildews of forest trees include *Uncinula* species on maples and *Microsphaera* and *Sphaerotheca* species on oaks. In Europe, *M. alphitoides* causes death of leaves and shoot deformation of *Quercus petraea* and *Q. robur*, and also occurs on several species of oak in North America. Species in the *M. penicillata* complex affect a number of broadleaved host genera including *Acer*, *Betula*, *Carya*, *Castanaea*, *Cornus*, *Corylus*, *Fagus*, *Fraxinus*, and *Platanus*. Although powdery mildew is seldom seriously damaging to mature trees, nursery stock may need to be protected by fungicides.

Taphrina species are yeastlike ascomycetes that form a thin, superficial layer penetrating just the epidermis of leaves of several broadleaved hosts. Like the powdery mildews, *Taphrina* species are specialized, host-specific parasites. *Taphrina* symptoms are typically patchy swelling and gall-like deformations of leaves (leaf blisters), sometimes coalescing and causing 'leaf curl.' *Taphrina* gall of alder (*Alnus* spp.) also causes a hypertrophy in shoots and can be a persistent problem in nurseries, requiring control by fungicides. Other hosts commonly affected by *Taphrina* are *Quercus*, *Populus*, *Prunus*, and *Salix*.

Anthracnose diseases are characterized by sunken, often confluent, necrotic lesions on foliage, and are caused by several genera of ascomycetes, particularly those with acervular asexual states. In general, anthracnose pathogens infect foliage in spring, and more severe symptoms are associated with rain in late spring and early summer. Several anthracnose pathogens initially infect leaves and spread to shoots by hyphal growth, causing dieback. *Glomerella cingulata*, together with its anamorph *Colletotrichum gloeosporioides*, is one of the most widely distributed foliar parasites in temperate and tropical forests worldwide, and one of the most common fungi associated with anthracnose symptoms on numerous broadleaved woody hosts in nurseries, plantations, and forests. Some of the hosts affected by *G. anthracnose* include poplar, cashew, mango, citrus, papaya, *Robinia*, *Hevea*, and many others. *Glomerella anthracnose* has been reported as a particular problem in establishing plantations of *Gmelina arborea* in Malaysia.

Other fungus species associated with anthracnose symptoms include *Apiognomonia errabunda*, *A. tiliae*, *A. veneta*, and *A. quercina*, the causes of beech, lime (*Tilia*), plane (*Platanus*), and oak anthracnoses, respectively, in Europe and North America. *Kabatiella apocrypta* is common on several maple species in North America, causing interveinal necrosis and scorchlike blight of leaves and shoots. In Europe, *K. apocrypta* is associated with necrotic lesions around feeding sites of psyllid larvae on oak leaves. In North America, *A. errabunda* causes a damaging anthracnose of ash that can cause severe defoliation and shoot dieback when spring rain favors heavy infection. Oak anthracnose can also be particularly damaging in years when conditions are conducive to infection. Rain-dispersed spores produced on killed twigs infect emerging leaves and quickly generate more fruiting bodies, multiplying the amount of inoculum during rainy periods. Several oak species are susceptible, but white oak in the northeastern USA and California live oak are the most severely affected by shoot dieback and foliage blight from this disease. *Discula destructiva*, the cause of dogwood anthracnose in the USA, apparently was introduced almost simultaneously in the 1970s from an unknown source to both the eastern and northwestern USA, where it has spread rapidly, attacking the native species *Cornus florida* and *C. nuttallii*.

Tar spots of maple and willows are conspicuous, black, disk-like, 1–2 cm diameter spots, caused by *Rhytisma* spp. The tar spots are fungal stromata that complete their maturation during the winter and spring after leaves are abcised. Ascospores are released in the spring, coinciding with the emergence of new foliage.

A number of serious foliage diseases of broad-leaved forest trees are associated with species classified in *Mycosphaerella*, or in the several genera of asexual states connected to it. *Septoria, Cercospora, Coniothyrium, Dothistroma, Lecanosticta, Ramularia*, and several other form-genera are used for different asexual forms of *Mycosphaerella*. A large number of *Mycosphaerella* species are associated with leaf spots of *Eucalyptus*. A recent monograph lists 55 *Mycosphaerella* species that cause leaf diseases of *Eucalyptus* worldwide, many of which are host-limited and cause injury only to certain species or hybrid clones. For example, *Mycosphaerella* leaf blotch disease has been shown to cause growth reduction in *E. nitens*, and also has been particularly damaging to *E. globulus* in South Africa and Australia. *Ramularia* shoot blight, caused by the fungus *Ramularia* (= *Quambalaria*) *pitereka*, causes a severe leaf and shoot blight of several of the *Eucalyptus* subgenus *Corymbia* species in eastern Australia.

Since *Eucalyptus* species are some of the most widely planted forest crops in Asia, Australia, South Africa, and South America, their pathogens are economically important. The emergence of specialized foliage pathogens on certain species and clones in plantations has forced changes in selection of *Eucalyptus* species in several regions where the diseases occur. The susceptibility of *E. globulus* to the leaf spot pathogen *M. nubilosa*, considered one of the most important leaf pathogens in South Africa, caused the planting of this species to be abandoned in parts of South Africa. *Phaeoseptoria eucalytpti* causes severe defoliation of lower branches and is particularly damaging to certain clones of *E. grandis*. It can also cause severe damage to seedlings in nurseries and hedges used for clonal propagation. *Eucalyptus* leaf and shoot blight caused by *Cryptosporiopsis eucalypti* is particularly damaging to *E. camaldulensis* in nurseries and plantations in Southeast Asia. An undescribed species of *Gleosporidina* has recently been reported associated with leaf lesions and shoot dieback of *E. nitens* and *E. globulus* in Tasmania, but apparently is infrequent.

Wattle (*Acacia* spp.), particularly black wattle (*Acacia mearnsii*), also has been planted in many parts of the world outside its native range in Australia, including India, Sri Lanka, and South Africa, and has led to the appearance of new pathogens of this host. Foliage pathogens of wattle include *Calonectria indusiata*, which caused complete defoliation of trees in parts of India and Sri Lanka. *Glomerella acaciae* is the cause of *Acacia anthracnose* in Japan.

Several important foliage diseases affect species of poplars (*Populus* spp.) and their hybrids grown for fiber. *Melampsora* rusts are probably the most significant foliage pathogens of poplars. Leaf and shoot blight caused by *Venturia macularis* on *P. tremuloides* and *V. populina* on *P. trichocarpa* can be particularly damaging in years with favorable mild wet weather in spring. Certain hybrid clones are resistant. Symptoms include discolored, blighted foliage and a characteristic blackened shoot dieback. *Septoria populicola* causes a severe leaf spot and defoliation of *P. deltoides* and susceptible hybrids in western North America. In eastern North America, *S. musiva* also causes severe leaf spots as well as cankers. The related *Venturia saliciperda* causes a similar dieback of willow, often in association with *Glomerella miyabeana*. *Linospora* leaf blight caused by *L. tetrasperma* affects *P. balsamifera* and *P. deltoides* as well as several hybrids, occurring across northern North America from eastern Canada to the Pacific Northwest. *Linospora* blight tends to be local in occurrence, but damage can be heavy in years when wet spring weather favors infection. Species of *Marsonnina* cause leaf spots and blights of several broadleaved woody hosts. The species *M. brunnea*, *M. castagnei*, and *M. populi* are particularly important as forest pests of *Populus* plantations worldwide, causing defoliation and dieback of several poplar species and hybrids. Subspecies and pathovars of *M. brunnea* differing in pathogenicity to different hosts are recognized.

Diseases Caused by Bacteria

Bacteria are single-celled microscopic prokaryotes of the kingdom Eubacteria. Unable to penetrate plants on their own, bacteria require natural openings such as lenticels, stomata, hydathodes, and leaf scars; or wounds due to events such as pruning, breakage, herbivory, or insects. Local dispersal of bacteria from an infected tree occurs via water splash, wind, insects, and rubbing together of infected and healthy foliage. Long-distance dispersal is primarily through transport of infected material such as seed, stools, and cuttings.

Although bacterial pathogens are widespread, information on bacterial diseases of forest trees is limited. In general, bacterial diseases of trees in mixed-forest systems (not trees isolated in landscapes, in fringes around cities, or in forest nurseries) are minor, often because they occur in low incidence or in more severe but sporadic outbreaks, during which they can cause heavy losses locally. The most serious losses occur in monoculture of same-age plantings, especially when derived from a single clone, or when the trees are exotic to the area.

Symptoms caused by bacteria on foliage range from small round leaf spots from which the tissue drops out, leaving a hole (shothole leaf spots); angular, water-soaked leaf spots; whole leaf blight; leaf scorch; and chlorosis or reddening of leaves, often associated with lesions or marginal necrosis. Bacteria can also cause blighting of small twigs or whole branches; cankers of twigs, branches and main stems; galls of branches, stems, or roots; vascular plugging leading to wilting; and death. Leaf spots and blights, occasionally leading to blighting and dieback of small twigs, are often caused by bacteria of the genera *Pseudomonas*, *Xanthomonas*, and *Erwinia*. Such blights are often limited to the current year's growth, and, in the case of *Pseudomonas syringae*, disease often follows cold injury. For this reason, leaf spots, leaf blight, and twig dieback are of minor significance, since complete defoliation is rare. Some bacteria can cause dieback of older branches, or, by infecting the trunk and causing large cankers, have a greater impact. This includes bacteria such as *Erwinia amylovora* (cause of fire blight), *Xanthomonas campestris* pv. *populi*, and some species of *Pseudomonas* on particularly susceptible hosts. Vascular diseases are caused by the xylem-inhabiting *Xylella fastidiosa* and *Ralstonia solanacearum* (= *Pseudomonas solanacearum*) and, by their systemic nature, can cause either rapid death or chronic stress via impedance of water movement throughout the canopy, rendering the tree more susceptible to additional stresses.

Specific bacterial pathogens of forest trees include *P. syringae* and its pathovars which affect a wide range of broadleaved hosts worldwide, including *Acer, Fraxinus, Populus, Quercus*, and *Salix*. *Ralstonia solanacearum* also affects a variety of hosts, primarily with tropical and southern distributions (China, South America, Australia, southern Africa) including *Acacia*, *Casuarina*, and *Eucalyptus*. Xanthomonads occur on both tropical and temperate woody hosts. *Xanthomonas populi* is widely distributed throughout Europe and causes a serious disease of *Populus* species and hybrids, resulting in blighted buds and shoots and the formation of persistent cankers. *Xylella fastidiosa*, a xylem-limited bacterium which causes Pierce's disease of cultivated grapes, causes leaf scorch and may contribute to a general decline in *Acer*, *Aesculus*, *Fraxinus*, *Platanus*, *Quercus*, and *Ulmus* in North America. Bacterial wilt of bamboo caused by *Erwinia sinocalami* has been reported from Fujian and Taiwan.

In situations where bacterial diseases require control, copper sprays and the antibiotics streptomycin and tetracycline have been used with varying success on cultivated trees with fire blight, but use in situations other than nurseries is extremely rare. Tetracycline is not as effective as streptomycin, and bacterial populations can become resistant to both streptomycin and copper. The loss of efficacy of these chemicals makes it imperative that sanitation measures be carried out, and sanitation is often the only option in situations where the trees are outside a nursery setting. This includes cutting and destroying affected limbs (with nonvascular diseases) or entire trees, establishing quarantines, clonally propagating from disease-free material, and preventing the reintroduction of the pathogen.

Diseases Caused by Phytoplasmas

Phytoplasma is the name given to microscopic, plant pathogenic, cell wall-less prokaryotes of the class Mollicutes that were formerly known as mycoplasma-like organisms or MLOs. Phytoplasmas are obligate parasites and have not been grown in axenic culture. Because of this, they have not been fully characterized and their pathogenic nature has not classically been confirmed, although it is assumed. Until the plant-inhabiting pleomorphic mollicutes can be cultivated and characterized apart from their hosts, they are provisionally classified as *Candidatus* Phytoplasma, with species delineated by genome size and phylogeny as inferred by the nucleic acid sequence of the 16S ribosomal RNA. Phytoplasmas cause 'yellows' diseases (named for the response of infected foliage) and other disorders in over 300 species of plants. Systemic and limited within the plant to the phloem cells, phytoplasmas are vectored by over 100 species of phloem-feeding insects, primarily leaf hoppers, plant hoppers, sharpshooters, and psyllids of the families Cicadellidae, Fulgoroidae, and Psylloidae. Parasitic plants of the genera *Cuscuta* and *Cassytha* may also transmit phytoplasmas.

Symptoms with which phytoplasmas have been associated may include several of the following: leaf stunting (little leaf); pinkish, or more commonly, yellow discoloration of the foliage (yellows); greening of flower petals; precocious or suppressed flowering; precocious shoot growth, proliferation of shoots or branches (witches' brooming); loss of apical dominance of the shoots, leading to deliquescent branching; phloem necrosis; branch dieback; progressive loss of vitality; suppressed root development; wilting; and eventual plant death. Phytoplasmas have also been detected in plants with no apparent symptoms, possibly indicating the existence of tolerance in the asymptomatic plants. Alternatively, it may be that plants with phytoplasmal diseases die due to multiple causes, with the phytoplasma being one of several contributory factors. Virus particles are often found in plants coinfected with phytoplasmas, as are other pathogens and pests.

Phytoplasma-affected plants may not be cured, although symptom remission does occur with treatment by tetracycline antibiotics. For this reason, effective disease management must consist of prevention, such as establishment of quarantines to prevent introduction into a new area, removal and destruction of infected trees, clonal propagation from only healthy trees, vector control, and breeding for genetic resistance.

Phytoplasma diseases are relatively rare in comparison with fungal diseases. Although important in agricultural production, the impact of phytoplasmal diseases in most forest ecologies is rather limited, probably due to the diversity of species present in most forests and the feeding preferences of the vectors. Phytoplasmal diseases will do most damage in situations where monoculture, especially of clonally propagated material, is predominant and where vectors flourish. Some phytoplasma diseases have been extremely important to the local economy, even while they are severely limited in geographic distribution (e.g., sandal spike, which only occurs in southern India). This is in contrast to diseases such as lethal yellowing of coconut, which has spread rapidly throughout the Caribbean, and a related disease of palms found in equatorial Africa, both caused by group IV phytoplasmas. It is difficult to assess the true distribution (and hence impact) of phytoplasmas on forest ecosystems, since many early reports of phytoplasma diseases are based on symptoms which are not exclusive to phytoplasmas. Commonly reported and substantiated (via light or electron microscopy, or molecular analyses) phytoplasma-caused diseases in forest trees include, from the tropics, witches' broom of *Paulownia* spp. in China (16S ribosomal RNA group I) and spike disease of *Santalum album* from India (group I). There are few reports of phytoplasma diseases in Europe, but alder yellows on *Alnus glutinosa* (group V) can cause problems. In North America elm yellows of *Ulmus* spp. (group V) occurs in the USA, whereas witches' broom of *Salix* spp. (group VI) and ash yellows of *Fraxinus* spp. (group VII) are widely distributed in the USA and southern Canada.

Diseases Caused by Viruses

Viruses are submicroscopic agents of disease composed of nucleic acids, either single or double strands of DNA or RNA, encased in a protein coat or capsid. Viruses are transmitted mechanically, by contact of infected plant material with healthy tissues (e.g., root grafts); by insect, fungal, or nematode vectors; by pollen; and via seed. Grafting of diseased material on to healthy trees is a primary means of spreading viruses in cultivated trees, but is less common in forest trees.

The mixed-species composition of most forests is a limiting factor to the impact of viruses in forest ecosystems. Viruses are often implicated in forest declines, in which a majority of trees exhibit poor vigor leading to reduced growth, decline, and eventual death. Although viruses may be detected in trees showing slow growth, poor color, branch dieback, and other nonspecific symptoms of poor performance, trees with these symptoms in the same area may not have any detectable levels of virus. The inconsistent association of virus particles in symptomatic trees has confounded the understanding of forest declines, and the role of viruses in these situations remains in many cases undetermined.

Sources of viruses in forest ecosystems include insect and nematode vectors, infected seed or pollen, forest soils, surface waters, and even fog, as with tomato mosaic tobamovirus in New York state. Many of the viruses documented in forest situations are nepoviruses, tobamoviruses, potexviruses, and ilarviruses. Cherry leaf roll nepovirus has been reported from several forest trees, including species of *Betula*, *Cornus*, *Fagus*, *Fraxinus*, *Juglans*, *Prunus*, and *Ulmus* in Europe and North America. Elm mottle ilarvirus affects *Ulmus* spp. in Europe. Tobacco necrosis necrovirus affects both conifer (*Larix*, *Picea*) and broadleaved (*Betula*, *Fagus*, *Populus*, *Quercus*) species. Bamboo mosaic potexvirus has been found in several species of *Bambusa* and *Dendrocalamus* from Taiwan and Brazil.

Trees infected with viruses may be asymptomatic or show one or more of the following: variations in leaf color, including light-green/dark-green mottling, striking rings or jagged lines of yellow or shades of red; leaf speckling; leaf spots; foliar distortion; shot hole; stunted leaves; reduced shoot or root growth; or branch dieback. Symptoms are best documented for domesticated trees which may also grow wild, such as apple mosaic virus on *Malus* or *Prunus* necrotic ringspot virus on *Prunus* spp. Virus infections are systemic, and there is no cure for infected trees.

Diseases Caused by Viroids

Viroids are the smallest known plant pathogens. Consisting of a single circular strand of ribonucleic acids a few hundred basepairs in length and without benefit of even a capsid, it is unknown exactly how these organisms are capable of infecting plant cells and causing disease. However, viroids can cause extensive damage in some hosts. There are fewer than 30 known diseases of viroid etiology, primarily of fruit trees, potatoes, and a few ornamentals. Their natural mode of transmission is largely unknown, but it is suspected that human activities play some part. In at least one temperate forest, trees showing symptoms of decline were assayed for the presence of viroids. None were found and so far there are no known viroid diseases of temperate forest trees. In contrast, in the Philippines, a viroid disease known as cadang-cadang of coconuts (*Cocos nucifera*) has been devastating. The disease has been spreading since it was first recorded in 1931; there is no known vector, no known means of control, and no known resistant coconuts. It is estimated that 30 million coconut palms died, as of 1980, from cadang-cadang. It is caused by a viroid of the potato spindle tuber viroid group, based on the sequence of their central conserved region, and exists as four distinct molecular forms which occur over the course of infection. A related viroid, causing tinangaja disease, has permanently destroyed the commercial coconut industry on Guam. Both diseases can be difficult to diagnose due to the long period over which the disease develops (7–16 years) and the similarity of symptoms to those produced by water stress, poor nutrition, typhoon damage, physiological sterility, and insect feeding damage. Foliar symptoms, which may take as long as 2 years after infection to develop, begin as nonnecrotic water-soaked spots which eventually enlarge with time. Spots may grow together to give an appearance of general chlorosis. With increased time, leaflets become brittle, the crown size is reduced, and death follows. Other palms found to be naturally infected with cadang-cadang include oil palm (*Elaeis guineensis*) and buri palm (*Corypha elata*). Artificial inoculations have resulted in disease of other members of the Arecaceae, but inoculations failed in 44 species from 12 other families. Viroidlike molecules have been detected in oil and coconut palms in other parts of the southwest Pacific, but cadang-cadang disease has not been identified in these areas.

Diseases Caused by Nutrient Deficiencies

Foliar abnormalities may be caused by factors other than pathogens. Insects, mites, and other arthropods may cause distortion, speckling, or the destruction of leaf or shoot tissues. However the arthropods are often present or at least leave evidence of their presence in the form of frass, eggs, or skins cast during molting. Abiotic factors of foliar problems, such as nutrient deficiencies and injury from air pollutants, are not as easily diagnosed or recognized. Symptoms of nutrient deficiencies appear when plants are grown in soils low in organic matter, in soils with extremely high or low pH, in heavily leached soils, or when growing in soils derived from native rock which is nutrient-poor. Nutrient deficiency symptoms are rarely diagnostic in themselves. Often one nutrient is essential in the metabolism of another, so that a deficiency in one will produce a concomitant deficiency in the other. Deficiency symptoms may be similar for more than one element and can resemble those caused by waterlogged soils, salt spray, drying winds, drought, compacted soils, or pathogens. Broadleaved plants will show symptoms differently than conifers, and even within a given species of plant symptoms may vary depending on time of year and plant maturity. If deficiencies are suspected, a leaf tissue and soil analysis can help target the insufficient element.

Diseases Caused by Air Pollution

Anthropogenic air pollution may also produce abnormalities in leaf color, size, and vigor, and has been implicated in forest decline, especially in northern temperate forests. Pollution may arise from point sources, e.g., power generation plants or industrial smelters, or from nonpoint sources such as automobiles. Injury may be due to long-term exposure of low levels of pollutants (chronic exposure) or from short- or long-term exposure to high levels of pollutants (acute exposure). Injury is most likely to occur when downwind from factory smokestack plumes, at edges of cities, or in areas of air inversions.

Diagnosis is difficult as pollutants are rarely present singly and symptoms often mimic those caused by other abiotic or biotic factors. Degree of injury will vary by species, physiological age of the tissues, and proximity to the source. Generally, chronic exposure results in yellowing, stippling, dwarfing, reduced vigor, and premature senescence. Acute exposure often results in well-defined areas of dead tissues, dwarfing, or plant death.

See also: **Pathology**: Diseases affecting Exotic Plantation Species; Diseases of Forest Trees; Rust Diseases. **Tree Breeding, Practices**: Breeding for Disease and Insect Resistance.

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Rust Diseases

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Rust Fungi are All Parasites

Symbionts of forest trees may be parasites, mutualists, commensalists, amensalists, competitors, or neutralists. Rust fungi are unquestionably all parasites in that their interactions with plants are of benefit to their own fitness but detrimental to their hosts. There may be some, as-yet-unknown benefits to some hosts of rust infection, but detriments are obvious. Forest trees do not seem to constitute a special class of plant hosts for rust fungi, although herbaceous and woody perennials alike do afford opportunities for long-lasting infection unlike annuals.

Rust Fungi in Relation to Other Fungi

Systematists tend to accept between 5000 and 7000 species of rust fungi belonging to somewhere between 100 and 125 genera in from 10 to 15 families. Rust fungi constitute the order Uredinales, and they represent most of the species diversity in the class Urediniomycetes.

Some rust genera appear to be monophyletic, or natural groups of species descended from a common ancestor. *Chrysomyxa*, *Coleosporium*, *Cronartium*, *Gymnosporangium*, *Melampsora*, *Phragmidium*, and *Tranzschelia* appear to be in this category. However, some of the other genera that affect forest trees and woody plants and that are listed in **Table 1**, are not monophyletic: *Puccinia*, *Pucciniastrum*, *Thekopsora*,