

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*,

**Table 1** Distribution of rust fungi on selected genera of plants that are primarily of the northern hemisphere and 'woody'. 'Nonhost genera' are only genera that include species native to the US, for which the detailed databases of the US National Fungus Collections were consulted, and for which there were no rust records. Use of these databases also explains the North American bias that is evident in columns 3 and 4. The fifth column lists rust genera that are not necessarily North American in distribution.

Family	Nonhost genera (no susceptible species)	Host genera (but N. American species appear to be non-hosts)	Host genera (at least one N. American sp. is a host)	Rust genera parasitizing susceptible hosts
<i>Aceraceae</i>		<i>Acer</i>		<i>Aecidium</i> , <i>Pucciniastrum</i>
<i>Anacardiaceae</i>			<i>Rhus</i>	<i>Pileolaria</i> , <i>Uredo</i>
<i>Aquifoliaceae</i>			<i>Ilex</i>	<i>Chrysomyxa</i>
<i>Berberidaceae</i>			<i>Berberis</i>	<i>Aecidium</i> , <i>Cumminsia</i> , <i>Edythea</i> , <i>Puccinia</i> , <i>Puccinosira</i>
<i>Betulaceae</i>		<i>Corylus</i>		<i>Melampsorium</i> , <i>Pucciniastrum</i>
			<i>Alnus</i>	<i>Melampsorium</i>
			<i>Betula</i>	<i>Melampsorium</i>
			<i>Carpinus</i>	<i>Melampsorium</i>
			<i>Ostrya</i>	<i>Melampsorium</i>
<i>Bignoniaceae</i>	<i>Catalpa</i> <i>Chilopsis</i> <i>Paulownia</i>			
			<i>Tabebuia</i>	<i>Aecidium</i> , <i>Prospodium</i> , <i>Sphaerophragmium</i>
<i>Caprifoliaceae</i>			<i>Lonicera</i>	<i>Aplopsora</i> , <i>Puccinia</i>
			<i>Sambucus</i>	<i>Puccinia</i>
			<i>Symphoricarpos</i>	<i>Puccinia</i>
			<i>Viburnum</i>	<i>Coleosporium</i> , <i>Puccinia</i>
<i>Celastraceae</i>	<i>Pachistima</i>			
		<i>Celastrus</i>		<i>Uredo</i>
		<i>Euonymus</i>		<i>Melampsora</i>
<i>Cornaceae</i>			<i>Cornus</i>	<i>Aplopsora</i> , <i>Puccinia</i>
<i>Cupressaceae</i>	<i>Thuja</i>			
			<i>Calocedrus</i>	<i>Gymnosporangium</i>
			<i>Chamaecyparis</i>	<i>Gymnosporangium</i>
			<i>Cupressus</i>	<i>Gymnosporangium</i> , <i>Uredo</i>
			<i>Juniperus</i>	<i>Gymnosporangium</i> , <i>Uredo</i>
<i>Ebenaceae</i>		<i>Diospyros</i>		<i>Aecidium</i> , <i>Uredo</i>
<i>Elaeagnaceae</i>			<i>Elaeagnus</i>	<i>Ceraceopsora</i> , <i>Puccinia</i> , <i>Ochropsora</i>
<i>Ericaceae</i>	<i>Kalmia</i> <i>Oxydendrum</i>			
			<i>Arbutus</i>	<i>Pucciniastrum</i>
			<i>Arctostaphylos</i>	<i>Chrysomyxa</i> , <i>Pucciniastrum</i>
			<i>Chamaedaphne</i>	<i>Chrysomyxa</i>
			<i>Gaultheria</i>	<i>Chrysomyxa</i>
			<i>Gaylussacia</i>	<i>Pucciniastrum</i> , <i>Thekopsora</i>
			<i>Ledum</i>	<i>Chrysomyxa</i>
			<i>Menziesia</i>	<i>Pucciniastrum</i>
			<i>Rhododendron</i>	<i>Chrysomyxa</i> , <i>Pucciniastrum</i>
			<i>Vaccinium</i>	<i>Calypsoptera</i> , <i>Naohidemyces</i> , <i>Pucciniastrum</i>
<i>Fabaceae</i>	<i>Cercidium</i> <i>Cladrastis</i> <i>Gymnocladus</i> <i>Robinia</i>			
		<i>Cercis</i>		
			<i>Acacia</i>	<i>Aecidium</i> <i>Atelocauda</i> , <i>Endoraecium</i> , <i>Ravenelia</i> , <i>Sphaerophragmium</i> , <i>Uromycladium</i>
			<i>Albizia</i>	<i>Sphaerophragmium</i> , <i>Uromycladium</i>
			<i>Amorpha</i>	<i>Uropyxis</i>
			<i>Gleditsia</i>	<i>Ravenelia</i>
			<i>Leucaena</i>	<i>Ravenelia</i>

Table 1 Continued

Family	Nonhost genera (no susceptible species)	Host genera (but N. American species appear to be non-hosts)	Host genera (at least one N. American sp. is a host)	Rust genera parasitizing susceptible hosts
<i>Fagaceae</i>		<i>Castanopsis</i> <i>Fagus</i>	<i>Prosopis</i> <i>Sophora</i>  <i>Castanea</i> <i>Lithocarpus</i> <i>Quercus</i>	<i>Ravenelia</i> <i>Uromyces</i> <i>Pucciniastrum</i> <i>Cronartium</i> , <i>Pucciniastrum</i> <i>Cronartium</i> , <i>Pucciniastrum</i> <i>Cronartium</i> <i>Cronartium</i>
<i>Ginkgoaceae</i> <i>Grossulariaceae</i>	<i>Ginkgo</i>		<i>Ribes</i>	<i>Coleosporium</i> , <i>Cronartium</i> , <i>Melampsora</i> , <i>Puccinia</i>
<i>Hamamelidaceae</i>	<i>Liquidambar</i>	<i>Hamamelis</i>		<i>Aecidium</i> <i>Puccinia</i> <i>Pucciniastrum</i> <i>Gymnosporangium</i>
<i>Hippocastanaceae</i> <i>Hydrangeaceae</i>			<i>Aesculus</i> <i>Hydrangea</i> <i>Philadelphus</i>	
<i>Juglandaceae</i>	<i>Carya</i>		<i>Juglans</i>	<i>Gymnosporangium</i>
<i>Lauraceae</i>	<i>Persea</i> <i>Sassafras</i> <i>Umbellularia</i>			
<i>Magnoliaceae</i>	<i>Liriodendron</i> <i>Magnolia</i>			
<i>Moraceae</i>		<i>Morus</i>		<i>Cerotelium</i> <i>Cerotelium</i> <i>Cronartium</i> , <i>Gymnosporangium</i>
<i>Myricaceae</i> <i>Myrtaceae</i>			<i>Maclura</i> <i>Myrica</i> <i>Eucalyptus</i> <i>Melaleuca</i> <i>Nyssa</i>	<i>Puccinia</i> <i>Puccinia</i> <i>Aplopsora</i> , <i>Uredo</i> <i>Aecidium</i> <i>Aecidium</i> , <i>Zaghouania</i> <i>Coleosporium</i> , <i>Puccinia</i> <i>Puccinia</i> , <i>Macruropyxis</i>
<i>Nyssaceae</i> <i>Oleaceae</i>		<i>Chionanthus</i> <i>Osmanthus</i>		<i>Calyptospora</i> , <i>Hyalopsora</i> , <i>Melampsora</i> , <i>Melampsorella</i> , <i>Milesina</i> , <i>Peridermium</i> , <i>Pucciniastrum</i> , <i>Uredinopsis</i> <i>Melampsora</i> , <i>Melampsoridium</i> , <i>Triphragmiopsis</i>
<i>Pinaceae</i>			<i>Forestiera</i> <i>Fraxinus</i> <i>Abies</i>  <i>Larix</i>  <i>Picea</i>  <i>Pinus</i>  <i>Pseudotsuga</i> <i>Tsuga</i>	<i>Thekopsora</i> <i>Ceropsora</i> , <i>Chrysomyxa</i> , <i>Peridermium</i> , <i>Pucciniastrum</i> , <i>Coleosporium</i> , <i>Cronartium</i> , <i>Endocronartium</i> , <i>Melampsora</i> , <i>Peridermium</i> <i>Melampsora</i> <i>Chrysomyxa</i> , <i>Melampsora</i> , <i>Naohidemycetes</i> , <i>Pucciniastrum</i> , <i>Thekopsora</i>
<i>Platanaceae</i> <i>Rhamnaceae</i>	<i>Platanus</i>		<i>Ceanothus*</i> <i>Rhamnus</i>	<i>Puccinia</i> <i>Puccinia</i>
<i>Rosaceae</i>	<i>Cercocarpus</i> <i>Holodiscus</i> <i>Physocarpus</i> <i>Purshia</i> <i>Pyracantha</i>	<i>Spiraea</i>	<i>Amelanchier</i>	<i>Triphragmium</i> <i>Gymnosporangium</i>

continued

**Table 1** Continued

Family	Nonhost genera (no susceptible species)	Host genera (but N. American species appear to be non-hosts)	Host genera (at least one N. American sp. is a host)	Rust genera parasitizing susceptible hosts
			Aronia Chaenomeles Crataegus Malus Prunus Pyrus Rosa Rubus	Gymnosporangium Gymnosporangium Gymnosporangium Gymnosporangium Thekopsora, Tranzschelia Gymnosporangium Phragmidium Arthuriomyces, Gerwasia, Gymnoconia, Hamaspora, Kuehneola, Phragmidium, Pucciniastrum Gymnosporangium, Ochropsora
Rutaceae	Poncirus		Sorbus  Ptelea Zanthoxylum	Puccinia Aecidium, Coleosporium, Puccinia, Uredo
Salicaceae			Populus Salix	Melampsora Melampsora Aecidium
Staphyleaceae		Staphylea		
Taxaceae	Taxus		Torreya	Caeoma
Taxodiaceae	Sequoia Sequoiadendron Taxodium			
Tiliaceae		Tilia		Pucciniastrum
Ulmaceae	Planera Ulmus			
		Celtis		Uredo, Uromyces

\*Only ever identified as *Ceanothus* sp.

and *Uromyces*. Such artificial groups of species cloud interpretation of host–parasite trends at the generic level, but these are presented regardless in **Table 1** so as to reflect current knowledge.

In spite of considerable research, even today rust fungi are far from fully known at the species level, and there are at least two reasons to believe that considerable species diversity in this group remains to be elucidated: (1) plants of many parts of the world, especially in the tropics, host rust fungi that have been little studied; and (2) even in North America, Europe, Japan, Australia, and New Zealand where rust fungi have received the most attention, single, poorly delimited taxa may actually represent large complexes of cryptic or sibling species. The latter may not be distinguishable morphologically but they may still be species that are reproductively isolated from their ‘look-alike’ congeners.

The host specialization of rust fungi is clearly a major factor in speciation, and thus evolution of such cryptic complexes. Specialization provides a special form of sympatric isolation for parasite populations; gene flow will stop in the absence of a common host. Divergence at many levels may then follow.

Rust fungi parasitizing the forest trees and woody plants of the tropics are only beginning to receive study that could add substantially to species diversity in the order. Perhaps even more importantly, discoveries of ecologically unusual rust fungi in the tropics could deepen understanding of the entire group.

### Importance of Rust Fungi in Causing Diseases of Forest Trees

All reviews of the interactions of rust fungi with plants emphasize negative consequences for the plant hosts. Negative effects vary from mortality of seedling, sapling, and even mature trees to reduced growth in all age classes. Rust diseases of trees include foliar and needle rusts, cone rusts, limb rusts, stem rusts, and broom rusts. Cankers, galls, premature defoliation, and broken limbs and tops can all be the work of rust fungi.

### Symptoms Caused by Rust Fungi

Signs (cells and tissues of the parasite itself) typically accompany symptoms of infection by rust fungi.

Timing is an issue in that symptoms such as chlorosis, or yellowing of normally green leaves or needles, may frequently precede signs. In stems, swellings or galls (symptoms) may be evident long before signs, and this is also true of abnormally dense clusters of stems or twigs that are called 'witches' brooms', or just 'brooms.' In some cases, genetic resistance of the host prevents signs from ever appearing (i.e., the host prevents the parasite from reproducing). When the host is susceptible, rust fungi parasitize its living cells, and their pustules may then frequently be surrounded by what appears to be healthy and normal host tissue.

In **Figure 1**, dark spermatogonia are surrounded by orange, swollen tissue in which a *Gymnosporangium* rust has proliferated. However, the host tissue contiguous with the rust is typically green, even as it supplies the parasite with the products of photosynthesis. Once spermatia (**Figure 2**) from spermatogonia of opposite mating type are transferred by insects to effect fertilization, aecia develop on the lower leaf surface (**Figure 1**). Once again, host tissue immediately surrounding the aecia typically appears green or 'healthy.'

When signs do appear in the form of sporulating structures or pustules (e.g., spermatogonia, aecia, and subsequent uredinia, and telia), rusts are not easily mistaken for other fungi. This is especially true when spores from the pustules can be examined microscopically, either in the light microscope or scanning electron microscope, as in **Figure 2**.

## Life Cycle of Rust Fungi

Rust fungi are macrocyclic when their life cycle includes five spore states that are often designated by Roman numerals: spermatia (0), aeciospores (I), urediniospores (II), teliospores (III), and basidiospores (IV). A representative of each of the five is shown in **Figure 2**. However, it is important to note that the spore states are not recognized through morphology or appearance alone; the spore states are related to the nuclear cycle, as will be briefly explained.

Basidiospores, and the spermatia that follow them in the 'typical' sequence of spore states, are both genetically haploid and structurally small and simple with thin, smooth walls (**Figure 2**). They differ in that basidiospores are the haploid products of meiosis in addition to being unicellular and relatively ephemeral. Basidiospores must also infect and parasitize a host, whereas spermatia serve only in mating. In rust fungi, mating initiates a dikaryotic phase that encompasses the aecial (I), uredinial (II), and telial (III) states. It is only in the teliospore that the two nuclei of the dikaryon fuse to undergo meiosis to produce basidiospores once again.



**Figure 1** Intimate association of spermatogonia and aecia in the 'aecial host' of a heteroecious rust. Dark spermatogonia embedded in orange rust tissue on the upper, adaxial surface of a leaf of the host, and following fertilization, aecial 'horns' emerging on the lower surface. A sp. of *Gymnosporangium* on *Amelanchier alnifolia* in mid-summer in the northern Rocky Mountains. Aeciospores released from the 'horns' must infect *Juniperus*, the 'telial host' to complete the life cycle. Magnification  $\times 10$ .

Given the role of spermatia in mating, spermatogonia and aecia are typically close together (**Figure 1**). Urediniospores and teliospores are sometimes closely associated also; they can even be produced in the same pustule. However, more often uredinia are produced in repeating cycles of infection until finally some host and/or environmental cue provokes the rust fungus to produce telia. Some rust fungi overwinter in a dormant telial state but others form teliospores that immediately produce infectious basidiospores. For example, non-dormant teliospores of the white pine blister rust fungus, *Cronartium ribicola*, produce basidiospores in fall that infect white pines. Those rusts that produce dormant teliospores require some ambient conditioning before they will produce basidia and haploid basidiospores.

Some rust fungi are heteroecious in that the so-called 'aecial host' supports the 0 and I phases of the life cycle, but an unrelated plant is the telial host for the II, III, and IV states. Whereas heteroecious rust fungi have alternate hosts, autoecious rusts lack





**Figure 2** LM and SEM micrographs representative of different spore states, and of the association of uredinia and telia. The LM photo in the upper left is of spermatia from a spermogonium of **Figure 1**. In general, when spermatia of one mating type are transferred by an insect to a spermogonium of the opposite mating type, the aecia develop ( $\times 1000$ ). To the right of the spermatia is a 'warty' aeciospore, produced within an aecium ( $\times 2500$ ). Below the spermatia is a spiny urediniospore; these spores develop within uredinia and may repeatedly infect the same host ( $\times 2000$ ). However, not all aeciospores of rust fungi are warty and not all urediniospores are spiny. The LM micrograph at the lower right shows closely associated uredinia (round pustule in the middle) and telia (hairs or horns) or *Cronartium ribicola* on *Ribes* ( $\times 10$ ). The hairs are chains of teliospores that produce basidia and through meiosis, haploid basidiospores that infect white pines. Note the superficial but misleading, macroscopic similarity of aecial 'horns' and telial 'hairs'.

them. Life cycles from which some spore states are absent are commonly classified as demicyclic (no uredinia) or microcyclic (neither uredinia nor aecia). However, many other variations of life cycle are known. Finally, the life cycles of many rust fungi are still poorly studied.

### Host Specialization

If current estimates were correct and there are from 250 000 to 300 000 species of plants, and 7000 species of rust fungi, one might calculate that the average rust fungus thus possesses a host range of roughly 35 to 43 host species. However, well-studied rust fungi are known to be specialists with much narrower host ranges. The discrepancy results from

the following factors: (1) not all plant species are parasitized by rust fungi, and (2) not all species of rust fungi are known.

The first factor is demonstrated in **Table 1**. The 120 genera of woody plants in **Table 1** represent genera, primarily of the northern hemisphere, for which the research literature and the databases of the US National Fungus Collections could be used to summarize some major trends. Although rust fungi do parasitize a wide variety of angiosperms, gymnosperms, and even 'primitive,' vascular plants such as *Selaginella*, there are surprisingly genera of woody plants in which resistance to rust fungi has evidently become fixed in evolutionary time (i.e., nonhost genera). It is important to note also that within many genera that do host rust fungi (e.g., *Cornus*,

dogwoods), there are many species that appear to be nonhosts. Interestingly, in *Cornus* it is the tree and shrub species that appear to be nonhosts, whereas the circumboreal, herbaceous species are hosts. The one exception is the giant dogwood, *Cornus controversa*, which in Japan hosts a rust fungus in the genus *Aplopsora*.

Another trend that is apparent in Table 1 and is intriguing, has to do with the number of genera in which North American species are nonhosts for rusts in contrast to at least some of their Eurasian congeners: maple (*Acer*), hazel-nut (*Corylus*), bittersweet (*Celastrus*), Euonymus, persimmons (*Diospyros*), redbud (*Cercis*), chinquapin (*Castanopsis*), beech (*Fagus*), witch hazel (*Hamamelis*), mulberry (*Morus*), fringe-tree (*Chionanthus*), devilwood (*Osmanthus*), bladdernut (*Staphylea*), basswood or linden (*Tilia*), and hackberry (*Celtis*).

Among the 33 nonhost genera that are scattered across families that include woody plants of the northern hemisphere, there may be species that host rust fungi that have not been observed. However, most of these genera are quite well studied, and it would seem unlikely that rust infection has been missed. This seems especially true of the 10 nonhost genera that are endemic to North America (including Mexico): *Kalmia*, *Oxydendrum*, *Robinia*, *Umbellaria*, *Cercocarpus*, *Purshia*, *Sequoia*, *Sequoiadendron*, *Taxodium*, and *Planera*. The proportion of nonhost to host genera also seems significant: it is 33 to 87. In any case, there is evidently only a subset of the plant kingdom that hosts rust fungi. This fact transcends the artificial dichotomy between woody and herbaceous plants in that there are also many nonhosts among the latter although such plants are not the focus of this article. It is also true that many rust species or taxa are unknown or improperly delimited. In the latter case, complexes of cryptic or sibling species, among which morphological variation is subtle and continuous, present a considerable challenge to species delimitation.

Ideally, the host ranges of rust fungi would be experimentally determined so as to avoid the conflation of host ranges of cryptic species. To date however, few host ranges have been so determined. In any case, on the one hand there are fewer host species and on the other hand there are more rust species, than may be generally believed.

### Rust Fungi Are Specialists in Relation to Plant Tissues and Age

Typically, woody plants are more susceptible to rust fungi when they are young. On a seasonal basis,

young tissues are typically also more susceptible than older tissues. However, there may be exceptions to these generalizations about host ontogeny in relation to resistance. In the case of box rust (i.e., *Puccinia buxi* on *Buxus sempervirens* in the UK) there is at least circumstantial evidence that older individuals are more susceptible.

Rust fungi are not known to infect the roots of forest trees, but they may infect all portions of the aboveground shoot system. Similarly, there do not appear to be any clear examples of vertical transmission of seedborne rust, although introductions of rust fungi to new regions may cause the question to be raised.

### Genes for Resistance to Rust Fungi

Most of what is known about genetic resistance to parasites of forest trees has been learned by studying rust fungi. Various researchers have identified major genes for resistance to the fungi causing white pine blister rust, poplar rust, western gall rust, and fusiform rust. If other rust fungi parasitizing forest trees received similar attention, it is likely that major genes for resistance would characterize those interactions as well.

Major genes that have been cloned can be proven to function in resistance in transgenic assays. Although major genes for rust resistance from forest trees have not been cloned, they would presumably be like such genes in crop plants in passing such a test. In contrast, partial resistance, that has also been described as quantitative or horizontal, is thought to be under polygenic control in that many genes of minor effect are thought to act in concert (see **Tree Breeding, Practices: Breeding for Disease and Insect Resistance**).

### Interactions of Rust Fungi with Other Fungi

Less is known about the effects of other fungi on rust infection. *Sphaerellopsis filum* parasitizes rust fungi, and can thus be described as a hyperparasite or mycoparasite. However, *S. filum* is not found on all rust fungi, nor is it always found in all parts of the geographic range of any particular rust fungus. Many other fungi are associated with rust pustules; these may be hyperparasites or opportunists that consume host cells parasitized or killed by the primary parasite, or rust fungus. Some fungal symbionts of forest trees could conceivably stimulate host resistance to rust fungi. However, in general, other fungi

have not been developed as tools to control rust diseases of forest trees.

## Control of Rust Fungi of Forest Trees

Forest pathology has been greatly influenced by attempts to control rust diseases. Avoidance of areas of high inoculum is generally recommended for new plantings of all forest trees. In the famous case of the introduced *Cronartium ribicola*, or white pine blister rust, extensive and expensive efforts were made to eradicate the alternate host (i.e., species of *Ribes*), albeit without much success. Pruning, avoidance of areas in which the environment favors infection by *C. ribicola*, nursery applications of fungicide, and programs to breed for resistance are all components of the arsenal deployed against white pine blister rust.

Breeding for resistance to the native, fusiform rust of loblolly and slash pines in the southern United States has also been combined successfully with silvicultural techniques of intensive management. Breeding for resistance to poplar rust is an ongoing battle both in Europe and North America, but again this subject is presented in more detail in this volume and elsewhere.

**See also:** **Pathology:** Diseases of Forest Trees. **Tree Breeding, Practices:** Breeding for Disease and Insect Resistance.

## Further Reading

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## Stem Canker Diseases

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## Introduction

Canker diseases are caused by a diverse array of pathogenic fungi, and are grouped together based on similarities in the symptoms they produce on their host plants. Our treatment will be restricted to diseases caused by fungi in the group known as Ascomycetes. This includes most of the biotic pathogenic agents responsible for cankers, but does exclude at least one noteworthy group: the obligate parasites known as rust fungi, some of which cause diseases referred to as cankers (see **Pathology:** Rust Diseases). Even with this limitation, canker diseases represent a heterogeneous grouping, which is unified more by the nature and location of the damage on the tree than the appearance of the diseased tissue.

## Pathology

A canker would typically be defined as a more or less sunken area on a stem or branch where pathogen growth has killed the underlying cambium, and which is often bordered by host-produced callus tissue. Thus, it is the combination of no growth where host tissue is killed and a somewhat elevated border of callus produced in response to infection that defines a depressed area known as a canker. However, many so-called canker diseases do not have symptoms at all similar to the foregoing description, and among the pathogens that produce typical cankers, some will do so only on certain plant parts, such as large-diameter branches, because younger branches die too quickly after infection for a canker to develop.

To account for variation in the appearance of cankers induced by different pathogens, three sub-groupings have been recognized: perennial, annual, and diffuse cankers. Perennial cankers would most closely match the description given above. As the