



**Figure 12** Hyphae of the brown rot fungus *Fomitopsis pinicola* can readily colonize and degrade cell walls of the unaltered sapwood. Due to their limited enzymatic ability they cannot readily penetrate reaction zones in beech. Reproduced with permission from Schwarze FWMR, Engels J and Mattheck K (1999) *Hozzersetzende pilze in Bäumen – Strategien der Holzersetzung*. Rombach, Freiburg, Germany.

(Figure 11). Failure of *Fomitopsis pinicola* to invade and defeat reaction zones in beech is apparently related to the limited enzymatic ability and inflexible behavior of brown rot fungi (Figure 12).

On the basis of these observations, it is postulated that *I. hispidus* and other basidiomycetes have the ability to cause a soft rot either in addition or alternatively to their more typical mode of action, i.e., a white rot may be a common phenomenon, which may play a significant role in lesion expansion for a range of other decay fungi. By contrast, more aggressive decay fungi may have a broader enzymatic potential capable of degrading polyphenols deposited in the wood cell lumina.

The relative aggressiveness of decay fungi seems to be a function of their ability to degrade both lignin and polyphenolic compounds formed in response to lesion expansion in the wood. The fact that less-invasive fungi appear to avoid polyphenolic deposits by tunneling into the cellulose-rich regions of the wood cell wall and do not display an ability to penetrate through the lignin-rich middle lamella adds weight to this view.

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

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## Disease Affecting Exotic Plantation Species

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### Introduction

Tree pathogens in natural forests are typically in balance with their environment. This delicate balance can easily be disturbed through the introduction of an exotic pest or pathogen (see **Pathology:** Diseases of Forest Trees). In natural forests, pathogens play an important role in maintaining genetic diversity of the tree species in these ecosystems. They are also important in removing weak trees from the

forests and contribute to decomposition of forest biomass. Thus, management of natural forests, especially for commercial forestry, is complicated and often poorly understood.

Plantation forestry is a relatively modern undertaking and has been practiced for just over 100 years. These forests are primarily propagated to produce solid-wood products for construction, fuelwood, or secondary products such as charcoal, pulp, and paper. Demand for some of these products has grown rapidly during the course of the last century and huge commercial industries are now based on plantation forestry.

Plantations are established either using native or exotic species. In the northern hemisphere, the tendency has been to establish plantations of native species such as loblolly (*Pinus taeda*) and slash (*P. elliottii*) pines in the southeastern USA, scots pine (*P. sylvestris*) in Europe and various species of *Populus* in North America and Europe. In contrast, huge plantation areas have been established in the tropics and southern hemisphere using primarily exotic species of *Pinus*, *Eucalyptus*, and *Acacia*. These include *Pinus radiata* in Australia, Chile, and New Zealand, *P. patula* in Southern Africa, *P. taeda* in Brazil, hybrids of *P. elliottii* and *P. caribaea* in Australia and South Africa, *Eucalyptus grandis* and hybrids of this and other species in Brazil, South Africa and Southeast Asia, *E. globulus* and *E. nitens* in Chile, and *Acacia mangium* in various parts of Southeast Asia.

There are fundamental differences between natural forests and trees grown and managed intensively in plantations. Natural forests are typically made up of a mixture of species. In some ecosystems, such as the boreal forests, this can be a relatively small number of species, while others such as tropical forests include a great diversity of species. This is very different to the composition of plantations of exotic species where uniform families or even single genotypes are planted across extensive areas.

The establishment of plantations of exotic tree species in the tropics and southern hemisphere has been hugely successful. Growth and yield generally surpass those obtained in plantations using native species and the performance of the exotic trees has been likened to that of weeds. Although the reasons for the superior performance of exotic trees in plantations can be debated, there is substantial evidence to suggest that this is strongly linked to the so-called pest and pathogen release hypothesis. Here, the trees have been released from their natural enemies and are able to grow vigorously in the absence of competition. Indeed, in many cases, a problem with exotic tree species is that they commonly 'escape' from plantation lands and establish themselves as serious weed plants in natural ecosystems.

The absence of pests and pathogens has provided forestry companies growing exotic trees with a valuable window of opportunity. However, pathogens have gradually appeared in these plantations and in some cases they have resulted in considerable loss. These losses are usually exacerbated due to the large areas planted to single species where the trees are often genetically related. There are thus examples where the tree species being grown has had to be abandoned due to the appearance of a serious disease problem.

## Examples of Diseases in Exotic Plantations

Diseases affecting exotic plantation forestry occur in two distinct categories. These include those caused by exotic pathogens, which have usually originated on the trees or related tree species in their areas of origin. Alternatively, they are caused by pathogens native to the new environments in which the trees have been established. In some instances, the pathogens are well known in their areas of origin or elsewhere in the world and their appearance in new environments might even have been predicted. However, in many situations, native pathogens are unknown in their areas of origin because they are not associated with an obvious disease problem or a commercially important species of tree. This often means that the source of a pathogen affecting exotic tree species is unknown and complex molecular genetic studies are required before its origin can be discovered.

Generally, when plantations of exotic tree species have been established in areas where very closely related native species grow naturally, serious disease problems have emerged. Thus, although different, the exotic tree species are sufficiently similar to the native trees to enable pathogens to move on to them. For example, where European *Pinus* spp. have been planted in areas of the USA that has a diverse ecosystem of native *Pinus* spp., serious disease and pest problems have been experienced on the exotics. Likewise, where *E. globulus* has been planted as an exotic in western Australia, these trees have been severely infected by a wide range of pathogens, presumably originating on nearby native *Eucalyptus*.

## Diseases Caused by Native Pathogens

There are many examples of diseases of exotic plantation trees that are caused by native pathogens. Amongst the first of these to be discovered were root pathogens such as species of *Armillaria*, *Ganoderma*, *Heterobasidion annosum*, and *Phytophthora* that tend to have wide host ranges. However, in recent years, numerous examples of native stem and shoot pathogens that infect exotic plantation trees have

emerged. Some of these were thought to be reasonably host-specific but this is clearly not the case. Now it is of particular concern that these 'new' pathogens that have become adapted to infect the exotic species might be accidentally introduced into areas where the trees are native. Such situations where native trees are invaded by exotic pathogens could lead to epidemics of a magnitude equivalent to chestnut blight and Dutch elm disease, discussed elsewhere (see **Pathology**: Insect Associated Tree Diseases). This section includes a selection of examples of native pathogens that have caused serious disease problems in plantations of exotic tree species.

**Armillaria root rot** *Armillaria* root rot is a well-known disease of woody plants that can be caused by one of numerous species of *Armillaria*. Most of these fungi have wide host ranges and are best known in the northern hemisphere, where disease centers in native forests caused by single clones of the pathogen can become very large. *Armillaria* spp. such as *A. ostoyae* have thus gained notoriety for representing the largest and oldest living organisms on earth.

*Armillaria* spp. are native in natural woody ecosystems, generally killing weakened trees and moving through the soil via bootlace-like rhizomorphs. When trees have been felled to provide land for planting exotics, stumps are colonized by the *Armillaria* spp. The fungus thus acquires energy (inoculum potential), enabling it to infect healthy trees adjacent to the colonized stumps. Large numbers of newly planted seedlings can be killed in this way and it can be virtually impossible to establish stands without removing the source of inoculum.

In more established trees, infection centers usually originate from colonized stumps of felled trees. Infection passes from one tree to another via root contacts or by rhizomorphs. This can result in large disease centers that continuously increase in size, during the rotation.

*Armillaria* spp. have been amongst the first pathogens noted after the establishment of exotic tree species, generally but not exclusively in plantations of *Pinus* spp. For example, *A. limonea* and *A. novae-zealandiae* have resulted in serious losses to newly established stands of *P. radiata* in New Zealand. Similarly, *A. limoneae* and *A. luteobubalina* are associated with *P. radiata* establishment problems in Chile. In South Africa, *A. fuscipes* has caused serious losses in newly established plantations of various *Pinus* spp., but especially *P. elliottii* and *P. patula*.

**Eucalyptus rust** Rust diseases are caused by a group of pathogens generally known to be highly host-specific. These fungi tend to have complex life cycles

and many have both primary and alternate hosts, which bear different parts of these life cycles. Amongst the three most important genera of trees grown as exotics in plantations, *Pinus* spp. have the largest number of rust diseases. It is thus interesting that none of these have appeared on exotic *Pinus* spp., grown in the tropics and southern hemisphere. *Eucalyptus* is a very large genus including more than 600 species, mostly native to Australia. It is thus interesting that no rust diseases are known on these trees in their native environment.

*Puccinia psidii* that causes eucalyptus rust is an unusual pathogen. This fungus is native in South and Central America where it occurs on various genera and species of native Myrtaceae. The fungus has, however, developed the capacity to infect *Eucalyptus* spp. In countries such as Brazil and Uruguay it has caused severe damage to these trees, especially in young plantations of susceptible species. As trees become older, they are less severely damaged by the pathogen and thus, established plantations are not considered at risk due to rust.

The eucalyptus rust pathogen is widely considered to be amongst the most important threatening organisms linked to forestry. This is collectively because rust fungi have powdery spores that facilitate spread, and the fact that some native Myrtaceae, especially in Australia, are highly susceptible to this pathogen. Accidental introduction of *P. psidii* into that country could have disastrous consequences for the natural environment.

**Ceratocystis wilt** *Ceratocystis* species are well-known pathogens of woody plants and many cause important wilt diseases. Examples include the causal agents of oak wilt, *Ceratocystis fagacearum*, and sapstreak of sugar maple and other hardwood trees caused by *C. virescens*. These fungi are primarily dispersed by casual insects such as flies and picnic beetles (Coleoptera: Nitidulidae), which are attracted by the fruity aromas produced by the fungi, sporulating on infected trees. The insects are attracted to the sap produced by fresh wounds, and in this way the fungi enter the vascular systems of trees (see **Entomology**: Sapsuckers). Because infections lead to the blockage of sap flow, these fungi tend to kill trees relatively rapidly.

*Ceratocystis* wilt is a relatively newly discovered disease in plantations of exotic trees. *C. albobundus* was the first species belonging to the group shown to cause a rapid wilt disease of trees. This fungus infects wounds on exotic *Acacia mearnsii* (black wattle) and *A. dealbata* (green wattle) in South African plantations. Large numbers of trees can be killed rapidly and this is the most important disease of *A. mearnsii*

in South Africa. There is good evidence to show that *C. albobundus* originated on native Proteaceae in South Africa. This is unusual given that Proteaceae are very distantly related to *Acacia* spp. The fungus has not been found in Australia and might pose a threat to native *Acacia* spp. in that country.

*Ceratocystis fimbriata* is a well-known wilt and canker pathogen on many forest and fruit trees. This fungus has recently been discovered to cause rapid wilt and death of *Eucalyptus* spp. in Brazil, Uruguay and the Congo. Phylogenetic studies have shown that the fungus in the former two countries is probably native, but it appears to be exotic in the Congo. There is no evidence that *C. fimbriata* occurs in Australia. Thus, strains of the fungus that infect *Eucalyptus* elsewhere in the world are clearly threatening to native stands of these trees.

### Diseases Caused by Introduced Pathogens

Many pathogens found on exotic plantation trees are thought to have been introduced from the areas of origin of these trees. As mentioned previously, these assumptions could be incorrect given that the origin of most pathogens has not been established experimentally. Relatively large numbers of foliage pathogens occur on exotic plantation trees such as *Eucalyptus* and they are assumed to have been introduced into the new areas on contaminated seed. Many are relatively unimportant and have been afforded little attention.

Most of the more serious diseases of exotic plantation trees are caused by introduced pathogens. Some have been present in exotic plantations for many years and others have appeared relatively recently. New introductions continue to occur regularly and this is a trend that is not likely to change. The following examples have been selected based on relative importance and to reflect differences in infection strategy and host range.

**Diplodia canker and dieback of pines** In most countries where species of *Pinus* have been established as exotics in plantations, *Diplodia* canker and dieback caused by *Diplodia pinea* (also known as *Sphaeropsis sapinea*) was the first disease to be recorded. This is apparently due to the fact that the fungus is seed-borne and was, therefore, introduced into new areas probably close to the time of plantation establishment. The fungus is found in every country where pines are grown as exotics. Contemporary studies have shown that those countries that have restricted the importation of seed have populations of the pathogen with lower levels of

genetic diversity than those where more regular seed introductions have been made.

For many years, *D. pinea* was thought to be a secondary, wound-infecting fungus. In contrast, recent research has shown that the fungus is a common latent pathogen in asymptomatic pine tissue. Onset of disease is closely linked to environmental stress such as drought, cold, poor site-species matching, and hail damage. The fungus is perhaps best known in South Africa where the highly susceptible *Pinus patula* is widely planted and commonly damaged by hail storms. A combination of latent infections by the pathogen, together with the susceptible species and hail damage, can lead to the death of very large areas of trees.

**Dothistroma needle blight** In exotic plantation forestry, *Dothistroma* needle blight caused by *Dothistroma septospora* is perhaps the best-known disease. This is due to the tremendous damage that it has caused to *P. radiata* plantations in Africa, South America, Australia, and New Zealand, particularly during the 1960s and 1970s. Many plantation programs based on this tree species were abandoned, especially those in Africa where the climate was highly conducive to infection by *D. septospora*.

*Dothistroma septospora* is native to the northern hemisphere where it is well known and occurs in both its sexual and asexual forms. In many areas, the fungus is relatively unimportant but there are examples of severe damage to plantations and ornamental *P. ponderosa* in the USA and *P. nigra* where it is grown as an exotic in the USA and plantations in some parts of Europe. The fungus was first discovered in exotic *P. radiata* plantations in Africa in 1957 and it rapidly spread to other areas such as Australia, New Zealand, and Chile, where *P. radiata* was being intensively propagated. The disease remains important in these areas and wide-scale aerial spraying continues to be used to reduce the impact of the disease.

**Mycosphaerella leaf blotch on Eucalyptus** Many species of *Mycosphaerella* infect the leaves and green branches of *Eucalyptus* spp. In exotic plantations, these fungi have been amongst the first to be recorded associated with disease. Although there is no experimental evidence to substantiate this, observations regarding disease occurrence suggest that these fungi are seed-borne and that they have been widely distributed together with seed used for plantation establishment.

Most *Mycosphaerella* spp. on *Eucalyptus* appear to be relatively unimportant. However, some species, such as *Mycosphaerella nubilosa*, have caused serious

defoliation of juvenile leaves of *E. globulus* in South Africa and West Australia. *Eucalyptus nitens* is also severely damaged by this fungus in South Africa. *Mycosphaerella nubilosa* is well-known on native *Eucalyptus* in Australia and this is certainly the origin of the fungus. In contrast, *Phaeophloeospora destructans*, which phylogenetically is an asexual state of a *Mycosphaerella* species, is of unknown origin and causes serious shoot and leaf blight on various *Eucalyptus* spp. including *E. grandis*, *E. urophylla*, and *E. camaldulensis* in Indonesia, Thailand, and Vietnam. This fungus was first found in Sumatra and it has gradually spread southwards. It was possibly introduced into the area from Australia or other parts of Indonesia where *E. urophylla* is native, or it has moved on to *Eucalyptus* from some other host. Irrespective of its origin, *P. destructans* has become one of the most important pathogens of *Eucalyptus* and it now threatens plantation programs elsewhere in the world.

**Pitch canker** Pitch canker has become one of the most important diseases threatening exotic pines in plantations. The disease (see **Pathology: Stem Canker Diseases**) is caused by *Fusarium circinatum*, which is known in its sexual state as *Gibberella circinata*. This fungus was discovered for the first time in the southeastern USA in 1945 on *P. virginiana* and it has caused occasional outbreaks of disease in that area. More recently, the fungus appeared in California where it was discovered causing branch and stem cankers on *P. radiata* planted along streets and in parks. The disease has spread rapidly to trees in natural stands where it has caused very serious damage and possibly threatens *P. radiata* in its native range.

The pitch canker fungus requires wounds to infect trees. These wounds can arise from physical damage to trees, for example, by wind and forestry operations. Insects are also associated with infection and these include cone- and shoot-infesting bark beetles (Scolytidae) and weevils (Curculionidae), as well as lepidoptera that damage shoots. When infections reach the main stems, parts of trees above the stem cankers and often whole trees will die. The name 'pitch canker' refers to the deep resin impregnation of the wood associated with infections.

The pitch canker fungus was first discovered in exotic pine plantations in South Africa in 1991. In this situation, it caused extensive losses to *P. patula* seedlings in a major pine production nursery. The fungus has subsequently spread to virtually all pine-producing nurseries in this country and it has also recently been associated with serious losses associated with the establishment of new lands. The pitch canker disease, typified by infections on above-

ground parts of trees, has not been seen and, strictly speaking, pitch canker disease does not occur in South Africa.

A situation very similar to that in South Africa has recently been discovered in Chile. Here, *P. radiata* plants in nurseries are severely damaged by *F. circinatum*. The disease affects seedlings in containers and open-rooted nurseries, and most importantly, valuable clonal hedges used to produce clonal cuttings. Infections of established trees in plantations have not been seen in Chile. However, the presence of various primary insects, such as shoot moths known to be associated with pitch canker in the southeastern USA, suggests that it is only a matter of time before the disease appears in plantations.

An early hypothesis from the southeastern USA was that the pitch canker fungus might have originated in Haiti. Recent studies using DNA-based markers have shown that the fungus in California probably originated in the eastern USA. The fungus in South Africa most probably originated in Mexico, where the disease is now well-known on native *Pinus* spp. Pitch canker is known to occur in Japan, and has recently been found in Korea and in Spain. All indications are that *F. circinatum* is spreading around the world, presumably on seed, which is known to carry the fungus. Countries such as New Zealand and Australia, with substantial resources of susceptible *P. radiata*, have instituted rigorous legislation to prevent the introduction of the pathogen.

**Phytophthora root rot** Phytophthora root rot is a well-known disease of woody plants and can be caused by numerous species of *Phytophthora*. These fungi are unusual in that they belong to a group of organisms that are not strictly fungi (Kingdom: Stramenopila). They are soil-borne and produce structures enabling them to survive in the soil for extended periods of time. They also produce motile spores that are water-borne and move through the soil-water interface. Contamination of new areas can occur easily through the movement of soil or contaminated irrigation water.

*Phytophthora* spp. generally infect the feeder roots of plants and give rise to a slow decline as these infections move towards the root collars of trees. In exotic plantation forests, they are often moved into newly established areas with infected plants from nurseries. Trees can die during the first year after planting but more commonly die after 2 years or more. Disease distribution tends to be scattered in plantations. Where highly susceptible trees are planted in infected lands, they too become infected.

By far the best known *Phytophthora* species is *P. cinnamomi*. This fungus has a very wide host range

and is thought to be native to Papua New Guinea, although the origin of the fungus has been deeply debated. It has caused serious losses in plantations and wind breaks of *P. radiata* in Australia. In South Africa, important species of *Eucalyptus* such as *E. fastigata*, *E. fraxinoides*, and *E. smithii* have been severely damaged.

### Management of Diseases in Plantations

Many opportunities exist to reduce the impact of diseases in exotic plantations. Thus, quarantine measures to prevent the introduction of new pathogens are among the most important approaches to disease management. Eradication of pathogens after early detection might, in some cases, also be possible. Chemical control has been very successful in the case of some foliar diseases such as *Dothistroma* needle blight, where aerial spraying of fungicides has been used for many years.

Of all the approaches to disease control in exotic plantations, minimization through breeding and selection of pathogen-tolerant planting stock is most important and widely used. Considerable success has been achieved in reducing the impact of diseases through matching species to sites and planting species tolerant of the diseases, in areas where these diseases occur. Classical forest genetics has contributed substantially to the improvement of exotic plantation forestry as well as to disease resistance. Large industrial corporations that are involved in plantation forestry have generally invested in forest genetics programs and especially in ensuring access to a wide range of provenances of desired tree species. Breeding programs have also moved rapidly towards producing hybrids between species. They have thus been able to capitalize on hybrid vigor and to gain the advantages of a mixture of traits not available in single species. Hybrids have also been very useful in combatting various disease problems.

Contemporary trends are to produce clones of the best-performing genotypes and, after thorough testing, to deploy them on sites where they will grow best. Consequently, in some areas, plantation forestry has become technologically advanced, using techniques such as tissue culture and somatic embryogenesis to multiply clones. Management of clonal forests is complicated and, from a disease standpoint, maintaining reliable plantation records and establishing safe numbers of clones to plant is important. Thus, large corporations rely on geographic information systems to determine planting strategy and to ensure effective disease avoidance or resistance.

Genetic modification of exotic plantation trees to improve traits including disease tolerance and

resistance is being actively pursued at the experimental level. Various genes associated with disease resistance are available and these have been transformed into trees such as *Eucalyptus* and *Pinus* that are widely grown as exotics in plantations. Tissue culture protocols are widely available for these trees, thus facilitating genetic modification. Clonal forestry and experience in deploying relatively small numbers of genetically identical clones for short rotations will also positively influence opportunities to deploy genetically modified trees. However, rotations longer than those associated with agronomic crops and the fact that forest trees are wind-pollinated, potentially producing clouds of genetically modified pollen, have raised concern. As soon as the potentially negative impacts of deploying genetically modified trees have been resolved, it is likely that these trees will play an important role in minimizing the impacts of disease.

Biological control of insect pests is well established in exotic plantation forestry but has not been used commercially to reduce the impact of pathogens. There is, however, considerable opportunity in this field and recent advances in the manipulation of fungal viruses for pathogen control deserve notice. Certainly, as diseases in forest exotic forest plantations become increasingly important, and together with the negative environmental impact of most chemical fungicides, it is likely that interest in biological control will increase.

### Future Prospects

Plantations of exotics, particularly in the tropics and southern hemisphere, have yielded outstanding productivity during the last 100 years. Separation of the trees in these plantations from their natural enemies has been an important component of this success. However, disease and pest problems in exotic plantations have gradually increased due to the accidental introduction of new pathogens and the adaptation of native pathogens to be able to infect the exotic trees.

In the future, it is likely that increased investments will be needed in order to reduce the impact of pathogens in plantations of exotic trees. These will be essential if the impressive productivity that has been associated with these plantations is to be maintained. New technologies, including those associated with molecular genetics and computer science, are likely to become increasingly important in ensuring the long-term sustainability of exotic plantation forestry.

*See also:* **Entomology:** Sapsuckers. **Pathology:** Diseases of Forest Trees; Insect Associated Tree Diseases;

*Phytophthora* Root Rot of Forest Trees; Root and Butt Rot Diseases; Rust Diseases; Stem Canker Diseases. **Tree Breeding, Practices:** Breeding for Disease and Insect Resistance.

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# PLANTATION SILVICULTURE

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## Forest Plantations

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### Definition

Forest plantations embrace a range of forest types, with the common feature that the majority of the trees present were established by planting (or deliberate seeding). However, this simple statement belies the fact that when mature, many planted forests can appear similar to natural forest formations. While a geometrically shaped forest monoculture of a nonnative species is plainly artificial, many old and famous forests in Europe appear

natural and reveal little of their mainly planted origin. Examples include the New Forest (UK), parts of the Black Forest (Germany), parts of the Forêt de Compiègne (France), and almost all the forests of Denmark.

There is no internationally agreed definition of a forest plantation, or ‘planted forest,’ the expression now widely used to embrace the continuum of forest types where forest origin is known to be by planting or direct seeding. Successive international experts meeting on The Role of Planted Forests in Sustainable Forest Management in Chile (1999) and New Zealand (2003) have recommended that the question of definition be considered. This is because the boundary between planted and natural forests is often indistinct and, among countries, there are different degrees of management, and different