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Insect Associated Tree Diseases

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Introduction

The causes of tree diseases range from the simple – with one principal damaging agent – to the complex – where a number of damaging agents interact.

A key role for insects in some simple diseases is that of vector for a pathogen. This is particularly important for certain fungal diseases. However, insects also play a vital part in the dissemination of some tree-pathogenic nematodes, phytoplasmas, xylem-limited bacteria, and viruses.

In complex tree diseases insects may play a variety of roles. At an early stage, leaf-eating insects may act as agents of stress. At a later stage it may be bark- or wood-inhabiting beetles that deliver the final death blow to the tree.

Fungal Diseases Vectored by Insects

Among the fungi, there are three main taxonomic groups: the Oomycotina, the Basidiomycotina, and the Ascomycotina (plus the closely allied Fungi Imperfecti). The majority of fungal pathogens with known insect vectors are either Ascomycotina or Fungi Imperfecti, and most of the ascomycetes fall within two genera of the family Ophiostomataceae – *Ophiostoma* and *Ceratocystis*. In addition, most of the imperfect fungi are *Chalara*, *Leptographium*, or *Verticicladiella*, genera that would be expected to have *Ophiostoma* or *Ceratocystis* perfect states. The nature of the insect–fungus relationship with this group of pathogens is discussed in some detail later in this article. Among other ascomycetes, recent attention has focused on the role of insects as vectors of *Fusarium circinatum*, the cause of pitch canker. This major pathogen, first recognized in the eastern USA, was reported from California in 1986. Studies there on *Pinus radiata* have focused on the twig-feeding bark beetles *Pityophthorus* spp., but other beetles, including the cone beetle *Conophthorus radiata*, have also been implicated. In southern Europe, a cone-feeding insect, the seed bug *Orsillus maculatus*, has been found to transmit the important canker pathogen *Seiridium cardinale* to *Cupressus sempervirens* cones. Once the cones are colonized by the fungus they become a source of inoculum for branch infection. Interestingly, it seems that when *S. cardinale* arrived in Europe, it took over a long-established relationship between the insect and a nondamaging fungus *Pestalotiopsis funerea*.

Although the Basidiomycotina include many fungal pathogens of trees, the only indubitable case of insect transmission concerns the *Amylostereum* species that are transmitted by woodwasps in the genera *Sirex* and *Urocerus*. In most parts of the world these organisms do little damage but in Australia and New Zealand, *Sirex noctilio* and *Amylostereum areolatum* can cause significant losses in *Pinus radiata* plantations, especially during periods of drought.

The fungus is carried by the adult siricids in a pair of small invaginated intersegmental sacs protruding into the body. These are connected by ducts to the anterior end of the ovipositor. During oviposition (**Figure 1**), spores of the fungus are 'injected' into the sapwood of trees and developing mycelium then invades the wood around the oviposition hole and larval tunnels. As is commonly the case with xylem pathogens, a zone of reduced moisture content develops around the tissue occupied by *Amylostereum* and this ensures that the *Sirex* eggs hatch and the larvae develop in relatively dry wood. In addition, host resinosis is reduced in colonized tissue, and this also favors larval development. Female larvae, from the second instar onwards, carry the

Figure 1 *Sirex* woodwasp, vector of basidiomycete *Amylostereum* ovipositing on pine. Courtesy of Forest Commission.

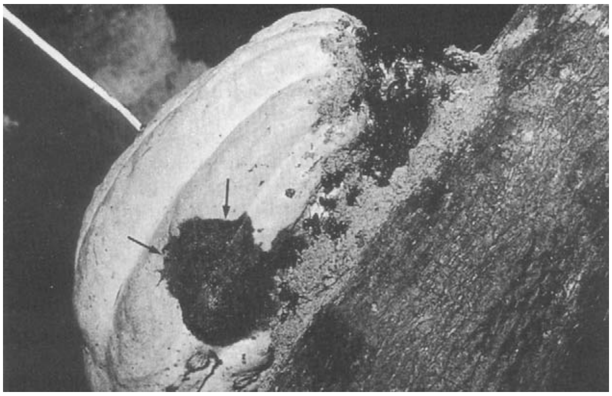

Figure 2 A soil tent (arrowed) produced by ants, causing *Phytophthora megakarya* infection of cocoa pods. Courtesy of CM Brasier.

fungus in deep skinfolds called hypopleural organs sited in the abdomen. The young adult then acquires the fungus during eclosion when, by reflex actions, it breaks up the hypopleural organs in the cast-off larval skin. Interestingly, inoculation with the fungus alone has relatively little effect and the insect's mucus secretions are believed to play an important part in 'conditioning' the tree for invasion by *A. areolatum*.

The only oomycetes known to be insect-vectored are *Phytophthora palmivora* and *P. megakarya*. They cause black pod disease of cocoa and can also cause stem cankers and wilt of flower cushions. Although these fungi can be disseminated via rain splash and contact with plant litter, several species of ants have been found to act as vectors. Transmission occurs when ants collect particles of soil contaminated with *Phytophthora* and build them into tents on the cocoa plants, including on the pods (**Figure 2**). These can then become infected with the pathogen, which appears to be capable of invading both wounded and uninjured pods.

The Ophiostomoid Pathogens of Standing and Freshly Felled Trees and their Insect Dispersal

Because of their economic importance, diseases caused by this group of fungi have been subject to detailed research, evaluation of which has thrown much light on the principles underlying the process of insect transmission.

Two contrasting patterns of host invasion can be found in the Ophiostomataceae and these have a significant influence on the nature of the relationship with potential insect vectors. In the vascular wilts the fungus shows extensive vertical distribution in the xylem elements (vessels or tracheids), but is unable to colonize xylem parenchyma, the medullary rays, the cambium, and the inner bark (phloem tissue) until the host becomes moribund. Examples from temperate

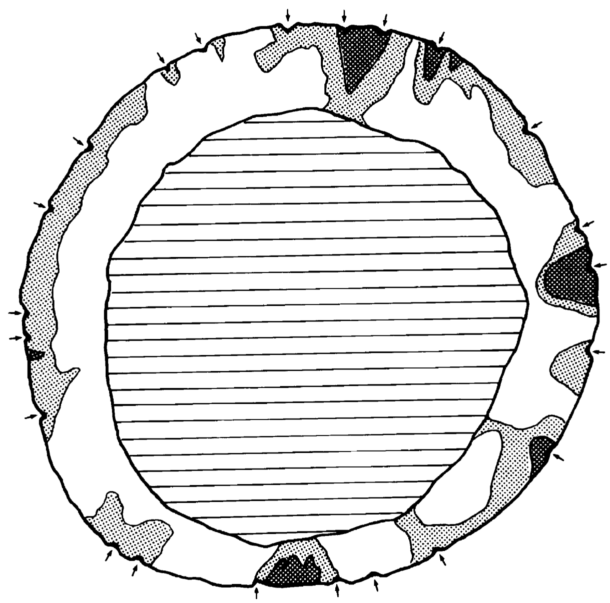

Figure 3 Cross-section of xylem of a lodgepole pine a few weeks after it has been successfully colonized by *Dendroctonus ponderosae*. Arrows show the position of egg galleries. The zone of blue-stained wood and the surrounding zones of wood with reduced moisture are shown with different degrees of stippling. The heartwood is hatched. Some of the patterns are due to the presence of other egg galleries above or below the section. Reproduced with permission from Reid RW, Whitney HS, and Watson JA (1967) Reactions of lodgepole pine to *Dentroctonus ponderosae* and blue stain fungi. *Canadian Journal of Botany* 45(7): 1115–1126.

regions of the world include Dutch elm disease caused by *Ophiostoma ulmi* and *O. novo-ulmi*, oak wilt (*Ceratocystis fagacearum*), and black stain root disease (*Verticicladiella wageneri*), which affects pines and Douglas-fir. A tropical example is takamaka wilt in the Seychelles caused by *Leptographium calophylli*. By contrast, in the vascular stains the fungus invades the rays, ray parenchyma, and inner bark at the same time as it colonizes the xylem elements. Some vascular stain diseases occur in standing trees. Examples are the *Ceratocystis* canker of deciduous trees caused by *C. fimbriata* and the pathogenic bluestain, caused by *C. polonica*, that develops in Norway spruce following trunk invasion by *Ips typographus*. Another pathogenic bluestain occurs in *Pinus contorta* in western North America following attack by the mountain pine beetle *Dendroctonus ponderosae* (**Figure 3**). Here two fungi, *C. clavigera* and *O. montia*, are carried to the trees on the beetles and are strongly implicated in overcoming host resistance. Other bluestains only develop if the trees lack active host resistance following felling or windblow. A European example is the stain caused by *Leptographium wingfieldii* that develops in *Pinus sylvestris* logs following attack by *Tomicus piniperda*.

Establishment of the Link Between Insect and Ophiostomoid Fungus in the Diseased Tree

Specialized plant pathogens are characterized by an expanding phase of parasitic growth in the living host and a declining phase of saprotrophic growth in the dead host. This is because qualities which fit the fungus for parasitism tend to put it at a disadvantage when it comes to prolonged survival in competition with other microorganisms. Any potential vector must have a life cycle that is completed before the disappearance of the fungus, and some likely candidates can prove to be of no significance.

An example is provided in myrtle wilt, a vascular stain disease of *Nothofagus* in Tasmania caused by *Chalara australis*. Very large numbers of the mountain pin hole borer, *Platypus subgranosus*, breed in trees killed by the fungus but while the *Platypus* has a 2–22-year life cycle, *C. australis* survives in the stems of dead trees for only 12–18 months. Hence, the lack of synchrony between the two species prevents the borer from vectoring the pathogen.

Of course, it is not enough for the fungus just to survive in the tree. It also needs to produce propagules that are suitable for insect dispersal. The ophiostomatoid fungi are typically very well adapted for this purpose, as illustrated in **Figure 4** for the Dutch elm disease pathogen *Ophiostoma novo-ulmi*.

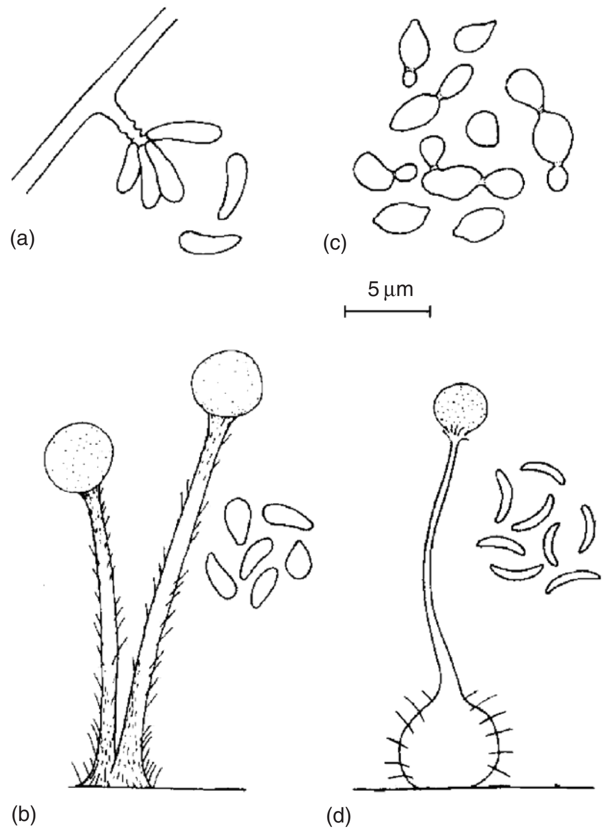

Figure 4 Spore forms and fruit bodies in *Ophiostoma novo-ulmi*. The scale applies to the spores only: (a) conidial or sporothrix stage; (b) stalk-like coremium (c. 1 mm tall) and coremiospores; (c) budding yeast-like stage; (d) flask-shaped perithecium (0.5 mm tall) and ascospores. The coremium and the perithecium are particularly well-adapted for insect dispersal. Courtesy of CM Brasier.

Transport of Ophiostomoid Fungi from Diseased to Healthy Trees

By definition a vector must move from a diseased to a healthy tree, or at least from a diseased part to a healthy part of the same tree. Scolytid beetles act as vectors of Dutch elm disease because, following emergence from their pupal chambers, the young adults often fly to feed in the twig crotches of healthy trees (**Figure 5**) before seeking out suitable fresh bark for breeding.

The method of spore transport, the behavior of the vector and the environmental conditions during dissemination can all influence the chances of successful disease transmission. With some vectors, spores are simply carried externally on the insect's exoskeleton and so are directly exposed to desiccation and ultraviolet radiation during flight. Studies on *Scolytus scolytus* in the UK during the 1980s showed that the mean percentage of beetles carrying *O. novo-ulmi* was over 89% in the pupal chambers but only 17% after emergence and flight.

Although fungi are much better protected if they are contained within the specialized carrying organs, mycangia, possessed by many bark and wood-boring beetles, it is a matter of record that few of the fungi transported in this way have much ability to cause tree disease or bluestain.

Temperature may also play an important part in disease transmission by regulating insect behavior. Although most vectors are commonly assumed to fly, the threshold temperatures for flight can often be quite high – at least 20°C in the case of the Dutch elm disease scolytid vectors. Indeed, the very temperatures which encourage insect activity can often be detrimental to the fungi they transport. For this reason, crawling may be more important than is generally recognized, and is crucial in the dissemination of *Verticicladiella wageneri* by various root-inhabiting beetles and weevils, which actively seek out stressed and diseased roots for oviposition.

Transfer and the Establishment of Infection with Ophiostomoid Fungi

Once the vector has reached a potential host tree, successful transfer of the fungus to susceptible plant tissue and the initiation of sustained disease again

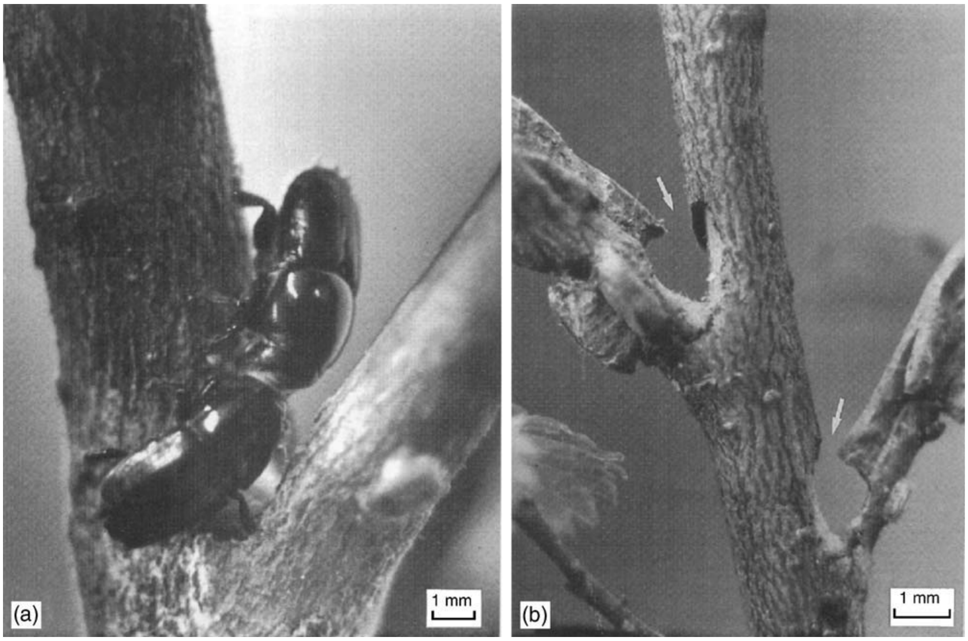

Figure 5 (a) Larger European elm bark beetle *Scolytus scolytus*, vector of Dutch elm disease; (b) feeding grooves (arrowed) produced by *S. scolytus* on *Ulmus procera*. Courtesy of Forestry Commission.

depend on several factors. These include the nature of the infection court, and the quantity of inoculum that is introduced to it.

Wounds are required in all known cases of infection by the Ophiostomataceae involving insect transmission, and, where bark beetles and weevils are involved, the insects are able to make the wounds themselves. However, with other kinds of insects, such as the sap-feeding nitidulids that vector the oak wilt pathogen *Ceratocystis fagacearum*, there is a dependence on wounds made in other ways, e.g., through the use of pruning tools or tree-climbing irons.

The depth of the wound may also be important. With the vascular wilt diseases like Dutch elm disease and oak wilt, the wound must reach the wood if the pathogen is successfully to penetrate and invade the xylem elements, whereas with a vascular stain disease like the *Ceratocystis* canker of fruit trees, a wound exposing live inner bark is all that is required.

The arrival of viable fungal spores in a suitable wound does not necessarily lead to disease. Infection depends on the number and physiological condition of the spores, and on the effects of competing microorganisms. Simultaneous host invasion from many infection points may also be necessary to overwhelm the resistance of a host which might otherwise be able to check the development of a single infection. This has been shown to be important with the vascular stain pathogen *Ophiostoma polonica* on Norway spruce, where doubling the number of inoculation points produced an almost eightfold increase in the amount of wood which succumbed to the pathogen.

Relationships in the Brood Galleries Between Insects and Ophiostomoid Fungi Causing Vascular Wilt Diseases

In a vascular wilt disease like Dutch elm disease, the pathogen can move rapidly away from the point of infection as spores are carried along in the transpiration stream. The result is that symptoms arising from a single infection can appear rapidly throughout the crown. Bark beetles can successfully establish breeding colonies in the trunk and major branches of such trees and, as the larval brood develops, there is the opportunity for a link to be reestablished with the fungus in the xylem. At the same time colonization of the inner bark can also take place from propagules of the pathogen still present on the parent beetles as the latter begin to establish breeding galleries. The subsequent ecological interactions between the beetle larvae and the various 'sources' of the fungus are quite complicated.

The survival of the fungus on the parent beetles also means that it can establish itself in brood galleries that are made in the bark of logs or windblown limbs from healthy trees. Young beetles emerging from such material can be just as effective in spreading the pathogen as beetles emerging from diseased trees. Failure to recognize this point greatly hampered early attempts to eradicate Dutch elm disease from the USA in the 1930s.

Insects as Agents for Fertilization in the Ophiostomoid Fungi

It is important to realize that, in the Ophiostomataceaea, as in many other groups of fungi, spore dispersal may be as important, or more important, for fertilization as for infection or substrate colonization. This is because they comprise two mating types and these have to be brought together for the sexual stage of the fungus to be produced. There may also be a link between dissemination for fertilization and dissemination for transmission. For example, in *C. fagacearum*, the cause of oak wilt, the switch from asexual spore to sexual spore production following fertilization prolongs the period over which inoculum is available for disease transmission.

Pine Wilt Disease: Caused by a Nematode, Vectored by Longhorn Beetles

The pine wood nematode *Bursaphalenchus xylophilous* is a native of North America where it causes little damage. However, following its introduction to Japan and subsequently to other countries in Asia, it has caused enormous losses to the native pines. Transmission is by several species of *Monochamus* (longhorn beetles in the Cerambycidae), and, as with the scolytid vectors of Dutch elm disease, these insects can introduce the pathogen both during maturation feeding and during oviposition (**Figure 6**). Within the vector, the nematode exists as a special larval stage, the dauerlarva, but once in the xylem of the healthy tree, the dauerlarvae molt to reproductive adults that mate and begin egg-laying. The first-stage larvae molt while still in the egg and then hatch as second-stage larvae that feed on host parenchyma cells. The larvae molt to third and fourth larval stages and then to adults that continue feeding and breeding. Once the tree dies, the nematodes survive on fungi (principally ophiostomoid bluestain fungi) before forming an overwintering stage. In the same trees, *Monochamus* larvae develop through various instars before pupating and emerging as adults in spring. The overwintering form of the nematode changes into dauerlarvae and these enter the tracheae of the callow *Monochamus* adults via the thoracic spiracles.

Diseases Caused by Phytoplasmas, Xylem-Limited Bacteria and Viruses and their Insect Vectors

These diseases are caused by a loose grouping of tree pathogens that share the characteristic of being unable to replicate except within living host tissue. *Inter alia*, this means that transmission from one host to another is essentially a passive operation. Insects

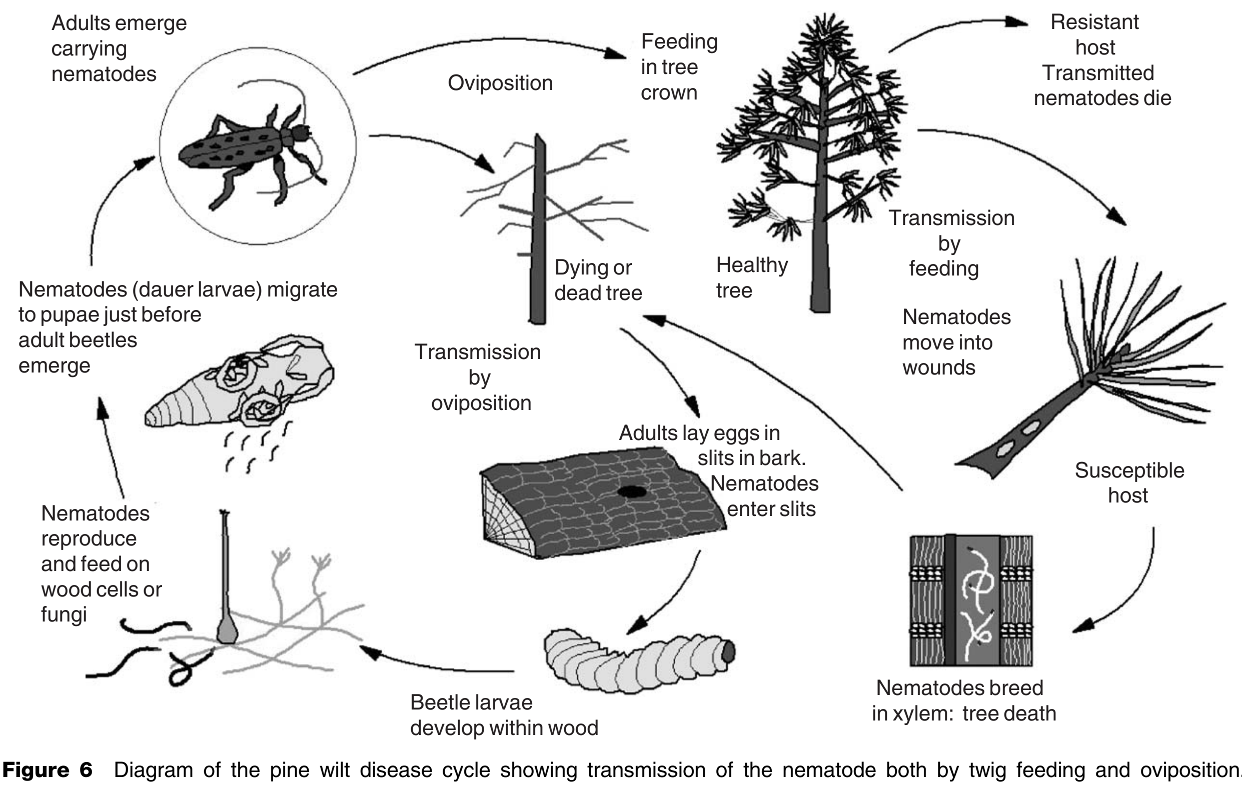

Figure 6 Diagram of the pine wilt disease cycle showing transmission of the nematode both by twig feeding and oviposition. Courtesy of HF Evans.

implicated in the process are all in the Homoptera, a group (suborder) that contains sucking insects such as aphids, leaf-hoppers, psyllids, and spittlebugs. However, only in comparatively few cases are the vectors known with certainty. Phytoplasmas, formerly known as mycoplasma-like organisms (MLOs), have the general characteristics of bacteria but lack cell walls. They can only invade the phloem where they replicate in the sieve tubes. Symptoms typically involve a yellowing of the foliage, followed by progressive dieback. Shoot proliferation resulting in the formation of witches' brooms may also occur. Important examples include elm and ash yellows in North America, lethal yellowing of coconut (widely distributed in the tropics) and, recently, sudden death of cabbage tree in New Zealand.

Detailed knowledge of the role of insects in transmission has been obtained from studies on elm yellows where the white-banded leafhopper, *Scaphoideus luteolus*, is known to be a vector. The pathogen is picked up by the insect during feeding on phloem sap in the leaf veins. It multiplies in the insect's salivary glands and is transmitted to the phloem of healthy trees during further feeding. Almost a year can elapse between infection and the development of symptoms. A planthopper *Myndus crudus* appears to be the principal vector of lethal yellowing of palms. This insect often lives among the roots of various grasses by day but migrates to palm trees at night.

The xylem-limited bacteria are smaller than other plant-pathogenic bacteria and, as the name indicates, are restricted to the host xylem. Strains that cause diseases of trees have been given the name *Xylella fastidiosa*. Symptoms in genera such as elm, plane, and oak include delayed leaf expansion, late-season leaf scorch, and dieback. Given the biology of the pathogen, it follows that their vectors are all xylem-feeding sucking insects. Many species have been identified through studies of the pathogen in the economically important Pierce's disease of grapevine but those involved in transmission to trees are not yet known. However, it is probable that nymphs as well as adult insects will be able to acquire and transmit *X. fastidiosa*. It is suggested that the bacteria form a plaque in the foregut and are flushed out by the sucking pump.

Many of the above-mentioned diseases were originally thought to be caused by viruses. When it comes to tree diseases caused by the true viruses (viruses consist of a nucleic acid core and a protein coat), very few have important insect vectors. One exception is plum pox where up to 20 species of aphid are thought to be involved in transmission.

Role of Insects in Complex Tree Diseases

Tree diseases of complex cause often go under the names of diebacks or declines. A good model for this type of disease involves various agents of stress acting on the tree which is then so much altered that it becomes vulnerable to organisms of secondary action, i.e., organisms that would be unable to cause significant damage to a healthy tree. Defoliating insects very often act as agents of stress, preventing the tree from carrying out photosynthesis and hence causing a depletion in essential food reserves. For example, the introduced gipsy moth (*Lymantria dispar*) plays this role in the condition known as oak decline in the northeastern USA, and so does the native oak roller moth (*Tortrix viridana*) in the somewhat similar condition in northern Europe known as oak dieback. Similarly, sucking insects can act as agents of stress by removing large quantities of sugars from the phloem. Thus in the condition known as beech bark disease, the scale insect *Cryptococcus fagisuga* builds up huge populations on the trunks of beech (*Fagus sylvatica* in Europe and *F. grandifolia* in North America) and renders the bark vulnerable to attacks by fungi (*Nectria* spp.) that would not normally be capable of damage.

Insects often also act as organisms of secondary action. Thus many beetles that are incapable of initiating a successful attack on a healthy tree will quickly establish breeding galleries in one that has been altered by various agents of stress. In North American oak decline, for example, it is the two-lined chestnut borer *Agrilus bilineatus* that often delivers the coup de grâce to a tree weakened by successive gipsy moth defoliations. Similarly many of the conifer bark beetles can cause mortality in trees weakened by drought.

See also: **Entomology**: Bark Beetles; Foliage Feeders in Temperate and Boreal Forests; Sapsuckers. **Pathology**: Diseases of Forest Trees; Pine Wilt and the Pine Wood Nematode; Vascular Wilt Diseases. **Tree Breeding, Practices**: Breeding for Disease and Insect Resistance. **Wood Formation and Properties**: Biological Deterioration of Wood.

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Heart Rot and Wood Decay

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Introduction

In natural ecosystems, there is a dynamic equilibrium between the accumulation of woody biomass and its breakdown. In this way, a permanent cover of trees or shrubs is maintained, while the carbon and minerals that they have fixed are recycled. At the same time, the survival of a range of woodland plants is fueled by the energy released in the breakdown of wood. Decay fungi play a major role in the processes of breakdown since, alone among microorganisms, they have evolved the means to break down large volumes of wood completely.

The balance between trees and decay fungi represents the state of play in a coevolutionary battle that has lasted for hundreds of millions of years, and in which wood has been the main prize. The success of trees as a dominant form of land vegetation has depended on their being able to maintain a perennating woody structure, which is their means of attaining both height and longevity. This defensive strategy protects the woody stem against loss of integrity of both its water-conducting and its mechanical properties. A range of agents, especially decay fungi, whose mode of attack is the degradation of the woody cell wall, can cause such damage.

Colonization of the Standing Tree

Heart rots were for a long time regarded as the primary cause of decay in standing trees. Whilst it is now clear that this is a considerable oversimplification, it remains true that in high forest and mature amenity trees heart rots are still a major cause of economic loss and deterioration. Based on the concept that either the distribution of water and its mutual relation with aeration are primary determinants of colonization patterns, five distinctive colonization strategies are recognized:

- heart rot
- active pathogenesis
- specialized opportunism
- unspecialized opportunism
- desiccation tolerance.

Most heart rot fungi have a stress-tolerant colonization strategy, i.e., they colonize the tree via exposed heartwood or ripewood (**Figure 1**). Although the heartwood of many tree species does exhibit a high concentration of antifungal extractives (e.g., polyphenols, tannins), heart rot fungi have adapted to the adverse conditions (low oxygen concentrations, high carbon dioxide concentrations, low moisture content). Thus, those features that render functionally intact sapwood nonsusceptible to decay are avoided. Moreover, after colonization of the tree via infection courts such as logging scars, branch stubs, fire scars, broken tops, pruning wounds, and severed roots, decay fungi can degrade the heartwood without inducing the host response system of the tree.

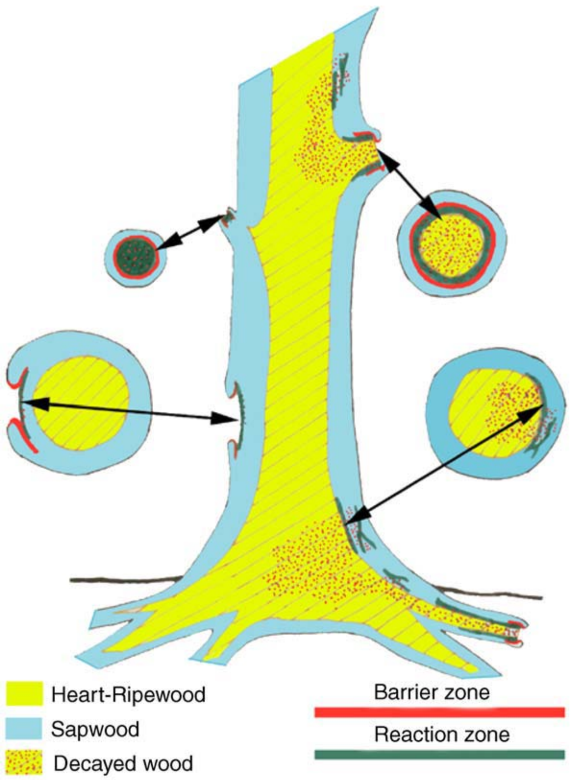

Figure 1 Infection points for decay fungi and associated host response mechanisms within the tree.