11 Ceratocystis Diseases

Thomas C. Harrington*
Iowa State University, Ames, Iowa, USA

11.1 Pathogens, Significance and Distribution

Most species of *Ceratocystis* are at least weakly pathogenic to woody plants, and some cause substantial losses. The genus *Ceratocystis* defines a closely related group of ecologically unique ascomycetes, and there are a number of epidemiological aspects and management considerations that are common to the diseases they cause. *Ceratocystis* spp. are generally associated with insects, mostly with beetles (Coleoptera). In their native ecosystems, these fungi are primarily wound colonizers and do not cause substantial damage to native hosts. However, some species have caused substantial tree mortality after being introduced to new forest ecosystems or to new cultivated hosts, and humans have fostered epidemics by plant wounding and mechanical transmission of the pathogens.

The focus of this chapter is the epidemiology and management of forest tree diseases caused by *Ceratocystis* spp., with emphasis on the three most important and studied diseases: oak wilt, canker stain on plane tree, and Ceratocystis wilt on eucalyptus. Kile (1993) wrote on diseases caused by *Ceratocystis* spp., and Harrington (2009) gave a brief overview of the biology of the genus. A recent symposium proceedings and a review on oak wilt cover a wealth of further information (Billings and Appel, 2009; Juzwik *et al.*, 2011). Panconesi *et al.* (2003) provide an account of canker stain on plane tree in Europe. Ceratocystis wilt on eucalyptus is an emerging disease in Brazil (Ferreira *et al.*, 2011).

Ceratocystis once included the much larger genus of *Ophiostoma*, which, along with the anamorph genera *Leptographium* and *Raffaelea*, are mostly saprophytic bark and ambrosia beetle associates, with a few plant pathogens: the cause of Dutch elm disease (*Ophiostoma ulmi* (Buisman) Nannf. and *O. novo-ulmi* Brasier), blackstain root disease on conifers (varieties of *Leptographium wageneri* (W.B. Kendr.) M.J. Wingf.), and laurel wilt (*Raffaelea lauricola* T.C. Harr., Fraedrich & Aghayeva) (Harrington, 2005; Harrington *et al.*, 2010). The biology of *Ceratocystis* spp. differs substantially from that of *Ophiostoma* spp., but the two genera have converged in respect of long-necked perithecia (sexual fruiting bodies) with sticky ascospore masses at their tip for insect dispersal. In contrast to *Ophiostoma* and its strong ties to bark beetles, most species of *Ceratocystis* produce fruity

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* E-mail: tcharrin@iastate.edu

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volatiles, presumably to attract their vectors, and their relationships with insects are varied (Harrington, 2009).

A number of asexual states have been noted for *Ceratocystis* spp., but these have been reduced to the genus *Thielaviopsis* (Paulin-Mahady *et al*., 2002; Harrington, 2009). All *Ceratocystis* spp. have one or two endoconidial states, in which asexual spores (conidia) are produced within deep-seated phialides. The cylindrical to barrel-shaped endoconidial states were earlier placed in the anamorph genus *Chalara*, which is now restricted to anamorphs of discomycetes. In addition to the thin-walled and short-lived endoconidia, many species of *Ceratocystis* form aleurioconidia, which are pigmented, thick-walled, clamydospore-like spores borne on specialized conidiophores.

Phylogenetic analyses (Harrington, 2009) indicate that there are at least five species complexes within *Ceratocystis*, but *C. fagacearum* (Bretz) J. Hunt (the cause of oak wilt), *C. adiposa* (E.J. Butler) C. Moreau, and some ambrosia beetle symbionts (members of the anamorph genus *Ambrosiella*) do not appear to have close relatives. The species complexes include the *C. coerulescens* (Münch) B.K. Bakshi complex, the large *C. fimbriata* Ellis & Halst. complex, the *C. paradoxa* (Dade) C. Moreau complex (on monocotyledon hosts, including palms), the *C. moniliformis* (Hedgc.) C. Moreau complex (saprophytic sap-stain fungi or weakly pathogenic wound colonizers) and a group of apparently asexual species, the *Thielaviopsis* complex (soil-borne pathogens of minor importance to forestry).

11.1.1 The *Ceratocystis coerulescens* complex

Most of these species cause blue-stain in the sapwood of *Pinaceae*, and some are associated with tree-killing bark beetles (Harrington and Wingfield, 1998). Angiosperm pathogens include *C. virescens* (R.W. Davidson) C. Moreau, the cause of sap streak of sugar maple (*Acer saccharum* Marsh.), and the related asexual species *Thielaviopsis australis* (J. Walker & Kile) A.E. Paulin, T.C. Harr. & McNew, which causes myrtle wilt on myrtle beech (*Nothofagus cunninghamii* (Hook.) Oerst.). *C. virescens* is native to eastern North America (Harrington *et al*., 1998) and has been locally important in reducing sugar yield and lumber quality in sugar maple ('sugar bush') stands managed for the collection of sap for maple syrup from Wisconsin to Maine (Houston, 1993). Myrtle wilt is important in the dynamics of myrtle beech-dominated temperate rainforests of Australia (Victoria and Tasmania), but is not of major commercial importance (Kile, 1993).

11.1.2 *Ceratocystis fagacearum*

The oak wilt pathogen is well placed in the genus *Ceratocystis*, but it is not closely related to any other species. It is unique in its capacity to cause a true vascular wilt disease and in its tight association with sap beetles (Coleoptera: Nitidulidae) (Harrington, 2009). Oak wilt is known only in the eastern USA, where it is a major cause of oak (*Quercus* spp.) mortality in many locations. The susceptibility of European and other exotic oaks has been demonstrated (MacDonald *et al*., 2001), and Chinese chestnut (*Castanea mollissima* Blume) is also susceptible, suggesting that *C. fagacearum* could be a threat to other forest ecosystems if accidentally introduced.

It has been suggested that *C. fagacearum* evolved in Mexico or Central America and was naturally introduced to the eastern USA in recent times (Juzwik *et al*., 2008b; Harrington, 2009). The fungus was first reported in the Upper Mississippi River Valley and may have spread from there to the Appalachian Mountains. It was probably killing oak trees in the Upper Midwest in the late 1800s (Gibbs and French, 1980), but was not confirmed in Texas until 1961, although it may have been present there since the 1930s (Appel, 1995a). Oak wilt is scattered across much of the eastern USA, but it is still 'filling in' within that range and is also expanding at the fringes (Juzwik *et al*., 2008b, 2011; Appel, 2009). The disease was recently reported in New York at about 300 km northeast of its previously known range (Jensen-Tracy *et al*., 2009). However, mortality due to oak wilt is generally not severe at the eastern edge of its distribution, where incidence may actually be decreasing (Juzwik *et al*., 2011).

The disease is known in 52 of 55 counties in West Virginia, but is sporadic in that region and losses are generally not heavy (Juzwik, 2009). In the Upper Midwest, loss of timber value due to oak wilt can be heavy (Haugen *et al.*, 2009), but losses of amenity trees are of greater economic importance. In Minnesota, oak wilt is in only 25 of the 65 counties with suitable forest types, but the disease can be severe, especially on sandy soils north of Minneapolis and east of Rochester (Juzwik, 2009). Members of the red oak group (section *Lobatae*), such as northern red oak (*Q. rubra* L.) and northern pin oak (*Q. ellipsoidalis* E.J. Hill), are highly susceptible, but some members of the white oak group (section *Quercus*), such as bur oak (*Q. macrocarpa* Michx.) and to a lesser extent white oak (*Q. alba* L.), are also affected. To the south, in the Ozarks of Missouri, the disease is widespread, but the disease centres are relatively small and losses are not great (Juzwik, 2009).

Oak wilt is very important in some locations in Texas, where the pathogen appears to be expanding its range (Appel, 2009). At least 2500 ha are affected by the disease in central Texas, but the wilt has not yet expanded to eastern Texas or Louisiana, where there are many susceptible oaks. The live oak (*Q. virginiana* Mill.) and the Texas live oak (*Q. fusiformis* Small) are members of section *Quercus* (series *Virentes*) but are susceptible to oak wilt, as are the epidemiologically important red oaks, Buckley oak (*Q. buckleyi* Nixon & Dorr) and blackjack oak (*Q. marilandica* Münchh.). Loss of property values and of historically significant trees, and the ecological impacts, have been considerable in central Texas, where thousands of aesthetically important oak trees are killed each year – probably millions of trees in total (Appel, 1995a; Juzwik *et al.*, 2011). The loss of oak habitat is a further threat to the endangered golden-cheeked warbler (*Dendroica chrysoparia*) (Greene and Reemts, 2009).

11.1.3 The *Ceratocystis fimbriata* complex

This complex is further broken up into clades: the African, Asian, North American (NAC) and Latin American (LAC) clades (Johnson *et al.*, 2005; Harrington, 2009). The African species *C. albofundus* M.J. Wingf., De Beer & M.J. Morris has been reported from Uganda and South Africa, where it can cause substantial mortality in plantations of black wattle (*Acacia mearnsii* De Wild.) (Barnes *et al.*, 2005). A canker disease of tapping panels on the rubber tree (*Hevea brasiliensis* (Willd. ex A. Juss.) Müll. Arg.) in Asia is also caused by a member of the complex (South and Sharples, 1925), and *C. larium* M. van Wyk & M.J. Wingf. was recently described from styrax (*Styrax benzoin* Dryand.) used for incense production (van Wyk *et al.*, 2009).

Three species in the NAC are capable of causing tree mortality. *C. populicola* A. Johnson & T.C. Harr. (Ceratocystis canker on poplars, *Populus* spp.) forms conspicuous cankers and causes some mortality on quaking aspen (*P. tremuloides* Michx.) in the USA and Canada (Hinds, 1972a; Johnson *et al.*, 2005). It has also been introduced to Poland, where it caused mortality of various *Populus* spp. in a limited area (Przybyl, 1984), but the pathogen apparently has not spread. *C. variospora* (R.W. Davidson) C. Moreau causes an important disease on almond and other stone fruits (*Prunus* spp.) in California, but it is only a minor wound pathogen on native forest trees in the Midwest (Johnson *et al.*, 2005). *C. smalleyi* J.A. Johnson & T.C. Harr. causes a wilt of bitternut hickory (*Carya cordiformis* (Wangenh.) K. Koch) and other hickories in the Midwest in association with the hickory bark beetle, *Scolytus quadrispinosus* Say (Johnson *et al.*, 2005).

The LAC includes *C. fimbriata s.s.*, *C. platani* (J.M. Walter) Engelbr. & T.C. Harr., and also *C. cacaofunesta* Engelbr. & T.C. Harr., the cause of Ceratocystis wilt or mal de machete on cacao (*Theobroma cacao* L.) (Engelbrecht and Harrington, 2005). *C. cacaofunesta* is native to the upper Amazon but has caused substantial mortality in cacao plantations wherever the fungus has been introduced (Engelbrecht *et al.*, 2007).

Ceratocystis platani

Canker stain is a lethal disease on sycamores or plane trees (*Platanus* spp.) in the USA and Europe. Epidemics were initially recognized in the eastern USA on the commonly planted street tree, London plane tree (*P. hybrida* Brot.; syn. *P. acerifolia* (Aiton) Willd.), a hybrid of the American sycamore (*P. occidentalis* L.) and the oriental plane tree (*P. orientalis* L.), though *C. platani* has also been found on American sycamore in natural riparian forests (Walter, 1946). An estimated 10,000 London plane trees out of an initial population of 153,000 were killed in the Philadelphia area, and some communities lost more than 80% of these trees during the 1930s and 1940s (Walter *et al*., 1952). However, the disease is no longer common in eastern US cities.

American sycamore trees are moderately resistant to the disease, and are generally scattered in natural stands, and rarely wounded, so losses due to canker stain in natural forests were considered minimal by Walter (1946) and Walter *et al*. (1952). Later, McCracken and Burkhardt (1979) reported losses of up to 30% in natural stands, and the potential losses in commercial plantations are high, especially in short-rotation stands managed from coppice or 'silage sycamore' for fibre production. However, there are several canker diseases on American sycamore, and some of the reported canker stain mortality in plantations may have been due to the presence of bacterial leaf scorch (*Xylella fastidiosa*) followed by secondary pathogens (*Botryosphaeria* spp.) (Britton *et al*., 1998) that cause cankers and xylem discoloration similar to that caused by *C. platani*.

C. platani is native to the eastern USA, but there have been at least two introductions: one to Modesto (California) and the other to Europe (Engelbrecht *et al*., 2004; Ocasio-Morales *et al*., 2007). In California, the disease was reported on street trees in the city of Modesto (Perry and McCain, 1988), where it has killed most of the London plane trees, the American sycamores and the California sycamores (*P. racemosa* Nutt.). The pathogen has probably been in Modesto for 50 years or more, but it has not been reported outside the city, though there is native riparian California sycamore nearby. The threat to native California sycamore and street trees in other communities remains substantial.

In Europe, the fungus was first recognized at Forte dei Marmi (Italy), although mortality attributable to canker stain was reported near Naples in the 1960s (Panconesi *et al*., 2003). It has been speculated that the fungus was brought into the Naples/Caserta area from the USA on wooden packing material used for military supplies during World War II (Panconesi, 1999). Genetic analyses (Engelbrecht *et al*., 2004) suggest that a single genotype of the pathogen was introduced into Europe and apparently spread throughout Italy, Switzerland and southern France, where the disease spread from the port of Marseilles (Ferrari and Pinchenot, 1976). In France alone, more than 50,000 trees have died, and the removal and replacement of each tree costs thousands of euros (Mollet, 2007). *C. platani* is now in the Toulouse region, and since 2006 has been found along the historic Canal du Midi, which is lined with more than 50,000 mature London plane trees, thousands of which have already died (A. Vigouroux, France, 2011, personal communication). There were earlier unconfirmed reports of canker stain in Spain, but the disease was recently confirmed in a small plantation near Girona (Riba, 2011).

Canker stain was reported from the Peloponnese peninsula in Greece in 2003, the fungus apparently having originated from Italy (Ocasio-Morales *et al*., 2007). This was the first report for canker stain in the native range of oriental plane tree, though the disease was severe on naturalized oriental plane trees in Sicily (Granata and Pennisi, 1989). In Greece, it has caused substantial mortality of oriental plane trees in natural stands along streams and rivers, as well as in ornamental plantings of both London and oriental plane trees. The disease could cause devastating losses to this important and historic riparian species, which extends naturally east into Turkey.

Ceratocystis fimbriata s.s.

The name *C. fimbriata* is herein restricted to populations that are native to South and Central America and the Caribbean (Harrington *et al*., 2011). On forest trees, *C. fimbriata* has its greatest economic impact on eucalyptus (*Eucalyptus* spp. and hybrids) plantations in Brazil, but it also can cause cankers (mouldy rot) on tapping panels of the rubber tree (Martin, 1949) and causes a lethal canker stain in gumhar (*Gmelina arborea* Roxb.) plantations in the lower Amazon (Muchovej *et al.*, 1978). Some strains on mango (*Mangifera indica* L.) in Brazil are closely related to the strains on eucalyptus (Ferreira *et al.*, 2010). A Brazilian strain introduced to Pakistan attacks mango and a valuable forest tree known as Indian rosewood (*Dalbergia sissoo* Roxb. ex DC.) (Poussio *et al.*, 2010).

C. fimbriata was first observed on dying eucalyptus trees in the south of Bahia, Brazil, in 1997 and is now common in former cerrado forests in Minas Gerais (Ferreira *et al.*, 2011). It has been discovered in six other Brazilian states, appears to be increasing in importance, and may now be considered the most important disease on *Eucalyptus* spp.

Several *Ceratocystis* spp. have been isolated from eucalyptus around the world, but these species are mostly simple wound colonizers that do not cause tree mortality (Harrington *et al.*, 2011). New *Ceratocystis* spp. that are probably synonymous with *C. fimbriata* have been found on wounds of eucalyptus in north-western South America, but it is not clear whether they are important pathogens. Reported mortality of eucalyptus in Uruguay, Congo, Uganda and South Africa is likely to have been caused by Brazilian strains of *C. fimbriata* (Roux *et al.*, 2000; Ferreira *et al.*, 2011; Harrington *et al.*, 2011).

11.2 Diagnosis

The important *Ceratocystis* spp. on forest trees colonize the sapwood and eventually kill their hosts. Crown or branch dieback often precedes death. Leaves on affected branches may fall off, or may be poorly developed or show chlorosis or other colorations before dying, giving a characteristic 'wilt' appearance to the crown (McCracken and Burkhardt, 1979; Houston, 1993). On some species, oak wilt may cause diagnostic leaf symptoms, including a bronzing of the leaf tips on members of the red oak group, and live oaks may show a striking necrosis and chlorosis along the leaf veins (Appel, 2009; Juzwik *et al.*, 2011). In general, sapwood discoloration is more characteristic of these diseases than leaf symptoms.

Only *C. fagacearum* causes a true vascular wilt (Harrington, 2009), and the deep sapwood staining following along the ray parenchyma, typical of other Ceratocystis diseases, is not evident in oak wilt. Oak wilt may be distinguished based on a ring of brown vascular discoloration visible in cross-sections of wilted branches, but the staining may not always be conspicuous (Juzwik *et al.*, 2011). The discoloration is often concentrated around certain vessels, and more or less evenly spaced within the growth ring. Oak wilt can sometimes be diagnosed by mat production under the bark of recently killed trees of the red oak group (Engelhard, 1955), but a more typical diagnostic characteristic is a cluster of symptomatic and killed trees in a discrete pocket (an infection centre).

Apart from the findings in oak wilt, the xylem discoloration caused by *Ceratocystis* spp. is not restricted to a particular annual ring. If there is branch dieback, extensive xylem discoloration can generally be found below the dying branch, on the main stem or, especially, at the base of the tree if the tree was infected through the root system (Walter, 1946). The discoloration is a combination of host response to infection and the pigmented hyphae and spores of the pathogen. Microscopic examination will show dark brown aleurioconidia in the stained sapwood (Panconesi *et al.*, 2003). Other fungi can induce xylem discoloration, especially in stressed hosts, but *Ceratocystis* spp. tend to stain the ray parenchyma more intensely than *Botryosphaeria* spp. or *Lasiodiplodia theobromae* (Pat.) Griffon & Maubl., which cause symptoms that are frequently confused with those caused by *Ceratocystis* spp.

In some hosts, *Ceratocystis* spp. can move out from the sapwood and attack the cambium and inner bark tissue, causing a canker. In aspen (*Populus* spp.), cankers may have substantial callus production and be flared at the margins (Hinds, 1972a). Long, inconspicuous cankers or a spiral–vertical series of small cankers may form in *Platanus* spp. that have little callus growth at the canker margins (Walter, 1946; McCracken and

Burkhardt, 1979; Panconesi, 1999). Older cankers on plane trees may be slightly sunken, with the dead bark dried and cracked.

Another common feature of these diseases is attack by ambrosia beetles (Curculionidae: Scolytinae and Platypodinae), which bore through the bark and into the xylem to excavate their galleries (Kile, 1993; Ocasio-Morales *et al*., 2007). Chopping into the tree where the ambrosia beetle frass is seen may reveal that the beetle bore holes are precisely placed in streaks of discoloured xylem. As adult ambrosia beetles tunnel in the sapwood of killed or dying trees, they push their frass outside the tree, and the fine powder accumulates in bark crevices or at the base of the tree, or is perhaps left as a 'toothpick' sticking out from the tree trunk. The pathogen may be isolated from the ambrosia beetle frass.

Because the above symptoms are not unique, isolation of the causal agent from discoloured sapwood or twigs is necessary for accurate diagnosis. No selective agar media are available, although some species, notably members of the *C. fimbriata* complex, can be isolated on fresh slices of carrot root (Moller and DeVay, 1968a). Many important *Ceratocystis* pathogens are homothallic and produce perithecia and ascospores rapidly on isolation media or on discoloured wood chips. Incubation of colonized plant tissue in a moist chamber may result in the production of perithecia with sticky ascospore droplets within a week. Even for heterothallic species like *C. fagacearum*, conidia will form within a few days on agar media. However, with any sample of discoloured wood, the ubiquitous *Fusarium solani* (Mart.) Sacc. may also grow on agar media or carrot slices and could be mistaken as a pathogen. Members of the LAC of the *C. fimbriata* complex may be isolated from soil using the carrot baiting technique (Laia *et al*., 2000) or from water using sycamore twigs (Grosclaude *et al*., 1988).

C. fagacearum does not form aleurioconidia and is more sensitive to heat and drying than other *Ceratocystis* spp., and it does not survive long in stem tissues (Merek and Fergus, 1954). Samples of living, discoloured wood are best be kept on ice or refrigerated before plating. Chips of the discoloured xylem or discs from small branches can be aseptically excised or surface sterilized and placed in acidified medium. Like the other *Ceratocystis* spp., the oak wilt fungus has a fruity smell in culture, though it may not be as strong as the banana-like smell of the *C. fimbriata* complex.

There are many cryptic species in *Ceratocystis* that differ little in morphology. Thus, accurate identification relies on DNA sequencing. The internal transcribed spacer (ITS) region of the nuclear ribosomal DNA region (rDNA) is useful for identifications (Harrington *et al*., 2011). For some species (such as *C. smalleyi* and *C. variospora*), the ITS-1 region has repetitive bases that may make PCR and DNA sequencing difficult. In the LAC, there are many regions of insertions/deletions in the ITS region, and there may be heterogeneity among the rDNA repeats, thus making sequencing difficult; the ITS region may then provide little useful phylogenetic information for the delineation of species.

11.3 Infection Biology

Inoculum may come in the form of conidia or ascospores carried by insects, or on tools and equipment, in frass of ambrosia beetles or other wood-boring insects, or in sawdust. All *Ceratocystis* spp. on woody hosts infect through wounds and move through sapwood tissue, mostly in ray parenchyma, and some also cause cankers (Harrington, 2009). However, *C. fagacearum* moves systemically through the host's xylem without attacking parenchyma tissue in the early stages of colonization. In some diseases in large trees, the pathogen may move from an infected to a healthy tree through functional root grafts (anastomosed roots). Species that form aleurioconidia are potentially soil-borne or water-borne and can directly infect roots.

11.3.1 Inoculum

Conidia and ascospores are produced on short-lived mats of mycelium that form on cut surfaces or on cankers (Harrington, 2009). Spores from mats may be important in dispersal via rain or animal vectors, or by the contamination of tools and equipment. However, the mats may be more important as a site for fungal feeding and the acquisition of spores by insects.

Black perithecia with long necks position wet masses of ascospores above the sporulating mat. Ascospores are thought to survive longer than conidia and may be more effectively dispersed (Merek and Fergus, 1954). Unlike conidia, ascospores are held together in a sticky, hydrophobic matrix, so the spores are not readily separated by water but, instead, have an affinity for the hydrophobic exoskeleton of insects. Many *Ceratocystis* spp. are capable of 'selfing' (homothallism), perhaps because of the unreliability of insect dispersal of conidia for the cross-fertilization of mycelial mats (Harrington, 2009). All species in the *C. fimbriata* complex and *C. virescens* are homothallic through unidirectional mating type switching. *C. fagacearum* is heterothallic, meaning that it can only reproduce sexually if two strains of opposite mating type come in contact; nitidulids visiting various mats acquire conidia and cross-fertilize mats. The importance of ascospores in the epidemiology of oak wilt is supported by the fact that the two mating types occur in nature in roughly equal proportions (Yount, 1954; Appel *et al.*, 1985).

Members of the *C. fimbriata* complex produce long-lived aleurioconidia on mats and in wood, and these probably contribute to survival of the fungus in the frass of wood-boring insects and sawdust (Harrington, 2009). Fungal propagules expelled from the trees during tunnel cleaning by adult ambrosia beetles may be dispersed by wind or rain splash for relatively short distances. The frass is highly infectious when placed on wounds.

T. australis does not produce aleurioconidia, but viable conidia and conidiophores are expelled by ambrosia beetle tunnelling (Kile, 1993). *C. fagacearum* was not isolated from frass expelled by ambrosia beetles attacking trees with oak wilt (Peplinski and Merrill, 1974), although it was isolated from the mycangia of ambrosia beetles, but it is unlikely that ambrosia beetles introduce *C. fagacearum* into living oaks (Harrington, 2009).

Aleurioconidia in frass or sawdust are likely sources of soil-borne inoculum. Members of the LAC are mostly soil-borne pathogens, as exemplified in Ceratocsystis wilt on coffee (*Coffea*) and citrus (*Citrus*) (Marin *et al.*, 2003), mango (*Mangifera*) and eucalyptus (Laia *et al.*, 2000; Ferreira *et al.*, 2011), and canker stain on plane tree (Mutto Accordi, 1989). The infection of roots via soil-borne inoculum has not been well studied, but it occurs quickly and commonly in eucalyptus planted on former forested sites (Ferreira *et al.*, 2011), and wounding may not be necessary.

11.3.2 Insect vectors

Most *Ceratocystis* spp. produce fruity odours in the form of small chain aliphatic alcohols and their esters, or fusel oils (fusel alcohols), which are thought to attract fungal-feeding insects (Lin and Phelan, 1992; Kile, 1993). Ethyl acetate and ethyl alcohol are particularly common. These compounds are toxic and may reduce grazing by insects that are not regular fungal feeders, thus leaving the mats for vectors, such as nitidulids, that typically tolerate high concentrations of mycotoxins (Harrington, 2009).

Many different groups of insects can acquire spores of *Ceratocystis* spp., but most of them do not transmit the pathogen to new wounds and are not vectors. Drosophilid flies (Diptera) and nitidulids have frequently been associated with mycelial mats, but most *Ceratocystis* spp. do not have specific insect vectors (Kile, 1993; Harrington, 2009). Nitidulids are commonly believed to be the primary vectors, but it is not always clear that they transmit spores to suitable infection courts, i.e. fresh wounds. *C. variospora* and *C. populicola* have been associated with nitidulids, but also with other insects (Moller and DeVay, 1968b; Hinds, 1972b; Johnson *et al.*, 2005). Nitidulids are contaminated with *C. albofundus* (Heath *et al.*, 2009) and *C. platani* (Crone and Bachelder, 1961), but the importance of these potential vectors is not known.

The association of nitidulids with *C. fagacearum* is particularly strong (Harrington, 2009). The fungus has a unique capability of producing mats under the bark of freshly killed trees and exposing the mats by splitting the bark (Gibbs and French, 1980; Juzwik *et al*., 2011). Pressure pads form in the middle of the mats on the xylem and phloem, and as the pads grow and push against each other, the bark is pushed away and cracks open. The sweet, melon-like odour emitted from the mat is believed to be attractive to nitidulids, which can enter through the cracked outer bark.

Many species of nitidulids inhabit *C. fagacearum* mats, but only a few species carry spores of the pathogen to fresh wounds (Juzwik *et al*., 2004; Ambourn *et al*., 2005; Hayslett *et al*., 2008, 2009; Juzwik *et al*., 2011). *Colopterus truncatus* (Randall) is an important vector in the Upper Midwest, Missouri and Texas; *Carpophilus sayi* (Parsons) also is a likely vector in the Upper Midwest; and *Colopterus niger* (Say) and *C. semitectus* (Say) also may be important in Missouri.

Only four species of *Ceratocystis* (*C. smalleyi*, *C. laricicola* Redfern & Minter, *C. polonica* (Siemaszko) C. Moreau and *C. rufipennis* M.J. Wingf., T.C. Harr. & H. Solheim) are known to be adapted to bark beetle vectors (Harrington, 2009). These species lack fruity odours, perhaps because their fusel oils are toxic, and bark beetles may not tolerate these volatiles. *C. smalleyi* is associated with the hickory bark beetle and mortality of bitternut hickory, but the aetiology of this mortality is not well understood, and the vector relationships need further study (Johnson *et al*., 2005).

Bark beetles may be significant vectors of *C. fagacearum* in regions where nitidulids are less effective (Rexrode and Jones, 1970). However, there is a growing consensus that bark beetles are much less important than nitidulids as vectors of *C. fagacearum* (Gibbs and French 1980; Hayslett *et al*., 2009; Juzwik *et al*., 2011).

11.3.3 Wound colonization and xylem movement

Fresh wounds to the xylem are the most important infection court for most species of *Ceratocystis*. On natural hosts, wound colonization is typically limited to a small area around the wound site, and the pathogen quickly sporulates on the exposed xylem and inner bark tissue around the wound, often under flaps of the bark surrounding the wound (Johnson *et al*., 2005). On highly susceptible hosts, a *Ceratocystis* sp. may extensively colonize sapwood tissue, causing a discoloration or stain and wilting and death of branches or whole trees as the host responds with tyloses and gums (Clérivet *et al*., 2000). Some of these diseases may also involve necrosis of the inner bark (cankers), which may be subtle (e.g. on plane tree and eucalyptus) or conspicuous (e.g. on almond and aspen) due to host responses, such as gummosis or rings of flared callous tissues, leaving a perennial or target canker.

Infected trees may die over a period of months to years. Vertical colonization of London plane tree may be greater than 2 m a year, and a tree of 30–40 cm diameter may be girdled within 2–3 years (Panconesi *et al*., 2003). Large American sycamores die within 6 years (McCracken and Burkhardt, 1979). *C. fagacearum* moves systemically through the non-living vessels as conidia, at least in the early stages of colonization, and longitudinal colonization may be particularly rapid. Red oaks and live oaks usually die within months, but bur oak survives longer, and white oak may survive many years with oak wilt (Juzwik *et al*., 2011).

Phytotoxins have been implicated in a number of diseases caused by *Ceratocystis* spp. Limp leaves and bright coloration patterns on the leaves of affected branches are evident in many of these diseases, including canker stain on plane tree and oak wilt. Aromatic fusel oils produced by *Ceratocystis* spp. are thought to be important in the attraction of insects, but these same compounds are phytotoxic and may have an important role in host–pathogen interaction (Tabachnik and DeVay, 1980). There has been substantial work on the importance of cerato-platinin in canker stain on plane tree (Bernardi *et al*., 2011).

Sapwood movement through functional root grafts can lead to extensive mortality in stands of mature trees. *T. australis* moves readily from tree to tree through functional root grafts (Kile, 1993), as does *C. platani* (Mutto Accordi, 1986). The oak wilt pathogen also moves through functional root grafts between trees (Juzwik *et al.*, 2011), and self-grafting (grafts among roots of the same tree) is important in the colonization of the root system of an individual oak tree (Blaedow and Juzwik, 2010).

11.4 Epidemiology

With many different potential sources of inoculum and dispersal mechanisms, Ceratocystis disease cycles are complicated and varied. Epidemics may occur where several favourable factors coincide, such as abundant sporulating mats, vector activity, wounding, mechanical transmission, root grafting or high levels of soil-borne inoculum. There is a history of localized outbreaks of short duration for some of these diseases.

11.4.1 Sporulation and vector activity

Sporulating mats are obvious sources of inoculum, but the dispersal of spores from mats to wounds has not been clearly demonstrated with many of these diseases. There is little doubt, however, that sporulating mats are important in oak wilt and canker stain on the plane tree.

Sporulating mats on firewood or logs may lead to the introduction of *C. fagacearum* to a new area (Appel, 1995b; Juzwik *et al.*, 2011). A recently discovered focus of oak wilt 300 km north-east of its previous known range was associated with the movement of firewood (Jensen-Tracy *et al.*, 2009). However, *C. fagacearum* only produces sporulating mats when the bark/wood interface is moist (Gibbs and French, 1980), so the intercontinental movement of the pathogen in debarked logs is not likely. In general, large sporulating mats of *C. fagacearum* are produced on members of the red oak group, suggesting that the fungus is naturally adapted to red oaks (Harrington, 2009; Juzwik *et al.*, 2011). No mats, or only a small number of small mats, are found on members of the white oak group (Engelhard, 1955).

Most oak wilt mats are produced in the spring and autumn in Minnesota. Spring mat production is dependent on minimum February temperatures and spring precipitation (Juzwik, 2009). Mats are also produced in the summer, but the most important nitidulid species are not frequently contaminated between late August and mid-October, and fresh wounds on oak are not as attractive to nitidulids at that time of year (Ambourn *et al.*, 2005; Juzwik, 2009). Mats produced in the spring are most important, and optimal mat production in the spring is usually on trees that became infected or wilted the summer before. The highest frequency of pathogen-contaminated nitidulids on oak wounds was in May in Minnesota and April in central Missouri (Juzwik *et al.*, 2004; Hayslett *et al.*, 2008, 2009).

Colopterus truncatus is an important vector because a high percentage of the population may be contaminated with *Ceratocystis*, and the beetle is strongly attracted to fresh wounds on oak. It has been found on wounds within 10 min of their creation (Juzwik *et al.*, 2011). Even so, the transmission of *C. fagcearum* is inefficient, sporadic and mostly local. Much higher numbers of contaminated *C. truncatus* were found in oak wilt stands than in stands free of oak wilt (Ambourn *et al.*, 2005). There is a higher efficiency of vector spread over shorter distances, and longer distance spread is spotty (Menges and Loucks, 1984; Shelstad *et al.*, 1991; Juzwik, 2009). Nitidulid transmission may be mostly limited to 1 km (Juzwik *et al.*, 1985), meaning that local sanitation programmes may be effective.

In Texas, live oaks are frequently killed, but they do not produce significant numbers of sporulating mats. Therefore, Buckley oak and blackjack oak provide most of the inoculum for insect dispersal, and these hosts are the target of sanitation programmes (Appel, 2009). Mats typically form in Texas from late winter through to the spring, and nitidulids are active and carry *C. fagacearum* from February to July (Hayslett *et al.*, 2009; Juzwik *et al.*, 2011).

Bark beetles probably do not play a major role in oak wilt epidemics, in part because the fungus is not adapted for sporulation in bark beetle galleries, and even if contaminated, bark beetles would not frequently feed in the xylem of healthy oak species and introduce spores to the vessels. In oak wilt infection centres in Minnesota, only four to 13 adults per thousand of the small oak beetle, *Pseudopityophthorus minutissimus* (Zimmermann), were contaminated with *C. fagacearum* in May and June (Ambourn *et al.*, 2006). In Europe, the bark beetle *Scolytus intricatus* (Ratzeburg) has been suggested as a potential vector of *C. fagacearum* because it has a life history and behaviour more suited to overland transmission than *Pseudopityophthorus* spp. (Webber and Gibbs, 1989). However, it is questionable whether *C. fagacearum* could become established in an ecosystem without suitable nitidulid vectors.

The thin bark of London plane tree allows for subtle cankers with inconspicuous sporulating mats, which produce inoculum that can be acquired by tools and equipment. *C. platani* sporulates within 24–48 h on canker surfaces, wounded parts of diseased trees and pruning cuts (Panconesi *et al.*, 2003). In the eastern USA, sporulation occurs during periods of high moisture content from May until October (Walter, 1946). These spores may be spread by insects or rain and enter soil or waterways (Walter, 1946; Crone and Bachelder, 1961; Panconesi *et al.*, 2003), but are probably most importantly spread by mechanical transmission on tools and equipment. Spores from mats do not normally spread far by rain or insects; only wounds on trees within 8 m of diseased London plane tree became infected in a field trial reported by Walter (1946).

11.4.2 Frass of wood-boring insects and sawdust

The activities of ambrosia beetles and other wood-boring insects appear to be particularly important in diseases caused by members of the LAC. The contaminated frass of the boring insects may be important for the wound colonization of nearby trees, for contributing to soil-borne inoculum and for contamination of waterways. Similarly, sawdust created in the removal of diseased trees is important in canker stain on plane trees.

The boring activities of the oak pinhole borer (*Platypus cylindricus* Burmeister; Curculionidae: Platypodinae) may be contributing to the rapid spread of canker stain in natural riparian forests in Greece (Ocasio-Morales *et al.*, 2007). Other wood-boring insects are thought to be similarly important in Italy (Panconesi *et al.*, 2003). More important in urban forests are the aleurioconidia that are released in sawdust. *C. platani* may remain viable in killed trees for 2 years or more (Grosclaude *et al.*, 1993; Panconesi, 1999), so the trees remain a continued source of inoculum as they are degraded by the activities of insects. However, removal of the trees produces abundant infectious sawdust that can blow in the wind to infect wounds or enter waterways.

The frass of ambrosia beetles attacking diseased eucalyptus trees is known to harbour viable inoculum of *C. fimbriata*, and frass from ambrosia beetles, termites and other wood-boring insects probably contributes to soil-borne inoculum (Ferreira *et al.*, 2011). Although soil-borne inoculum from cleared natural forests or cultivated woody crops may lead to high levels of mortality of planted eucalyptus, it is not clear whether rotations of susceptible eucalyptus clones increase the levels of soil-borne inoculum. This is of particular concern where *C. fimbriata* has been brought into new regions or to former pasture sites in eucalyptus cuttings because such introductions could lead to high disease levels in later rotations.

There has been speculation that *C. platani* was introduced into Italy from the eastern USA on solid wood packing material (Panconesi, 1999). Although it is possible that *C. platani* produced mycelial mats on the cut surfaces of such wood, it is unlikely that the fungus would produce a fresh mat with spores on dried wood after arrival in Europe. It is more likely that ambrosia beetle activity in the wood released *C. platani* in frass (Ocasio-Morales *et al.*, 2007). The sporulation of *C. fimbriata* on or in eucalyptus wood shipped from Brazil to South Africa may have led to the introduction of the pathogen (van Wyk *et al.*, 2009), but the fungus could also have been introduced in eucalyptus cuttings (Ferreira *et al.*, 2011; Harrington *et al.*, 2011).

11.4.3 Wounding and new infection centres

Many epidemics caused by *Ceratocystis* species have been associated with a high incidence of wounding (Kile, 1993). Wounding is important for sap streak of maple in managed sugar bush stands in which the bases of trees are often wounded by equipment during the collection of maple sap. Most of the infections are along roads or near work buildings, and wounds made in the spring when the soils are wet are particularly subject to infection (Houston, 1993). In Wisconsin, 5% of wounded maple trees had sap streak (Mielke and Charette, 1989).

Wounding during commercial harvesting and timber stand improvements can lead to substantial levels of oak wilt in Wisconsin and Michigan (Haugen *et al.*, 2009). However, the pruning of amenity trees, tree damage during building construction and other human activities are more commonly associated with new oak wilt infection centres in non-commercial forests. Wounds on oak are suitable for infection for only a few days (Zuckerman, 1954; Cobb *et al.*, 1965), and timing is critical. The highest frequency of successful nitidulid transmission is during the spring, when the mycelial mats are most abundant, there are large numbers of nitidulids carrying the fungus and wounds to the xylem are most susceptible to infection (Juzwik, 2009).

Because the vector–pathogen relationship is inefficient, new introductions to an oak stand are rare but important events in predicting losses (Menges and Loucks, 1984). The initiation rates of new oak wilt infection centres vary greatly among regions, and these rates generally relate to the severity of the disease. Juzwik (2009) summarized reported rates of new foci that ranged from 0.42 ha^{-1} yr^{-1} in Minnesota and Wisconsin to <0.07 in Missouri and <0.006 in Illinois. Rates of new infection centres were much lower in Pennsylvania and West Virginia and even lower still in North Carolina and Tennessee. In a survey of the Fort Hood Military Installation in Texas, there was only one new disease centre per 150 ha^{-1} $year^{-1}$ (0.007 foci ha^{-1} $year^{-1}$) (Appel, 2009), but the large and rapidly expanding infection centres resulted in substantial mortality of live oaks.

Although some stream-side American sycamores were infected through natural wounds made by driftwood, human-caused wounds were the only important infection court in the London plane tree (Walter, 1946). At an undisturbed (no wounds) study site of London plane trees with high levels of disease, no new infections occurred after 4 years. Only small wounds are needed for infection, and the thin outer bark of the London plane tree makes it highly susceptible to wounding. Wounds are only susceptible to infection for a few days (Walter, 1946; Vigouroux and Rouhani, 1987).

In the eastern USA, it was realized that pruning activities not only provided an infection court for the pathogen, but that the wound dressings commonly applied to pruning cuts carried inoculum in the form of sawdust that had fallen into the open cans of pruning paint that hung from the belts of tree trimmers (Walter, 1946; Walter *et al.*, 1952). Pruning followed by the application of tree paint to the wounds so caused led to higher infection levels than did pruning alone (Walter *et al.*, 1952). Inoculated wounds and unpainted wounds on London plane trees were not infected from 1 December to 15 February in New Jersey, though wounds sealed during this period with sterile tree paint resulted in 25–50% infection, apparently due to the insulation of the wounds from cold winter temperatures (Walter, 1946).

11.4.4 Mechanical transmission

Although *C. fagacearum* could possibly be moved tree to tree on pruning equipment (Bretz, 1951), it survives in sawdust for <1 day (Merek and Fergus, 1954) and only sporulates under the bark. *C. variospora* and other species that are known to be mechanically transmitted form aleurioconidia in sapwood, but sporulation on the outside of the tree may be more important (Teviotdale and Harper, 1991).

The mechanical transmission of *C. platani* is central to epidemics of canker stain on London plane trees. Contaminated pruning saws, tree paint and climbing ropes were important in the early epidemics in the eastern USA. The pathogen infected 40% of the wounds made by saws that had been previously used on diseased trees (Walter, 1946). Sawdust from diseased trees contaminated tree paint, in which *C. platani* was viable for months, and treating pruning wounds with this paint greatly increased infection probability (Walter *et al.*, 1952). Climbing ropes used on diseased trees and then used on healthy trees on the same day resulted in infection of 50% of the trees, and on the next day, 25% of trees were infected via the ropes (Walter, 1946). The fungus is also transmitted on saws in plantations of American sycamore managed from coppice.

The epidemiology of canker stain in Europe is complicated by modern machinery, especially terracing (earth-moving) equipment, which may acquire the fungus from sporulating cankers or bits of wood and mechanically transmit it to new locations as it wounds the thin-barked trees (Blankart and Vigouroux, 1982; Panconesi *et al.*, 2003). Such equipment is frequently moved within and among cities and is believed responsible for initiation of many new disease centres. The very rapid spread of *C. platani* from city to city in Italy (Panconesi, 1999) was most likely due to mechanical transmission on tools and equipment. The recent introduction to Gerona (Spain) was associated with terracing equipment (A. Vigouroux, France, 2011, personal communication).

Mechanical transmission is likely to be responsible for the dramatic rates of tree mortality within cities. In Gloucester (New Jersey), a canker stain epidemic began in 1926 in a 1915 planting of 279 London plane trees (Walter *et al.*, 1952). Some 14 years later, in 1940, the percentage of trees that were symptomatic or killed was 63%; after 17 years it was 73%, after 20 years it was 86% and after 23 years it was 91%. In the first 20 years after canker stain was discovered in Forte dei Marmi (Italy), 90% of the London plane trees had died (Panconesi, 1999). Well after the initial establishment of canker stain in Marseilles, 1850 mature London plane trees (about 13% of the initial population) were killed between 1960 and 1972 (Ferrari and Pichenot, 1976).

C. fimbriata will produce mycelial mats on wounded eucalyptus trees and stumps, so mechanical transmission may be important. Eucalyptus trees in plantations are commonly wounded during weed control operations and other activities. High incidence of Ceratocystis wilt has been noted in plantations that were cut and managed for sprout production for rooted cuttings (Ferreira *et al.*, 2011), and these stools may have been infected by contaminated saws during the harvest or by contaminated scissors and other tools used to collect the cuttings for rooting. It is likely that the fungus is spread throughout nurseries as workers harvest cuttings from hedge plants with contaminated tools.

11.4.5 Vegetatively propagated material

An often unappreciated fact is that many species in the *C. fimbriata* complex have been introduced to new areas in vegetatively propagated material. Corms, storage roots and slips of vegetable and ornamental crop plants have been known to harbour these fungi (Engelbrecht and Harrington, 2005; Thorpe *et al.*, 2005). Mechanical transmission may facilitate contamination of the propagated material in the nursery. Source plants, rooted cuttings and grafted scions may be asymptomatic when heavily watered, allowing for the unwitting distribution of thousands of infected plants.

C. fimbriata may have been moved from Brazil to Pakistan and Oman in infected mango stock (Ferreira *et al.*, 2010; Harrington *et al.*, 2011), *C. cacaofunesta* has been moved among various research stations in Latin America in cuttings from cacao trees (Englebrecht *et al.*, 2007), *C. populicola* was found in vegetatively propagated poplar in Canada and Poland (Przybyl, 1984; Vujanovic *et al.*, 1999; Johnson *et al.*, 2005), and the recent introduction of *C. platani* to Greece was thought to be on grafted cuttings of London plane tree from a nursery in Italy (Ocasio-Morales *et al.*, 2007). Infected eucalyptus cuttings have been shown to be important in bringing *C. fimbriata* to new regions and to former pastureland that had little or no soil-borne inoculum of the fungus (Ferreira *et al.*, 2010, 2011; Harrington *et al.*, 2011).

11.4.6 Root graft transmission

Movement through functional root grafts is potentially important for diseases affecting trees of sufficient age and size. The initiation of new disease centres is relatively rare in myrtle wilt, but many massive trees can be killed through the expansion of infection centres by root graft transmission (Kile *et al.*, 1989).

Many more oak trees are infected by *C. fagacearum* through root grafts than through wounds (Bruhn *et al.*, 1991; Appel, 1995b). Root grafting varies greatly among oak species, from 70% in northern pin oak to only 6% in bur oak (Parmeter *et al.*, 1956). A higher percentage of oak trees infected through root graft transmission and larger disease centres were found in stands with higher percentages of red oak (Menges and Loucks, 1984). The probability of transmission between two trees of the same species increases with tree size and decreases with distance between the two trees, but the speed of underground transmission is not related to these two factors (Menges and Kuntz, 1985). More root graft transmission is seen in lighter textured soils than in heavier soils (Prey and Kuntz, 1995). Some grafting also occurs between different species of oaks, but the importance of interspecific grafting in transmission is unknown (Juzwik, 2009).

The regional importance of oak wilt may correspond with the amount of root grafting of susceptible species. Expansion of disease foci averages 1.9–7.6 m yr^{-1} in Minnesota and up to 12 m yr^{-1} in Michigan, with the highest rates found on the sandiest soils where there may be mortality of 8–11 red oaks ha^{-1} yr^{-1} (Bruhn and Heyd, 1992; Juzwik, 2009). The mortality rate is lower in Pennsylvania (1–3 oaks $centre^{-1}$ yr^{-1}) and West Virginia (0.19–0.39 oaks $centre^{-1}$ yr^{-1}) (Jones, 1971; Mielke *et al.*, 1983). Expansion rates of up to 50 m yr^{-1} were estimated in infection centres in live oak stands in Texas (Appel, 2009).

As an affected tree dies, water flow is disrupted owing to the formation of tyloses, and the transpiration pull of the tree diminishes. This pulls the water and the fungus into the root system of a grafted healthy (transpiring) tree. Cutting a diseased tree also facilitates such undesirable pathogen movement into a root-grafted, healthy tree (Nair and Kuntz, 1975). *C. fagacearum* may survive for up to 5 years in the grafted roots of killed trees (Skelly and Wood, 1974).

Root graft transmission is also important in the movement of *C. platani* (Mutto Accordi, 1986). Clonal propagation of the London plane tree may facilitate root graft transmission because trees planted along a street are likely to be genetically identical and likely to form functional grafts. The pathogen can quickly move from tree to tree along avenues of mature London plane trees, and sanitation measures must include not only symptomatic trees but also their asymptomatic neighbours.

Root graft transmission of American sycamore in natural forest stands may not be important because the trees are generally scattered in floodplain forests. Plantations of American sycamore are typically harvested within 15 years, so root grafting may not be common. Eucalyptus plantations in Brazil are typically harvested after 7 years, and grafting is not likely to be common or important.

11.4.7 Soil-borne and waterborne inoculum

Aleurioconidia of *C. platani* are abundant in stained sapwood and, once liberated, can infest soil (Mutto Accordi, 1989) and waterways (Grosclaude *et al.*, 1988, 1991; Vigouroux and Stojadinovic, 1990). As *Platanus* spp. are riparian and frequently planted along waterways, the pathogen may be able to spread quickly in water. Canker stain is spreading rapidly through the London plane trees that line the Canal du Midi (A. Vigouroux, France, 2011, personal communication). The production of ambrosia beetle frass from diseased oriental plane trees in Greece is apparently leading to the rapid spread of *C. platani* on this species in natural watercourses (Ocasio-Morales *et al.*, 2007). The similarly rapid spread of canker stain on naturalized oriental plane trees in Sicily was also thought to be due to water movement (Granata and Pennisi, 1989).

C. fimbriata appears to be native to certain forest types of Brazil (Ferreira *et al.*, 2010; Harrington *et al.*, 2011). Eucalyptus planted to former cerrado forest sites in Minas Gerais can have very high levels of disease due to soilborne inoculum (Ferreira *et al.*, 2011). Susceptible clones planted on former forest sites may begin to show symptoms and mortality at 15–20 months after planting, and the disease then progresses in a manner typical of a soilborne disease; that is, a monomolecular model in which infections are due to an initial inoculum level, and the inoculum level does not increase during the rotation of the crop (Ferreira, 2009). Greater than 60% mortality has been noted 3 years after planting (Ferreira *et al.*, 2011). It is not known whether soil inoculum levels increase during eucalyptus rotations or during harvest of the plantation, but this could be a major consideration for future rotations of that species.

11.5 Management Strategies and Tactics

11.5.1 Avoidance

Wound avoidance is key to management of some diseases caused by *Ceratocystis* spp., including sap streak of sugar maple (Houston, 1993). There was no difference in sap streak incidence between stands logged during frozen versus non-frozen conditions in Wisconsin (Mielke and Charette, 1989), but Houston (1993) found that most infections occurred through wounds made during spring (the mud season) when soils were wet and roots were frequently injured by tractors and other equipment. Avoidance of such activity at that time of the year was recommended.

Most oak wounds infected by *C. fagacearum* are made in spring or early summer, so harvests should be curtailed during these periods (Haugen *et al.*, 2009; Cummings Carlson and Martin, 2010). In urban settings, pruning wounds made in the spring and early summer have a much higher probability of infection than pruning wounds made in late summer, autumn and winter. In a wounding study in Minnesota (Juzwik *et al.*, 1985), wounds made from May to mid June became infected, and the advertised slogan in Minnesota is 'Do not prune in May or June'. Based on the activity of vectors, April is the month of highest risk of wound infection in Missouri, but avoidance of wounds from April to June has been recommended (Hayslett *et al.*, 2008, 2009). In Texas, wounding should be avoided in late winter and spring (Hayslett *et al.*, 2009). It is not advisable, however, to delay treatment of storm-damaged trees. When pruning is absolutely necessary, a protective layer of latex paint can be applied immediately after pruning to protect the wound from infection (French and Juzwik, 1999).

The canker stain epidemics in eastern USA during the 1920s to the 1940s were associated with pruning wounds (Walter *et al.*, 1952), and avoidance of pruning was an important management strategy. Sporulation on cankers occurred during the moistest periods from May through to October, but Walter (1946) recommended that pruning should be done between 1 December and 15 February. Sanitation was the primary management tool, however, because total avoidance of wounding was not feasible.

In Europe, pruning was just part of the problem because terracing and other equipment had proven to be major wounding agents and a means of mechanical transmission (Blankart and Vigouroux, 1982; Panconesi *et al.*, 2003). None the less, it is recommended that pruning should be avoided or done in the coldest and driest months of the year, along with the application of fungicide to the pruning cut (Panconesi, 1999).

Ceratocystis wilt on eucalyptus on pastureland in Brazil can be avoided if disease-free cuttings are planted (Ferreira *et al.*, 2011). Disease incidence is low in such locations because soil inoculum levels are low due to the absence of woody hosts. Clean nursery stock can be produced if care is taken to avoid the collection of cuttings from diseased mother trees. Carefully monitored mini hedges in nurseries appear to be the best source of disease-free cuttings (Ferreira *et al.*, 2011).

11.5.2 Exclusion

Ceratocystis spp. have been frequently introduced to new areas by human activity, and international quarantines have been considered or are in place. Infected planting stock (especially rooted cuttings or grafted scions) is the most likely pathway of introduction, but restrictions on the movement of such stock are inadequate. The frass from wood-boring insects or spore-producing mats on wood taken from diseased trees is another potential pathway. Lastly, contaminated pruning tools and equipment can introduce pathogens such as *C. platani*.

Although the biology and history of oak wilt suggests that accidental introduction of *C. fagacearum* over long distances is unlikely (Harrington, 2009), *C. fagacearum* is categorized as an A1 quarantine pest by the European and Mediterranean Plant Protection Organization (EPPO) and is of quarantine significance for the Inter-African Phytosanitary Council (IAPSC) and the North American Plant Protection Organization (NAPPO). EPPO (2010) has requirements for the import of plants for planting and seed of *Quercus* spp. from the USA because of *C. fagacearum*, even though oaks are not normally vegetatively propagated, oak wilt does not commonly occur in nurseries, and seed transmission of the pathogen is highly unlikely. Options for importing oak wood (timber) from the USA include bark removal in conjunction with heat treatment, radiation or fumigation, though treatment of debarked logs may not be necessary. Mycelial mats form under the bark but only when the sapwood and inner bark tissue are moist (Gibbs and French, 1980), and the fungus does not survive long in stem wood, especially if it is debarked (Merek and Fergus, 1954). EPPO also includes in its regulations the quarantine of potential vectors – the timberworm *Arrhenodes minutus* (Drury) and the bark beetles *Pseudopityophthorus minutissimus* and *P. pruinosus* (Eichhoff) – though these are not considered to be efficient vectors. Nitidulid vectors are not listed.

In contrast to *C. fagacearum*, *C. platani* has been frequently introduced to new regions through human activity. Planting material of *Platanus* spp. should be obtained from regions where canker stain does not occur (EPPO/CABI, 1997). The recent introduction in Greece is likely to have been through infected planting stock from Italy, where canker stain is widespread (Ocasio-Morales *et al.*, 2007). It is further recommended that pruning tools are disinfected, even when used in uninfested regions (EPPO/CABI, 1997). All terracing machinery used in the vicinity of canker stain should be treated before moving it to another site. Blankart and Vigouroux (1982) recommended cleaning with a water jet and 8-hydroxyquinoline sulfate. Saws and climbing ropes are other important means of mechanical transmission and introductions to new areas. The single introduction of *C. platani* to Europe from the USA on solid wood packing material is unlikely to be repeated because there are no longer epidemics of canker stain in urban areas of the USA to supply cheap wood for packaging. Also, there are now better safeguards for treating solid wood packing material (FAO, 2009), which should help to control the activity of wood-boring insects and the release of *C. platani* in insect frass.

11.5.3 Eradication

Complete eradication of an exotic *Ceratocystis* sp. from even a limited area is a difficult task, but local introductions may be eliminated if recognized quickly, and sanitation practices have proven effective in managing local epidemics.

Because overland spread of *C. fagacearum* by nitidulids tends to be localized, the probability of infection can be reduced if symptomatic oak trees in the area are removed before mats form. Removal of all symptomatic and recently killed trees is generally recommended, as well as that of neighbouring asymptomatic trees that may already be infected. The goal is twofold: to remove potential mat-producing trees and to produce a barrier to root graft transmission. Trees that die in late summer are most likely to retain sufficient moisture and produce mats the next spring, so they are the focus of sanitation practices. Treatment of stumps of diseased trees with ammate, aresenite, or 2,4,5-trichlorophenoxyacetic acid (2,4,5-T) has been shown to somewhat reduce the survival time of *C. fagacearum* in roots (Merek and Fergus, 1954).

Portions of diseased trees greater than 5 cm diameter should be removed or destroyed before spring mat production and nitidulid activity (Haugen *et al.*, 2009). Cutting the diseased trees while still alive risks the rapid movement of conidia in the sapwood into adjacent, root-grafted trees, so it is recommended that roots are severed before felling. Mats can be produced on felled trees left on site (Morris, 1955), but the wood of diseased trees can be utilized for wood products, or chipped, burned or buried, so long as the bark is removed and the wood is dry before mats can form in the spring (French and Juzwik, 1999). Firewood can be used if it is debarked to promote drying or if stacked firewood is covered with plastic to prevent access by nitidulids (Haugen *et al.*, 2009).

An alternative to felling and removing symptomatic trees is girdling, which generally reduces the moisture content of the trees and lessens the probability of mat production (Gillespie *et al.*, 1957). Basal girdling of diseased red oaks in Texas reduced mat production, but was not effective in reducing disease levels, probably because most of the trees there are infected through root graft transmission (Greene *et al.*, 2008). Girdling trees that are part of a large, common root system probably does not slow underground spread of the pathogen.

Attempts have been made to eradicate *C. platani* from pockets of infection in southern Europe, but these attempts have mostly proven unsuccessful and are quite costly. The eradication of small, isolated infection centres that have not yet spread far, such as the recent effort in north-eastern Spain (Riba, 2011), can be successful. The widespread nature of the affected area in the Peloponnese peninsula in Greece may have led to the decision not to eradicate *C. platani*.

Sanitation was effective in managing canker stain in urban settings in the eastern USA (Walter, 1946). If a branch is infected, a London plane tree could be saved by severing the branch, if there was a clearance of 1 m between the cankered branch and the nearest trunk, but most symptomatic trees should be removed. Tools and equipment used on diseased trees should be disinfected with alcohol, sodium hypochlorite or other chemicals. These efforts began to quickly quell the epidemics in the eastern USA (Walter *et al.*, 1952), but a well-designed sanitation programme was not effective in stopping the epidemic of canker stain in Modesto, California (Perry and McCain, 1988), and canker stain remains a major issue in Europe in spite of sanitation efforts.

The prompt removal of diseased trees is recommended in Europe. In addition to the removal of symptomatic trees, at least one healthy plane tree should be removed on either side of the infected trees (Panconesi, 1999). Treatments with glyphosate or other herbicides are used to kill the root systems and prevent further spread via root graft transmission. When diseased trees are removed, a minimum of cutting is recommended, and all sawdust generated should be collected in tarps and properly disposed of (Plate 13). Traffic in the area should be minimized to prevent the wind movement of sawdust, and trees should not be sawn on a windy day. As much of the root system should be removed as possible, as well as removing the contaminated soil. The entire area should be treated with disinfectant or fungicide. Equipment can be treated with alcohol or sodium hypochlorite (Panconesi, 1999; Panconesi *et al.*, 2003).

Care should be taken to avoid mechanical transmission during sanitation practices in diseased commercial stands of American sycamore. Initially, McCracken and Burkhardt (1979) recommend felling diseased trees and suggested that the trees need not be removed because the fungus does not remain alive long. However, it is now known that the fungus survives for long periods as aleurioconidia in sapwood, and that the logs should be removed or otherwise disposed of before ambrosia beetles and other wood-boring insects enter and release contaminated frass.

11.5.4 Protection

Fungicide injections

Wilts of trees are difficult to manage with fungicides because of the large mass of xylem tissue to treat and the difficulty of delivering a sustained dose of protection throughout the tree at a reasonable cost. The high cost and the injury to the tree in the injection process must be balanced with the likelihood that the treatment will lower the risk of infection. Preventive treatment for oak wilt may only delay disease development rather than give complete protection. Therapeutic or protective fungicide treatments for London plane trees have not met with success (Panconesi, 1999).

The most effective treatments for oak wilt have been below-ground injection of large volumes of dilute systemic triazoles (namely, propiconazole) into root flares. Soil application or injections of lower volumes of more highly concentrated propiconazole may also be effective (Wilson, 2005), but even the high volume injections do not completely stop colonization of the host nor completely eradicate the fungus (Blaedow *et al.*, 2010). Beside the cost, the limitations of propiconazole are its somewhat restricted movement into the root system (where preventive doses are needed) and its short-lived nature in a living tree. The concentration of propiconazole in injected trees decreases substantially in the first year and is below detectable levels within 2 years.

Preventive treatment of red oaks within grafting distance of diseased red oaks only delays progression of the disease, so treatments may need to be applied every 2 years (Eggers *et al.*, 2005; Blaedow *et al.*, 2010). Preventive treatment of bur and white oak may be effective (Eggers *et al.*, 2005), but because the disease progresses slowly in these species, arborists often wait until the trees show symptoms and then apply a therapeutic treatment (Haugen *et al.*, 2009). Injection of propiconazole is widely practised in Texas, but treatments generally delay development of disease symptoms rather than prevent infection (Appel and Kurdyla, 1992; Billings *et al.*, 2001). The pathogen may pass through the root system of an injected live oak and move on to the next tree (Juzwik *et al.*, 2011). Spring injections may work better than injections later in the season (Billings *et al.*, 2001).

Wound dressings

Fungicidal wound dressings have been recommended for the protection of pruning or other wounds from infection by *C. variospora* (DeVay *et al.*, 1968) and other *Ceratocystis* spp. When wounding cannot be avoided, a variety of wound treatments are known to be effective in preventing infection by *C. fagacearum*, but latex paint is the recommended treatment because of its effectiveness and its lack of toxicity to the tree (French and Juzwik, 1999; Camilli *et al.*, 2007).

Wound dressings also can inhibit the growth of *C. platani* (Davis and Peterson, 1973). Walter (1946) recognized that wound dressings commonly had sawdust with viable *C. platani* inoculum that could survive for months. He recommended the addition of phenylmercury nitrate to kill the pathogen in tree paint, but such highly toxic compounds are no longer used. Panconesi (1999) recommended a fungicide dressing for the protection of wounds against canker stain.

Trenching and other barriers

Reduction in the root graft transmission of the oak wilt pathogen by the use of root-free zones has been practised for many years and can be highly effective in reducing losses (Bretz, 1951; Gehring, 1995; Cummings Carlson and Martin, 2010; Juzwik *et al.*, 2011). Generally, a trench is made to delimit infected from healthy trees. The placement of the trench can be calculated based on the probability of disease spread (Bruhn *et al.*, 1991), but generally involves a primary barrier of at least one ring of healthy trees beyond the symptomatic trees and a secondary barrier placed inside this to help protect that ring of healthy trees. For live oaks in Texas, the primary barrier should be a minimum of 30 m from a symptomatic tree because of rapid spread of the pathogen in the common root systems of these hosts (Juzwik *et al.*, 2011).

Trenches 1.5 m deep are recommended (Bruhn and Heyd, 1992), but shallower trenches still lower the risk of transmission. However, many sites are too steep or have other physical limitations that make trenching impracticable. Vibratory ploughs with a long blade (Plate 14), belt trenchers, or heavy rotating discs that can cut through rock have been recommended, but such equipment is not available in all regions (Juzwik *et al.*, 2011). Backhoes can also be used, but site disturbance is substantial with such equipment. Plastic barriers placed inside the trenches increase their effectiveness but add to the cost (Wilson, 2005). Killing trees by herbicide treatment has not been considered effective in protecting healthy trees at the edge of expanding oak wilt centres (Haugen *et al.*, 2009).

Soil trenching was effective in reducing oak wilt spread in live oak at Fort Hood Military Installation, where 11.2 km of trenches were put in place over 4 years (Greene and Reemts, 2009). The Texas Oak Wilt Suppression Project has resulted in over 1000 km of trenches, and a recent evaluation found a nearly 80% success rates, that is, slightly more than 20% of the trenches were breached by oak wilt within 3 years (Billings, 2009). Such 'breakouts' are usually attributed to insufficient depth of the trenches.

11.5.5 Resistance

With most Ceratocystis diseases, there is substantial variation in aggressiveness in the pathogen and also in resistance among host species and within host species or hybrids. For instance, variation in resistance to *C. populicola* was noted among poplar clones in Poland (Przybyl, 1984).

C. fagacearum has a broad host range among *Quercus* spp. and also can attack chestnuts (*Castanea* spp.) under experimental conditions, but host species vary widely in susceptibility. Such variation in resistance among species can be used to favour more resistant species in plantings and in stand management. A diversity of oak species lessens the risk of root graft transmission. Commercial forest stands should encourage diversity and avoid dense stands of highly susceptible species, such as red oak. Breeding oak for resistance to oak wilt may be feasible. There appears to be some inheritance of tolerance in Texas live oak, but it is not clear whether it will be possible to breed tolerant trees (Gray and Appel, 2009). The genetic uniformity of *C. fagacearum* should favour the durability of any resistance that is deployed (Harrington, 2009).

The high susceptibility of (the hybrid) London plane trees to canker stain comes from the oriental plane tree component. Genetic variation is limited in London plane tree (Panconesi *et al.*, 2003), but there is some variability in susceptibility to canker stain in existing cultivars of the species (Pilotti *et al.*, 2009). There is more resistance available in American sycamore, which is being utilized to develop resistant London plane trees (Vigouroux and Olivier, 2004). Resistant American sycamores were crossed with oriental planes and screened through repeated inoculations, leading to the London plane cultivar 'Vallis Clausa', which has been commercially available for 5 years. About 2000 trees have been planted in France without reported canker stain (A. Vigouroux, France, 2011, personal communication). Pure American sycamore is not a suitable street tree in Europe because of its high susceptibility to anthracnose caused by *Apiognomonia veneta* (Sacc. & Speg.) Höhn., but 'Vallis Clausa' has good resistance to anthracnose and some resistance to powdery mildew and to lacebugs (*Corythucha ciliata* (Say)). More resistant clones are to be developed. The limited availability and higher cost of London plane trees that are resistant to canker stain suggests that only limited plantings can be made in the near future. Because the European population of *C. platani* originated from a single genotype and the species reproduces asexually or through selfing (Engelbrecht *et al.*, 2004), the pathogen has limited potential to overcome the resistance developed in 'Vallis Clausa'.

In contrast, soil-borne populations of *C. fimbriata* in Brazil can be quite diverse, and individual isolates vary greatly in aggressiveness to eucalyptus and other hosts (Harrington *et al.*, 2011). Planting *Eucalyptus* clones on former forested sites naturally infested with soil-borne inoculum may select for strains of the fungus that are particularly aggressive to eucalyptus, and such strains have been distributed in infected rooted cuttings. However, in both *E. grandis* W. Hill ex Maid. and *E. urophylla* S.T. Blake, there are clones that range from highly resistant to highly susceptible, and in crosses of the two species, there is a high degree of heritability of resistance (Goncalves-Rosado *et al.*, 2010). There is great variability among commercially available hybrid clones, but there is some clone × isolate interaction, which may make selection for resistance more difficult (Zauza *et al.*, 2004). Some of the most susceptible clones have already been eliminated from commercial use. Efforts are under way to deploy resistance to particular local genotypes or populations of *C. fimbriata* (Alfenas and Ferreira, 2008), which may be the best way to manage the disease when there are high levels of aggressive strains in the soil (Ferreira *et al.*, 2011).

11.5.6 Therapy

The oak wilt pathogen moves too quickly to remove affected limbs in the hope of restricting the spread of *C. fagacearum* within the crown. Fungicide treatment of symptomatic red oaks is also not recommended. However, therapeutic treatments of white and bur oaks with propiconazole are effective in delaying symptom development and mortality (Osterbauer *et al.*, 1994; Eggers *et al.*, 2005), though follow-up treatments may be needed.

Pruning out infected limbs has been recommended for almond trees with mallet canker (DeVay *et al.*, 1968) and in canker stain of plane trees (Walter, 1946), but *C. platani* generally moves too quickly in London plane tree to use this therapy on a routine basis. Therapeutic fungicide treatments are not considered to be effective for canker stain (Panconesi *et al.*, 2003).

11.5.7 Integrated disease management

As with the management of most forest diseases, an integrated approach involving several strategies is necessary to control diseases caused by *Ceratocystis* spp., especially in urban settings. Both oak wilt and canker stain require integrated programmes of detection, sanitation and prevention, and these only succeed with educational efforts and coordination among public and private interests (Walter *et al.*, 1952; Panconesi, 1999; Haugen *et al.*, 2009; Koch *et al.*, 2010; Juzwik *et al.*, 2011).

Juzwik (2009) reviewed some of the models and risk maps for oak wilt, and the measures that can be utilized to manage the disease in high-risk areas. Barriers to prevent underground spread (e.g. trenching to sever root grafts) may not be effective without sanitation. In Wisconsin, where the disease risk is high, there are appropriate guidelines for harvesting and timber stand improvement (Juzwik *et al.*, 2008a). Integrated measures in central Texas include avoiding wounding in the spring, treating fresh wounds with latex paint, cautious removal of firewood, trenching and, occasionally, fungicide injections (Appel, 2009).

Various formal suppression programmes, largely supported by the US Department of Agriculture Forest Service and state governments, have been enacted for oak wilt (Starkey, 2009). Early projects in eastern states were abandoned as largely ineffective, but with a better understanding of epidemiology and management techniques, successful programmes have been developed in Minnesota and Texas. In both cases, most of the spread of the pathogen is by root contact, and most direct control involves trenching.

The Texas Oak Wilt Suppression Project is an integrated, multi-agency management effort that began in 1988 and is coordinated by the Texas Forest Service (Billings, 2009). The prevention and control of oak wilt are based upon public education on proper timing of pruning, treatment of wounds, destroying diseased red oaks, proper handling of firewood, propiconazole injections and the planting of resistant species. Direct control efforts are based on detection, field evaluations and the control of expanding infection centres, primarily through root trenching.

Although the integrated management strategies outlined by Walter (1946) eventually led to a dramatic reduction of canker stain of plane trees in urban areas in the eastern USA, similar efforts in California and Europe have not had the same desired effect. Some factors contributing to the difficulties in Europe may include the mobility of construction equipment, the complexities of international commerce under the European Union (EU), and the difficulties of forming and executing the large, multilevel programmes needed to manage a problem as large as canker stain. None the less, education has led to early detection, and coordinated efforts have led to more effective sanitation, and prevention measures have undoubtedly reduced losses. London plane trees that are resistant to canker stain are another promising tool.

The epidemiology of Ceratocystis wilt on eucalyptus is still being unravelled, but an integrated approach that includes the sanitization of tools and use of clean nursery stock has been proposed (Ferreira *et al.*, 2011). Highly susceptible clones of otherwise productive hybrids have been abandoned in regions with a high level of disease, and resistant clones are being developed (Zauza *et al.*, 2004; Goncalves-Rosado *et al.*, 2010). It is to be hoped that this disease will be another case where integrated strategies lessen the importance of a disease caused by *Ceratocystis* spp.

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