The oak wilt pathogen *Ceratocystis fagacearum* is only known in the north central, south central and eastern parts of the US (Sinclair and Lyon, 2005). First clearly identified in the 1940s in the upper Mississippi valley, its apparent spread in the subsequent 20 years (1945-65) may be primarily the result of surveying rather than actual spreading (Appel, 1995). The epidemic in live oak trees in central Texas is an exception. All tested species of oak as well as related genera are susceptible, thus the fungus is a significant threat to oaks in the western US, Europe, and temperate parts of Asia. Transmission over distances is mediated by nitulid and bark beetle species of which there are relatives on other continents. Introduction to new continents would most likely be due to transport of infected logs. So far, spread in North America appears to have southern and northern limits due to climatic and ecological factors.

*Ceratocystis fagacearum* (Bretz) J. Hunt

Perithecia immersed in mycelial mat, base black, globose, unornamented, to 240-360 µm diam, neck emergent, black, tip pale brown to hyaline, 250 to 450 µm at base, 60-80 µm diam near tip; ostiolar hyphae erect, pale brown to hyaline filamentous, to 125 µm, average 75 µm.

Asci evanescent, globose, 8-spored, 7-10 µm diam.

Ascospores hyaline, aseptate, elongate-ellipsoid, 5-11 x 2.5-3.5 µm, collecting in white mucilaginous mass at ostiole.

Conidiophores resemble hyphal branches.

Conidiogenous cells integrated, terminal, subhyaline to brown, 2.5-4.5 x 20-40 µm, tapering slightly to apex; conidia endogenous, hyaline, cylindrical, 1-celled, truncate at both ends, 4-22 x 2.4-5.5 µm, in chains. Bretz (1952) reports "resting spores" appearing in culture, olivaceous to brown, thick-walled, varying in shape, 3.5-5.5 x 5-20 µm, intercalary.

Culture on 2% malt agar slow-growing, floccose, white, later grey to live-green, hyphae 2.5-6 µm, reverse hyaline to olive-green in various patterns.

Mycelial mats formed on surface of sapwood and opposing inner bark. Mats elliptic, 2.5-20 x 1-10 cm, grey or occasionally buff. Edges white, black in age, denser cushion in center. Endoconidia produced on mat, followed by perithecia after mating. (Sinclair and Lyon, 2005)

NOTES ON TAXONOMY AND NOMENCLATURE

*Ceratocystis* was revived as the accepted name for the genus in 1950.

Recent evidence showing the form genus *Chalara* to be polyphyletic led Paulin et al. (2002) to amend the genus *Thielaviopsis* to include all *Chalara* species with *Ceratocystis* affinities. Analysis of ITS and partial LSU rDNA sequences grouped *C. fagacearum* with some species in the imperfect genus *Ambrosiella* Brader.

DISTRIBUTION

The oak wilt disease was likely present, at least in the north central region of the United States for decades before it was identified and studied (Juzwik et al., 2008) Southern line/ Northern Line (Gibbs & French, 1980). Initial concern due to the rapid death of some oak species and the ongoing epidemics of diseases on other native species caused by introduced fungal pathogens, was followed by decline, since losses abated and the apparent spread of the pathogen was less rapid and dramatic than in the other forest epidemics. In 1965, it was noted that, in the preceding decade, the fungus spread only to Ark and TX; spread was limited in Arkansas during six years of repeated surveying (Wilson et al., 1964). No additional spread in TX was noted until 1975 (Appel, 1995) Wilson (2001) notes that reports from southern states of Louisiana, Mississippi, and Alabama were based on symptoms, not isolation of pathogen, although the pathogen may be present, though limited in effect by ecological conditions and so not highly visible. The discovery of oak wilt near Houston, TX places it, nevertheless, in the warm coastal zone of live oak habitat (Wilson, 2001). Recently, although the Susquehanna River in central Pennsylvania had long appeared to be a boundary of oak wilt incidence in the northeast (Gibbs & French, 1980), the disease was found in central New York state, at a distance of 136 miles (300 km) from the river (Jensen-Tracy et al., 2009).

*Ceratocystis fagacearum* has not been identified in Europe (IMI Map 254).

SIMILARITIES TO OTHER SPECIES
Henry (1944) compared the asexual form to other Chalara spp. then known as saprophytes on oak logs and leaves (C. affinis, C. fusidioidea, C. heterospora, C. setosa) and noted that their conidia were either septate or narrower (2 µm) than those of the oak wilt pathogen. Thielaviopsis (= Chalara) ovoidea is a soilborne pathogen of oak in Europe that produces endoconidia of the same size as C. fagacearum but also one-celled dark terminal aleuroconidia 8-16 × 4-10 µm (Paulin et al., 2002).

Ceratocystis species with similar ascospores (C. paradoxa and C. radicicola) are primarily pathogens of tropical plants (Rossman and Farr, 2009). Their perithecia are ornamented basally and have longer and thinner necks (Hunt, 1956). C. virescens, which causes sapstreak in other trees, can colonize oak logs and stumps (Sinclair & Lyon, 2005); its perithecia also differ in ornamentation and neck shape from C. fagacearum, and its ascospores are narrower, 5.5-7.5 x 1.7-2 µm (Davidson, 1946).

Conditions which may cause some of the symptoms of oak wilt include attack by various insects, including foliage-feeding and wood-boring larvae. These do not generally cause leaf drop, and the bodies or other signs of the insects (frass, holes in bark or leaves, etc.) can be found. Likewise, other fungal diseases affecting the foliage or stem do not cause leaf drop. Injuries from human activity can result in browning of foliage and dieback (Texas Natural Resources Conservation Service, 2009).

DETECTION AND INSPECTION METHODS

Surveys for detection of oak wilt first were done from the ground (Young, 1949; Jewell, 1956). In addition to observing symptoms, the particular pattern of leaf discoloration, leaf drop, dieback and death of trees, surveyors looked for bark cracking and the attraction of insects which are produced by fungal mats primarily on red oaks (Cones, 1967; Gibbs and French, 1980). The bark must be cut off to allow confirmation of the presence of mats. Isolation of the fungus from twigs, branches and wood chips is necessary to confirm infection of white or live oaks (Henry et al., 1944; Young, 1949; Wilson, 2005).

Aerial surveys were found to be a more effective and efficient means of detecting oak wilt over large areas (Fowler 1952; Wilson et al., 1964; Appel and Maggio, 1984). Suspected centers of disease should be confirmed by examination from the ground to the extent possible. Use of infrared photography can increase accuracy by distinguishing oak wilt from other causes of foliage symptoms (Appel and Maggio, 1984).

NOTES ON OTHER PLANTS AFFECTED

No tested species of Quercus are immune to C. fagacearum (Appel, 1995). This includes all species in the affected area of the United States (Farr & Rossman 2009), but there are at least 500 species worldwide. The oak forests of California are at risk, due to the demonstrated susceptibility of at least some species (Appel, 1995; Wilson, 2001). Some European (Young, 1949; McDonald et al., 2001) and Asian species (Bretz, 1952; Houston et al., 1965) have been tested and found susceptible and, in the case of some European oaks (Q. robur, Q. petraea), highly so (McDonald et al., 2001). The severity of disease in these species of the white oak group (Quercus section Quercus) is in contrast to the more moderate disease seen in North American white oaks, which are not killed as quickly as red oaks. The evergreen “live” oaks of Texas and southern coastal regions of North America are in a somewhat intermediate class, with high mortality but some show resistance (Appel, 1995).

Trees in other genera of the Fagaceae have also been found to be susceptible, including Castanea sativa (European chestnut), C. mollissima (Asian chestnut); Lithocarpus densiflorus Hook. & Am.) Rehder) (tanoak), and Chrysolepis (= Castanopsis) sempervirens Kellogg) Hjelmq (Sierra chinkapin) (Bretz, 1952; Farr & Rossman 2009).

SYMPTOMS - DESCRIPTION

Loss of green color, water-soaking, bronzing and browning from leaf edge to midrib, wilting, curling and blackening of young leaves, from top of tree or outer ends of branches. Leaf drop at any stage on mature leaves, so that there is a mixture of symptoms on fallen leaves. In live oaks, yellowing, browning and necrosis more often occur along the midrib and veins. Brownish discolored streaks occur frequently in the sapwood from the twigs down; more of this appears in white oak species. Generally, red oaks die within weeks of infection while white oaks show leaf and branch symptoms only in parts of the canopy and die more slowly if at all. (Henry et al, 1944).

BIOLOGY AND ECOLOGY

Genetics: There is a striking lack of genetic variation, both nuclear and mitochondrial, within the species, (Kurdyla et al., 1995) which strongly supports the hypothesis that C. fagacearum is an introduced, rather than native, pathogen in the United States (Juzwik et al., 2008). No evidence has been detected of specialization to a host (Young, 1949; Cobb & Fergus, 1964; Sinclair and Lyon, 2005). Given the heterothallic, outcrossing nature of sexual reproduction in C. fagacearum, the amount of variation suggests that an initial introduction could have consisted of a single ascospore mass (Juzwik et al., 2008).
The influence of sexual recombination in the epidemic not known 1995, but very little genetic variation was detected among isolates from different parts of the species range (Kurdyla et al., ).

**Reproductive biology:** *Ceratocystis fagacearum* is heterothallic (Bretz, 1944). Endoconidia serving as spermatia are produced in the fungal mats on the surface of the sapwood and on the opposing inner bark of red, and sometimes white, oaks (). (No reports concerning the non-oak hosts.) Generally, only one mating type occurs in each tree and insects are the obvious agents of mating (Jewell?). The role of insects in mating is different from that in transmission, since it is nonspecific, and only repeated visiting of fungal mats is required. Insects can carry both mating types (Jewell, 1956). Perithecia are produced in mats with necks and spore masses above surface. Fungal mats can form on logs and stumps, as well as on infected trees (Wilson, 2005). In Texas mats occur only on the red oaks ( *Q. texana, Q. marilandica*) not on live oaks. Mats form in spring or fall, depending on time of infection and death, as well as on temperature and moisture conditions in the parts of the tree. (Gibbs & French, 1980)

**Associations:** Insects have a significant role in the transmission of inoculum as well; they are the primary known means of “overland” movement of the fungus to initiate new disease centers and of transmission between the different types of oaks (Hayslet et al., 2008). The sweet smell of fungal mats (composed of a number of chemical (Lin & Panlin, ) attracts insects of different orders, but beetles have been predominantly identified in trapping experiments (Jewell, ) found species of families at fungal mats in PA? Nevertheless, an effective vector must pick up the pathogen propagules and carry them to an infection court of a susceptible tree. Attention has therefore focused on the Nitidulid and Scolytid beetles that transmit or could transmit ascospores from infected to healthy trees.

The nitidulids or sap beetles are small beetles that are attracted to feed and breed in fresh wounds of trees. Various species have been trapped in oak wounds bearing significant numbers of propagules of *C. fagacearum*. The maximum effective vector population of *Colopterus truncatus* and *Carpophilus sayi* in MN occurred in the spring. In other areas, other species, including the larger *Glischrochilus* spp, appear to have a larger role ( Cease & Juzwik, 2001 ). Male nitidulids produce an aggregation pheremone which can serve to attract both males and females to infection courts in oak trees. Knowledge of the vectors’ behavior through the growing season is important for timing of control measures against oak wilt.

Members of one genus of the Scolytidae, the bark beetles *Pseudopityophthorus minutissuimus* and *P. pruinosus* in the US have also been implicated in transmission, after either emergence as adults or breeding in the bark of branches(Ambourn et al, 2006) (G & F, 1980) in spring but not likely to transmit in summer Adults of *P. minutissuimus* were found to be carrying fungus at low % in MN Ambourn et al, 2006). The European bark beetle has been investigated as a potential vector if *C. fagacearum* were ever introduced.

**Environmental requirements:** Temperature and moisture are factors which appear to govern to some extent the distribution and spread of *C. fagacearum*. Optimum growth in vitro occurs in the range 24-28 C (Henry, 1944) and ascospore germination is at 25 C (Bretz, 1952). Growth of the fungus is inhibited by temperatures greater than 32 C, with the same apparent affect in infected trees as in culture (Houston et al., 1965), and this limitation has been considered a major factor in preventing spread into the southern states (Appel, 1995). Nevertheless, once introduced, the pathogen was not inhibited from causing an epidemic in central TX where summer temperatures exceed 32 C. Regardless of the air and bark temperatures, it survives inside tree trunks and root systems (Appel, 1995). No evidence has been found for a high temperature race of the pathogen, and transmission between live oaks does not require or involve growth and sporulation near the tree surface, where temperature could be a limiting factor (Appel, 1995).

Fungal mats are not produced in dry conditions (Sinclair & Lyon, 2005) and this was thought to suppress spreads in the southwest towards Texas (Appel, 1995: White, 2001). Reduced moisture, in addition to heat, was suggested to limit the development of disease and survival of the pathogen in trees in the southeastern state of South Carolina (Tainter and Ham, 1983). Rapid drying has been employed as a control method to prevent transmission from red oaks; girdling at the base of the trees (True and Gillespere, 1961; Greene et al, 2008). The fungus survives in dry wood of live oaks in Texas.

**MOVEMENT AND DISPERAL**

Natural dispersal (non-biotic)

The fungus is transmitted from tree to tree in centers of infection through natural root grafting between trees, usually within a species, although cross species grafts can occur (Gibbs and French, 1980). In MN, approximately 90% trees are infected in this way (Cook, 2001). Red oaks form these grafts more readily than white oaks (). Soil aspects, including moisture and texture, affect the frequency and distance over which roots extend. Thin sandy soils favor root extension and grafting (Bruhn et al., 1991). The pure stands of live oak in central Texas exhibit root grafting, (McDonald et al, 1998) in addition to the extensive shallow clonal root systems which connect trees growing from root sprouts (Appel, Wilson,
Accidental introduction

Logs bearing fungal mats, predominantly those from harvested oak trees, may be present in white oaks and can carry the fungus in a condition that will attract insect vectors. The outbreaks of oak wilt in southern Texas and central Michigan are likely to have been the result of transportation of fungal mat-containing logs for firewood (Juzwik et al., 2008). The appearance of the disease in eastern North Carolina (Grand and Doggett, 1973) and central New York (Jensen-Tracy et al., 2009), many miles from its nearest known locations, may also be due to human transport of infected tree material.

Wilson (2005) suggests there is a yet unidentified means of long distance dispersal responsible for the increase in infection centers in Texas.

SEEDBORNE ASPECTS OF DISEASE

Acorns tested did not contain pathogen (Young, 1949).

IMPACTS

The differences in effects on different oak species can result in a change in their distribution (Gibbs and French, 1980). On the other hand, human activity which contributed to conditions favoring increase and spread of the disease had done so by shifting species distribution or prevalence in some areas. Changes in genotypes among live oaks surviving in Texas presumably reflect selection towards characters related to resistance (MacDonald et al., 1998).

MANAGEMENT

SPS measures: Countries worldwide have responded to the threat of oak wilt by imposing strict regulations to prevent introduction of *C. fagacearum* on imported oak materials. The Canadian FIA identifies particular states of the United States for its regulation of oak imports (CFIA, 2008). Oak planting material, as a Schedule V “Restricted Plant Species”, must be free from this pathogen for import to India (Plant Quarantine Organisation of India, 2009). New Zealand refers specifically to *C. fagacearum* as a species which must be absent from imports of oak material.

Cultural control and sanitary measures: A measure aimed at preventing spread to managed and urban trees is the avoidance of wounding of healthy trees during the period of insect vector activity (Wilson, 2005). Because fungal mats can survive or be produced in cut logs, warnings about transportation of oak firewood over distances are published. Instructions are provided on methods for drying and storing of firewood so that insects do not have access to fresh fungal mats that may be present or may develop. Cook (2001) describes treatment of firewood that encourages competition of fungal growth under cover, which should eliminate the fungus.

Physical/mechanical control: A significant effort to control the disease in infection centers is the digging of trenches deep enough to cut roots. Wilson and Lester review the added necessity to include an insert as a physical barrier to root regrowth and grafting in the trenched soil. Dead or dying trees inside the trench are removed and roots must be severed, but the primary trench must be placed correctly with respect to the delay between infection and appearance of symptoms in trees beyond those showing symptoms (Wilson, 2005). The rate of movement in roots is 25 m/yr or more in Texas, greater than in the northern areas (Wilson, 2005). This trenched and tree removal is more readily accomplished thoroughly and successfully in rural areas than in urban ones, where buildings, roads, etc. are barriers and there is greater need to preserve certain trees. Trenches 4.5 ft deep (1.2 m) were 88% successful (Cook, 2001).

Earlier control programs in the eastern US included deep girdling of infected trees to speed drying out and prevent the formation of fungal masts before the trees (True and Gillespie, 1961) were felled and cut up. Without cutting of roots, this would not prevent local spread of the pathogen (Wilson, 2005), and Hayslett et al. (2008) noted that the effort had to take effect before spring. However, Jones (1971) found that these physical methods were only marginally effective.

Biological control: A certain amount of “natural” biological control of the pathogen, limiting its persistence in infected trees in certain areas/circumstances, has been observed to be due to other oak-infecting fungi, but it is unlikely that these other less threatening pathogens would be used deliberately. The failure of the pathogen to spread in the southwest was attributed to competition from *Hypoxylon atropunctatum*, which colonizes affected sapwood.

Juzwik, 2001 identified saprophytic fungi *Gliocladium* and *Trichoderma* spp. on fungal mats. These, as well as *Ophiostoma quercus*, may be carried by nitulids, and interfere physically with the contamination of beetles with spores.

Host resistance: Some choice in species and varieties of white oaks for planting in managed areas, at
least, is available due to natural differences in susceptibility. Natural selection for resistance to oak wilt appears to be occurring in live oaks (Kurdyla et al., 1995)

**Integrated pest management:** Where insect vectors are clearly involved in overland spread, modeling of the insects feeding and mating behavior through the growing season can contribute to control by determining appropriate periods for pruning or other deliberate or accidental wounding of trees (Juzwik et al., 2004; Ambourn et al., 2005, 2006; Juzwik, 2001). Such efforts must be combined with trenching, destruction of infected trees, creation of buffer zones around centers of infection, and education of the public to slow the pace of spread.

References


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