Oak wilt

Oak wilt is a systemic vascular disease caused by the invasive fungus *Bretziella fagacearum* (Bretz) (Microascales: Certocystidaceae) (formerly *Ceratocystis fagacearum*) [158,159]. The Upper Mississippi River Valley was the first place where oak wilt was discovered in the US, and historical records indicate that *B. fagacearum* might have been present as early as the 1890s [160,159,161]. It was first discovered in Wisconsin in 1942 [159] and was recognized as a major disease by the 1950s [162]. The population structure of *B. fagacearum* provides evidence of a genetic bottleneck which supports the hypothesis that the fungus was introduced to the US [163]. Many *Quercus* spp. in midwestern, northeastern, and southern states are currently affected by oak wilt disease [164].

The most common method of infection propagation in *Q. alba* is root grafting between healthy and infected trees of the same species, however, its frequency varies with different locations and habitats [165,152,166,167]. The pathogen may also be transmitted by contaminated oak bark beetles or sap-feeding beetles (Scolytidae and Nitidulidae, respectively). Sap-feeding beetles are lured to new wounds on healthy oaks in the spring season and release fungal spores, whereas bark beetles that breed in previously infected oaks introduce the fungus to healthy oaks by forming new wounds in small twigs and branches [168]. Infections can survive for years on twigs, branches, and even roots [165].

Fungal colonies grow quickly in vessel elements, releasing spores into the water moving through the tree xylem column [169]. Spores, mycelium, and phytotoxic chemicals produced by *B. fagacearum* eventually clog xylem vessels. In the middle of the growing season, leaves from infected limbs become water-soaked or bronzed, droop, and abscise [161]. In the dead host tree, the pathogen grows saprophytically further into the sapwood from the present growth ring, where it can live for one to three years in stems and bigger branches. *Q. alba* is somewhat resistant to oak wilt and disease symptoms develop more slowly when compared to *Q. rubra* (red oak) or other *Quercus* species [159]. The only visible symptoms are black and grey fungal mats, which are common in *Q. rubra* but less visible in *Q. alba* species [170,161]. Many of the affected trees completely recover or show symptoms of remission. Fungus fruiting is also more frequent on red oaks (Section *Lobatae*) than on white oaks (Section *Quercus*) [166]. Hot and dry environments, especially southern locations, have lower incidence of oak wilt overall and reduced fungus fruiting on all hosts [160,166]. For a long time, oak wilt control options were limited to preventative measures such as disrupting shared root systems and removal of infected trees. Currently, to reduce the risks associated with the spread of the oak wilt fungus, oak logs meant for export must be fumigated with 240 g/m3 methyl bromide for 72 hours [171,172,173]. However, methyl bromide is recognized as a class I ozone-depleting substance by the United Nations Environmental Programme. A recent study found that sulfuryl fluoride is a promising alternative to methyl bromide in killing the oak wilt fungus in both naturally infested and artificially inoculated *Q. alba* logs [174] Further investigation into its efficacy as a phytosanitary treatment is warranted [174].

4.2.3. Oak decline

Oak decline has a complex disease etiology that affects mature *Q. alba* trees. It is caused by the interaction between severely stressed trees, secondary invaders such as the two-lined chestnut borer (*Agrilus bilineatus* Weber) [175] and root diseases like armillaria root rot (caused by *Armillaria mellea* [Vahl. Ex Fr.] and possibly other *Armillaria* spp.) as well as ink disease by *Phytophthora cinnamomi*. An initial onset of severe stress caused by an extensive drought, insect defoliation, or late frost affects physicochemical processes in mature trees to the extent that photosynthesis stops and starch deposited in roots is transformed into soluble sugars to sustain metabolism [167]. This alteration in carbohydrate chemistry promotes *A. mellea*, a saprophytic fungus common in *Q. alba* stands, to acquire larger root density, compromising water conductivity and overall tree health [177]. As oak decline progresses, branches and twigs die off gradually to accommodate a compromised root system [178]. This dieback usually spreads downward and inward from the crown's top and outside, and it is frequently accompanied by canker caused by less pathogenic fungal species, *Hypoxylon atropunctatum* (Schw. ex Fr.) Cke. [179]. The two-lined chestnut borer, *A. bilineatus*, is attracted to strained *Q. alba* trees, and along with root rot disease, kills the trees [180]. As with oak wilt, *Q. alba* is less susceptible to oak decline than other North American species such as *Q. rubra* and *Q. velutina* [181]. Oak decline is more severe in homogenous species stands and is most severe in trees over approximately 70 years of age [166].

4.2.4. Foliage and twig pathogens

Several leaf and twig diseases can adversely impact oak reproduction and wildlife food resources by reducing *Q. alba* acorn production. Oak anthracnose, caused by the pathogen *Dendrostoma leiphaemia* (Fr.) Senan. & K.D. Hyde (previously known as *Discula quercina*) is the most damaging disease in this category [182]. While usually causing only minor damage, ideal weather conditions can cause severe outbreaks. Frequent rains along with mild temperatures in early spring offer an ideal environment for disease development and spore generation, and during this period young oak leaves are more susceptible due to their lack of a thick, protective cuticle [183].

Some of the additional opportunistic fungal pathogens that can induce twig or branch dieback in *Q. alba* are *Botryosphaeria* spp. (including *B. rhodina* [Berk. & Curt.] von Arx, *B. dothidea* [Moug. ex Fr.] Ces. & de Not., *B. obtusa* [Schw.] Shoemaker, and *B. quercum* [Sch.: Fr.] Saccardo) and *Botryodiplodia gallae* (Schw.) Petrak & Sydow [183]. Often associated with oak cankers, these pathogens are most successful on trees with drought stress or cold-induced damage or wounds caused by insects and animals96. All can be part of the oak decline syndrome described above and may contribute to the characteristic symptom of branch dieback. All these fungal species are common in forests, although the climatic variables that predispose trees to infection rarely last more than a few growing seasons [348].

4.2.5. Spongy moth

Throughout the Northern Hemisphere, the spongy moth (*Lymantria dispar*, formerly gypsy moth) is a significant insect pest of *Q. alba* forests [192].

It remains in low population numbers in most locations for the bulk of the year, although it occasionally surges into a severe outbreak. It was unintentionally introduced to North America near Boston, Massachusetts in 1868 [184]. The spongy moth took 130 years to expand from Massachusetts to the present infection range in Minnesota, Illinois, Indiana, Ohio, and North Carolina, because the female adults cannot fly [185,184]. In North America, spongy moth epidemics occur at unpredictable periods but are documented around every decade [186–188].

Spongy moth caterpillars have been observed feeding on hundreds of different tree species, but *Q. alba* is preferred over others [189,190]. Caterpillar feeding can reduce acorn production of *Q. alba* by severe defoliation and consequent elimination of carbohydrate reserves [191]. Acorn production decreased by 50–100% in Maryland, Pennsylvania, and Virginia, US during defoliation years, and acorn production was essentially eliminated in years of heavy defoliation [191]. Spongy moth defoliation has several additional consequences for stand dynamics, including overstory mortality, altered regeneration potential, and changes in successional pathways. The susceptibility of forest stands to spongy moth defoliation is largely determined by the proportion of preferred tree species in the stands.

4.2.6. Oak acorn weevil

Nut weevils (*Curculio* and *Conotrachelus* spp.) are the major seed predator of oak species in the eastern United States, and result in seed crop losses ranging from 0–100 %, varying among tree species and with seed crop size [193–196]. Weevils can be a factor in the reduced regenerative ability of oak species in the hardwood forests of eastern North America, with management treatments such as fire being employed in an effort to reduce weevil population sizes [349]. Steele et al. [122] recently published a study on the interactions of weevils and oaks over an extensive geographic area and several years. They reported on patterns of infestation in both northern red oak (*Q. rubra*) and white oak (*Q. alba*) over an eight-year period along a latitudinal transect covering much of the shared range of the species. Weevil prevalence did not differ significantly between the two oak species, however in white oak the highest infestation prevalence was observed at lower latitudes than for red oak. Also, lower cotyledon damage observed in red oak acorns than those of white oak were attributed in part to be due to larger acorn size at the lower latitudes. The authors recommended future research to determine if the distribution of weevil species (using DNA barcoding) and geographic variation in acorn chemistry determine patterns of weevil damage in acorns [122].