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INSECT TRANSMISSION OF OAK WILT[1]

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Abstract. A review of the research done in attempts to identify the insect vectors of the oak wilt fungus *Ceratocystis fagacearum.* Oak bark beetles *Pseudopityophthorus* sp. are believed to be the most important vectors of the oak wilt fungus. Nitidulids, sap-feeding beetles, probably aid in the transmission of the fungus when mycelial mats of the fungus develop on diseased trees.

Oak wilt, a disease of oaks caused by the fungus *Ceratocystis fagacearum* (Bretz) Hunt, was first identified in Wisconsin in 1942. It has since been reported from 646 counties in 21 eastern and midwestern states. Although the disease has been studied for more than 30 years, we do not completely understand how it is spread overland. Certain characteristics of the organism, the pattern of disease occurrence, and a substantial body of research implicate insects as likely vectors.

For an insect to be judged an important vector of the oak wilt fungus, four criteria need to be met: 1) it must, with a fair degree of regularity, visit a diseased tree; 2) it must leave the diseased tree, bearing propagules of the fungus, either spores or mycelial fragments; 3) it must visit healthy oaks under conditions conducive to inoculation and infection; and 4) infection must follow these visits.

I will review the research done in attempts to identify the vectors of the oak wilt fungus.

Insects Associated with Oak Wilt Trees

An insect must visit the source of inoculum, the fungus-infected tree, to meet the first requirement for a vector; and there are many that meet this requirement. For example, Curl (1955) found 40 species of insects, including representatives of 19 families, associated with mycelial mats on wilt trees. Dorsey and Leach (1956) collected specimens representing 31 families of Coleoptera and a few families of Hymenoptera, Diptera, and Orthoptera from oak wilt mats. During the same year, Dorsey and Leach also reared 72 species of Coleoptera alone from two wilted trees. The list of potential vectors is very long. Dorsey and Leach also pointed out that, of all the insects found, the Nitidulidae were most numerous and most consistently present when fungus mats were present on the diseased tree.

Oak bark beetles are also abundant. Rexrode and Jones (1970) found practically every wilt tree attacked by *Pseudopityophthorus* sp. Much of the earlier research on oak bark beetles as vectors of the oak wilt fungus was concerned with the association of insects with the diseased trees. In 1952, Craighead and Morris reported that oak bark beetles were abundant in twigs of diseased oaks in Pennsylvania; and in 1953, Griswold and Neiswander found three species of *Pseudopityophthorus* breeding in oak trees that had been killed by the disease in Ohio. Buchanan (1956) reported that *P. minutissimus* (Zimm.) breeds in most diseased scarlet and black oak trees in Missouri. Rexrode et al. (1965) found that *P. pruinosus* (Eichoff) breeds commonly in diseased oaks in West Virginia (Fig. 1).

Rexrode and Jones (1970) found that of 86 trees killed by oak wilt in Missouri, every tree was attacked by bark beetles. Attacks before diseased trees were defoliated were commonly abortive; the beetles tunneled into the cambium but backed out without making egg galleries, and moved on to other trees. Successful attacks, resulting in egg-gallery construction and oviposition, were recorded in 50 percent of the dis-

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eased trees. When egg-gallery construction and oviposition were completed, more than 50 percent of the parent adults emerged and presumably moved to other trees. Under caged conditions, parent adults attacked oak bolts, laid eggs, and re-emerged three times in a growing season (Rexrode 1969).

Other Coleoptera that commonly infest wilt trees are the two-lined chestnut borer, *Agrilus bilineatus* (Web.); the flatheaded apple tree borer, *Chrysobothris femorata* (Oliv.); the Columbian timber beetle, *Corythlus columbiana* (Hopk.); and several species of ambrosia beetles and other wood borers.

Figure 1. *P. pruinosus* egg galleries in diseased oak.

Dissemination of the Fungus by Insects

It seems logical that any insect coming into intimate contact with a fungus mat would become contaminated with endoconidia and/or ascospores of *C. fagacearum.* It also seems reasonable that any insect that breeds or feeds in a diseased tree will become contaminated with propagules of the oak wilt fungus. Several species of Diptera, Collembola, and Coleoptera carry the oak wilt fungus when they leave the sources of inoculum (Bart and Griswold 1953, Berry and Bretz 1966, Buchanan 1956, Dorsey et al. 1953, Himelick et al. 1954, Jewell 1954 and 1956, McMullen et al. 1955, Norris 1953, Rexrode et al. 1965, Rexrode and Jones 1971, Skelly 1968, Stambaugh et al. 1955, Thompson et al. 1955, Wertz et al. 1971), thus meeting the second requirement for a vector.

Since the first vector studies in 1952, oak bark beetles, *Pseudopityophthorus* sp., have received more attention as a direct vector of the oak wilt fungus than any other tree-wounding insect. Studies in Missouri by Buchanan (1956), in which healthy trees contracted oak wilt after they were inoculated with a mixture of the macerated beetles in water, demonstrated that the beetles carried sufficient amounts of the pathogen to cause infection. Stambaugh et al. (1955) found that a small percentage of oak bark beetles carry viable spores of *C. fagacearum* upon emergence from diseased trees in late summer. Rexrode et al. (1965) showed that 2 to 22 percent of the re-emerging parent adult beetles carry spores of the oak wilt fungus. Berry and Bretz (1966) also found that a fairly high percentage of the oak bark beetle, *P. minutissimus,* reared from wilt-infected material, carry oak wilt fungus.

Rexrode and Jones (1971) found that the oak bark beetles, *P. minutissimus* in Missouri and *P. pruinosus* in West Virginia, carry the oak wilt fungus when they emerge in April and May after overwintering in wilt-killed trees. Beetles from 47 percent of all trees sampled carried the fungus. The percentage of contaminated beetles emerging from wilt-killed trees ranged from 0 to 33.

Insects Directly Associated with Healthy Oaks

Since so many species of insects feed and/or breed on diseased oaks, the list of potential vec-

tors of the oak wilt fungus is long. However, a large number of them are not directly associated with healthy oaks; thus they do not meet the third requirement for a vector. Insect species of Diptera, Collembola, and Nitidulidae are commonly present on mycelial mats of the fungus on diseased oaks, but they are not directly associated with healthy oaks. One of the primary groups of suspect vectors of the oak wilt fungus are the Nitidulids, the sap-feeding beetles; but they do not make their own feeding or breeding wounds on healthy oaks: most are found where plant fluids are fermenting or souring. The mere association of an insect with the diseased tree or the presence of inoculum on or in the insect's body is not sufficient justification for concluding that the insect is a vector of the oak wilt fungus.

Several species of Coleoptera, such as the two-lined chestnut borer, the flatheaded apple tree borer, the Columbian timber beetle, and other wood borers do feed and/or breed in healthy oaks as well as diseased oaks; but oak bark beetles are the most common. Oak bark beetles commonly feed on healthy oaks throughout the known range of the oak wilt disease. Craighead and Morris (1952) thought that adult bark beetles feed in leaf axils and in dormant buds. Griswold and Neiswander (1953) reported that *P. minutissimus* makes deep feeding cavities in the twig crotches and in the bud, leaf, and immature acorn axils on small twigs of healthy oaks of both the red and white oak groups.

Griswold and Bart (1954) reported the same kind of feeding by *P. pruinosus* adults. In 1955, Stambaugh et al. observed frequent attacks by these beetles on twigs of healthy oaks when beetles were abundant on nearby trees killed by oak wilt. Buchanan (1958) reported that *P. minutissimus* feeds in twig crotches, at the base of leaf petioles, and on roughened areas of bark on small stems.

During the spring of 1968, Rexrode and Jones (1970) found adults of *P. pruinosus* and *P. minutissimus* commonly feeding on healthy oaks of the red and white groups in Missouri, Ohio, and West Virginia. The beetles feed mainly at the node between the previous year's growth and the current year's growth (Fig. 2) but will also feed in leaf axils, female flower axils, and bud axils on the current growth. Adults bore through the bark, cambium, and xylem to the center of the twig (Fig. 3). Feeding appeared to be most common in the spring, but was observed in all three states throughout the growing season. Feeding was concentrated in the top branches of dominant trees, but was also noted lower in the crown as well as on twigs of trees in all crown classes.

Figure 2. *P. pruinosus* feeding on black oak.

Transmission

In the early 1950s, most research on transmission of the oak wilt fungus concentrated on insects that frequent mycelial mats on diseased trees. Leach et al. (1952) pointed out that insects, principally Nitidulids, were attracted to fungus mats on wilt trees. These workers also predicted that Nitidulids, since they also visited wounds in the bark of healthy trees, would be found to be important vectors of the oak wilt fungus.

This has been proved experimentally by Dorsey et al. (1953) in West Virginia and Norris (1953) in Iowa. Additional confirmation was pre-

Figure 3. *P. pruinosus* feeding on scarlet oak.

sented by Himelick et al. (1954), Jewell (1954), McMullen et al. (1955), and Thompson et al. (1955). Because the sap-feeding beetles are dependent on mycelial mats of the fungus on diseased trees and fresh wounds in the bark of healthy trees for successful transmission, they cannot be considered as a primary vector in the absence of one of these factors. In Missouri, mats seldom form on wilt-killed trees; yet the disease is well established, and each year new infections occur that can be attributed only to overland spread of the fungus.

The amount of sporulation of the oak wilt fungus in the xylem of diseased trees remains unknown (Fergus 1953). However, evidence that such sporulation occurs has been presented by several workers (Young 1949, Parmeter et al. 1956). Sporulation in moist wounds that penetrate the bark into the xylem of infected trees (Craighead et al. 1975, Cobb et al. 1965), and in insect galleries (Curl et al. 1953, Fergus 1953) has been reported. Thus, it seems logical that insects not associated with oak wilt fungus mats but in intimate contact with the diseased trees would become infested with the oak wilt fungus.

Griswold and Bart (1953) and Griswold (1958) demonstrated that the oak wilt fungus was transmitted by *P. pruinosus* and *P. minutissimus* by exposing the beetles to sporulating cultures of the fungus and then caging large numbers of small trees of susceptible oak species. In 1958, Buchanan reported two specific cases of fungus transmission by *P. minutissimus* under caged conditions.

In studies conducted by Rexrode and Jones (1970), bark beetles transmitted the oak wilt fungus in 2 of 30 attempts. Beetles were exposed to sporulating cultures or to a suspension of conidia and then were caged (32-mesh screen) on small trees of susceptible oak species. In one case, oak wilt symptoms developed on, and the fungus was reisolated from, a nursery-grown red oak tree (3 feet tall) on which five beetles had been caged. The only feeding wound on this tree was at the base of the twig where wilting first appeared. Identical results were obtained on another tree where 10 beetles had been caged. Here too, the only feeding wound was at the base of the twig displaying initial symptoms.

Discussion

The oak bark beetles are one of the few groups of insects that satisfy all the requirements for a vector of the oak wilt fungus. Nearly all wilt-infected oaks are attacked by these insects. Breeding attacks on diseased trees during the wilting and defoliation phase of symptom expression are usually not successful. Even in these abortive attacks, however, the beetles penetrate the cambium before moving on to another tree and, theoretically, could become contaminated with the fungus.

About half of all trees killed by wilt sustain successful attacks; that is, breeding, egg-gallery

construction, and oviposition are completed. After oviposition about half of the parent adults emerge and move on to feed and/or breed in other trees. This commonly involves thousands of beetles per tree, and adults may attack, lay eggs, and re-emerge up to three times in a growing season. Varying percentages of the emerging adults are contaminated with the wilt fungus.

The beetle progeny develop in the diseased tree in about 6 weeks during the growing season. They then emerge and move on to other trees to feed and/or breed. A portion of these beetles carry the fungus.

Some bark beetles overwinter in diseased trees. In the spring, these adults emerge and move to healthy trees to feed. Some of these beetles carry the oak wilt fungus.

Feeding occurs throughout the growing season, but is particularly heavy in the spring. Beetle-feeding wounds are ideal infection courts for the oak wilt fungus, and infection can occur when contaminated beetles feed on healthy oaks.

Today, oak bark beetles are believed to be the most important vectors of the oak wilt fungus. In areas where mycelial mats of the fungus develop on diseased trees, sap-feeding beetles, Nitidulids, probably aid in the transmission of the fungus. However, the fungus is not entirely dependent on these two groups of insects for overland spread. Any insect that feeds and/or breeds on oak wilt fungus-infected oaks and then visits healthy oaks under conditions conducive to inoculation and infection can also be a vector of the fungus.

Although I feel that oak bark beetles and sap-feeding beetles, Nitidulids, are the most important and most capable vectors of the oak wilt fungus, many factors limit their efficiency. Nitidulids are dependent on mycelial mats on diseased oak for a source of inoculum, and they are also dependent on fresh (less than 24 hours old) wounds on healthy trees to perform the transmission process. We do not know the frequency of natural wounds on healthy oaks in nature, but we do know that fungus mats rarely develop on wilt trees in some sections of the country and in other sections are rarely found on more than 25 percent of the diseased trees.

Although oak bark beetles naturally breed in diseased oaks, most studies indicate that only a small percentage of beetles emerging from wilt-killed trees carry the fungus. There are several possible explanations for the apparent low incidence of beetle contamination. The oak wilt fungus rarely fruits in diseased trees. Fungus longevity in the bole and crown of infected trees of the red oak group rarely exceeds 1 year, and is often much shorter, particularly in the branches where bark beetles commonly breed. Also, fungus distribution is irregular in many diseased trees.

Oak bark beetles are native insects, and there appears to be a balance between them and their natural enemies. Beetle population levels remain rather constant year after year as does the occurrence of oak wilt. However, about every 3 to 4 years the populations collapse. The incidence of oak wilt normally declines following the collapse of oak bark beetle populations. However, we have no evidence that the decline in the incidence in oak wilt is due to the collapse of oak bark beetle populations.

Following some hardwood logging operations in the eastern United States, the occurrence of oak wilt often increases for 1 to 3 years. We do not know what to attribute this increase to other than oak bark beetle build-up in the slash and/or wounding of the remaining healthy trees.

Experiments for the control of oak wilt, now being conducted by the U.S. Forest Service, Northeastern Forest Experiment Station, in cooperation with the West Virginia Department of Agriculture, Forest Pest Control, are aimed primarily at reducing fungus-mat production and oak bark beetle breeding in diseased oaks. We believe that oak wilt losses can be suppressed if we reduce the source of inoculum for Nitidulids and reduce oak bark beetle breeding in diseased oaks.

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ABSTRACT

Smith, E.M. and T.A. Fretz. 1976. **Chemical weed control recommendations for Ohio nursery and landscape plantings.** Cooperative Extension Service Publication MM-297. The Ohio State University, Columbus, Ohio. 19p.

Herbicides are an efficient and effective means of controlling weed growth in nursery and landscape situations. Use of a well designed chemical weed control program can result in a number of benefits including: 1) Reduced labor and operation costs, 2) Improved plant quality by reducing cultivation damage, and 3) Increased growth and yield of plants by reducing weed competition for light, nutrients, and water. In order to achieve a better understanding of the practices of chemical weed control, some knowledge of the classification, types, and methods of application of herbicides must be understood.