Overland Transmission of *Ceratocystis fagacearum*: Extending Our Understanding

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Oak wilt is an important disease of oaks (*Quercus* spp.) in 22 states of the eastern United States. The causal fungus, *Ceratocystis fagacearum* J. Hunt, causes mortality of thousands of native oaks annually across the upper midwestern states. The pathogen is transmitted from diseased to healthy trees below ground via functional root connections and above ground via insect vectors. Spread of the disease across the landscape is considered slow and erratic, especially when compared with that of introduced exotic diseases of trees such as Dutch elm disease and chestnut blight. The inefficient insect vector relationship in the disease cycle is cited as the reason that oak wilt has not had the major impact that Dutch elm disease has had in the United States (25). Overland transmission of the pathogen via insect vectors is less effective, occurs less frequently, and is less predictable than local root graft spread. Nonetheless, insect transmission is significant as the means by which new infection centers are initiated either within the same oak stand or in adjacent to more distant stands.

Average rates of new oak wilt center establishment in the Midwest have been reported (1,17,24,30) to range from 0.004 to 0.042 new centers per hectare of oak forest type per year. The distances of new centers from the nearest documented infection center have also been reported, ranging from several hundred meters to several kilometers (19,25,30). Shelstad et al. (30) documented the distance of new centers from existing oak wilt centers over a 10-year period in east central Minnesota and found most new centers occurred within 300 m of an existing center. However, 24% of the new centers were >300 m from existing centers, and these centers had a significant impact on total area of oak forest affected over time.

The direction of newly established centers from the nearest existing center has also been studied (4,18,25). In general, new infection centers are initiated by insect vectors that are carried downwind until they impact on the edges of stands or openings, on dominant trees protruding above the forest canopy, or on the windward sides of ridges.

In the most recent review of insects and the epidemiology of oak wilt, Merrill and French (25) concluded that several different species of the order Coleoptera could indeed vector *C. fagacearum*. However, the relative importance of each of these species in establishing new infection centers in different areas of the oak wilt range is not known. Current research efforts in the Midwest are addressing this and other issues related to insect transmission of the oak wilt fungus. This paper specifically addresses a cursory view of the importance of different insect vector groups by region or state, and the current research efforts to extend our understanding of the overland spread phenomenon.

IMPORTANCE OF DIFFERENT INSECT VECTOR GROUPS

Within the Existing Oak Wilt Range

Sap beetles, or nitidulids (Coleoptera: Nitidulidae), are considered the primary vectors of *C. fagacearum* in the north central states (9,11) based on several decades of observational and experimental evidence. To the contrary, oak bark beetles, or *Pseudopithyophthorus* spp. (Coleoptera: Scolytidae), have long been considered the primary vectors of *C. fagacearum* in Missouri. Nitidulids were not considered important vectors due to the apparently rare occurrence of oak wilt mats in the state (12). Based on recent observations of mats and their nitidulid associates in Missouri (J. Bruhn, *personal communication*), the importance of both these vector groups in establishing new infection centers in that state need clarification. The ability of oak bark beetles, nitidulids and ambrosia beetles to serve as vectors of the pathogen in Ohio, Pennsylvania, and West Virginia has been documented along with some evidence for the relative importance of at least two of these vector groups (12). Less is known about insect vector groups of *C. fagacearum* in Texas. Viable pathogen propagules have been detected on bodies of several different free-flying nitidulid species in Texan oak wilt centers (3). The crowns of numerous oaks were examined in central Texas over several weeks for evidence of feeding by oak bark beetles. No evidence was found, however, and nitidulids are currently viewed as the most important insect vector group (D. Appel, *personal communication*).

Potential for Disease Increase and Spread

It is likely that an increased rate of overland spread as well as an extension of the range of oak wilt in the United States could occur if the European oak bark beetle, *Scolytus intricatus* (Coleoptera: Scolytidae), becomes established in the country. Based on comparisons of the biology and behavior of the European species to U.S. species of oak bark beetles, *S. intricatus* would likely be a very effective vector of the pathogen compared with the existing inefficient vectors currently in the United States (13). *S. intricatus* has been intercepted at least seven times in the past 2 years at U.S. ports of entry (13).

Species of the other two commonly cited vector groups already occur in states outside the known oak wilt range in the United States. If *C. fagacearum* were inadvertently introduced into these states, there is potential for the disease to become established and, thus, expand the known range of oak wilt. Nitidulid species are of particular interest, as they are known to vector other *Ceratocystis* species in western states. For example, *Carpophilus freemani* and *C. hemipterus* are vectors of *Ceratocystis fimbriata* in deciduous fruit trees in California (26). Furthermore, the susceptibility of predominant oaks in California to *C. fagacearum* has been demonstrated (2). Nitidulids also serve as vectors of *Ceratocystis* spp. pathogens on sugarcane (Hawaii) and on trembling aspen (Colorado) (7, 14).

CURRENT RESEARCH EFFORTS ON OVERLAND TRANSMISSION

Principal Nitidulid Species Associated with Transmission

A major research effort to determine the principal nitidulid species associated with the transmission of *C. fagacearum* to fresh wounds on oak in Minnesota was initiated in 1994. The variety of nitidulid species implicated in oak wilt spread and the relatively inefficient manner of overland spread have led to generalizations about nitidulids as *C. fagacearum* vectors (20), two of which are being questioned in this research.

The first generalization is that a wide range of nitidulid species are involved in the overland spread of oak wilt. Our research, however, points to two species as the principal nitidulids vectors involved in carrying the pathogen from mats to fresh wounds in Minnesota. Although six species accounted for 94% of all members of the family Nitidulidae on spring mats between 1994 to 1996 in two east central Minnesota locations (Figs. 8.1 and 8.2) (5,6), only two of these species accounted for >90% of the members of the family Nitidulidae found on fresh wounds during spring 1998 in the same locations (Fig. 8.3) (23). *C. fagacearum* was isolated from a high percentage of the wound-inhabiting beetles (Table 8.1). The two predominant species, *Carpo-*

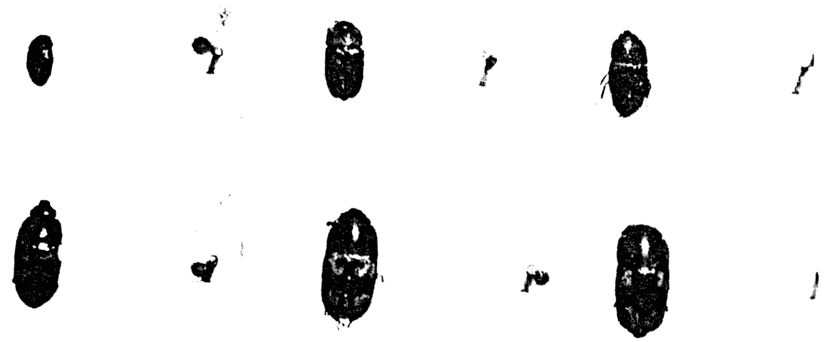

Fig. 8.1. Predominant nitidulid species associated with spring oak wilt mats in east central Minnesota, 1994 to 1996: Top row (l to r) *Colopterus truncatus*, *Epuraea corticina*, *Carpophilus sayi*; bottom row (l to r) *Glischrochilus sanguinolentus*, *Glischrochilus fasciatus*, *Glischrochilus quadrisignatus*.

philus sayi and *Colopterus truncatus*, are now the primary suspects in pathogen transmission in Minnesota.

The second generalization in question is that the members of the family Nitidulidae associated with the *C. fagacearum* disease cycle are ecological generalists and casually visit oak wilt mats and oak wounds in addition to various other food sources. Our current hypothesis (T. C. Skalbeck and J. Juzwik, *unpublished data*) is that ecological specialization to the oak wilt disease cycle exists for several members of the family Nitidulidae. This hypothesis was also raised by Norris (28) following his investigation of insects associated with oak wilt in Iowa between 1952 and 1955. Recent observational evidence also supports this hypothesis. First, a progression of nitidulid species was correlated with advancing biological age of oak wilt mats in our 1994 to 1996 studies (Fig. 8.2). *Colopterus truncatus*, *Epuraea corticina*, and *Carpophilus sayi* are associated with younger mats that, we speculate, produce different volatiles than do older mats that are commonly colonized by various other microorganisms (5). *Glischrochilus* species, however, are most frequent on the older mats and are generally known to be associated with various decaying fruit and vegetable material. Secondly, *Colopterus truncatus*, *Colopterus semitectus*, and *Carpophilus sayi* were predominant on fresh (≤7-day-old) oak wounds during spring 1998 (Fig. 8.3). *Glischrochilus* species were commonly observed on these wounds 15 to 30 days after wounding and were apparently feeding on fermenting sap. In summary, I suggest that *Colopterus truncatus*, *Carpophilus sayi*, and *Epuraea corticina* have a much higher degree of ecological specialization for the oak wilt disease cycle than do the *Glischrochilus* species.

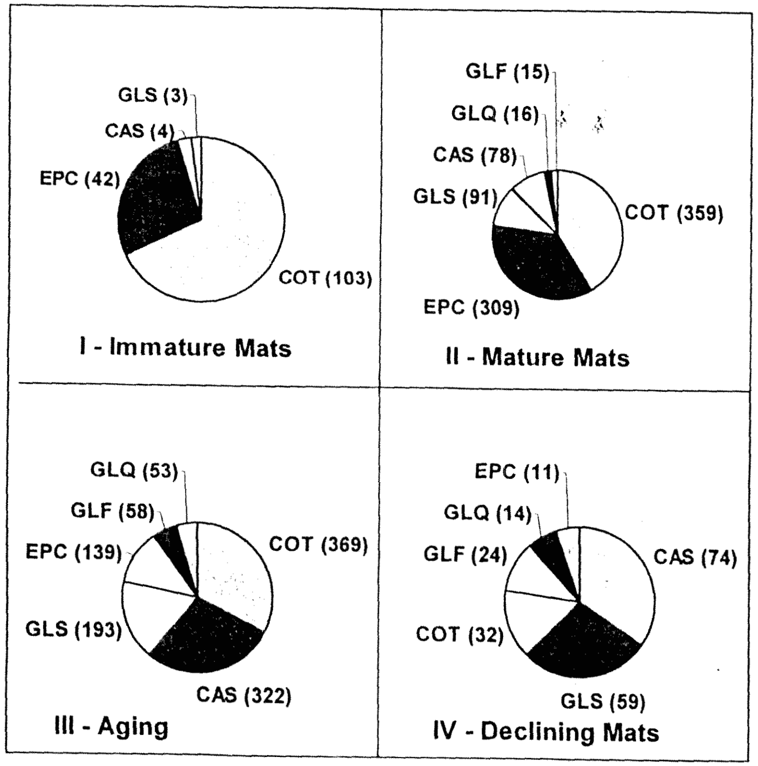

Fig. 8.2. Number of nitidulid species collected from different biological ages of spring oak wilt mats in east central Minnesota, 1994 to 1996. Cot = *Colopterus truncatus*; Epp = *Epuraea corticina*; Cas = *Carpophilus sayi*; Gls = *Glischrochilus sanguinolentus*; Glf = *Glischrochilus fasciatus*; and Glq = *Glischrochilus quadrisignatus*. Based on collection of nitidulids from the following number of mats per mat state: 34 mats, immature; 151 mats, mature; 188 mats, aging; and 57 mats, declining.

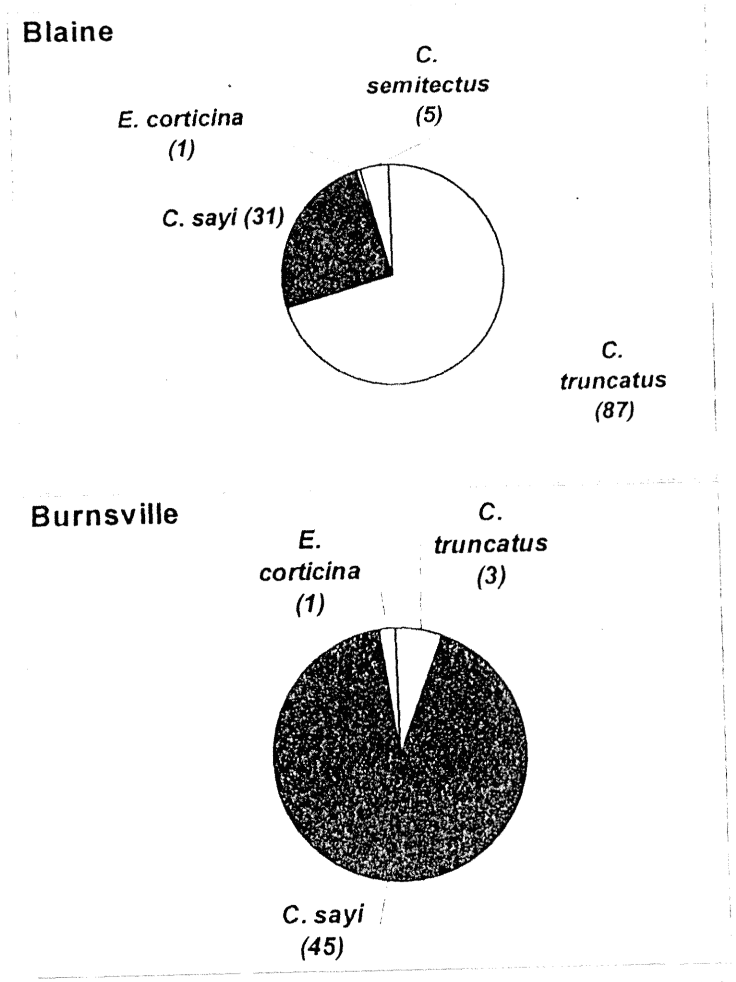

Fig. 8.3. Number (in parentheses) of nitidulid species *Carpophilus sayi*, *Colopterus semitectus*, *Colopterus truncatus*, and *Epuraea corticina* found on ≤7-day-old wounds during mid-May 1998 in two locations in east central Minnesota.

Research has recently been initiated that will increase our knowledge about these putative ecological specialists. Results of life history investigations on *Colopterus truncatus* and *Carpophilus sayi* may suggest points in their life cycles that could be disrupted and lead to vector-based disease control. Results of chemical ecology investigations of the same species may also lead to a new control strategy. Behavioral responses of *Colopterus truncatus* and *Carpophilus sayi* to different attractants and pheromones are being documented. Related species of both genera are known to produce pheromones that show potential as tools in managing nitidulid pests in other crops (15,33).

Availability of Inoculum During the Critical Spring Period

Much is known about the production of oak wilt spore mats in the north central states. Mats are commonly formed on recently killed red oaks (*Q. ellipsoidalis* and *Q. rubra*) during the spring and fall. The production peaks during the spring are of special interest, as this is the time when most overland transmission of *C. fagacearum* has been documented in the region. The common message publicized each spring in Minnesota has advised landowners, arborists, and developers to "not prune in May or June" (or otherwise damage healthy oaks!) to prevent overland transmission of the pathogen. Peaks in spore mat formation, however, vary annually and may indeed occur in early April. Temperature is thought to play a major role in triggering mat production in Minnesota (18). Baseline data on mat production on various diameter red oaks and on cambial temperatures have been collected for the past 3 years. Statistical analyses of these factors are currently underway, with the goal being to develop a model to annually predict onset and peak production dates. Of course, degree-day models concerning the population levels of *Colopterus truncatus* and *Carpophilus sayi* during the same time period would also be of value.

TABLE 8.1. Isolation of *Ceratocystis fagacearum* from nitidulid species collected daily from wounds made between 1 and 7 days prior on red oaks in mid-May 1998 in two east central Minnesota locations

Location	Nitidulid species	No. of nitidulids assayed	Percent with *C. fagacearum*[z]	Average CFU per beetle ($\times 10^3$)
Blaine	*Colopterus truncatus*	87	94	9.1
	Colopterus semitectus	5	60	1.3
	Carpophilus sayi	31	94	44
	Other	2	0	0
Burnsville	*Colopterus truncatus*	3	100	13
	Carpophilus sayi	45	69	18
	Other	2	100	1.2

[z]Based on plating of aqueous suspensions of beetle washings onto acidified potato dextrose agar.

Role of Other Fungi in Deterring Pathogen Transmission

Oak wilt mats and adjacent moribund xylem are colonized by a variety of microorganisms (31,32). The role of these organisms in reducing the availability of viable pathogen propagules for insect vector acquisition is largely unknown. *Ophiostoma quercus* (previously the hardwood type of *O. piceae*) is a common colonizer of mats in Minnesota (21), West Virginia (16), and probably Illinois (8). The overgrowth of fresh oak wilt mats by *O. quercus*, however, does not significantly impact the viability of *C. fagacearum* propagules on the mats (21) or their acquisition by nitidulids visiting those mats (Table 8.2) (22). Other mat-associated fungi have been shown to negatively affect *C. fagacearum* viability in laboratory studies (31,32). For example, *Gliocladium roseum* and *Trichothecium roseum* prevented growth or caused mycelial death of *C. fagacearum* (31). In subsequent laboratory screening trials, no viable propagules of *C. fagacearum* were isolated from colonies (single mating type) of *C. fagacearum* overgrown by 12 of 19 *G. roseum* isolates in potato dextrose agar petri dish culture studies (27). Similar effects were observed for two of five *T. roseum* isolates tested in the same manner. Three *G. roseum* isolates were further tested in a preliminary field trial in Minnesota in spring 1998. Reduced isolation of *C. fagacearum* propagules from treated mats was associated with *G. roseum* treatment compared with the higher isolation rate from nontreated mats (M. F. Neuman and J. Juzwik, *unpublished data*). Additional in vitro and in vivo studies with *G. roseum* isolates are currently underway.

The availability of suitable xylem-penetrating wounds is one of several conditions needed for successful nitidulid-mediated transmission of *C. fagacearum*. Numerous experimental field studies have been conducted to elucidate the length of time such wounds on healthy oaks remain susceptible to infection by *C. fagacearum* (12). Susceptibility decreased rapidly as the numbers of days after wounding increased, with many reports indicating that the susceptible wounds were ≤3 days old. Colonization of wounds by other microorganisms occurs quickly after xylem-penetrating wounds are made in the spring (J. Juzwik, *personal observation*), and such organisms may well serve as deterrents to infection by *C. fagacearum*. *O. quercus* is commonly

TABLE 8.2. Isolation of *Ceratocystis fagacearum* and *Ophiostoma quercus* from nitidulids collected from *O. quercus*-treated and nontreated oak wilt mats[x]

Treatment	No. of nitidulids assayed	Percent beetles yielding fungi[y]			Average CFU per beetle ($\times 10^3$)	
		O. quercus	*C. fagacearum*	Both	*O. quercus*	*C. fagacearum*
O. quercus	98	74 a[z]	92 a	70 a	53 a	83 a
Control	85	41 b	84 a	35 b	68 a	145 a

[x]Mats were in aging and declining conditions, per Curl (8).
[y]Based on plating of aqueous suspensions of beetle washings onto acidified potato dextrose agar.
[z]Values followed by the same letter within a column are not different ($P \geq 0.05$).

associated with wounds on healthy oaks (31) and has been shown to prevent *C. fagacearum* infection of fresh wounds (24-h old) when it is introduced 24 h prior to challenge inoculation with the pathogen (10). Immediate treatment of pruning wounds with *O. quercus* was later found to be as effective as tree paints in preventing overland disease spread (28). Nitidulids are common carriers of *O. quercus* (Table 8.2) but they are probably not involved in natural biological control of overland transmission of *C. fagacearum* in which *O. quercus* is involved (22). Nitidulids also commonly carry *G. roseum* and infrequently carry *T. roseum* (J. Juzwik, *unpublished data*) but their role as vectors of these other potentially antagonistic fungi is unknown.

SUMMARY AND CONCLUSIONS

In summary, there continue to be large gaps in our understanding of the importance of different insect vector groups in transmission of the oak wilt fungus. Over 20 years of observational and circumstantial data support the case that nitidulids are the most important vector group in Minnesota (19). Perhaps new technologies (e.g., molecular biology and geographic information systems [GIS]) will provide tools for better addressing this question in the different parts of the oak wilt range. Recent gains in knowledge and understanding of the principal members of the family Nitidulidae associated with wound-related spread of *C. fagacearum* may help in quantifying the importance of nitidulids in pathogen transmission and may lead to the development of new insect-based control strategies.

The role of oak bark beetles in *C. fagacearum* transmission needs further examination. In particular, their importance in long-distance spread of oak wilt in Missouri in relation to nitidulids is now in question. The potential for greater efficiency in overland disease spread should European oak bark beetles become established in the United States deserves consideration as well.

Finally, recent research results concerning the conditions associated with nitidulid-mediated transmission of *C. fagacearum* have increased our understanding of the role of selected antagonistic and competitor fungi in the overland transmission cycle and will hopefully lead to better predictive systems for when oak wilt mats are available each spring as well as when principal nitidulid vector species are present and transmitting the pathogen to healthy oaks.

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Current Practices and Suppression Methods for Managing Oak Wilt Disease

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Approximately 10,000 years ago the glaciers receded from the region now known as the Twin Cities metropolitan area of Minneapolis and St. Paul, MN, leaving tens of feet of glacial outwash sand as the new soil. This area is geographically termed the Anoka Sand Plain. Minnesota's oak species grow well in this soil type and, consequently, for centuries there has existed a vast forest with thousands of acres of contiguous forest type, composed primarily of northern pin oak (*Quercus ellipsoidalis*), but also northern red oak (*Q. rubra*), bur oak (*Q. macrocarpa*), and white oak (*Q. alba*).

The expansion of the Twin Cities area has meant the residential and commercial development of the Anoka Sand Plain over the last 30 years. This development has resulted in thousands of oak wilt sites across thousands of acres involving hundreds of thousands of trees. The wooded lots and forest areas, so desperately sought after by the suburban population, are truly threatened by this population's encroachment into the oak forest.

Human activity of many kinds, including construction, leads to the wounding of trees during the months of May and June, which directly leads to the establishment of oak wilt sites. Initial infections spread within the same species via root grafts. Contiguous oak stands lead to ever-expanding disease sites. Some may be tens of acres in size. However, this disease's dependence on spread by root graft transmission, and the fact that the insect vectors of this disease depend on wounds to oaks during a particular time of the year, makes management of this disease possible.

The management practices addressed in this chapter are those commonly and currently in use in Minnesota in both community-wide management programs and programs made available to individual property owners. However, this chapter will deal primarily with the procedures undertaken in two community oak wilt programs administered in northern Anoka County: Columbus Township and the City of Ham Lake just north of St. Paul and Minneapolis, MN.

These management practices have five main phases: (i) detection and diagnosis; (ii) public education and involvement; (iii) containment of root spread; (iv) prevention of loss within the infection center; and (v) prevention of overland spread.