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COMPARISON OF VOLATILES FROM BEETLE-TRANSMITTED *Ceratocystis fagacearum* AND FOUR NON-INSECT-DEPENDENT FUNGI

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Abstract—*Ceratocystis fagacearum* (Bretz) Hunt is the causative agent of oak wilt disease, which is transmitted primarily by nitidulid beetles. This fungus was compared with four non-insect-dependent fungi for their volatile profiles using gas chromatography and mass spectrometry (GC-MS) and for their attractiveness to nitidulids using a wind-tunnel bioassay. The four additional fungi included *Xerula radicata* Sing, *Pluteus atricapillus* Kumm, *Tyromyces chioneus* Karst, and *Botrytis cinerea*. Nitidulids have been reported in association with each of these fungi, but unlike *C. fagacearum*, they are dispersed primarily by wind or rain. Significant attraction of three nitidulid species, *Carpophilus hemipterus* (Linne), *C. lugubris* Murray, and *Stelidota geminata* (Say) was elicited by *C. fagacearum* and to a lesser extent by *X. radicata*, but not by the others. A comparison of headspace volatile profiles showed that the odor of *C. fagacearum* was the strongest, both with regard to the number of components and in their rates of production. Chemical characterization of the headspace profile of *C. fagacearum* revealed 16 components: one aldehyde, one ketone, five alcohols, and nine esters. These components were all common fruit-odor constituents and many of them were previously shown to be attractive to nitidulid beetles. The results of this study suggest that, by mimicking food odors, *C. fagacearum* odor is an adaptation for attracting nitidulid and possibly other insect vectors.

Key Words—Oak wilt, *Ceratocystis fagacearum*, headspace volatiles, Coleoptera, Nitidulidae, *Carpophilus hemipterus*, *Carpophilus lugubris*, *Stelidota geminata*.

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INTRODUCTION

Oak wilt, caused by the fungus, *Ceratocystis fagacearum* (Bretz) Hunt, is a severe disease of oak trees and occurs over much of the United States (True et al., 1960; Gibbs and French, 1980; Appel et al., 1985). Insect vectors play an important role in its aboveground transmission by initiating new infection centers (Gibbs and French, 1980), and activity of nitidulid beetles is considered one of the three major factors responsible for the spread of oak wilt (Appel et al., 1987). Since the transmission of oak wilt by nitidulid beetles was first demonstrated (Dorsey et al., 1953; Norris, 1953), many studies have focused on the occurrence of nitidulid beetles in oak-wilt areas and the transmission of this disease to healthy trees (Dorsey and Leach, 1956; Skalbeck, 1976; Juzwik and French, 1983, 1985; Appel et al., 1986, 1987). *C. fagacearum* forms mycelial mats under the bark of oak trees that generate sufficient pressure to split the bark and expose their fruiting surface (Dorsey and Leach, 1956). The mycelial mats produce sticky spores that can not be transmitted by wind or rain (Dorsey and Leach, 1956; Collins and Kalnins, 1965); spores are characterized by a strong fruity odor, which is detectable around infected trees (Collins and Kalnins, 1965; Skalbeck, 1976). To better understand the relationship between *C. fagacearum* and nitidulids, we compared the volatile profile and attractiveness of *C. fagacearum* with those of four other wood-infecting, but non-nitidulid-dependent fungi.

METHODS AND MATERIALS

Fungal Cultures. A culture of oak-wilt fungus, *Ceratocystis fagacearum* (Bretz) Hunt, was initiated with an isolate from Department of Plant Pathology and Physiology, Virginia Polytechnic Institute and State University (Blacksburg, Virginia). *Xerula radicata* Sing, *Pluteus atricapillus* Kumm, and *Tyromyces chioneus* Karst were initiated with isolates from the Center for Forest Mycology Research, USDA (Madison, Wisconsin), and *Botrytis cinerea* was obtained from the Department of Plant Pathology, OARDC/The Ohio State University. All fungi were maintained on potato-dextrose agar (PDA) medium (BBL Microbiology System, Cockeysville, Maryland) at room temperature and were transferred every two to three weeks. Fungal cultures used for headspace-volatile collection and for bioassay were grown on the same medium in 240-ml Qorpak straight-sided jars at 24–26°C until at least $\frac{3}{4}$ of the medium surface was covered by fungal mycelia. Jars with PDA medium alone were incubated under the same condition to serve as the control. The lid of each jar was equipped with a 0.2-μm Bacterial Air Vent (Gelman Science, Ann Arbor, Michigan) for ventilation and a rubber septum (Thomas Scientific) for collection of headspace air samples.

Beetles and Wind-Tunnel Bioassay. Laboratory colonies of *Carpophilus hemipterus* (L.), *C. lugubris* Murray, and *Stelidota geminata* (Say) were maintained on artificial diet (Hall et al., 1978) under the conditions of 24 ± 1°C, 16:8-hr light–dark and 75–85% relative humidity. After eclosion from the pupae, both sexes were held with moisture in 360-ml plastic cups, but without contact with food or food odors. Six- to 7-day-old *C. hemipterus* and *C. lugubris* and 4-day-old *S. geminata* were used for bioassays, and beetles were discarded after each test.

Orientation of nitidulid beetles to fungal cultures and to PDA medium were evaluated in a wind tunnel as previously described (Lin and Phelan, 1991a). Conditions in the wind tunnel were 35–65% relative humidity, 24–27°C, 17 lx light at the wind-tunnel floor and wind speed of 0.5 m/sec. Two jars were placed on the tunnel floor 20 cm apart in the center of the upwind end of the tunnel. One jar was empty and the other contained the odor source; positions of the two jars were rotated between replicates. Ten beetles were released on the floor at the center of the downwind end of the tunnel at a distance of 180 cm from the jars, and those walking or flying to within 10 cm downwind of the jar in 10 min were counted as responders (Phelan and Lin, 1991). *S. geminata* was released at a distance of 120 cm from the jars because this beetle moved slower than the two *Carpophilus* species. Percent responses to the odorous and empty jars were compared by *t* test after arcsin-square root transformation.

Volatile Collection and Identification. Headspace-volatile collections followed the previously described method in which volatiles were trapped on Tenax GC and then thermally desorbed to a gas chromatograph (Phelan and Lin, 1991). Jars containing fungal cultures were opened for 3 min prior to collecting headspace samples. For a comparison of the volatile constituents of different fungi, a 20-ml headspace sample was injected into the Tenax trap using a gas-tight syringe, followed by a 2-min flush of the trap with helium (20 ml/min). The trap then was heated to 200°C and the helium flow through the trap was reversed, such that the retained constituents were desorbed and backflushed to the GC capillary column. This flushing method, used for qualitative comparisons, reduced the amounts of the highly volatile major components, ethanol and acetaldehyde, while enriching the levels of minor components of the profiles (Phelan and Lin, 1991). Volatile constituents were chromatographed using a Hewlett-Packard 5890A gas chromatograph (GC) with a direct interface to a Hewlett-Packard 5970C Mass Selective Detector. DB-FFAP column (30 m × 0.25 mm ID, 0.25 μm film thickness) was used in the among-fungi comparisons of headspace profiles. For a quantitative analysis of the *C. fagacearum* volatile profile, the trap was only flushed for 0.5 min, which removed air from the trap but retained all volatile constituents, as determined by breakthrough studies. Separation was carried out on a DB-1 capillary column (30 m × 0.32 mm ID, 5.0 μm film thickness). GC analyses were temperature-programmed from 30 to

200°C at 10°C/min, with a helium flow rate of 0.7 ml/min on DB-FFAP and 0.9 ml/min on DB-1. Volatile components were identified by comparison of mass spectra and retention times of authentic compounds. Amounts were peak areas with those of known quantities of authentic compounds. All chemicals were purchased from Aldrich Chemical Co. (Milwaukee, Wisconsin).

RESULTS

Beetle Attraction. C. fagacearum elicited significant levels of up-tunnel attraction in all three nitidulid species (Figure 1). PDA medium alone did not attract any beetles, and of the four non-nitidulid-dependent fungi, only *X. radicata* evoked beetle response at a level greater than that to a blank jar (Figure 1).

Comparison of Headspace Volatile Profiles. The volatile profiles of *C. fagacearum*, four non-nitidulid-dependent fungi, and PDA medium are shown in Figure 2. Ten components were identified from the profile of *C. fagacearum* (Figure 2, Table 1). Four of these constituents also were detected from *X. radicata*, and at a lower concentration from *P. atricapillus*: ethanol, 2-methylpropanol, 3-methylbutanol, and 2-methylbutanol. Only ethanol was found in the profiles of *T. chioneus* and PDA medium, and *B. cinerea* emitted none of the *C. fagacearum* components but produced two unidentified later-eluting vol-

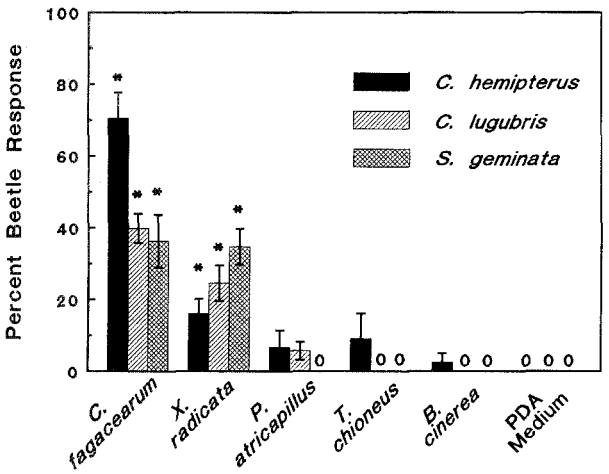

FIG. 1. Percent orientation ($\bar{X} \pm$ SEM) by *Carpophilus hemipterus*, *C. lugubris*, and *Stelidota geminata* to fungal cultures in a wind tunnel. N = four groups of 10 beetles. Bars marked with an asterisk indicate response significantly greater than that to a blank jar to which beetles never responded (Student's t test, $P < 0.05$).

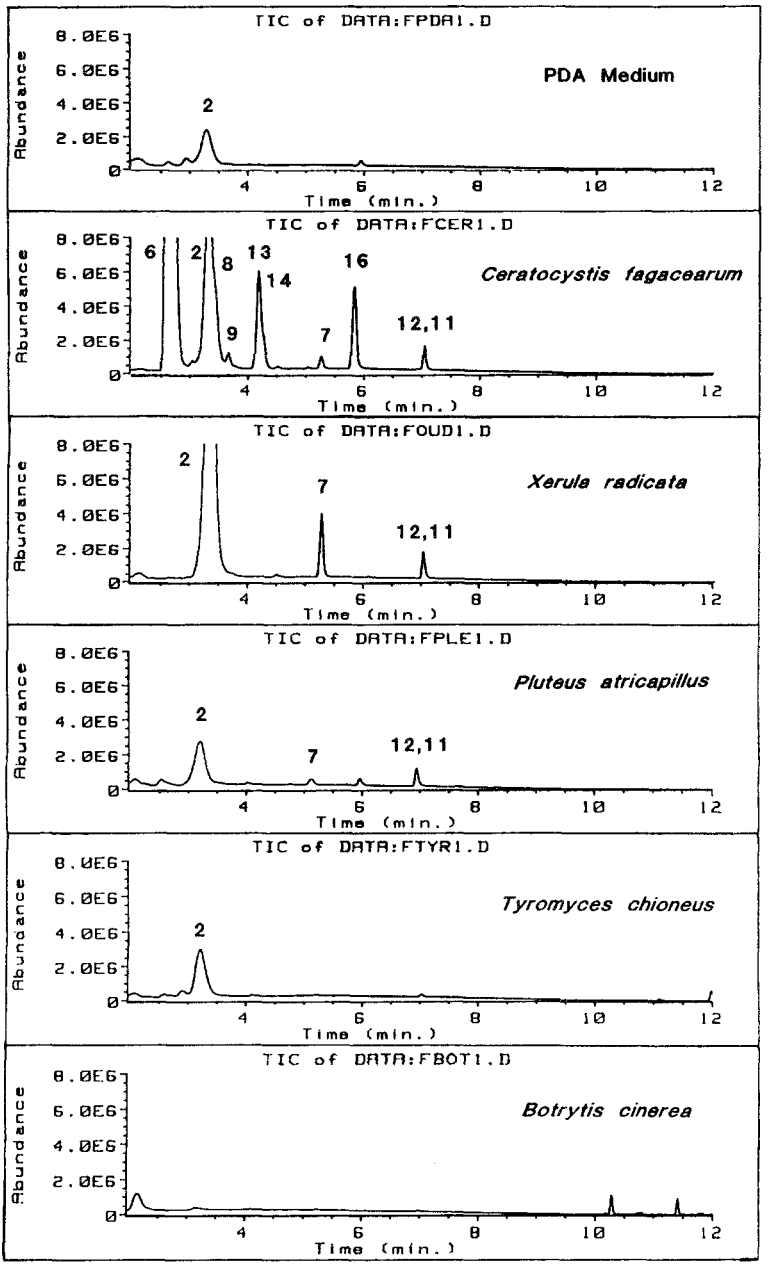

FIG. 2. Comparison of the volatile profiles of five fungi on PDA medium and of PDA medium alone. Note that the profiles were analyzed on DB-FFAP capillary column; component numbering follows Table 1, which was based on an analysis using DB-1. See text for explanation of methods for volatile collection and analysis.

TABLE 1. CHEMICAL CHARACTERIZATION AND QUANTIFICATION OF HEADSPACE ABOVE *Ceratocystis fagacearum* ON PDA

No.	Identity	*RT*[a]	Mass spectra (*m/z*)[b]	Amount (ng/ml)[c]	Percent[c]
1	Acetaldehyde	0.5	29, 41, 43, 44	<0.1	<0.1
2	Ethanol	1.4	27, 29, 31, 45, 46	4.0	2.8
3	Methyl acetate	2.9	29, 42, 43, 59, 74	0.4	0.3
4	1-Propanol	3.6	27, 29, 31, 42, 59, 60	0.1	0.1
5	2-Butanone	4.3	27, 29, 43, 57, 72	0.2	0.2
6	Ethyl acetate	4.9	43, 45, 61, 70, 73, 88	101.0	70.0
7	2-Methylpropanol	5.3	31, 33, 41, 42, 43, 55, 74	4.3	3.0
8	Ethyl propionate	7.3	29, 45, 57, 74, 75, 102	2.4[d]	1.7
9	Propyl acetate	7.4	27, 31, 41, 42, 43, 61, 73		
10	Methyl butyrate	7.6	27, 41, 43, 59, 71, 74, 87	0.1	0.1
11	3-Methylbutanol	7.9	41, 42, 43, 55, 56, 57, 70	8.7[d]	6.0
12	2-Methylbutanol	8.0	29, 41, 55, 56, 57, 70		
13	Isobutyl acetate	8.6	27, 29, 41, 43, 56, 62, 73	5.0	3.4
14	Methyl isovalerate[e]	9.0	39, 41, 43, 57, 59, 74, 85	6.1	4.2
15	Butyl acetate	9.8	27, 29, 41, 43, 56, 61, 73	0.3	0.2
16	Isopentyl acetate	11.2	39, 41, 43, 55, 61, 70, 87	11.9	8.2

[a] *RT* = retention time in minutes eluted from DB-1 column.
[b] Major ions of mass spectra, with the base ions underlined.
[c] Mean of three replicates (ng/ml headspace air sample, and percent of the total profile).
[d] Components were combined due to their unresolved GC peaks. Estimated ratio of ethyl propionate and propyl acetate is 1 : 1 and that of 3-methylbutanol and 2-methylbutanol is 4 : 1.
[e] Authentic compound was unavailable, identification based on mass spectrum alone.

atiles. Thus, the volatile profile of *C. fagacearum* appeared quantitatively and qualitatively richer than did those of the non-beetle-dependent fungi.

Characterization of Headspace Profile of C. fagacearum. A more extensive analysis of *C. fagacearum* odor aimed at quantifying individual components of the volatile profile revealed six additional minor components ($\leq 0.3\%$ of total profile; Table 1, Figure 3). Ethyl acetate was the most abundant component of *C. fagacearum* odor; its headspace concentration was 101.0 ng/ml and it made up 70.0% of the odor. Concentrations of other odor constituents ranged from <0.1 (acetaldehyde) to 11.9 ng/ml (isopentyl acetate).

DISCUSSION

Nitidulids have been reported in association with a number of plant pathogens. Because of their sap-feeding habit, those beetles that come to feed on fungal mycelial mats or infected tissues pick up pathogens and may transmit

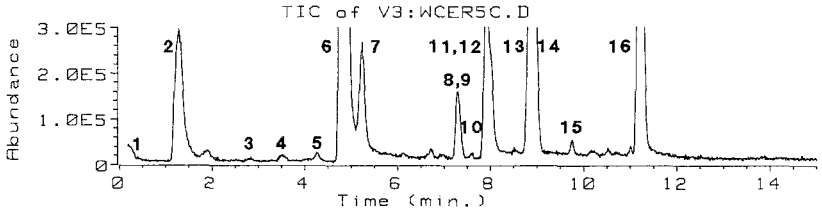

FIG. 3. Volatile profile from oak-wilt fungus, *C. fagacearum* on DB-1. See Table 1 for identity of peaks, and see text for explanation of methods for volatile collection and analysis.

them to healthy trees or fruits when they visit fresh wounds or ripening fruits. Nitidulids are important vectors of *Ceratocystis* canker of aspen in Colorado (Hind, 1972) and of almond in California (Moller and DeVay, 1968). In Hawaii, several species of nitidulids were proven to be important vectors of pineapple disease in sugarcane caused by *C. paradoxa* (Chang and Jensen, 1974). Nitidulids also were reported in association with *Monilinia fructicola*, the causative agent of brown rot in stone fruit in California (Tate and Ogawa, 1975), with *Fusarium* pathogens of corn (Windels et al., 1976; Attwater and Busch, 1983), and with yeasts responsible for diseases of figs (Miller and Mrak, 1953). Juzwik and French (1983) demonstrated that a seasonal peak for nitidulids coincided with the time of maximum mat production for *C. fagacearum*. Furthermore, both adults and larvae of *Glischrochilus* species have been observed feeding on mycelial mats of *C. fagacearum* in the field and adults may overwinter underneath these mats (Dorsey and Leach, 1956). *C. fagacearum* is hermaphroditic but self-sterile and, in addition to inoculating new hosts, nitidulids moving between mats bring about sexual reproduction by fertilizing receptive hyphae of one mat with endoconidia from another (Dorsey and Leach, 1956).

If this association represents a form of mutualism, it is not an obligatory one for the beetles. Nitidulids are not dependent on fungi as they can feed on a variety of ripening or decaying fruits and plant tissues; however, fungal infection does increase the attractiveness or even the nutritional value of food substrates for some nitidulids. *C. paradoxa*-infected sugarcane stalks were nine times more attractive to nitidulid beetles than healthy stalks in the field, and larvae of the nitidulid *Urophorus humeralis* reared on a diet of mixed sugarcane juice and the pathogen developed faster and gained more weight than those on sugarcane juice only (Chang and Jensen, 1974). Similarly, adults of *C. hemipterus* showed higher attraction to yeast-inoculated banana than to aseptic banana, and larvae feeding on yeast-inoculated banana developed faster and gained more weight than those on the aseptic substrate (Lin and Phelan, in preparation, a).

Our chemical characterization of *C. fagacearum* odor revealed 16 components including one aldehyde, one ketone, five alcohols, and nine esters (Table

1). Collins and Kalnins (1965) previously identified four aldehydes and one ketone from steam distillates of *C. fagacearum*; of these, only acetaldehyde was detected in the present study. All of the 16 components identified from the headspace profile of *C. fagacearum* have been found previously in the odors from various food substrates (Jennings, 1977; Macku and Jennings, 1987; Maarse and Visscher, 1988; Phelan and Lin, 1991; Lin and Phelan, 1991a), and 11 of them have been tested at natural release rates with one or more nitidulid species: *C. lugubris* (Lin and Phelan, 1991a), *C. hemipterus* (Phelan and Lin, 1991), *Glischrochilus quadrisignatus* and *G. fasciatus* (Lin and Phelan, 1991b), and *Stelidota geminata* (Lin and Phelan, in preparation, b). Acetaldehyde and ethyl acetate are essential components of attractive odor blends for all these species, except *C. lugubris*, for which ethyl acetate can be partially replaced by ethanol. The five alcohols present in the profile of *C. fagacearum* are attractive to these beetles except 2-methylpropanol and 3-methylbutanol, which have a negative effect on the response of *S. geminata*. Butyl acetate and isopentyl acetate are components of blends attractive to *S. geminata* , while isobutyl acetate has a negative effect on response (Lin and Phelan, in preparation, b). We have found ethanol to be attractive to all of the above species except *C. hemipterus* (Phelan and Lin, 1991). Alm et al. (1985, 1986, 1989) demonstrated that butyl acetate was attractive to *G. quadrisignatus* in the field but only at unnaturally high release rates (70–2000 mg/24 hr). Other components identified from the odor of *C. fagacearum* either have not been tested or have no significant effect on the nitidulid response.

In contrast to *C. fagacearum*, the volatile profiles of the other fungi in our studies were rather depauperate. These fungi were chosen for comparison because they are primarily dispersed by wind or rain, they can infect woody tissue, and they have been reported in association with nitidulids. *S. geminata* has been collected from *X. radicata*, *P. atricapillus*, and *T. chioneus* in nature (Weiss and West, 1921), and Wildman (1933) reported increased capture of nitidulids when cooked figs or peaches were inoculated with a *Botrytis* sp. However, the results of this study suggest that when these fungi are placed on agar, they elicit little or no attraction of nitidulids and generally do not produce attractive volatile blends. Of the non-insect-dependent fungi, only *X. radicata* elicited attraction at a level significantly greater than a blank jar, and this response was less than that to *C. fagacearum*.

We have contended previously that fungi generally enhance attraction of nitidulids through a simple increase in the release of volatiles common to fruit substrates rather through a qualitative change in the odor profile (Phelan and Lin, 1991). This quantitative change is likely brought about by some combination of increased fruit-cell lysis and/or fungal catabolism of fruit constituents that parallels processes characteristic of fruit ripening. Our results here support this contention for non-insect-dependent fungi inasmuch as such fungi involved

in the present study produced no or only small amounts of fruity volatiles in the absence of fruit. In contrast, *C. fagacearum*, a fungus dependent on insects for transmission of spores and for sexual reproduction, produced an odor blend that was both quantitatively and qualitatively rich when cultured on agar. We would submit that production of this more complex odor profile may represent an adaptation on obligatory dispersal by insects.

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