Journal of Chemical Ecology, Vol. 24, No. 6, 1998

PRIMARY ATTRACTION OF THE FIR ENGRAVER, *Scolytus ventralis*

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(Received May 6, 1997; accepted February 6, 1998)

Abstract—In laboratory bioassays, Porapak Q-captured and steam-distilled volatiles from the bark of host trees, *Abies grandis*, particularly from root-rot-infected trees, attracted 50–70% of male and female fir engravers, *Scolytus ventralis*. Gas chromatographic–electroantennographic detection (GC-EAD) analyses of Porapak Q-captured bark volatiles revealed 19 EAD-active compounds of which 13 (mostly monoterpenes) were identified by GC–mass spectrometry (GC-MS). In separate field experiments, multiple-funnel traps baited with two blends of these 13 synthetic volatiles released at 280 and 340 mg/24 hr attracted 66 and 93% of the total *S. ventralis* captured, respectively. The clerid predator, *Thanasimus undulatus*, also responded strongly to the kairomonal volatiles. Additional experiments produced no evidence for aggregation pheromones in *S. ventralis*. These included laboratory bioassays and GC and GC-EAD analyses of Porapak Q-captured volatiles from male- and female-infested logs or trees undergoing mass attack in the field, GC analyses and/or bioassays of extracts from female accessory glands, extracted volatiles from emerged, attacking and juvenile hormone-treated beetles of both sexes, and videotape analysis of the behavior of attacking beetles on the bark surface. We argue against the hypothesis of pheromone-mediated secondary attraction in *S. ventralis* and conclude that the attack dynamics of this species can be explained solely by its sensitive primary attraction response to host volatiles.

Key Words—Semiochemicals, primary attraction, kairomones, *Scolytus ventralis*, *Thanasimus undatulus*, *Abies grandis*, monoterpenes, sesquiterpenes.

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0098-0331/98/0600-1049/$15.00/0

INTRODUCTION

Bark beetles must locate and detect not only the right host species but also the most susceptible trees within the host population (Raffa and Berryman, 1987). There is conflicting evidence as to whether all bark beetles land on potential hosts at random, making a decision on host suitability at close range, or whether they orient toward host volatiles (primary attraction). It is widely accepted that after pioneer beetles have initiated attack the majority of the population orients to the host in response to secondary attractants, usually a blend of pheromones released by conspecifics and kairomones released by the tree (Wood, 1982; Birch, 1984; Borden, 1985).

Volatiles released by the host are attractive to subcortical scolytids in the genera *Dendroctonus*, *Hylastes*, *Hylurgops*, *Hylurgopinus*, *Ips*, *Pityogenes*, *Pseudohylesinus*, *Scolytus*, *Tomicus*, and *Trypodendron* (Goeden and Norris, 1964; Rudinsky, 1966a,b; Meyer and Norris, 1967; Moeck, 1970; Moeck et al., 1981; Byers et al., 1985, 1990; Miller et al., 1986; Lanne et al., 1987; Swedenborg et al., 1988; Voltz, 1988; Byers, 1989; Miller and Borden, 1990a; Moeck and Simmons, 1991; Lindelöw et al., 1992; Hobson et al., 1993; Tunset et al., 1993). Monoterpenes such as α-pinene, myrcene, terpinolene, β-pinene, β-phellandrene, and 3-carene, as well as sesquiterpenes like α-atlantone, α-cubebene, and cadinene are primary attractants when tested alone for bark beetles (Chararas, 1980; Byers et al., 1985; Millar et al., 1986; Philips et al., 1988; Schroeder, 1988; Chénier and Philogène, 1989; Schroeder and Lindelöw, 1989; Miller and Borden, 1990b; Phillips, 1980; Byers, 1992; Hobson et al., 1993). Synergistic effects on attraction often occur when terpenes are combined with the host kairomone ethanol or with insect-produced pheromones (Borden, 1985).

The fir engraver, *Scolytus ventralis* LeConte (Coleoptera: Scolytidae), is a major cause of mortality of true firs, especially white fir, *A. concolor* Hildebr. and grand fir, *A. grandis* (Dougl.) Lindl., in North America. Outbreaks of this bark beetle have occurred at least once a decade over the last 60 years (Ferrell, 1986; Wood and van Sickle, 1991). In the last decade, fir engravers have killed hundreds of thousands of grand and white fir in western North America (Wood and van Sickle, 1991; Campbell and Liegel, 1996; unpublished records from USDA, Forest Service, Northern Region). Mortality caused by the fir engraver depends on a strict mutualistic association with the plant–pathogenic fungus, *Trichosporium symbionticum* Wright, that is apparently essential for successful reproduction and colonization of trees (Wright, 1935; Livington, 1971; Wong and Berryman, 1977).

Some observations suggest that *S. ventralis* selects its host through random landing on both resistant and susceptible trees (Struble, 1957; Ashraf and Berryman, 1969; Berryman and Ashraf, 1970). However, a high correlation occurs

between root-rot infections and successful fir engraver attacks (Cobb et al., 1973; Hertert et al., 1975; Ferrell and Smith, 1976; Wright et al., 1984), which suggests that the insect can detect root-rot-infected trees. There is increasing evidence that diseased and healthy conifers can be detected by released volatiles. White fir trees that survived fir engraver attacks had a different monoterpene composition than trees that were killed (G. T. Ferrell, USDA Forest Service, Redding, California, personal communication). Concentrations of five monoterpenes, tricyclene, α-pinene, camphene, γ-terpinene, and bornyl acetate were significantly higher in lodgepole pine, *Pinus contorta* Dougl., attacked by one or more diseases (dwarf mistletoe, comandra blister rust, and root rot) than in healthy ones (Nebeker et al., 1995). Similarly, spruce, *Picea excelsa* Lk., infested with *Armillaria* root rot, contained increased amounts of oils (Madziara-Borusiewicz and Strzelecka, 1977). Moreover, needles of drought-stressed Norway spruce, *Picea abies* (L.), had a higher total monoterpene content and greater amounts of tricyclene, α-pinene, and camphene than control trees (Kainulainen et al., 1993).

Several attempts have been made to find evidence for primary and secondary attraction of the fir engraver. Vité and Pitman (1967) reported that *S. ventralis* and *S. unispinosus* LeConte respond to host odors in field trials and suggested that an insect-produced attractant was not indicated. Ferrell's (1969, 1971) field experiments showed that the fir engraver can land on different species but will land preferentially on its host, white fir. Fir engravers were trapped twice as frequently on girdled or severed-standing trees as on ungirdled controls. However, these experiments could not differentiate between primary and secondary attraction, because test trees were not protected from insect attacks, and thus secondary attraction was not prevented. In laboratory bioassays, both male and female *S. ventralis* were highly attracted to aged host phloem and less so to frass produced by virgin females (Ferrell, 1969).

Fir engravers exposed to constitutive grand fir oleoresin or to its volatile monoterpenes (individually presented) died at significant rates within 4–12 hr after exposure (Ferrell, 1969; Raffa et al., 1985). The monoterpenes tricyclene, α-pinene, β-pinene, camphene, myrcene, sabinene, limonene, β-phellandrene, bornyl acetate, and terpinolene are present in the constitutive resin. The composition of traumatic resin induced by wounding is similar, except for the addition of Δ^3-carene, the absence of bornyl acetate, and a significant increase in the quantities of β-pinene and myrcene (Russell and Berryman, 1976; Raffa and Berryman, 1987; Lewinsohn et al., 1990). Each of these compounds was repellent to walking beetles in laboratory bioassays (Bordash and Berryman, 1977). Growth of *T. symbionticum* was inhibited by camphene, β-pinene, myrcene, Δ^3-carene, and limonene (Wong and Berryman, 1977; Raffa et al., 1993).

Possible evidence for secondary attraction in *S. ventralis* was found by Ashraf and Berryman (1969). They observed that grand fir logs attacked by the

fir engraver attracted more flying conspecific beetles than uninfested control logs. Ethanolic extracts of *S. ventralis* frass were strongly attractive in the field. However, there were only two replicates, the frass-producing sex was not reported, and there was no control for ethanol, a known semiochemical for other bark beetles (Pitman et al., 1975; Moeck, 1970). However, Ferrell (1969) found that *S. ventralis* were not arrested by ethanol in laboratory bioassays. As the season progressed, attacks by *S. ventralis* became increasingly aggregated, but because attack density is directly related to gallery elongation (Ashraf and Berryman, 1969), an attractant could either be released by the beetle or by the host tree.

In a 1968 study by Ferrell and Borden (unpublished), laboratory bioassays revealed that virgin female frass and fresh grand fir phloem sawdust arrested equal numbers of *S. ventralis* at high doses, but at progressively lower doses the response to the frass disappeared before the response to sawdust. Virgin male- and female-produced frass was equally attractive. Grand fir phloem disks containing a mining female remained highly attractive for hours, while disks lacking a beetle rapidly lost potency. Fecal pellets separated from virgin female frass proved no more attractive on an equal weight basis than whole frass. The above results support the hypothesis of primary attraction for *S. ventralis*, but do not rule out the possibility of a pheromone.

Secondary attraction does occur in the genus *Scolytus*. The smaller European elm bark beetle, *S. multistriatus* Marsham, produces and responds to the pheromones 4-methyl-3-heptanol and multistriatin in combination with the sesquiterpene α-cubebene; the large elm bark beetle, *S. scolytus* F. utilizes only 4-methyl-3-heptanol and α-cubebene (Lanier et al., 1977; Blight et al., 1978). Field tests with these three components have also caught *S. pygmaeus* F. and *S. laevis* Chapuis (Minks and Van Deventer, 1978; Bejer, 1979), suggesting that the same compounds are involved in secondary attraction for these beetles. For *S. quadrispinosus* Say (Goeden and Norris, 1964), *S. numidicus* Brisout (Chararas, 1980), and *S. rugulosus* Ratzeburg (Kovach and Gorsuch, 1985), there is evidence only for primary attraction.

We report the results of laboratory and field experiments supporting the hypothesis that primary attraction occurs for *S. ventralis* and elucidating the kairomones involved. We argue against the hypothesis that *S. ventralis* requires secondary attraction for successful host selection.

METHODS AND MATERIALS

Collection of Insects and Host Material. Bolts of grand fir from healthy and root-rot-infected trees (Hagle et al., 1987), as well as from trees infested with *S. ventralis*, were collected in August and September 1993–1995 from

felled trees near Coeur d'Alene, Idaho. All logs were kept at 2°C until used. Infested logs were transferred to mesh screen cages at 24–30°C, and water was sprayed on them every five to six days to prevent desiccation. Emerged beetles were collected daily and sexed by comparing morphological characteristics of the abdominal sternites and the frons (Blackman, 1934; Edson, 1967).

Collection and Analysis of Beetle Host Volatiles. Volatiles from logs were obtained by drilling entrance holes (1.5 mm diam.) approximately 3 cm apart in the bark of fresh grand fir bolts ca. 21 cm long × 12 cm diam. These bolts were set inside separate glass aeration chambers (28 cm long × 15 cm diam.), and either 130 males or 130 females were allowed to bore into the bark, or the log remained without beetles as an uninfested control. Air was drawn through the chamber at 1.7 liters/min, and then through glass tubing (14 mm OD × 20 cm long) containing Porapak-Q (Byrne et al., 1975). Volatiles were eluted from the trap with 150 ml of distilled pentane and the effluent was concentrated to 5 ml by distillation in a 30-cm Dufton column.

Differential diagnosis (Vité and Renwick, 1970) of male- and female-produced volatiles was used to search for sex-specific compounds. GC analyses employed Hewlett Packard 5830A, 5880A, and 5890A instruments equipped with capillary inlet systems and FID. Capillary columns (30 m × 0.25 or 0.32 mm ID) coated with SP-1000 (Supelco, Bellefonte, Pennsylvania) or DB-1 (J & W Scientific Inc., Folsom, California) were used. Coupled GC–mass spectrometry (GC-MS) employed a DB-23 column and a Varian Saturn ion trap. Helium was the carrier gas for GC and GC-MS.

Isolation of Bark Oil. Bark tissue (cortex plus phloem) was peeled from fresh logs of either healthy or root-rot-infected grand fir and cut into small chips (approx. 1 cm^2). Bark oil was obtained by steam distillation. A concurrent steam distillation–continuous extraction still head (Flath and Forrey, 1977) was employed for the isolation of volatile oil from bark chips. The steam distillation was conducted for 4 hr after boil-up, and pentane was used as the extraction solvent. After evaporation of most of the pentane under a stream of nitrogen, residual solvent was removed by brief vacuum pumping.

Fractionation of Bark Oil. A Varian 1200 gas chromatograph (GC) equipped with a 10:1 effluent splitter and thermal gradient collector (Brownlee and Silverstein, 1968) was employed for micropreparative fractionation of *A. grandis* bark oil. The column was a stainless steel tube (3.05 m × 3.18 mm OD) packed with 10% SP-1000 on Supelcoport (100/120 mesh) (Supelco). The temperature program was 70°C for 2 min, then 4°C/min to 180°C and held for 20 min. The injection port and flame-ionization detector (FID) temperatures were 260°C and 270°C, respectively, and helium was the carrier gas. Typically, 1.5-μl aliquots of oil were used per run, and fractions were rinsed from the collection tubes with pentane into 1-ml volumetric tubes that were made up to volume. A Hewlett Packard 5830 GC fitted with a glass column (30 m × 0.50 mm ID) coated with

SP-1000 and FID was employed for determination of components in the fractions by the external standard method. The temperatures and carrier gas were as above. The FID was calibrated by analyzing a solution containing a known concentration of bark oil. Fraction 1 contained monoterpenes (slightly beyond the retention time of phellandrene), and fraction 2 contained the remaining compounds, mostly sesquiterpenes.

GC-EAD Analysis. Extracts and oils obtained by steam distillation and by laboratory and field aerations were subjected to coupled gas chromatographic–electroantennographic detection (GC-EAD) analyses (Arn et al., 1975) adapted for an intact bark beetle (Gries, 1995) or an excised bark beetle antenna. A Hewlett Packard 5890 A instrument equipped with a DB-23-coated fused silica column (30 m × 0.32 mm ID; J & W Scientific) was used. Responses of excised antennae were amplified by utilizing a custom-built amplifier with a passive low pass filter and a cutoff frequency of 10 kHz. Compound identities were confirmed by comparison of their mass spectra with those of authentic samples.

Analysis of the chirality of α- and β-pinene, camphene, and limonene was performed as follows: ca. 10 μg of grand fir steam-distilled oil was injected twice under split conditions into a Varian 3400 GC remodified according to Brownlee and Silverstein (1968) to a preparative GC. The GC was equipped with a DB-23 column (30 m × 0.32 mm ID; J & W Scientific; GC conditions: 40°C hold for 5 min, then program 5°C/min up to 200°C; the injector was set to 240°C and the auxiliary heater for the preparative unit at 250°C). At these conditions α-pinene eluted at 3.64 min retention time, camphene at 4.66, β-pinene at 5.70, and limonene at 7.83, respectively. They were condensed in glass tubes (25 cm long × 1 mm ID), which were then rinsed with 25 μl of hexane into a 1.5 ml vial. The two collections were combined to give a total of 50 μl, and the samples of camphene and limonene were concentrated to ca. 10 μl. Each singly collected monoterpene was then injected (1 μl) into another Varian 3400 GC equipped with a Cyclodex-B-column (30 m × 0.25 mm ID, J & W Scientific; GC conditions: split injection, 80°C isothermal, injector and detector at 200°C). Chiral monoterpenes coincided with authentic standards of (+)-α-pinene and (−)-α-pinene, (−)-camphene, (−)-β-pinene, and (−)-limonene.

Preparation of Test Stimuli for Laboratory and Field Bioassays. Bark and sapwood sawdust from fresh logs of grand fir were obtained by drilling with a 1.5-mm-diam. bit. Frass produced by the insects was obtained by confining male or female beetles in gelatin capsules attached to a fresh bolt of grand fir. Frass deposited into the capsules was collected on days 2–8 after the insects began to bore into the bark. Frass was stored in air-tight vials and kept at −15°C until used.

All chemicals used in preparation of test stimuli, their purity, and their

sources are listed in Table 1. Two synthetic blends (SB1 and SB2) (Table 2) were prepared to mimic as closely as possible the spectrum of antenally active volatiles in the bark. SB1 was prepared with crude β-phellandrene, which had limonene as an impurity in a 2:1 proportion (limonene–β-phellandrene), much higher than the 1:10 ratio in the grand fir bark oil. SB2, containing synthetic β-phellandrene of greater purity (53%) and without limonene, was prepared as follows. A solution of dimsyl anion was prepared by adding, after washing, 29.6 g (0.77 mol) of 60% sodium hydride dispersion to 400 ml dimethyl sulfoxide (DMSO). The mixture was slowly warmed, and stirred for 3 hr until H_2 evolution had ceased. To this was added methyltriphenylphosphonium bromide, 289 g (0.71 mol), to produce a yellow mixture that was difficult to stir until more DMSO was added. A solution of 100 g (0.68 mol) 4-isopropyl-2-cyclohexenone (Aldrich Chemical Co.) in 100 ml DMSO was added via a dropping funnel, and the mixture was stirred overnight. The reddish mixture was quenched with 50% aqueous methanol and extracted with hexane. The combined hexanes were filtered, washed with more 50% methanol, then with saturated salt solution,

TABLE 1. CHEMICAL PURITY AND SOURCES OF COMPOUNDS USED IN THIS STUDY

Chemical	Purity (%)	Source
(±)-α-Pinene	98	Sigma Chemical Co.
Camphene	81	Matheson, Coleman & Bell
(−)-β-Pinene	99	Aldrich Chemical Co.
(+)-β-Pinene	98	Aldrich Chemical Co.
Myrcene	90	Aldrich Chemical Co.
(*S*)-(−)-Limonene	96	Aldrich Chemical Co.
(*R*)-(+)-Limonene	97	Aldrich Chemical Co.
β-Phellandrene (synthetic)	53	Synthesized
β-Phellandrene (comm.)	30	*Glidco Organics*
α-Terpinolene	29	Givaudan Lab.
p-Cymene	99	Aldrich Chemical Co.
(−)-α-Cubebene	98	Fluka Chemical Corp.
(+)-Longifolene	90	Sigma Chemical Co.
(*E*)-Pinocarveol	90	Phero Tech Inc.
Bornyl acetate	98	Matheson, Coleman & Bell
α-Terpineol	95	Aesar
(−)-Borneol	99	Aldrich Chemical Co.
Cadinene	72	Phero Tech Inc.
Verbenone	93	Phero Tech Inc.
(*E*)-Nerolidol	95	Aldrich Chemical Co.
Nerolidol	98	Aldrich Chemical Co.
Methyl-isoeugenol	99	Aldrich Chemical Co.

TABLE 2. CHEMICAL COMPONENTS AND THEIR PERCENTAGES IN SYNTHETIC BLENDS SB1 AND SB2[a]

Chemical	Percent composition in blend	
	SB1	SB2
(±)-α-Pinene	13.4	15.6
Camphene	3.0	3.2
β-Pinene	41.7	45.7
Myrcene	1.5	1.5
(±)-Limonene	17.5	1.3
β-Phellandrene (synthetic)		18.8
β-Phellandrene (comm.)	9.2	
α-Terpinolene	0.8	0.8
α-Cubebene	0.03	0.03
(±)-Longifolene	0.5	0.5
Bornyl acetate	7.0	7.3
(−)-Borneol	2.5	2.5
Nerolidol	2.6	2.6
Methyl-isoeugenol	0.2	0.2

[a]The commerical β-phellandrene used in SB1 includes limonene as an impurity. β-Pinene was deployed in a 1:50 ratio of (−) and (+) enantiomers, and nerolidol was deployed in a 2:1 ratio of *E* and *Z* isomers. α-Cubebene and methyl-isoeugenol were present in the bark oil in 3.53 and 0.49%, respectively. However, due to short supply they were deployed in the low percentages that appear in this table.

and dried over sodium sulfate. The crude product was distilled at 120°C, 20 torr, to yield 22.7 g of β-phellandrene, which was identical to authentic β-phellandrene by GC and GC-MS analysis.

Laboratory Experiments. The bioactivity of captured volatiles was tested in an arena olfactometer in which beetles made a choice between responding to a photic and an olfactory stimulus (Moeck, 1970). A light source (microscope lamp, low power) was located 49 cm from the insect release point (which received a light intensity of 76.6 lux), and the air carrying test stimuli was delivered perpendicular to the light beam 6.5 cm from the release point. The arena surface, a filter paper strip (Whatman chromatographic 3 MM) 30 cm long × 15 cm wide, was replaced every time a different sex or stimulus was tested. Prior to bioassays, beetles were held in groups of five (sexes kept separately) in Petri dishes with moistened paper at 21°C and 69 lux for 2 hr. Bulk stimuli (frass or sawdust) were placed in weighing boats directly below the air outlet and even with the arena surface. Extracted or captured volatiles were released from a glass tube (9 mm ID) lined with filter paper (10 cm diam.)

impregnated with volatile extract in pentane. Medical-quality air was passed continuously through the tube at 1200 ml/min. A positive response was recorded if a beetle entered and stayed inside a rectangular area (3 × 15 cm) transverse to the runway just in front of the air outlet.

Attractiveness of stimuli was tested in eight bioassay experiments. Experiments 1–5 and 7 used male and female beetles; experiments 6 and 8 employed only females, the most responsive sex. Experiment 1 tested volatiles emanating from 250 mg of freshly ground grand fir sapwood, bark, or frass produced by males or females; medical-quality air was the control stimulus. Experiment 2 tested Porapak Q-trapped volatiles from female-infested grand fir logs at doses of 0.03, 0.3, 3, 30, and 90 beetle-hours (bh) (1 bh = volatiles released by 1 female in 1 hr). Porapak Q-trapped volatiles from an uninfested grand fir log were used as the control stimulus. Experiment 3 tested Porapak Q-trapped volatiles from male-infested grand fir logs at doses of 0.3 and 3 bh. Trapped volatiles from an uninfested grand fir log were used as the control stimulus. Experiment 4 tested steam-distilled bark oil from a healthy tree at doses of 0.009, 0.097, 0.975, 9.75, and 97.5 mg equivalents, with pentane as a control stimulus (1 mg equiv = amount of oil distilled from 1 mg of starting material). Experiment 5 tested Porapak Q-trapped volatiles from an uninfested grand fir log at doses of 0.001, 0.01, 0.1, 1, and 10 mg/μl, with pentane as a control stimulus. Experiment 6 compared female responses towards steam-distilled bark oil from healthy and root-rot-infected grand fir at doses of 0.0006, 0.006, 0.06, 0.6, 6, and 60 mg equiv, with pentane as a control stimulus. Experiment 7 tested two fractions of steam distilled bark oil from root-rot-infected grand fir at 1 μg equiv, with pentane as a control stimulus. Experiment 8 compared the activity of the two fractions tested in experiment 7 with the activity of two tentative synthetic fractions[3] without complete confirmation of the bioactivity of all components.

Field Experiments. Synthetic blends of compounds that were antennally active, attractive in the laboratory, and available in sufficient quantity were field tested in a mature *Abies grandis/Acer rubrum* forest with moderately abundant Douglas fir (Steel and Gier-Hayes, 1992), located 10 km north of Coeur d'Alene, Idaho. Twelve-unit, multiple-funnel traps (Lindgren, 1983) (Phero Tech, Inc.) baited with candidate kairomonal blends were deployed in 10 randomized complete blocks, with $\geq$ 15 m between traps and 15 m between trap lines. Captured beetles were bagged and frozen until they could be counted and sexed. Experiments 9 and 10, respectively, tested attraction to two different synthetic blends

[3]Composition (μg) of synthetic fraction 1: α-pinene (6.9), camphene (1.2), β-pinene (21.4), myrcene (0.2), limonene (0.5), and crude β-phellandrene (3). Composition of synthetic fraction 2: α-terpinolene (0.3), *p*-cymene (0.001), longifolene (0.02), (*E*)-pinocarveol (0.04), bornyl acetate (1), α-terpineol (0.3), borneol (0.4), cadinene (0.8), verbenone (0.06), (*E*)-nerolidol (0.04), (*Z*)-methyl isoeugenol (0.04), and (*E*)-methyl isoeugenol (0.08).

(SB1 and SB2) of 13 components each (Table 2), as well as steam-distilled bark oil, and an unbaited control. The synthetic blends used in these experiments differ from those employed in experiment 8 only by the presence of α-cubebene and the lack of *p*-cymene, (*E*)-pinocarveol, and verbenone. α-Cubebene was present in the bark oil and was erroneously identified as an antennally active peak. It was incorporated as 0.03% of the synthetic blends SB1 and SB2. Release rates of SB1, SB2, and the bark oil, determined under laboratory conditions at 32°C, were 340, 280, and 50 mg/24 hr, respectively.

Statistical Analysis. Percentages of male and female beetles responding in laboratory bioassays were transformed by $\arcsin\sqrt{x}$ to normalize the data and stabilize the variances between replicates (Zar, 1984), except for experiment 6, and were analyzed by ANOVA followed by the Ryan-Einot-Gabriel-Welsh (REGW) multiple range test (Day and Quinn, 1989). For experiment 6, responses to the volatiles from healthy or root-rot-infected trees at each dose were compared by *t* tests. The REGW test was also used for data from field experiments, but with a $\log_{10}(x + 1)$ transformation (Zar, 1984). All analyses employed SAS computer software (SAS Institute, 1994) with $\alpha = 0.05$.

RESULTS

In most laboratory bioassays, females were more responsive and less variable in their responses than males. All stimuli in experiment 1 (Figure 1) were significantly more attractive to males and females than the air control. Host bark, sapwood sawdust, and male or female frass were equally attractive. Captured volatiles from female-infested logs were no more attractive at any of five doses than those from uninfested logs in experiment 2 (Figure 1). In experiment 3, volatiles from male-infested logs were less attractive to females than were volatiles from uninfested logs, but for males there was no difference in response to treatments (Figure 1).

In experiment 4 (Figure 2), responses by females to steam-distilled bark extract were significantly higher than those to pentane at doses of 0.975 and 9.75 mg equiv; males responded significantly to stimuli at these doses and also at a dose of 0.975 mg equiv. Experiment 5 (Figure 2) showed a similar trend for captured volatiles; females responded significantly at doses of 0.1, 1.0, and 10.0 mg/μl, while males responded only at the two highest doses. Steam-distilled bark volatiles from root-rot-infected trees were more attractive to walking beetles at most doses than volatiles from uninfected trees, and significantly at two doses (Figure 2, experiment 6). At doses >0.0006 mg equiv and <60 mg equiv, 61% of all responses were to the volatiles from infected trees.

In experiment 7, neither fraction of bark beetle oil distillate alone was more attractive to walking beetles than the pentane control stimulus, but there was a

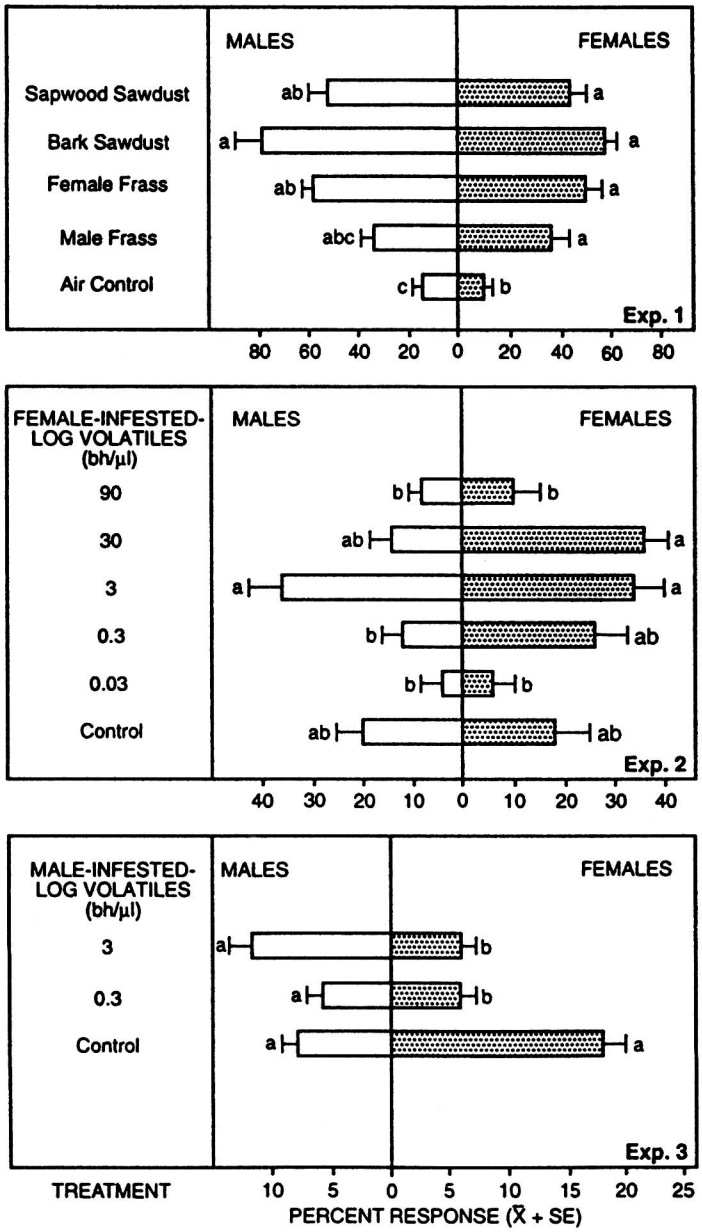
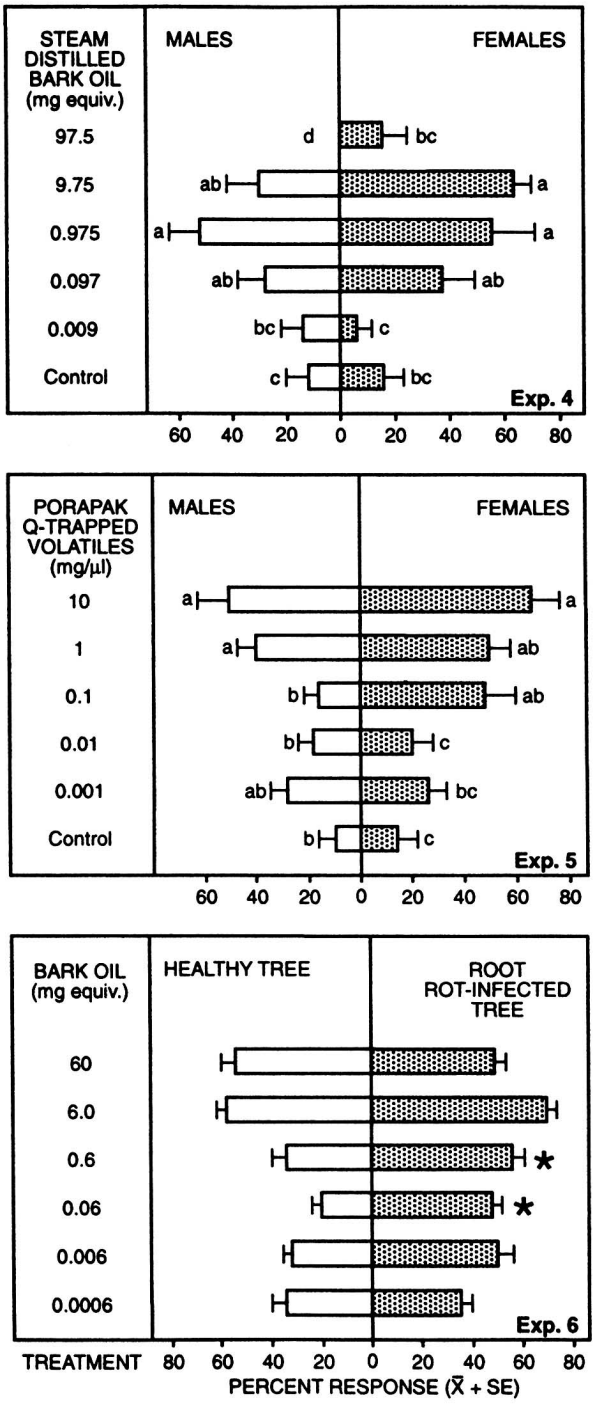


FIG. 1. Results of laboratory bioassays showing the percent responses of walking male and/or female *S. ventralis* tested in 10 groups of five insects (males or females) to sawdust or frass presented in 250 mg doses (experiment 1), Porapak Q-trapped volatiles from logs infested with female *S. ventralis* (experiment 2) or with males (experiment 3). Bars for each sex with the same letter are not significantly different, REGW test, $P < 0.05$.


STEAM DISTILLED BARK OIL (mg equiv.)
MALES
FEMALES
97.5
9.75
0.975
0.097
0.009
Control
d
bc
ab
a
a
a
ab
ab
bc
c
c
bc
Exp. 4
60 40 20 0 20 40 60 80
PORAPAK Q-TRAPPED VOLATILES (mg/µl)
MALES
FEMALES
10
1
0.1
0.01
0.001
Control
a
a
a
ab
b
ab
b
c
ab
bc
b
c
Exp. 5
60 40 20 0 20 40 60 80
BARK OIL (mg equiv.)
HEALTHY TREE
ROOT ROT-INFECTED TREE
60
6.0
0.6
0.06
0.006
0.0006
*
*
Exp. 6
TREATMENT
80 60 40 20 0 20 40 60 80
PERCENT RESPONSE (X̄ + SE)

very clear synergistic effect of combining the two fractions, especially for females (Figure 3). This effect was reproduced in experiment 8 by combining the defined synthetic fractions (Figure 3).

In GC-EAD analyses of *A. grandis* volatiles, female *S. ventralis* antennae responded to many compounds, including (±)-α-pinene, (−)-camphene, (−)-β-pinene, myrcene, (−)-limonene, β-phellandrene, α-terpinolene, longifolene, bornyl acetate, borneol, (*E*)-nerolidol, and methyl-isoeugenol (Figure 4). When the synthetic blends SB1 and SB2 (the latter with a correct ratio of limonene–β-phellandrene) were tested in the field in experiments 9 and 10, both *S. ventralis* and the clerid predator, *Thanasimus undatulus* Say, were captured in significant numbers in traps baited with the synthetic blends (Figure 5). Neither species responded to the bark oil distillate.

A summary of negative results from experiments searching for evidence of secondary attraction in *S. ventralis* is given in Table 3. These experiments included laboratory and field aerations, hormone treatments, GC analysis of gland extracts, and videotaping of behavior.

DISCUSSION

When examined in detail our results consistently support the primary attraction aggregation hypothesis. Both sexes of *S. ventralis* displayed the same general trend of response to any material tested, with females attracted in slightly higher numbers to a broader dose range of stimuli than males. This finding is concordant with the role of females as the pioneer sex that must perceive and select the most suitable host trees. The superior attraction of volatiles from female-infested logs over those from male-infested logs can be accounted for by the higher rate of boring by females, which would release more host volatiles than boring by males. The results from experiment 3 suggest that boring males produced a repellent pheromone, but this hypothesis was not followed further.

The results from GC-EAD analyses, bioassays that indicate a requirement for a blend of host volatiles to achieve attraction, and the finding that attraction can be reproduced by substituting synthetic blends for natural ones are all indicative of a species highly adapted to respond to host kairomones. Further evidence

FIG. 2. (Opposite) Results of laboratory bioassays showing the percent responses of walking male and/or female *S. ventralis* tested in 10 groups of five insects (males or females) to steam distilled bark oil (experiment 4), Porapak Q-captured volatiles from grand fir bark chips (experiment 5), and steam-distilled bark oil from root rot-infected or healthy grand firs (experiment 6). For experiments 4–5, bars for each sex with the same letter are not significantly different, REGW test, $P < 0.05$. Asterisks in experiment 6 indicate significant difference in paired responses within a dose, t test, $P < 0.05$.

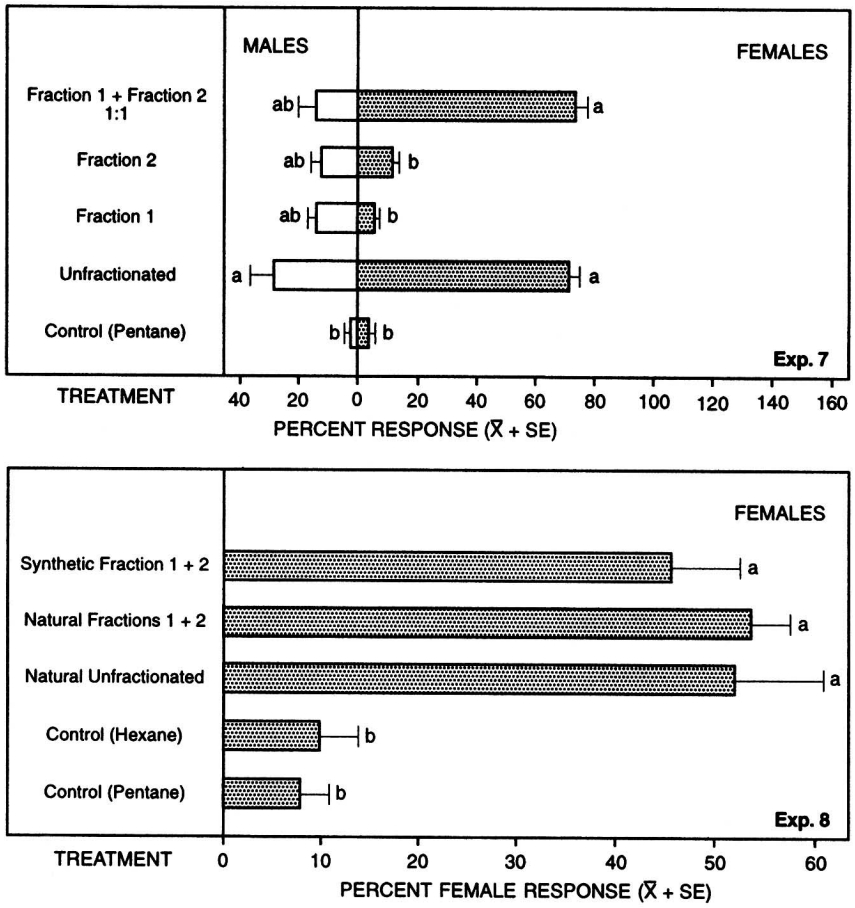


FIG. 3. Results of laboratory bioassays showing the percent responses of walking male and/or female *S. ventralis* tested in 10 groups of five insects (males or females) to fractionated and unfractionated steam-distilled bark oil from root-rot-infected grand fir presented in 1-μg doses (experiment 7), and combinations of fractions of natural and synthetic bark oil from grand fir presented in 100-ng doses (experiment 8). Within each experiment and sex of beetles, bars with the same letter are not significantly different, REGW test, $P < 0.05$.

of the sensitivity of *S. ventralis* to specific volatiles from its host is that it is repelled in laboratory bioassays at equivalent doses by bark oil from subalpine fir (unpublished results). Although both *A. grandis* and *A. lasiocarpa* are similar in their major volatile components, some minor components are not shared by both (Zavarin, 1968; von Rudolf, 1975).

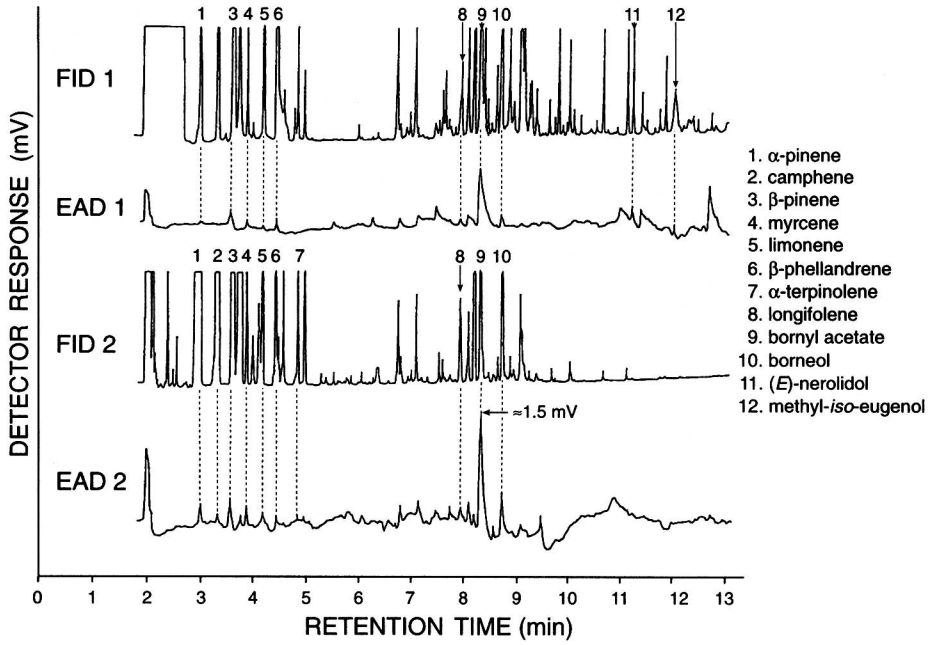


FIG. 4. Representative paired recordings of FID and EAD with female *S. ventralis* antenna to steam-distilled grand fir bark volatiles. Chromatography: DB-23 column (30 m × 0.32 mm ID) splitless injection; injector and FID temperature 240°C. Temperature program: 50°C for 1 min, then 10°C/min to 200°C, FID 1 = Porapak Q-trapped volatiles from female-infested logs; FID 2 = Porapak Q-trapped volatiles from field aeration of a 1-m section of a root-rot-infected, uninfested standing grand fir.

The repellent effect of individual terpenoid components found by Bordash and Berryman (1977) was apparently overturned by offering a blend of the same materials in a ratio of components similar to that found in the naturally occurring bark volatiles. An equivalent situation was found by Visser and Avé (1978), in which the Colorado potato beetle, *Leptinotarsa decemlineata* Say, was attracted to a specific blend of green leaf volatiles, but when these compounds were tested individually or incorporated into the blend at different ratios, the attraction ceased or decreased, respectively. Similarly, Anderson et al. (1993) reported that oviposition by the cotton leafworm, *Spodoptera littoralis* (Boisd.), was strongly deterred by a mixture of six compounds from conspecific larval frass. If one of the compounds was excluded from the mixture, the deterrent effect was lost.

The response of the predator *T. undatulus* to the same blend that attracts its prey is analogous to similar predator–host interactions in which *T. undatulus* responded to the pheromone frontalin produced by the Douglas fir beetle,

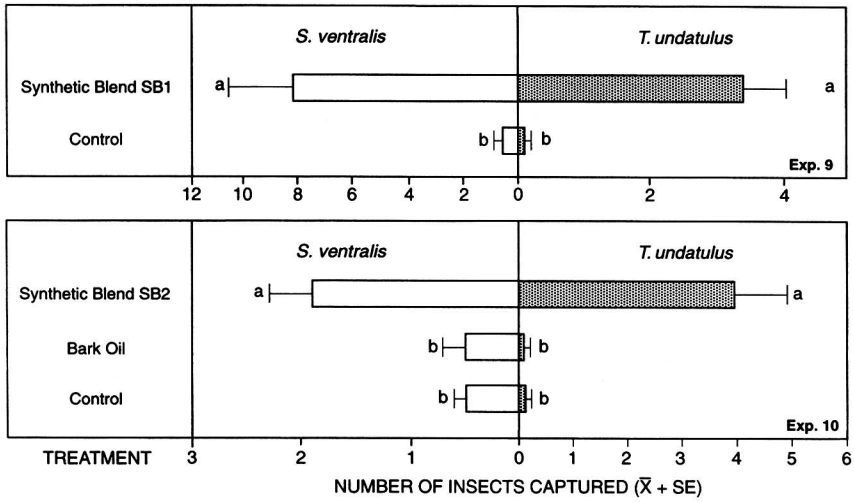


FIG 5. Numbers of *S. ventralis* and *T. undatulus* captured in multiple-funnel traps in experiment 9 (July 7–16, 1996) and experiment 10 (July 2–9, 1996), Coeur d'Alene, Idaho; $N = 10$. Release rate for SB1 was 340 mg/24 hr; for SB2, 280 mg/24 hr; and for the bark oil, 50 mg/24 hr. For each experiment and insect, bars with the same letter are not significantly different, REGW test, $P < 0.05$.

TABLE 3. SUMMARY OF ADDITIONAL EXPERIMENTS (MACÍAS-SÁMANO, 1997) PERFORMED TO TEST HYPOTHESIS OF SECONDARY ATTRACTION IN *S. ventralis*

Experiments	Results
Laboratory aerations Volatiles collected on Porapak-Q from groups of 20–500 male, female, or mixed-sex *S. ventralis* held in glass tubes (Rudinsky et al., 1973). Beetles were virgin-unfed, virgin-fed, or mated-fed. Aerations also made of grand fir bolts infested with males, females or both.	GC and GC-EAD analyses of captured volatiles revealed no sex-specific compounds. No preferential response by beetles of either sex to volatiles from either sex or type of treatment.
Field aerations Adapting the methodology of Browne et al. (1979), 1-m-long sections of bole of standing grand fir trees under attack by *S. ventralis* were wrapped in a plastic sheet open at the top with the bottom attached to a Porapak Q trap under vacuum from a portable pump. Aerations continued for 50 hr. Volatiles from unattacked control trees captured in identical manner.	GC analysis of the captured volatiles revealed no volatiles specific to attacked trees and no differences in ratios of components. This was confirmed by comparative GC-EAD analysis of extracts from one infested and one uninfested tree.

TABLE 3. CONTINUED

Experiments	Results
Hormone treatment	
With Harring's (1978) technique, 120 *S. ventralis* of each sex were treated topically with 1 and 10 μg of methoprene in 1 and 10 μl of pentane. After 24 hr, treated and control beetles were extracted in pentane. Extracts also made of male and female fir engravers allowed to bore into phloem pieces treated with 1 and 10 μg of methoprene.	No sex-specific volatiles revealed by GC analysis of extracted beetles.
Gland extracts	
Exploring the hypothesis of Gore et al. (1977) that accessory glands at the base of vaginal palpi of *S. multistriatus* were associated with pheromone production, we excised 276 abdominal tips (containing the palpi and gland) from unfed female *S. ventralis* as well as from females that had been fed for two days. Excised tips were macerated in ice-cold pentane.	GC analysis of abdominal tip extracts revealed trace amounts of *exo*-brevicomin as confirmed by GC-MS. No attraction to *exo*-brevicomin in laboratory bioassays or field experiments was observed.
Videotaping	
Over 20 hr of videotaping of male and female *S. ventralis* walking on surface of grand fir logs, females initiating attack, and males courting females were evaluated.	Several females were observed rubbing the tip of the abdomen on bark in apparent marking behavior, and a few others possibly calling while running with protruded, swollen abdominal tips.[a] There was no observed response by males to either marking or calling females, and no sex-specific volatiles were revealed by GC analysis of aerated or extracted beetles (above). Gallery initiation and courtship similar to that by *S. multistriatus* (Svihra and Clark, 1980) was observed, but no behavior observed that would suggest pheromone release.

[a] J. E. Macías-Sámano and J. H. Borden: Host finding and mating behavior of the fir engraver. Paper presented at the annual meeting of the Entomological Society of America, Indianapolis, Indiana, December 13–15, 1993.

Dendroctonus pseudotsugae Hopkins (Ross and Daterman, 1995), and ipsdienol produced by *Ips* spp. (Miller et al., 1991). In each instance, the predators and their prey responded to identical stimuli, suggesting that *T. undatulus* may have distinct semiochemical-based, prey-adapted races. *Thanasimus* spp. are characteristically attracted to the pheromones of several host scolytid species (Vité

and Williamson, 1970; Bakke and Kvamme, 1981; Mizell et al., 1982; Payne et al., 1984; Raffa and Klepzig, 1989; Herms et al., 1991; Miller et al., 1991). Another predator, the blackbellied clerid, *Enoclerus lecontei* (Wolcot), reported as the most abundant predator of the fir engraver (Struble, 1957; Ashraf and Berryman, 1969; Berryman and Ferrell, 1988), was not trapped in response to the synthetic blends, but at the same field site was attracted (Macías-Sámano, 1997) by the aggregation pheromone (Macías-Sámano et al., 1997) of *Pityokteines elegans* Swaine, which implies that this clerid is following *P. elegans* and not *S. ventralis*.

The thresholds for perception of and response to bark oil and the blend of synthetic host kairomones are similar to those for pheromones in the genera *Dendroctonus* and *Ips* (Borden, 1985), and much lower than for kairomones in other genera (Dickens, 1979). In particular, the threshold for response near 0.1 mg equiv of bark oil distillate is easily equivalent to the response of male *S. multistriatus* in laboratory bioassays to 10 mg of pheromone-laden frass from virgin females (Peacock et al., 1973). The ability of the synthetic blends released at 340 and 280 mg/24 hr for SB1 and SB2, respectively, to attract *S. ventralis* in the field is also remarkable, considering the competition from natural odor sources in the forest, and the fact that these are the summed release rates for 13 components (Table 2). In comparison, red turpentine beetles, *Dendroctonus valens* (LeConte, were attracted in the field to specific enantiomers of α- and β-pinene released at 0.8–70 ml/24 hr (Hobson et al., 1993), doses ranging from 2 to 200 times those at which SB1 and SB2 were released.

Although grand fir bark oil was highly attractive to *S. ventralis* in laboratory bioassays, its failure to attract *S. ventralis* in the field when released at 50 mg/24 hr suggests that the release rates of 340 and 280 mg/24 hr for SB1 and SB2, respectively, were just above the threshold for attraction. Additional experimentation has shown bark oil to be attractive to fir engravers when released at 386 mg/24 hr (Macías-Sámano, 1997).

Because of the intolerance of *S. ventralis* to resin and the inhibition of growth by *T. symbionticum* in the presence of monoterpenes (Raffa et al., 1985), there is a low likelihood that fir engravers could overcome the induced defense system of healthy trees (Raffa, 1991), even by mass attack. Therefore, avoidance of stimuli associated with host resistance would be adaptive (Raffa and Berryman, 1987), as would orientation toward stimuli associated with susceptible weakened hosts. Mass attack behavior would be adaptive only to the extent that slightly resistant trees could be included as suitable hosts. A preference for weakened hosts is supported by the high correlation of root-rot infections and fir engraver attacks (Cobb et al., 1973; Hertert et al., 1975; Ferrell and Smith, 1976; Wright et al., 1984) and by our findings that fir engravers are more attracted to oil from the bark of root-rot-infected trees than from the bark of healthy trees. Other bark beetles can apparently also detect fungus-infested hosts.

For example, seven times more pine engravers, *Ips pini* (Say), bored into trees infected by *Leptographium terebrantis* Barras and Perry, than into healthy ones (Raffa and Klepzig, 1996). Nebeker et al. (1995) showed that lodgepole pines infested with *Armillaria* root rot had a 20 times higher bornyl acetate content in the resin than healthy trees. Conversely, traumatic resin from grand fir contains no bornyl acetate (Russell and Berryman, 1976; Raffa and Berryman, 1987; Lewinsohn et al., 1990) and may not be attractive to host-seeking fir engravers. In our experiments bornyl acetate elicited a very clear and strong EAD response in fir engraver antennae and was attractive to walking *S. ventralis* when tested alone at doses ranging from 10 to 100 ng in laboratory bioassays (results not shown).

In a kairomone-driven system, it would be adaptive for both sexes to respond at high levels to a host kairomonal signal, and to rely on close-range recognition factors for mate selection. Accordingly, one would not expect the sex ratio of responding beetles to be altered if the host were under attack by conspecifics. Field investigations by Ferrell (1969) support this hypothesis; the sex ratios of *S. ventralis* caught on girdled unattacked and girdled attacked trees did not differ, nor did they differ from the sex ratio at emergence. Results from experiment 1 and from the female–male sex ratios of 12:8 and 47:35 in experiments 9 and 10, respectively, are consistent with Ferrell's (1969) observations.

There are other bark beetles that are attracted to host resin and/or some of its components and that also do not seem to have aggregation pheromones. The red turpentine beetle is attracted to mixtures of α-pinene, myrcene, and 3-carene (Hobson et al., 1993) and demonstrates a remarkable chiral specificity toward (*S*)-(−)-α-pinene (White and Hobson, 1993). The native elm bark beetle, *Hylurgopinus rufipes* (Eichhoff), is attracted to cut elm wood (Martin, 1936), wounded elms (Landwehr et al., 1981), and to naturally and artificially moribund elms (Gardiner, 1979; Millar et al., 1986). Several sesquiterpenes were attractive to *H. rufipes* when deployed in traps (Millar et al., 1986), but no pheromone could be demonstrated in this species (Swedenborg et al., 1988).

Historically, research on the chemical ecology of scolytids has disclosed occasions when species were considered to be kairomone-driven but were later shown to employ aggregation pheromones. For example, Meyer and Norris (1967) attributed the higher attraction of *S. multistriatus* to female- than male-infested logs to the greater release of host volatiles by the actively boring females. However, Peacock et al. (1971) demonstrated the presence of a female-produced aggregation pheromone by showing much higher attraction to logs infested with 40 females than to logs infested by 400 males. The contention by Byers et al. (1985) and Vité et al. (1986) that the pine shoot beetle, *Tomicus piniperda* (L.), relies solely on primary attraction in host selection has recently been countered by Teale (1996), who used GC-EAD analysis as the basis for demonstrating that this species also uses an aggregation pheromone. Therefore, we pursued an

exhaustive series of experiments using GC and GC-EAD techniques as well as other approaches to test the hypothesis of secondary attraction in *S. ventralis*, with consistently negative results. Moreover, a review of 50 years of published information on the fir engraver failed to yield compelling evidence for a pheromone-driven system and supported the hypothesis that from an evolutionary perspective the fir engraver has become well adapted to rely on host kairomones to mediate host selection.

One significant adaptation is the transverse orientation of *S. ventralis* galleries, which allows *T. symbionticum* to be inoculated into the greatest possible amount of vascular tissue (Wong and Berryman, 1977). This in turn results in a large area invaded by the fungus and a correspondingly large area in which the insect can breed. Because *S. ventralis* can avoid encountering large amounts of constitutive resin, which is localized primarily in cortical pitch blisters (Bannan, 1936; Littelfield, 1973; Ferrell, 1969, 1983), there is little selective pressure to develop a resin detoxification system (Raffa and Berryman, 1987), a process by which other bark beetles produce pheromones (Renwick, 1988).

Because exposure to resin can be avoided, fir engravers produce single galleries in living trees that can be as successful, or more so, as those in mass-attacked trees (personal observation). Several reports (Struble, 1957; Johnson and Shea, 1963; Berryman, 1969; Berryman and Ashraf, 1970; Felix et al., 1971; Ferrell, 1973) describe the scars of old isolated attacks, both successful and unsuccessful, embedded in the xylem of living firs. The ability to kill a patch of bark and potentially reproduce in it (Ferrell, 1973; personal observation) is found in very few other bark beetles. Among them is *Dendroctonus micans* Kugelann, which like *S. ventralis* is not known to orient by pheromonal communication (Grégoire, 1985).

Scolytus ventralis flies over an eight-week period (Struble, 1957; Ashraf and Berryman, 1969) and can respond to stressed trees throughout the growing season as they become available (Raffa and Berryman, 1987). Linking the long period of flight with the absence of strong mass attack behavior (Ashraf and Berryman, 1969), and great variability in attack density when trees are mass attacked (Berryman, 1968a,b), there is presumably less advantage to synchronous flight and attack than in other species of tree-killing bark beetles (Raffa and Berryman, 1987) that are driven by pheromones. This hypothesis is supported by the fact that grand fir is incapable of induced responses to wounding under conditions of intense water stress (Lewinsohn et al., 1993).

As hypothesized for pheromone-mediated mass attack (Alcock, 1982), mass attack by *S. ventralis*, when it does occur, would simply be a consequence of each beetle attempting to maximize its fitness by responding to the volatiles emitted by a potentially suitable host. In support of this hypothesis, Berryman and Ashraf (1970) found that aggregation on a host by the fir engraver is directly associated with the degree of gallery elongation.

Based on our findings and the above discussion, we hypothesize that both sexes of *S. ventralis* are attracted to and aggregate on a tree, first because of odors emitted by the tree, and subsequently because the pioneer boring insects (females) liberate host kairomones, not insect-produced pheromones, by exposing vascular tissue to the air. These compounds would signal other insects of the presence of a suitable host. Close-range phagostimulatory signals might stimulate boring, and mating might be regulated by a combination of stridulatory signals (Ferrell, 1969; Rudinsky et al., 1978) and close-range pheromonal stimulation. Such close-range signals and their regulation have been suggested by observations of apparent calling and marking behavior revealed by videotape analysis.

Acknowledgments—We thank M. M. Furniss, P. DeGroot, K. F. Raffa, P. L. Lorio, Jr., J. G. Millar, D. R. Miller, A. Savoie, and E. S. Tomlin for their comments and discussion of some of the ideas presented in this work; D. E. Bright, Jr., for insect identifications; L. J. Chong, B. Cinel, S. L. Van Learhoven, M. E. Greenwood, and G. A. Yakel for field assistance; and S. J. Kegley, J. Schwandt, J. L. Wallace, C. Bell-Randall, and R. Oaks, USDA, Forest Service, Idaho Panhandle National Forest, for advice and support with field sites and laboratory facilities. The research was supported by the Natural Sciences and Engineering Council of Canada, the Canadian Forest Service, the Science Council of B.C., the Coast Forest and Lumber Sector, the Interior Lumber Manufacturers' Association, the Cariboo Lumber Manufacturers' Association, seven forest industry companies, and by scholarships to J.E.M.-S. from the Comisión Nacional para el Desarrollo de la Ciencia y la Tecnologia (CONACyT), México and Organization of American States, Washington, D.C.

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