Bark and Ambrosia Beetle (Coleoptera: Scolytidae) Responses to Volatiles from Aging Loblolly Pine Billets

C.A.H. FLECHTMANN,[1] M. J. DALUSKY,[2] AND C. W. BERISFORD[2]

Environ. Entomol. 28(4): 638–648 (1999)

ABSTRACT Many species of bark and ambrosia beetles use host volatiles as cues for breeding site location. In a study where the objectives were to identify the different volatiles released by *Pinus taeda* L. billets as they age, to determine the arrival sequence of scolytids (Coleoptera: Scolytidae), and to correlate volatile emission by the billets with beetle catches, 25 species of scolytids were trapped. Bark beetles were more attracted to the billets in the beginning of the period, whereas ambrosia beetles arrived later. Among the bark beetles, *Dendroctonus terebrans* (Olivier) was significantly more attracted during the 1st 3 wk after tree felling, *Hylastes tenuis* Eichhoff in the 1st 2 wk, *Pityophthorus pulicarius* (Zimmermann) in weeks 2 and 3, and *Ips grandicollis* (Eichhoff) was more attracted on weeks 3 and 4. Among the ambrosia beetles, *Xyleborinus saxeseni* (Ratzeburg) was more attracted to billets during weeks 4–6, whereas *Xyleborus pubescens* Zimmermann and *Xyleborus californicus* Wood were more attracted during week 6. The billets showed marked decline in attractiveness to all scolytids after 8 wk. Volatiles collected during the beetle trapping periods included 15 hydrocarbon monoterpenes, 18 oxygenated monoterpenes, 4-allylanisole, and ethanol. The hydrocarbon monoterpenes and 4-allylanisole decreased sharply over time, but oxygenated monoterpenes and ethanol increased up to weeks 4–6, after which they also decreased. Good correlations between certain billet volatiles and catches for some beetle species were obtained, but their biological significance could not be determined.

KEY WORDS Scolytidae, arrival sequence, hydrocarbon monoterpenes, oxygenated monoterpenes, ethanol, correlation

BARK BEETLES ARE among the most economically important forest insects (Paine et al. 1997). The losses caused by tree mortality result in damage totaling millions of dollars annually (Wood 1982). In the Southeast, the bark beetle guild, composed of *Dendroctonus frontalis* Zimmermann, *Dendroctonus terebrans* (Olivier), *Ips calligraphus* (Germar), *Ips grandicollis* (Eichhoff), and *Ips avulsus* (Eichhoff) (Birch et al. 1980) is considered to be the most destructive group of these insects (Smith et al. 1993).

Ambrosia beetles are sometimes associated with bark beetle attacks, but they attack and kill healthy trees only sporadically (Beaver 1988). Ambrosia beetles cause less damage than bark beetles, but their damage is difficult to quantify (Samaniego and Gara 1970). The most important losses from ambrosia beetles are degradation of lumber (Dobie 1978) and export problems (Hosking 1969). In sawmills, those problems can compound and result in millions of dollars of losses (Lindgren and Fraser 1994).

There is a well-established sequence of arrival for various scolytid groups, once a live or recently felled host is first attacked by one beetle species (Birch et al. 1980, Lindgren et al. 1982, Smith et al. 1993). The most comprehensive study in this field was done by Dixon and Payne (1979), who studied the scolytid arrival sequence on *Pinus taeda* L. and *Pinus echinata* Miller after an initial attack by the southern pine beetle (*D. frontalis*).

The 2 main hypotheses for how bark beetles are able to locate and select their hosts are as follows: (1) scolytids are attracted to host volatiles, or (2) pioneer beetles randomly land on hosts and on nonhosts alike (Byers 1989). Apparently aggressive bark beetles (species able to attack healthy standing trees) are weakly or nonattracted by host kairomones (Byers 1989, 1995). Secondary bark beetles however, those that colonize dying or decaying trees, are considered to be strongly attracted to either host volatiles, ethanol, or a combination of both (Phillips et al. 1988, Werner 1995).

Although the host selection mechanism of many bark beetle species has been intensively studied, host selection behavior of the ambrosia beetles has received relatively little attention (Phillips et al. 1989). Ambrosia beetles colonize mainly dead or dying trees, and they must be able to detect and locate suitable breeding material, which is usually scattered and ephemeral (Lindelöw et al. 1992). A number of ambrosia beetles are known to respond to host monoterpenes (Phillips et al. 1988). Ethanol, however, which is produced in stressed trees (MacDonald and Kimmerer 1991) and mainly in aging fallen trees

[1] Department of Biology–FEIS/UNESP, Av Brasil, 56, 15 385-000-Ilha Solteira-SP, Brasil.
[2] Department of Entomology, University of Georgia, 413 Biological Sciences Building, Athens, GA 30605-2655.

0046-225X/99/0638–0648$02.00/0

(Moeck 1970, Lindelöw et al. 1992), seems to be the most consistent cue for host location by many ambrosia beetles (Moeck 1970, Samaniego and Gara 1970, Phillips et al. 1988, Flechtmann et al. 1995), and it often acts as a synergist to monoterpenes (Liu and McLean 1989).

Traditional methods to collect volatiles include the use of adsorbents such as Porapak Q, Tenax or charcoal (Golub and Weatherston 1984), and direct gas injections of headspace samples (Hunt et al. 1989, Kelsey 1996). Solid-phase microextraction (SPME) is a relatively new and efficient technique for analyzing volatile organic compounds (Zhang and Pawliszyn 1993, Bartelt 1997). The SPME technique concentrates trace compounds (Zhang and Pawliszyn 1993), and it is considered ideal for analyzing many of the complex mixtures released by biological systems (Czerwińsky et al. 1996, Bartelt 1997).

The objectives of our experiments were to determine the change in volatiles released by billets of loblolly pine, *P. taeda*, over time; to monitor the arrival sequence of the different scolytid beetles responding to the emitted billet semiochemicals, and correlate beetle catches with the emitted volatiles. We also were interested in comparing qualitatively both SPME and headspace sample gas injection techniques.

Materials and Methods

1996 Field Season. Two sites were used, both located on the Chattahoochee National Forest (Stephens County, GA), and composed primarily of *P. echinata.* One site was a recent southern pine beetle "cut-and-leave" area (site CH 1); the other had an active southern pine beetle infestation (site CH 2a). The "cut-and-leave" technique is used for southern pine beetle control by felling infested trees plus an uninfested buffer to induce lethal temperatures under the bark and to disrupt pheromone-mediated behavior (Thatcher et al. 1980). Ambrosia beetle attacks were evident at both sites.

We used billets of loblolly pine (70 cm long, 16–20 cm diameter) as attractive baits. Three of these billets were put inside each tent trap; this trap allows volatiles released by the billets to escape into the environment and to catch attracted insects before they can land on and attack the billets (Flechtmann and Gaspareto 1997).

Each site had 5 blocks of traps, with 2 traps per block. Each block was composed of a trap baited with loblolly pine billets and an unbaited (control) trap. Trap spacing within and between blocks was 20 m.

The billets were cut from Whitehall Forest, Clarke County, GA, on 27 May and taken to the trapping sites within 2 d. Traps were checked weekly for 10 wk, and after each collection the baits were rotated between traps of each block to reduce position effects (Volz 1988).

A 2nd deployment was made to site CH 2a, hereafter called site CH2b, using the same methods. Tent traps were baited on 21 August and insects were collected weekly for 7 wk.

Concurrent with trap collection, 1 billet from each of the 5 baited traps was brought to the laboratory for headspace volatiles collection. One end of each billet was covered with a 7.6-liter freezer bag and the billets were placed in an incubator at 30°C for at least 1 h to allow volatiles eluted into the bag to reach an equilibrium. Sample billets were returned to their corresponding tent traps in the field the following day.

One microliter of a standard composed of 500 ng/μl each of undecane:ethyl caprate was injected through the bag onto a piece of filter paper inside a small aluminum pan (previously placed on top of each billet) 30 min before each headspace gas analysis. A gas-tight syringe was flushed 3 times in the headspace, then a 1-ml sample of gas was injected into a gas chromatograph–mass spectrometer (GC-MS) (Kelsey 1996). The airtight syringe was rinsed 5 times in redistilled pentane immediately after use, and was kept in an oven at 43°C until reused. The GC-MS was a Hewlett–Packard GCD G1800A GC-MS system equipped with a HP-FFAP fused-silica capillary column (49.5 m by 0.2 mm; 0.33 μm film thickness) (Hewlett–Packard, Palo Alto, CA). The temperature program was 32°C for 1 min, then 8°C/min to 220°C for 12 min. The carrier gas was helium at a flow rate of 0.7 ml/min. The volatile compounds were identified based on their mass spectra and retention times matching known standards. No quantification of released volatiles was attempted. The volatile abundance of each compound was expressed as the relative abundance compared with the undecane standard.

1997 Field Season. Two plantations of longleaf pine, *Pinus palustris* Miller, located at the U.S. Department of Energy's Savannah River Plant, Barnwell County, SC, were used as study sites. The loblolly pine billets came from Whitehall Forest, and they were cut on 25 August with the same dimensions as previously described, then deployed inside the tent traps on the following day. Each site had the same number of traps and design as used in the 1996 season. Beetles trapped were collected weekly for 8 wk.

Volatiles released by the billets and control traps were collected directly from inside the tent traps in the field. The volatiles were collected using the SPME technique, with a fiber coated with 100 μm of polydimethylsiloxane as the stationary phase (Supelco, Bellefonte, PA). The fibers were extruded from a needle inside the tent trap and exposed for 15 min to absorb volatiles present in the headspace, after which they were retracted into the needle, sealed at the tip with a rubber septum, and kept on dry ice until desorption in the laboratory.

Injections were done manually using a specialized SPME holder (Supelco, Bellefonte, PA). The injector liner had an inside diameter of 0.75 mm, which markedly improves the GC-MS results (Yang and Peppard 1994); runs were performed in the splitless mode (Czerwiński et al. 1996). The fibers were thermally cleaned in the injector port (Yang and Peppard 1994) and reused until the end of the experiment (Bartelt 1997). The same GC-MS and column used in the 1996 season were used in the identification of the volatiles.

The temperature program was 40°C for 1 min, then 16°C/min to 80°C then 7°C/min to 202°C, then 40°C/min to 230°C for 6 min; 0.7 ml/min helium flow rate.

An external calibration was used (Yang and Peppard 1994), where fibers were exposed to the headspace of an undecane and ethyl caprate standard (1 μl of 250 μg/μl) inside a 500-ml mason jar. Quantification of volatiles was not attempted because an external calibration method is not suitable for quantification in SPME techniques (Yang and Peppard 1994). The volatile abundance was expressed as the relative abundance based on undecane abundances.

Temperature measurements were taken inside baited and control tent traps and compared with ambient values.

Voucher specimens collected in both field seasons were deposited in the Entomology Museum of the University of Georgia, Athens, and the Faculdade de Engenharia de Ilha Solteira (FEIS/UNESP), Ilha Solteira, São Paulo state, Brazil.

Experimental Design and Data Analysis. The experimental design was a randomized complete block design. Beetle catch data as well as volatile abundance data were transformed into $\sqrt{(x + 0.5)}$ to remove heteroscedasticy. Beetle catches in baited and unbaited traps were compared by Kruskal–Wallis (PROC NPAR1WAY; SAS Institute 1990a) and beetle catches among weeks by Friedman's χ^2 (PROC FREQ; SAS Institute1990a); the significance level used was 5%. Volatile relative abundance over weeks and temperature measurements were analyzed by PROC GLM with mean separation by the Tukey test (SAS Institute 1990b). The relationship between volatiles and beetle catches was examined using stepwise regression analyses (PROC REG; SAS Institute1990b); only data from weeks where catches in baited traps were statistically higher than those in control traps were analyzed to identify volatiles potentially attractive to beetles. For 1997, we used PROC STEPDISC combined with PROC DISCRIM (SAS Institute 1990b) as a tool to determine if data from the 2 sites could be combined (Snyder et al. 1996); scolytid catches and volatiles released by the pine billets were used to classify sites.

Results

1996 Field Season. *Trap Collections.* In total, 24 species of Scolytidae were trapped—*D. frontalis* and *D. terebrans* in the Tomicini; *I. calligraphus, I. grandicollis,*and *Orthotomicus caelatus* (Eichhoff) in the Ipini; *Hylastes porculus* Erichson, *Hylastes salebrosus* Eichhoff, and *Hylastes tenuis* Eichhoff in the Hylastini; *Hypothenemus miles* (LeConte) in the Cryphalini; *Gnathotrichus materiarius* (Fitch), *Monarthrum fasciatum* (Say), *Pityophthorus confusus* Blandford, and *Pityophthorus pulicarius* (Zimmermann) in the Corthylini; and *Ambrosiodmus rubricollis* (Eichhoff), *Xyleborinus gracilis* (Eichhoff), *Xyleborinus saxeseni* (Ratzeburg), *Xyleborus affinis* Eichhoff, *Xyleborus atratus* (Eichhoff), *Xyleborus celsus* Eichhoff, *Xyleborus ferrugineus* (F.), *Xyleborus pubescens* Zimmermann, *Xyleborus* sp.n., *Xylosandrus crassiusculus* (Motschulsky), and *Xylosandrus germanus* (Blandford) in the Xyleborini.

Significantly more bark beetles were caught on baited than on control traps in the beginning of the period. Significantly more *D. terebrans* were caught on baited traps during week 2 and week 3 at site CH 1, and at site CH 2b on week 1 and week 2. Significantly more *H. tenuis* on site CH 2b were caught on baited traps during weeks 1, 2, and 3. For all other species and sites, no statistically significant differences were observed (Table 1).

Significant differences in baited over control trap catches for the ambrosia beetles were found during later weeks. At site CH 1, significant differences for *X. saxeseni* occurred on weeks 4 and 5, and for *X. pubescens* on weeks 4, 5, and 6. On site CH 2a, *X. pubescens* was captured significantly more on baited traps on weeks 6 and 7 (Table 1).

Significantly more bark beetles were trapped in log-baited traps in the 1st 2 wk than in later weeks, whereas significantly more ambrosia beetles were trapped in later weeks than in earlier weeks (Fig. 1).

Volatile Analysis. The hydrocarbon monoterpenes α-pinene, β-pinene, camphene, myrcene, limonene, tricyclene and β-phellandrene, in addition to the phenylpropanoid 4-allylanisole, were identified from all 3 experiments as released by loblolly pine billets; terpinolene, terpinen-4-ol, and ethanol were identified only from billets used at site CH 2b.

The relative abundance of the identified volatiles varied over time. All monoterpenes (except for terpinen-4-ol) and the phenylpropanoid 4-allylanisole were significantly higher in abundance on the day the trees were cut, decreasing rapidly afterward. Ethanol, identified in only one experiment, was present immediately after trees were cut (week 0); its abundance then dropped markedly on week 1 then reached a 2nd peak on week 4, decreasing afterward (data not shown).

No correlation was obtained for the data from sites CH 1 and CH 2a because no volatile variable met the significance level of $P = 0.15$ for entry into the regression model. A significant correlation between catches and volatiles was found only for *H. tenuis,* and it was based on data from weeks 1 and 2 of the experiment conducted on site CH 2b. The compounds terpinen-4-ol and limonene correlated positively with *H. tenuis* catches ($P = 0.0379$; $r^2 = 0.61$).

1997 Field Season. *Trap Collections.* Seventeen species of Scolytidae were trapped at Savannah River Plant—*D. terebrans* in the Tomicini, *I. grandicollis* and *O. caelatus* in the Ipini, *H. porculus, H. salebrosus,* and *H. tenuis* in the Hylastini, *Gnathotricus materiarius, M. fasciatum,* and *P. pulicarius* in the Corthylini, and *A. rubricollis, X. saxeseni, X. affinis, X. ferrugineus, X. pubescens, Xyleborus* sp.n., *Xyleborus californicus* Wood, and *X. crassiusculus* in the Xyleborini.

By using scolytids to classify sites, site 2 was classified as such 100% of the time; site 1 was classified correctly only 43% of the time (i.e., 57% of the time it was classified as site 2). When volatiles were used as

Table 1. Mean ± SE of baited versus control Scolytidae trap catches in the Chattahoochee National Forest, Stephens County, GA, and mean comparison, within weeks and beetle species

Site Ch1

Week	*D. terebrans*		*H. Porculus*		*X. saxeseni*		*X. pubescens*		*X. ferrugineus*		*G. materiarius*	
	Baited[a]	Control[a]	Baited	Control	Baited	Control	Baited	Control	Baited	Control	Baited	Control
1	0.40 ± 0.24a	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	0.80 ± 0.58a	0.80 ± 0.20a	0.00 ± 0.00a	0.00 ± 0.00a
2	2.40 ± 0.98a	0.00 ± 0.00b	0.40 ± 0.24a	0.00 ± 0.00a	0.20 ± 0.20a	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	0.20 ± 0.20a	0.00 ± 0.00a	0.40 ± 0.40a	0.00 ± 0.00a
3	0.80 ± 0.37a	0.00 ± 0.00a	0.20 ± 0.20a	0.00 ± 0.00a	0.60 ± 0.40a	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	0.80 ± 0.37a	1.00 ± 0.56a	0.00 ± 0.00a	0.20 ± 0.20a
4	0.40 ± 0.40a	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	3.60 ± 1.40a	0.00 ± 0.00b	1.20 ± 0.37a	0.00 ± 0.00b	0.00 ± 0.00a	0.00 ± 0.00a	0.40 ± 0.24a	0.40 ± 0.24a
5	0.40 ± 0.40a	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	0.80 ± 0.37a	0.00 ± 0.00a	1.40 ± 0.51a	0.00 ± 0.00b	0.00 ± 0.00a	0.40 ± 0.40a	0.20 ± 0.20a	0.20 ± 0.20a
6	0.20 ± 0.20a	0.00 ± 0.00a	0.60 ± 0.60a	0.00 ± 0.00a	0.40 ± 0.40a	0.20 ± 0.20a	2.20 ± 0.58a	0.00 ± 0.00b	0.60 ± 0.40a	0.00 ± 0.00a	1.00 ± 0.63a	0.60 ± 0.24a
7	0.20 ± 0.20a	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	0.40 ± 0.40a	0.40 ± 0.24a	0.00 ± 0.00a	0.40 ± 0.24a	0.00 ± 0.00a	0.80 ± 0.58a
8	0.00 ± 0.00a	0.00 ± 0.00a	0.40 ± 0.24a	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	1.00 ± 0.32a	0.20 ± 0.20a	0.20 ± 0.20a	0.00 ± 0.00a	2.40 ± 1.36a	0.40 ± 0.24a

Site Ch2a

Week	*H. tenuis*		*I. grandicollis*		*X. saxeseni*		*X. pubescens*		*X. ferrugineus*		*G. materiarius*	
	Baited[a]	Control[a]	Baited	Control	Baited	Control	Baited	Control	Baited	Control	Baited	Control
1	0.00 ± 0.00a	0.00 ± 0.00a	0.20 ± 0.20a	0.20 ± 0.20a	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	0.20 ± 0.20a	0.20 ± 0.20a	0.20 ± 0.20a	0.40 ± 0.40a	0.40 ± 0.24a
2	0.00 ± 0.00a	0.00 ± 0.00a	0.20 ± 0.20a	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	0.20 ± 0.20a	0.00 ± 0.00a
3	0.00 ± 0.00a	0.20 ± 0.20a	0.20 ± 0.20a	0.00 ± 0.00a	0.40 ± 0.24a	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	0.20 ± 0.20a	0.20 ± 0.20a	0.60 ± 0.60a	1.00 ± 0.55a
4	0.40 ± 0.24a	0.00 ± 0.00a	0.20 ± 0.20a	0.20 ± 0.20a	0.20 ± 0.20a	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	0.20 ± 0.20a	1.20 ± 0.97a	1.40 ± 0.93a
5	0.00 ± 0.00a	0.00 ± 0.00a	0.20 ± 0.20a	0.20 ± 0.20a	0.20 ± 0.20a	0.00 ± 0.00a	0.00 ± 0.00a	0.20 ± 0.20a	0.00 ± 0.00a	0.00 ± 0.00a	1.20 ± 0.49a	5.40 ± 4.92a
6	0.00 ± 0.00a	0.40 ± 0.24a	0.20 ± 0.20a	0.40 ± 0.40a	0.00 ± 0.00a	0.00 ± 0.00a	0.60 ± 0.24a	0.00 ± 0.00b	0.40 ± 0.24a	0.20 ± 0.20a	9.60 ± 7.88a	4.40 ± 2.46a
7	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	1.40 ± 0.51a	0.20 ± 0.20b	0.00 ± 0.00a	0.00 ± 0.00a	7.40 ± 5.07a	9.80 ± 8.75a
8	0.20 ± 0.20a	0.40 ± 0.24a	0.40 ± 0.24a	0.20 ± 0.20a	0.00 ± 0.00a	0.00 ± 0.00a	0.40 ± 0.40a	0.20 ± 0.20a	0.20 ± 0.20a	0.00 ± 0.00a	8.00 ± 6.14a	9.80 ± 7.36a

Site Ch2b

Week	*D. terebrans*		*H. porculus*		*H. salebrosus*		*H. tenuis*		*X. pubescens*		*G. materiarius*	
	Baited[a]	Control[a]	Baited	Control	Baited	Control	Baited	Control	Baited	Control	Baited	Control
1	4.40 ± 1.36a	0.00 ± 0.00b	0.00 ± 0.00a	0.40 ± 0.24a	0.00 ± 0.00a	0.00 ± 0.00a	1.60 ± 0.51a	0.00 ± 0.00b	0.20 ± 0.20a	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a
2	1.60 ± 0.81a	0.00 ± 0.00a	0.80 ± 0.37a	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	2.00 ± 0.63a	0.00 ± 0.00b	0.00 ± 0.00a	0.20 ± 0.20a	0.00 ± 0.00a	0.20 ± 0.20a
3	0.60 ± 0.60a	0.00 ± 0.00a	0.00 ± 0.00a	0.20 ± 0.20a	0.60 ± 0.60a	0.00 ± 0.00a	1.80 ± 0.91a	0.40 ± 0.24a	0.20 ± 0.20a	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a
4	0.00 ± 0.00a	0.00 ± 0.00a	1.40 ± 1.40a	0.00 ± 0.00a	0.80 ± 0.80a	0.00 ± 0.00a	2.40 ± 1.44a	0.20 ± 0.20a	0.20 ± 0.20a	0.00 ± 0.00a	0.20 ± 0.20a	0.00 ± 0.00a
5	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	0.20 ± 0.20a	0.20 ± 0.20a	0.20 ± 0.20a	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a
6	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	0.20 ± 0.20a	0.00 ± 0.00a	0.20 ± 0.20a	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a
7	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	0.20 ± 0.20a	0.00 ± 0.00a	0.20 ± 0.20a	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a

[a] Means back-transformed from $\sqrt{(x + 0.5)}$; within each species, means within rows followed by the same letter are not significantly different ($P > 0.05$; Kruskal–Wallis test).

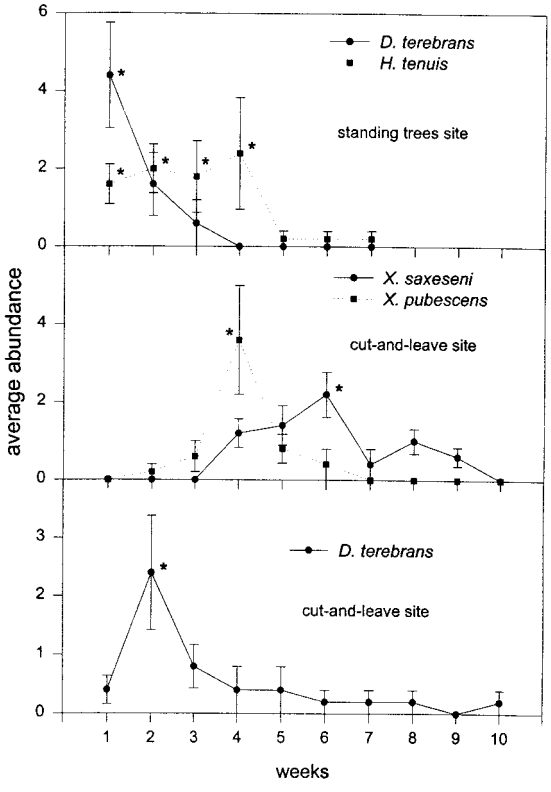

Fig. 1. Mean ± SE number of Scolytidae caught in traps baited with loblolly pine logs over time in the Chattahoochee forest, Stephens County, GA. Means of weeks followed by * are statistically higher than remaining weeks ($P < 0.05$) within each species.

the classificatory variables, site 1 was classified correctly 100% of the time but site 2 was classified as such just 13% of the time (data not shown). Based on the poor classifications obtained for one or another site, we combined sites 1 and 2 for the remainder of the analyses.

The baits (billets) were attractive to a number of scolytids for almost 7 wk. The baited traps had higher catches of the bark beetles *D. terebrans* and *I. grandicollis* than the control traps from week 1 through week 5 and week 2 through week 6, respectively (Table 2). The ambrosia beetles *X. saxeseni* and *X. pubescens* were more attracted to baited than to control traps for 5 and 4 wk, respectively, of the 8 wk of sampling (Table 2). *P. pulicarius* and *X. californicus* had higher catches on baited traps only on week 2 and week 6, respectively (Table 2).

Significantly more *D. terebrans* and *P. pulicarius* were caught on baited traps on weeks 2 and 3, *I. grandicollis* on weeks 3 and 4, *X. saxeseni* on weeks 4 and 6, *X. californicus* on week 6, and there were no statistically significant differences for *X. pubescens* (Fig. 2).

Overall, 36 semiochemicals emitted by the loblolly pine billets were identified, mainly hydrocarbon monoterpenes and oxygenated monoterpenes. The

Table 2. Mean ± SE of baited versus control Scolytidae trap catches in the Savannah River Plant forest, Barnwell County, SC, and mean comparison, within weeks and beetle species

Week	*D. terebrans*		*I. grandicollis*		*P. pulicarius*		*X. pubescens*		*X. saxeseni*		*I. calligraphus*	
	Baited[a]	Control[a]	Baited	Control	Baited	Control	Baited	Control	Baited	Control	Baited	Control
1	1.20 ± 0.53a	0.00 ± 0.00b	0.10 ± 0.10a	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	0.80 ± 0.20a	0.00 ± 0.00b	1.10 ± 0.41a	0.00 ± 0.00b	0.00 ± 0.00a	0.00 ± 0.00a
2	3.20 ± 0.74a	0.30 ± 0.74b	0.60 ± 0.22a	0.00 ± 0.00b	0.70 ± 0.33a	0.00 ± 0.00b	0.40 ± 0.16a	0.00 ± 0.00b	2.40 ± 0.56a	0.00 ± 0.00b	0.00 ± 0.00a	0.00 ± 0.00a
3	3.40 ± 0.97a	0.00 ± 0.00b	1.20 ± 0.39a	0.00 ± 0.00b	0.20 ± 0.13a	0.00 ± 0.00a	0.80 ± 0.59a	0.00 ± 0.00a	0.90 ± 0.41a	0.00 ± 0.00b	0.00 ± 0.00a	0.00 ± 0.00a
4	1.80 ± 0.74a	0.20 ± 0.13b	1.40 ± 0.048a	0.00 ± 0.00b	0.10 ± 0.10a	0.00 ± 0.00a	0.10 ± 0.10a	0.00 ± 0.00a	5.10 ± 0.85a	0.00 ± 0.00b	0.00 ± 0.00a	0.00 ± 0.00a
5	1.50 ± 0.50a	0.00 ± 0.00b	0.60 ± 0.22a	0.00 ± 0.00b	0.00 ± 0.00a	0.00 ± 0.00a	0.50 ± 0.22a	0.00 ± 0.00b	0.60 ± 0.22a	0.20 ± 0.13a	0.20 ± 0.13a	0.00 ± 0.00a
6	0.50 ± 0.27a	0.10 ± 0.10a	0.40 ± 0.16a	0.00 ± 0.00b	0.00 ± 0.00a	0.00 ± 0.00a	0.50 ± 0.17a	0.00 ± 0.00b	4.60 ± 1.24a	1.00 ± 0.42b	1.10 ± 0.69a	0.00 ± 0.00a
7	0.40 ± 0.16a	0.00 ± 0.00b	0.20 ± 0.13a	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	0.20 ± 0.20a	0.10 ± 0.10a	0.50 ± 0.34a	0.40 ± 0.22a	0.40 ± 0.31a	0.10 ± 0.10a
8	0.00 ± 0.00a	0.20 ± 0.13a	0.10 ± 0.10a	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	0.10 ± 0.10a	0.00 ± 0.00a	0.40 ± 0.22a	1.50 ± 0.60a	0.10 ± 0.10a	0.30 ± 0.21a

[a] Means back-transformed from $\sqrt{(x + 0.5)}$; within each species, means within rows followed by the same letter are not significantly different ($P > 0.05$; Kruskal–Wallis test).

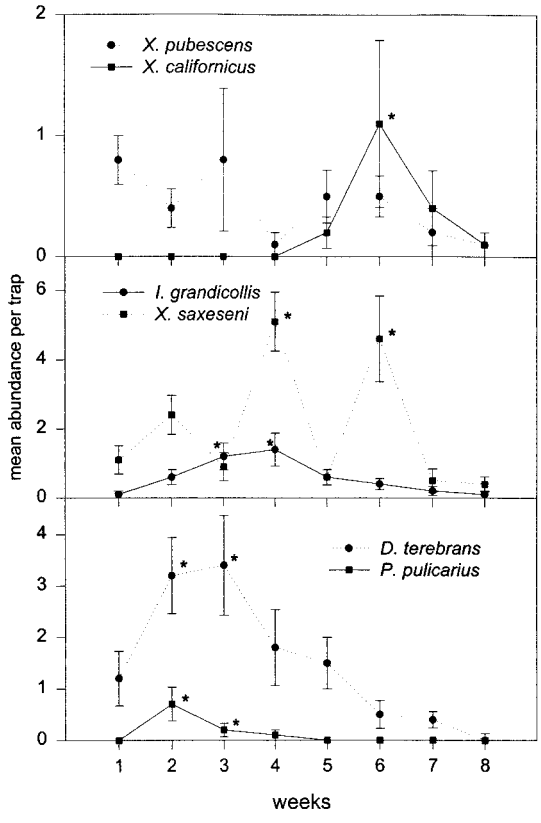

Fig. 2. Mean ± SE number of Scolytidae caught in traps baited with loblolly pine logs over time in the Chattahoochee forest, Stephens County, GA. Means of weeks followed by * are statistically higher than remaining weeks ($P < 0.05$) within each species.

compounds α-pinene, β-pinene, limonene, β-phellandrene, myrcene, 4-allylanisole, camphene, tricyclene, bornyl acetate, caryophyllene, terpinolene, γ-terpinene, α-phellandrene, α-humulene, α-terpinene, and δ-3-carene, mostly hydrocarbon monoterpenes, were significantly more abundant shortly after the trees were cut into billets (week 0), decreasing sharply thereafter (Fig. 3). However, for other semiochemicals, primarily oxygenated monoterpenes, such as verbenone, isopinocamphone, pinocamphone, borneol, α-terpineol, terpinen-4-ol, *trans*-verbenol, myrtenol, pinocarvone, carvone, isoborneol, ethanol, p-cymene, *trans*-carveol, fenchone, p-cymene-8-ol, fenchyl alcohol, fenchene, and myrtenal, there was a gradual increase in their abundance, followed by a corresponding decrease (Fig. 4).

Using data from weeks 2 and 3, a highly significant correlation ($P = 0.0019, r^2 = 0.60$) was found between *D. terebrans* catches and volatiles; p-cymene-8-ol and pinocamphone correlated positively and isopinocamphone correlated negatively. Using data from weeks 3 and 4, *I. grandicollis* catches correlated positively with carvone and negatively with myrcene and ethanol ($P = 0.0062, r^2 = 0.62$). Data for *P. pulicarius* in weeks 2 and 3 showed that pinocarveol and ethanol correlated positively and pinocarvone correlated negatively with beetle catches ($P = 0.0049$, $r^2 = 0.54$). For *X. californicus*, p-cymene-8-ol correlated positively and myrtenal negatively with trap catches ($P = 0.0003$; $r^2 = 0.90$). For *X. pubescens* (wk 1 to wk 3) and *X. saxeseni* (wk 4 and wk 6) no variable met the significance level ($P = 0.15$) for entry into the model.

Overall, average temperatures inside tent-traps were ≈3°C higher than the ambient temperature ($F = 242.73$; df = 1, 314; $P = 0.0001$).

Discussion

Sites and years were similar in the composition of the most abundant scolytid species arriving at loblolly billets.

The black turpentine beetle, *D. terebrans*, is a pest of pine forests throughout southern and eastern United States (Payne et al. 1987). Attacks occur more frequently on weakened and dying trees and stumps (Drooz 1985), but it is known also to attack green billets (Drooz 1985, Phillips et al. 1989). In our study, *D. terebrans* arrived during the 1st 2–3 wk (Figs. 1 and 2). This agrees with the report by Godbee and Franklin (1976) that loblolly pine bolts attract these beetles during the 1st 3 wk.

Bark beetles of the genus *Hylastes* usually breed in dying pines or billets in contact with the ground. The biology of *H. tenuis* is not well studied, but it breeds in pine trees (Drooz 1985, Furniss et al. 1992). Dixon and Payne (1979) observed that *H. tenuis* arrived in 2 peaks, one at 10–12 d and the other at 25–27 d after trees were attacked by the southern pine beetle. In our studies, *H. tenuis* was more attracted to the billets during the first 2 wk (Figs. 1 and 2).

Ips grandicollis attacks recently felled pines and slash, but healthy trees can be attacked when in concert with other bark beetle species (Drooz 1985). Following a southern pine beetle attack, *I. grandicollis* reaches a peak after 18 d (Dixon and Payne 1979), after which an intermediate attack rate is maintained until day 30 (Smith et al. 1993). Similar results were found in our study, where the peak of attractiveness for this species was found to be centered around the 3rd and 4th week (Fig. 2).

The response of *P. pulicarius*, with peak attraction between the 2nd and 3rd week (Fig. 2), was somewhat unexpected because this species is myelophagous and usually breeds in the pith of small pine twigs (Wood 1982). This beetle apparently responded to monoterpene odors, but it may not have attacked the billets if it had a chance to land and probe them.

Xyleborus saxeseni is a common ambrosia beetle species throughout the United States, breeding in a variety of trees; shortleaf and loblolly pines are among its more important hosts (Drooz 1985). This species is known to attack billets, but not immediately after felling (Hosking 1969). It showed 2 peaks in arrival, one at 12 d and another at 27 d after the initiation of southern pine beetle attacks (Dixon and Payne 1979).

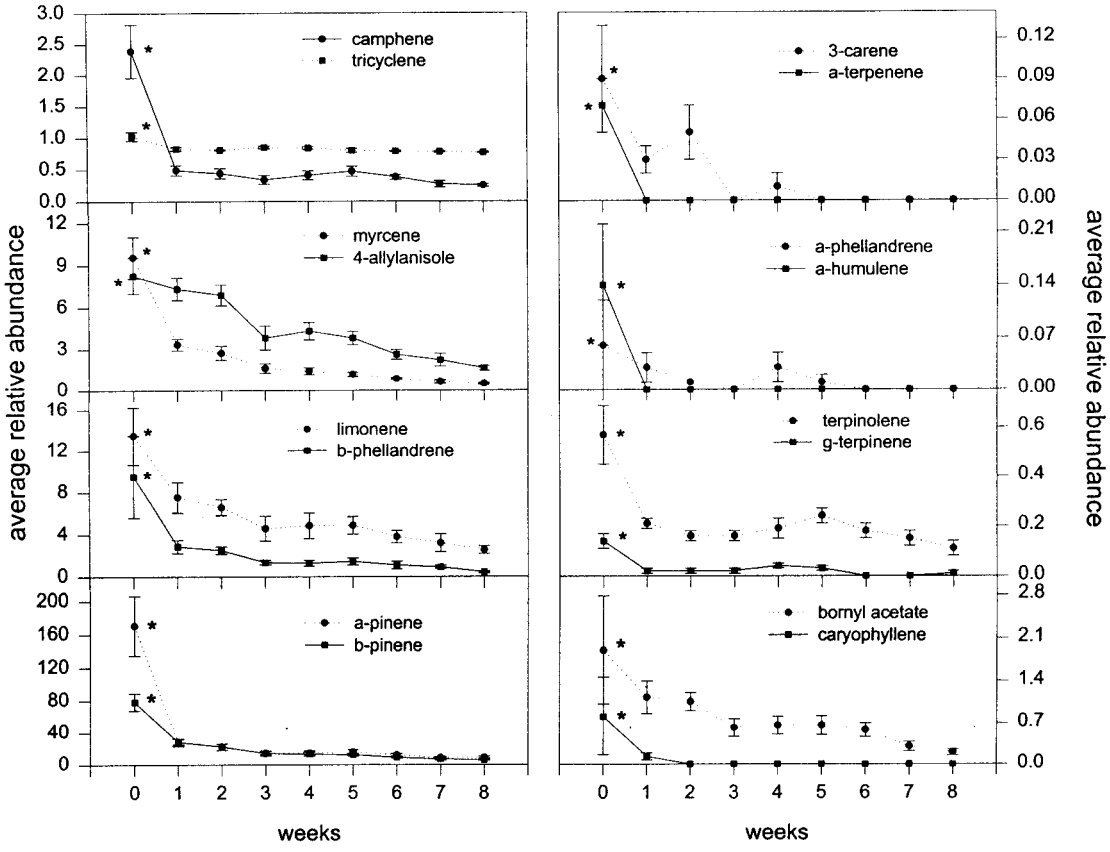

Fig. 3. Mean ± SE of the relative abundance of different loblolly pine billet hydrocarbon monoterpenes over time in the Savannah River Site Plant forest, Barnwell County, SC. Means of weeks followed by * are statistically higher than remaining weeks ($P < 0.05$) within each volatile.

In our experiments, peak attraction of *X. saxeseni* occurred 4 and 6 wk after felling (Figs. 1 and 2).

One of the few host-specific *Xyleborus* species is *X. pubescens*, which breeds in trunks of several pine species (Wood 1982). This ambrosia beetle arrived at southern pine beetle-infested pine trees at ≈27 d following bark beetle attack (Dixon and Payne 1979). Our Chattahoochee forest sites had catches of this species peaking at week 6.

Xyleborus californicus, a rare species (Furniss et al. 1992), apparently responds to stressed deciduous trees (Furniss et al. 1992). We trapped this species only at Savannah River Plant, where its highest catches were observed on week 6 (Fig. 2).

Our results showed that there was a clear arrival sequence among bark and ambrosia beetles, which generally confirmed past observations (Lindgren et al. 1982). Aggressive bark beetle species responded first to the billet volatiles, overlapping but generally followed by *D. terebrans* and *H. tenuis*. The ambrosia beetles *X. saxeseni*, *X. pubescens*, and *X. californicus* arrived later, during the 4th and 6th wk. Attractiveness of the billets to scolytid beetles declined noticeably after 8 wk of exposure (Fig. 1).

It is noteworthy to emphasize that the objectives of this experiment were to study the arrival sequence of scolytids without the interference of secondary attractants. If the pheromone component were present, we would expect some changes in the species composition and time of arrival because of the cross-attraction and repellent action by some of these semiochemicals (Smith et al. 1993).

The SPME technique was superior to the direct headspace gas injections in qualitative analyses of volatiles released by the pine billets. In the gas injections, only 11 compounds were identified, none of them oxygenated monoterpenes. Conversely, 35 volatiles were identified in samples collected with the SPME technique, including all volatiles detected in the gas injection.

In all experiments, a decline over time in the relative abundance of the hydrocarbon monoterpenes and 4-allylanisole was evident (Fig. 3), with the only exception being p-cymene (Fig. 4). Those results generally agree with published information. In contact with air, the compound α-pinene autoxidizes and produces the oxygenated monoterpenes *cis*-verbenol and *trans*-verbenol, and the latter is further autoxidized to

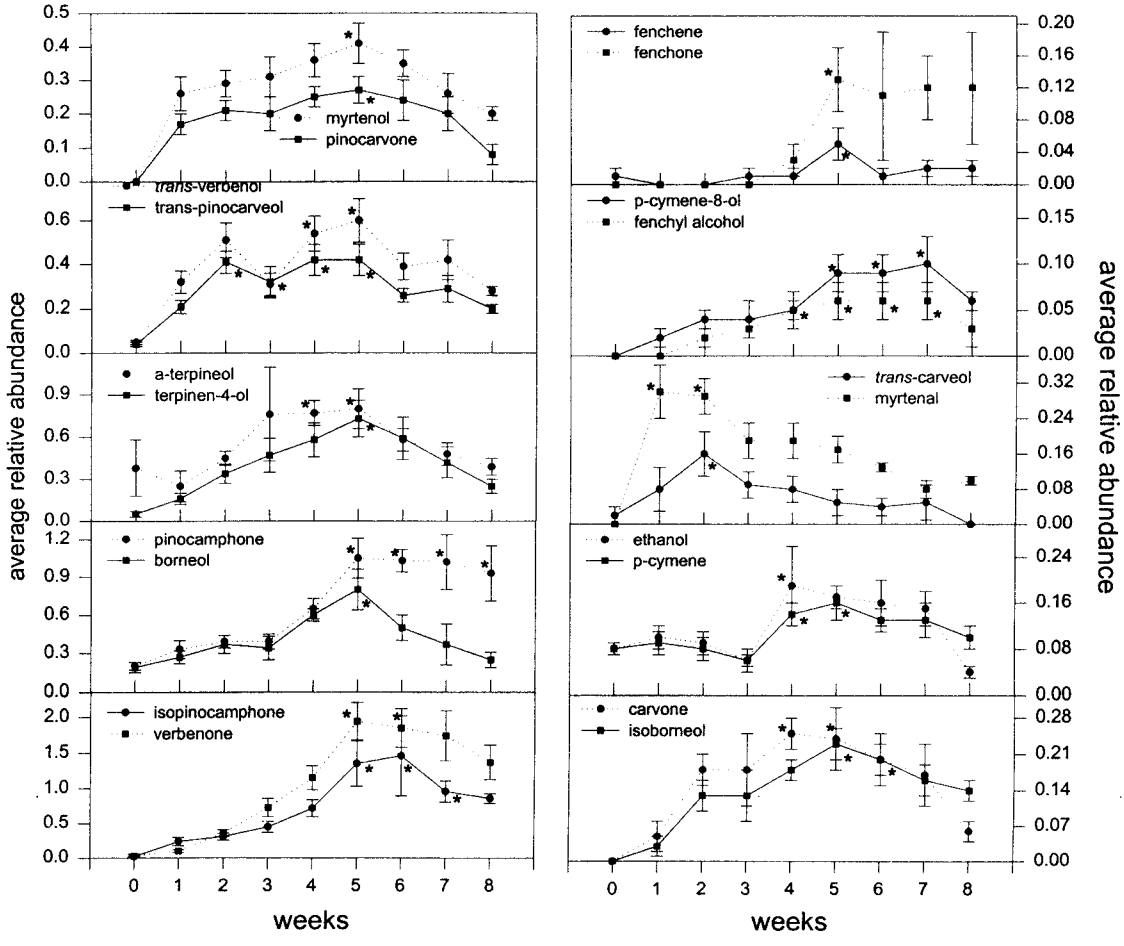

Fig. 4. Mean ± SE of the relative abundance of different loblolly pine billet oxygenated monoterpenes over time in the Savannah River Site Plant forest, Barnwell County, SC. Means of weeks followed by * are statistically higher than remaining weeks ($P < 0.05$) within each volatile.

verbenone (Hunt et al. 1989). Werner (1972a) found that α-pinene and β-pinene were lower in felled than in live trees, and Byers et al. (1989) reported a decline in hydrocarbon monoterpenes in felled trees over time. The relative abundance of the hydrocarbon monoterpenes dropped sharply in the first few weeks. This was the period when the billets were most attractive to bark beetle species.

As hydrocarbon monoterpene abundance decreased, the relative abundance of oxygenated monoterpene and ethanol increased. The exception was bornyl acetate (Fig. 3), which decreased in successive weeks. Overall, the abundance of oxygenated monoterpenes and ethanol peaked around weeks 4–6, then declined (Fig. 4). Scolytids or their associated microorganisms can produce oxygenated monoterpenes from host hydrocarbon monoterpenes (Leufvén and Birgersson 1987, Byers 1995). However, although we prevented scolytid attacks on our billets, fungal invasion (mainly carried by other insects that managed to reach the billets) was not deterred. Leufvén and Birgersson (1987) observed an increase in oxygenated monoterpenes in the phloem of pines after attack by *Ips typographus* L., and one of their hypotheses for the origin of these compounds was the autoxidation of hydrocarbon monoterpenes. Verbenone is known to be the final product of the autoxidation of α-pinene (Hunt et al. 1989), and this semiochemical increases in concentration as fallen trees begin to decay (Byers et al. 1989, Byers 1995).

During the period of highest oxygenated monoterpene release, we found the highest abundance of ethanol (Byers 1995), a semiochemical attractant for several ambrosia beetles (Samaniego and Gara 1970, Flechtmann et al. 1995), the lowest abundance of hydrocarbon monoterpenes, attractants for several bark beetles (Billings 1985), and the highest abundance of verbenone, a repellent for bark beetles (Miller et al. 1995). However, the phenyl propanoid, 4-allylanisole, a putative repellent for many bark beetles (Werner 1995), was found at its lowest concentration during this period.

It appears that the attractiveness of the billets to bark beetles in the first weeks was caused by high concentrations of attractive monoterpenes and low quantities of repellents. As the billets aged, the presence of bark beetle attractive semiochemicals decreased, and the abundance of compounds with repellent qualities increased. Aging billets then produced increasing amounts of chemicals attractive to ambrosia beetles. It appears ambrosia beetles are unaffected by the higher oxygenated monoterpene abundance, or they actually use some of them as cues for host location.

The black turpentine beetle is attracted to odors of pine volatiles (Payne et al. 1987, Phillips et al. 1989). Turpentine is very attractive, and ethanol acts as a synergist to this attractant (Phillips et al. 1988). Compounds that were strongly correlated with black turpentine beetle catches (p-cymene-8-ol, pinocamphone, and isopinocamphone) are all oxygenated monoterpenes. Although p-cymene-8-ol and pinocamphone were negatively correlated with catches, it is difficult to explain how a species that is attracted to billets during the period characterized by a predominance of hydrocarbon monoterpenes would be positively correlated with isopinocamphone, an oxygenated monoterpene. One explanation is that our results were spurious, with no biological significance.

Hylastes tenuis is attracted to odors from artificially injured *Pinus virginiana* Miller (Hines and Heikkenen 1977), and in our experiment catches of *H. tenuis* were correlated with the relative abundance of limonene and terpinen-4-ol. Limonene acts as a synergist of pheromones of some species of primary bark beetles (Werner 1972b) but has not been associated with the attraction of secondary species such as *H. tenuis.* The positive correlation between attraction of *H. tenuis* and the oxygenated monoterpene, terpinen-4-ol, also may have no biological significance.

Pine phloem odors attract *I. grandicollis* (Werner 1972a, Billings 1985, Fatzinger 1985), and it responds to a bait composed of α-pinene, limonene, camphene, myrcene, and ethanol (Chénier and Philogéne 1989). In our model, catches of *I. grandicollis* were negatively correlated with the abundance of ethanol and myrcene, and positively correlated with carvone. Carvone is a terpenoid with bactericidal and fungicidal activity (Naigre et al. 1996, Oosterhaven et al. 1996) and an antifeedant (Salom et al. 1994). There are no previous reports of positive responses to carvone by *I. grandicollis.* Ethanol and myrcene responses in our experiments differed from those reported in the literature and suggest that the correlation was an artifact.

Catches of *P. pulicarius* were negatively correlated to pinocarvone and positively correlated to pinocarveol and ethanol. Pinocarvone reduces catches of *Dendroctonus ponderosae* Hopkins when added to an attractive bait (Libbey et al. 1985), whereas ethanol is a general attractant to secondary bark beetles and ambrosia beetles alike (Chénier and Philogéne 1989, Byers 1995). There are no previous reports on the responses of *P. pulicarius.*

Many Xyleborini are attracted to ethanol (Flechtmann et al. 1995), and some also respond to turpentine (Fatzinger 1985) or a combination of both (Phillips et al. 1988). In our study, catches of *X. californicus* were positively correlated with p-cymene-8-ol and negatively correlated with myrtenal. Surprisingly, ethanol was not positively correlated with *X. californicus* catches.

Field tests with baits composed of artificially synthesized chemicals are necessary to ascertain the accuracy of the model in predicting beetle catches using the putative semiochemicals previously described for each scolytid species.

Acknowledgments

We thank James Hanula and Gary DeBarr (Forestry Sciences Laboratory, U.S. Forest Service, Athens, GA) for critical review of the manuscript; Catherine Teare-Ketter (Division of Biological Sciences, University of Georgia) for assistance in part of the statistical analyses; and the U.S. Forest Services at Chattahoochee National Forest, Savannah River Plant, and Whitehall Forest for the use of their sites.

References Cited

Bartelt, R. J. 1997. Calibration of a commercial solid-phase microextraction device for measuring headspace concentrations of organic volatiles. Anal. Chem. 69: 364–372.

Beaver, R. A. 1988. Biological studies on ambrosia beetles of the Seychelles (Col., Scolytidae and Platypodidae). Z. Angew. Entomol. 105: 62–73.

Billings, R. F. 1985. Southern pine bark beetles and associated insects: effects of rapidly- released host volatiles on response to aggregation pheromones. J. Appl. Entomol. 99: 483–491.

Birch, M. C., P. Svihra, T. D. Paine, and J. C. Miller. 1980. Influence of chemically mediated behavior on host tree colonization by four cohabiting species of bark beetles. J. Chem. Ecol. 6: 395–414.

Byers, J. A. 1989. Chemical ecology of bark beetles. Experientia 45: 271–283.

Byers, J. A. 1995. Host-tree chemistry affecting colonization in bark beetles, pp. 154–213. *In* R. T. Cardé and W. J. Bell [eds.], Chemical ecology of insects 2. Chapman & Hall, New York.

Byers, J. A., B. S. Lanne, and J. Löfqvist. 1989. Host tree unsuitability recognized by pine shoot beetles in flight. Experientia 45: 489–492.

Chénier, J.V.R., and B.J.R. Philogène. 1989. Field responses of certain forest Coleoptera to conifer monoterpenes and ethanol. J. Chem. Ecol. 15: 1729–1745.

Czerwiński, J., B. Zygmunt, and J. Namieśnik. 1996. Headspace solid phase microextraction for the GC-MS analysis of terpenoids in herb based formulations. Fresenius J. Anal. Chem. 356: 80–83.

Dixon, W. N., and T. L. Payne. 1979. Sequence of arrival and spatial distribution of entomophagous and associate insects on southern pine beetle-infested trees. Tex. Agric. Exp. Stn. Bull. MP-1432.

Dobie, J. 1978. Ambrosia beetles have expensive tastes. Can. For. Serv. Pac. For. Res. Centre Rep. BC-P-24.

Drooz, A. T. 1985. Insects of eastern forests. U.S. Dep. Agric. Misc. Publ. 1426.

Fatzinger, C. W. 1985. Attraction of the black turpentine beetle (Coleoptera: Scolytidae) and other forest Coleoptera to turpentine-baited traps. Environ. Entomol. 14: 768–775.

Flechtmann, C.A.H., and C. L. Gaspareto. 1997. A new trap for capturing Scolytidae (Coleoptera), based on primary attraction. Z. Angew. Entomol. 121: 357–359.

Flechtmann, C.A.H., H.T.Z. Couto, C. L. Gaspareto, and E. F. Berti. 1995. Scolytidae em Reflorestamento com Pinheiros Tropicais. IPEF, Piracicaba, Brazil.

Furniss, M. M., J. B. Johnson, R. L. Westcott, and T. R. Torgersen. 1992. List of Oregon Scolytidae (Coleoptera) and notes on new records. Great Basin Nat. 52: 373–378.

Godbee, J. F., Jr., and R. T. Franklin. 1976. Attraction, attack patterns and seasonal activity of the black turpentine beetle. Ann. Entomol. Soc. Am. 69: 653–655.

Golub, M. A., and I. Weatherston. 1984. Techniques for extracting and collecting sex pheromones from live insects and from artificial sources, pp. 223–285. *In* H. E. Hummel and T. A. Miller [eds.], Techniques in pheromone research. Springer, New York.

Hines, J. W., and H. J. Heikkenen. 1977. Beetles attracted to severed Virginia pine (*Pinus virginiana* Mill.). Environ. Entomol. 6: 123–127.

Hosking, G. P. 1969. *Xyleborus saxeseni.* Rep. For. Res. Inst. 1968: 63–65.

Hunt, D.W.A., J. H. Borden, B. S. Lindgren, and G. Gries. 1989. The role of autoxidation of α-pinene in the production of pheromones of *Dentroctonus ponderosae* (Coleoptera: Scolytidae). Can. J. For. Res. 19: 1275–1282.

Kelsey, R. G. 1996. Anerobic induced ethanol synthesis in the stems of greenhouse-grown conifer seedlings. Trees 10: 183–188.

Leufvén, A., and G. Birgersson. 1987. Quantitative variation of different monoterpenes around galleries of *Ips typographus* (Coleoptera: Scolytidae) attacking Norway spruce. Can. J. Bot. 65: 1038–1044.

Libbey, L. M., L. C. Ryker, and K. L. Yandell. 1985. Laboratory and field studies of volatiles released by *Dendroctonus ponderosae* Hopkins (Coleoptera, Scolytidae). J. Appl. Entomol. 100: 381–392.

Lindelöw, Å., B. Risberg, and K. Sjödin. 1992. Attraction during flight of scolytids and other bark- and wood-dwelling beetles to volatiles from fresh and stored spruce wood. Can. J. For. Res. 22: 224–228.

Lindgren, B. S., J. H. Borden, D. R. Gray, P. C. Lee, D. A. Palmer, and L. Chong. 1982. Evaluation of two trap log techniques for ambrosia beetles (Coleoptera: Scolytidae) in timber processing areas. J. Econ. Entomol. 75: 577–586.

Lindgren, B. S., and R. G. Fraser. 1994. Control of ambrosia beetle damage by mass trapping at a dryland log sorting area in British Columbia. For. Chron. 70: 159–163.

Liu, Y. B., and J. A. McLean. 1989. Field evaluation of responses of *Gnathotrichus sulcatus* and *G. retusus* (Coleoptera: Scolytidae) to semiochemicals. J. Econ. Entomol. 82: 1688–1690.

MacDonald, R. C., and T. W. Kimmerer. 1991. Ethanol in the stems of trees. Physiol. Plant. 82: 582–588.

Miller, D. R., J. H. Borden, and B. S. Lindgren. 1995. Verbenone: dose-dependent interruption of pheromone-based attraction of three sympatric species of pine bark beetles (Coleoptera: Scolytidae). Environ. Entomol. 24: 692–696.

Moeck, H. A. 1970. Ethanol as the primary attractant for the ambrosia beetle *Trypodendron lineatum* (Coleoptera: Scolytidae). Can. Entomol. 102: 985–995.

Naigre, R., P. Kalck, C. Roques, I. Roux, and G. Michel. 1996. Comparison of antimicrobial properties of monoterpenes and their carbonylated products. Planta Med. 62: 275–277.

Oosterhaven, K., A. C. Leitao, L.G.M. Gorris, and E. J. Smid. 1996. Comparative study on the action of S-(+)-carvone, *in situ,* on the potato storage fungi *Fusarium solani* var. *coeruleum* and *F. sulphureum.* J. Appl. Bacteriol. 80: 535–539.

Paine, T. D., K. F. Raffa, and T. C. Harington. 1997. Interactions among scolytid bark beetles, their associated fungi, and live host conifers. Annu. Rev. Entomol. 42: 179–206.

Payne, T. L., R. F. Billings, J. D. Delorme, N. A. Andryszak, J. Bartels, W. Francke, and J. P. Vité. 1987. Kairomonal-pheromonal system in the black turpentine beetle, *Dendroctonus terebrans* (Ol.). Z. Angew. Entomol. 103: 15–22.

Phillips, T. W., A. J. Wilkening, T. H. Atkinson, J. L. Nation, R. C. Wilkinson, and J. L. Foltz. 1988. Synergism of turpentine and ethanol as attractants for certain pine-infesting beetles (Coleoptera). Environ. Entomol. 17: 456–462.

Phillips, T. W., J. L. Nation, R. C. Wilkinson, and J. L. Foltz. 1989. Secondary attraction and field activity of beetle-produced volatiles in *Dendroctonus terebrans.* J. Chem. Ecol. 15: 1513–1533.

Salom, S. M., J. A. Carlson, B. N. Ang, D. M. Grosman, and E. R. Day. 1994. Laboratoy evaluation of biologically-based compounds as antifeedants for the pales weevil, *Hylobius pales* (Herbst) (Coleoptera: Curculionidae). J. Entomol. Sci. 29: 407–419.

Samaniego, A., and R. I. Gara. 1970. Estudios sobre la actividad de vuelo y selección de huéspedes por *Xyleborus* spp. (Coleóptera: Scolytidae y Platypodidae). Turrialba 20: 471–477.

SAS Institute. 1990a. SAS/STAT user's guide, vol. 1. SAS Institute, Cary, NC.

SAS Institute. 1990b. SAS/STAT user's guide, vol. 2. SAS Institute, Cary, NC.

Smith, M. T., S. M. Salom, and T. L. Payne. 1993. The southern pine bark beetle guild: an historical review of the research on the semochemical-based communication system of the five principal species. Va. Agric. Exp. Stn. Bull. 93–94.

Snyder, M. A., B. Fineschi, Y. B. Linhart, and R. H. Smith. 1996. Multivariate discrimination of host use by dwarf mistletoe *Arceuthobium vaginatum* subsp. *cryptopodum:* inter- and intraspecific comparisons. J. Chem. Ecol. 22: 295–305.

Thatcher, R. C., J. L. Searcy, J. E. Coster, and G. D. Hertel. 1980. The southern pine beetle. Pineville U.S. Dep. Agric. For. Serv. Tech. Bull. 1631.

Volz, H. A. 1988. Monoterpenes governing host selection in the bark beetles *Hylurgops palliatus* and *Tomicus piniperda.* Entomol. Exp. Appl. 47: 31–35.

Werner, R. A. 1972a. Aggregation behaviour of the beetle *Ips grandicollis* in response to host- produced attractants. J. Insect Physiol. 18: 423–437.

Werner, R. A. 1972b. Response of the beetle, *Ips grandicollis,* to combinations of host and insect produced attractants. J. Insect Physiol. 18: 1403–1412.

Werner, R. A. 1995. Toxicity and repellency of 4-allylanisole and monoterpenes from white spruce and tamarack to the spruce beetle and eastern larch beetle (Coleoptera: Scolytidae). Environ. Entomol. 24: 372–379.

Wood, S. L. 1982. The bark and ambrosia beetles of North and Central America (Coleoptera: Scolytidae): a taxonomic monograph. Great Basin Nat. Mem. 6: 1–1361.

Yang, X., and T. Peppard. 1994. Solid-phase microextraction for flavor analysis. J. Agric. Food Chem. 42: 1925–1930.

Zhang, Z., and J. Pawliszyn. 1993. Headspace solid-phase microextraction. Anal. Chem. 65: 1843–1852.

Received for publication 14 July 1998; accepted 16 December 1998.