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ATTRACTION OF BARK BEETLES, *Tomicus piniperda*, *Hylurgops palliatus*, AND *Trypodendron domesticum* AND OTHER INSECTS TO SHORT-CHAIN ALCOHOLS AND MONOTERPENES

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Abstract—Several Scandinavian forest insects, *Hylurgops palliatus*, *Tomicus piniperda*, and *Trypodendron domesticum* (Coleoptera: Scolytidae), *Rhizophagus ferrugineus* (Coleoptera: Rhizophagidae) and *Pollenia* spp. (Diptera: Calliphoridae) were attracted to window traps baited with ethanol and placed on Scots pine trees (*Pinus sylvestris*) in May–June, 1986. Release of ethanol at increasing relative rates of 0, 0.01, 0.1 and 1.0 (800 mg/day) from the window traps on trees in 1987 caused *H. palliatus*, *T. domesticum*, and *R. ferrugineus* to be increasingly attracted, while *T. piniperda* was equally attracted at both 0.1 and 1.0 rates. The attraction of *T. piniperda* to ethanol was weak compared to attraction to a monoterpene mix, (±)-α-pinene, (+)-3-carene, terpinolene. The terpene mix plus ethanol was significantly more attractive to *H. palliatus* than ethanol alone, but terpenes significantly reduced the attraction of *T. domesticum* to ethanol. Baiting of pipe traps with a series of short-chain alcohols (methanol to hexanol) each alone showed that ethanol was greatly preferred by *H. palliatus*, *T. domesticum*, and *R. ferrugineus* over alcohols of one more or one less carbon, while longer-chain alcohols were not attractive. However, *Glischrochilus hortensis* (Col.: Nitidulidae) was attracted only to propanol. A series of 10-fold increasing release rates of ethanol (0.0001–1.0, where 1.0 = 800 mg/day) with either a "low" or "high" release of the terpene mix had various effects on the sexes during their attraction to pipe traps and subsequent entering of holes. Release of (−)-verbenone at 0.25 mg/day had no significant effect on *H. palliatus* or *R. ferrugineus* attraction to ethanol, but the response of *T. domesticum* to ethanol was reduced. Several theories on olfactory mechanisms of host selection by *T. piniperda* are integrated and placed in ecological perspective.

Key Words—Host-plant selection, Coleoptera, Scolytidae, Nitidulidae, Rhi-

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zophagidae, Calliphoridae, Diptera, semiochemical, monoterpenes, methanol, ethanol, propanol, terpinolene, α-pinene, 3-carene, verbenone.

INTRODUCTION

Bark beetles and associated beetles feeding on or living in trees must locate a suitable host from among the relatively few scattered widely in the forest during their dispersal from brood or hibernation sites. The host tree is restricted usually to one or a few species and in most cases the insects seek weakened, less-resistant trees, or trees that are in the initial stages of decay. Thus, it is expected that species have evolved behavioral responses to volatile host-plant chemicals that indicate the presence of a suitable host in which reproduction can occur. It is well known that ethanol, probably released by microorganisms in decaying woody tissue (Graham, 1968; Moeck, 1970; Cade et al., 1970) and stressed plants (Kimmerer and Kozlowski, 1982), is attractive to a wide variety of species of forest Coleoptera (Moeck, 1970, 1981; Kerck, 1972; Roling and Kearby, 1975; Magema et al., 1982; Montgomery and Wargo, 1983; Kohnle, 1985; Dunn et al., 1986; Klimetzek et al., 1986; Schroeder 1987, 1988; Schroeder and Eidmann, 1987; Witcosky et al., 1987; Atkinson et al., 1988; Phillips et al., 1988; Volz, 1988; Chénier and Philogène, 1989; Schroeder and Lindelöw, 1989). Similarly, various tree monoterpenes (e.g., α-pinene, myrcene, terpinolene, β-pinene) and turpentine are attractive to a large number of species (Fatzinger, 1985; Byers et al., 1985; Witcosky et al., 1987; Phillips et al., 1988; Schroeder, 1988; Chénier and Philogène, 1989; Schroeder and Lindelöw, 1989; Miller and Borden, 1990; Phillips, 1990). Synergism between ethanol and various monoterpenes (or turpentine) has also been widely reported (Nijholt and Schönherr, 1976; Kohnle, 1985; Tilles et al., 1986; Vité et al., 1986; Phillips et al., 1988; Volz, 1988; Schroeder, 1988; Chénier and Philogène, 1989; Schroeder and Lindelöw, 1989; Phillips, 1990). These compounds are not only important for primary attraction to plants but also may play a role in enhancing the bark beetles' response to aggregation pheromone (Bedard et al., 1969; Pitman et al., 1975; McLean and Borden, 1977; Borden et al., 1981; Paiva and Kiesel, 1985; Byers et al., 1988; Miller and Borden, 1990).

Bark beetle species that aggressively attack and kill living trees have been shown invariably to possess an aggregation pheromone, usually of two or more components, and are weakly, if at all, attracted by host volatiles (Byers, 1989). However, so-called "secondary" bark beetle species, those that colonize dying or decaying trees, less often use an aggregation pheromone, but generally are strongly attracted to host volatiles and ethanol (Kohnle, 1985; Klimetzek et al., 1986; Schroeder, 1988; Schroeder and Lindelöw, 1989). The pine shoot beetle, *Tomicus piniperda* (L.) (Scolytidae), sometimes kills living Scots pine (*Pinus*

sylvestris L.), but more often prefers recently fallen (still living) trees (Långström, 1984). Byers et al. (1985) used the subtractive-combination bioassay and fractionation method (Byers, 1992a) to rigorously identify the semiochemicals responsible for aggregation of *T. piniperda*. A combination of (−)-(*S*)-α-pinene, (+)-(*R*)-α-pinene, (+)-3-carene, and terpinolene, or each alone, was effective in attracting both sexes. During the isolation study, designed for detection of synergistic pheromone components, no evidence was found for beetle-produced compounds being attractive, in contrast to most bark beetles that aggregate en masse on hosts (Byers, 1989).

Following the paper of Byers et al. (1985), Vité et al. (1986) reported that ethanol plus two of the above monoterpenes (α-pinene and terpinolene) were about eight times more attractive than these terpenes to *T. piniperda*. Unfortunately, the release rates of neither the monoterpenes nor ethanol was reported. The activity of ethanol alone was also not determined. Earlier, Magema et al. (1982) had suggested ethanol is attractive to *T. piniperda*, although statistical evidence was lacking (and no release rates were given). However, the evidence of Vité et al. (1986) that ethanol could play a role in aggregation of *T. piniperda* is not in conflict with Byers et al. (1985), since the latter study used Porapak Q to collect organic volatiles, and this adsorbent is inefficient with small molecules like ethanol. In apparent contrast to the ethanol–monoterpene synergism reported by Vité et al. (1986), Klimetzek et al. (1986) tested different release rates of ethanol (24–125 mg/day) with an unreported release rate of α-pinene and terpinolene and found that the higher releases of ethanol inhibited attraction of *T. piniperda*. However, a control with ethanol alone, or terpenes alone, was not reported. Two other studies, also in seeming contrast to Vité et al. (1986), showed that ethanol at higher rates inhibited attraction of *T. piniperda* to α-pinene (Schroeder, 1988; Schroeder and Lindelöw, 1989).

Vité et al. (1986) proposed that ethanol in combination with monoterpenes are used by *T. piniperda* to locate diseased, and therefore susceptible host trees. Since chemical release rates in their study were not measured, and it is not known how much ethanol is released from diseased trees, this hypothesis remained in doubt. A way to probe the question is to assume that monoterpene releases from healthy trees are similar to diseased trees, but that ethanol releases are higher from the latter. Then, by placing ethanol on healthy trees, these trees will appear diseased and should attract more *T. piniperda*.

The objectives of the present study concerning *T. piniperda* were to determine: (1) whether ethanol is attractive when placed on standing Scots pine; (2) the relative attractiveness of ethanol, a more complete blend of monoterpenes alone, or a combination of monoterpenes with ethanol; and (3) the relative attractancy of various short-chain primary alcohols (C_1–C_6) and ethylene glycol. The attraction of other scolytids and associated fauna was also monitored. In addition, the attraction of *Hylurgops palliatus* (Gyll.) and *Trypodendron domes-*

ticum (L.), among other beetles, to ethanol alone, (−)-(*S*)-verbenone alone, or both in combination was tested. Verbenone also was tested with ethanol since the former compound is released as Scots pine logs age and has been shown to inhibit the attraction of *T. piniperda* to host volatiles (Byers et al., 1989).

METHODS AND MATERIALS

Both the window/barrier trap type (Byers et al., 1989) and the pipe trap with funnel (Bakke et al., 1983; Byers et al., 1988) were used for testing semiochemicals. The pipe trap can reveal behavioral differences between the sexes as they orient to the attractant source since the trap collects beetles in two bottles (wire screen bottoms), as they bounce off the pipe barrier into a large 33-cm-diameter funnel, and as they enter any of the 900 holes in the pipe.

Window traps of transparent plastic (17 × 35 cm high) with funnel and collection bottle were wired to Scots pine trees (about 25–35 cm DBH) at 2 m height (all experiments in a pine plantation, Sjöbo, southern Sweden). The traps on trees were spaced 90 m apart in two parallel lines 90 m apart. Ethanol was released from two open, plastic-vial dispensers per trap (total 800 mg/day) from 13 traps while 13 traps were unbaited controls. Collections of insects were done five times. The plastic vial dispensers (730 type, Kartell Inc., Italy) were made of polyethylene (0.6 cm diam. × 3 cm). Treatments were assigned at random and remained stationary during the test (April 29–May 12, 1986). A second test in 1987 (April 24–May 6) used the same traps and general methods; 11 traps/tree each were baited with either 0 (unbaited), 0.01, 0.1, or 1.0 ethanol release rates (1.0 equivalent to 800 mg/day). The diffusion-dilution method was used (Byers, 1988) to dilute ethanol with water based on mole percentages to obtain the desired rates.

A comparison of the relative attraction rates of ethanol alone (800 mg/day), the same dose plus a monoterpene mix, and the monoterpene mix alone was done using pipe traps with funnel (April 29–May 12, 1986). The monoterpene mix consisted of several monoterpenes and release rates: terpinolene (>97.3% GLC, Carl Roth KG) at 2.5 mg/day, (+)-3-carene (> 99%, $[\alpha]_D^{20} = 17°$) at 6 mg/day, and (−)-α-pinene (99%, $[\alpha]_{546}^{20} = 50°$) and (+)-α-pinene (99.5%, $[\alpha]_{546}^{20} = 57°$) each at 14 mg/day (Fluka AG). Each of the monoterpenes was placed in two plastic vial dispensers with 200 μl neat compound each, and all were placed inside the pipe. The three traps per treatments were placed 10 m apart in a line and were replicated in three areas on four dates for a total of 12 replicates. Baits were randomized after each test day.

In 1987 (April 23–May 11), two release rates of the above monoterpene mix, one at the same or "high" release rate and a "low" rate of about 3.3% that of the high rate (based on 3-cm-long tubes with an opening 3.3% that of

the dispenser above), were tested alone and in combination with a series of 10-fold increased release rates of ethanol: 0.0001, 0.001, 0.01, 0.1, and 1.0. Diffusion–dilution was again used to dilute the ethanol appropriately with water. Twelve pipe traps with funnel, six for each series, were placed in one line with traps 10 m apart. Treatments were randomized after each collection (once or twice a day) for a total of 15 replicates. In another test, eight pipe traps were baited with a series of increasing length primary alcohols (methanol, ethanol, propanol, butanol, pentanol, and hexanol) and ethylene glycol plus an unbaited trap. Exponential regression was used on vapor pressure statistics (Weast, 1971) for the primary alcohols to predict the tube opening diameters necessary to approximate the same release as the standard 1.0 ethanol rate (800 mg/day). Thus, methanol was released from one dispenser, ethanol from two, propanol from three, and butanol from seven, pentanol from 20, and hexanol from 35. For ethylene glycol, a glass container with an opening about 137 times that for methanol was used to obtain an equivalent rate of release.

The effects of verbenone on attraction of insects to ethanol was tested in 1987 (April 23–May 11) in two areas with tree traps each spaced 10 m apart in a line. The trap consisted of two window traps placed back-to-back at 1.2 m height on a metal pole. Ethanol was released at 800 mg/day from two of the traps, one of these also had two dispensers of (−)-verbenone releasing 0.25 mg/day (>99%, $[\alpha]_D^{20} = -246°$, 99.2% ee, Bedoukian). The third trap released only (−)-verbenone.

RESULTS

Window Traps Baited with Ethanol on Scots Pine Trees. Three species of bark beetle, *Tomicus piniperda*, *Hylurgops palliatus*, and *Trypodendron domesticum* were caught in the ethanol-baited window traps placed on the Scots pine trees (Table 1). The beetle *Rhizophagus ferrugineus* Payk. (Coleoptera: Rhizophagidae) and several cluster flies, *Pollenia* spp. (Diptera: Calliphoridae), were also caught only on the ethanol baited traps. Catches were relatively low in 1986 and not all of the 65 trap replicates caught insects, so use of conventional statistical tests for comparing catches was inappropriate. However, a chi-square test comparing the proportions of traps catching to those that caught none was used to compare the baits within a species between release rates. Using this method, all species above were significantly attracted to ethanol-baited traps on trees (Table 1). In 1987 a similar experiment had window traps on trees baited with either 0, 0.01, 0.1 or 1.0 ethanol equivalent (800 mg/day), and again the three bark beetle species and *R. ferrugineus* were principally caught on higher release rates of ethanol (Figure 1, Table 2). *H. palliatus* and *T. domesticum* were significantly attracted to relative rates of 0.01 ethanol and higher on the

TABLE 1. CATCH OF FOREST INSECTS ATTRACTED TO WINDOW TRAPS BAITED WITH ETHANOL (800 mg/day) OR UUBAITED AT BREAST HEIGHT ON SCOTS PINE TREES (APRIL 28–MAY 12, 1986)

Species[a]	Males	Females	Total	Percentage of traps catching[b]		*P* value chi square
				Baited traps	Unbaited traps	
H. palliatus	27	21	48	37	1.5	<0.001
T. domesticum	26	24	50	55	0	<0.001
T. piniperda	3	2	5	6	0	0.04
R. ferrugineus	—	—	82	46	0	<0.001
Pollenia spp.	14	4	18	20	0	<0.001

[a] *Hylurgops palliatus*, *Trypodendron domesticum*, *Tomicus piniperda*, *Rhizophagus ferrugineus*, and *Pollenia* spp. (see text).
[b] N = 65 trap replicates for each treatment.

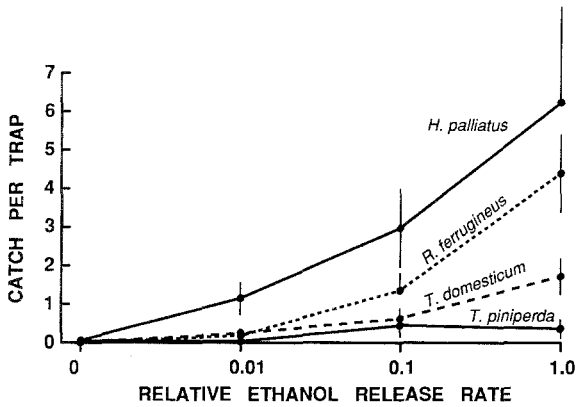

FIG. 1. Catch of *Hylurgops palliatus*, *Trypodendron domesticum*, *Tomicus piniperda*, and *Rhizophagus ferrugineus* attracted to window traps releasing different relative rates of ethanol at breast height on Scots pine trees (1.0 ethanol rate equivalent to 800 mg/day; April 24–May 6, 1987, Sjöbo, Sweden). Bars represent 95% confidence intervals (N = 66).

trees, while *T. piniperda* was not significantly attracted at 0.01 but appeared to be attracted at the 0.1 and 1.0 rates (Table 1), although attraction at the 1.0 rate was not increased as in the other three species (Figure 1, Table 1). In 1987, 10 male flies (*Pollenia* spp.) were caught only in the ethanol baited traps (one in 0.01, three in 0.1, and six in 1.0 baits). Nine of these individuals were separated to species by genitalia differences and were composed of one *P. amentaria*

TABLE 2. CATCH OF VARIOUS FOREST COLEOPTERA ATTRACTED TO WINDOW TRAPS BAITED WITH DIFFERENT RELATIVE RATES OF ETHANOL (1.0 RATE EQUIVALENT TO 800 mg/day) AT BREAST HEIGHT ON SCOTS PINE TREES (APRIL 24–MAY 6, 1987, SJÖBI, SWEDEN)

Species[a]	Catch				Catch range	Percent of traps catching[b]
	Male	Female	Male proportion	95% BCL		
Blanks						
H. palliatus	1	3	0.25	0.05–0.70	0–2	4.5
T. domesticum	0	0				0
T. piniperda	2	1	0.67	0.21–0.94	0–1	4.5
R. ferrugineus	0	0				0
0.01 Etnanol						
H. palliatus	35	40	0.47	0.36–0.58	0–6	51.5a
T. domesticum	9	7	0.56	0.33–0.77	0–1	24.2a
T. piniperda	0	2			0–1	3
R. ferrugineus	(6)[c]	(6)			0–2	12.1a
0.1 Ethanol						
H. palliatus	102	94	0.52	0.45–0.59	0–23	65.2a
T. domesticum	26	26	0.50	0.37–0.63	0–5	47ab
T. piniperda	8	20	0.29	0.15–0.47	0–7	19.7ab
R. ferrugineus	(44.5)[c]	(44.5)			0–9	54.5ab
1.0 Ethanol						
H. palliatus	218	193	0.53	0.48–0.58	0–61	83.3abc
T. domesticum	44	61	0.42	0.33–0.51	0–9	75.8abc
T. piniperda	13	11	0.54	0.35–0.72	0–4	15.2ab
R. ferrugineus	(145)[c]	(145)			0–15	84.8abc

[a] *Hylurgops palliatus*, *Trypodendron domesticum*, *Tomicus piniperda*, and *Rhizophagus ferrugineus*.
[b] $N = 66$ trap replicates for each treatment; letters indicate proportion of traps catching were significantly different ($P < 0.05$) from corresponding treatments, where a = blanks, b = 0.01, c = 0.1 ethanol.
[c] Assumes equal sex ratio.

(Scop.), two *P. rudis* (Fbr.), four *P. angustigena* Wainwr. and two *P. labialis* R.-D.

Attraction of Forest Beetles to a Series of Primary Alcohols. In the series of increasing length primary alcohols, only methanol, ethanol, and propanol caught insects (Figure 2). There appeared to be a subtle shift in the response spectrum of the species, in which *H. palliatus* preferred ethanol but sometimes was attracted to propanol, *T. domesticum* restricted its response to ethanol, *R. ferrugineus* also preferred ethanol but would orient to methanol, while *Glis-*

chrochilus hortensis Fourcroy was caught only on propanol (Figure 2). No insects were caught on butanol, pentanol, hexanol, ethylene glycol, or in the unbaited pipe trap.

Attraction of Forest Insects to Monoterpenes and Ethanol. The catches of the above beetle species and others on pipe traps baited with either ethanol (800 mg/day), monoterpenes mix (see methods), or both are shown in Table 3.

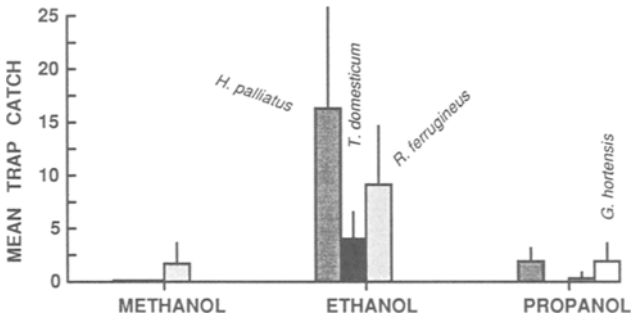

FIG. 2. Catch of *Hylurgops palliatus*, *Trypodendron domesticum*, *Rhizophagus ferrugineus*, and *Glischrochilus hortensis* attracted to pipe traps with funnel releasing either methanol, ethanol, or propanol at similar rates (about 800 mg/day; April 23–30, 1987, Sjöbo, Sweden). Bars represent 95% confidence limits ($N = 9$). Traps with either butanol, pentanol, hexanol, ethylene glycol, or unbaited caught no insects.

TABLE 3. CATCHES (MALE–FEMALE) OF VARIOUS FOREST COLEOPTERA ATTRACTED TO PIPE TRAPS WITH FUNNEL AND BAITED WITH EITHER ETHANOL (800 mg/day), MONOTERPENES (SEE TEXT), OR BOTH (APRIL 29–MAY 12, 1986, SJÖBO, SWEDEN)

	Total catch (male:female)					
	Ethanol		Terpenes		Ethanol + terpenes	
Species[a]	Entering pipe	Funnel	Entering pipe	Funnel	Entering pipe	Funnel
H. palliatus	0:2	3:7	0	0	24:19	21:22
T. domesticum	3:4	16:14	0	0	0:1	1:1
T. piniperda	0	0	1:1	17:21	2:2	26:16
R. ferrugineus	0	9	0	1	10	5
G. quadripunctatus	0	6	0	0	0	0
H. ater	0	1:0	0	0	0	5:2
H. abietis	0	0	0	0	0	4

[a] *Hylurgops palliatus*, *Trypodendron domesticum*, *Tomicus piniperda*, *Rhizophagus ferrugineus*, *Glischrochilus quadripunctatus*, *Hylastes ater*, and *Hylobius abietis*.

Wilcoxon signed-rank tests indicated a synergism of ethanol and monoterpenes in attraction of *H. palliatus* ($P < 0.01$, $N = 10$). The attraction of *T. domesticum* to ethanol was inhibited by the monoterpenes ($P < 0.001$, $N = 12$). *T. piniperda* was not attracted to ethanol but was caught on the terpene baits ($P < 0.01$, $N = 10$).

A second test with pipe traps in 1987 attempted to determine the effect of increasing release rates of ethanol combined with two release rates of the monoterpene mix, either a "high" rate or a "low" rate (3.3% of the high rate). At the higher monoterpene release rate, the attraction of *T. piniperda* was apparently unaffected by increasing release rates of ethanol over the ranges tested (Figure 3A). However, at the lower monoterpene release rate, the attraction of *T. piniperda* increased when ethanol rates increased from 0.01 to 1.0 (Figure 3A, the 1.0 rate was significantly different from the 0.01 rate, Wilcoxon test,

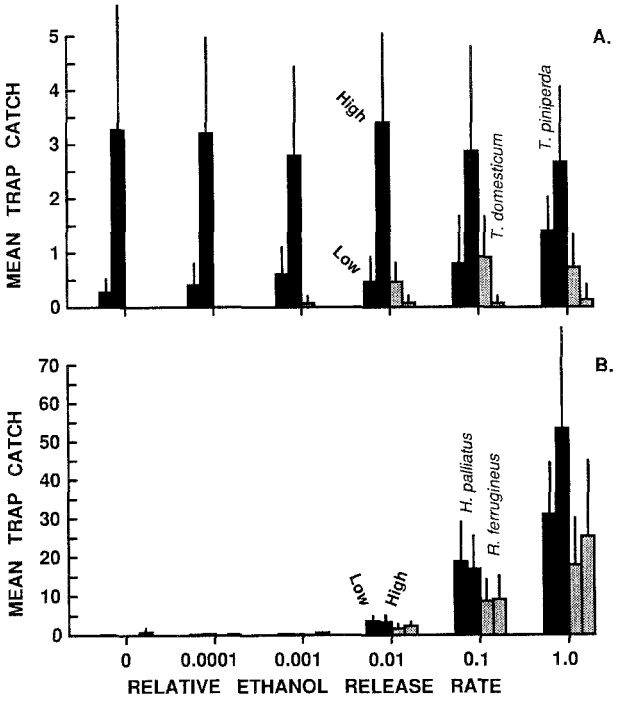

FIG. 3. (A) Catch of *Tomicus piniperda* and *Trypodendron domesticum* attracted to pipe traps with funnel releasing monoterpenes [terpinolene, (+)-3-carene, and (+)- and (−)-α-pinene] at either a "low" or "high" rate (see text) with various relative rates of ethanol (1.0 dose equivalent to 800 mg/day). (B) Catch of *Hylurgops palliatus* and *Rhizophagus ferrugineus* attracted to the same pipe traps (April 23–30, 1987, Sjöbo, Sweden). Bars represent 95% confidence limits ($N = 15$).

$N = 12$, $P < 0.05$). *T. domesticum* response increased with ethanol rates from 0.001 to 1.0 at the low monoterpene rate but remained low at the high monoterpene rate (Figure 3A), consistent with the inhibition by monoterpenes in earlier tests (Table 3). The attraction of *H. palliatus* and *R. ferrugineus* increased with ethanol rates from 0.01 to 1.0 at both the low and high monoterpene releases (Figure 3B). Although not significant, the higher rate of monoterpenes caught more *H. palliatus* at the highest ethanol release.

In the above test, beetles were collected in the outer large funnel or after they entered one of the 900 holes in the pipe. The percentage of *R. ferrugineus* entering holes was about twice as much as for *H. palliatus* at higher ethanol release rates regardless of monoterpene rate (Figure 4A). However, at the high monoterpene rate, both species increased their entering of holes as the ethanol rate was increased, but not at the low monoterpene rate (Figure 4A). At the

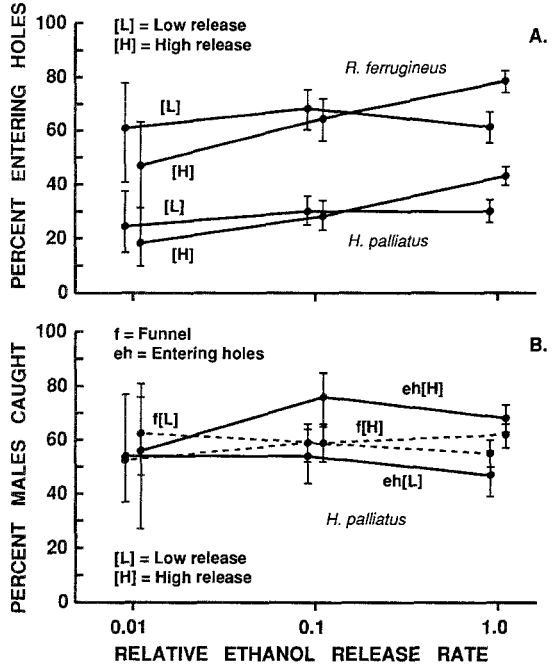

FIG. 4. (A) Percentage of *Hylurgops palliatus* and *Rhizophagus ferrugineus* entering holes in pipe traps with funnels that released monoterpenes [terpinolene, (+)-3-carene, and (+)- and (−)-α-pinene] at either "low" or "high" rates (see text) with various relative rates of ethanol (1.0 dose equivalent to 800 mg/day). (B) Male percentages of *Hylurgops palliatus* caught in the funnels or caught after entering holes in pipe traps as in Figure 4A (April 23–30, 1987, Sjöbo, Sweden). Bars with brackets represent 95% binomial confidence intervals for proportions.

higher ethanol rates (0.1 and 1.0) with monoterpenes, the percentage of males of *H. palliatus* that entered holes was significantly higher at the high monoterpene rate than at the low monoterpene rate (Figure 4B).

Effect of (−)-Verbenone on Attraction of Beetles to Ethanol. Window traps (back-to-back) baited with ethanol caught, as expected, *H. palliatus*, *T. domesticum*, and *R. ferrugineus* (Table 4). *T. piniperda* was not caught, consistent with its nonresponse to ethanol baits in Table 3. The addition of (−)-verbenone to ethanol did not decrease the attraction of *H. palliatus* but the response of *T. domesticum* was significantly reduced (Table 4). Fourteen *Rhinosimus planirostris* Fbr. (Coleoptera: Salpingidae) were caught on baits with ethanol (compared to none on verbenone). The pollen beetle, *Meligethes aeneus* Fbr.

TABLE 4. CATCH OF VARIOUS FOREST COLEOPTERA ATTRACTED TO WINDOW TRAPS (BACK-TO-BACK) BAITED WITH ETHANOL (800 mg/day), (−)-VERBENONE (0.25 mg/day), OR BOTH (APRIL 23–MAY 11, 1987, SJÖBO, SWEDEN)

Species[a]	Catch					Percent of traps catching[b]
	Male	Female	Male proportion	95% BCL	Catch range	
Ethanol						
H. palliatus	46	33	0.58	0.47–0.68	0–9	90
T. domesticum	24	26	0.48	0.35–0.61	0–6	85
R. ferrugineus	(70)[c]	(70)			0–23	90
M. aeneus	(1)[c]	(1)			0–1	10
G. quadripunctatus	(3)[c]	(3)			0–3	20
Ethanol +(−)-verbenone						
H. palliatus	64	48	0.57	0.48–0.66	0–22	85
T. domesticum	14	10	0.58	0.39–0.76	0–3[d]	70
R. ferrugineus	(103.5)[c]	(103.5)			0–38	90
M. aeneus	(11)[c]	(11)			0–4[d]	40
G. quadripunctatus	(5.5)[c]	(5.5)			0–3	45
(−)-Verbenone						
H. palliatus	1	2	0.33	0.06–0.79	0–1	15
T. domesticum	0	0			0	0
R. ferrugineus	(1)[c]	(1)			0–1	10
M. aeneus	(5.5)[c]	(5.5)			0–3	20
G. quadripunctatus	0	0			0	0

[a] *Hylurgops palliatus*, *Trypodendron domesticum*, *Rhizophagus ferrugineus*, *Meligethes aeneus*, and *Glischrochilus quadripunctatus*.
[b] $N = 20$ trap replicates for each treatment.
[c] Assumes equal sex ratio.
[d] Wilcoxon signed-rank tests indicated catch was different from that on ethanol alone ($P < 0.05$).

(Coleoptera: Nitidulidae), an important pest of oilseed rape (*Brassica napus*) was attracted to baits with verbenone (Table 4). No other insects were attracted to verbenone.

DISCUSSION

Primary alcohols other than ethanol have not been reported as being attractive to scolytids. However, only a few studies have tested methanol (Moeck, 1970; Montgomery and Wargo, 1983), while longer-chain alcohols were not investigated. It might be considered surprising that methanol (wood alcohol) had little activity (Figure 2). The fact that ethanol is a common by-product of glycolysis while methanol is not probably explains the evolution of the use of ethanol by forest insects. Moeck (1970) found methanol to be a minor constituent and ethanol a major constituent of extracts from Douglas-fir sapwood attractive to *Trypodendron lineatum*. Although *Tomicus piniperda* was not attracted by ethanol alone, the beetle was attracted when ethanol was placed on trees (Table 1, Figure 1) or combined with monoterpenes (Figure 3). Schroeder and Eidmann (1987) baited Scots pine trees with ethanol (1800 mg/day) and induced attacks by *T. piniperda*. Electroantennogram (EAG) responses of *T. piniperda* to a series of straight-chain alcohols indicated that the antennae respond increasingly with longer chain length, up to a maximum between pentanol and heptanol and then decrease (Lanne et al., 1987). The response spectrum can be due in part to differences in volatility. Thus, although ethanol plays a role in host selection (discussed subsequently), the EAG for ethanol is lower than for longer-chain alcohols (which probably are not involved in behavior). The attraction of the occasional crop pest *Glischrochilus hortensis* (Nitidulidae) (Alford, 1976) to propanol (Figure 2) is unusual since few insects are attracted to propanol. For example, in addition to the report here, only two nitidulid species in the genus *Carpophilus* are reported to be attracted to propanol in the Coleoptera (Lin and Phelan, 1991; Dowd and Bartelt, 1991).

Verbenone inhibited the response of *Trypodendron domesticum* but not *Hylurgops palliatus* to ethanol (Table 4). Response to ethanol by *T. domesticum* was also inhibited by the monoterpene mix, (±)-α-pinene, (+)-3-carene, and terpinolene, while the response of *H. palliatus* was enhanced (Table 3). α-Pinene has been shown earlier to inhibit *T. domesticum* response to an attractive bait of ethanol plus lineatin (Paiva and Kiesel, 1985), and Norway spruce resin or α-pinene has been shown to enhance response of *H. palliatus* to ethanol (Kohnle, 1985; Schroeder and Lindelöw, 1989). Verbenone has been shown to be increasingly released from aging Scots pine logs (Byers et al., 1989). *H. palliatus* is a "secondary" colonizing species and prefers moribund trees, hence the attraction to ethanol and insensitivity to verbenone. *T. domesticum* does not

feed in Scots pine but colonizes deciduous trees (in the study area: *Fagus sylvatica*, *Quercus* spp. *Betula* spp.) and is known to be attracted to ethanol (Magema et al., 1982; Paiva and Kiesel, 1985). Thus, conifer monoterpenes and verbenone (from decaying conifers) that are repellent would provide a mechanism for avoiding unsuitable colonization areas.

Verbenone is found in hindguts of the important pest bark beetles of the United States, *Dendroctonus frontalis* and *D. brevicomis* (Renwick and Vité, 1968), and the compound inhibited response of both beetles to their pheromone (Renwick and Vité, 1969, 1970). Verbenone from *D. brevicomis* was later shown to inhibit aggregation response of *Ips paraconfusus* to natural and synthetic pheromone (Byers and Wood, 1980), and verbenone inhibited *I. typographus* response to synthetic pheromone components (Bakke, 1981). A third genus of bark beetles was added to the list when *T. piniperda* response to the monoterpene mix above was inhibited (Byers et al., 1989). This led Byers (1989) to speculate that verbenone, as a consistent signal of microbial activity in decaying hosts, would be used by bark beetles earlier in evolution as a kairomone to avoid less suitable hosts and then subsequently serve additionally as a pheromone to reduce intraspecific competition and/or as an allomone to reduce interspecific competition. Verbenone production in beetles would coevolve in several species since the same chemical could serve as the signal for all three types of beneficial information. Recently, verbenone was found to inhibit the aggregation pheromone response of another important pest bark beetle of Europe, *Pityogenes chalcographus* (Byers, 1992b).

The attraction of *H. palliatus*, *T. domesticum*, *Glischrochilus quadripunctatus* L., and *Rhizophagus ferrugineus* to ethanol alone, with monoterpenes, and on trees (Tables 1–4, Figures 1–3) is consistent with earlier reports (Moeck, 1970; Nijholt and Schönherr, 1976; Magema et al., 1982; Kohnle, 1985; Paiva and Kiesel, 1985; Klimetzek et al., 1986; Schroeder, 1988; Volz, 1988; Schroeder and Lindelöw, 1989). The attraction of the cluster fly, *Pollenia rudis* (and related species above, Table 1), to ethanol was unexpected since this fly parasitizes earthworms (Thomson, 1973). However, it has been caught at baits with meat (Steinborn, 1981), where ethanol was probably released due to fermentation. Both sexes of *Pollenia* species may respond to ethanol, indicating food sources, but more males may have been caught due to their more extensive foraging patterns (typical of flies in Muscidae and Calliphoridae). Only one other report has proven ethanol, from fermenting sugar, attractive to pest flies in the genera *Musca*, *Muscina*, and *Fannia* (Hwang et al., 1978).

An explanation for the higher percentage of both *H. palliatus* and *R. ferrugineus* entering the holes in the pipe trap at the higher release rate of monoterpenes with the highest ethanol release is that the ratio of monoterpenes to ethanol may be closer to the natural ratio and indicates an appropriate host (Figure 4A). Host-tree compounds, monoterpenes and ethanol, elicited increased

entering rates of bark beetles *T. lineatum* and *P. chalcographus* into pipe traps baited with aggregation pheromone (Vité and Bakke, 1979; Bakke, 1983; Byers et al., 1988). The relatively large differences between the species in entering holes may not be due only to behavioral differences, but also to the fact that *H. palliatus* is easier to catch in the funnels than *R. ferrugineus*. The differences between the sexes of *H. palliatus* in entering holes at the high monoterpene release and higher ethanol releases (Figure 4B) are difficult to explain without more experiments and a deeper understanding of the biology.

The main purpose of the present experiments was to investigate the role of ethanol, in conjunction with monoterpenes, in the location of suitable hosts by *T. piniperda*. Byers et al. (1985) quantified the release rates of α-pinene, terpinolene, and 3-carene from a freshly cut log of Scots pine (28 cm $\times$ 13 cm diam.) and found them each to be about 15 mg/day (terpinolene somewhat less). Release of these amounts in the field competed favorably with a host log in attracting *T. piniperda*. Byers et al. (1985) theorized that since healthy trees were not expected to release appreciable amounts of these monoterpenes compared to broken tops and storm-felled trees where oleoresin wounds are numerous, the aggregation response to monoterpenes functioned in the beetle's recognition of both host species (other trees have less monoterpenes) and host susceptibility to colonization (wounded trees have less capacity to produce more oleoresin for defense).

Vité et al. (1986) presented evidence that ethanol enhanced the attraction of *T. piniperda* to α-pinene and terpinolene by about eight times, but as stated above chemical release rates were not given, making it difficult to replicate the results. They proposed that "contrary to" the theory of Byers et al. (1985) "we present evidence that aggregation and olfactory recognition of susceptible host material depends on the synergism between monoterpenes and ethanol." However, since ethanol release from aging Scots pine has not been quantified, there is some doubt to the validity of the theory. The two theories are not mutually exclusive, however. One way to test the hypothesis of Vité et al. (1986) would be to place ethanol baits on healthy trees as was done here (Table 1, Figure 1). The attraction of *T. piniperda* to these traps on trees (Table 1, Figure 1) supports the hypothesis. Schroeder and Eidmann (1987) also found that trees baited with ethanol (or each of the monoterpenes) were attacked by *T. piniperda*. Vité et al. (1986) did not test ethanol alone, but it has very little activity alone (Table 3, and none caught in Table 4 and Figure 2), a finding also made by Schroeder (1988) and Schroeder and Lindelöw (1989).

Klimetzek et al. (1986) "qualified" the ethanol–monoterpene synergism theory when they reported that increasing ethanol release rates from 24 to 120 mg/day reduced the response of *T. piniperda* to a mixture of racemic α-pinene and terpinolene. Since monoterpenes alone were not tested, it was not possible to confirm the synergism of ethanol and monoterpenes. In fact, the decline in

response did not support the theory that ethanol played a role in selection of susceptible hosts. Schroeder (1988) also attempted to confirm the theory of Vité et al. (1986) by increasing the release of ethanol in five steps over an even wider range from 0 to 50 g/day in combination with a 10 mg/day release of α-pinene. The attraction of *T. piniperda* linearly declined with the logarithm of ethanol release, supporting Klimetzek et al. (1986) but not Vité et al. (1986).

Schroeder and Lindelöw (1989) provided evidence that could explain the discrepancies between the above results. In their Figure 1 for *T. piniperda* it can be seen that a high release of α-pinene was most attractive to the beetle and that ethanol releases from 0 to 3 g/day had little, if any, effect on the attraction. Ethanol released at even higher rates, 120 mg/day (Klimetzek et al., 1986) or 50 g/day (Schroeder, 1988), would inhibit the response to monoterpenes. However, at a low release rate of monoterpene (2.4 or 22 mg/day), the lower releases of ethanol from 0 to 3 g/day had a synergistic effect on the weak response (Schroeder and Lindelöw, 1989). These latter results are similar to those found here (Figure 3B). Therefore, the beetle could find diseased, but physically uninjured, trees by a weak response to a synergism between low monoterpene release rates and moderate ethanol rates—the hypothesis of Vité et al. (1986). These trees would be tested occasionally by beetles and, if low in resistance, this would permit beetles to continue feeding. Resinosis and monoterpene release would elicit increased numbers joining in a mass-attack. Injured trees with wound oleoresin, and trees under attack with "pitch tubes," would have a higher monoterpene release and attract the most beetles, a scenario in line with the hypothesis of Byers et al. (1985). Trees with high ethanol release rates would indicate a tree in advanced decay and unsuitable for reproduction, thus to be avoided, as in the hypothesis of Klimetzek et al. (1986) (high monoterpenes releases would normally not occur with high ethanol rates). In addition, verbenone from decaying hosts would inhibit response to monoterpenes (Byers et al., 1989). Measurements of ethanol and monoterpene release rates from various host and nonhost substrates would be of interest and are necessary for further integration and refinement of these ecological perspectives.

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