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LIMONENE INHIBITS ATTRACTION TO α-PINENE IN THE PINE WEEVILS *Hylobius abietis* AND *H. pinastri*

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Abstract—The field responses of *Hylobius abietis* (L.) and *H. pinastri* (Gyllenhal) (Coleoptera: Curculionidae) to various combinations of two host monoterpenes and ethanol were studied using baited pitfall traps. Both species were attracted to α-pinene, and when ethanol was added the attraction increased by 5–16 times. Limonene completely inhibited the attraction to α-pinene, even when the release rate of limonene was only about 1/50 that of α-pinene. The catches in traps with α-pinene and limonene as well as with limonene alone were similar in size to catches in empty control traps, i.e., no true repellent effect was demonstrated. When limonene was added to the combination of α-pinene and ethanol on old clear-cuttings, the catch of *H. pinastri* was completely inhibited while that of *H. abietis* was reduced by two thirds. On fresh clear-cuttings the inhibitory effect of limonene on the attraction to the α-pinene–ethanol combination was small or absent. Some aspects of host interactions are discussed as are practical implications regarding the choice of seedling material for planting and prospects of finding deterrents for protecting seedlings from pine weevil damage.

Key Words—*Hylobius abietis*, *Hylobius pinastri*, Coleoptera, Curculionidae, limonene, α-pinene, ethanol, olfactory orientation, attraction, inhibition, deterrent.

INTRODUCTION

The two Palaearctic pine weevil species *Hylobius abietis* (L.) and *H. pinastri* (Gyllenhal) are biologically very similar (Eidmann, 1974). Both species oviposit in roots of freshly killed or dying coniferous trees, and the larvae develop under the bark of the roots. Adult weevils feed mainly on the tender bark of

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stems and twigs of young conifers. Planted seedlings in reforestation areas are commonly killed by feeding pine weevils. Considerable economic losses are caused primarily by *H. abietis*, which is generally much more abundant than *H. pinastri*.

The olfactory orientation of *H. abietis* to its coniferous hosts has been the subject of several recent studies. Host monoterpenes and the biodegradation product ethanol have been found to be important attractants, while no pheromone has been demonstrated in *H. abietis* (Nordlander et al., 1986; Tilles et al., 1986a,b), except for a close-range mating stimulant present on the body surface of female weevils (Tilles et al., 1988). Nordlander et al. (1986) showed that weevils walking on the ground are able to locate underground roots suitable for oviposition by utilizing volatiles emanating from these roots and diffusing through the soil. A condensate of volatiles from stems of Scots pine, *Pinus sylvestris* L., was found to be highly attractive to *H. abietis* in a bioassay where the weevils responded by burrowing through a layer of sand towards the hidden odor source. When tested alone, the main component of this condensate, α-pinene, elicited about two thirds of the response obtained with the complete condensate, in which 14 monoterpenes were identified. Moreover, strong synergism between α-pinene and ethanol, when evaluated as attractants for *H. abietis*, has been demonstrated in field tests with baited pitfall traps (Tilles et al., 1986b; Nordlander, 1987).

The present study was initiated after discovering that the host monoterpene limonene can completely inhibit the strong attraction of walking pine weevils to α-pinene when both substances are released from baited pitfall traps (Nordlander, unpublished). Although limonene is known to repel or deter several insects associated with conifers (e.g., Rudnew and Smeljanez, 1969; Bordasch and Berryman, 1977), the observed effect on *H. abietis* and *H. pinastri* appears to be unusually conspicuous.

In previously published laboratory studies, *H. abietis* showed a neutral response or slight attraction to both (+)- and (−)-limonene (Selander et al., 1973, 1974; Nordlander et al., 1986). In the white-pine weevil, *Pissodes strobi* (Peck), Alfaro et al. (1980) found that limonene stimulated feeding at low concentrations but caused feeding inhibition when concentrations rose above a particular threshold. Limonene also has been found to be the most toxic of several host monoterpenes for the scolytid beetles *Dendroctonus brevicomis* LeConte, *D. frontalis* Zimmermann, and *Scolytus ventralis* LeConte (Smith, 1965; Coyne and Lott, 1976; Raffa et al., 1985). Moreover, there are strong indications that *D. brevicomis* preferentially attacks host trees with low concentrations of limonene (Smith, 1966; Sturgeon, 1979), and it has been shown that such trees are less resistant to attack than individuals with high limonene concentrations (Smith, 1969).

Limonene is present in variable amounts in Scots pine and Norway spruce, *Picea abies* (L.) Karst, which are the two main hosts of *H. abietis* and *H. pinastri* in northern Europe. In Swedish Scots pines limonene constitutes about 3–20% of the total cortical monoterpene content, and there is a distinct clinal pattern, with limonene proportions increasing with latitude (Yazdani et al., 1985; Yazdani and Nilsson, 1986). In Norway spruce investigated in Germany, the limonene content showed a bimodal pattern: high limonene levels were associated with low levels of β-phellandrene and vice versa (Heemann and Francke, 1977). Generally, the main cortical monoterpene hydrocarbon components of Scots pine as well as Norway spruce are α-pinene, β-pinene, 3-carene, myrcene, limonene, and β-phellandrene.

Monoterpene variation in conifers is largely genetically determined, and, in general, is not considered to be influenced much by environmental factors (e.g., Squillace, 1976). One exception, however, is the local, drastic increase in the proportions of limonene and certain other monoterpenes that sometimes occurs in response to infection by fungi associated with bark beetles attacking living trees (Raffa and Berryman, 1982, 1987). Mechanical wounding in the absence of the fungi does not appear to result in any major changes in monoterpene composition (Raffa and Berryman, 1982). However, mortal injuries, like girdling or felling, have been reported to increase the limonene–α-pinene ratio in *Pinus taeda* L. (Werner, 1972) while moisture stress has been found to decrease this ratio in *P. taeda* (Gilmore, 1977).

In this study the inhibitory effect of limonene on the attraction of pine weevils to host odors is investigated. The experiments deal with field attraction to various odor combinations employing the technique with baited pitfall traps described by Nordlander (1987). The effects on weevil attraction of adding limonene to either α-pinene or to the combination of α-pinene and ethanol were studied. In addition, different release rates of limonene were tested, and the effects of its two enantiomers were compared. It was also possible to compare the responses of *H. abietis* and its close relative *H. pinastri*. The olfactory behavior of the latter has not been studied previously.

Early field tests indicated that the relative catches on the various baits changed after the weevils had migrated in early June from 2-year-old clear-cuttings to fresh ones (i.e., cut during the previous winter). Therefore, comparative trapping was conducted (1) during May and June on 2-year-old clear-cuttings, where the newly emerged weevils were in a premigratory maturation feeding phase, (2) during June and July on fresh clear-cuttings, where arriving migrants were searching for oviposition sites, and (3) during August and September on 1-year-old clear-cuttings, where part of the adult population that had developed from eggs laid the previous summer had emerged and were feeding prior to hibernation.

METHODS AND MATERIALS

Odor-baited pitfall traps were used in field tests on clear-cuttings ca. 20–25 km N, NE, and E of Uppsala in central Sweden during 1984, 1985, and 1987 (Table 1). Each test compared the attractivity of two or four different treatments, consisting of odor baits placed in pitfall traps or of empty control traps. Traps were set out in blocks containing one representative of each treatment and with ca. 2 m between traps within a block and ca. 20 m between blocks. About 15 (13–17) such blocks were placed in a line across the clear-cutting. Differences between treatments were tested statistically with Friedman's test followed by a multiple-range test paralleling the Student-Newman-Keuls procedure (Zar, 1974) when four treatments were included, while a two-tailed Wilcoxon paired-sample test was used when only two treatments were compared.

The pitfall traps used in this study, with the exception of the extra control trap (C2) in the 1987 experiments, were all of the type illustrated in Nordlander (1987). The trap was constructed from a transparent polypropylene jar with a white polyethylene cap (height 121 mm, upper diam. 116 mm, lower diam. 95 mm). Eight 1-cm-diam. holes were equally spaced around the circumference of the jar, ca. 2 cm below its rim. The traps were placed with their holes just above ground level to allow walking weevils to enter. The C2 trap was made

TABLE 1. FIELD TESTS WITH ODOR-BAITED PITFALL TRAPS

Year	Test[a]	Age of clear-cutting	Trapping periods	No. of days in the field[b]	No. of replicates
1984	1a	2-year	May 17–23	6	15
	1b	fresh	June 7–20	13 (6 + 7)	15
	2a	2-year	May 23–30	7	17
	2b	fresh	June 15–28	13 (6 + 7)	15
	3	2-year	May 25–June 4	10 (5 + 5)	15
	4a	2-year	May 30–June 4	5	17
	4b	fresh	June 7–14 and June 20–27	14 (7 + 7)	15
	5	fresh	July 3–14	11 (6 + 5)	17
1985	6a,7a,8a	2-year	May 24–29	5	15, 13, 14
	6b,7b,8b	fresh	June 27–July 7	5	15
	6c,7c,8c	1-year	Aug. 26–Sept. 4	9 (4 + 5)	15
1987	9–12	2-year	May 6–July 1	56 (8 × 7)	15

[a]Treatments and results presented in Tables 3–5.
[b]Numbers in parentheses refer to intervals (days) at which traps were emptied and dispensers renewed.

from the same kind of jar but lacked the cap and the entrance holes of the other type of trap. This trap was placed with its rim level with the ground surface, like a conventional pitfall trap. All traps were filled with 0.15 liters of water.

The dispensers for volatile substances consisted of test tubes (depth 54 mm, inner diam. 8.5 mm) supplied with a strip of filter paper (50 × 8 mm, Munktell No. 3) reaching from the rounded bottom up to about 1 mm from the opening of the tube (the dispenser releasing limonene at a low rate lacked this filter paper). These dispensers were filled with either 1 ml (1984, 1985) or 1.5 ml (1987) of α-pinene, limonene, or a mixture of 95% α-pinene and 5% limonene, or with 2 ml (1984, 1985) or 3 ml (1987) of 70% ethanol. The volumes released of these substances were measured under conditions similar to those used in the field tests (Table 2). The baits consisted of an individual dispenser or a combination of dispensers containing different substances. The dispensers were suspended vertically with the openings ca. 2 cm below the center of the trap lid (illustrated and further described in Nordlander, 1987).

The following monoterpenes, supplied by Fluka AG, CH-9470 Buchs, were used in the field tests: (1*S*)-(—)-α-pinene (>97%, $[\alpha]_D^{20}$ −42 ± 3°), (*R*)-(+)-limonene (>98%, $[\alpha]_D^{20}$ + 115 ± 5°), (*S*)-(—)-limonene (≈97%, $[\alpha]_D^{20}$ − 90 ± 5°), and (±)-limonene (techn., = "dipentene").

RESULTS

The presence of limonene generally reduced the number of pine weevils attracted to α-pinene as well as to α-pinene and ethanol (Tables 3–5). As described below, this inhibitory effect varied with clear-cutting age, strength of attractive source, amount of limonene released, and pine weevil species. No sex-related differences in response were apparent for either of the pine weevil species. This conclusion was based on the use of contingency tables, when appropriate.

Sex ratios varied between clear-cuttings and between trapping periods on the same clear-cutting. However, no particular trends or patterns were observed regarding variation with clear-cutting age or time of year. In *H. abietis* the percentage of females varied between 40 and 65% in 23 test periods (tests 9–12 divided into two periods, tests 6c and 7c excluded); in 13 of these 23 cases the percentage ranged between 52 and 58%. The average percentage of females calculated for the total catch in all tests was 55% for *H. abietis* (N = 8509) and 52% for *H. pinastri* (N = 672).

Both pine weevil species were attracted to traps with an α-pinene dispenser. When (±)-limonene was added, trap catches were reduced to about the level of empty control traps. This inhibition of the attraction occurred when limonene was released from a separate dispenser located alongside the α-pinene

TABLE 2. AMOUNTS OF SUBSTANCES USED IN FIELD TESTS RELEASED FROM DISPENSERS PLACED IN PITFALL TRAPS DURING PERIOD WITH TYPICAL MAY TEMPERATURE CONDITIONS AND PERIOD WITH UNUSUALLY HIGH TEMPERATURES IN JUNE

Substance	Amount in dispenser (ml)[a]	No. of days in the field	Amount released per 5 or 7 days ($\bar{X} \pm$ SD μl)[b]		Average amount released per day (μl)	
			Typical temp.[c]	High temp.[d]	Typical temp.[c]	High temp.[d]
70% Ethanol[e]	2	5	910 ± 33	1256 ± 178	182	251
(−)-α-Pinene	1	5	578 ± 116	646 ± 170	116	129
(±)-Limonene	1	5	264 ± 29	332 ± 53	53	66
(±)-Limonene	1[f]	5	18 ± 16	64 ± 36	4	13
70% Ethanol[e]	3	7	1844 ± 197	1968 ± 284	263	281
(−)-α-Pinene	1.5	7	806 ± 27	984 ± 149	115	141
(±)-Limonene	1.5	7	416 ± 35	538 ± 126	59	77

[a] Ethanol 2 ml and terpenes 1 ml correspond to baits used in tests 1–8, ethanol 3 ml and terpenes 1.5 ml correspond to baits used in tests 9–12 (see Table 1).
[b] $N = 5$; single dispenser in each trap.
[c] Typical temp.: mean air temperature for the five-day period (May 20–25, 1988) 9.4°C; for the seven-day period (May 20–27) 11.3°C.
[d] High temp.: mean air temperature for the five-day period (June 22–27, 1988) 19.8°C; for the seven-day period (June 22–29) 20.1°C.
[e] The exact amount of ethanol released is not known since 70% ethanol was used in accordance with previous studies (Tilles et al., 1986b; Nordlander, 1987).
[f] Dispenser lacking filter paper.

TABLE 3. PINE WEEVIL CATCHES ON BAITS WITH AND WITHOUT LIMONENE IN 1984 FIELD TESTS ON 2-YEAR-OLD AND FRESH CLEAR-CUTTINGS

Test	Baits[a]	Catch *H. abietis*[b] 2-year	Catch *H. abietis*[b] fresh	Catch *H. pinastri* 2-year	Catch *H. pinastri* fresh
1a, b	A	149 a	171 a	6	5
	L	0 b	10 b	0	0
	A & L	0 b	25 b	0	0
	C	2 b	23 b	0	2
2a, b	A	353 a	102 a	10	7
	L(low)	3 b	14 b	1	1
	A + L5%	3 b	18 b	4	0
	C	0 b	14 b	4	2
3	A	49 a		9	
	A & (±)L	7 b		1	
	A & (+)L	3 b		2	
	A & (−)L	2 b		0	
4a, b	A	83 a	85 a	5	1
	A + (±)L5%	6 b	21 b	3	0
	A + (+)L5%	25 ab	23 b	2	1
	A + (−)L5%	24 ab	22 b	1	2
5	A & E		434 a		24
	A + (±)L5% & E		335 b		16

[a] A = (−)-α-pinene; L = (±)-limonene (techn.); (±)L, (+)L, and (−)L = (±)-, (+)-, and (−)-limonene (97%); (low) = low release rate; +L5% = mixture containing 5% limonene; C = control (trap without bait); E = ethanol.
[b] Column figures followed by the same letter are not significantly different at the 5% level (tests 1–4: Friedman's test followed by a multiple comparison, test 5: Wilcoxon paired-sample test, two-tailed).

TABLE 4. PINE WEEVIL CATCHES WITH VARIOUS BAITS IN 1985 FIELD TESTS ON CLEAR-CUTTINGS EITHER 2 YEARS OLD, FRESH, OR 1 YEAR OLD

Test	Baits[a]	Catch *H. abietis*[b] 2-year	Catch *H. abietis*[b] fresh	Catch *H. abietis*[b] 1-year	Catch *H. pinastri* fresh
6a, b, c	A	85	54	4	5
	A & L	0***	9*	1	0
7a, b, c	A	168	30	2	15
	A & E	785***	180***	6	42
8a, b, c	A & E	743	181	31	15
	A & E & L	240***	177NS	2**	13

[a] A = (−)-α-pinene; L = (±)-limonene (techn.); E = ethanol.
[b] Pairwise comparisons with two-tailed Wilcoxon paired-sample tests (*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$).

TABLE 5. PINE WEEVIL CATCHES WITH VARIOUS BAITS IN 1987 FIELD TESTS ON 2-YEAR-OLD CLEAR-CUTTINGS

		Catch *H. abietis*[b]			Catch *H. pinastri*[b]
Test	Baits[a]	May 6–June 3	June 3–July 1	May 6–July 1	May 6–July 1
9	A	49	202	251 a	17 a
	A & L	3	3	6 b	1 b
	C	1	1	2 b	5 b
	C2	8	9	17 b	3 b
10	A	72	184	256 a	24 a
	A + L5%	8	30	38 b	2 b
	C	4	2	6 b	4 b
	C2	10	19	29 b	5 b
11	A	38	66	104 b	13 b
	A & E	458	729	1187 a	203 a
	C	2	0	2 c	3 b
	C2	3	3	6 c	3 b
12	A & E	512	861	1373 a	173 a
	A & E & L	185	318	503 b	6 b
	C	1	1	2 c	3 b
	C2	12	11	23 c	8 b

[a] A = (−)-α-pinene; L = (±)-limonene (techn.); +L5% = mixture containing 5% L; E = ethanol; C = control (trap without bait); C2 = control (trap without bait), open type.
[b] Column figures for the entire trapping period (May 6–July 1) followed by the same letter are not significantly different at the 5% level (Friedman's test followed by a multiple comparison).

dispenser as well as when a mixture containing 5% limonene and 95% α-pinene was released from a common dispenser (tests 1a, 1b, 2a, 2b, 9, 10). Traps baited exclusively with either a high- or a low-release limonene dispenser caught about as many weevils as the empty control traps and the traps with both α-pinene and limonene (tests 1a, 1b, 2a, 2b).

The relative catches of *H. abietis* in α-pinene-baited traps were usually considerably lower on fresh clear-cuttings than on 2-year-old ones seen in relation to the catches in both empty control traps and in traps baited with α-pinene and limonene (Table 6). During 1987, when pine weevil catches were recorded weekly from May 6 to July 1 on 2-year-old clear-cuttings (tests 9–12), no similar changes were observed in relative catches over time. (Owing to cold and rainy weather in May and June that year, only part of the pine weevil populations participated in the migration, which was observed to occur on June 6 and 22.) Thus, the observed decrease in relative catch for the α-pinene-baited traps on fresh clear-cuttings appears to have been attributable to the presence of fresh

TABLE 6. CATCHES OF *H. abietis* IN α-PINENE-BAITED TRAPS RELATED TO CATCHES IN TRAPS WITH COMBINATIONS OF α-PINENE AND LIMONENE AND IN CONTROL TRAPS

Test	Catch ratio[a]				Catch in A
	A/A & L	A/A + L5%	A/C	A/C2	
2-Year old clear-cuttings					
1a	>149		75		149
2a		118	>353		353
3	12[b]				49
4a		5[b]			83
6a	>85				85
9:(May 6–June 3)	16		49	6	49
9:(June 3–July 1)	67		202	22	202
10:(May 6–June 3)		9	18	7	72
10:(June 3–July 1)		6	92	10	184
Fresh clear-cuttings					
1b	7		7		171
2b		6	7		102
4b		4[b]			85
6b	6				54

[a] A = α-pinene; L = limonene; +L5% = mixture containing 5% L; C = control traps without bait; C2 = control traps without bait, open type.
[b] Ratio calculated using the mean catch of traps baited with (±)-, (+)-, and (−)-limonene.

host material and host odors competing with the baits rather than to a seasonal change in pine weevil behavior. Moreover, a comparison of the catches in the two types of control traps (C and C2; tests 9–12) did not reveal any tendency for interest in entering traps with holes to increase over time, which otherwise could have been an alternative for explaining the decreased A/C catch ratio.

In most of the tests an inexpensive (±)-limonene of technical purity was used. Limonene of higher purity (purum), consisting predominantly of either the (+)- or the (−)-enantiomer, was nevertheless used in three tests in order to check whether the inhibitory effect might be influenced by chirality or the presence of impurities. In test 4a, a racemic mixture of (+)- and (−)-limonene tended to have a stronger inhibitory effect than either of the enantiomers alone. However, in the two other tests (3, 4b), no difference in inhibitory effect between the racemate and the two enantiomers was found. The catch in traps with a combination of α-pinene and limonene tended to be larger in relation to the catch with α-pinene alone when the purer preparation was used. However, this relationship varied considerably between tests with the technical grade and was sometimes similar to that of the purer preparation (Table 6).

The combination of α-pinene and ethanol attracted many more pine weevils of both species than α-pinene alone. In tests 7a (on a 2-year-old clear-cutting) and 7b (on a fresh one), the catch of *H. abietis* with the combined bait was five and six times larger, respectively. The α-pinene–ethanol bait attracted even more weevils in relation to α-pinene alone in test 11, made on a 2-year-old clear-cutting; the combined bait caught about 11 times more of *H. abietis* and 16 times more of *H. pinastri*. No substantial differences in these relations were observed between the trapping periods before and after June 3.

When limonene was added to the α-pinene–ethanol bait the catch of *H. abietis* was reduced by two thirds in the tests on 2-year-old clear-cuttings (tests 8a and 12, both periods). The inhibitory effect of limonene on the catch of *H. pinastri* was much stronger (2 × 2 contingency table: $\chi^2_c = 47$, $P < 0.001$); traps supplied with a limonene dispenser caught about as many *H. pinastri* as the empty control traps. On the fresh clear-cuttings, adding limonene had no effect on the catch of *H. abietis* in test 8b, while in test 5 the mixing of limonene with α-pinene (5:95) caused a small but significant decrease in trap catch. In test 5 the response of *H. pinastri* was similar to that of *H. abietis*, while no *H. pinastri* were caught in test 8b. Although few *H. abietis* were caught on 1-year-old clear-cuttings in late summer, it is clear from the data that limonene strongly inhibited attraction to α-pinene and ethanol in these presumably newly emerged weevils (test 8c).

DISCUSSION

That limonene inhibits attraction of pine weevils to α-pinene was discovered during the search for an effective standardized bait for trapping *H. abietis* (cf. Nordlander, 1987). Previous laboratory studies had indicated that limonene was one of several host monoterpenes eliciting digging behavior in *H. abietis* (Nordlander et al., 1986). Thus limonene was included as a potential attractant when first tested in the field (test 1a).

Since insects are commonly repelled or deterred by high concentrations of substances that are attractive or stimulatory in some way at lower dosages (e.g., Alfaro et al., 1980), the response to comparatively low release rates of limonene also was tested in the present study. However, when limonene was added to α-pinene, forming a mixture containing only 5% limonene, this was enough to completely or almost completely inhibit pine weevil attraction. The release rate from such a dispenser can be roughly estimated to have been around 2–3 μl limonene and 120 μl α-pinene per day at the prevailing temperature conditions during the tests, taking into account the proportions of the two substances and the lower volatility of limonene (cf. Table 2). This suggests that high concentrations are unlikely to have been responsible for the inhibitory effect of limonene observed in the field.

Substances inhibiting specific types of behavior, such as feeding or oviposition, are termed deterrents according to the designations of Dethier et al. (1960). This term might apply to limonene in the present case. However, it is not known whether limonene actually inhibits the normal response to α-pinene or if it is affecting some type of behavior counteracting the end result of the behavior induced by α-pinene. Any one of several behavioral changes, elicited either very close to the trap or at some larger distance from the odor source, could lead to the observed decrease in numbers of weevils entering the traps. Because these behavioral mechanisms are still unknown, I have preferred to use expressions such as "inhibited attraction" and "inhibitory effect" to account for what was actually observed in the field. These observations showed that the addition of limonene to the attractive odor source reduced the number of pine weevils captured; however, capture levels were no lower than those of empty control traps. Similarly, the low catch in traps baited with limonene alone was nevertheless about as high as the catch in control traps. Thus, a true repellent effect of limonene was not demonstrated.

Biological data on *H. pinastri* are scarce in the literature, and no information concerning responses to specific host substances in this species was available prior to the present study. The few published observations to date suggest that the life history of *H. pinastri* is roughly similar to that of *H. abietis* (Eidmann, 1974; Långström, 1982). However, a slight difference in habitat preferences has been found in some studies; in northern Europe it appears as if *H. pinastri* prefers moist sites dominated by Norway spruce, whereas *H. abietis* prefers drier Scots pine-dominated areas (Ozols, 1967; Långström, 1982). During the present study it was noted that *H. pinastri* was particularly abundant on wet parts of the clear-cuttings. This description of two biologically similar species with some modest differences in their habits is in agreement with the results of this study regarding responses to odors. Both pine weevil species were similarly attracted by α-pinene and by the synergistic combination of α-pinene and ethanol, while limonene more or less inhibited their attraction to these odor sources. However, this effect of limonene appeared to be more pronounced in *H. pinastri*. In test 12, for example, the addition of limonene to the combination of α-pinene and ethanol reduced the catch of *H. abietis* by only about two-thirds, whereas the attraction of *H. pinastri* was inhibited completely.

Host monoterpenes constitute essential cues for pine weevils in the process of locating the ephemeral breeding substrate they utilize (Nordlander et al., 1986). The monoterpenes play a role in defending the tree against various herbivores and pathogens. However, ovipositing females do not currently act as a selective force influencing the evolution of this defense system since living, reproductive trees are not used as breeding material by these species. In contrast, weevil feeding may be a significant selective factor acting on the seedling. This should be the case if the genetically determined variation in monoterpene composition and other qualities affects (1) the risk of discovery by weevils, (2) palatability to weevils, or (3) tolerance of the seedling against damage. Little is known about whether levels of weevil-induced mortality differ between conspecific seedlings with different monoterpene compositions (see Selander and Kalo, 1979), but the findings regarding the effects of limonene in the present study indicate that such differences may exist. Further investigations in this area should be of practical interest also, inasmuch as the knowledge gained might help in determining the suitability of seedling material for planting. Particularly in clonal forestry, it should be worthwhile to consider any relationship between chemical composition of the seedling and damage caused by pine weevils.

In living natural host material, the relative amount of limonene is frequently higher than the 5% concentration found to be inhibitory in this study. For example, in cortical oleoresin samples taken from a large number of Swedish Scots pine populations (Yazdani et al., 1985; Yazdani and Nilsson, 1986), the amount of limonene was of the same magnitude as the amount of α-pinene, and in relation to the total monoterpene content the percentage of limonene was usually above 5% (3–20%). How then is it possible that pine weevil attraction to α-pinene can be completely inhibited at such low limonene levels whereas freshly cut or wounded Scots pines always appear to be attractive? One possibility is that limonene released as a part of the complete monoterpene bouquet from natural host material does not have the same inhibitory effect as it has together with only a single attractive monoterpene. It should not be assumed, however, that pine weevil attraction to natural host material cannot be inhibited by limonene. The degree of limonene-induced inhibition may vary—depending, for example, on whether the host material being considered consists of (1) either intact or injured seedlings used as food for adult weevils or (2) dying roots used as breeding material. In view of the urgent need to protect planted seedlings from pine weevil damage (e.g., Eidmann, 1981; Brunberg et al., 1986), the possibilities for using limonene, or related substances, for this purpose should be examined thoroughly.

Conventional insecticides and, to a lesser extent, some comparatively costly mechanical devices are used currently for seedling protection in northern Europe (e.g., Brunberg et al., 1986). No deterrents or repellents affecting pine weevils are in use. A turpentine distillate with deterrent or repellent effects on many insects, including *H. abietis*, has been tested recently by applying it to planted seedlings, but sufficient protection was not achieved (Eidmann, 1987). Thus, the finding reported here of a specific substance that can completely neutralize the strong attraction of another host monoterpene is encouraging. These results might be useful in future attempts to search methodically for substances capable of reducing pine weevil damage, whether or not limonene eventually proves to be useful.

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