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ABSTRACT

Field tests were conducted in East Texas in 1973–77 to evaluate the influence of 7 behavioral chemicals on the flight and landing behavior of the southern pine beetle, *Dendroctonus frontalis* Zimmerman. A mixture of frontalin plus host tree volatiles attracted flying beetles within an infestation. *Trans*-verbenol synergized the activity of frontalin and substituted for host tree volatiles, α-pinene and loblolly turpentine. Verbenone in a 1:1 ratio with frontalin did not significantly affect trap catch. At higher concentrations of verbenone, trap catch was significantly reduced. *Endo*-brevicomin inhibited trap catch when added to an attractant-baited trap. *Exo*-brevicomin showed no inhibitory effect. Traps with a 1:4 mixture of *endo*-brevicomin and verbenone plus an attractant caught significantly fewer beetles than traps with the attractant plus either one of the inhibitors.

Secondary attraction behavior in the scolytid genus *Dendroctonus* has been shown to be affected by several compounds (Borden 1974). The roles of these compounds as either attractants, synergists, or inhibitors have been assigned on the basis of either field trap tests, laboratory bioassays, or electrophysiological studies (Vité and Francke 1976). We questioned the assigned roles of the various behavioral chemicals due to the following points: (1) the discrepancies between laboratory and field testing of compounds, (2) the use of crushed beetles as attraction sources being indicative of a natural phenomenon, (3) the lack of detailed methodology (specifically, elution rates of the compounds), (4) the lack of adequate controls, and (5) the absence of statistical analysis of test results. Wood and Silverstein (1970) provided a detailed criticism of the research relating to the role of 2 of these behavioral chemicals.

The goal of the research presented here was to verify the roles of several behavioral chemicals associated with secondary attraction of the southern pine beetle, *D. frontalis* Zimmerman. Furthermore, these compounds were tested over a wider range of concentrations and in different combinations than previously reported.

Methods and Materials

Test Sites

Field tests were conducted June through Sept. 1973, 1976, and 1977. In 1973, tests were run in southern pine beetle infestations < 10 ha in size, in the Sam Houston National Forest in Montgomery Co., Tex. The forests were an equal mixture of shortleaf (*Pinus echinata* Mill.) and loblolly pine (*P. taeda* L.). Stands were even-aged, pulpwood size trees, 25–50 cm dbh and 15–25 m high.

The 1976 and 1977 field tests were run in infestations < 10 ha in Chambers, Hardin, and Montgomery Co. in southeastern Tex. Site and stand characteristics were similar to the 1973 test sites.

Test Compounds

Seven behavioral chemicals were evaluated in 1-, 2-, 3-, and 4-way combinations for their effect on the response of *D. frontalis* to baited traps. (Table 1). Three attractants were used as standards during the course of our testing: a 1:4 mixture of frontalin and alpha-pinene, a 1:12 mixture of frontalin and loblolly turpentine, and a 1:1:12 mixture of frontalin, *trans*-verbenol and loblolly turpentine.

Elution Devices

The test compounds were eluted by evaporation. Desired elution rates were obtained by use of glass planchets and vials of varying sizes (Table 1) (W. D. Bedard and P. E. Tilden, pers. comm.). In the 1973 tests, the elution devices were placed inside inverted glass jars with perforated lids. In the 1976 and 1977 tests, the elution devices were placed in inverted aluminum film cannisters with perforated lids. Each jar or cannister was positioned on the center pole of a wing-vane trap 2 m above the ground. Sufficient amounts of chemicals were used to provide the desired elution rate for a 10-h test period (from 1100 h of one day to 1200 h of the following day CDST). Elution rates of the behavioral chemicals were determined by Bedard and Brown (pers. comm.) during their research on the western pine beetle, *D. brevicomis* LeConte. The elution devices were rinsed with acetone and provided with new compound(s) once daily between 1000 h and 1200 h outside the effective trapping area.

Monitor Traps

Beetle response to the test compounds was monitored with 4-vaned wing–traps coated with Stickem-Special®. Each vane was 61×61 cm giving a total trapping area of ca. 1.5m². The vanes were made of 18×14-mesh fiberglass-coated nylon screening. The wing-trap design has been published elsewhere (Payne et al. 1978).

All field tests were conducted within active infestations. Traps were placed ca. 25 m apart in a zone between infested trees with emerging beetles (both emerging brood adults and re-emerging parent adults) and newly attacked trees (Payne et al. 1977). The hazard of placing traps adjacent either to trees just coming under attack or trees with emerging or re-emerging adults was minimized by placing traps in the zone of infestation containing mid-instar larvae. A daily survey of each test site was made to detect changes in brood development. Traps were moved accordingly to avoid positional effects and disproportionately high trap catches (Payne et al. 1978).

In the 1973 tests, treatments were initially assigned positions randomly. On subsequent days, the trap in the position with the highest catch was exchanged with the trap in the position with the lowest catch and all other traps were assigned randomly. Responding beetles were removed from the traps every 24 h and placed in labeled vials for subse-

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Table 1.—Compound purity, volume delivered, and elution containers used in evaluation of behavioral chemicals on the response of *D. frontalis*. (After W. D. Bedard and P. E. Tilden, pers. comm).

Compound[a]	% purity	Elution rate (mg/h)	Elution containers[c]
Alpha-pinene (a)	—	2.0	1 dram × 33 mm cup
Loblolly turpentine[b] (a)	—	6.0	1 dram × 20 mm cup
Frontalin (b) (Renwick et al. 1969)	100.0	0.5	3 mm × 21 mm planchet
Trans-verbenol (d) (Renwick 1967)	99.4	0.5	0.5 dram × 5 mm cup
Verbenone (d) (Renwick 1967)	99.1		0.5 dram × 5 mm cup
1x concentration		0.5	1 5 mm cup
5x concentration		2.5	5 5 mm cups
10x concentration		5.0	10 5 mm cups
20x concentration		10.0	20 5 mm cups
Endo-brevicomin (c) (Silverstein et al. 1968)	100.0	0.5	0.5 dram vial
Exo-brevicomin (e) (Silverstein et al. 1968)	99.9	0.5	0.5 dram vial

[a] Source of compounds: a = host tree; b = female *D. frontalis*; c = male *D. frontalis*; d = both sexes; and e = female *D. brevicomis* LeConte (western pine beetle).
[b] Loblolly turpentine obtained by short path distillation of loblolly pine oleoresin.
[c] Cups made by cutting appropriate size vial to desired height.

quent counting and sexing. Beetles were removed between 0800 and 1000 h CDST, prior to peak flight activity (Coster et al. 1977). Every 3rd day the wing-vanes were removed from all traps, labeled and washed in warm Varsol® solvent and the numbers of predators, parasites and other associated insects were recorded.

In the 1976 and 1977 tests, treatments were assigned on a random basis each day. After a 30-min trapping period, each trap was moved to an adjacent trap position. This rotation of traps with their respective elution devices was carried out to further reduce the variability in trap catch numbers due to trap placement (Payne et al. 1978). Trapped *D. frontalis* were removed from the traps every 30 min and placed in labeled vials for subsequent counting and sexing.

Data were analyzed using standard analysis of variance and non-parametric tests. In the 1973 tests, some data were statistically identified as outliers and were discarded from the analysis (Snedecor and Cochran 1967). These outliers represented high or low trap catches caused by trap position. In 1976–77 tests, using trap rotation techniques, no outlier data were found.

Results and Discussion

Single Compound Tests

Only frontalin elicited a field response from *D. frontalis* equivalent to the attractant mixture of frontalin + *alpha*-pinene. Previous field tests, using unspecified elution rates and ratios of compounds, have demonstrated that without the addition of host tree volatiles frontalin–baited trap catch was only 27% of the response to the frontalin-*alpha*-pinene mixture (Renwick and Vité 1969, Kinzer et al. 1969). The synergistic effect of *alpha*-pinene has been well proven (Renwick and Vité 1969). Host tree and beetle-produced volatiles in the test areas, which are unmeasured and uncontrollable variables, have unknown effects on beetle response in field testing of behavioral chemicals. Possibly, frontalin was synergized by host tree volatiles in the air in the testing sites. All other single compounds which we tested failed to elicit trap catches significantly greater than the blank wing-trap control (Table 2). Our tests substantiate the reports that frontalin at the concentrations tested is an attractant for the southern pine beetle (Renwick and Vité 1969, 1970).

Table 2.—Response of *D. frontalis* to single compounds (1973).

Treatment	Elution rate (mg/h)	$\bar{x} \pm$ SE trap catch replicate[ab]	Sex ratio ♀ : ♂
Frontalin + alpha-pinene	0.5 + 2.0	23±7 a	0.44
Frontalin	0.5	37±11 a	0.46
Verbenone	0.5	10±2 b	0.93
Exo-brevicomin	0.5	7±3 b	0.88
Endo-brevicomin	0.5	6±2 b	0.59
Trans-verbenol	0.5	5±1 b	0.68
Turpentine	0.5	4±1 b	0.70
Blank wingtrap	—	4±1 b	0.57

[a] 24 replicates/treatment except frontalin + alpha-pinene with 11; 24 h/replicate.
[b] Means followed by same letters are not significantly different at $P < 0.05$ level (pairwise comparison of means using Fisher's LSD test).

Trans-verbenol Tests

The addition of either *trans*-verbenol or loblolly turpentine to frontalin-baited traps resulted in a significant increase in mean trap catch (Table 3). However, *trans*-verbenol added to a mixture of frontalin and host volatiles did not significantly enhance trap catch (Table 3, 4). Kinzer et al. (1969) reported a similar synergistic activity for this compound. These data substantiate the report that *trans*-verbenol can substitute for host tree volatiles as a synergist for frontalin (Renwick and Vité 1969, 1970). This synergistic activity was not evident in the presence of host tree volatiles in our tests.

Varied alpha-pinene Concentrations

Trap catch of *D. frontalis* was not significantly affected by varying the elution rate of *alpha*-pinene in traps containing either frontalin or frontalin and *trans*-verbenol (Table 4). These results are in agreement with those for tests with 1:2 to 1:10 and higher ratios reported by Vité (1970).

Verbenone Tests

Significantly fewer beetles were caught on traps baited with either standard I or II + either the 10x or 20x concentration of verbenone than on traps baited with either of the 2 standards alone (Table 5). Lower concentrations of ver-

Table 3.—Evaluation of the role of *trans*-verbenol as a substitute for host tree turpentine (1976).

Treatment[a]	$\bar{x}$ ± SE trap catch[bc]	Sex ratio ♀ : ♂
Frontalin	10.3±1.6a	0.75
Frontalin + *trans*-verbenol	25.1±2.4b	0.98
Frontalin ± *trans*-verbenol + loblolly turpentine	24.3±2.8b	0.92
Frontalin + loblolly turpentine	22.4±2.9b	0.94
Blank wingtrap	0.7±0.3c	0.60

[a] Elution ratio for test compounds were: frontalin and *trans*-verbenol = 0.5mg/h each; loblolly turpentine = 6.0 mg/h.
[b] Ten 30-min trapping periods.
[c] Means followed by the same letter are not significantly different at the 1% level based on a pairwise comparison of means using the Mann-Whitney test.

Table 4.—Influence of *alpha*-pinene concentrations on response of *D. frontalis* to frontalin and frontalin plus *trans*-verbenol (1976).

Treatment[a]	Elution rate (mg/h)	$\bar{x}$ ± SE trap catch/ replicate[b]	Sex ratio ♀ : ♂
Frontalin + alpha-pinene	0.5 + 2.0	18.5±4.6 a	0.46
Frontalin + alpha-pinene	0.5 + 6.0	11.9±2.4 a	0.50
Frontalin + *trans*-verbenol + alpha-pinene	0.5 + 0.5 + 2.0	18.6±2.8 a	0.64
Frontalin + *trans*-verbenol + alpha-pinene	0.5 + 0.5 + 6.0	15.6±1.70 a	0.49
Blank wingtrap		4.8±1.0 b	0.57

[a] 11 replicates/treatment; 30 min/replicate.
[b] Means followed by same letter are not significantly different at 5% level based upon pairwise comparison of means using one-way analysis of variance.

benone added to attractant baited traps had no significant affect on the number of beetles caught. Renwick and Vité (1969) reported that high concentrations inhibited male response to known attractants. They did not specify elution rates of the attractant mixture, therefore, a comparison with data presented is not possible. Based upon Renwick and Vité (1969) and our data, high concentrations of verbenone effectively reduce the number of beetles caught on traps.

Brevicomin Tests

There was a significant reduction in the number of beetles caught on traps baited with either *endo*-brevicomin or a 50:50 mixture of the *endo*- and *exo*-isomers of brevicomin plus either of the 3 standard attractants tested (Table 6, 7). *Exo*-brevicomin failed to show any inhibitory activity. Vité and Renwick (1971) reported *exo*-brevicomin to be less inhibitory than *endo*-brevicomin in a different bioassay system. Rudinsky et al. (1974), Payne et al. (1977), and Vité and Renwick (1971) reported similar evidence for inhibition of male response to attractants with low concentrations of *endo*-brevicomin. Rudinsky et al. (1974) reported laboratory bioassay response while Vité and Renwick (1971) evaluated the response of flying beetles.

Verbenone–Brevicomin Test

1976 test data demonstrated the inhibitory activity of both verbenone at 4x concentration and *endo*-brevicomin at 1x concentration (Table 5, 6, 7). Addition of 4x concentration of verbenone and 1x concentration of *endo*-brevicomin to frontalure baited traps resulted in a significant reduction in the number of beetles caught on traps (Table 7). This reduction in trap catch was significantly less than the trap catch of both frontalure baited traps baited with each inhibitor separately. These data suggest that the behavioral mechanisms which terminate aggregation behavior of the southern pine beetle may be a multi-compound system (Vité 1970).

Sex Ratio

There was a large variation in the sex ratio of beetles caught in traps baited with the synthetic behavioral chemicals. There was no significant difference in the sex ratio of responding beetles to any of the 4 attractant standards used in this study (Table 8). Furthermore, only the 4x concentration of verbenone + attractant standard effected a sex ratio significantly different than the ratio of the nested (Snedecar and Cochran 1967) attractants. Coster et al. (1977) reported that the sex ratio of beetles responding to naturally attacked trees was 1:0.86 (male:female) but that this ratio varied within days. Other studies cited by Coster et al. (1977) reported sex ratios ranging from 1:0.72 to 1:1. In 5 yr of field testing attractant standards, we have observed sex ratios of responding beetles ranging from 1:0.44–1:1.12. Given

Table 5.—Response of *D. frontalis* to synthetic attractants with varying concentrations of verbenone (1976).

Treatment	$\bar{x}$ ± SE trap catch/replicate[ab] ♀ : ♂ — Frontalin & α-pinene	$\bar{x}$ ± SE trap catch/replicate[ab] ♀ : ♂ — Frontalin + turpentine	T prob[c]
Attractant	11.9±4.5 (0.59) a	9.8±1.9 (0.63) a	NS
Attractant +			
1x verbenone[d]	11.5±2.6 (0.55) a	6.6±2.8 (0.64) a	NS
5x verbenone	6.8±1.7 (0.84) ab	5.9±1.6 (1.40) ab	NS
10x verbenone	5.8±1.3 (1.07) b	4.3±0.6 (1.27) b	NS
20x verbenone	4.2±1.5 (1.47) b	3.2±0.9 (0.81) b	NS
Blank wingtrap	1.4±0.6 (1.00) c	2.2±0.4 (0.94) c	NS

[a] 25 replicates; 30 min/replicate.
[b] Means followed by same letters within columns not significantly different at $P < 0.5$ level based upon pairwise comparison of means using Mann-Whitney test.
[c] T-test run on total trap catch/replicate between 2 standards.
[d] Elution rates of 1x, 5x, 10x, and 20x verbenone concentrations are presented in Table 1.

Table 6.—Influence of *endo*- and *exo*-brevicomin on the response of *D. frontalis* to synthetic attractants (1976).

Treatment[a]	$\bar{x} \pm$ SE trap catch/30 min replicate[b]	
	Frontalin + turpentine[d]	Triplicate[cd]
Attractant	16.4±3.6 a (0.8)	85.9±20.6 a (0.9)
Attractant + *exo*-brevicomin	16.4±3.8 a (1.0)	98.9±21.4 a (1.1)
Attractant + *endo*-brevicomin	8.8±2.6 b (0.5)	31.2±6.1 b (0.9)
Attractant + *endo*-*exo*-brevicomin	8.2±2.0 b (0.5)	23.9±5.8 b (0.5)
Blank wingtrap	3.5±0.6 (0.8)	5.4±2.1 c (1.8)

[a] Elution rates for compounds are presented in Table 1.
[b] Means followed by the same letter within columns are not significantly different at the 5% level based upon pairwise comparison of means using the Mann-Whitney test.
[c] Triplicate attractant is a 1:1:12 mixture of frontalin, *trans*-verbenol and loblolly turpentine, respectively.
[d] Frontalin + turpentine = 12 replicates; triplicate = 10 replicates.

this wide range of variation in reported sex ratios, one should be cautious in ascribing a function of a behavioral chemical based upon a deviation of an observed sex ratio varying from the 1:1 ratio of attacking adults (Coulson et al. 1976). It may be that the sex ratio of beetles landing on attacked trees is different than the sex ratio of beetles actually attacking the trees.

Conclusion

The role of all compounds tested and reported here and by others cited have used the response of either flying beetles to baited traps or in laboratory pedestrian bioassays. As such, only a portion of the total beetle behavioral response to compounds has been evaluated. Precisely assigned roles of these compounds will necessitate evaluation of preflight, flight, and postflight behavior as well as trap catch and electrophysiological data. However, on the basis of data from studies by other researchers (see text) and our field evaluation series, the following functions for these compounds are proposed:

(1) Frontalin is, by itself, attractive to both sexes of the southern pine beetle, and attracts more male than female beetles.

(2) *Trans*-verbenol, when added to traps baited with frontalin, synergizes the activity of frontalin and appears to substitute for host tree volatiles.

(3) Both the host tree turpentine and *alpha*-pinene synergize the activity of frontalin. The ratio of host volatiles to frontalin does not appear to affect beetle response to baited traps.

(4) Low concentration of verbenone (0.5mg/h) does not affect trap catch to attractant-baited traps. Higher concentrations (5mg/h) inhibit beetle response.

(5) *Exo*-brevicomin shows no activity in trap catch tests.

(6) *Endo*-brevicomin added to attractant-baited traps significantly reduces the number of beetles caught.

(7) High concentrations of verbenone + *endo*-brevicomin affect an increased inhibitory activity on attractant baited traps over each compound alone.

(8) None of the behavioral compounds except high concentrations of verbenone significantly affect the sex ratio of responding beetles. Verbenone appears to balance the ratio of responding beetles by reducing the number of male beetles responding.

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Table 7.—Influence of verbenone and *endo*-brevicomin on the response of *D. frontalis* to traps baited with an attractant (1977).

Treatment[a]	Total no. caught	± SE trap catch[bc]	Sex ratio
Attractant	750	50.0±10.4 a	0.69
Attractant + verbenone (10mg/h)	486	32.4±7.4 ab	0.66
Attractant + *endo*-brevicomin (0.5mg/h)	317	21.1±4.2 b	0.58
Attractant + verbenone (10mg/h) + *endo*-brevicomin (0.5mg/h)	177	11.8±3.2 c	0.65
Blank wingtrap	43	2.9±0.7 d	1.05

[a] Elution rates for compounds tested are presented in Table 1. The attractant was a 1:4 mixture of frontalin and alpha-pinene.
[b] Means followed by same letters are not significantly different at $P < 0.5$ level based upon pairwise comparison of means using the Mann-Whitney test.
[c] 15 replicates 30 min/replicate.

Table 8.—Sex ratio of southern pine beetles responding to flight traps baited with behavioral chemicals and attractants.[a]

Compounds	No. of replicates	Sex ratio (♀:♂)[b]
Attractants[c]	149	0.89 b
Verbenone		
1x concentration	44	1.45 ab
2x concentration	21	1.33 ab
3x concentration	20	1.76 ab
4x concentration	34	1.93 a
Endo-brevicomin	35	1.41 ab
Exo-brevicomin	44	1.03 b
Endo-exo-brevicomin[d]	20	0.78 b
Trans-verbenol	48	1.06 b

[a] Attractants used were frontalin + *alpha*-pinene, frontalin + turpentine and frontalin + *trans*-verbenol + turpentine.

[b] Ratios followed by the same letter are not significantly different at $P < 0.05$ level based upon Duncan's Multiple Range Test for variable ratios.

[c] Attractants tested were frontalin; frontalin + *alpha*-pinene; frontalin + turpentine; and frontalin + *trans*-verbenol + turpentine. Analysis of variance of nested attractants (Snedecor and Cochran, 1967) with an $F_{3,1,45} = 0.79$, F probability of 50%.

[d] A 50:50 mixture of the *endo-exo*-isomers was used.

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