EFFECTS OF GREEN LEAF VOLATILES ON THE RESPONSE TO AGGREGATION PHEROMONES BY TWO SPECIES OF AMBROSIA BEETLES, *GNATHOTRICHUS SULCATUS* AND *G. RETUSUS*

by

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EFFECTS OF GREEN LEAF VOLATILES ON THE RESPONSE TO AGGREGATION PHEROMONES BY TWO SPECIES OF AMBROSIA BEETLES.

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ABSTRACT

Experiments were conducted to test the null hypothesis that green leaf volatiles, abundant in herbaceous plants and angiosperm trees, have no effect on the aggregative response by the conifer-infesting ambrosia beetles, *Gnathotrichus sulcatus* (LeConte) and *G. retusus* (LeConte) (Coleoptera: Scolytidae), to pheromone-baited multiple-funnel traps. A blend of four green leaf alcohols, 1-hexanol, (*E*)-2-hexen-1-ol, (*Z*)-2-hexen-1-ol, and (*Z*)-3-hexen-1-ol, released at ca. 4 mg per 24 hr per compound, combined with a blend of two green leaf aldehydes, hexanal and (*E*)-2-hexenal, released at ca. 13.0 mg per 24 hr per compound, reduced trap catches to levels not significantly different from those to unbaited control traps for both sexes of each species. Green leaf alcohols, released alone or in a quaternary blend, also demonstrated varying degrees of disruptive capacity. For *G. sulcatus*, an evaluation of all possible binary and ternary blends of green leaf alcohols revealed additive rather than synergistic disruptive effects; binary blends reduced trap catches 60% to 88% while ternary combinations caused reductions of 80% to 93%. No specific blend was superior, demonstrating redundancy in the disruptive effect. Released together, the two green leaf aldehydes enhanced trap catches for both species; (*E*)-2-hexenal alone cause a weak enhancement. The attractive effects were consistently masked when the aldehydes were combined with the alcohols. These results lead to rejection of the null hypothesis on the basis of both positive and negative effects. The enhancement of response to pheromones caused by the green leaf aldehydes suggest that they or other compounds represent as yet unidentified host kairomones for conifer-infesting ambrosia beetles. Long-range repellency by green leaf alcohols would be adaptive for both species, because host-seeking beetles would minimize the risk of predation, desiccation, and the expenditure of energy involved in close-range inspection of non-host angiosperms. A summary of known responses by eight other scolytids to green leaf volatiles in field trapping studies reveals consistent repellency, but variations between and within species in bioactive compounds. An exception occurs for *Pityogenes knetchteli* Swaine, which uses 1-hexanol as a multifuncional pheromone. Disruptive green leaf volatiles may offer promise as forest product protectants against ambrosia beetles, by disguising hosts as non-hosts.

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DAMAGE AND ECONOMIC IMPACT

Gnathotrichus sulcatus (LeConte) and *G. retusus* (LeConte) (Coleoptera: Scolytidae) are forest products pests in western North America (Furniss and Carolin, 1977). Together with the striped ambrosia beetle, *Trypodendron lineatum* Olivier, they infest the highly valued sapwood of felled timber and freshly milled green timber (McLean and Borden, 1975a). *Gnathotrichus sulcatus* and *G. retusus* attack nearly all species of conifers (Furniss and Carolin, 1977), and attacks on logs can begin within the first week of felling (Cade et al., 1970); vulnerable host material occurs at logging sites, booming grounds, dryland sorts, and sawmills (McLean and Stokkink, 1988). Damage does not result in a structural defect (Shore, 1992). However, the beetles' galleries, darkly stained by their symbiotic ambrosia fungi, cause conspicuous defects on dimension lumber and veneer (McLean, 1985). In turn this degrade causes direct financial loss in selling price, and indirect losses due to increased culling, heavier slabbing, and resorting and resawing damaged lumber (Gray and Borden, 1985; Orbay and McLean, 1994). Further costs result from export restrictions, altered forest harvesting practices to remove vulnerable inventory, and ambrosia beetle pest management programs (Borden, 1988). The annual economic impact of ambrosia beetles is estimated to range from $95 to $189 million (Can.) on the British Columbia coast alone (Lindgren and Fraser, 1994).

BIOLOGY AND HOST SELECTION

Gnathotrichus sulcatus and *G. retusus* have no true diapause, overwintering mainly as adults (Liu and McLean, 1993) or larvae (J.H. Borden, pers. comm.) in coniferous host materials. Adult emergence and flight begins in the spring when daily temperatures exceed 15°C (Daterman et al., 1965; Liu and McLean, 1993); both species have a bimodal diurnal flight pattern with a small flight peak in the morning and a large peak at dusk (Rudinsky and Schneider, 1969), primarily regulated by light intensity (Liu and McLean, 1993). Attacks are semiochemical mediated. Guided in flight by primary host attractants, such as ethanol (Cade et al., 1970) and α-pinene (Rudinsky, 1966; Borden et al., 1981; but see Liu and McLean, 1989), pioneer males select hosts and initiate attack, releasing an aggregation pheromone in the frass (Borden, 1974). Secondary attraction to pheromone and the host kairomones ethanol and α-pinene results in aggregation by conspecific males and females (Borden et al., 1980b); mating and further attack ensues. Species specificity in sympatric *Gnathotrichus* populations is essentially maintained by the enantiomeric composition of the pheromone sulcatol, 6-methyl-5-hepten-2-ol (Byrne et al., 1974). *Gnathotrichus sulcatus* aggregates to (±)-sulcatol and requires both enantiomers to elicit a response (Borden et al., 1976). *Gnathotrichus retusus* responds only to (*S*)-(+)-sulcatol ("retusol") and is inhibited by the antipode (Borden et al., 1980a). Males mate with a single female. Following mating, the female continues excavating the gallery (Prebble and Graham, 1957). Species-specific fungal spores are released from forecoxal cavities of males; these germinate and the resulting mycelia and fruiting bodies serve as the food of larvae and adults which crop the fungus from the gallery walls (Farris, 1963). In the sapwood, egg galleries are constructed off the entrance gallery at intervals, more or less following annual rings (Furniss and Carolin, 1977). Eggs are laid in niches cut in the sides of a gallery, and the larvae construct "cradles" in which they feed on the fungus growing in the surrounding wood (McLean, 1976). Following pupation within the cradles, emergent callow adults mature by consuming more fungi, presumably from the large, non-brood-producing distal portions of egg galleries (Zanuncio, 1981; Liu and McLean, 1993).

In the Pacific Northwest, *G. sulcatus* appears to have two overlapping generations, with extended adult flight peaks in late spring and late summer (Shore, 1992). *Gnathotrichus retusus* is primarily univoltine, with populations peaking in May; however some flight may occur up to late September (Liu and McLean, 1993).

MANAGEMENT

Until the late 1960's ambrosia beetle management relied upon aerially or ground applied pesticides, such as DDT or lindane, to protect logs from attack (Borden, 1988). However, due to safety concerns for the worker and the environment, no chemical pesticides are currently registered in Canada for use against ambrosia beetles (Shore, 1992). Today, management strategies primarily involve reducing host availability in the forest and at timber processing sites, and semiochemical-based mass trapping in the latter locations. Removing logs quickly from forest settings after felling, and avoiding stockpiling logs at processing sites is effective (Shore, 1992), but weather and market conditions, and resistance to change within the industry can interfere with success

(McLean and Stokkink, 1988; Shore, 1992). Water misting can effectively protect high value logs from attack (Nijholt, 1978), but is restricted to sites adjacent to an abundant source of water. Other disadvantages of water misting include frequent maintenance, wet working conditions and potential environmental hazards from leaching (Borden 1988; Shore, 1992). Ambrosia beetle populations can be effectively reduced with semiochemical baited traps and trap log bundles (Borden, 1988). These two tactics are employed at dryland sorts and sawmills. Semiochemical-baited multiple-funnel traps (Lindgren, 1983) are used to mass trap beetles before they can reach their hosts, and secondarily to provide spatial and temporal distribution data (Lindgren, 1990). Suitably-aged semiochemical-baited cull logs are deployed around timber-processing sites. Attacking beetles are diverted away from high-value inventory and are induced to attack these trap logs. They and their brood are killed by processing the logs through a chipper before beetle emergence (Shore, 1992). Integrating the above strategies and tactics where possible provides the most effective ambrosia beetle management (Borden, 1988).

CURRENT NEEDS

Despite recent advances in ambrosia beetle management, the need remains for an efficient, cost-effective repellent that could be used to protect logs from attack. Such a tactic would be complementary to current management practices, and could enhance protection of timber in processing areas. Additionally, because of reduced size of clearcuts mandated by B.C.'s Forest Practices Code (Petter, 1994) and the attendant logistic difficulties in timely removal of timber from harvesting sites, there is a renewed need for protection of felled and bucked timber in the woods (J.H. Borden, pers. comm.).

To date, only a few potentially-repellent materials have been rigorously evaluated. Experiments testing the capability of pine oil and oleic acid to mask primary and secondary odors provided significant results; against *G. sulcatus* and *T. lineatum*, pine oil and oleic acid protected logs from attack for 49.5 and 41.2 days, respectively (Nijholt, 1980). However, both materials are relatively expensive, and pine oil is particularly unpleasant and difficult to work with; consequently neither has been developed operationally (J.H. Borden, pers. comm.).

Other compounds with conceivable protectant ability include antiaggregation pheromones and repellent interspecific synomones (Borden, 1996). However, there is no evidence for antiaggregation pheromones in any species of ambrosia beetle (Borden, 1996), there is no significant interspecific repellancy among *T. lineatum*, *G. sulcatus* and *G. retusus* (Borden et al., 1981), and repellent semiochemicals from other heterospecific scolytid beetles have not been discovered.

Another possible source of repellency is non-host volatiles that could be used to disguise the resource as an inappropriate host (Borden, 1996). Most conifer-infesting scolytids, such as *Gnathotrichus* spp., seek hosts which are relatively scarce and distributed unevenly in space and time (Atkins, 1966; Schroeder, 1992). Consequently, it would be of adaptive significance for these insects to reduce time and energy costs and the risk of mortality during dispersal by using olfactory cues to reject non-hosts quickly (Gries et al., 1989; Schroeder, 1992). One abundant non-host olfactory cue for such scolytids are green leaf volatiles (GLVs). GLVs are six-carbon alcohols, aldehydes, and derivative esters common to a wide variety of plant families (Visser et al., 1979). These chemicals are especially abundant in herbaceous plants and angiosperm shrubs and trees; produced by oxidative degradation of leaf lipids, they are continuously released by leaves (Visser and Ave, 1978).

Recent research has demonstrated the ability of GLVs to disrupt host selection in conifer-infesting scolytids. Dickens et al. (1992) reported that hexanal and 1-hexanol disrupted the response of three species of coniferous bark beetles, the southern pine beetle, *Dendroctonus frontalis* Zimmerman, the eastern fivespined ips, *Ips grandicollus* (Eichhoff), and the small southern pine engraver, *Ips avulsus* (Eichhoff), to traps baited with attractant semiochemicals. When placed in multiple-funnel traps baited with the aggregation pheromones (*E*)-verbenol and *exo*-brevicomin and the host tree kairomone myrcene, (*E*)-2-hexen-1-ol and (*Z*)-3-hexen-1-ol reduced trap catches of both sexes of mountain pine beetle, *Dendroctonus ponderosae* Hopkins, to levels not significantly different from those in unbaited control traps (Wilson et al., 1996). In addition, the same GLV combination reduced attack on attractant-baited trees to levels not significantly different from those on unbaited trees. Borden et al. (1997) reported that, for the ambrosia beetle *T. lineatum* in the British Columbia interior, four green leaf alcohols [1-hexanol, (*E*)-2-hexen-1-ol, (*Z*)-2-hexen-1-ol, and (*Z*)-3-hexen-1-ol] released alone or in a quaternary blend resulted in a 63% to 78% reduction in catches in traps baited with aggregation pheromone, and two aldehydes [hexanal and (*E*)-2-hexenal] released as a binary blend were weakly disruptive. At the B.C. coast, the quaternary alcohol blend was weakly inhibitory to *T. lineatum* in one of two experiments, and in one of two experiments the binary aldehyde blend caused a moderate enhancement of catches in lineatin-baited traps. In this study I tested the null hypothesis that non-host GLVs (both aldehydes and alcohols) would have no effect on the aggregative response of *G. sulcatus* and *G. retusus* to their respective pheromones.

MATERIALS AND METHODS

TRAPPING EXPERIMENTS

Experiments on *G. sulcatus* were located at the University of British Columbia's Malcolm Knapp Research Forest, Maple Ridge, B.C. The study site is in the Coastal Western Hemlock (CWH) biogeoclimatic zone (Pojar et al., 1991), at 100-150 m elevation. The stand is naturally regenerated mixed second growth, dominated by western hemlock, *Tsuga heterophylla* (Raf.) Sarg., with occasional Douglas-fir, *Psuedotsuga menziesii* (Mirb.) Franco, and western red cedar, *Thuja plicata* Donn ex D.Don., with scattered paper birches, *Betula papyrifera* Marsh, bigleaf maples, *Acer macrophyllum* Pursh, vine maples, *Acer circinatum* Pursh, and black cottonwood, *Populus trichocarpa* Torr. & Gray.

Experiments on *G. retusus* were set up in an abandoned dryland log sort at an elevation of 500 m, at North Bend, B.C. in the Interior Douglas-fir (IDF) biogeoclimatic zone (Hope et al., 1991). The forest is dominated by Douglas-fir, with some black cottonwoods, paper birches, and mixed deciduous brush occurring near the edge. The sort itself was largely empty, except for some old Douglas-fir and western red cedar logs stacked in the central area, and scattered piles of coarse woody debris.

At both sites, 12-unit multiple funnel traps (Lindgren, 1983) were set up at least 15 m apart, and away from deciduous trees. Traps were hung from ropes or poles, along the rights-of-way of forestry roads at the Malcolm Knapp Research Forest, and around the perimeter of the dryland sort at North Bend. Eight randomized complete block experiments (Exp.) were conducted for *G. sulcatus*, and three for *G. retusus*, with dates and numbers of replicates as in Table 1, and chemical stimuli, sources, purities, release devices and release rates as in Table 2. The GLVs were chosen because they often are reported in the literature, and are inexpensive and readily available. In each experiment, the pheromone for the test species was combined with the GLV treatments. Pheromone-baited and unbaited control traps served as positive and negative control treatments, respectively, against which the bioactivity of GLV treatments could be assessed.

GLV treatments for Exp. 1-3 and 9-11 were identical for *G. sulcatus* and *G. retusus*, respectively. Exp. 1 and 9 tested an aldehyde blend, hexanal and (*E*)-2-hexenal, and an alcohol blend, 1-hexanol, (*E*)-2-hexen-1-ol, (*Z*)-2-hexen-1-ol, and (*Z*)-3-hexen-1-ol, alone. Exp. 2 and 10 tested the two aldehydes alone and together, and Exp. 3 and 11 tested the four alcohols alone and in a quaternary blend. For the remaining *G. sulcatus* experiments, Exp. 4 and 5, respectively, tested all possible binary and ternary combinations of the alcohols. Exp. 6 examined the two aldehydes alone at the standard release rate of 13 mg per 24 hr (Table 2), the two aldehydes alone at twice that rate, and the two aldehydes together at the low release rate to determine if enhanced attraction observed in Exp. 1 and 2 was dose-dependant or synergistic in nature. Exp. 7 tested the aldehyde blend and ethanol alone and together, to compare relative attractive ability. Exp. 8 repeated Exp. 2, to re-examine aldehyde treatment effects. Captured insects from all experiments were stored frozen in plastic bags prior to later sexing and counting of all captured *Gnathotrichus* spp.

TABLE 1. Numbers, dates, and numbers of replicates for field trapping experiments on *G. sulcatus* at the Malcolm Knapp Research Forest, Maple Ridge, B.C., and *G. retusus* at North Bend, B.C.

Target species	Exp. No.	Dates	Number of replicates[a]
G. sulcatus	1	15 March-12 May, 1996	10
	2	12-24 May, 1996	10
	3	24 May-21 June, 1996	19
	4	22 June-16 Aug., 1996	21
	5	16 Aug.-9 Sept., 1996	18
	6	9-13 Sept., 1996 27 Sept.-2 Oct., 1996	17
	7	13-27 Sept., 1996	12
	8	2-19 Oct., 1996	10
G. retusus	9	8 May-4 June, 1996 24-29 June, 1996 29 June-6 July, 1996	♂ 14, ♀ 17
	10	4-12 June, 1996 6-13 July, 1996	♂ 13, ♀ 17
	11	13 July-30 Aug., 1996	♂ 6, ♀ 10

[a] Low numbers of *G. retusus* limited the number of experiments that could be conducted. For *G. retusus*, all replicates with no captured beetles in response to any trap for a given sex were discarded, causing uneven numbers of replicates between sexes.

TABLE 2. Description of semiochemicals employed in the randomized block trapping experiments, for the effect of GLVs on *G. sulcatus* and *G. retusus*.

Chemical[a]	Source[b]	Purity(%)[b]	Experiments	Release devices (P)[b]	Release rate (mg per 24 hr)[c]
sulcatol[d]	P	99.6	1-8	bubble cap	3.5
retusol[d]	P	100	9-11	bubble cap	5.0-6.0
hexanal	A	98	1,2,6-8,9,10	bubble cap	13.0
(*E*)-2-hexenal	A	99	1,2,6-8,9,10	bubble cap	13.0
1-hexanol	A	98	1,3-5,9,11	bubble cap	3.8
(*E*)-2-hexen-1-ol	A	95	1,3-5,9,11	bubble cap	3.8
(*Z*)-2-hexen-1-ol	B	92	1,3-5,9,11	bubble cap	3.8
(*Z*)-3-hexen-1-ol	A	98	1,3-5,9,11	bubble cap	3.8
ethanol	P	95	7	pouch	30.0-50.0

[a] All GLVs stabilized with 1-2% (wet weight) Ethanox® 330 antioxidant, Ethyl Chemicals Group, Baton Rouge, LA.

[b] Symbols as follows: P=Phero Tech Inc., Delta, B.C.; A=Aldrich Chemical Company, Milwaukee, WI; B=Bedoukian Research Inc., Danbury, CT. Purities as determined by manufacturer.

[c] Determined by Phero Tech in the laboratory at 22-24° C.

[d] Chemical name 6-methyl-5-hepten-2-ol.

DATA ANALYSIS

To satisfy criteria for normality and homoscedasticity, all data for *G. sulcatus* were converted to proportions of total beetles captured by sex within each replicate and transformed by arcsin $\sqrt{x}$, and all data for *G. retusus* (except Exp. 9, males) were transformed by $\log(x+1)$ (Zar, 1996). The numbers of *G. retusus* captured were too low to convert to proportions. For all but Exp. 9, means were compared by ANOVA (GLM procedure, SAS institute Inc., 1988) and the Ryan-Einot-Gabriel-Welsh Multiple Q-test (REGWQ procedure, SAS Institute Inc., 1988; Day and Quinn, 1989). For male *G. retusus* in Exp. 9, Friedman's nonparametric randomized block analysis of variance (Zar, 1996) was used, as the data were non-normal and heteroscedastistic. Dunnett's t-test (GLM procedure, SAS Institute Inc., 1988) was also used to compare treatment means for *G. sulcatus* in Exp. 2 (males) and Exp. 3 (females). In all cases $\alpha=0.05$. For *G. sulcatus* and *G. retusus*, 2 and 6 values, respectively, for missing data were estimated using Li's (1964) procedure (Zar, 1996).

RESULTS

G. sulcatus

Green leaf alcohols consistently caused a significant reduction in trap catches of *G. sulcatus* relative to sulcatol baited controls (Figs. 1,3-5). Relative trap catch reductions varied both within and between experiments, for green leaf alcohol treatments. Conversely, in two of four experiments the two green leaf aldehydes when tested together significantly enhanced trap catches over those to sulcatol alone (Figs. 2,6-8). Aldehyde-alcohol blends always lowered trap catches significantly, relative to sulcatol alone (Fig. 1).

In Exp. 1, the alcohol and the aldehyde-alcohol blends reduced response by *G. sulcatus* to sulcatol by 73% and 84%, and 76% and 74%, for males and females, respectively (Fig. 1). Both treatments reduced trap catches for both sexes to levels not significantly different from those to unbaited control traps. The aldehyde blend in combination with sulcatol caused a significant increase in the numbers of captured males. In Exp. 2, the aldehyde blend again caused enhanced trap catches, in this instance significantly so for both sexes (Fig. 2). Neither hexanal nor (*E*)-2-hexenal had any effect alone. Although the REGWQ procedure failed to detect a difference between the unbaited control and the sulcatol, hexanal, and (*E*)-2-hexenal treatments for males, (Fig. 2), Dunnett's test demonstrated that traps baited with sulcatol alone or with hexanal captured significantly more males than unbaited traps.

When single alcohols were compared in Exp. 3, only (*E*)-2-hexen-1-ol caused a significant reduction in trap catches. Although this effect occurred only for males

FIG. 1. Percent captures of 134 male and 658 female *G. sulcatus* in Exp.1 in multiple-funnel traps baited with sulcatol alone or with blends of two green leaf aldehydes and four alcohols. Long dash indicates no treatment. Bars associated with the same letter are not significantly different, REGW test, $P < 0.05$, $n = 10$.

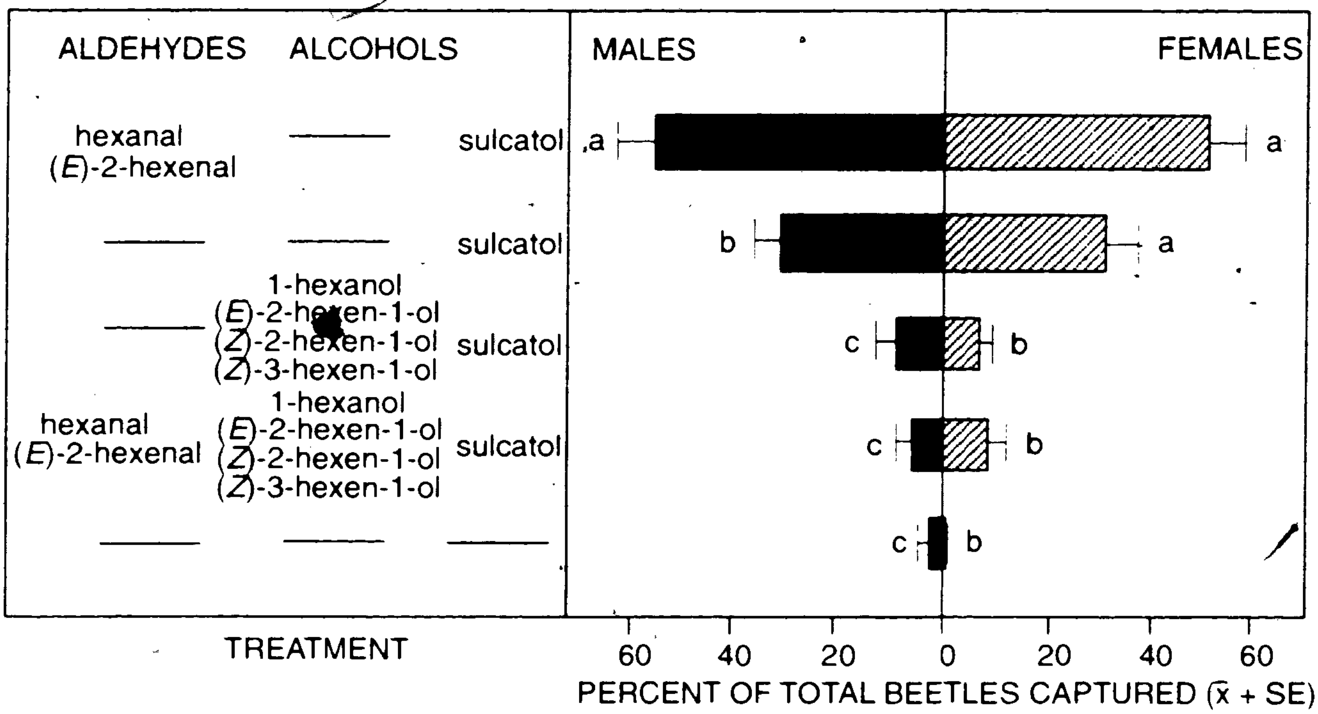
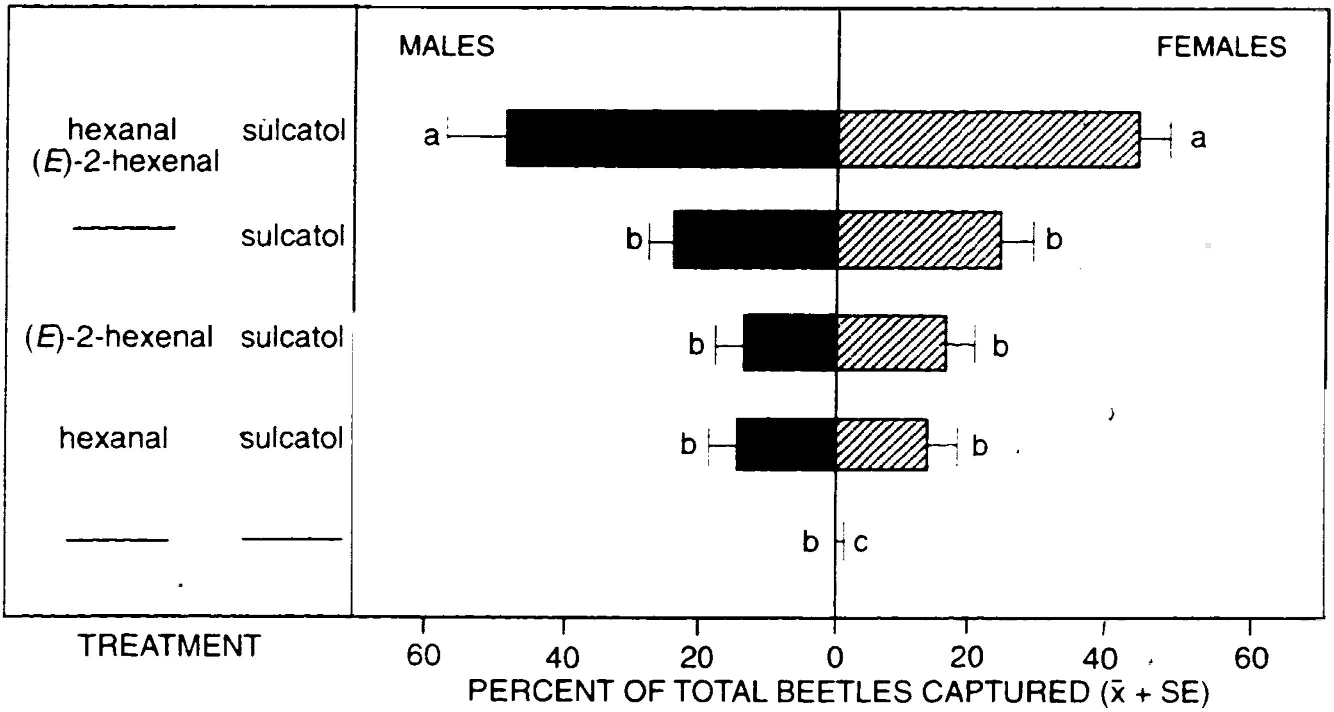

ALDEHYDES
ALCOHOLS
MALES
FEMALES
hexanal
(E)-2-hexenal
sulcatol
a
sulcatol
b
a
1-hexanol
(E)-2-hexen-1-ol
(Z)-2-hexen-1-ol
(Z)-3-hexen-1-ol
sulcatol
c
b
hexanal
(E)-2-hexenal
1-hexanol
(E)-2-hexen-1-ol
(Z)-2-hexen-1-ol
(Z)-3-hexen-1-ol
sulcatol
c
b
c
b
TREATMENT
60
40
20
0
20
40
60
PERCENT OF TOTAL BEETLES CAPTURED (x̄ + SE)

FIG. 2. Percent captures of 200 male and 1161 female *G. sulcatus* in Exp. 2 in multiple-funnel traps baited with sulcatol alone, with one of two green leaf aldehydes, or with both together. Long dash indicates no treatment. Bars associated with the same letter are not significantly different, REGW test, $P < 0.05$, n = 10.


MALES
FEMALES
hexanal (E)-2-hexenal
sulcatol
sulcatol
(E)-2-hexenal
sulcatol
hexanal
sulcatol
a
a
b
b
b
b
b
b
b
c
TREATMENT
60
40
20
0
20
40
60
PERCENT OF TOTAL BEETLES CAPTURED (x̄ + SE)

(Fig. 3), the response to sulcatol was reduced by 80% and did not differ from that to unbaited control traps. (*Z*)-3-hexen-1-ol, the alcohol blend, and 1-hexanol caused trap catches of males to fall to levels intermediate between those to sulcatol-baited and unbaited traps. Although the REGWQ procedure failed to detect a significant effect of any green leaf alcohol treatment for females (Fig. 3), Dunnett's test, using sulcatol as the control, showed that catches in sulcatol-baited traps were significantly larger than those in unbaited traps or traps in which (*E*)-2-hexen-1-ol or 1-hexanol was combined with sulcatol.

In Exp. 4, all binary combinations of green leaf alcohols reduced trap catches for both sexes to levels significantly lower than to sulcatol-baited control traps (Fig. 4). For males, trap catches from six of seven binary alcohol combinations reduced trap catches to levels not significantly higher than those to unbaited control traps. Females responded at statistically equal levels to all alcohol treatments. The combination of (*E*)-2-hexen-1-ol with (*Z*)-2-hexen-1-ol produced the largest trap catch reductions, 88% and 85% for males and females, respectively. Similarly, the combination of 1-hexanol with (*Z*)-2-hexen-1-ol was the weakest disruptant, with reductions of 64% and 60% for males and females, respectively.

All four ternary combinations of green leaf alcohols and the quaternary blend reduced the response of males in Exp. 5 to levels not different from those to unbaited control traps (Fig. 5). Reductions relative to sulcatol ranged from 80% to 92% for males and 81% to 91% for females, but only two ternary combinations and the quaternary blend were capable of reducing catches of females to levels not different from those in unbaited control traps.

FIG. 3. Percent captures of 247 male and 1287 female *G. sulcatus* in Exp. 3 in multiple-funnel traps baited with sulcatol alone or with one or all of four green leaf alcohols. Long dash indicates no treatment. Bars associated with the same letter are not significantly different, REGW test, $P<0.05$, $n=19$.

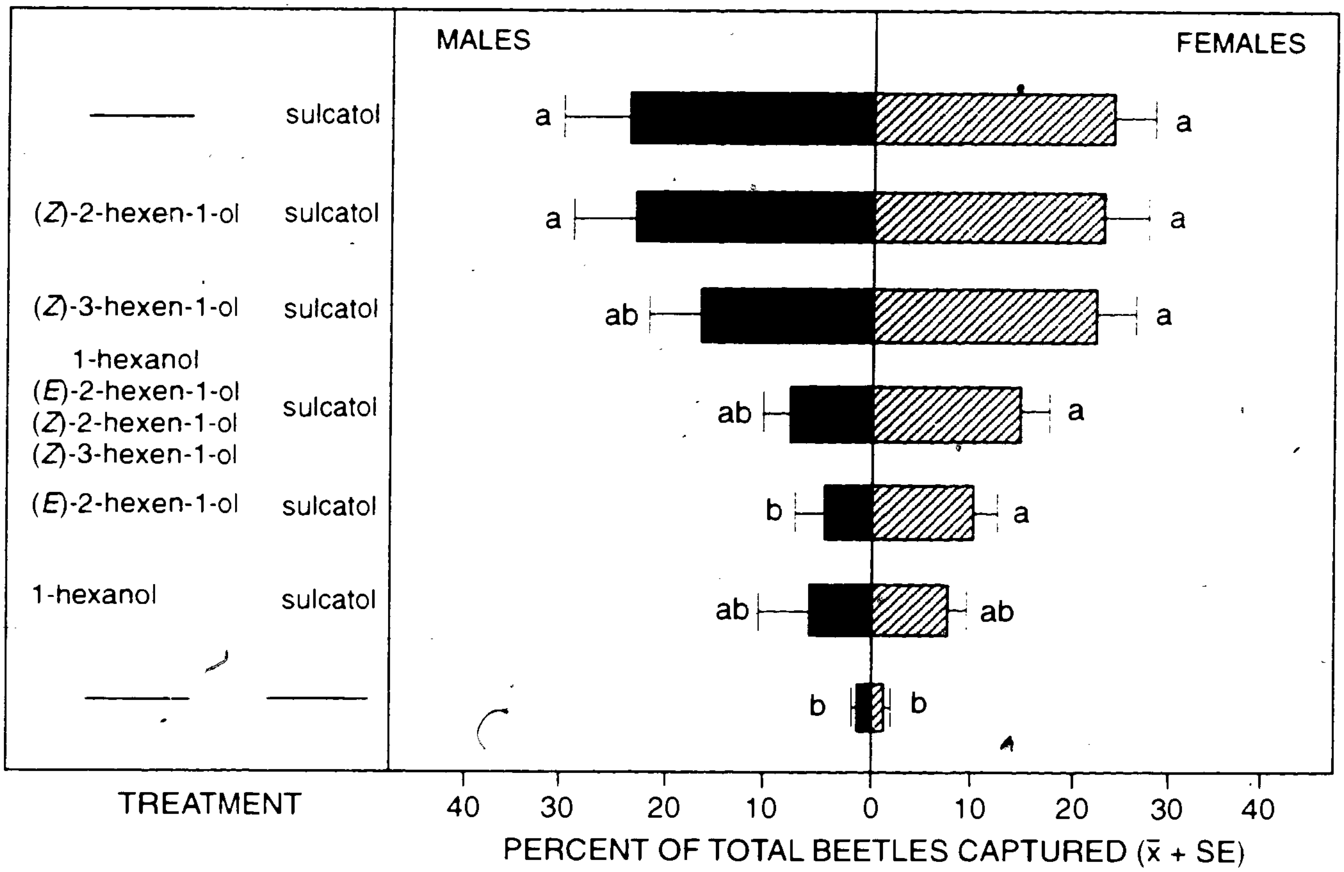

MALES
FEMALES
sulcatol
(Z)-2-hexen-1-ol sulcatol
(Z)-3-hexen-1-ol sulcatol
1-hexanol
(E)-2-hexen-1-ol
(Z)-2-hexen-1-ol
(Z)-3-hexen-1-ol
sulcatol
(E)-2-hexen-1-ol sulcatol
1-hexanol sulcatol
a
a
a
a
ab
a
ab
a
b
a
ab
ab
b
b
TREATMENT
40
30
20
10
0
10
20
30
40
PERCENT OF TOTAL BEETLES CAPTURED ($\bar{x}$ + SE)

FIG. 4. Percent captures of 314 male and 1462 female *G. sulcatus* in Exp. 4 in multiple-funnel traps baited with sulcatol alone, with four green leaf alcohols together or in all possible binary combinations. Long dash indicates no treatment. Bars associated with the same letter are not significantly different, REGW test, $P<0.05$, n=21.

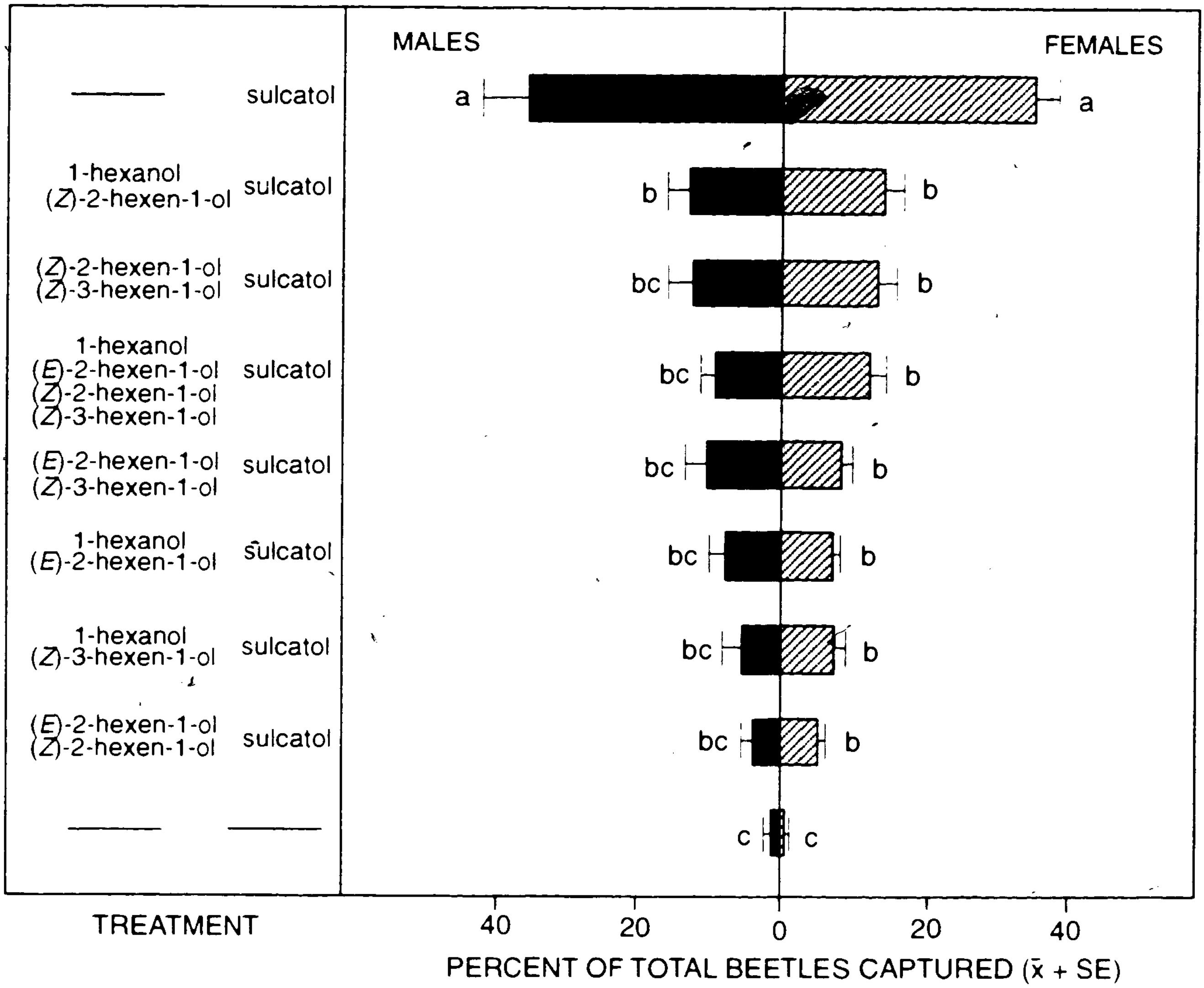
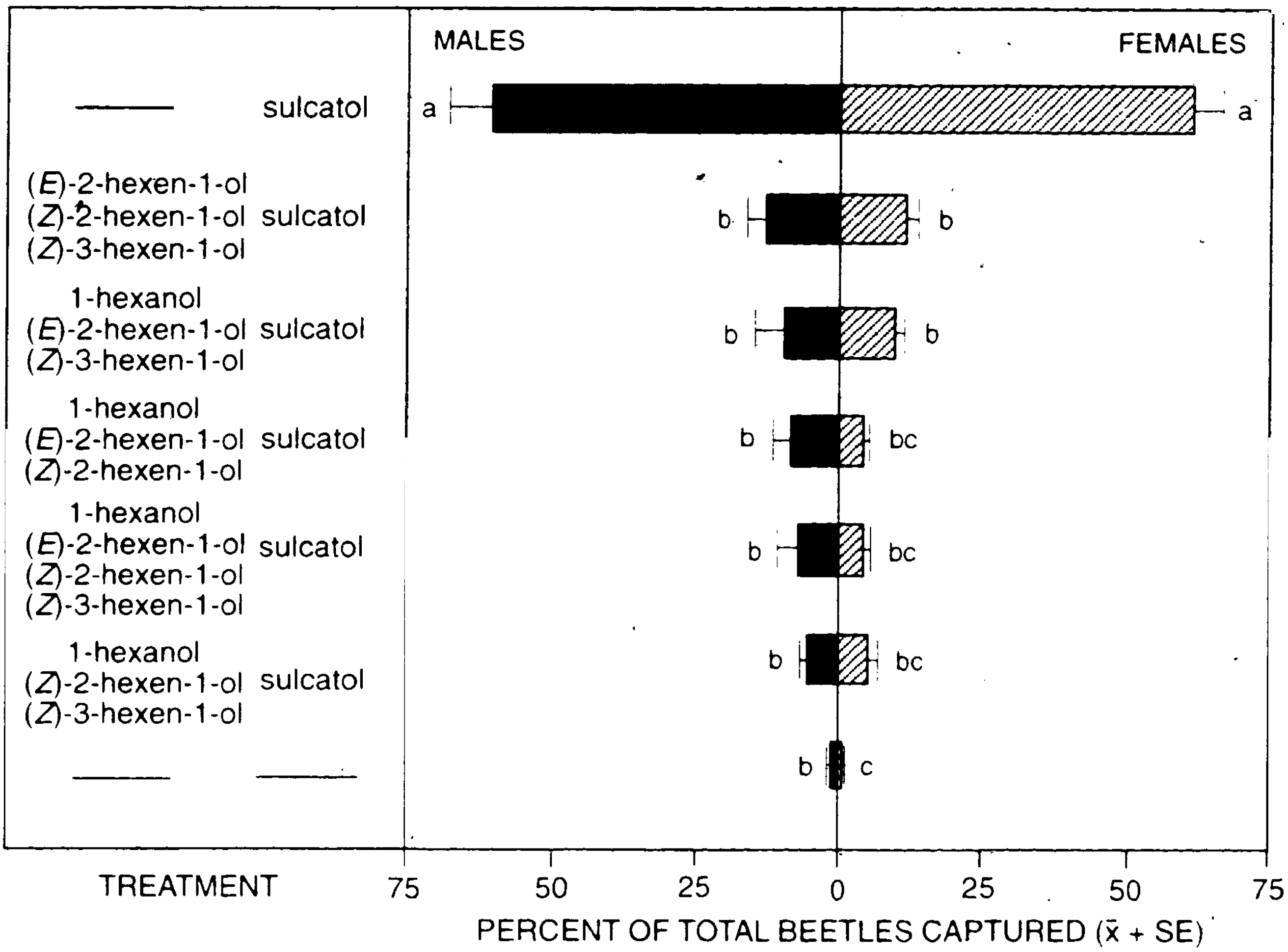

MALES
FEMALES
sulcatol
1-hexanol
(Z)-2-hexen-1-ol
sulcatol
(Z)-2-hexen-1-ol
(Z)-3-hexen-1-ol
sulcatol
1-hexanol
(E)-2-hexen-1-ol
(Z)-2-hexen-1-ol
(Z)-3-hexen-1-ol
sulcatol
(E)-2-hexen-1-ol
(Z)-3-hexen-1-ol
sulcatol
1-hexanol
(E)-2-hexen-1-ol
sulcatol
1-hexanol
(Z)-3-hexen-1-ol
sulcatol
(E)-2-hexen-1-ol
(Z)-2-hexen-1-ol
sulcatol
a
a
b
b
bc
b
bc
b
bc
b
bc
b
bc
b
bc
b
c
c
TREATMENT
40
20
0
20
40
PERCENT OF TOTAL BEETLES CAPTURED (x̄ + SE)

FIG. 5. Percent captures of 249 male and 1544 female *G. sulcatus* in Exp. 5 in multiple-funnel traps baited with sulcatol alone or with four green leaf alcohols together or in all possible ternary combinations. Long dash indicates no treatment. Bars associated with the same letter are not significantly different, REGW test, $P<0.05$, $n=18$.


MALES
FEMALES
sulcatol
(E)-2-hexen-1-ol
(Z)-2-hexen-1-ol sulcatol
(Z)-3-hexen-1-ol
1-hexanol
(E)-2-hexen-1-ol sulcatol
(Z)-3-hexen-1-ol
1-hexanol
(E)-2-hexen-1-ol sulcatol
(Z)-2-hexen-1-ol
1-hexanol
(E)-2-hexen-1-ol sulcatol
(Z)-2-hexen-1-ol
(Z)-3-hexen-1-ol
1-hexanol
(Z)-2-hexen-1-ol sulcatol
(Z)-3-hexen-1-ol
a
a
b
b
b
b
b
bc
b
bc
b
bc
b
c
TREATMENT
75
50
25
0
25
50
75
PERCENT OF TOTAL BEETLES CAPTURED (x̄ + SE)

In Exp. 6, neither male nor female *G. sulcatus* was more strongly attracted to sulcatol plus aldehydes than to sulcatol alone, including the previously active blend (Figs. 1,2) of hexanal with (*E*)-2-hexenal (Fig. 6). Traps with hexanal released at low and high rates captured males at levels intermediate between those to sulcatol-baited and unbaited control traps.

In Exp. 7 the aldehyde blend again did not significantly enhance attraction to sulcatol for both sexes (Fig. 7). In contrast, the blend of sulcatol with the known kairomone ethanol was very attractive to both sexes, greatly increasing trap captures relative to sulcatol alone. Combining ethanol with the green leaf aldehyde blend had no effect on catches of either sex.

In Exp. 8, response by females to sulcatol was enhanced by both the aldehyde blend and (*E*)-2-hexenal (Fig. 8). This is the only experiment in which a single aldehyde significantly enhanced attraction. For males, sulcatol in combination with the aldehyde blend was the only stimulus that resulted in trap catches significantly greater than to unbaited control traps.

G. retusus

The response of *G. retusus* to green leaf volatiles was generally similar to that of *G. sulcatus*, but low numbers of beetles captured may have obscured some biologically significant effects. In Exp. 9, the aldehyde-alcohol blend reduced responses to retusol by females to levels not significantly different from those to unbaited control traps (Fig. 9). The aldehyde blend demonstrated weak evidence for enhanced attraction to females. Males did not discriminate at all between treatments. In Exp. 10, males

FIG. 6. Percent captures of 535 male and 3410 female *G. sulcatus* in Exp. 6 in multiple-funnel traps baited with sulcatol alone or with one of two green leaf aldehydes at low and high release rates (Table 2), or with both aldehydes together at the low release rate. Long dash indicates no treatment. Bars associated with the same letter are not significantly different, REGW test, $P < 0.05$, n=17.

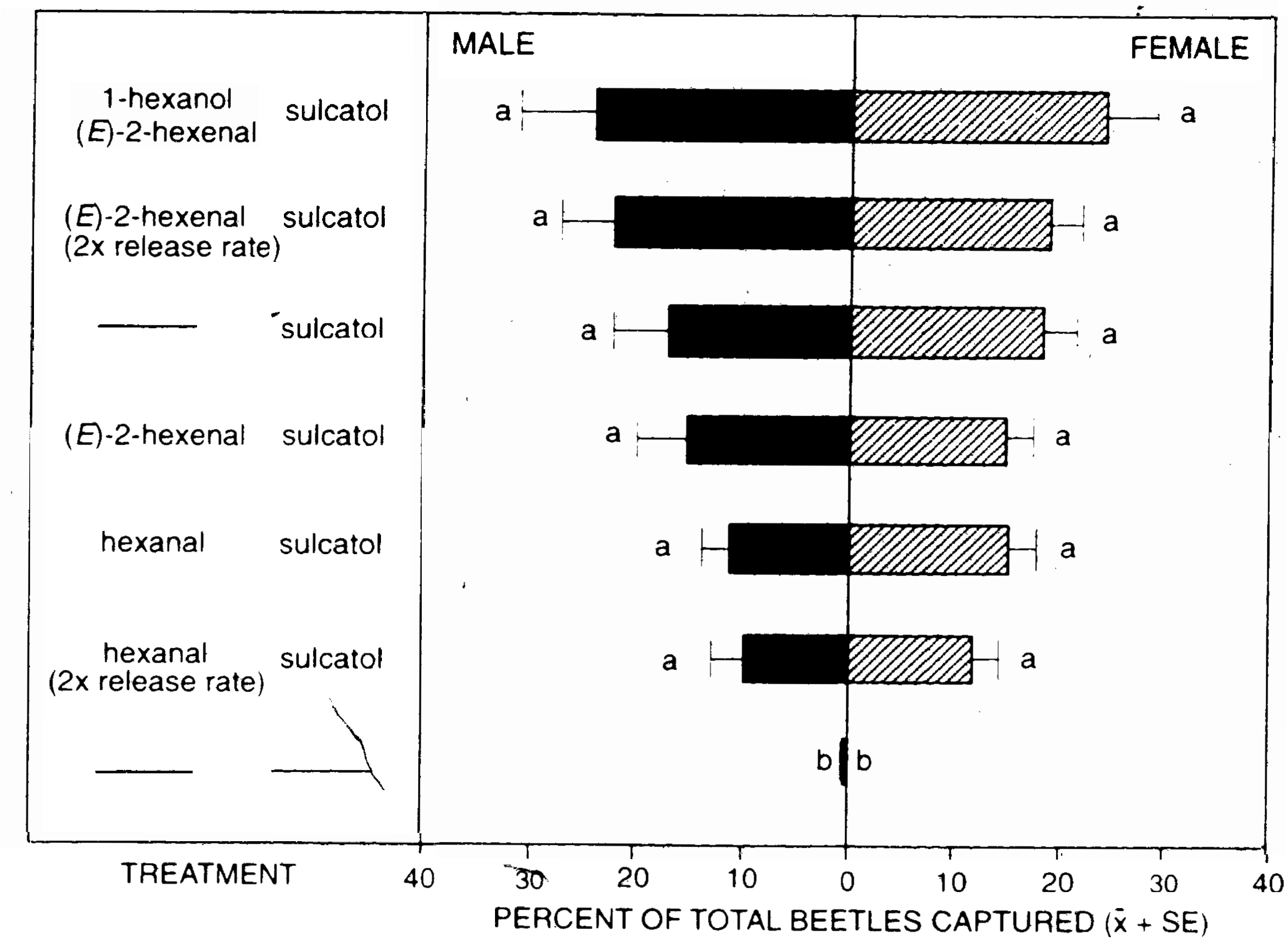

MALE
FEMALE
1-hexanol
(*E*)-2-hexenal
sulcatol
(*E*)-2-hexenal
(2x release rate)
sulcatol
sulcatol
(*E*)-2-hexenal
sulcatol
hexanal
sulcatol
hexanal
(2x release rate)
sulcatol
a
a
a
a
a
a
a
a
a
a
a
a
b
b
TREATMENT
40
30
20
10
0
10
20
30
40
PERCENT OF TOTAL BEETLES CAPTURED ($\bar{x}$ + SE)

FIG. 7. Percent captures of 1058 male and 3297 female *G. sulcatus* in Exp. 7 in multiple-funnel traps baited with sulcatol alone or with a blend of two green leaf aldehydes, ethanol, or both. Long dash indicates no treatment. Bars associated with the same letter are not significantly different, REGW test, $P < 0.05$, $n = 12$.

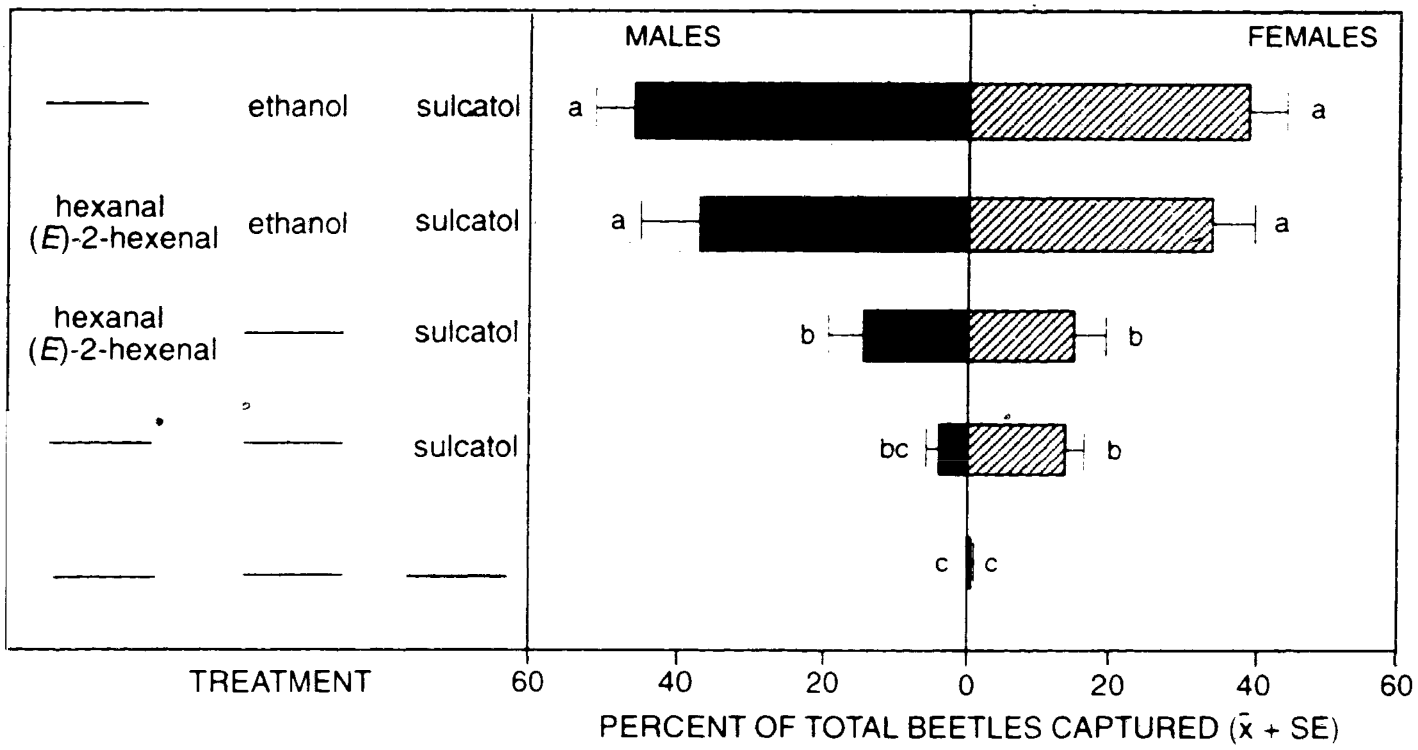

MALES
FEMALES
ethanol
sulcatol
hexanal
(E)-2-hexenal
ethanol
sulcatol
hexanal
(E)-2-hexenal
sulcatol
sulcatol
a
a
a
a
b
b
bc
b
c
c
TREATMENT
60
40
20
0
20
40
60
PERCENT OF TOTAL BEETLES CAPTURED (x̄ + SE)

FIG. 8. Percent captures of 72 male and 351 female *G. sulcatus* in Exp. 8 in multiple-funnel traps baited with sulcatol alone or with one of two green leaf aldehydes, or both together. Long dash indicates no treatment. Bars associated with the same letter are not significantly different, REGW test, $P < 0.05$, n=10.

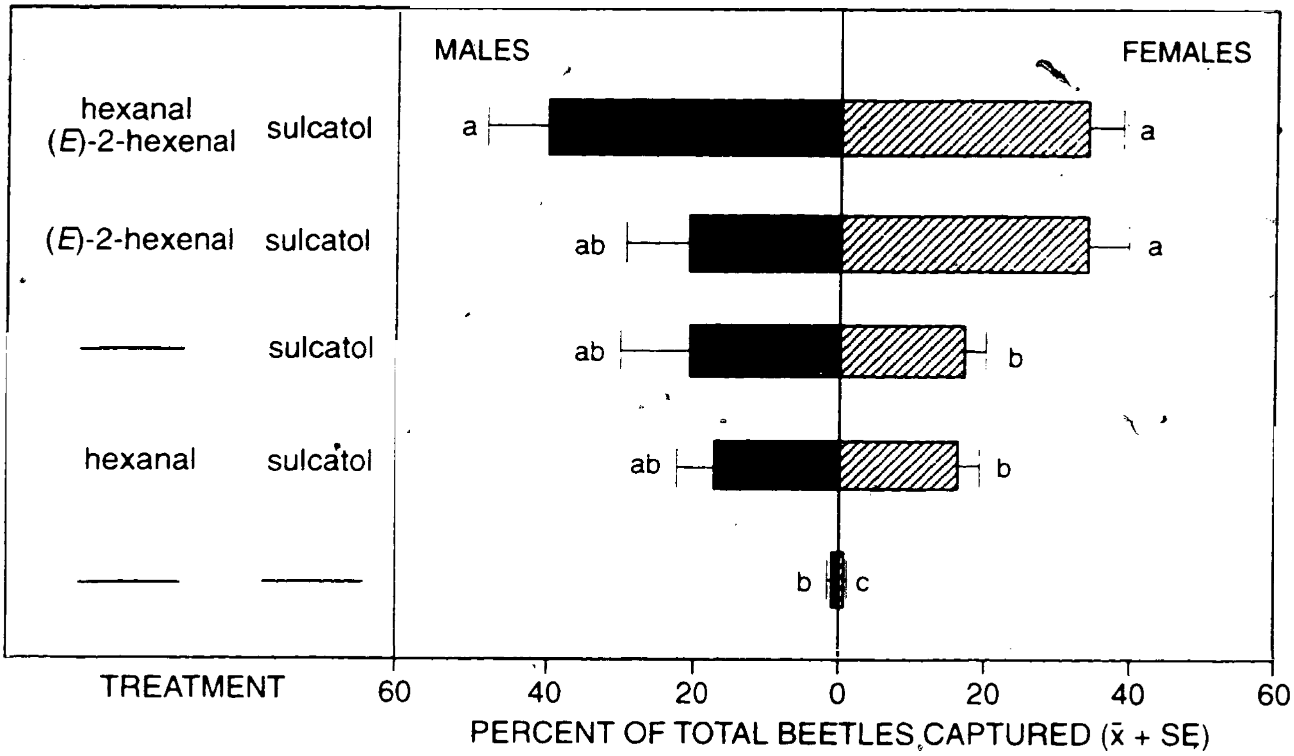
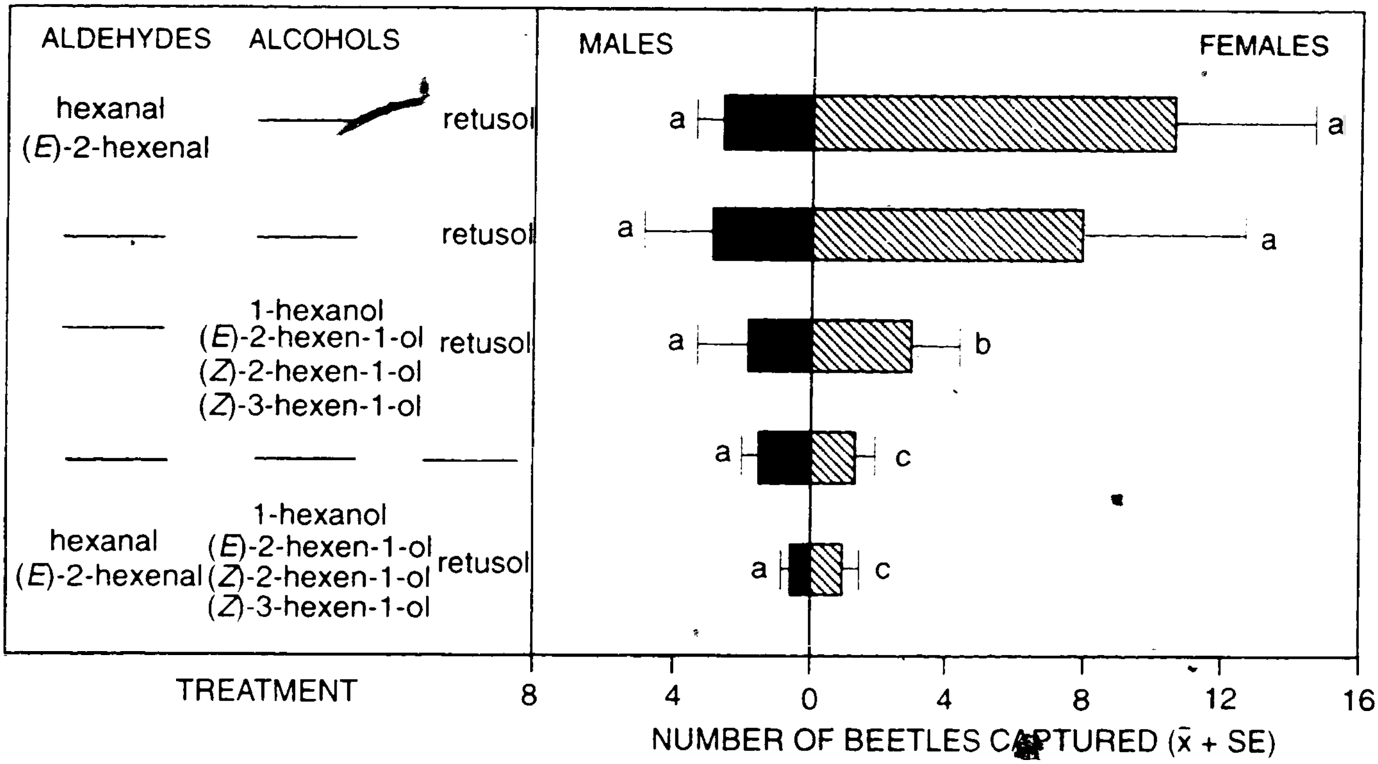

MALES
FEMALES
hexanal
(*E*)-2-hexenal
sulcatol
(*E*)-2-hexenal
sulcatol
sulcatol
hexanal
sulcatol
a
a
ab
a
ab
b
ab
b
b
c
TREATMENT
60
40
20
0
20
40
60
PERCENT OF TOTAL BEETLES CAPTURED (x̄ + SE)

FIG. 9. Captures of 120 male and 394 female *G. retusus* in Exp. 9 in multiple-funnel traps baited with retusol alone or with a blend of two green leaf aldehydes and four alcohols. Long dash indicates no treatment. For females, bars associated with the same letter are not significantly different, REGW test, $P < 0.05$, n=17. For males, Friedman's nonparametric randomized block analysis of variance failed to detect significant differences, $0.10 < P > 0.25$, n=14.


ALDEHYDES
ALCOHOLS
MALES
FEMALES
hexanal
(E)-2-hexenal
retusol
a
a
retusol
a
a
1-hexanol
(E)-2-hexen-1-ol
(Z)-2-hexen-1-ol
(Z)-3-hexen-1-ol
retusol
a
b
a
c
hexanal
(E)-2-hexenal
1-hexanol
(E)-2-hexen-1-ol
(Z)-2-hexen-1-ol
(Z)-3-hexen-1-ol
retusol
a
c
TREATMENT
8
4
0
4
8
12
16
NUMBER OF BEETLES CAPTURED (x̄ + SE)

responded at levels significantly greater than to unbaited control traps when retusol was combined with the aldehyde blend or (*E*)-2-hexenal (Fig. 10). Females did not discriminate between retusol alone or with either or both green leaf aldehydes. Both 1-hexanol and (*E*)-2-hexen-1-ol reduced responses by males to levels significantly lower than to retusol, and not different from those to unbaited control traps (Fig. 11). For females, all alcohol treatments produced catches significantly lower than to retusol alone, and all but (*Z*)-3-hexen-1-ol reduced catches to levels that could not be discriminated from levels of unbaited control traps.

FIG. 10. Captures of 100 male and 380 female *G. retusus* in Exp. 10 in multiple-funnel traps baited with retusol alone or with one of two green leaf aldehydes, or both together. Long dash indicates no treatment. Bars associated with the same letter are not significantly different, REGW test, $P<0.05$, males n=13, females n=17.

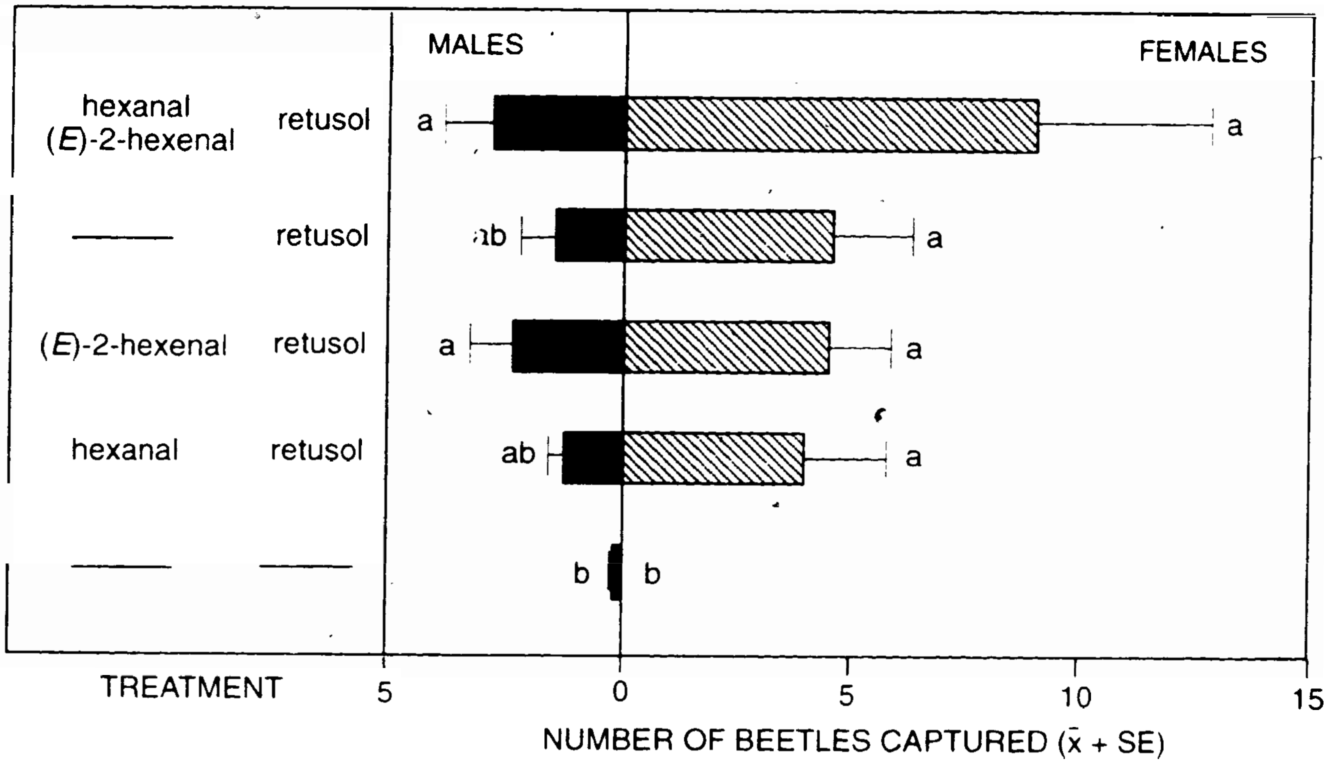
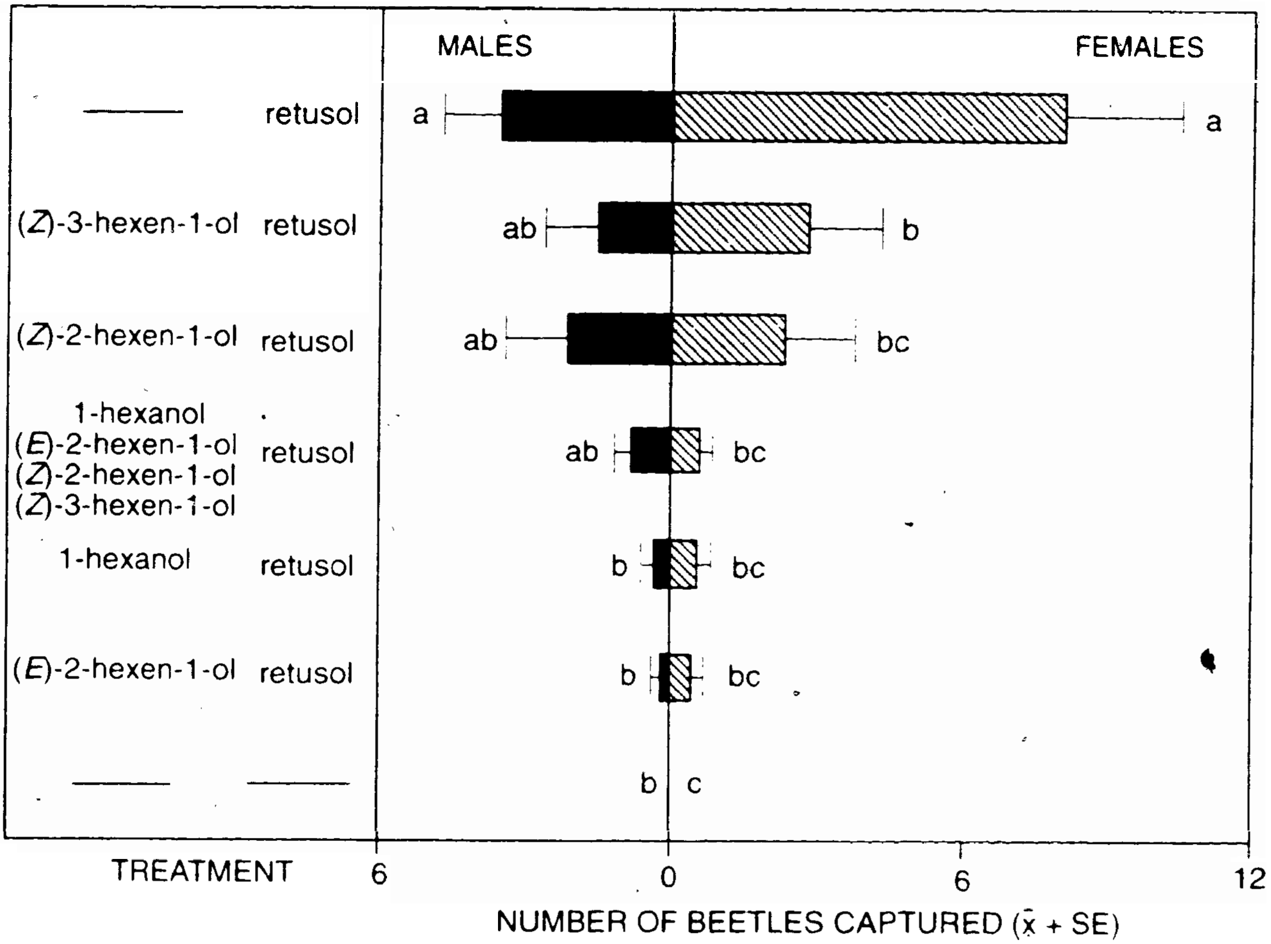

MALES
FEMALES
hexanal (E)-2-hexenal retusol
retusol
(E)-2-hexenal retusol
hexanal retusol
a
ab
a
ab
b
a
a
a
a
b
TREATMENT
5
0
5
10
15
NUMBER OF BEETLES CAPTURED (x̄ + SE)

FIG. 11. Captures of 48 male and 151 female *G. retusus* in Exp. 11 in multiple-funnel traps baited with retusol alone or with one or all of four green leaf alcohols. Long dash indicates no treatment. Bars associated with the same letter are not significantly different, REGW test, $P < 0.05$, males $n = 6$, females $n = 10$.


MALES
FEMALES
retusol
(Z)-3-hexen-1-ol retusol
(Z)-2-hexen-1-ol retusol
1-hexanol
(E)-2-hexen-1-ol
(Z)-2-hexen-1-ol
(Z)-3-hexen-1-ol retusol
1-hexanol retusol
(E)-2-hexen-1-ol retusol
a a
ab b
ab bc
ab bc
b bc
b bc
b c
TREATMENT
6
0
6
12
NUMBER OF BEETLES CAPTURED (x̄ + SE)

DISCUSSION

My results demonstrate that green leaf volatiles can both enhance and disrupt the aggregative response of both sexes of *G. sulcatus* and *G. retusus* to their respective pheromones. Therefore, the null hypothesis is rejected on the basis of both positive and negative effects. The disruptive effect is similar to that achieved with various green leaf volatiles on other conifer-inhabiting scolytid species in North America (Table 3). However, enhancement of response to aggregation pheromones is rare, occurring only in response to aldehydes by *T. lineatum*, another ambrosia beetle (Borden et al., 1997) and to 1-hexanol, a multifunctional pheromone for *Pityogenes knechteli* Swaine (Savoie et al, 1997).

In this study, the sex ratio of captured beetles for each treatment always favored females; as the responding sex, females are more likely to orient precisely to pheromone sources than are males, and thus are most likely to be captured in pheromone-baited traps (Borden, 1982). However, from ecological, evolutionary, and practical perspectives the disruptive effect on males is intriguing. As the pioneer sex, it would be highly adaptive for male *Gnathotrichus* spp. to respond negatively to any olfactory signal that would allow them to discriminate between potential hosts and non-hosts, thereby avoiding the risks of predation, desiccation, and metabolic expenditure associated with close-range inspection and rejection of non-hosts (Gries et al., 1989; Schroeder, 1992). Although conifer-inhabiting ambrosia beetles occasionally make the mistake of attacking an angiosperm host (Nijholt, 1981; Lindgren, 1986) the rarity of

TABLE 3. Responses of North American conifer-inhabiting scolytids to green leaf volatiles in field trapping experiments, with selected references. A=attractant; a=weak attractant; D=disruptant; d=weak disruptant; I=inactive. Unless specified, response applies to both sexes.

Scolytid species	Green leaf volatile	Behavioural response	Reference
Dendroctonus brevicomis Hopkins	hexanal	♂d ♀I	J.H.Borden, A.J. Stock, and L.J. Chong, pers. comm.
	(*E*)-2-hexenal	♂D ♀I	
	aldehyde blend[a]	I	
	alcohol blend[b]	I	
	aldehyde/alcohol blend[c]	I	
Dendroctonus frontalis Zimmerman	hexanal	D	Dickens et al., 1992
	1-hexanol	D	
	hexanal/1-hexanol blend	D	
Dendroctonus ponderosae Hopkins	hexanal	I	Wilson et al., 1996
	(*E*)-2-hexenal	I	
	aldehyde blend[a]	I	
	1-hexanol	D	
	(*E*)-2-hexen-1-ol	D	
	(*Z*)-2-hexen-1-ol	D	
	(*Z*)-3-hexen-1-ol	D	
	alcohol blend[b]	D	
	aldehyde/alcohol blend[c]	D	
Dendroctonus rufipennis (Kirby)	hexanal	I	T.H. Poland and J.H. Borden, pers. comm.
	(*E*)-2-hexenal	I	
	aldehyde blend[a]	I	
	1-hexanol	♂I ♀D	
	(*E*)-2-hexen-1-ol	♂I ♀d	
	(*Z*)-2-hexen-1-ol	♂I ♀d	
	alcohol blend[b]	I	
	aldehyde/alcohol blend[c]	D	

TABLE 3 (con't).

Scolytid species	Green leaf volatile	Behavioural response	Reference
Gnathotrichus retusus (LeConte)	hexanal	I	Deglow, 1997
	(*E*)-2-hexenal	I	
	aldehyde blend[a]	a	
	1-hexanol	D	
	(*E*)-2-hexen-1-ol	D	
	(*Z*)-2-hexen-1-ol	♂d ♀D	
	(*Z*)-3-hexen-1-ol	♂d ♀D	
	alcohol blend[b]	♂d ♀D	
	aldehyde/alcohol blend[c]	♂I ♀D	
Gnathotrichus sulcatus (LeConte)	hexanal	I	Deglow, 1997
	(*E*)-2-hexenal	I	
	aldehyde blend[a]	a	
	1-hexanol	d	
	(*E*)-2-hexen-1-ol	♂D ♀I	
	(*Z*)-2-hexen-1-ol	I	
	(*Z*)-3-hexen-1-ol	♂d ♀I	
	alcohol blend[b]	D	
	aldehyde/alcohol blend[c]	D	
Ips avulsus (Eichhoff)	hexanal	D	Dickens et al., 1992
	1-hexanol	d	
	hexanal/1-hexanol blend	D	
Ips grandicollis (Eichhoff)	hexanal	D	Dickens et al.,1992
	1-hexanol	d	
	hexanal/1-hexanol blend	d	
Pityogenes knechteli Swaine	1-hexanol	a/D[d]	Savoie et al., 1997
Scolytus ventralis LeConte	hexanal	I	J. Macias, pers. comm.
	(*E*)-2-hexenal	I	

TABLE 3 (con't).

Scolytid species	Green leaf volatile	Behavioural response	Reference
Trypodendron lineatum[e] (Olivier)	hexanal	I	Borden et al., 1997
	(*E*)-2-hexenal	I	
	aldehyde blend[a]	d	
	1-hexanol	D	
	(*E*)-2-hexen-1-ol	D	
	(*Z*)-2-hexen-1-ol	D	
	(*Z*)-3-hexen-1-ol	D	
	alcohol blend[b]	D	
	aldehyde/alcohol blend[c]	D	
Trypodendron lineatum[f] (Olivier)	hexanal	♂a ♀I	Borden et al., 1997
	(*E*)-2-hexenal	♂I ♀d	
	aldehyde blend[a]	a	
	1-hexanol	I	
	(*E*)-2-hexen-1-ol	I	
	(*Z*)-2-hexen-1-ol	I	
	(*Z*)-3-hexen-1-ol	I	
	alcohol blend[b]	d	
	aldehyde/alcohol blend[c]	D	

[a] includes hexanal, (*E*)-2-hexenal

[b] includes 1-hexanol, (*E*)-2-hexen-1-ol, (*Z*)-2-hexen-1-ol, (*Z*)-3-hexen-1-ol

[c] includes both a and b above

[d] in this case a multifunctional pheromone, attractive at low release rates, and repellant at high release rates

[e] *T. lineatum* population in Interior Douglas-fir biogeoclimatic zone

[f] *T. lineatum* population in Coastal Western Hemlock biogeoclimatic zone

these instances suggests that such events would be strongly disadaptive. It is possible that the conifer-adapted ambrosia fungi are unable to colonize angiosperm hosts or that they are outcompeted by other fungi in this habitat. From a practical perspective, any negative response to a naturally-occurring volatile could potentially be exploited (Borden, 1988) in the protection of high-value conifer logs from attack by ambrosia beetles.

The enhancement of responses to pheromones in combination with green leaf aldehydes in some experiments (Figs. 1,2,8) was unexpected. The lack of consistently enhanced attraction may be attributable to seasonal microclimatic differences that altered the release rates and ratio of aldehydes to pheromone, or to seasonal variations in the relative responsiveness of dispersing beetles to the two types of stimuli. Numerically, the responses to the aldehydes by *G. sulcatus* males, the host finding sex, were proportionally greater than those of females, supporting the hypothesis that green leaf aldehydes may actually be produced by conifers, and may play a kairomonal role in host selection. However, the relative attractiveness of the aldehydes was much less than that of ethanol (Fig. 7), a potent host kairomone for ambrosia beetles (Cade et al., 1970; Moeck, 1970; Bauer and Vité, 1975; Nijholt and Shönner, 1976). As well, the enhanced attraction to sulcatol was least evident when competing treatments were either attractive or without effect; only when repellant alcohol treatments were included did attraction to the aldehyde blend appear strongest. Nonetheless, the repeated positive responses by ambrosia beetles to green leaf aldehydes (Figs. 1,2,8), (Borden et al., 1997) suggest that they, and possibly other compounds, may represent as yet unverified host kairomones. Although ethanol and α-pinene are proven host kairomones for both *Trypodendron* and *Gnathotrichus* spp. (Rudinsky, 1966; Bauer and Vité, 1975; Nijholt and Shönherr, 1976; Borden et al., 1981; Schroeder, 1988; Schroeder and Lindelöw, 1989) it is highly unlikely that they represent the only active host kairomones. Variations in host preferences by *T. lineatum* (Johnson, 1958; Chapman, 1963) could lie in the presence or absence of as yet unknown kairomones or in the release of partially repellent volatiles. In electrophysiological studies, Tømmerås and Mustaparta (1989) recorded strong olfactory receptor cell responses from European *T. lineatum* to unidentified host volatiles, lending support to the hypothesis of undiscovered host kairomones. With the capability of conducting coupled gas chromatographic-electrophysiological research with bark beetle antennae (Wadhams, 1984; Gries, 1995), a renewed search for attractive host kairomones for ambrosia beetles could lead to significant new discoveries.

For *G. sulcatus*, the increasing degree of repellancy of green leaf alcohols achieved in Exp. 3-5 offers strong evidence for an additive rather than synergistic effect of combined stimuli. Ternary blends were more disruptive than binary blends, which were more disruptive than single alcohols (Figs. 3-5), but the disruptive effects were not strikingly different. Moreover, the similarity in disruptive effect between binary, ternary, and quaternary blends indicates a high degree of redundancy between these compounds, a phenomenon also noted between semiochemical mediators of mass attack by the mountain pine beetle (Borden et al., 1990). In both cases, redundancy in responses may be adaptive. During peak flights, with a small optimal window for successful attack, response by bark or ambrosia beetle to any semiochemical that signals the proximity of a potentially suitable host might ensure successful reproduction (Borden et al., 1990). Similarly, if different non-host species released green leaf volatiles in different combinations and ratios, an ability to respond equally to a wide range of redundant signals would ensure that ambrosia beetles could avoid the maximal range of non-host species.

By preventing host-seeking *Gnathotrichus* spp. from landing at or near attractive sources, disruptant green leaf alcohols offer considerable promise as log protectants. In some settings, it could provide the much needed "push" in the push-pull tactic (Lindgren and Borden, 1993) to divert attacking beetles to semiochemical-baited traps or trap logs. Most likely it would be necessary to formulate and apply green leaf alcohols as a spray for them to be most effective, because extensive coverage may be needed to ensure that the resource is adequately protected. An important consideration, however, would be the need to select GLV disruptant blends that are also effective against *T. lineatum*, or to incorporate other disruptants into the blend. As a possible attractant, the aldehyde blend could easily be incorporated into existing trapping systems.

Further research is necessary to improve our understanding of disruption by non-host volatiles. For conifer-inhabiting ambrosia beetles, a clear comprehension of both host and non-host odor profiles is needed to allow researchers the means to identify all of the semiochemicals critical in host selection. For an individual insect species, optimal repellancy may depend upon the release rate and ratio of disruptive components. As well, the blend of volatiles utilized to recognize non-hosts may differ between insect species, or even between ecotypes. There is evidence that the response to GLVs can vary within a species; Borden et al. (1997) reported that responses by *T. lineatum* to GLVs varied between two geographically separated populations in two biogeoclimatic zones in British Columbia. Moreover, Wilson (1995) suggested that the extent of GLV-mediated disruption of the mountain pine beetle in operational trials may depend upon initial population levels. As future research provides further insight into the signals and mechanisms involved in host aggregation for both *G. sulcatus* and *G. retusus*, enhanced management tactics using both attractants and disruptants will doubtless emerge, thereby increasing the yield and value of forest products.

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