4-Allylanisole as an Inhibitor of Bark Beetle (Coleoptera: Scolytidae) Aggregation

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J. Econ. Entomol. 87(6): 1586–1594 (1994)

ABSTRACT To assess the extent of inhibitory activity of the host compound 4-allylanisole, we conducted field studies with three scolytid species. These species are geographically widespread and economically important. Trials were completed with *Dendroctonus brevicomis* LeConte (California), *D. ponderosae* Hopkins (Oregon), and *Ips pini* (Say) (Wisconsin) by using multiple-funnel traps with appropriate pheromone-based attractants. With the *Dendroctonus* species, the effects of 4-allylanisole were compared with verbenone, an aggregation inhibitor produced by beetles themselves. We also determined effects of the treatments on the most abundant coleopterous predators in each trial. Inhibition of bark beetle aggregation behavior by 4-allylanisole was demonstrated for *D. ponderosae* (Oregon) and *I. pini* (Wisconsin). In Oregon, 4-allylanisole reduced the catch of *D. ponderosae* at attractant-baited traps by 77%, whereas verbenone reduced the catch by 91% compared with attractant alone. Although both reductions were significant, the effect of verbenone was significantly greater than that of 4-allylanisole. In Wisconsin, addition of 4-allylanisole to attractant-baited traps resulted in a significant reduction (43%) in numbers of *I. pini* caught, compared with attractant alone. In the California trials, mean trap catches of *D. brevicomis* were reduced by both 4-allylanisole (35%) and verbenone (27%) compared with attractant alone, but neither reduction was significant. Sex ratios of target scolytids were not affected by inhibitory treatments in any trial. The predator *Temnochila chlorodia* (Mannerheim) (Coleoptera: Trogositidae) was not affected by 4-allylanisole in California; however, verbenone significantly reduced the number caught. Although captures were low, numbers of *T. chlorodia* caught by traps containing 4-allylanisole in Oregon were significantly higher than those containing verbenone or attractant alone (numbers in verbenone and attractant traps were not significantly different). Numbers of the predatory beetles counted in Wisconsin—*Thanasimus dubius* (F.) (Coleoptera: Cleridae), *Platysoma parallelum* Say (Coleoptera: Histeridae), and *P. (Cylistix) cylindrica* (Paykull) (Coleoptera: Histeridae)—were not affected by elution of 4-allylanisole with the attractant. Implications of these results for protection of individual trees and management of bark beetle populations are discussed.

KEY WORDS Scolytidae, 4-allylanisole, antiaggregation behavior

FOR WILDLIFE, CULTURAL, and recreational resource management, as well as in suburban and urban settings, high-value stands and single trees threatened by pine bark beetles (Coleoptera: Scolytidae) need to be protected. Considerable attention has been devoted recently to the development of suppression, and to a lesser extent protection, tactics that use synthetic semiochemicals. In particular, pheromones that inhibit aggregation (or congregation; see Discussion by Turchin 1994) such as verbenone (e.g., Bedard et al. 1980a,b; Borden et al. 1987, Payne & Billings 1989, Vité & Baader 1990, Paine & Hanlon 1991, Payne et al. 1992, Salom et al. 1992, Shea et al. 1992), *endo-* and *exo*-brevicomin (e.g., Payne et al. 1977, Borden et al. 1987, Salom et al. 1992), and methylcyclohexenone (e.g., Rudinsky et al. 1972, 1974), as well as allomones produced by competitive species of bark beetles (e.g., Werner 1972b, Paine & Hanlon 1991, Borden et al. 1992, Miller & Borden 1992) have been tested. In contrast, host compounds (Nijholt et al. 1981, O'Donnell et al. 1986, Berisford et al. 1986, Werner et al. 1986, Dubbel 1992) and compounds obtained from plants other than hosts (Dickens et al. 1992, Kohnle et al. 1992) have received less attention as attack deterrents or repellents.

Nonhost, green-leaf volatiles (including hexanal or hexan-1-ol [or both]) (Dickens et al. 1992), and plant (lippia) oil (containing ipsdienone [≈50%], and myrcene [≈11%]) (Kohnle et al. 1992) have shown some promise as deterrents, although their effects are generally not as dramatic as those found with beetle pheromones. Attempts to apply pine oil products, which are mixtures of various host and other compounds (Nijholt 1980), to unattacked standing pines as a

Table 1. Location, dates, target insect and bait information from field trapping studies

Location	Sites	Inclusive dates	Target insect	Compound[a]	Elution rate[b,c]	Proposed semi-chemical role
California	3	20 May–23 June	*D. brevicomis*	*exo*-Brevicomin	2–3	Attractant
				Frontalin	1–2	
				Myrcene	100	
				Verbenone	8–12	Inhibitor
				4-Allylanisole	160	Inhibitor
Wisconsin	2	29 May–28 July	*I. pini*	Ipsdienol	0.2–0.3	Attractant
				Lanierone	0.02–0.03	
				4-Allylanisole	160	Inhibitor
Oregon	2	18 July–6 August	*D. ponderosae*	*trans*-Verbenol	2–4	Attractant
				exo-Brevicomin	0.01	
				Myrcene	100	
				Verbenone	8–12	Inhibitor
				4-Allylanisole	160	Inhibitor

[a] All attractants were purchased as complete units and verbenone was purchased in bubble-caps from Phero Tech, Delta, BC, Canada. 4-Allylanisole was purchased from Berjé Chemical, Vineland, NJ, and was eluted from 20-ml wicked-vials.
[b] milligrams per 24 h.
[c] Elution rates of *exo*-brevicomin, frontalin, myrcene, *trans*-verbenol, and verbenone were determined at 25°C (Phero Tech). Rate of 4-allylanisole determined gravimetrically at 22–27°C.

repellent for several scolytid species have met with limited success (Nijholt et al. 1981, Berisford et al. 1986, O'Donnell et al. 1986, Werner et al. 1986). Presumably, host compounds contained in these mixtures are responsible for repellent properties, but further research is needed to identify active compounds. Certain host compounds such as α-pinene, limonene, and camphene have been shown to be repellents in walking olfactory assays, but these same compounds are also attractants for the same species during flight (Rudinsky 1966).

4-Allylanisole (also referred to as estragole or methyl chavicol) is present in numerous pine species; its concentrations usually range from 1 to 11% of the volatile component of the oleoresin (Drew & Pylant 1966, Werner 1972a, Hayes et al. 1994b). Hayes et al. (1994a, b) demonstrated repellent properties of 4-allylanisole for various bark beetle species. In laboratory behavioral assays with *Dendroctonus frontalis* (Zimmermann), *D. brevicomis* LeConte, *D. ponderosae* Hopkins, *D. rufipennis* (Kirby), and *Ips pini* (Say), all species were highly (>80%) repelled by 4-allylanisole. Only with *D. frontalis*, however, have these laboratory results been corroborated by field studies through a significant reduction in catch by attractant-baited traps and by the protection of vulnerable trees in natural populations. Because 4-allylanisole is present in a wide range of conifer species, and because repellency in laboratory assays was evident in numerous scolytid species, we designed field studies to test the extent of inhibitory activity of 4-allylanisole on three broadly distributed species of economic and ecological significance: *D. brevicomis*, *D. ponderosae*, and *I. pini*.

Materials and Methods

Field Tests. Multiple-funnel traps (Lindgren 1983, Phero Tech, Delta, BC, Canada) were used to test the response of local beetle populations to simultaneous elution of 4-allylanisole or verbenone, with commercially available attractants. Eight-unit funnel traps were used in Wisconsin; 12-unit traps were used in California and Oregon. Traps were placed in areas with active target insect populations in the spring and summer of 1993; locations, elution data, and inclusive dates for each trial are given in Table 1. The trials consisted of the following treatments: 1) an appropriate (commercially available) attractant for each species, 2) attractant + verbenone (with the exception of *I. pini* where verbenone was excluded; see below), and 3) attractant + 4-allylanisole. Attractants and verbenone were purchased from Phero Tech as complete units (Table 1). Verbenone influences *I. pini* (Borden et al. 1992), but it was not included as a treatment for this species because an established product was not available. 4-Allylanisole was purchased from Berjé, Bloomfield, NJ. Elution devices consisted of a 20-ml polyethylene vial (Kimble Glass, Vineland, NJ) with an alcohol-burner wick (Fisher, Pittsburgh, PA) that released the active ingredient through a hole in the cap. Except for one site in Oregon (see below), treatments were first assigned to trap locations at random and then moved in sequential order at the end of each collection period so that each treatment appeared in each location. Duration of collection periods varied because of weather conditions; number of collection periods (4–6) depended on the number of treatments. In the Wisconsin trials and one site (see below) in Oregon, baits were moved at each collection period among stationary traps; in the California trials, traps with baits were moved. Except where noted in the California trials, collection cups contained a piece (5.5 by 2 cm) of 2,2-dichlorovinyldimethylphosphate (Peststrip, Loveland Industries, Greeley, CO).

California Trials. *D. brevicomis* was the target insect in the California trials. Trapping was done at three field sites, all of them near Long Barn, CA (Tuolumne County) on the Mi-Wok Ranger District of the Stanislaus National Forest. All sites were mixed species of pine, cedar, and various hardwoods; ponderosa pine (*Pinus ponderosa* Laws.) was the dominant species. Each site was a minimum of 2 km apart at approximately equal elevations (1,600–1,700 m). Traps (six per site) were suspended at least 100 m apart on branches of nonhost trees at a height of 2–5 m. The traps with their baits were moved in sequential order on an irregular schedule (depending on the weather) from 20 May through 23 June 1993. All treatments included commercially available *D. brevicomis* lures, which contained *exo*-brevicomin, frontalin, and myrcene. Two traps were baited with this attractant alone; two traps also contained the inhibitory pheromone verbenone, and two traps also contained 4-allylanisole. To increase attractiveness of the traps at sites 1 and 2, and to provide a better test for the potential inhibitors, a single pinhole was punched through caps of each component of the attractant (microcentrifuge tubes), but elution devices for 4-allylanisole and verbenone were not modified. At site 3, baits were not changed. Site did not have a significant effect on catch of *D. brevicomis*, indicating that the attempt to increase elution of attractants at sites 1 and 2 had little effect on the number of beetles caught.

To examine potential differences among individuals responding to each treatment in the field, *D. brevicomis* were trapped alive (i.e., pest strip was omitted from collection vessel) from 20 to 25 May and shipped overnight to our laboratory in Pineville, LA. In the laboratory, individual *D. brevicomis* were subjected to a walking olfactory test (Hayes et al. 1994a, b). We used a 17-cm circle of 4-allylanisole painted on cardboard; individual beetles were released near the center. Only apparently healthy individuals were used for these tests. A beetle was consided to be repelled if it remained in the circle or not repelled if it left the circle during a 30-s exposure in reduced light.

Trap captures of *D. brevicomis* and the predator *Temnochila chlorodia* (Mannerheim), the only predator caught in sufficient numbers for testing, were counted and recorded. In addition, subsamples of *D. brevicomis* from 20 to 23 May, 17 June, and 20 June were sexed as described by Tate & Bedard (1967).

Wisconsin Trials. The target insect in Wisconsin, *I. pini*, was trapped at two sites located ≈6 km apart near Colfax, WI (Dunn County). Both sites were owned and managed by Woods Run Forest Products, Colfax, WI. The sites contained plantations of red pine (*Pinus resinosa* Ait.), 30–34 yr-old, with a basal area of 13.9–14.9 m^2 and a mean diameter at breast height (dbh) of ≈20 cm. Within each site, four funnel traps were suspended at least 20 m apart between red pines at a height of ≈2.2 m. All traps contained the attractants ipsdienol and lanierone (Teale et al. 1991); two traps per site also contained 4-allylanisole. Traps were emptied and bait positions changed on 21 June, 29 June, 10 July, and 28 July 1993.

Associated coleopterons that were counted in Wisconsin included the predatory clerid, *Thanasimus dubius* (F.) (Coleoptera: Cleridae), and two species of histerids, *Platysoma parallelum* Say, and *P. (Cylistix) cylindrica* (Paykull) (Coleoptera: Histeridae). The sex of subsamples of *I. pini* (up to 30 individuals per trap sample) was determined by examination of the third declivital tooth (or spine) (Lanier & Cameron 1969).

Oregon Trials. The target insect in Oregon, *D. ponderosae*, was trapped at two sites located near the Deschutes River Bridge (Deschutes County, Oregon) in the Deschutes National Forest. Treatments consisted of a three-component attractant, which contained *exo*-brevicomin, *trans*-verbenol, and myrcene; attractant + verbenone; and attractant + 4-allylanisole. Sites were ≈2 km apart. At one site (site P), along a power line in a lodgepole pine, *Pinus contorta murrayana* (Balf.), (15–40 cm dbh) stand, 12 funnel traps were suspended from 2-m tripods placed at 30–40-m intervals. The tripods were arranged in a staggered pattern. Treatments were assigned in repeating sequence of attractant alone, attractant + verbenone, and attractant + 4-allylanisole. The second site (site Q) was a thinned stand of lodgepole near a mixed stand of lodgepole and ponderosa pine. At this site, six traps were suspended on tripods placed at least 50 m apart. Treatments were assigned at random and changed in sequence when collections were made. Depending on weather conditions, collections were made at irregular intervals between 22 July and 6 August.

The contents of each trap from each collection period were identified to species. *D. ponderosae* were sexed by examining the seventh abdominal tergite (Lyon 1958) of all trapped individuals from site Q. *Dendroctonus brevicomis*, *T. chlorodia*, and a clerid species were also collected and counted. Because few individuals were caught, the clerid species at both sites (n = 3) and *D. brevicomis* at site P (n = 7) were excluded from statistical analyses.

Statistical Analyses. Where possible, trap-count data were subjected to standard parametric analysis of variance (ANOVA) procedures (PROC GLM; SAS Institute 1988). The mean daily trap catch for a treatment within a site was used as the experimental unit for analysis; i.e., individual traps were treated as subsamples. When F-values were significant for an overall ANOVA model ($P < 0.05$) and the overall effect

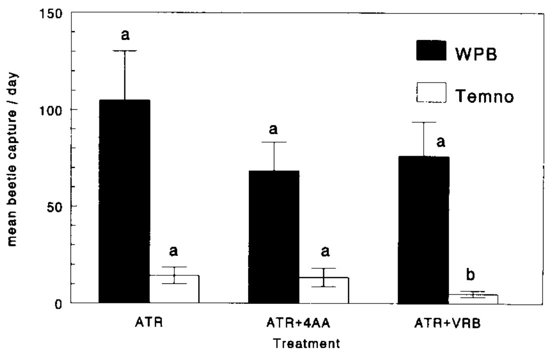

Fig. 1. Trapping results from three sites in California using funnel traps baited with attractant for *D. brevicomis*, either alone or in combination with an inhibitor. Mean number of *D. brevicomis* (black bars) and *T. chlorodia* (open bars) caught per day by attractant alone (ATR), attractant and 4-allylanisole (ATR + 4-AA), or attractant and verbenone (ATR + VRB). Different letters above bars indicate significant difference between treatment means within a beetle species by protected least significant differences ($P \leq 0.05$; SAS Institute 1988).

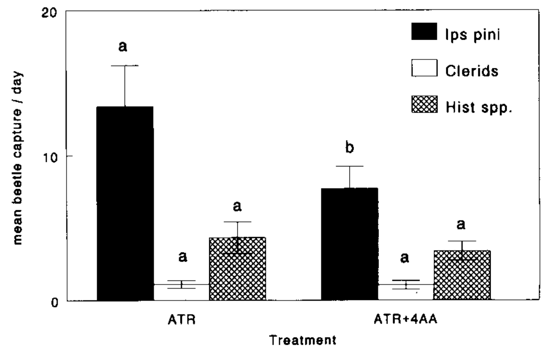

Fig. 2. Trapping results from two sites in Wisconsin using funnel traps baited with attractant for *I. pini*, either alone or in combination with 4-allylanisole. Mean number of *I. pini* (black bars), *T. dubius* (open bars), and the histerid species, *P. parallelum* and *P. (cylistix) cylindrica*, (hatched bars) caught per day by attractant alone (ATR), or attractant and 4-allylanisole (ATR + 4AA). Different letters above bars indicate significant difference between treatment means within a beetle species (or genus) by protected least significant differences ($P \leq 0.05$; SAS Institute 1988).

for treatment was significant ($P < 0.05$), treatment means were compared with the least significant difference procedure (PROC GLM; LSMeans PDIFF option; SAS Institute 1988). Interaction terms were included unless they were not significant ($P < 0.05$). When graphical analysis of data or residual plots, or both, suggested departure from normality, data were transformed by square root(y), $\ln(y + 1)$, or rank transformed (Conover & Iman 1981), in that order of preference, before analysis. As a result, untransformed data were never subjected to statistical analysis. All factors in the ANOVA models were considered fixed. To test for the effect of semiochemical treatment on the percentage of female beetles caught in traps, a chi-square test of independence was done with combined samples (PROC FREQ; SAS Institute 1988).

Results

California. Neither verbenone nor 4-allylanisole significantly affected the number of *D. brevicomis* caught in attractant-baited funnel traps in California (Table 2; Fig. 1) (overall effect for treatment, $P = 0.51$). However, traps containing 4-allylanisole + attractant caught 34.8% fewer *D. brevicomis* per day (mean ± SEM = 68.4 ± 14.9; n= 35) and traps containing verbenone + attractant caught 27.4% fewer *D. brevicomis* per day (76.1 ± 17.6; n = 35) compared with traps that contained attractant alone (104.9 ± 25.4; n = 35). Site did not significantly affect the number of *D. brevicomis* caught ($P = 0.40$).

Catch of *T. chlorodia* among treatments differed significantly (Table 2; Fig. 1) ($F = 5.08$; df = 2, 85; $P \leq 0.0082$). Simultaneous release of verbenone with the attractant mixture resulted in a significantly lower catch of *T. chlorodia* (4.9 ± 1.6; n = 35) compared with attractant alone (13.4 ± 4.7; n = 35; $P \leq 0.0196$), or attractant with 4-allylanisole (14.2 ± 4.3; n = 35; $P \leq 0.0036$). Traps baited with the attractant + 4-allylanisole did not catch significantly different numbers of *T. chlorodia* ($P = 0.54$). Site had a significant effect on catch of *T. chlorodia* ($F = 4.87$; df = 2, 85; $P \leq 0.0098$); significantly fewer *T. chlorodia* were caught at site 3 (7.1 ± 2.4; n = 11) than in either site 1 (12.9 ± 3.8; n = 12; $P \leq 0.0063$) or site 2 (12.1 ± 4.8; n = 12; $P \leq 0.0119$). Results for sites 1 and 3 did not differ from each other ($P = 0.76$).

D. brevicomis trapped live from each treatment in the field did not respond differently to 4-allylanisole in the laboratory assay. *D. brevicomis* collected from traps baited with attractant alone were highly repelled (98%, n = 120; 54 females, 66 males), as were those collected from traps also containing 4-allylanisole (99% repelled, n = 92; 49 females, 43 males) or verbenone (99% repelled n = 105; 58 females, 47 males). These results are comparable with those obtained in previous assays with newly emerged *D. brevicomis* (Hayes et al. 1994a, b).

The percentage of female *D. brevicomis* caught in traps was not influenced by treatment ($\chi^2 = 4.48$, df = 2, $P = 0.11$) (Table 2). For all treatments, more females (the sex which initiates attack in *Dendroctonus* species, the so-called pioneering sex) than males were captured. Traps baited with attractant alone caught 56.7% (1,458/2,572) females; traps baited with 4-allylanisole plus attractant caught 56.8% (870/1,531) females, and traps baited with verbenone plus attractant

Table 2. Daily trap catches (mean ± SEM) of target insects and associated Coleoptera at each location.

Location	Insect species	Treatment[a,b]					
		ATR	% ♀♀[c]	ATR + 4-AA	% ♀♀	ATR + VRB	%♀♀
California	*D. brevicomis*	104.90 ± 25.42a	56.7a	68.41 ± 14.87a	56.8a	76.11 ± 17.65a	53.4
	T. chlorodia	13.41 ± 4.73a		14.20 ± 4.30a		4.89 ± 1.64b	
Wisconsin	*I. pini*	13.39 ± 3.99a	57.5a	7.69 ± 2.03b	58.6a		
	T. dubius	1.10 ± 0.35a		1.05 ± 0.41a			
	Histerid[d] spp.	4.31 ± 1.07a		3.38 ± 0.93a			
Oregon	*D. ponderosae*	5.53 ± 1.68a	48.5a	1.26 ± 0.43b	49.5a	0.50 ± 0.17c	44.1a
	D. brevicomis[e]	1.83 ± 1.03a	23.0a	1.09 ± 0.41a	13.3a	0.13 ± 0.07b	42.9a
	T. chlorodia	0.09 ± 0.08b		0.19 ± 0.05a		0.01 ± 0.01b	

[a] Different letters across rows indicate significant differences among means when comparing treatment or percent females by protected least significant differences test ($P \leq 0.05$; SAS Institute 1988).
[b] ATR, attractant (see Table 1 for descriptions); 4-AA, 4-allylanisole; VBR, verbenone.
[c] % female was determined only for scolytids.
[d] Histerid category consists of *Platysoma parallelum* and *P. (Cylistix) cylindrica.*
[e] Site Q only; site P not included because the total catch was only seven *D. brevicomis.*

caught 53.4% (704/1,318) females. These results generally agree with previously published studies which report that catches with the attractant mixture of *exo*-brevicomin, frontalin, and myrcene are slightly biased toward capture of females (Vité & Pitman 1969; Bedard et al. 1980a, b).

Wisconsin. In Wisconsin, the mean daily catch (mean ± SEM) of *I. pini* in traps containing attractant and 4-allylanisole (7.7 ± 2.0; $n = 8$) was significantly lower than those traps that contained attractant alone (13.4 ± 4.0; $n = 8$; $P \leq 0.0206$) (Table 2; Fig. 2). This difference indicates that 43% fewer *I. pini* were trapped as a result of the addition of 4-allylanisole to the attractant-baited trap. Site significantly affected numbers of *I. pini* in traps ($P \leq 0.0151$), with traps at site 2 catching significantly more beetles per day (13.2 ± 4.0; $n = 8$) than site 1 (7.9 ± 2.1; $n = 8$) (treatments combined).

Numbers of neither the clerid *T. dubius* ($F = 1.85$; df = 1, 10; $P = 0.20$), nor the histerids *P. parallelum* and *P. cylindrica* ($F = 0.78$; df = 1, 10; $P = 0.40$) were significantly affected by the presence of 4-allylanisole (Table 2, Fig. 2). However, site and date significantly affected numbers of *T. dubius* ($F = 61.26$; df = 1, 10; $P \leq 0.0001$ for site, $F = 81.18$; df = 3, 10; $P \leq 0.0001$ for date) and of the histerid species caught per trap ($F = 15.50$; df = 1, 10; $P \leq 0.0028$ for site, $F = 11.68$; df = 3, 10; $P \leq 0.0013$ for date).

The subsamples for which sex was determined indicated that the percentage of female *I. pini* caught in traps was not influenced by the addition of 4-allylanisole to the attractant mixture (Table 2). The response of *I. pini* to the combination of ipsdienol and lanierone was biased toward females (males are the pioneering sex), with 57.5% (241/419) of the trap catch being female. These results generally agree with those of Teale et al. (1991), who caught ≈55% females when 10 mg ipsdienol was eluted with 1.0 mg lanierone, the same ratio used in our study (Table 1). Traps that contained attractant plus 4-allylanisole captured 58.6% (236/403) females. This percentage was not significantly different from the ratio caught in traps baited with attractant alone ($\chi^2 = 0.09$; df = 1; $P = 0.76$).

Oregon Trials. In the Oregon tests with *D. ponderosae*, mean daily trap catch was significantly reduced by the addition of verbenone (mean ± SEM = 0.5 ± 0.2; $n = 11$; $P \leq 0.0001$) or 4-allylanisole (1.3 ± 0.4; $n = 11$; $P \leq 0.0001$) when compared to attractant alone (5.5 ± 1.7; $n = 11$). These results indicate a 91% or 77% reduction in trap catch with the addition to the attractant of verbenone or 4-allylanisole respectively; the difference between verbenone and 4-allylanisole was also significant ($P \leq 0.0342$) (Table 2; Fig. 3). Besides the effects of treatment, date ($F = 10.46$; df = 6, 24; $P \leq 0.0001$) and site ($F = 66.13$; df = 1, 24; $P \leq 0.0001$) had highly significant influences on trap catch of *D. ponderosae.* Traps at site P caught more *D. ponderosae* per day (3.8 ± 1.1; $n = 18$) than those at site Q (0.7 ± 0.2; $n = 15$). The interaction treatment * site also significantly affected numbers of this insect caught ($F = 8.48$; df = 2, 24; $P \leq 0.0016$). A significant interaction term generally suggests that main effects—in this case site and treatment—may need to be reevaluated. Visual inspection of the interaction plot (treatment * site) indicated that this effect was caused by the traps baited with attractant. These traps at site P ($\bar{X} = 8.7$; $n = 18$) caught many more *D. ponderosae* (relative to the other two treatments) than the same treatment at site Q ($\bar{X} = 1.6$; $n = 15$). This difference probably resulted from a large, active infestation of *D. ponderosae* near site P.

Although capture numbers were relatively low, treatments also significantly affected trap catches of the *D. ponderosae* associates, *D. brevicomis* and *T. chlorodia* (Table 2, Fig. 3). The verbenone treatment significantly reduced trap catch of *D. brevicomis* (mean ± SEM = 0.13 ± 0.07; $n = 5$) compared with the attractant alone (1.83 ± 1.03; $n = 5$; $P \leq 0.0013$), a reduction of 93%, and compared with the 4-allylanisole treat-

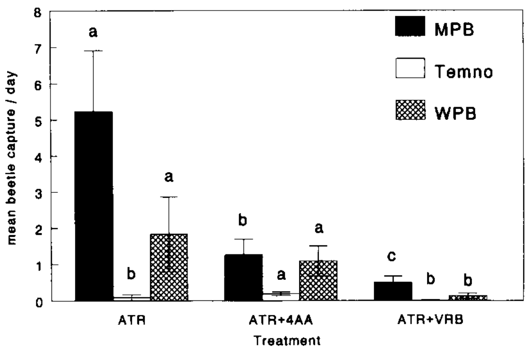

Fig. 3. Trapping results from two sites in Oregon using funnel traps baited with attractant for *D. ponderosae*, either alone or in combination with an inhibitor. Mean number of *D. ponderosae* (black bars), *T. chlorodia* (open bars) and *D. brevicomis* (hatched bars) caught per day by attractant alone (ATR), attractant and 4-allylanisole (ATR + 4-AA), or attractant and verbenone (ATR + VRB). Different letters above bars indicate significant difference between treatment means within a beetle species by protected least significant differences ($P \leq 0.05$; SAS Institute 1988).

ment (1.09 ± 0.41; n = 5; $P \leq 0.0117$). Although 4-allylanisole showed a 40% reduction in trap catch, the difference between this treatment and the attractant alone was not significant (P = 0.2144). Treatments containing 4-allylanisole caught a significantly greater number of the natural enemy *T. chlorodia* per day (0.19 ± 0.05; n = 11) than did verbenone (0.01 ± 0.01; n = 11; $P \leq 0.0001$) or attractant alone (0.09 ± 0.08; n = 11; $P \leq 0.0001$); the effects of verbenone and attractant did not differ significantly from each other (P = 0.37).

Treatments did not significantly affect the percentage of female *D. ponderosae* or *D. brevicomis* captured in traps (Table 2). For *D. ponderosae*, a species in which females are also the pioneering sex, numbers in all trap captures were slightly biased toward males (49.5% female [93/188] in 4-allylanisole, 48.5% [409/844] in attractant alone, 44.1% [30/68] in verbenone) (χ^2 = 0.59; df = 1; P = 0.75). Although direct comparisons among studies are made difficult by differing elution rates among compounds, the percentage of females caught in this study generally agrees with previously published results that found this three-component attractant caught *D. ponderosae* in approximately a 1:1 sex ratio (Conn et al. 1983, Borden et al. 1987). Because this attractant mixture was designed to attract *D. ponderosae*—and was missing frontalin, a female-biased attractor of *D. brevicomis* (Bedard et al. 1980a, b)—the sex ratio of *D. brevicomis* was strongly biased toward males (much more strongly than in California where *D. brevicomis* attractant was used). The inclusion of *trans*-verbenol, an inhibitor of *D. brevicomis* (Bedard et al. 1980b), may also have affected the sex ratio of this species. Verbenone and *trans*-verbenol reportedly act as synergists to inhibit aggregation of *D. brevicomis* (Bedard et al. 1980b). In Oregon, traps baited with attractant and verbenone had the highest percentage of female *D. brevicomis* (42.9%) (3/7), traps with attractant alone caught an intermediate percentage (23.0%) (20/87), and traps with attractant and 4-allylanisole caught the lowest percentage of females (13.3%) (6/45). Although these differences seem large, total catch of *D. brevicomis* by the verbenone treatment (n = 7) was insufficient for analysis.

Discussion

The potential inhibitory effects of host compounds on the semiochemical bouquet (and subsequent scolytid behavior) are poorly understood and have been largely overlooked. 4-Allylanisole significantly reduced the catch of *D. ponderosae* (Oregon) and *I. pini* (Wisconsin). These results demonstrate that this host compound has inhibitory properties in these scolytid-pheromone systems and substantiate results from laboratory bioassays (Hayes et al. 1994a, b). In California, fewer *D. brevicomis* were caught by the 4-allylanisole and verbenone treatments, but neither of these reductions was significant. Inconsistent results with inhibition of *D. brevicomis* have been reported previously. In one study, Bedard et al. (1980b) found that the addition of either verbenone or *trans*-verbenol to attractant-baited traps significantly reduced trap catch. In a second study, Bedard et al. (1980a), trapping in August with an unspecified enantiomeric composition, found that verbenone reduced catch of *D. brevicomis* at traps baited with *exo*-brevicomin, frontalin, and myrcene, but the difference was not significant. A significant reduction was demonstrated only when *trans*-verbenol, which alone did not significantly reduce trap catch, and verbenone were both eluted. Our laboratory assays, although preliminary, did not support the hypothesis that *D. brevicomis* caught in traps with an inhibitor would be less responsive to 4-allylanisole than those caught by attractant alone.

Although *D. brevicomis* were not significantly affected by treatments in California, verbenone inhibited their response to *D. ponderosae* attractant in Oregon. Four possible explanations, none of which is mutually exclusive, might explain this difference. First, the *D. ponderosae* attractant contained *trans*-verbenol (Table 1), a compound that may inhibit aggregation of *D. brevicomis* (Bedard et al. 1980b) when used alone or might act synergistically with verbenone (Bedard et al. 1980a, b). Second, the *D. ponderosae* attractant lacked frontalin, which is an important component for attracting female *D. brevicomis* (Vité & Pitman 1969). If either of the inhibitors affected males more than females, a more significant effect would have been seen when used with this attractant. Even though no significant sexual bias was demonstrated and the response in Oregon was quite low, traps containing verbenone caught the greatest percentage of females numerically (Table 2). Verbenone is known to inhibit male *D. frontalis* more strongly than females (Salom et al. 1991, Hayes et al. 1994a), and *D. frontalis* and *D. brevicomis* are closely related species (Hopkins 1909, Wood 1963). Third, mean numbers of *D. brevicomis* caught were considerably lower in Oregon than California (Table 2), and population levels may affect insect responses or any ability to demonstrate differences. Finally, as with *D. ponderosae* (Borden et al. 1987 and references therein), host- or geographically based differences in semiochemical responses by *D. brevicomis* may occur.

Although not the target of these trials, the effect of inhibitory treatments on responding predators provides potentially important information about the practical use of control techniques with these semiochemicals. In both the Oregon and California tests, trap captures of *T. chlorodia* were significantly influenced by the treatments (Table 2). At each location, the effect of treatment on the rank order of numbers caught was the same; i.e., 4-allylanisole + attractant > attractant alone > verbenone + attractant. In California, numbers caught in traps with verbenone were significantly lower than the other treatments. In Oregon, 4-allylanisole caught significantly higher numbers than the other two treatments. Our observation that verbenone reduced catch of *T. chlorodia* at traps baited with attractant in California supports the suggestion by Bedard et al. (1980a) that verbenone is an inhibitor of *T. chlorodia* response to the 3-component *D. brevicomis* attractant. Our experiments were not designed to test the attractiveness of 4-allylanisole alone; therefore, we do not know whether this compound by itself is attractive to *T. chlorodia*. Bedard et al. (1980b) determined that neither myrcene nor turpentine alone was attractive to *T. chlorodia*, suggesting that host compounds are not generally attractive. None of the associates recorded in the Wisconsin trials was significantly affected by the addition of 4-allylanisole to traps baited with attractant.

Knowledge about the effects of semiochemical treatments on various insect species is important for many reasons. For pest species with overlapping geographic ranges, behaviors of each pest in the presence of semiochemicals should be considered. Inhibitors may serve multiple functions (Rudinsky 1973a, b), and some of the most effective inhibitors are important aggregation pheromones for other pest species (Birch et al. 1980, Byers & Wood 1981, Paine & Hanlon 1991, Borden et al. 1992, Miller & Borden 1992). Although attracting competitors may be a compelling management option in certain instances (e.g., suppression of an infestation of an aggressive species with a less aggressive competitor), in other cases it is not acceptable. As forested areas become increasingly used for purposes other than timber production (e.g., aesthetics, wildlife, urbanization), goals of pest management often change from infestation or population management to resource protection. As a result, individual trees have become important management units. In a management scheme to protect individual trees, effects of semiochemical treatments on competitive species must be determined and probably must fall into one of two categories: either acting to inhibit their attack (in addition to inhibiting the target species) or at the very least not attracting them. Compounds that might inhibit or repel a wide range of bark beetle species are therefore important to meet these needs.

Our results have direct implications for management of scolytids. Knowledge that 4-allylanisole is an inhibitor of *D. ponderosae* and *I. pini* may have significance for management of infestations and for tree-protection strategies for these species. Besides providing an additional inhibitor for use with these bark beetles, the wide range (geographic and taxonomic) of 4-allylanisole's inhibitory effects suggests that this compound may be useful as an inhibitor, or resource protectant, for many scolytids. All species of scolytids tested were repelled by 4-allylanisole in laboratory assays (Hayes et al. 1994a, b), and recent field studies show that 4-allylanisole inhibits the response of *D. rufipennis* and *Dendroctonus simplex* LeConte to attractants (Werner 1994). Compounds produced by plants may be expected to have less specific effects than pheromones produced by insects, affording an advantage in those situations where the management goal is resource protection (versus management of a single pest species). Results with *D. brevicomis* further support the suggestion that many interacting factors in field trials (e.g., behavioral differences among insects, nonolfactory behaviors, variable biotic and abiotic environments, insect population levels, host effects) cause inhibitors to produce variable results. More research is needed to clarify important relationships so that the efficacy of inhibitors can be predicted, and management of aggressive bark beetles with semiochemicals can proceed with increased confidence.

Acknowledgments

This research would not have been possible without the help of personnel in Pineville and at each of the field locations. In Pineville, we thank J. Roton, J. Roshto, and C. Steiner for technical assistance and L. Roton for both his technical assistance and his insight throughout the project. In California, we thank personnel from RWU-PSW-4502 and RWU-PSW- 4503, USDA Forest Service, particularly J. Robertson and P. Shea, for providing supplies and technical assistance. S. Smith (USDA Forest Service, Forest Health, Sonora, CA), numerous personnel at the Mi-Wok Ranger Station (Stanislaus National Forest, Mi-Wuk Village, CA), and members of the Mi-Wuk Village Homeowners Association (especially G. Kirk) were also instrumental in completing our field trials. Their help is greatly appreciated. Trials in Wisconsin would not have been possible without the help of B. Ayres (Woods Run Forest Products, Colfax, WI) who provided insight and hospitality, bought field sites, and helped with collections. We also thank K. Raffa (University of Wisconsin, Madison, WI), who allowed us to use his laboratory, equipment, and field sites. In Oregon, we thank R. Mitchell, H. Hayes, and R. Hayes for their help with all aspects of the project and C. Carter for technical assistance. We thank R. Mitchell, R. Werner (USDA-FS, PNW), and S. Seybold (University of Nevada, Reno, NV) for helpful comments on the manuscript.

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Received for publication 21 June 1994; accepted 19 August 1994.