INHIBITION OF ATTRACTION TO AGGREGATION PHEROMONE BY VERBENONE AND IPSENOL

Density Regulation Mechanisms in Bark Beetle *Ips typographus*[1]

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Abstract—The semiochemicals verbenone (Vn), ipsenol (Ie), and ipsdienol (Id), present in late phases of host colonization, have been implicated as qualitative "shut-off" signals regulating attack density. Combinations of the three chemicals were released in pipe traps together with the aggregation pheromone components 2-methyl-3-buten-2-ol (MB) and *cis*-verbenol (cV) at different levels and in different ratios to MB + cV, and with two spacings of traps to test for possible effects on reducing catch at traps baited with aggregation pheromone. When they were released with the attractants Vn and Ie (alone or together) decreased the mean catch significantly at the higher release rates used (1 mg/day). Id alone or together with Vn at low release rates (0.1 mg/day), with the attractants, increased catch somewhat. A dose–response test of Vn, with the attractants held constant, showed a decline in catches, down to about < 10% of the control, at ratios of Vn to cV between 1:1 and 150:1. A larger spacing (25 m) of traps gave a stronger response to change in doses of Vn and MB + cV than a smaller (6 m) spacing. The sex ratio was more skewed towards females when two or three inhibitors were present and at higher doses of Vn. It is suggested that Vn could be the most important density-regulating signal in the natural system, as release of Vn from galleries is larger and starts earlier than that of Id and Ie.

INTRODUCTION

The eight-spined spruce bark beetle of Europe, *Ips typographus* (L.), regularly mass attacks standing, healthy host trees (Postner, 1974). In this respect, its population biology resembles the more aggressive Nearctic *Dendroctonus* species. The attack dynamics of the spruce bark beetle, i.e., the aggregation and density regulation process of initial attacks, mass attack, and then switching of attack focus to nearby trees, is only partly understood. The first part of the attack dynamics, where density is positively regulated by the attraction of both sexes to the aggregation pheromone released by the pioneering males, is empirically relatively well known (Bakke, 1976; Bakke et al., 1977; Bakke and Riege, 1982; Birgersson et al., 1984; Schlyter and Löfqvist, 1986; Schlyter et al., 1987a–c). A simple numerical model using these data (Schlyter and Anderbrant, 1989) described the first part of the process governed by the rapid release of 2-methyl-3-buten-2-ol (MB) and *cis*-verbenol (cV) from the males, up to and including the mass attack, but after this period the model was inadequate (Anderbrant et al., 1988).

The latter part of the dynamics includes a decline in attraction and the switch of attack focus in order to avoid the well-established negative effects of larval competition at high densities on the number and quality of offspring (Thalenhorst, 1958; Ogibin, 1973; Botterweg, 1983; Anderbrant et al., 1985; Mills, 1986). The mechanisms governing the latter part are much less known, but two mechanisms have been proposed in *Ips typographus* (Schlyter et al., 1987c): (1) the quantitative hypothesis based on sex-specific response of males to large amounts of pheromone (relative inhibition; Byers, 1983) and the decrease of pheromone quantity after mating (Byers, 1981; Birgersson et al., 1984; Schlyter and Löfqvist, 1986), and (2) the qualitative hypothesis based on male production in later "attack phases" of ipsdienol (Id) and ipsenol (Ie) (Birgersson et al., 1984, 1988; Schlyter et al., 1987c) as inhibitors of the attraction to the pheromone. These might function as a "shut-off" signal for the aggregation. Ie is more or less inhibitory at the doses tested (Bakke, 1981; Schlyter et al., 1987c). In contrast, Id is inhibitory only at higher doses, but slightly attractive (Bakke, 1976; Schlyter et al., 1987c) or neutral (Dickens, 1981) at lower doses.

The numeric model of attack dynamics (Schlyter and Anderbrant, 1989) indicated that production of Id and Ie may start too late to influence the dynamics of density regulation (limitation) and switching at the rate these processes proceed in nature. It is likely that other signals are present in the process. One such additional signal may be the release of verbenone (Vn), which (at an

unspecified release rate) alone or together with Ie, has been shown to reduce the catch of *I. typographus* (Bakke, 1981). Verbenone also inhibits response (lower the catch at attractant baits) of North American species (*Dendroctonus frontalis*, Payne et al., 1978; *D. brevicomis*, Bedard et al., 1980; Tilden and Bedard, 1988; *D. ponderosae*, Ryker and Yandell, 1983; *D. adjunctus*, Livingston et al., 1983; *Ips paraconfusus*, Byers and Wood, 1980). The amounts of oxygenated monoterpenes, such as Vn, are found to increase in gallery wall phloem during late attack phases of *Ips typographus* and are probably produced by microorganisms, such as yeasts, brought to the tree by the beetle (Leufvén et al., 1984, 1988; Leufvén and Birgersson, 1987). The release of Vn from beetle-infested logs (Schlyter et al., 1987a) or from male attacks on standing trees (Birgersson and Bergström, 1989) is relatively high, often of the same magnitude as cV. Since Vn may affect behavior of the beetle, but is produced mainly by associated organisms (Leufvén et al., 1984) and only in trace amounts by the beetle (Birgersson et al., 1984), we use the term "semiochemical" for Vn together with Ie and Id. The two later compounds may also be termed pheromone components.

    In order to test the relative importance of these three semiochemicals as "inhibitors" of attraction, we have released them, in racemic form, in all the seven possible combinations at two levels of release rates with the attractants MB + cV. We have also quantified the response to three decadic steps of Vn dose with MB + cV at two levels and spacing of traps in a factorial experiment.

METHODS AND MATERIAL

Compounds, Dispensers, Traps, and Study Area. The three proposed "inhibitors," which are all chiral molecules, were tested in racemic or close to racemic mixtures. For verbenone (Vn), which is probably derived from the chiral precursor α-pinene, which has a very high between-tree variation in enantiomeric composition (Lindström et al., 1989), both enantiomers of Vn could be expected to be equally active, as was also indicated by Bakke (1981). The Vn used was not far from racemic as it had a rotation (measured by polarimetry) of only $[\alpha]_D^{25} = +93.9°$ (c = 0.82g/100 ml, 99.5% ethanol) (corresponding to 34.9% *ee* of *R* or 67.5 : 32.5% *R/S*). The two compounds derived from the achiral precursor myrcene in nature, ipsenol (Ie) and ipsdienol (Id), could be produced by the beetle in nonracemic form (Francke et al., 1980), but were synthetic and racemic.

    The attractants 2-methyl-3-buten-2-ol (MB) and (4*S*)-*cis*-verbenol (cV) and their dispensers were identical to those earlier used by Schlyter et al. (1987a,c) (Table 1). Release rates were estimated in a mini wind tunnel in the laboratory as described earlier (Schlyter et al., 1987a).

TABLE 1. CHEMICALS, RELEASE RATES, AND DISPENSERS USED IN FIELD TEST OF
INHIBITORY EFFECTS OF SEMIOCHEMICALS ON ATTRACTION TO AGGREGATION
PHEROMONE IN *Ips typographus,* DENMARK, 1985

| Compound | Purity (%) | Source | Release rate (mg/day) | | | Dispensers[b] |
| | | | Nominal | Measured[a] | | |
				Mean	95% C.L.	
Attractant aggregation pheromone components						
MB	97	Aldrich	5	5.8 ± 0.3		Closed #730 w. 50-μl cap.
			50	57 ± 0.8		2-mm-diam., 3-ml vial
cV	99	Borregaard	0.1	0.052 ± 0.001		Closed #730 w. 150-μl cap.
			1.0	1.03 ± 0.05		9-mm-diam. hole, 2-ml vial
Semiochemicals						
Vn	99	KTH, Stockholm	0.1	0.11 ± 0.02		Closed #730
			1.0	1.1 ± 0.03		Two open #730
			10	7.7 ± 0.4		Three open, 3-ml vials
Ie	99	Borregaard	0.1	0.1 ± 0.02		Closed #730
			1.0	0.71 ± 0.09		Open #730
Id	95	Borregaard	0.1	0.1 ± 0.01		Two closed #730
			1.0	1.2 ± 0.1		Two open #730

[a] Measured in a mini wind tunnel at 20°C and 0.7 m/sec. Rate calculated as the slope ± its 95% confidence limits of the regression of weight loss vs. time.
[b] Dispensers were polyethylene vials that were either closed or closed but with hole drilled through the cap (x-mm-diam. hole) or with a capillary through the lid (w. x-μl cap.) or open. Vials were from Kartell, Italy, with the #730 being a 1-ml vial.

Traps were of type N79, i.e. black drainpipe traps without exterior funnel (Regnander and Solbreck, 1981; Bakke et al., 1983). These traps require beetles to orient, land, and enter holes to be caught. Tests were done in three old clear-cut felling areas (S, L, and J), all with relatively low beetle populations in Esrum Forest District, Grib Skov, North Zealand, Denmark, in May–June 1985. Randomization was "without replacement" (in the probability statistics sense) and followed a Latin-square design, i.e., with eight treatments and positions, a trap was assigned a random position after each replicate, but was tested exactly once in each position during eight replicates.

Qualitative Test of Verbenone, Ipsenol, and Ipsdienol Combinations. Vn, Ie, and Id were released in all possible combinations (singly or in binary or

trinary combinations) with the attractants, which with the control included eight treatments. Traps were placed at 6-m spacings in a clear-cut (site S), and their positions randomized after each replicate. A replicate, which lasted one day or longer, depending on flight activity, was completed when at least one trap was judged to have caught ≥ 50 beetles or when all traps had caught ≥ 100 beetles. For the first period (May 18–26, eight replicates), the "inhibitory" compounds were released at about 0.1 mg/day and for the second period (May 27–June 6, nine replicates) at about 1 mg/day (Table 1). In both cases, the control was a "low" level of attractant, MB + cV, at a release of 5 + 0.1 mg per day (Table 1).

   Dose–Response Test of Verbenone. A release dose range of approximately 0.1, 1, and 10 mg/day of Vn (exact laboratory rates in Table 1) was combined with two levels of attractant, MB + cV at 50 + 1 mg/day and 5 + 0.1 mg/ day, giving, with the two levels of attractants alone as controls, eight different baits. A 6-m spacing between traps was used for the two first replicates at each of the two sites (L and J) but was changed to a larger spacing (25 m) at site J, as the difference in catch between the two levels of attractant control baits was smaller than found in earlier studies (Schlyter et al., 1987c). Replications and randomizations were as described above, with the exception that the two first replicates at each site lasted for only half a day.

   Statistics. The mean catch ($\bar{x}$) of a bait (i) per replicate (j) is given as the proportion (p_{ij}) of the total catch per replicate (p_j) in Figures 1 and 2 below. To further facilitate comparisons between the different experiments, the proportion of total catch caught by a bait, p_i, is given in percent of the catch (100%) of the "low" control bait (release rate level MB + cV, 5 + 0.1 mg/day). This "low" control has been used in several earlier experiments (Schlyter et al., 1987a–c; Byers et al., 1989) and has about 10% of the release of commercial mass-trapping dispensers (Ipslure by Borregaard/Hercon; Schlyter et al., 1987a).

   Following Perry (1986) and Jones and Matloff (1986), we have used factorial MANOVA for analysis of the dose–response test. The variable used in ANOVA (Perry, 1986) was p_{ij} transformed by arcsin $p^{0.5}$, which was the transformation that gave the most homogenous variances as judged by Cochran's C test.

RESULTS

   Qualitative Test of Effects of Verbenone, Ipsenol, and Ipsdienol Combinations. The higher release rate (1 mg/day) of the three compounds, together with a constant release of the attractants, resulted in a reduced total catch for all combinations of "inhibitors" (Figure 1B). Except for Id alone, the reduction was significant. The pattern of qualitative influence by individual compounds

and their combinations on catch was quite similar between the two release rates of semiochemicals (Figure 1).

However, when the three compounds were released at their low rate (0.1 mg/day) alone or in any combination with attractant, only small and not statistically significant negative (inhibitory) effects on catch were seen (Figure 1A).

In all combinations and at both levels, addition of Id seemed to increase catch (low release rate) or at least not significantly decrease catch (high rate).

With the low rate of inhibitor candidates, all the binary and trinary combinations decreased the proportion of males down to around 22% at 6 m trap spacing (Table 2A), while the total catch was little affected (Figure 1A).
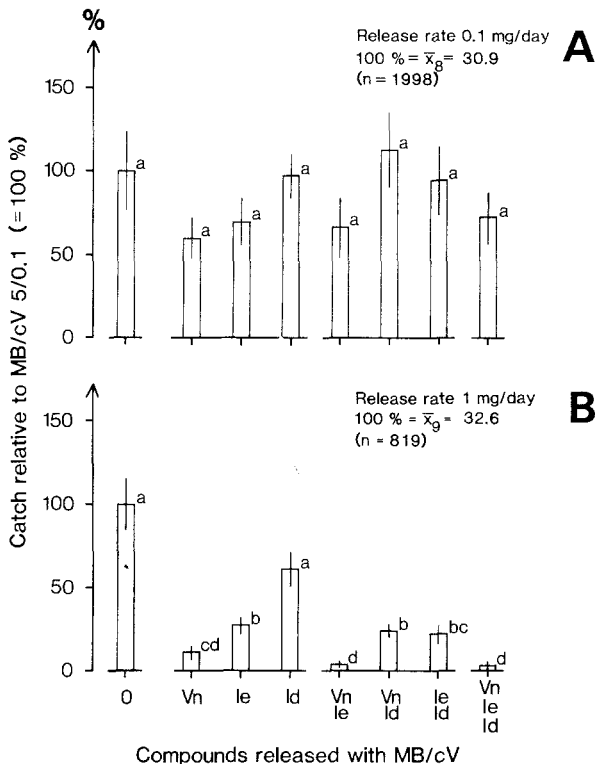

FIG. 1. Mean relative catches ($p \pm$ SE) of *Ips typographus* in pipe traps at 6-m spacing with qualitative addition in all possible combinations of verbenone (Vn), ipsenol (Ie), and ipsdienol (Id) in separate dispensers to attractant pheromone (MB + cV at "low" release 5 + 0.1 mg/day). Catches expressed as percent of the catch of the control ("low" level of the attractants MB + cV). Bars with the same letter are not significantly different by ANOVA on arcsin $p^{0.5}$ followed by Duncan's multiple-range test. (A) Added semiochemical compounds (Vn, Id, Ie) released at approx. 0.1 mg/day, (B) semiochemicals released at approx. 1 mg/day (see Table 1 for exact laboratory estimated release rates). For sex ratios, see Table 2.

TABLE 2. RESPONSE OF SEXES OF *Ips typographus* TO TESTS OF VERBENONE (Vn), IPSENOL (Ie), AND IPSDIENOL (Id) WITH ATTRACTANT PHEROMONE IN GRIB SKOV, DENMARK, 1985

Treatment release rates (mg/day)						Response	
						% Males	
MB	cV	Vn	Ie	Id	Ratio (Vn + Ie + Id)/cV	Mean (N)	95% CI
A. Combinations of compounds added at 0.1 mg/day, 6-m spacing, site S, May 18–26 (8 replicates)							
Control							
5	0.1					35.4 (237)	29.6–41.7
One compound							
5	0.1	0.1	0	0	2.1	30.1 (191)	24.1–36.9
5	0.1	0	0.1	0	1.9	33.3 (195)	27.1–40.2
5	0.1	0	0	0.1	1.9	35.5 (248)	29.8–41.6
Two compounds							
5	0.1	0.1	0.1	0	4.0	22.5 (169)	16.8–29.4[a]
5	0.1	0.1	0	0.1	4.0	21.5 (326)	17.4–26.2[a]
5	0.1	0	0.1	0.1	3.9	22.1 (263)	17.5–27.4[a]
Three compounds							
5	0.1	0.1	0.1	0.1	6.0	24.7 (186)	19.1–31.3
All baits						27.1 (1504)	25.0–29.5
B. Combinations of compounds added at 1 mg/day, 6-m spacing, site S, May 27–June 6 (9 replicates)							
Control							
5	0.1					34.8 (293)	29.6–40.4
One compound							
5	0.1	1	0	0	21	26.0 (34)	15.0–43.0
5	0.1	0	1	0	14	22.0 (85)	15.0–32.0
5	0.1	0	0	1	23	35.6 (222)	29.6–42.1
Two compounds							
5	0.1	1	1	0	35	(6.0) (16)	1.0–28.0[a]
5	0.1	1	0	1	44	26.0 (89)	18.0–36.0
5	0.1	0	1	1	37	29.0 (69)	20.0–41.0
Three compounds							
5	0.1	1	1	1	58	(33.0)[b] (12)	14.0–61.0
All baits						31.3 (820)	28.3–34.6
C. Dose–response test of Vn, 25-m spacing, site J, May 17–June 4 (12 replicates)							
Control, low-level attractants							
5	0.1					45.9 (98)	36.4–55.6
Vn dose with low-level attractants							
5	0.1	0.1			2.1	34.0 (79)	25.0–45.0
5	0.1	1			21.0	(50) (16)	28.0–72.0
5	0.1	10			148.0	(0) (7)	0–66
Control, high-level attractants							
50	1					24.6 (378)	20.5–29.2
Vn dose with high-level attractants							
50	1	0.1			0.11	18.9 (275)	14.7–24.0[a]
50	1	1			1.1	26.5 (215)	21.1–32.8[a]
50	1	10			7.8	31.0 (52)	20.0–44.0

[a] Significantly different from the control (low level attractants) at $P < 5\%$.
[b] Values for % males within parantheses are based on less than 20 individuals.

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For the high rate of "inhibitors," the proportion of males was very similar for both the control and addition of Id alone, while for the addition of Vn + Ie, the male proportion was significantly lower (6% males, Table 2B). However, the absolute catches were low, making estimates of sex-ratio differences less reliable.

In contrast to the spruce bark beetle, its predator *Thanasimus formicarius* was mostly attracted only to the bait including Ie + Id, which had 38% of the total 26 clerids caught.

Verbenone Dose–Response. Verbenone (Vn) decreased trap catch when released at 1 mg/day or more with both levels of attractants (Figure 2). At a 25-m spacing of traps, a significant inhibition began to occur at a ratio of Vn to cV of 0.1:1 (Figure 2B), corresponding to a ratio of Vn to Mb + cV as low as 0.002:1.

Of the factors (ANOVA) in the experiment, the level of attractant (MB + cV) had the largest main effect, followed by the dose of verbenone (Table 3). The factor spacing between traps had very little effect, as would be expected when relative catch, p_{ij}, per bait (i) per replicate (j), was the variable used in the analysis. The interaction of spacing with attractant level (Table 3) can be
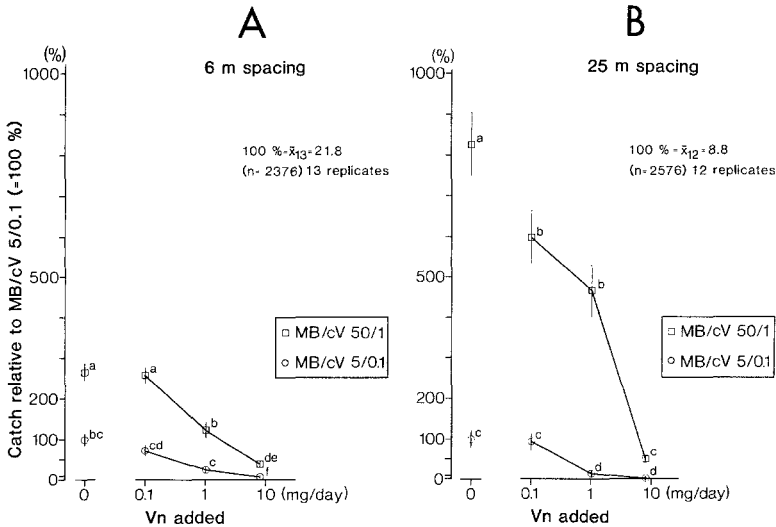

FIG. 2. Mean relative catches ($p \pm$ SE) of *Ips typographus* in pipe traps with doses of verbenone (Vn) added to two levels of attractants (MB + cV) at (A) 6-m spacing, and (B) 25-m spacing of traps. Catches expressed as percent of the catch of the "low" control (MB + cV, 5 + 0.1 mg/day) (cf. Figure 1). Within each spacing of traps, values with the same letter are not significantly different at $P > 5\%$ by ANOVA on arcsin $p^{0.5}$ followed by Duncan's multiple-range test.

TABLE 3. FACTORIAL MANOVA OF EFFECTS OF SPACING OF TRAPS, LEVEL OF ATTRACTANT (MB + cV), AND DOSE OF VERBENONE (0–10 mg/day) ON TRAP CATCHES OF *Ips typographus*, GRIB SKOV, DENMARK, 1985[a]

Factor	df	Mean square	F	Significance of F (%)
Within cells	180	0.1		
Constant	1	18.1	1923.6	<0.1 ***
Main effects				
SPACE (Distance between traps)[b]	1	0.04	4.2	4.2 *
ATTLEVEL (Level of attractant)[c]	1	4.1	437.8	<0.1 ***
VNDOSE (Dose of verbenone)[d]	3	1.1	119.1	<0.1 ***
Interactions				
SPACE × ATTLEVEL	1	0.2	18.6	<0.1 ***
SPACE × VNDOSE	3	0.01	1.1	33.6 NS
ATTLEVEL × VNDOSE	3	0.1	14.0	<0.1 ***
SPACE × ATTLEVEL × VNDOSE	3	0.04	4.3	0.6 **

[a] Catch was transformed by arcsin $p^{0.5}$ before analysis. Test of homogeneity of variances yielded Cochran's $C(11, 16) = 0.13$, $P = 23\%$ (approx.) after transformation.
[b] Two levels: 6 and 25 m spacing of traps. The factor SPACE was confounded with possible effects of location, as SPACE was not balanced between the two locations: there were two runs (replicates of each site) of 6 m at both sites before the change to 25 m spacing at one site. The total number of replicates was 2 + 11 for 6 m spacing and 0 + 12 for 25 m spacing. The results of the two first replicates at each of the two sites were very similar in absolute and relative catches ($P \gg 10\%$ in ANOVA), and the age, size, and proximity to naturally attacked trees (> 500 m) was also similar for the two sites. Thus, it was judged appropriate to do a simultaneous statistical comparison and to include the factor SPACE in the ANOVA.
[c] Two levels: MB + cV 50 + 1 or 5 + 0.1 mg/day (see Table 1).
[d] Four levels: 0, 0.1, 1, and 10 mg/day (see Table 1).

clearly seen when comparing Figure 2A and B, as the difference in catch levels between attractant levels is much larger in Figure 2B (25-m spacing). There was also a quite significant covariance between attractant level and verbenone dose (Table 3), graphically detectable as the different slopes for high and low attractant levels with increasing dose of Vn (Figure 2A and B) (cf. Tilden and Bedard, 1988). Also the third-order interaction was significant (Table 3), which can be seen graphically by the difference in slope between the attractant levels, which was not the same for the two trap spacings (Figure 2A and B). A direct test of the ratio between MB + cV and Vn as a factor was not possible as the ratio did not vary independently of Vn dose and attractant level.

The sex-ratio differences were large at the 6-m spacing of traps. At the low level of attractant (MB + cV, 5 + 0.1), the sex ratio decreased from 1 : 0.9 (male to female) at the control to 1 : 3 (24–31% males) at the higher Vn doses.
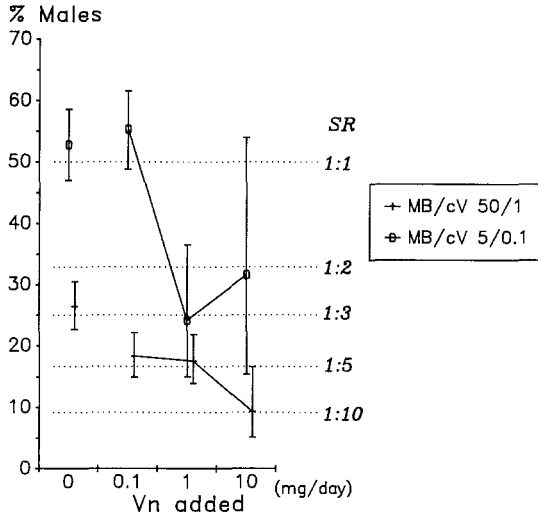
FIG. 3. Mean proportion of males ($p \pm 95\%$ C.I.) of *Ips typographus* in pipe traps with doses of verbenone (Vn) added to two levels of attractants (MB + cV) at the 6-m spacing. Values shown are retransformed from arcsin $p^{0.5}$, hence the asymmetric CI.

For the high level of attractant (MB + cV, 50 + 1), a threefold decrease in sex ratio, from 1:3.3 in the control to 1:10 (9% males) at the highest Vn dose, took place (Figure 3). At the 25-m spacing of traps, there was no effect on sex ratio by Vn dose alone (Table 2C).

DISCUSSION

The present study shows the inhibitory effects of ipsenol and verbenone on the attraction of *Ips typographus*. The effect is especially strong on the number of males, as both the total number of beetles and the proportion of males are reduced. The qualitative effects of Ie and Vn acting alone or in the pair Ie + Id were not unexpected as they agree with the findings of Bakke (1981) and Schlyter et al. (1987c). In the qualitative test Vn showed a negative effect on attraction, at both release rates (except in the binary combination with Id at the low rate). This agrees also with the effect of the binary combination of Ie + Vn with the attractants tested by Bakke (1981). Similar to previous reports (Dickens, 1981; Schlyter et al., 1987a, b), addition of Id to MB + cV had no significant effect on trap catches compared to MB + cV alone. Our current results do not show the effect shown in previous studies in which Id in combination with MB + cV was attractive at some dosages (0.005–0.04 mg/day,

Schlyter et al., 1987c; unspecified but relatively low doses, Bakke 1976; Bakke et al., 1977) but inhibitory at a high dose (0.58 mg/day, Schlyter et al., 1987c). Similar to the qualitative test, an increased dose of Vn (with both levels of attractant) decreased the trap catch linearly down to a level of 10% or less of the control (cf. Tilden and Bedard, 1988). The mechanism of this inhibitory effect of Vn is probably an inhibition of long-distance orientation, as the quantitative effect of verbenone dose was clearer at the 25-m than at 6-m spacing between traps (cf. Tilden and Bedard, 1988).

These experimental results must now be put into the framework of both how the semiochemicals (quantity and quality) are released from gallery systems in different attack phases (Birgersson et al., 1984; Leufvén and Birgersson, 1987; Birgersson and Bergström, 1989) and how they may affect the overall attack dynamics (Schlyter and Anderbrant, 1989; Anderbrant et al., 1988). The three compounds (Vn, Ie, Id) tested here were racemates or close to racemic, while their natural quality may be either as pure enantiomers or as mixtures with enantiomeric excess. For Vn, the racemate used is probably not a problem, as Vn chirality may depend on the pinan-skeleton of the α-pinene from which it is derived, and the chirality of α-pinene is known to vary widely between individual trees of Norway spruce (Lindström et al., 1989). Also, the activity of R- and S-enriched Vn tested by Bakke (1981) was equally high in reducing trap catch at the dose tested. For Id, however, it is possible that effects could have been distorted by the use of the racemate, because (1) the chirality of Id is known to be important in the behavior of *Ips* beetles (Birch et al., 1977, 1980; Wood, 1982), (2) Id produced by *I. typographus* has been reported as not racemic (Francke et al., 1980), and (3) it is known that a compound attractive in enantiomerically pure form may, as a racemate, show inhibitory effects at high release rates but attractive effects at low rates (Vité et al., 1985). However, we decided to test Id in racemic form as the compound was not available to us as pure enantiomers. In contrast, Ie seems to lack attractive effects at all rates tested both here and in a previous study (Schlyter et al., 1987c), and it would seem less likely that attractive properties of Ie were concealed by the racemic composition.

Estimates of the quantity of Ie, Id, and Vn released from logs (Schlyter et al., 1987a) and from galleries in attacked trees (Birgersson and Bergström, 1989) are now becoming available. These studies show that, although Ie and Id are undoubtedly present in beetle hindguts of males in late attack phases (Bakke, 1976; Birgersson et al., 1984, 1988), they are produced in such small quantities that they cannot be detected in the samples from airborne collections (Birgersson and Bergström, 1989). In contrast, Vn is readily detected and released in quantities similar to or larger than *cis*-verbenol from beetle infested logs and from galleries in trees (Schlyter et al., 1987a; Birgersson and Bergström, 1989).

The production mechanisms for the relatively large amounts of Vn, which

is found only in trace quantities in beetle hindguts (Birgersson et al., 1984, 1988), are not clear. Both autoxidation from α-pinene (Borden et al., 1986) and microbial mediated oxygenation of verbenols (Leufvén et al., 1984) have been shown. Irrespective of the relative and absolute release of the three semiochemicals (Id, Ie, and Vn), they could in theory all contribute to an odor message of an "old patch," as they are all produced in late attack phases by the beetle (Id, Ie) or by a sequence of oxidations of α-pinene in the defensive resin (Vn). At present, it seems that intraspecific attack density regulation by a qualitative change in the odor signal from a patch (such as a tree or a part of a tree) in *I. typographus* would be mostly dependent on Vn. The response of *I. typographus* to the beetle produced compounds (Id, Ie) may be more relevant in interspecific communication and competition, as Id and Ie are produced in larger quantities both by *Picea*-inhabiting sympatric *Ips* species such as *I. duplicatus* (Bakke, 1975) and *I. amitinus* (Francke et al., 1980) and by other sympatric species: *I. sexdentatus* (Vité et al., 1974), *I. acuminatus* (Bakke, 1978), *I. cembrae* (Stoakley et al., 1978), and *I. erosus* (Giesen et al., 1984). The attraction of the predatory *Thanasimus* beetles to baits with Ie and/or Id has been shown earlier (Bakke and Kvamme, 1981; Schlyter et al., 1987c).

An integration of the inhibitory effects of Vn and Ie into a quantitative model of attack dynamics (cf. Schlyter and Anderbrant, 1989) and into practical uses for forest protection would require more knowledge. Gathering of such data for time-dependent release (Birgersson and Bergström, 1988) and quantitative dose–response on attacks on logs (Schlyter et al., 1988) is now under way.

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