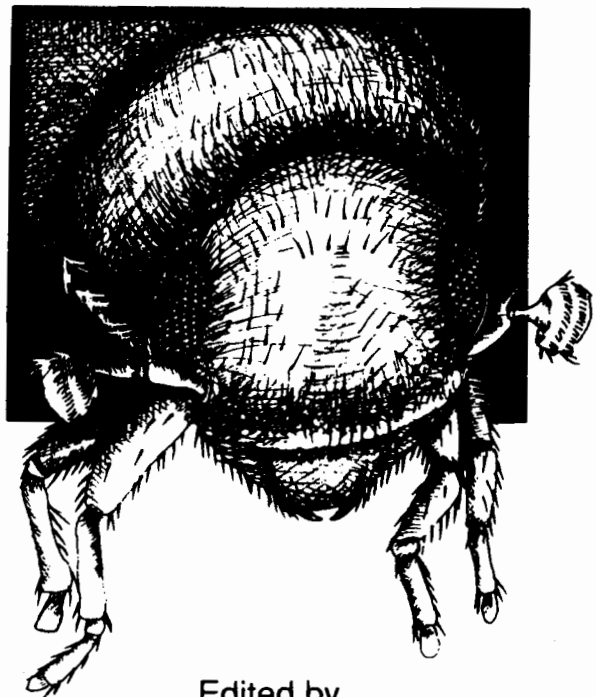# Integrated Control
## of
# Scolytid Bark Beetles

*Bigeia*

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Integrated Control

of

Scolytid Bark Beetles

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# Reduction of Attack Density of the bark beetles
## *Ips typographus* and *Tomicus piniperda* on host bark by
## Verbenone Inhibition of Attraction to Pheromone and Host Kairomone

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## ABSTRACT

An effective regulation of attack density in a bark beetle attack would
occur if individuals sought to avoid too close habitation with neighbours
on the bark surfaces in order to avoid competition for food and space
between their offspring. In aggressive species a positive regulation is
known to be driven by the aggregation pheromone during the mass attack to
overcome host-tree resistance, while a negative regulation leading to a
switching of attack to nearby patches may depend on several factors such
as a quantitative drop in pheromone signal, spacing behaviours on bark,
and production of semiochemical inhibitors. Ipsenol (Ie) and verbenone
(Vn), two oxygenated monoterpenes produced later during the attack in *Ips
typographus*, have earlier been shown to inhibit attraction to synthetic
aggregation pheromone. Verbenone has also been shown to inhibit
attraction of *Tomicus piniperda* to its host kairomone. In the first two
tests for *Ips typographus*, Ie and Vn were combined at a low dose, either
as a single point source, or with multiple dispensers spread over *Picea
abies* logs, but these treatments did not decrease attack densities. A
direct application of Vn gave an 88 % reduction in attacks. The fourth
test used Vn alone at three different doses applied over the surface and
showed a strong log-linear dose-response, with close to zero attacks at
the highest dose. Two tests with *Tomicus piniperda* on *Pinus sylvestris*
logs treated with Vn in a similar manner also showed significant
reductions in attacks. We suggest Vn to be one of several factors
involved in attack density regulation. The response of the two species to
this compound is highly dose-dependent; thus, Vn shows promise for
practical management by prevention of attacks when applied sufficiently.

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## 1. INTRODUCTION

The reproductive output of a bark beetle female is highly dependent on the competitive environment her larvae face. If strong inter-gallery competition lowers the amount of food available, the larvae may not gain enough biomass to pupate and will die (Anderbrant et al., 1985; DeJong and Grijpma, 1986). If the larvae survive to imago, they will be of small size and low quality in terms of pheromone production and reproductive output (Anderbrant et al., 1985). In both cases the fitness of the female will be lowered. Several tactics can be employed by beetles to avoid the deleterious effects of high density, such as earlier reemergence and/or shorter egg-galleries, and spacing of galleries. Of more strategical importance are mechanisms that will allow individuals to choose a patch where density is low (but high enough to diminish host resistance if living trees are mass-attacked), before investing time in preparing a gallery. Such mechanisms could be a direct sensing of density after landing in a patch by searching over the bark surface and then taking off if density is high, or by sensing a chemical signal before (and after) landing that has the message of an old, previously populated patch (cf. Byers, 1984; DeJong and Sabelis, 1988). A chemical signal is of special interest here as it can be experimentally manipulated to gain insight into the natural system or to control density and distribution of pest species for the purpose of forest protection. Such experiments have previously been done in some species, mostly for applied purposes, but have suffered from use of impure or even quite unknown compounds ("pineoil," Nijholt, 1980; Nijholt and McMullen, 1980; Berisford et al., 1986) or not precisely known release rates (Bakke, 1987).

In this study we aimed at testing the hypothesis that semiochemicals known to be released from infested host logs and/or to inhibit attraction to traps, in *Ips typographus* (L.) ipsenol (Ie) and verbenone (Vn) (Bakke, 1981; Schlyter et al., 1987b, 1989; Birgersson et al., 1988), and in *Tomicus piniperda* (L.) Vn (Byers et al., 1989), will also inhibit attacks on host material. To this end we have quantified the response in attacking and landing beetles on host logs treated with known release rates of the potential aggregation inhibitors.

## 2 MATERIALS AND METHODS

### 2.1 Tests A to D with *Ips typographus*

All tests with the eight-spined spruce bark beetle were run in Grib Skov, Esrum forest district, north Zeeland, Denmark. In 1985 the beetle population level was judged to be "semi-epidemic" with spontaneous attacks on standing trees occurring in several stands (Anderbrant et al., 1988), but in 1986 the level was lower and spontaneous attacks were not found.

*Tests A and B.* Groups of three logs (3 m long) of Norway spruce *Picea abies* (L.)Karst. were used with only the center log having an attractant bait. An adjoining log was untreated (control), while the other had ipsenol (Ie) and verbenone (Vn) either as a point source (test A) or 20

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smaller sources evenly spaced over the bark (test B). In both tests the hypothesis was that the treatment log, with Ie + Vn, would receive fewer attacks than the control. The experimental set-up was intended to represent the first part of switching of the attack focus from a tree under mass-attack releasing large amounts of aggregation pheromone (methylbutenol and cis-verbenol (MB + cV) = attractant bait on the center log) and males spilling over from the center to unattacked trees (control log) rather than to a fully colonized tree releasing inhibitors (Ie +Vn, treatment log). Test A was performed at six sites with two groups of three logs in each site giving a total of 12 replicates. Logs in each group came from the same tree to minimize effects of between tree variation in pheromone precursors (Lindström et al., 1988), and assignment of treatments/control to relative log diameters followed a latin-square design to avoid possible effects caused by the spruce bark beetles' preference for larger diameters with rougher bark. Logs within a group were placed parallel and spaced only 1.5 m apart while groups were at least 25 m apart and were oriented at $90^\circ$ with respect to each other. After each major flight period (1-3 days long), new attacks were located and marked with drawing pins over the exposed bark surface (2/3 of the bark total bark area). The experiment was run May 20 to June 5, 1985.

*Test B* was designed and run in the same way as test A, but in three sites. Since little effect had been noted by the point source of Ie+Vn in test A, we kept the same dose per log in test B while using 10 times the number of dispensers but each releasing 1/10 the previous rate and evenly dispersed over the whole area of the treatment log. In addition to marking of new attacks, small window traps were placed over logs in two of the six groups, and 6 bark samples (19 x 29 cm) were taken from all logs (upper and lower side at the middle section and at the end sections). Test B was run between May 19 and June 13, 1986.

*Test C* used pairs of 1 m long logs, one log baited with attractant only (control) and the other with attractant plus a direct spray application of Vn (treatment). Logs in pairs were adjacent sections of the same tree in order to be as similar in chemical and physical properties as possible. Logs in pairs were spaced $\geq 10$ m apart and pairs >25 m apart. Attacks were summarized for upper and lower sides in the field at the end of the experiment, which lasted from May 20 to June 5, 1986, in Grib Skov. Vn was applied a second time after 14 days (cf. Fig. 1).

*Test D* was a dose-response experiment with groups of 4 logs with three doses of Vn ("2," "20," and "200" nominal rate of Vn mg/day/log) released from dispensers spaced over the upper side of the treatment logs, plus control. All logs had an attractant bait and were spaced $\geq 20$ m apart, and groups were spaced 10 m apart. A latin-square design with 4 sites was used with 2 groups at each site, such that each treatment occurred exactly twice with each log size, and each group had logs cut from the same tree. Attacks were recorded as in test A. The test was run between May 20 and June 25, 1986.

## 2.2 Tests E and F with *T. piniperda*

Experiments with the pine shoot beetle were done at two localities, 110 km apart, from April 8 to May 6 at Brösarp and May 15 at Vegeholm, Skåne, Sweden, 1986. No synthetic pheromone was used with the pine shoot beetle, as logs of its host, Scots pine (*Pinus sylvestris* L.), are quite attractive (Byers et al., 1985), and the beetle seems to lack a long-range pheromone (Byers et al., 1985; Lanne et al., 1987).

*Test E* involved spraying of one of a pair of logs with Vn, and was, except for the attractants, done in the same way as test C, with six pairs in Vegeholm and two in Brösarp. Attacks were marked with drawing pins on the upper side only.

*Test F* was done like test D, but with only two doses of Vn ("2" and "20" nominal release of Vn mg/day/log). Three groups of logs were set up at each locality, and attacks were marked as in test E.

## 2.3 Chemicals, Dispensers and Estimation of Release Rates in the Field

In test A (1985), Ie (Borregaard A/S) was used in racemic form and 99% pure, and Vn was a mixture of enantiomers (66.5/33.5 $1S/1R$). The same compounds and dispensers were used in trap tests this year for *I. typographus* (Schlyter et al., 1989). In test B (1986), Ie was the same but Vn was almost pure (-)-enantiomer (99.2/0.8 $1S/1R$, Bedoukian) and 99% pure. This Vn was also used in tests C and D. The attractant pheromone components were 2-methyl-3-buten-2-ol (MB) and (4$S$)-*cis*-verbenol (cV) used in open vial dispensers at the "high" release rate (50 mg/day and 1 mg/day, respectively), which is comparable to the commercial attractant formulations (Ipslure©, Pheroprax©, Schlyter et al., 1987a, 1987b, 1989).
For *Tomicus piniperda* in test F, the (-)-enantiomer (98.6/1.4 $1S/1R$) of Vn was used at 94% pure (Chemicon/ Aldrich), and in test E the Vn used was the same as in tests B, C, and D.

As a starting point we used in test A (1985) the dispensers (and consequently release rates) that had proven active in inhibiting attraction to attractant pheromone in traps (Schlyter et al., 1989). The dispensers were open 1 ml PE-vials (#730, Kartell, Italy) and their approximate release was for Ie 0.6 and for Vn 0.5 mg/day at 20°. The dispensers used here have been reported earlier (Schlyter et al., 1989) and found, by gravimetrical analysis in the laboratory, to have a variation, measured as the range of the 95% confidence interval, of <10% of the average value. The lower dosages in test B (Ie 0.1 and Vn 0.11 mg/day per dispenser) were given by the same vials, but the vials were closed (Schlyter et al., 1989). The number and type of the dispensers for tests D and F were the same. Nominal release rate "2" for a log used 20 sources of closed 1-ml vials, rate "20" used 20 sources of 2 open 1-ml vials, and rate "200" 20 sources of 3 open 3-ml vials. The expected release rates would then be 2.2 (± 0.4), 22 (± 0.6), and 142 (± 8) mg/day per log ($\bar{x}$ ± 95 % C.I.), for the "2," "20" and "200" rates, respectively. Dispensers for the "2" rate were applied as in test B, but the open dispensers for rates "20" and "200" were put under rain-covers consisting

of a 6 x 7 cm rigid plastic sheet with a nail driven through its center. The nail was then driven in place on the log and dispensers fastened around the nail.

For tests C and, E Vn was sprayed directly on the bark in a quantity (about 15 ml per log) that was small enough to absorb completely into the outermost layer of the cortex bark. The release from this simple absorbent substrate was then monitored in test C by odour collections (see below).

Estimation of Vn release rates in the field was done by covering a portion of a log with a 50 x 60 cm form-fitting aluminum sheet and sucking the volatiles from the center of the semi-enclosed area through a plug of Porapak Q (80 -100 mesh) adsorbent. A plug of 300 mg adsorbent and an air flow of 200 ml/min generated by a small accumulator-fed pump (Birgersson and Bergström, 1989) was used. After a 2 h odour collection (aeration) period the plug was rinsed with 2 x 1 ml diethylether with 500 ng $C_7Ac$/ml as quantification standard. The extract was analysed, without pre-concentration, on a Finnigan MAT700 GC-ITD (Gas Cromatograph -Ion Trap Detector) using extracted ion current profiles (EICP) of characteristic fragments for quantification.

## 3.  RESULTS

### 3.1  Tests A to D with *I. typographus*

*Estimation of Vn release by odour collection from dispensers and sprayed logs (tests C and D).* The accuracy of the estimates in absolute terms could not be determined since no independent internal standard was released during the collections. In general the efficiency of trapping released Vn appeared to be low, <1 %. Estimates based on the two ions used for quantification, $m/z$= 91 and $m/z$= 107, correlated well (r =0.996), but $m/z$= 91 gave ~10% higher mean and median. Blank values, from forest air, untreated log etc., had a Vn estimate of 0.02 -0.03 ng/h for $m/z$= 107 and 0.1 -0.33 ng/h for $m/z$= 91.

The direct application by spraying of Vn in test C resulted in an exponential decline in release rate with time (Fig. 1A). However, despite the fast decline, appreciable amounts could still be detected after 10 days (Fig. 1A), equal to or larger than Vn release from logs with vials with a laboratory-estimated release of 140 mg/day/log (Fig. 1B).

The vial dispensers in test D showed a relatively stable release, with a weak, linear decline in release rates (Fig. 1B), as expected from open tubes (Byers, 1987).
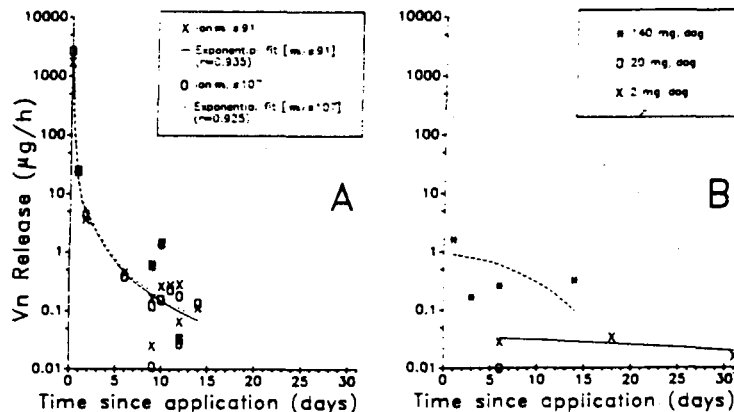
**Fig. 1.** **(A)** Release of verbenone (Vn) from logs sprayed with neat Vn (test C with *Ips typographus* ), estimated by odour collections with adsorbent eluted with solvent and analysed by GC-ITD, using two fragments, *m/z*= 91 and 107, characteristic for Vn. No data after 14 days due to new application after this time. **(B)** Odour collections as in A, but from logs with dispensers (test D with *Ips typographus)* with release rates estimated in the laboratory.

***Tests A and B.*** A total of 763 attacks were noted in test A, and 2083 in test B. In both tests the center log, with a high dose of attractant, received most attacks (Fig. 2), and in test B the center log had a lower proportion of males landing and found under the bark (Table 1).

However, the treatment (Ie+Vn) and control logs differed little in number of attacks (Fig. 2), although attacks were somewhat higher for the treatment log in test A. No formal analysis (ANOVA) was done, since it was obvious from Fig. 2 that the hypothesis that any of the treatment types (A: point source and B: area covering) would prevent "switching" of attacks from the center log was falsified.
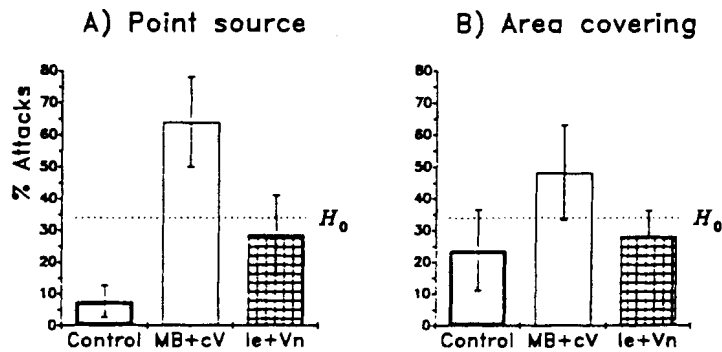
## A) Point source

## B) Area covering



**Fig. 2.** Relative number of attacks by *Ips typographus* on logs in groups of three *Picea abies* logs (untreated control, MB+cV synthetic pheromone treated, and ipsenol+verbenone (Ie+Vn) treated), $\bar{x}$ ±95% C. I. (retransformed from arcsin $\sqrt{p}$). Test (**A**) Ie and Vn released at a single point source (two dispensers), and test (**B**) Ie and Vn each released in 10 separate dispensers uniformly spread out over the area of the log. Dotted lines mark the zero hypothesis, $H_0$, of equal number of attacks on all types of logs.

**Table 1.** Number and sex-ratio of *Ips typographus* landing on and attacking logs in test B with uniform covering of dispensers with Ie and Vn, as estimated by barrier trap catches (2 of 6 groups) and bark samples (all 6 groups, n= 18) during May 21 -June 13, 1986.

| Treatment | Response | | | | | |
|---|---|---|---|---|---|---|
| | Landing (Traps) | | | Attacking (Bark Samples) | | |
| | Total | % Males | | Total | % Males | |
| | | Mean | 95 % C. I. | | Mean | 95 % C. I. |
| Control | 23 | 56 | 20 -80 | 49 | 43 | 30 -57 |
| MB+cV | 104 | 31.7 | 40 -50 | 144 | 33.3 | 26 -41 |
| Ie+Vn | 15 | 33 | 15 -75 | 88 | 45 | 35 -56 |

*Test C.* A total of only 226 attacks (50.7 % on the upper half) were noted, even though all logs in the 6 pairs were baited with strong synthetic attractant pheromone. However, since of the total attacks only 6.2 % occurred on Vn sprayed logs, Vn strongly reduced both the attack density and the relative numbers of attacks in a pair (Fig. 3).
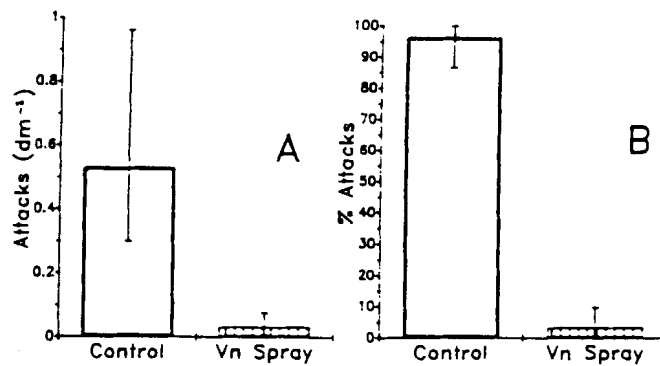


**Fig. 3. (A)** Attack density of *Ips typographus*, and **(B)** Relative number of attacks between pairs of *Picea abies* logs in test C, where the treatment log was sprayed with verbenone (Vn). Both logs had synthetic pheromone attractant (MB+cV). Means ±95% confidence intervals are given, retransformed from arcsin $\sqrt{p}$ [% Attacks] and $\log(x +1)$ [Attacks $(dm^{-2})$], respectively.

*Test D.* Similar to test C, the total number (n = 393) and attack densities (<1 $dm^{-2}$) were low, but an inhibitory effect of increased Vn dose could be seen in attack densities (Fig. 4A).

Multiple ANOVA showed Vn dose to be a quite significant factor, together with effects of site (Table 2). In addition there was a significant interaction between Vn dose and site (Table 2), which is also indicated by the non-parallel response lines in Fig. 4A.
The average relative number of attacks showed a negative and linear relation to Vn dose (Fig. 4B).
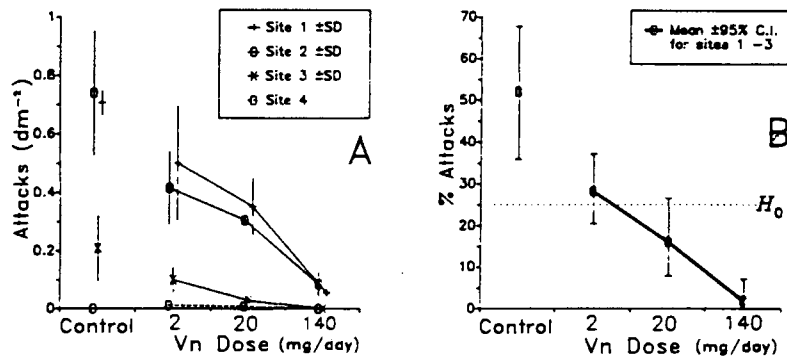
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**Fig. 4.** **(A)** Attack density of *Ips typographus* on *Picea abies* logs at different sites in test D, the dose - response experiment. Dispensers releasing rates of verbenone (Vn) estimated in the laboratory at 20° C (see Methods, sect. 2.3). All logs had synthetic pheromone attractant. **(B)** Mean relative number of attacks in groups of logs, test D, ±95% confidence intervals. Dotted line marks the zero hypothesis, $H_0$, of no difference between control and treatments.

**Table 2.** Multiple ANOVA of results of *Ips typographus* attack on verbenone treated logs and control logs (test D), as influenced by verbenone dose (2, 20, and 140 mg/day/log) and population levels on experimental forest sites.

*Tests of significance for* $arcsin(Relative\ number\ of\ attacks)^{0.5}$

| Source of variation | df | MS | F-value | Significance of F(%) |
|---|---|---|---|---|
| Within cells | 14 | 0.01 | - | - |
| Constant | 1 | 3.68 | 487 | <0.1*** |
| **Main effects (Factors):** | | | | |
| Verbenone-dose | 3 | 0.35 | 45.8 | <0.1*** |
| Site | 3 | 0.34 | 45.0 | <0.1*** |
| **Interaction:** | | | | |
| Verbenone-dose X Site | 9 | 0.06 | 7.8 | <0.1*** |

*Tests of significance for* $log(Attack\ density\ +1)$

| Within cells | 16 | .00 | - | - |
|---|---|---|---|---|
| Constant | 1 | .19 | 288 | <0.1*** |
| **Main effects (Factors):** | | | | |
| Verbenone-dose | 3 | .02 | 31.7 | <0.1*** |
| Site | 3 | .04 | 58.9 | <0.1*** |
| **Interaction:** | | | | |
| Verbenone-dose X Site | 9 | .00 | 5.5 | 0.2** |

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## 3.2 Tests E and F with *T. piniperda*

***Test E.*** Of 356 attacks on 8 pairs of logs only 17 % of the attacks were found on sprayed logs. Both mean relative number of attacks and attack densities were significantly different between treatment and control (Fig. 5).
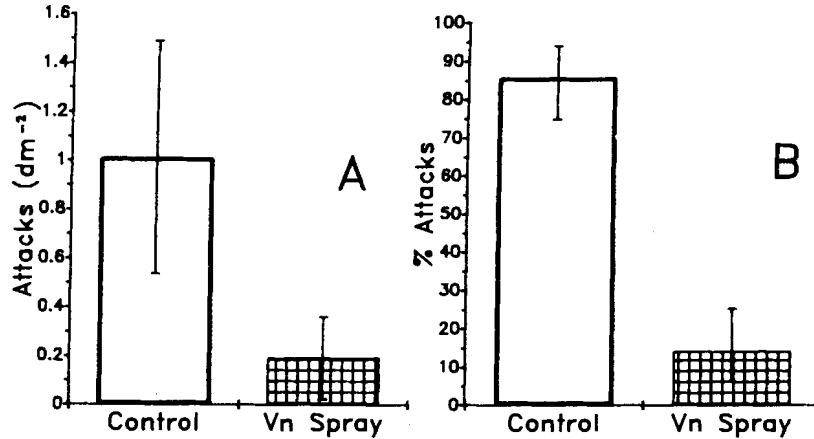


**Fig. 5. (A)** Attack density, and **(B)** Relative number of attacks by *T. piniperda* on pairs of attractive host *Pinus sylvestris* logs (test E), one treated with spay of verbenone (Vn). Means ± 95% confidence intervals are given, retransformed from arcsin $\sqrt{p}$ [% Attacks] and log(x+1) [Attacks (dm$^{-2}$)], respectively. See also Fig. 3.

***Test F.*** The dose-response experiment, with only two doses of Vn, gave a less clear picture than in *Ips typographus*, although the number of attacks (n = 1504) and attack density (>1.5 dm$^{-2}$) was fairly high. Of the two Vn doses used, "2" gave a somewhat, but not statistically significant, higher amount of attacks, while dose "20" gave half as many attacks as the control (Fig. 6).
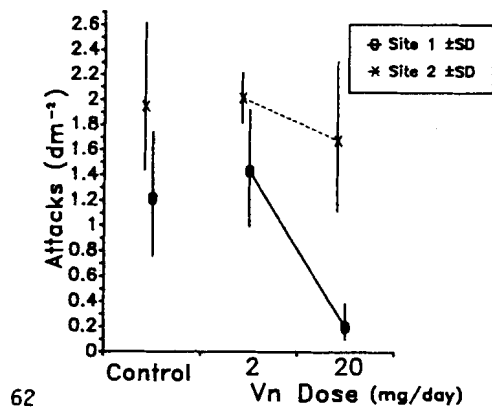


Fig. 6. Attack density of *T. piniperda* on *Pinus sylvestris* logs at different sites in test F, the dose - response experiment, with dispensers releasing rates of verbenone (Vn) estimated in the laboratory at 20° C. Site 1: Brösarp, Site 2: Vegeholm. Means ±SD are given, retransformed from log(x +1).

The diameter classes of the logs were included in ANOVA, partly because in one site diameters were imperfectly balanced and partly because log size and corresponding bark roughness are important for host selection in the pine shoot beetle.

MANOVA showed that Vn dose and diameter of logs were significant factors, as were the interactions of Vn dose with diameter and site for both relative number of attacks (P <1%) and attack density (Table 3). Site alone also had a significant effect on the attack density (Table 3), while the factor site was apparently not significant for the relative number of attacks (P >10%).

**Table 3.** Multiple ANOVA of results of *Tomicus piniperda* attack on verbenone treated logs and control logs (test F), as influenced by verbenone dose (2 and 20 mg/day/log), population levels on experimental forest sites, and diameter of host logs.

*Tests of significance for log(Attack density +1)*

| Source of variation | df | MS | F-value | Significance of F(%) |
|---|---|---|---|---|
| Within cells | 2 | | - | - |
| Constant | 1 | .002 | 8.8 | 9.7 NS |
| **Main effects (Factors):** | | | | |
| Verbenone-dose | 2 | .46 | 172 | 0.6 ** |
| Site | 2 | .74 | 279 | 0.4 ** |
| Diameter | 2 | .076 | 28.3 | 3.4 • |
| **Interactions:** | | | | |
| Dose X Site | 2 | .13 | 49.9 | 2.0 • |
| Dose X Diameter | 4 | .080 | 29.5 | 3.3 * |
| Diameter X Site | 2 | .009 | 3.4 | 23 NS |
| Dose X Diam. X Site | 2 | .001 | 1.0 | 88 NS |

## 4. DISCUSSION

Verbenone treatment showed a clear and significant effect in reducing attacks on host logs in 4 out of 6 tests. We have shown here that our hypothesis, that compounds inhibiting attraction to traps can also inhibit attacks on attractive host logs, is correct. Of the experiments (tests A -F), it was only in tests A and B, in which we hypothesised that inhibitors (Vn +Ie) -could stop "switching" in *Ips typographus* between closely (1.5 m) spaced logs, that there were apparently no significant effects of the inhibitors. In all the other tests, with spacings >10 m, clear inhibitory effects of Vn were shown. For *Ips typographus* we had to use a strong synthetic attractant in order to get any attacks on the control logs, a procedure which might have made the situation more like orienting to a trap. On the other hand, the results show that we can

inhibit attacks on logs which release an amount of synthetic pheromone corresponding to about 1000 attacking, unpaired males (Schlyter et al., 1987a); in other words, we succeeded in more or less inhibiting the attacks on a tree under mass-attack. The use of a strong synthetic pheromone attractant on the logs may have increased the attractant to an artificially high dosage and overpowered the effects of the inhibitors.

The effects shown here for Vn, a semiochemical (a compound produced by an organism that mediates an ecological interaction with (behaviour in) another organism in the system) are relatively clear, but what are the ecological implications in quantitative terms? Of interest are only the absolute amounts of Vn, but also, for *Ips typographus*, the relation of Vn to the pheromone component *cis*-verbenol (cV), from which Vn may be partly derived (Leufvén et al., 1984, 1988), and, for *Tomicus piniperda*, the relation of Vn to the kairomone (host-tree attractant) component α-pinene (Byers et al., 1985).

Schlyter et al. (1987a) collected volatile Vn and cV in the range 0.3 -0.7 and 0.1 -0.4 μg/day from small spruce logs with 50 males of *I. typographus*, corresponding to a ratio of Vn:cV of about 1:1. Birgersson and Bergström (1989) measured airborne release from individual beetles, which had about 30 -100 ng/3h/male of Vn and 100 -300 ng/3h/male of cV at different times after starting the attack, corresponding to a Vn:cV ratio of 1:10 in the beginning and 1:1 at the end (seven days later).
In *T. piniperda* Byers et al. (unpubl.) showed a release of up to 200 ng/h of Vn and 14 μg/h of α-pinene (a ratio of 1:70 , Vn:α-pinene) from small pine logs with 50 females. In traps they released Vn:α-pinene at a ratio of 1:110, which significantly inhibited attraction of *T. piniperda* to traps.

In our experiments with *I. typographus* we used higher ratios than obtained from the relatively early colonization phases (1 day - 1 week), from Vn:cV =1:0.5 (Vn dose "2", 2.2 mg/day per log) to 1:0.007 (Vn dose "200", 142 mg/day per log). Such high ratios together with high amounts of cV (1 mg/day), which correspond to a newly colonized patch, would probably not be found in nature. However, our experimental ratios may well be the case in old colonized patches where cV production by the beetles is low, but where Vn is produced by established microorganisms in the gallery wall phloem from verbenols and pinenes (Leufvén et al., 1984, 1988; Leufvén and Birgersson, 1987).

Several similar studies on protection of logs from bark beetle attack in *Trypodendron lineatum*, *Dendroctonus ponderosae* (Nijholt, 1980; Nijholt and McMullen, 1980; Berisford et al., 1986) and *Ips typographus* (Bakke, 1987) have shown the possibility to protect logs from attacks, but in these studies the treatment effects can not be understood in terms of the chemical ecology, since knowledge of release rates from treatment of logs and/or beetles is inadequate. Verbenone has long been known to inhibit attraction of *D. frontalis*, *D. brevicomis*, *D. pseudotsugae*, *D. adjunctus* and *D. ponderosae* to pheromone (Renwick and Vité 1970; Payne and Richerson, 1979; Rudinsky, 1974a; Bedard et al., 1980; Livingston et al., 1983; Ryker and Yandell, 1983). More recent work has utilized Vn to protect trees from *D. frontalis* attacks (T. Payne, pers. comm.). In addition to *T. piniperda* as shown by Byers et al. (unpubl.), *Ips*

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*paraconfusus* and *Ips typographus* also are inhibited from responding to their attractant pheromone (Byers and Wood, 1980; Bakke, 1981; Schlyter et al., 1989).

Thus, several species of phloem-feeding bark beetles have been found to respond to Vn in a similar manner, perhaps because Vn is consistently present in decaying trees (mostly by microbial catabolism) and its presence indicates that the host is no longer suitable for colonization (Leufvén and Birgersson, 1987). 3-Methyl-2-cyclohexen-1-one (MCH) is another important inhibitor for *D. pseudotsugae* and *D. rufipennis*, is known to be produced by the beetles, and has been used to protect trees from attacks (Rudinsky et al., 1974b; Furniss et al., 1974, 1981, 1983; McGregor et al., 1984).

The use of semiochemicals that inhibit aggregation and/or attack on host trees may prove to be useful tool in forest protection and management. In Europe, trees are harvested mainly during the winter and stored in large piles for transport later in spring or summer. These log piles must be moved out of the forest before beetles emerge from infested wood (by July 1 for *Tomicus piniperda* in Sweden and for *Ips typographus* in W. Germany). However, if the log piles can be protected by verbenone, then the logistic expenses and handling can be spread over a longer period with consequent savings. During epidemic conditions, when many stands are at risk of being mass-attacked during a short period of time, but not all stands can be accessed for cutting and removing attacked trees, Vn could be used to lower the probability that trees in such stands will be attacked, while traps and trap trees with attractant pheromone can concentrate the beetle population in more accessible areas.

From an applied point of view it is obvious that development of management strategies using inhibitory semiochemicals, such as Vn, would depend both on our basic knowledge of the semiochemicals' role in density regulation in the beetle and the development of suitable dispensers for releasing the compounds at the necessary rates. One point of interest is the mechanisms by which the inhibition of trap catches and log attacks takes place. Is it long-range orientation, landing or even after landing, or some other step in the behavioural sequence of attraction (Borden, 1982; Schlyter et al., 1987c) that is inhibited? The landing trap data from this study indicate that the steps up to and possibly including landing are involved, as landing corresponded roughly with attacks, but further behavioural experiments with natural and synthetic sources of attractants are needed here to elucidate the mechanisms of the effects of Vn found here.

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