

## Behavioural sequence in the attraction of the bark beetle *Ips typographus* to pheromone sources

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**ABSTRACT.** The functions of the two synergistic pheromone components, (4S)-*cis*-verbenol (cV) and 2-methyl-3-buten-2-ol (MB), and the role of ipsdienol in the attraction of *Ips typographus* (L.) (Scolytidae) to pheromone sources were studied in the field. Absolute and relative beetle catches were compared between several traps placed at and nearby a central pheromone source: a pipe trap containing the source, a surrounding sticky trap, a nearby window trap, and four distant window traps. A higher catch in the outer down-wind distant traps indicated an up-wind anemotaxis to the source. Increased MB release, with cV constant, increased the proportion caught in the central pipe trap, indicating MB as a landing stimulus. Release of MB alone gave a very small catch. Ipsdienol could not substitute for cV in the synergism with MB. An increase of cV, with MB constant, increased the number of beetles caught, but not the proportion caught in the pipe trap. The sex ratio was equal in the window traps, but fell to 30% males in both sticky and pipe traps, showing that a large proportion of the males attracted to the source did not land. The proportion of males in the pipe trap was reduced at the highest cV dose. The results support the idea of each pheromone component having a different relative importance in releasing different steps in the behavioural chain.

**Key words.** Synergism, pheromone components, behavioural sequence, 2-methyl-3-buten-2-ol, *cis*-verbenol, ipsdienol, sex-ratio, anemotaxis, orientation, pipe trap.

### Introduction

The original concept that species are characterized by single component attractant pheromones (Jacobson, 1965) has given way to multicomponent concepts (Wood *et al.*, 1967; Roelofs & Cardé, 1977; Linn & Roelofs, 1983), which

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stress that several components in a blend, acting synergistically, are usually necessary to affect a full response. Whether the synergism is due to the release of specific steps in a behavioural sequence by specific components (Bradshaw *et al.*, 1983) or, alternatively, that all compounds are equally important in releasing all steps (Linn & Roelofs, 1983) is still under debate.

Host selection and mate location behaviours in bark beetles (Coleoptera: Scolytidae) have

been described by Borden (1982) as a long behavioural sequence, which includes flight-initiation, dispersal flight with flight-exercise, orientation towards an odour source, landing, mating and establishment in the host. The orientation part of the sequence towards the odour source (host volatiles or aggregation pheromone) could take place by a series of behavioural steps which may be termed: up-wind anemotaxis (odour-modulated anemotaxis; David *et al.*, 1983), close-range orientation to the source, followed by landing and entering of galleries.

The aggregation pheromone of the palearctic spruce bark beetle, *Ips typographus* (L.), has been reported to consist of three synergistic compounds, 2-methyl-3-buten-2-ol (MB), *cis*-verbenol (cV) and ipsdienol (Id) (Bakke *et al.*, 1977). The male produces the largest amounts of MB and cV before mating. After mating, when females start to excavate their egg-galleries, MB and cV decrease while Id and ipsenol are produced in increasing amounts (Birgersson *et al.*, 1984). Of these, MB and cV are essential for the attraction and show strong synergistic effects on attraction (Schlyter *et al.*, 1987a). The synergism yields large trap catches but the numbers of males relative to females are low (Bakke *et al.*, 1983). The attractant activity of Id is less well established (Dickens, 1981; Bakke *et al.*, 1983).

On the basis of dose-response curves from electroantennograms, Dickens (1981) suggested that MB might act as a close-range/landing substance as it had a very steep dose-response profile. In contrast, cV showed both a more gradual dose-response curve and a lower threshold, and was suggested to act as a long-range orientation component of the aggregation pheromone. Id was assigned no specific function.

The strong synergism between cV and MB could be explained by a difference in importance of each compound in two parts of the behavioural sequence, long-range orientation (>1–3 m from the source) and short-range orientation/landing. In this hypothesis, the compounds could be of different importance either by acting as single substances or by acting in specific proportions. At least three predictions could be made from the hypothesis: (i) without MB there would be an attraction to, but little landing at, a source; (ii) an increase of MB with a constant amount of cV would cause an increased proportion of the flying beetles to be caught near

the centre of pheromone release; (iii) an increase in cV release with a constant dose of MB would increase the number of beetles attracted, but decrease the proportion landing.

The proportion of males in *Ips typographus* caught in pipe traps during mass-trapping is usually low, 21–31% (Bakke *et al.*, 1983). It is not known whether the low proportion is due to a low operative sex ratio in the population, a lower attraction of males to the pheromone source, or that attracted males for some behavioural reason are less likely to become caught by the pipe trap.

In order to test these predictions and to describe the attraction behaviour of the sexes in *Ips typographus* towards synthetic pheromone sources we have trapped beetles in the field at different distances from pheromone sources with the three components at different release rates and ratios over several decadic steps.

## Methods and test design

### *Experiment 1: variation of MB and Id*

The pheromone source (dispensers) was placed in the lower part of a pipe trap which was surrounded by a sticky trap, and had a near window trap on top of it (Fig. 4). This together with four distant window traps formed a trap group (Figs. 1 and 4). The pipe trap (Bakke *et al.*, 1983) with a trapping area of 0.55 m<sup>2</sup> caught beetles landing and entering holes/galleries. The sticky trap (no. 4 hardware cloth coated with Stickem Special®) with a trapping area of 0.06 m<sup>2</sup> encircled the lowest portion of the pipe trap and caught landing beetles. The near window trap consisted of a cross-barrier of Plexiglas® (with a trapping area of 0.36 m<sup>2</sup> over a funnel placed on top of the pipe trap), which caught beetles that were orienting close to the pheromone source.

Finally, four distant double-sided window traps (Helland *et al.*, 1984), with a trapping area of 0.36 m<sup>2</sup> on each side, were placed 3 m from the pipe trap in the four cardinal directions. These more distant traps together with wind data, recorded by SMHI (Sveriges Meteorologiska och Hydrologiska Institut) at Torsby airport 5 km south of the experiment site, allowed a correlative analysis of anemotactic long-range orientation towards the pheromone source (Fig. 1).

The substances were released from poly-

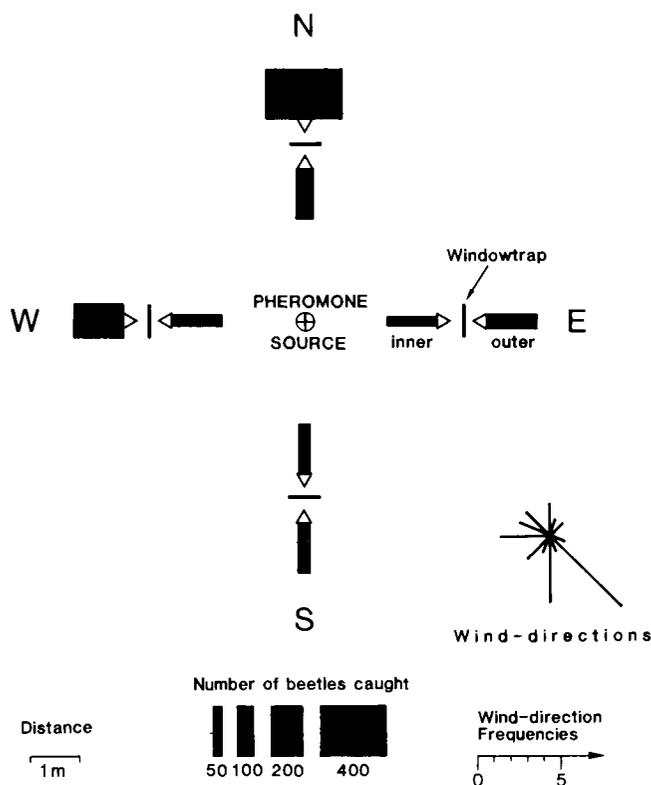


FIG. 1. Catch on outer and inner sides of the distant window traps, all baits containing both MB and cV combined. Size of distant window trap (0.60 m) is on scale with distance to pheromone source (3 m), experiment 1. Wind directions for afternoons with  $T_{\max} > 18^{\circ}\text{C}$  and wind velocity  $< 5$  m/s, i.e. when flight could take place, are indicated in lower right corner, as measured daily by SMHI at Torsby (5 km away), at 1 and 5 p.m.

ethylene vials of various openings or from glass capillaries (see Table 1). The release of 50 mg MB and 1 mg cV a day (our standard bait) corresponds to the release from a 1 m strip of the commercial Borregaard/Hercon IPSLURE<sup>®</sup> laminated dispenser aged 1 week (Schlyter *et al.*, 1987a).

The experiment was carried out on a 2-year-old clearing in a Norway spruce forest 7 km north of Torsby, Värmland, central Sweden in 1982 from 17 May to 6 June. The clearing widened towards the south giving a trough-like environment with a steady windflow from the south on most flight days. Trap groups were positioned at least 50 m apart and at a minimum of 20 m from forest edges. No attacked trees were present. Bait positions were randomized after each replicate, when sufficient numbers of beetles had been trapped.

#### Experiment 2: variation of cV

In the second experiment the release of cV in the pipe trap was varied over four decadic steps, with and without the standard release rate of MB (50 mg/day). The trap group was simplified and consisted of a pheromone baited pipe trap (same as above) and a near window cross barrier Plexiglas<sup>®</sup> trap (trapping area 0.72 m<sup>2</sup>, Fig. 4). In this case the near window trap was placed on the same height as the pipe trap at 0.75 m distance, catching beetles orienting close to the pheromone source.

The cV was purified by HPLC, removing for instance verbenone, giving a purity of  $> 99.5\%$  (courtesy of Peter Baeckström at the Royal Institute of Technology (KTH) in Stockholm). For dispensers and release rates see Table 1. The experiment was done on a fresh clearing, with

TABLE 1. Chemical release rates and dispensers used in field experiments testing the behavioural functions of 2-methyl-3-buten-2-ol, *cis*-verbenol and ipsdienol in *Ips typographus*.

Compound	Chemical purity (%) <sup>*</sup>	Source	Nominal release rate (mg/day)	Estimated release rate <sup>†</sup> (mg/day)	Dispensers <sup>‡</sup>
Experiment 1 (Torsby, 1982)					
2-Methyl-3-buten-2-ol (MB)	97	Aldrich	0.5	1.2±0.07	'730' with 2 µl cap
			5	5.8±0.3	'730' with 50 µl cap
			50	57±8	Hard vial, 1 mm hole
			500	570±80	Ten hard vials, 1 mm hole
			5000	1880±20	Ten hard vials, 3 mm hole
<i>cis</i> -Verbenol (cV)	96	Borregaard	1.0	1.03±0.05	Hard vial, 9 mm hole
Ipsdienol (Id)	98	Borregaard	0.1	0.04±0.003	50 µl capillary
			1	0.34±0.02	'730', 2.9 mm hole
			10	4.0±0.7	Hard vial, 9.2 mm hole
Experiment 2 (Lardal, 1983)					
MB	97	Aldrich	50	57±9	Soft vial, 2 mm hole
cV	99.5	KTH	0.01	0.003±0.002	'730' inside soft vial
			0.1	0.05±0.001	'730' with 150 µl cap
			1	1.03±0.05	Hard vial, 9 mm hole
			10	9.2±0.6	Seven soft vials with 13 mm hole

<sup>\*</sup>Chemical purity estimated by capillary GC. Optical purity for cV > 94% (-)-(4S) as estimated by its isopropyl urethane derivate separated on a XE-60-(S)-valine-(S)- $\alpha$ -phenylethylamide GC column.

<sup>†</sup>The release rates from polyethylene (PE) vials were estimated in the laboratory by measurements ( $n$ ) of the weight loss of the vials, placed in a wind tunnel at 0.7 m/s and 20°C, during 1 month. The rate of release was calculated as the slope, with its 95% confidence interval, from the regression of weight on time ( $n=8-35$ ). The 50 µl capillary was placed in the same wind tunnel and its release rate measured under a microscope as the decrease of its meniscus.

<sup>‡</sup>Dispensers were either PE vials (Kartell, Italy) of three types; '730' a 1 ml vial of soft PE, hard a 2 ml vial of hard PE and a soft vial of 3 ml size in soft PE, with capillaries or drilled holes in their lids, or a section of a 50 µl glass capillary sealed at one end.

numerous beetles hibernating in the litter, surrounded by forest on all sides, 15 km NE Skien, Lardal, southern Norway in 1983 from 6 June to 13 June. Positioning and randomization were as in experiment 1.

## Results

### *Up-wind anemotaxis and long-range orientation*

In the first experiment, the northern distant window traps caught the most beetles among the four outer distant window traps (all baits containing both MB and cV pooled,  $\chi^2=478$ ,  $df=3$ ,  $P<0.001$ ), followed by the western trap (Fig. 1). As the predominant wind direction was southeast/south, and since it was the outside of the northern trap that caught the most beetles, it strongly indicates that the beetles oriented

up-wind towards the pheromone source from a distance of more than 3 m.

In the second experiment, cV alone attracted some beetles to the trap group, and an increased release of cV increased the number caught (Fig. 2). However, of the four baits with cV alone, only 6% of the catch was caught in the pipe trap, compared to 59% for the five baits with cV+MB (Table 3). At a release rate of 10 mg/day for cV (alone), only 1% of the beetles trapped were caught in the pipe trap, while when MB was released alone the pipe trap caught 28% ( $\chi^2=28.2$ ,  $df=1$ ,  $P<0.001$ ). Thus, the first prediction of attraction to, but little landing at, the source without MB was correct.

Id could not substitute for cV in long-range orientation in combination with MB (experiment 1, Table 2) as the total catch was identical to that of MB alone.

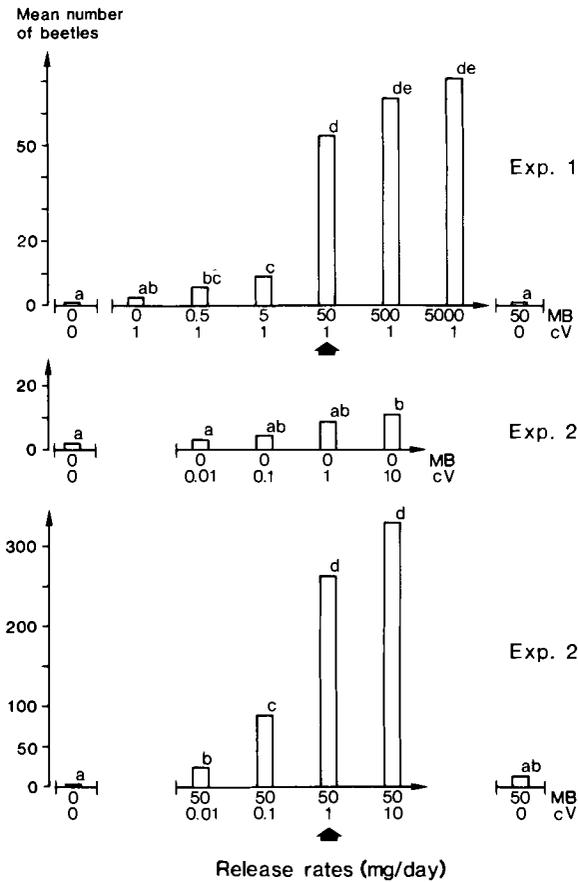


FIG. 2. Change in mean catch, combined for pipe and near window traps, at different release rates of MB and cV, experiments 1 and 2. Bars with the same letter are not significantly different by ANOVA followed by Duncan's multiple range test ( $P < 0.05$ ). Before the ANOVA, data from MB variation were transformed by  $\log(y+1)$ , data from cV variation without MB by  $(y+0.5)^{0.5}$  and data from cV variation with MB by  $\arcsin y^{0.5}$  to achieve homogeneous variances. Black arrows indicate standard bait, comparable to 1 m of commercial IPSLURE® dispenser.

#### Close-range orientation and landing

An increase in MB release from 1 to 2000 mg/day combined with a constant release of cV (1 mg/day) increased the proportion caught in the central pipe trap from 16% to 41% of the whole trap group (experiment 1, Fig. 3A). At the same time the proportion of catch in the near window traps decreased, while the sticky trap caught a constant proportion. The total number caught by the whole trap group increased substantially with the amount of MB released (Fig. 2). Thus, the second prediction of proportionately higher catch near the centre of phero-

mone release at higher MB levels was confirmed.

MB alone caught very few beetles in both experiments, and in the first experiment, where beetles may have had to orient over at least 100 m to reach a trap, the catch on MB alone did not differ from the blank. However, in experiment 2 where large numbers of beetles were believed to emerge from the litter around the traps, MB alone attracted small but significant numbers into the pipe trap (Table 3). Even a small addition of cV increased the total catch of the trap group and also the proportion caught in the pipe trap (Table 3). A further increase of cV did not

TABLE 2. Mean catches of *Ips typographus* in different trap types within trap groups with different rates of 2-methyl-3-buten-2-ol, *cis*-verbenol and ipsdienol released from the central pipe trap.

Nominal release rate* (mg/day)			Total catch of trap group	Catch in each trap type in the trap group					Sum
MB	cV	Id		Pipe	Sticky	Window			
						Near	Distant		
						Inner	Outer		
Experiment 1 (Torsby 1982), total catch ( <i>n</i> )=5008, six replicates									
0	0	0	4.0	0.8	1.5	0.2	0.7	0.8	1.5
0	1	0	5.0	0.8	0.5	1.5	0.7	2.3	3.0
0.5	1	0	16.7	2.7	4.2	3.3	3.3	3.2	6.5
5	1	0	18.0	3.7	4.5	5.7	1.2	3.0	4.2
50	1	0	91.5	27.2	22.2	25.8	5.2	11.2	16.3
500	1	0	110.0	37.5	23.3	27.2	4.5	17.5	22.0
5000	1	0	124.8	51.3	28.5	19.5	5.8	19.7	25.5
50	0	0	7.8	0.0	0.3	1.0	0.8	5.6	6.5
50	0	1	7.8	0.8	2.5	1.2	0.5	2.8	3.3
50	1	0.1	135.5	33.7	43.0	28.0	6.3	21.5	27.8
50	1	1	167.2	62.5	32.3	42.3	6.3	19.3	25.7
50	1	10	154.7	24.8	36.8	39.3	18.8	39.8	53.7
Experiment 2 (Lardal, 1983), total catch ( <i>n</i> ) = 7486, ten replicates									
0	0	0	2.5	0.0	—	2.5			
0	0.01	0	3.5	0.3	—	3.2			
0	0.1	0	4.6	1.4	—	3.2			
0	1	0	8.2	0.0	—	8.2			
0	10	0	10.1	0.1	—	10.0			
				1.8		27.1			
50	0	0	13.0	3.6	—	9.4			
50	0.01	0	24.5	14.7	—	11.6			
50	0.01	0	89.8	59.6	—	30.2			
50	1	0	263.0	150.1	—	113.0			
50	10	0	329.7	198.8	—	130.5			
				426.8		294.7			

Note: Sticky traps and distant window traps were not used in experiment 2.

\*For the estimated rates see Table 1.

TABLE 3. Proportion of *Ips typographus* caught in pipe trap releasing various rates of 2-methyl-3-buten-2-ol and *cis*-verbenol, experiment 2, 1983.

Baits (mg/day)		No. of baits	Total catch in trap types		Proportion caught in pipe trap	
MB	cV		Pipe	Near window	$\bar{x}$	95% CI
All baits without MB		5	18	271	0.06	0.02–0.11
All baits with MB		5	4268	2947	0.59	0.58–0.61
0	0	1	0 <sup>a*</sup>	25	0.00	0.00–0.13
0	10	1	1 <sup>a</sup>	100	0.01	0.002–0.05
50	0	1	36 <sup>b</sup>	94	0.28	0.21–0.36
50	0.01	1	147 <sup>c</sup>	116	0.56	0.50–0.62

\*Values followed by the same letter are not significantly different by Wilcoxon Signed-Ranks Matched Pairs test (at  $P < 0.05$ , corrected for number of comparisons).

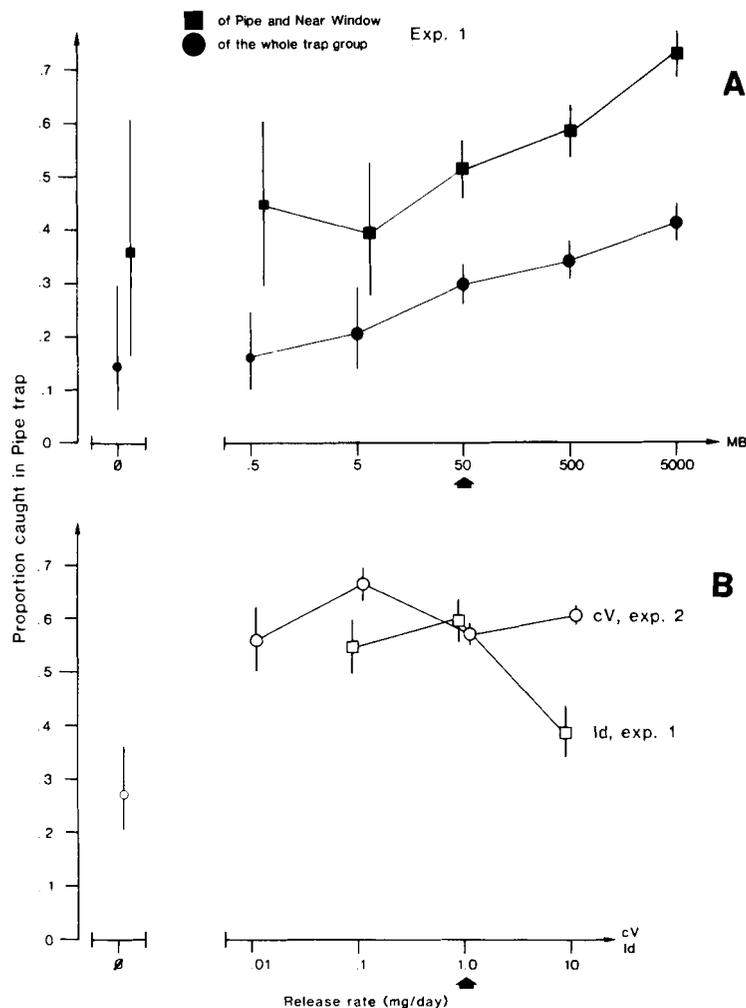


FIG. 3. (A) Relative catch in pipe trap (pheromone source/landing trap) at different release rates of MB, experiment 1, with cV constant at 1 mg/day. The results of the six replicates were pooled as no significant difference was found between replicates for any bait. Proportions calculated on total catch with 95% binomial confidence interval. (B) Change in relative catches within trap groups (pipe + near window trap) with change in cV and Id release. As cV was varied MB was kept constant at 50 mg/day, while as Id was varied, both MB and cV were kept constant at 50 and 1 mg/day, respectively. '0' indicates a blank trap in experiments 1 and 2, while black arrows indicate standard baits.

alter the proportion caught in the pipe trap, just the total number caught by the trap group (Figs. 2 and 3B). Thus, the third prediction was not fulfilled entirely as the proportion in the pipe trap did not decline.

Id at the lowest rate, less than one tenth that of cV, did not alter the catch from the standard 50/1 bait, but at the intermediate level the proportion caught in the pipe increased somewhat (N.S.) and also the catch of the whole trap group

(N.S.). However, at the highest release rate of Id, several times that of cV, the proportion of beetles caught in the pipe trap dropped drastically to only 16% of the whole trap group, while the catch of the distant window traps increased, which in turn lead to a high total catch of the group (Table 2). As much as 12% were caught in the inner distant window traps compared to 3.8–5.7% in other baits giving off 50 mg MB or more ( $P < 0.05$ ). Thus, the bait containing

the highest release of Id allowed many beetles to orient towards the pheromone source, while fewer entered the pipe (Fig. 3B) and a high proportion appeared to be deflected from the pheromone source.

#### Sex differences in close-range orientation

In the first experiment the proportions of males in the pipe trap were low, mean 30.2%,

and had a similar range, from 27% to 34%, for all baits which attracted more than 100 beetles into the pipe. In the landing trap (sticky) the proportion of males was as low as in the pipe (mean 34.3%, range 32–41%), while in both the near and distant window traps there was an equal sex ratio (mean 49.9% and 49.2% males respectively, range 44–63%) (see Fig. 4). Thus, about equal numbers of males and females were attracted and went from up-wind anemotaxis to

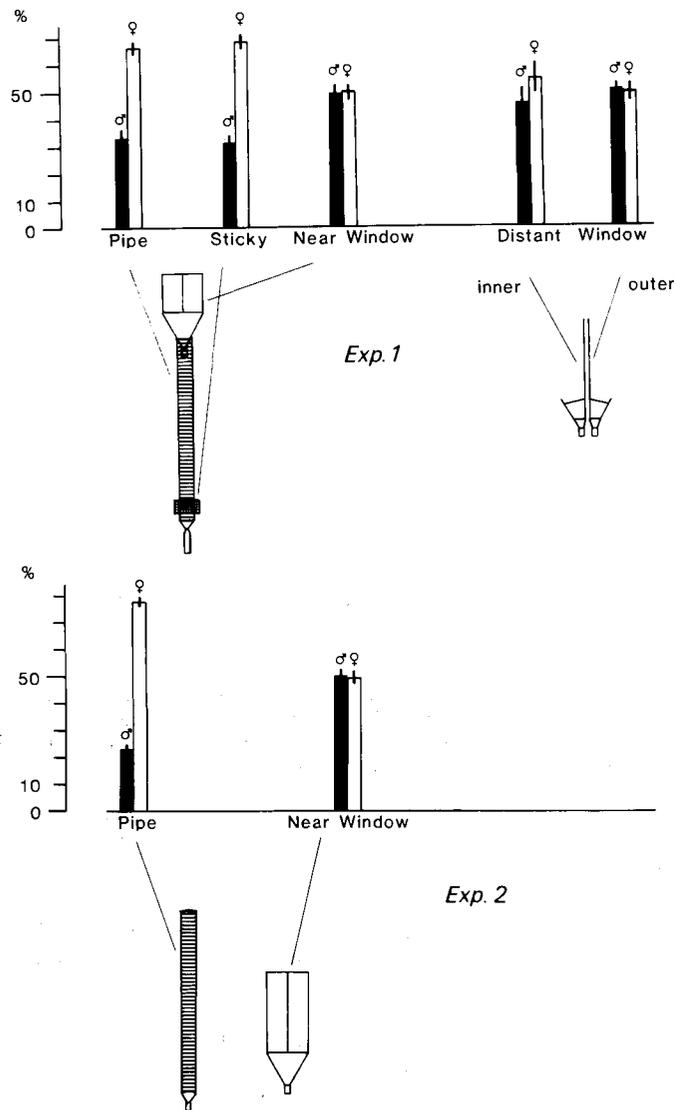


FIG. 4. Proportion of males (black bars) and females (open bars) caught in the different trap types within a trap group, combined for all baits. Proportions calculated on the total catch,  $\pm 95\%$  binomial C.I. Traps and inter-trap distances are approximately drawn to scale.

close-range orientation, but as sticky and pipe traps require the beetles to land to get caught, apparently a large proportion of the males orienting close to the pheromone source (pipe) did not land. In the second experiment, with only pipe and near window traps, there was again a low proportion of males in the pipe trap (mean 22.6%, range 14–38%), but an equal sex ratio in the near window trap (mean 50.4% males, range 41–62%) of the baits containing MB (Fig. 4).

When the standard bait was changed by increasing the cV release to 10 mg/day, the proportion of males decreased in the pipe trap ( $P < 0.01$ ) (Fig. 5). The high release also lured a slightly lower absolute number of males (N.S.) into the pipe trap. This means that the cV, although acting synergistically with MB to attract both sexes, at its highest release rate

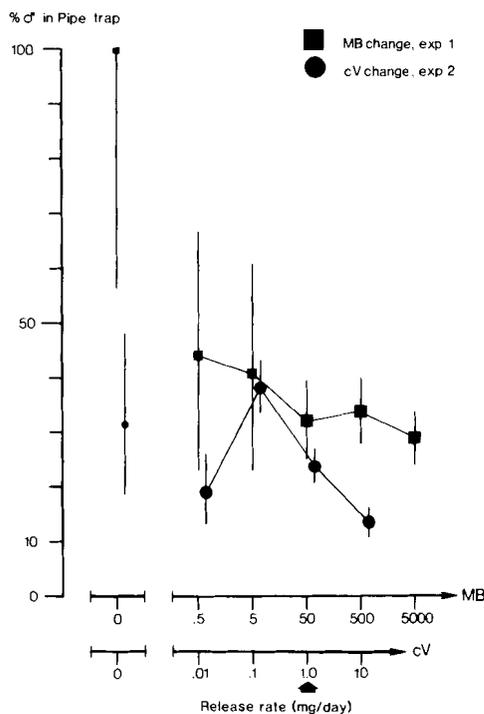


FIG. 5. Effect of MB and cV release rates on percentage of males ( $\pm 95\%$  C.I.) which have landed and entered holes in the pipe trap (pheromone source). As MB was varied, cV was kept constant at 1 mg/day, and as cV was varied, MB was kept constant at 50 mg/day. Addition of or change in Id (not plotted) changed the sex ratio very little. The black arrow indicates the standard bait.

inhibits male attraction, at least in the last steps in the behavioural sequence.

## Discussion

In chemical communication (hormonal, pheromonal, allomonal) activity of compounds should be termed synergistic in the strict sense only if the combined activity is significantly larger than the sum of their separate activities. For MB and cV the activity, measured as trap catch, was clearly synergistic, while Id seemed to be additive at intermediate levels. Similar activities were found in a parallel study, where MB and cV were tested together with a blend of all the major volatile components found in male hindguts. Both MB and cV were shown to be essential, as the removal of either of these from the blend reduced the attractive response nearly to zero (Schlyter *et al.*, 1987a). A significant additive effect on attraction by Id was later shown when Id was added to a medium dose of MB/cV (0.1 mg/day) at a release rate lower than or equal to that of cV (Schlyter *et al.*, 1987b).

Up-wind anemotaxis has been suggested to be the orienting mechanism of bark beetles by several authors, based on observations and trapping patterns on non-directional traps (McMullen & Atkins, 1962; Chapman, 1962; Byers, 1983a) but without quantitative wind data. Helland *et al.* (1984) showed with detailed trapping and quantitative wind data that *I. typographus*, released from platforms 10–50 m from a pheromone source, oriented over flat grassland, generally up-wind to the pheromone source (a pipe trap with IPSLURE, which is close to our 50/1 'standard bait'). In the laboratory a wind-tunnel study has also indicated anemotaxis (Choudhury & Kennedy, 1980). However, the present study is the first bark beetle study providing at least correlative evidence of up-wind anemotaxis in a natural setting, with un-manipulated beetles and with objective wind data (albeit with poor temporal and spatial resolution in the wind data).

The hypothesis of different importances of MB and cV, for short-range orientation/landing and for long-range orientation behaviour, is difficult to test directly but three predictions deduced from the hypothesis were tested here.

Only 1% of the beetles were caught in the pipe trap with a high release of cV as the only bait.

This conforms with prediction (i) of little landing without MB. The low proportion is significant, even if the total number of beetles caught by this bait is low, and it indicates that MB has a function for releasing such close-range behavioural steps as landing or entering of holes.

An increased amount of MB released, together with a constant amount of cV, increased substantially both the percentage caught in the pipe trap and the number caught by the whole trap group. Thus, prediction (ii) was confirmed, although the number of beetles caught by MB alone was very low. The increase in amount of MB also increased the ratio of MB to cV, and the ratio itself could be an important variable in modifying the behaviours (Linn & Roelofs, 1983). However, the ratio changed together with the total amount of pheromone released in both experiments, which means that the effect of the ratio MB/cV cannot be singled out.

Prediction (iii) was partially correct in that the proportion caught in the pipe did not increase with higher rates of cV release in the second experiment, but remained constant, although it should have declined somewhat.

These effects appear different from those in the western pine beetle (*Dendroctonus brevicornis*) where an increased release of attractant components had either no effect on (Tilden *et al.*, 1983) or decreased (Tilden & Bedard, 1985) the proportion caught near the source. However, the effects of MB and cV increase are not readily comparable to their studies, as the

trap types and component release ratios were not equivalent.

The three predictions, derived from the hypothesis of different importance in attraction behaviours of MB and cV, were not refuted, which allows us to accept the hypothesis at present. A simple diagram of how the hypothesis would fit into a behavioural sequence of attraction of *Ips typographus* is shown in Fig. 6.

However, the number of beetles attracted by the single substances, as judged by trap catch, is low, which makes exact judgement of their function difficult. In bark beetles little has been done so far on different functions of attractant components in the behavioural chain. In only a few studies have both release rates been varied and at the same time have different behaviours been quantified by observations or selective trapping devices (Tilden *et al.*, 1983; Rabalgia & Lanier, 1983; Tilden & Bedard, 1985). The specific role of MB and cV as well as the specific ratios between them should preferably be studied under the controlled conditions of a wind tunnel. However, wind-tunnel studies are inherently difficult to do on bark beetles (Choudhury & Kennedy, 1980) and the present orientation research for the well studied Lepidoptera, deduced mainly from wind-tunnel studies, is not conclusive. In moths, evidence has been found for separate functions of individual components, in *Grapholitha* and *Agyrotaenia* (Tortricidae; Cardé *et al.*, 1975; Baker *et al.*, 1976), and in *Panolis* (Noctuidae; Bradshaw *et al.*, 1983). However, recent detailed wind-tunnel studies

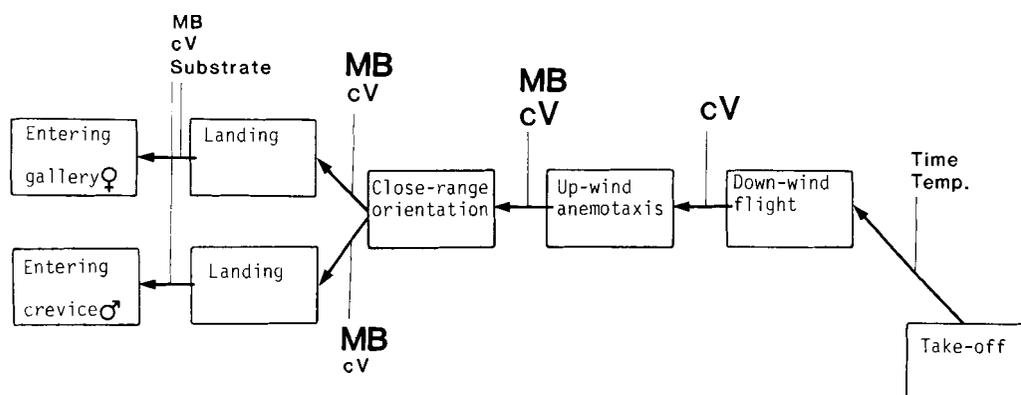


FIG. 6. Functions of the pheromone components cV (*cis-verbenol*) and MB (2-methyl-3-buten-2-ol) in the proposed behavioural sequence of attraction of *Ips typographus* towards an aggregation pheromone source. Thick arrows represent transitions between steps in the behavioural sequence and thin lines indicate variables releasing the transitions. Sizes of the MB and cV symbols indicate their relative importance as releasers.

have shown that a blend of long-range and short-range compounds was needed for orientation close to the source for *Trichoplusia* (Noctuidae; Linn & Gaston, 1981) or that all compounds are necessary for all behavioural steps (*Grapholitha*: Linn & Roelofs, 1983; Linn *et al.*, 1986; and *Agrotis* (Noctuidae): Löfstedt *et al.*, 1985).

Byers (1983a) reports that male *Ips paracon-fusus*, are less attracted to a centre of pheromone release than females, probably as part of a density regulation mechanism. Similarly, the proportion of male *I. typographus* caught in pipe traps used in the Scandinavian mass-trapping campaign has been low (Bakke *et al.*, 1983). The present study shows that the behavioural reason is that although the sexes are equally attracted from afar, many males do not closely approach or land at the source. The compound primarily responsible for this inhibitory effect is probably cV, as an amount of cV 10 times higher than standard decreased the proportion of males dramatically down to 14%, while an amount of MB 20 times higher than the standard decreased the percentage of males only slightly (and not significantly). It might be argued that the higher amounts of pheromone components released are too high to be behaviourally relevant. However, the release rates of the standard bait used in this study is of the same magnitude as that from a single tree under mass-attack (Schlyter *et al.*, 1987b).

A similar mechanism may operate in *Scolytus multistriatus* where multistriatin in excess of methylheptanol 'terminates colonization and deflects incoming beetles to crowns of elms' (Rabaglia & Lanier, 1983). In the western pine beetle (*D. brevicomis*) females and males are attracted equally to a pheromone source, but *trans*-verbenol at higher concentrations inhibits females, the gallery initiating sex (Byers, 1983b).

The basic knowledge gained in this study of elements in the behavioural sequence, the different behavioural functions of compounds, and the sex-specific behaviours can serve as a guide to the design of traps and dispensers used in the monitoring and control of spruce bark beetle populations. If the objective is to trap the highest possible number of both sexes of *Ips typographus* (mass-trapping), a barrier type trap with large amounts of MB (at 50/1 or 500/1 of MB/cV) would be preferable. For the monitoring of distribution and abundance, where it is

essential to have a large and constant attraction area per trap and a constant trapping efficiency, pipe traps with a large bait of cV+MB and dispensers with close to constant release rates, especially of MB, would be recommended.

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