THE EFFICACY AND PHOTODECOMPOSITION OF VERBENONE:

a repellent semiochemical of the mountain pine beetle, Dendroctonus ponderosae

by

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THE EFFICACY AND PHOTODECOMPOSITION OF VERBENONE:

A REPELLENT SEMIOCHEMICAL OF THE MOUNTAIN PINE

BEETLE, *Dendroctonus ponderosae*

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ABSTRACT

Verbenone is a known antiaggregation pheromone of the mountain pine beetle (MPB). In the vapor phase, it is unstable under natural daylight conditions, and its photodecomposition to chrysanthenone is caused by photons in the 300 to 380 nm range. Fifty per cent of the initial verbenone contained in pyrex test tubes decomposed within 1 to 2 h of exposure to daylight. Chrysanthenone had no effect on the MPB when tested alone or in conjunction with the synthetic attractants in the field. Therefore, verbenone decomposes to an inert compound that will not cause widespread disorientation. Verbenone released at 3.8 mg/day from impregnated polyethylene beads on the forest floor, reduced MPB response to attractant baited, multiple funnel traps by 50%, compared to a 100% reduction when verbenone was released at the same rate from the traps. Future experiments or operational treatments using verbenone beads applied aerially should compensate for its lack of vertical diffusion. Many beetles were unable to orient directly to an attractive point source when given a 4-silhouette visual cue, suggesting that vision is important in host selection. Verbenone released at 1.9 mg/day was 100% effective at preventing response by MPBs to multiple-funnel traps baited with the host compound myrcene at horizontal distances of 1 and 2 m from its source. Addition of the attractive pheromones, *trans*-verbenol and *exo*-brevicomin, to these traps caused the efficiency of verbenone to decrease 1 m from its source and to become ineffective 2 m from its release point, indicating that verbenone released in large quantities from a mass attacked tree would probably not prevent attack on nearby trees. The production of verbenone from a live standing tree was determined by drawing air from individual

MPB galleries through a Porapak Q trap. Verbenone production was equal in galleries containing either a single female or a male-female pair and remained constantly low for 3 days until the galleries were sealed with frass, depleting its output. The role of verbenone in the mechanism of 'host switching' may have been over emphasized in the attack dynamics of MPB within the lodgepole pine ecosystem.

ACKNOWLEDGMENTS

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INTRODUCTION

Traditional forestry practices and current pest management strategies are becoming unacceptable in today's environmentally conscious world. As social pressures mount, novel ideas to reduce the economic impact of pests, while respecting the integrity of the natural ecosystems must be considered. The use of naturally occurring semiochemicals to control insects, has proven to be an economically viable tool for the monitoring and control of many different pests (Ridgway et al. 1990). Semiochemicals include three commonly recognized types of chemical messengers: pheromones which convey a message between members of the same species, and allomones and kairomones, interspecific compounds of adaptive benefit to the producer and the perceiver, respectively (Nordlund 1981). One success story has been the use of semiochemicals to contain, concentrate and reduce mountain pine beetle outbreaks in lodgepole pine forests of British Columbia (Borden 1990). Continuing research in the use of semiochemicals has disclosed another possible control strategy: the use of an antiaggregation pheromone, verbenone, to protect trees from the mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae)(Amman et al. 1989; Lindgren et al. 1989; Amman et al. 1991; Gibson et al. 1991; Shea et al. 1992).

The Insect

The mountain pine beetle (MPB) is truly what its generic name suggests: a killer of trees. Its preferred hosts are large-diameter lodgepole pine, *Pinus contorta* var *latifolia* Engelmann, although it may be found in a wide range of other pines (Anhold and Jenkins 1987). *D. ponderosae* occurs throughout the pine forests of

British Columbia, south-western Alberta, the western United States and northwestern Mexico (Waters 1985).

D. ponderosae, *Dendroctonus monticolae* Hopkins and *Dendroctonus jeffreyi* Hopkins were synonymized by Wood (1963), but the latter species is now considered distinct (Lanier and Wood 1968). Some genetic differences can be found between widely separated populations of *D. ponderosae* (Stock and Guenther 1979), but classification into subspecies has not occurred, due to the wide variation of host species (Stock and Amman 1980; Wood 1982; Raffa 1988).

In lodgepole pine, *D. ponderosae* is generally univoltine. Adult beetles emerge in mid-summer and attack trees by chewing through the outer bark to the phloem-cambium layer. Initial host selection is apparently elicited primarily by the perception of vertical profiles (Borden et. al 1986). Moeck and Simmons (1991) have produced evidence for a primary chemical attraction to lodgepole pine volatiles, but beetles have been observed landing randomly on host and non-host species, as well as suitable and unsuitable lodgepole pines (Hynum and Berryman 1980). Aggregation results from the release of attractive pheromones and host volatiles caused from initial attack (Borden et. al 1987).

Mating occurs within the gallery, and females create vertical egg galleries, approximately 30 cm long (Reid 1962a,b). Ventilation holes to the outside are created at intervals along this gallery and the lower portion is usually packed with frass (Reid 1962a,b). The female deposits about 75 eggs into small niches cut to the side of the gallery, but this number varies greatly with attack density, phloem thickness and moisture content; potential fecundity ranges up to 260 viable eggs (Reid 1962a,b).

Hatching occurs about a week after oviposition; the larvae tunnel at right angles from the main gallery, feeding on the phloem tissue. Second or third instar larvae cease development and overwinter (Raffa 1988). Temperatures below -18° and -40°C are lethal to eggs and larvae, respectively (Safranyik et al. 1975; Safranyik 1978). The larvae resume feeding and finish their development by creating pupation chambers in the inner bark (Waters 1985). By mid-July or August, after approximately 1 month of maturation feeding, the adults emerge and seek new hosts (Waters 1985; Raffa 1988). Emergence occurs between 16° and 30°C and flight usually occurs between 21° and 38°C (Safranyik 1978).

Host/Insect Interactions

It is evident that the visual silhouette (standing tree), volatile host compounds and beetle produced attractants are essential for successful attack (Pitman and Vité 1969; Raffa and Berryman 1983; Borden et al. 1987). Thus, aggregation and successful attack is a complex sequence of events (Borden et al. 1987) that depends upon the resistance of an individual tree and the number of attacking beetles (Raffa and Berryman 1983). When populations are at suboutbreak levels, trees of low vigor are selected (Craighead et al. 1931; Amman 1978), but at epidemic population levels, vigorous trees of large diameter become the focal points of aggregation (Shepherd 1966; Amman 1978; Mitchell and Priesler 1991). It has not been resolved whether individual beetles select trees by random visitation (Hynum and Berryman 1980) or by orienting to primary attractant, semiochemical messages (Moeck and Simmons 1991).

About 90% of initially attacking beetles are female, but the sex ratio approaches 1:1 over time (Raffa 1988). Once beetles land, orientation is determined by visual, tactile and chemical cues. Rough surfaces are preferred (Shepherd 1965), and certain compounds can elicit feeding responses by females (Raffa and Berryman 1982). When the stimuli are unsuitable, the attack sequence is halted and the beetle leaves the host; if the cues are suitable, the female continues boring and the attack sequence progresses (Raffa and Berryman 1982). The exact chemicals that are used for the determination of suitable hosts have not been identified, but none of the host monoterpenes is strongly repellant (Raffa 1988). As the female bores into the host, she pushes frass and shredded bark out of the entrance hole causing the release of many host compounds.

After selecting a host, the female releases the pheromone *trans*-verbenol which attracts males and some other females. As the males arrive, they release the pheromone, *exo*-brevicomin, attracting mostly females to the host (Borden et al. 1987). The attraction to both pheromones is increased by the host tree kairomone, myrcene (Conn et al. 1983). Thus attack is concentrated on a host tree (Borden et al. 1987). Attack is terminated at least in part by the antiaggregation pheromone verbenone, produced primarily by yeasts associated with the beetles (Hunt and Borden 1990).

Fungi, bacteria and yeast spores carried by the beetles, soon start growing in the sapwood and phloem (Whitney 1982); within two weeks the fungi begin to form pigments, staining the infected tissue blue. These microorganisms assist the beetle in overcoming host resistance (Raffa 1988) and can be used by the brood as a food supplement (Whitney 1982).

Within a few weeks of infestation the trees usually begin dying from the actions of the fungi, *Ceratocytis montia* Rumb. and *Europhium clavigera* Robinson and Davidson, in association with the girdling of the living bark by the beetles (Safranyik et al. 1975; Raffa 1988). The following spring the foliage of these trees characteristically turns red and over the next 2 years the foliage gradually falls off the tree (B.C. Ministry of Forests 1985).

When beetles are not present in sufficient numbers or when host resistance is too great, attack is often unsuccessful and the host tree is able to "pitch out" the attacking MPBs with resin as they bore into the inner bark (Amman and Safranyik 1984). Host resistance has been shown to decline with age (Amman et al. 1977) and varies seasonally, usually peaking in early July and declining from that point (Reid and Shrimpton 1971). This seasonal reduction in host resistance corresponds with the initiation of flight and the attack period of the MPB (Amman and Safranyik 1984). Trees of diameter >25.4 cm at 1.3 m above ground (Shrimpton and Thomson 1983) and of an age >80 years (Amman et al. 1977) are considered to be prime hosts for MPB, provided there is a suitable climate for their development (Amman and Safranyik 1984). Therefore, current fire management strategies protecting stands that have reached maturity (>80 years) in British Columbia have provided the MPB with less resistant hosts (Waters 1985) and have allowed MPB populations to reach epidemic proportions.

During outbreaks the large number of dead or dying trees, create openings in the canopy and provide fuel for potential fires (Cole 1978; Peterman 1978) which are important for the regeneration of the lodgepole pine. Therefore, past MPB outbreaks and fires are responsible for the lodgepole pine stands one sees today (Cole 1978; Peterman 1978).

Economic and Environmental Importance

The MPB's devastating effects have been recognized since the early 1900's, when attempts were made to control or contain the beetle by felling and burning infested trees (Klein 1978). As the marketability of lodgepole pine has increased, the losses sustained have become much less tolerable and the problems have increased. In 1989, lodgepole pine was the major species harvested in B.C., accounting for 25% of the total harvested volume of 87.4 million m^3 (COFI 1990). As a timber species, lodgepole pine wood is used for light construction, panelling, trim, posts, poles, and other specialty uses (Waters 1985).

Lodgepole pine regenerates naturally after a forest fire, resulting in an even-aged dense stands. As these stands become overmature, tree vigor declines (Waters 1985), allowing the beetle to reach epidemic populations. These same stands are a major target for harvesting. Thus, the beetle is competing with man for prime timber. Borden (1990) noted that MPB killed approximately 195.7 million pines in British Columbia between 1972 and 1985, resulting in estimated potential losses of $14.4 - 19.6 billion (Can.). Even after salvage logging, real losses would be in the range of $4.1- 5.4 billion (Borden and Lindgren 1988).

Other problems encountered in infested areas, are an increased risk of fire and diminished accessibility for game and livestock caused by the dead and fallen trees (B.C. Ministry of Forests, undated). Also the need for rapid sanitation and salvage logging in large areas may cause substantial surface erosion often resulting from poor road construction with improper or damaged drainage patterns.

Current Controls

MPB infestations are very similar to forest fires (Safranyik 1985); since the composition of a lodgepole pine forest often allows epidemic populations of the beetle to flourish (if no control procedures are undertaken), all the timber on a parcel of land can be lost (Beal 1943; Berryman 1982). If control of forest fires is justified, there should be a similar justification for control of the MPB.

Control methods can be broken down into direct, short-term efforts and those methods which will ensure the long-term sustainability of the forest. Long-term control methods include the creation of vigorous stands of different age classes and species, and the adjustment of rotations (Niemann 1985). Little is known about what should be expected or the costs involved in implementing such practices. Because extensive susceptible stands are present today and will be present in the future, effective short-term methods will be continually needed.

When MPB infestations occur, harvesting is usually directed to problem areas. There are three options available: 1) prevent the attack of beetles by partial cutting of susceptible stands to 'beetle proof' them before the beetle reaches the area (Gibson 1989; Amman 1989); 2) harvest the stand immediately after attack to remove the beetles, while recovering the full value of the infested timber (sanitation-salvage logging); and 3) salvage log after the beetles have emerged to recover the residual value of the dead timber (Safranyik 1985; McMullen et al. 1986). Recently, attractive semiochemical baits (*trans*-verbenol, *exo*-brevicomin, and myrcene) placed at a density of 4/ha in lodgepole pine forests have been used in B.C. to contain and concentrate infestations prior to exercising the second option (Borden et al. 1983a,b; Borden and Lacey 1985; Borden 1990).

Single tree disposal can be effective for treatment of small or spot infestations (Safranyik 1985; McMullen et al. 1986). This management tactic relies on the identification of single or small groups of beetle-infested trees, and their subsequent removal or destruction by harvesting, felling and burning, application of MSMA (monosodium methane arsonate) killing both the tree and the beetles in it (Maclauchlan et al. 1988), or surface treatment of felled trees with an insecticide to kill emerging beetles (Fuchs and Borden 1985). Semiochemical tree baits are recommended to increase the efficiency of single tree treatment programs (B.C. Ministry of Forests 1985).

Amman et al. (1989) and Lindgren et al. (1989) demonstrated the potential of using the antiaggregation pheromone, verbenone, as a tool to disperse MPBs from an attacked stand, or to keep beetles from attacking high value or sensitive stands, e.g. wildlife corridors, recreational areas and riparian zones. As the social pressures mount to conserve natural forests, the use of new tools such as antiaggregation pheromones must be seriously considered.

Verbenone

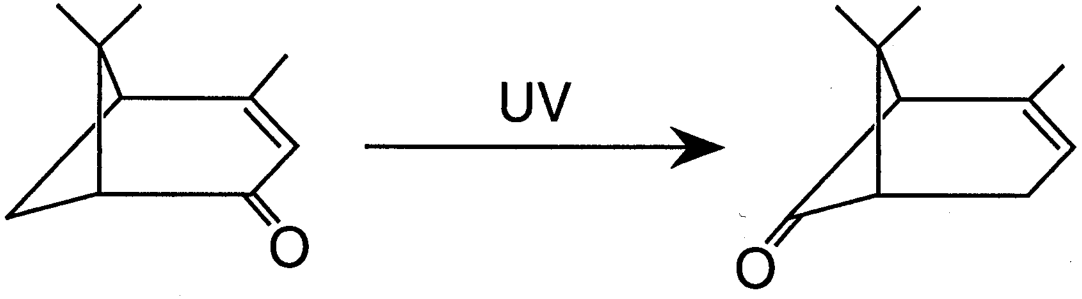
Verbenone, 4,6,6,-trimethylbicyclo [3.1.1] hept-3-en-2-one, was discovered in males of the southern pine beetle, *Dendroctonus frontalis* (Zimm.), and the western pine beetle, *Dendroctonus brevicomis* (LeC.)(Renwick 1967), and subsequently was shown to reduce aggregation of these species (Renwick and Vité 1970; Payne et al. 1978; Bedard et al. 1980). Verbenone has also been detected in the hindguts of feeding MPB's (Pitman et al. 1969) and in volatiles emanating from male-female pairs (Rudinsky et al. 1974). It has also been determined that verbenone is produced from the autoxidation of α-pinene and *trans*-verbenol (Hunt et al. 1989) and from the metabolism of these same compounds by symbiotic microorganisms occurring within the beetles' guts (Hunt and Borden 1989) and their galleries (Hunt and Borden 1990). Ryker and Yandell (1983) found that verbenone had antiaggregative properties for *D.ponderosae* when tested in conjunction with synthetic lures, and reported that (-)-verbenone was the most active enantiomer. Although the results of Amman et al. (1989) and Lindgren et al. (1989) look very promising from an operational point of view, subsequent tests have produced inconsistent results (B.S. Lindgren, pers. comm., Phero Tech Inc., Delta B.C.). One possible reason for this inconsistency is the instability of verbenone under daylight conditions (G.Gries, Dept. of Biological Sciences, Simon Fraser University, B.S. Lindgren, Phero Tech Inc., Delta B.C., pers.comm.) arising because of its photodecomposition under ultraviolet irradiation to chrysanthenone (Erman 1967)(Fig. 1).

There will likely be continual difficulties in management practices using verbenone, if its instability is not considered and compensated for.

Objectives

The objectives of this study were to assess verbenone stability under natural daylight conditions, and to determine the consequences of this breakdown; in addition to determining how effectively verbenone disperses both horizontally and vertically in the forest ecosystem.

Figure 1. Diagram illustrating conversion of verbenone to chrysanthenone under the influence of ultraviolet radiation.



Verbenone

Chrysanthenone

MATERIALS AND METHODS

Photodecomposition of Verbenone under Natural Daylight Conditions

Two experiments were conducted to assess verbenone decomposition. Each experiment consisted of placing a glass capillary (1 mm I.D.), open at one end and containing 20 μL of verbenone (96% pure, Phero Tech Inc. Delta B.C.) in each of 20, 10 mL screw-top pyrex test tubes. The test tubes were sealed with a teflon lined screw-cap and left in the dark, at room temperature for 48 h. Two control tubes were covered with black tape to prevent light from penetrating through the glass. After 48 h, the capillaries were removed, ensuring that at room temperature only verbenone in the vapor phase would be contained in each tube. The test tubes were placed in a rack at 45° off-vertical, and exposed to full sunshine. Exposure in the first experiment began at 1200 h on 6 Sept. 1990 at Burnaby B.C. and in the second experiment, exposure began at 1200 h on 23 Sept. 1990.

At 0,10,20,30,40,50,and 60 min after initial exposure on 6 Sept. and at these times plus 75 and 90 min on 23 Sept. two of the test tubes were removed, and placed in a light-tight container. The light intensity was measured with a radiometer (Li-cor, Model LI-185, pyranometer sensor) at each of the collection times. Control tubes were removed at 60 min (6 Sept.) and 60 and 90 min (23 Sept.).

The tubes were held at -15°C for 24 h, removed, and while still cold each was rinsed with 200 μL of pentane, containing an internal standard (6-undecanone, 25 ng/μL). 2 μL of this rinse was then subjected to gas chromatography employing a Hewlett Packard 5880 gas chromatograph equipped with a DB-1 column (30 m x 0.25 mm I.D.). The initial oven temperature was 100°C and increased at 5°C /min. Compounds formed during photolyzation and the rate of verbenone decomposition in the vapor phase, were analyzed.

Absorption Spectrum of Verbenone

The absorption spectrum of verbenone was determined by using a spectrophotometer (Philips PU8700 series, UV/visible) scan from 200 - 450 nm (250 nm/min) on 0.05% and 1.0% solutions of verbenone in hexane. Using two concentrations allowed an overall spectrum to be determined, and allowed a concentrated examination of the secondary absorption spectrum. The absorption spectrum of verbenone in the vapour phase, was also determined by adding 15 μL of verbenone (96% pure, Phero Tech Delta B.C.) to a quartz vessel (3 cm diam, 10 cm length) and allowing the compound to diffuse into the vapour phase before starting the spectrophotometer scan.

Capture of Volatiles Originating from Live Attacked Trees

Five lodgepole pine trees were selected approx. 20 km east of Penticton, B.C. To induce attack by MPB, they were baited with mountain pine beetle tree baits (Phero Tech Inc. Delta, B.C.) releasing myrcene, *exo*-brevicomin, and *trans*-verbenol at 6.5, 0.2, and 1.7 mg/day, respectively. After 36 h, the majority of galleries contained male and female MPBs, as determined by examination of individual galleries. At this time, one successfully attacked tree was selected on the basis of copious frass production and weak resin flow, and volatile capture apparatus (Gries et al. 1988) were set-up. Using an electric vacuum pump powered by a gas generator, volatiles were captured by drawing air from the gallery entrance at 1 L/min. through a glass tube (0.5 cm I.D.) containing 0.5 g of Porapak Q (Applied Science Lab, State College P.A.).

Volatiles were collected for 10-12 h on each of 4 days (21 -24 Aug. 1991) from 3 different galleries. A fresh Porapak Q trap was used each day. In addition, one trap was placed 10 cm from the trunk of the tree to capture volatiles emitted from the whole tree. Dissection of the galleries after 4 days revealed that 2 galleries were occupied by beetles of both sexes and one gallery contained a single female MPB.

Trapped compounds were removed from the Porapak Q, by solvent extraction, with a 90% pentane, 10% ether solution, until a volume of 1.5 mL was reached in the collection vial. The 16 samples (4 locations, 4 days) were analyzed by GC (SP-1000, 30 m x 0.25 mm I.D. Initial oven temp. 70°C, temp. rate 4°C/min) and compounds were confirmed by coupled gas chromatography-mass spectroscopy (GC-MS) (ion trap Varian Saturn, DB-5, 30 m x 0.25 mm I.D.).

Vertical Diffusion of Verbenone

A 10 replicate trapping experiment was set-up in a lodgepole pine forest, approx. 20 km east of Penticton B.C. from 20-24 Aug. 1991. In a randomized complete block design, 40, 12-unit multiple funnel traps (Phero Tech Inc., Delta B.C.) were placed 25 m apart. Ten traps were unbaited controls and the others were set-up with one of three treatments: 1) MPB funnel lure, releasing myrcene, *exo*-brevicomin, and *trans*-verbenol at 300, 0.01 and 1.7 mg/day, at a constant temperature of 24°C, respectively, 2) MPB funnel lures plus 2 g of verbenone impregnated polyethylene beads (85% (-) enantiomer, Phero Tech Inc. Delta B.C.), within a 8 x 3 cm plastic mesh bag placed within the central column of the funnel trap releasing 3.8 mg verbenone/day; and 3) MPB funnel lure and 2 g of verbenone beads scattered within a 2 x 2 m area below the centered trap. The bottoms of the traps were placed between

25 and 50 cm off the ground. Captured beetles from each trap were collected, sexed (Lyon 1958) and counted.

Horizontal Diffusion of Verbenone and its Ability to Protect Vertical Silhouettes and Attractant Sources

A 4-replicate, randomized complete block trapping experiment was completed from 20 -25 Aug. 1991 in the forest margins of a lodgepole pine forest approx. 20 km east of Penticton B.C. Groups of 4, 12-unit multiple funnel traps were placed 40 m apart. Each group of 4 traps consisted of a center trap and 3 surrounding traps placed equidistant from each other around the center trap. All surrounding traps were baited with myrcene released at 300 mg/day and four treatments were assigned in each block: 1) center trap baited with MPB funnel lure (as above) with surrounding traps 1 m from center; 2) as in (1) but with surrounding traps 2 m from center; 3) MPB funnel lure plus 1.0 g verbenone beads (release rate- 1.9 mg verbenone/day) suspended within a trap within a 5 cm x 3 cm plastic mesh bag, with surrounding traps 1 m from center; and 4) as in (3) with surrounding traps 2 m from center.

A second experiment from 25 Aug. to 10 Sept. 1991 was set-up with identical treatments to the above experiment except that all the surrounding traps were baited with MPB trap baits. Due to limited trap and bait availability this experiment was only replicated twice.

A final 4-replicate experiment was conducted from 25 Aug. to 10 Sept. 1991, in which the groups of 4 traps were assigned one of 4 treatments: 1) center trap baited with MPB funnel lure (as above), with surrounding traps baited with myrcene (as above) and placed 1 m from center; 2) as in (1) with surrounding traps 2 m from center; 3) center trap baited with MPB funnel lure, with surrounding traps unbaited and placed at 1 m; 4) as in (3) with surrounding traps at 2 m.

Captured beetles in all experiments were collected, sexed (Lyon 1958) and counted.

Bioactivity of Chrysanthenone

A 5-replicate, 4-treatment, randomized complete block experiment using 12-unit multiple funnel traps was completed in a lodgepole pine forest approx. 35 km east of Penticton B.C. from 25 July to 1 Aug. 1990. The traps were placed 25 m apart and the traps within a block were assigned one of 4 treatments: 1) unbaited control; 2) MPB funnel lure (as above); 3) chrysanthenone (67% pure, Phero Tech Inc. Delta B.C., released at approx. 2 mg/day); and 4) MPB funnel lure plus chrysanthenone. The experiment was repeated from 1-9 Aug. 1990. At the end of each experiment captured beetles were collected, sexed (Lyon 1958) and counted.

On 26 July 1990, a 10-replicate, randomized complete block, tree-baiting experiment was set up approx. 35 km north-east of Princeton, British Columbia. Lodgepole pine trees with diameter >20 cm at 1.3 m above ground were selected at 33 m intervals and baited with one of two treatments: 1) MPB tree baits, releasing *exo*-brevicomin, *trans*-verbenol and myrcene at 0.2, 1.7 and 6.5 mg/day at 24°C, respectively; or 2) MPB tree baits plus chrysanthenone (as above). This experiment was evaluated on 16 Sept. 1990 by counting the number of entrance holes in two 20 x 40 cm areas at eye level on the east and west sides of each tree.

Statistical Analysis

Since much of the data resulting from the above experiments contained zeros, non-parametric analyses and in particular the Friedman (1937) test, were used for statistical analysis. These tests were completed on SAS (Statistical Analysis System) within a Unix environment (Conover 1980, SAS 1985). Due to the low replicate number (N=2) no statistical analysis was performed on the experiment testing the horizontal diffusion of verbenone in the presence of the MPB lures. A Chi-square test (Conover 1980) was done to determine differences in sex ratios among the treatments, for all trapping experiments involving verbenone.

RESULTS AND DISCUSSION

Photodecomposition of Verbenone under Natural Daylight Conditions

Under natural sunlight, on two different days, verbenone in the vapor phase was converted to chrysanthenone, which was the only breakdown product detected by GC analysis (Fig. 2). On each day, the rate of verbenone decomposition was uniform (Fig. 3). No breakdown products were detected when light was excluded from the vessels (Fig. 2). Missing points in Fig.3 resulted from the loss of volatiles during the experiment, causing a reduction in levels of the compounds below detectable limits. The average light intensities on 6 and 23 Sept 1990 were 196 and 225 Wm^{-2}, respectively. Even though measuring the light intensity at discrete times did not provide a true indication of the average light intensity over the duration of the experiment, increased light intensity on 23 Sept. 1990 apparently caused the rate of decomposition to increase. On both days the weather conditions consisted of bright sunshine with a few scattered clouds.[1]

Erman (1967) reported several minor breakdown products in addition to chrysanthenone, when verbenone, at much higher concentrations in a solvent (cyclohexane or acetic acid), was irradiated with a wide spectrum lamp and a pyrex filter. It is possible that these compounds would have been found if the concentration of verbenone used was increased in the reaction vessel of this experiment.

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[1] A supplementary experiment demonstrated equal conversion rates in pyrex and quartz receptacles. Attempts to investigate the conversion reaction under controlled conditions in the laboratory were unsuccessful because of technical difficulties.

Figure 2. Representative gas chromatographic traces, showing the conversion of verbenone to chrysanthenone within 10 min of exposure to natural daylight.

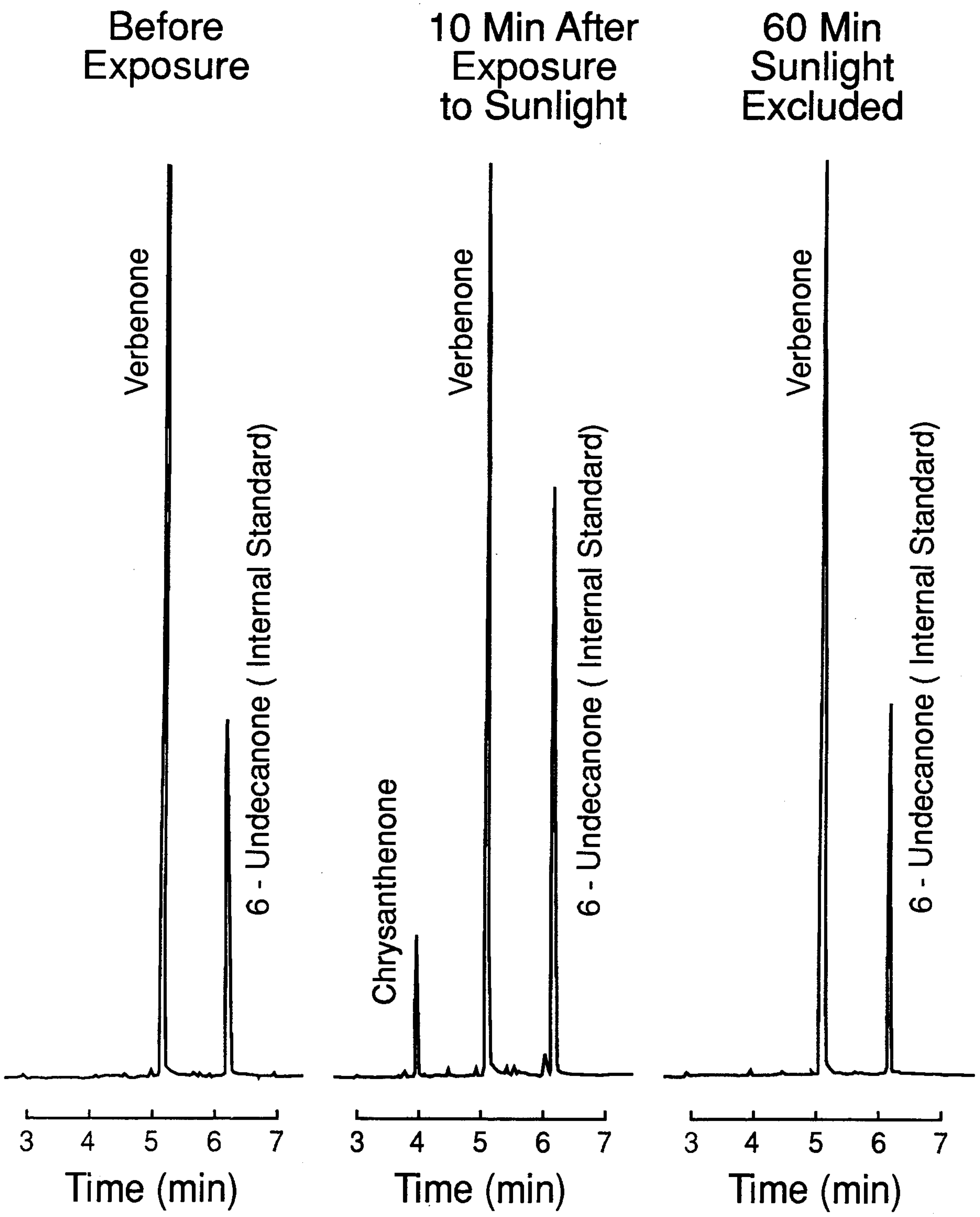
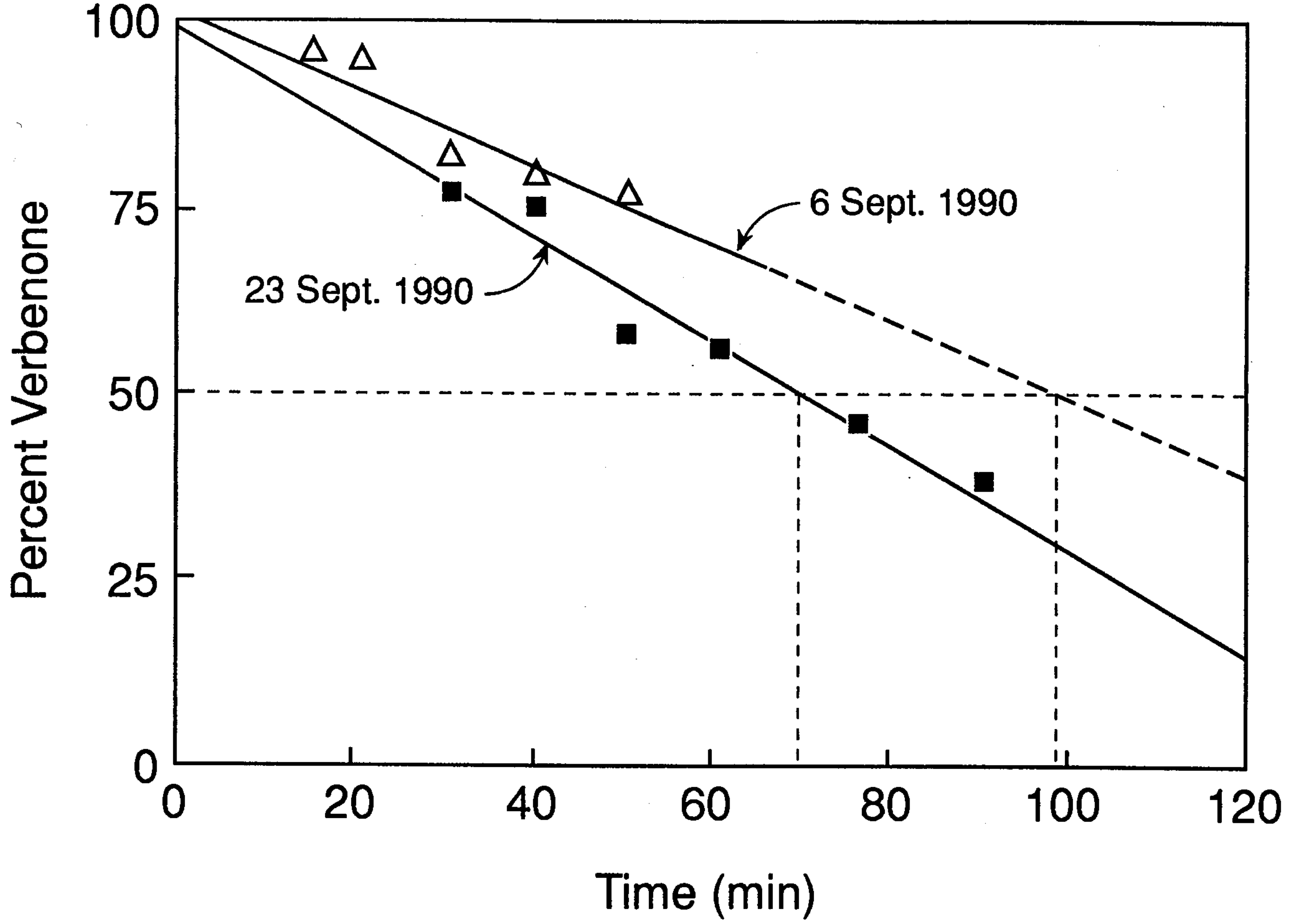

Before Exposure
10 Min After Exposure to Sunlight
60 Min Sunlight Excluded
Verbenone
6 - Undecanone (Internal Standard)
Chrysanthenone
3
4
5
6
7
Time (min)

Figure 3. Conversion of verbenone in the vapor phase to chrysanthenone, under natural daylight conditions within a pyrex test tube, on two different days in Burnaby, B.C.

6 Sept. 1990: $y = 102.1 - 0.53x$, $r^2 = 0.9063$, $P < 0.0034$.

23 Sept. 1990, $y = 99.5 - 0.70x$, $r^2 = 0.9815$, $P < 0.0001$.


100
75
50
25
0
Percent Verbenone
0
20
40
60
80
100
120
Time (min)
6 Sept. 1990
23 Sept. 1990

Absorption Spectrum of Verbenone

Fig. 4 clearly shows that verbenone has two distinct absorption spectra. However, since photons of wavelengths below 295 nm are not present in natural daylight when it reaches the earth's surface (Koller 1965) and only wavelengths of over 300 nm penetrate pyrex (Erman 1967), the second absorption spectrum, between 300 and 380 nm represents the basis for conversion of verbenone to chrysanthenone (Fig.1,4). The absorption spectrum for the vapour phase of verbenone revealed only the primary spectrum because the sample could not be concentrated to allow detection of the secondary spectrum. Erman (1967) also showed the production of chrysanthenone after exposing verbenone to photons at a wavelength of 350 nm.

Capture of Volatiles Originating from Live Attacked Trees

Porapak Q traps that were placed 10 cm away from the tree attacked by MPB did not contain known volatiles in concentrations high enough to be detected by GC-MS. Therefore, it was not possible to determine if verbenone was present in the atmosphere and if any decomposition had occurred.

Volatiles captured from galleries containing males and females (Fig.5) and the gallery containing only a female (Fig. 5) contained verbenone at similar concentrations. Chrysanthenone was not detected in the volatiles from any gallery. Frontalin, *exo*-brevicomin and *endo*-brevicomin were not detected, even though these compounds had been identified previously in air passed over previously fed male MPBs (Ryker and Libbey 1982; Libbey et al.1985). *trans*-Verbenol was detected, coeluting with estragol. Verbenone production did not change substantially during the period of the experiment. Aerations from male-female galleries during days 3 and

Figure 4. Absorption spectrum of verbenone, showing its primary spectrum using a 0.05% solution of verbenone in hexane. Arrow denotes secondary absorption spectrum. Inset shows the secondary spectrum using a 1.0% solution.

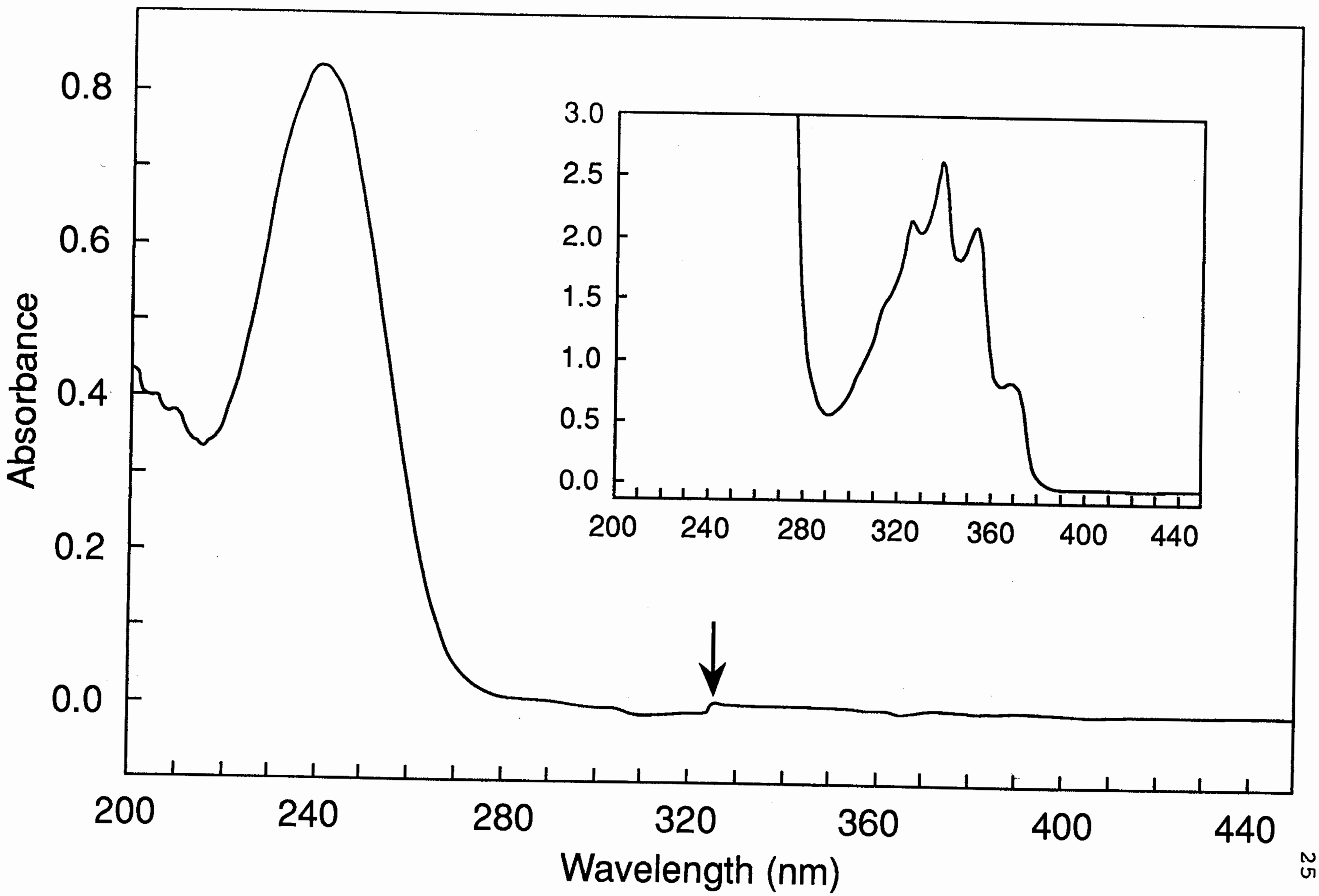
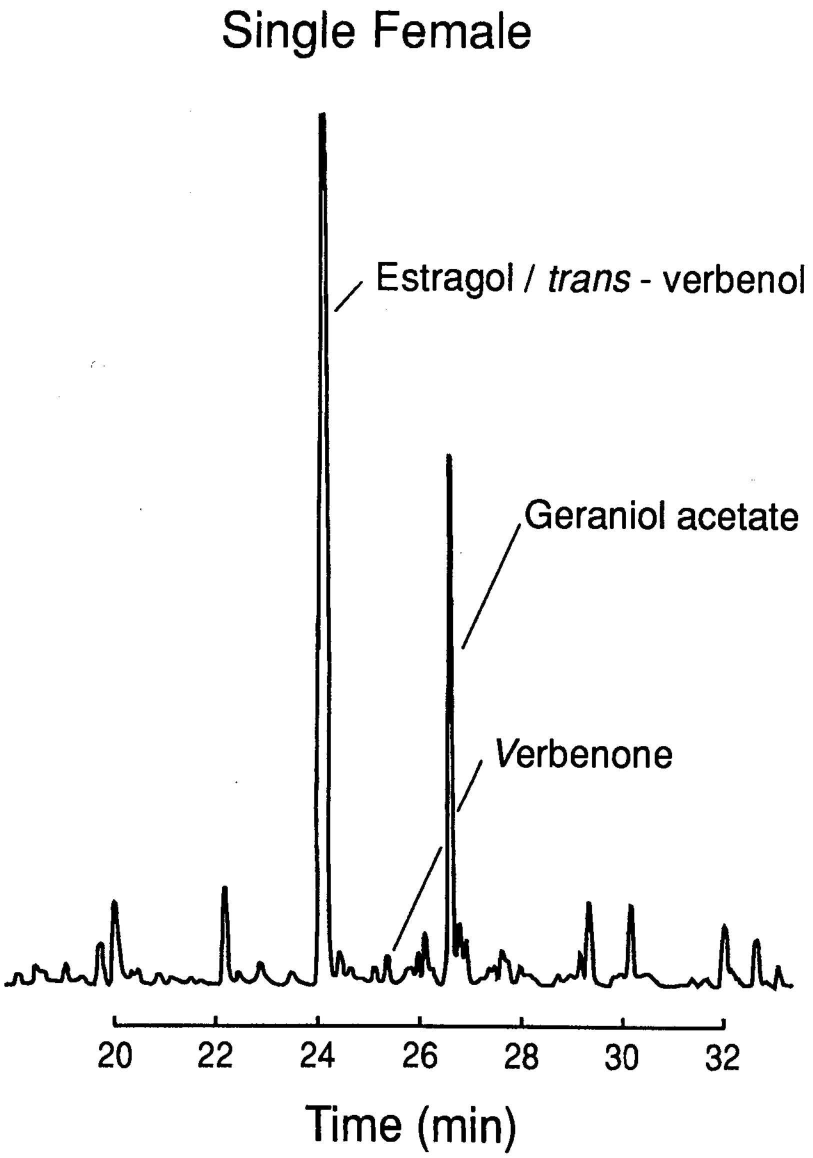
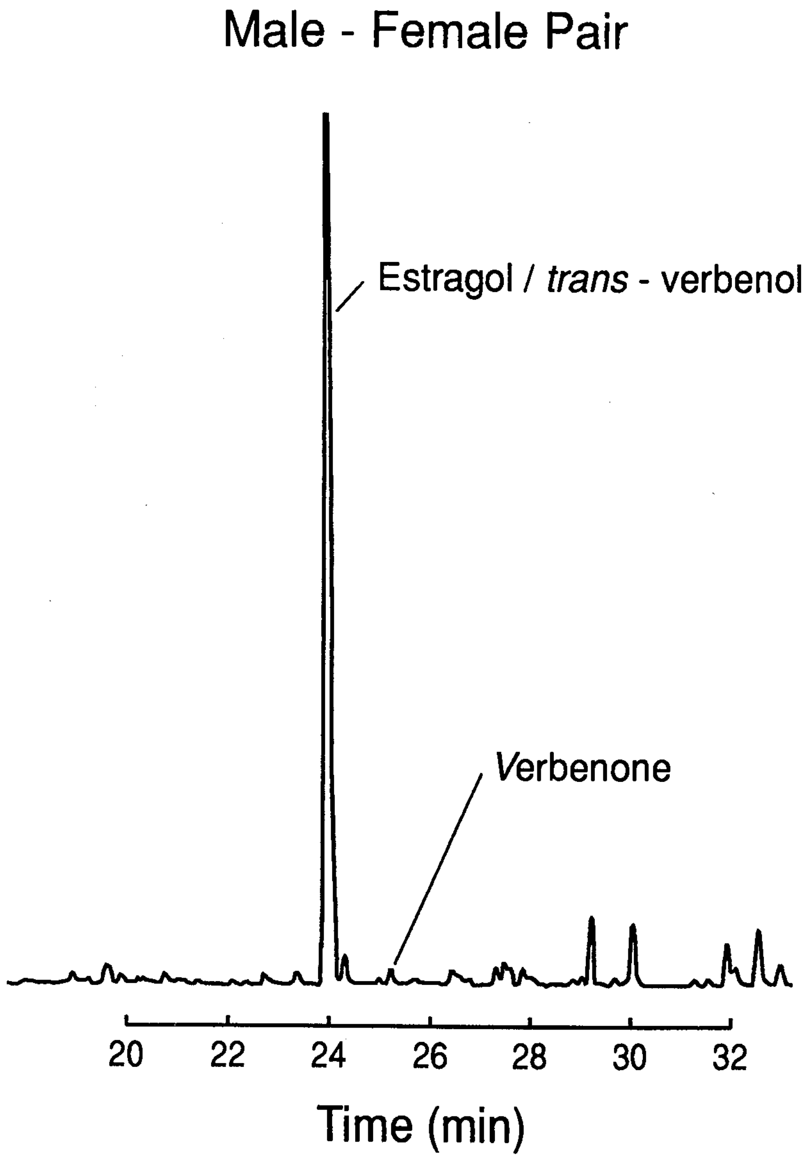

0.8
0.6
0.4
0.2
0.0
Absorbance
200
240
280
320
360
400
440
Wavelength (nm)
3.0
2.5
2.0
1.5
1.0
0.5
0.0
200
240
280
320
360
400
440

Figure 5. Gas chromatographic traces of captured volatiles from the entrance of a gallery containing a male-female pair and a single female MPB for a 10 h period 2 days after they attacked a standing lodgepole pine tree, approx. 20 km east of Penticton, B.C., 22 Aug. 1991.


Single Female
Estragol / *trans* - verbenol
Geraniol acetate
Verbenone
20
22
24
26
28
30
32
Time (min)


Male - Female Pair
Estragol / *trans* - verbenol
Verbenone
20
22
24
26
28
30
32
Time (min)

4 had greatly reduced volatile capture, presumably because the gallery entrances had been packed with frass (pers. obs.). Reduced emission of both attractive and repellant semiochemicals after gallery closing has also been reported by Byers and Wood (1980) for *D. brevicomis*.

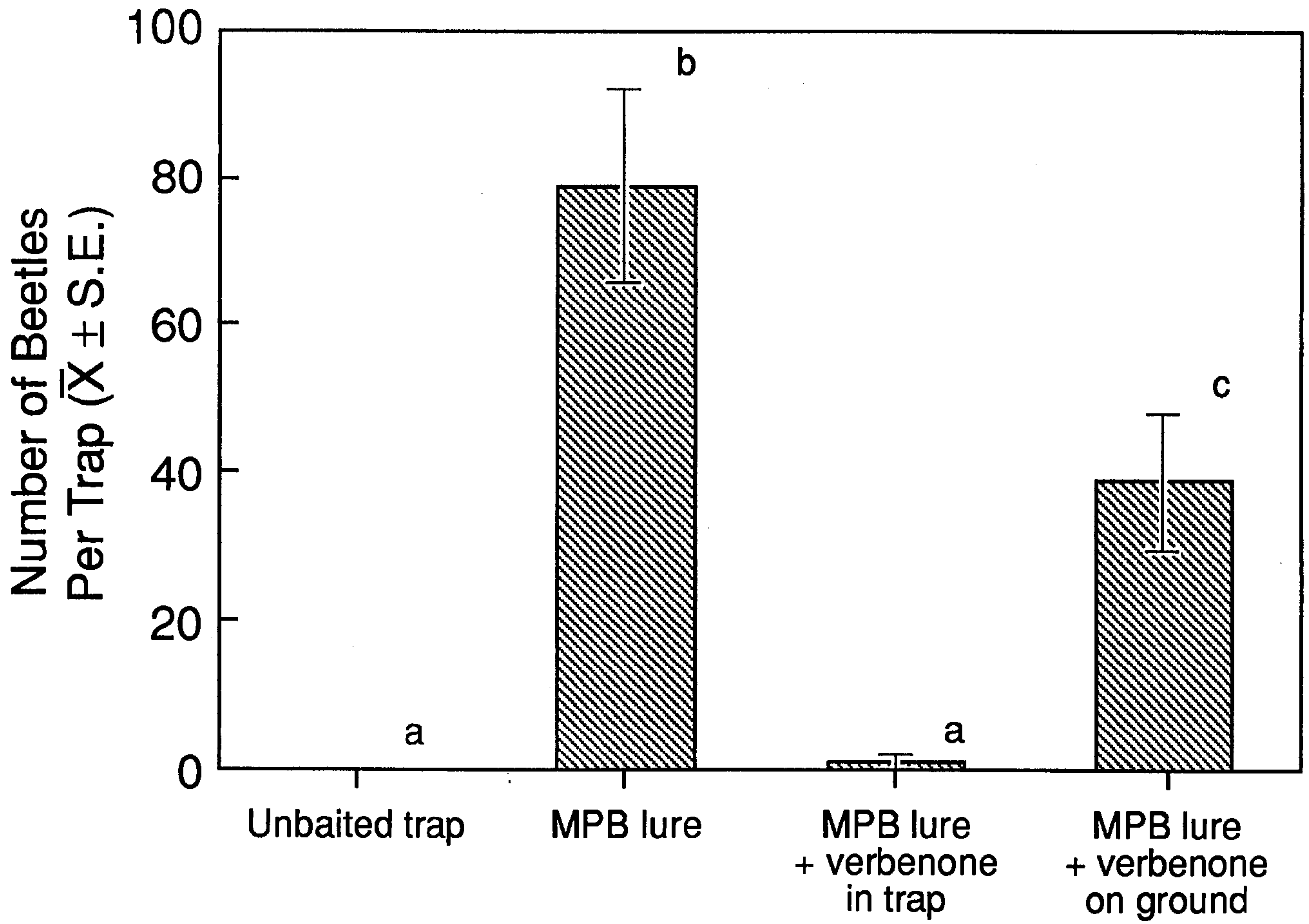
Geraniol acetate was present only in the volatiles from the female gallery (Fig. 5). This compound has not been associated previously with the MPB or other members of the Scolytidae (Mayer and McLaughlin 1991) and its occurrence and biological activity should be investigated.

Vertical Diffusion of Verbenone

When verbenone was contained within a multiple funnel trap it completely inhibited the response of MPBs to the MPB funnel lures (Fig. 6). However, when verbenone was released at the same rate (3.8 mg/day) from impregnated polyethylene beads on the ground, 25 - 50 cm below the base of the traps, it only partially inhibited the response.

The apparent lack of vertical diffusion may be caused by a number of factors: 1) its low volatility may keep the compound close to the ground, below the flight path of the MPB; 2) natural diffusion may reduce the dose to sub-optimal levels at trap height; 3) the reduction of exposed surface area, caused by the beads lying on the forest floor may reduce the release rate; 4) a significant amount of verbenone may be adsorbed on the soil and surface litter particles; 5) cool temperatures on the forest floor may reduce the release rate or inhibit diffusion; and 6) decomposition of verbenone to chrysanthenone (Fig. 1,3) may aid in reducing verbenone below optimal levels. Variation in the environmental factors, e.g. temperature, relative humidity, precipitation and wind, would presumably also affect the efficacy of verbenone-

Figure 6. Response by MPBs to multiple funnel traps when verbenone is contained within the trap and when it is applied on the forest floor, approx. 20 km east of Penticton, B.C. 25 Aug. - 10 Sept 1991. N = 10, Bars with same letter are not significantly different, Friedman Test, $P < 0.05$. No difference in the response of males or females among treatments, Chi-square test, $P < 0.05$. Total population: 52% male, 48% female.



Number of Beetles
Per Trap ($\bar{X} \pm$ S.E.)
100
80
60
40
20
0
a
b
a
c
Unbaited trap
MPB lure
MPB lure + verbenone in trap
MPB lure + verbenone on ground

impregnated beads on the ground. Thus the effective deterrence of aerially applied, verbenone impregnated beads, reported by Shea et al. (1992) in one year, could be offset by environmental effects or technological limitations in another year or on another site, as revealed by the inconsistent results when verbenone is applied in this manner (Shea et al. 1992; B.S. Lindgren, Phero Tech Inc., Delta B.C., pers. comm.).

Horizontal Diffusion of Verbenone and its Ability to Protect Vertical Silhouettes and Attractant Sources

Table 1, shows that when the MPB was presented with a four-component visual cue (multiple funnel traps) with only a single attractive plume originating from a MPB funnel lure in the central trap, the MPB responded to all traps. The same result was evident whether the surrounding traps were left unbaited or baited with myrcene (Table 1). Therefore, the traps' visual, tree-simulating silhouette stimulus is apparently a better close-range signal of a potential host than the known attractive semiochemicals are. Alternatively, the response of MPBs to the surrounding traps may be due to a phenomena similar to the 'threshold model of host switching' proposed by Geiszler et al. (1980). Under this model the attractive pheromones would be at a concentration high enough to stimulate the MPB to land when the attractive plume passes the outermost trap (silhouette). Support for this hypothesis comes from research data obtained on the southern and western pine beetles (Coster and Gara 1968; Coster and Gara 1968; Tilden et al. 1983) in which fewer beetles land on silhouettes farther away from the attractive source and with decreasing pheromone concentration. No preference for any trap in the silhouette component was noted (pers. obs) although response was expected to be higher in the prevailing

Table 1. Response of MPB to multiple funnel traps deployed so that central traps baited with MPB lures were surrounded at 1 or 2 m by groups of 3 traps baited with myrcene or left unbaited. 25 Aug. to 10 Sept. 1991, approx. 20 km east of Penticton, B.C.

	number of MPB captured(mean ± S.E.)[a]		percentage of MPB finding central trap (mean ± S.E.)[a]
Treatment	in central trap	in 3 surrounding traps	
unbaited traps 1 m from central MPB lure	45.2 ± 14.2a	68.0 ± 12.6a	37.7 ± 7.8a
unbaited traps 2 m from central MPB lure	48.7 ± 18.1a	46.0 ± 12.0a	46.2 ± 10.3a
myrcene-baited traps 1 m from central MPB lure	112.7 ± 63.0a	225.0 ± 92.8a	29.8 ± 4.7a
myrcene-baited traps 2 m from central MPB lure	111.0 ± 58.3a	156.5 ± 107.9a	48.3 ± 4.8a

[a] Means within a column followed by the same letter are not significantly different, Friedman Test, $P < 0.05$. No difference in the response of males or females among treatments, Chi-square test, $P < 0.05$. Total population: 49% male, 51% female.

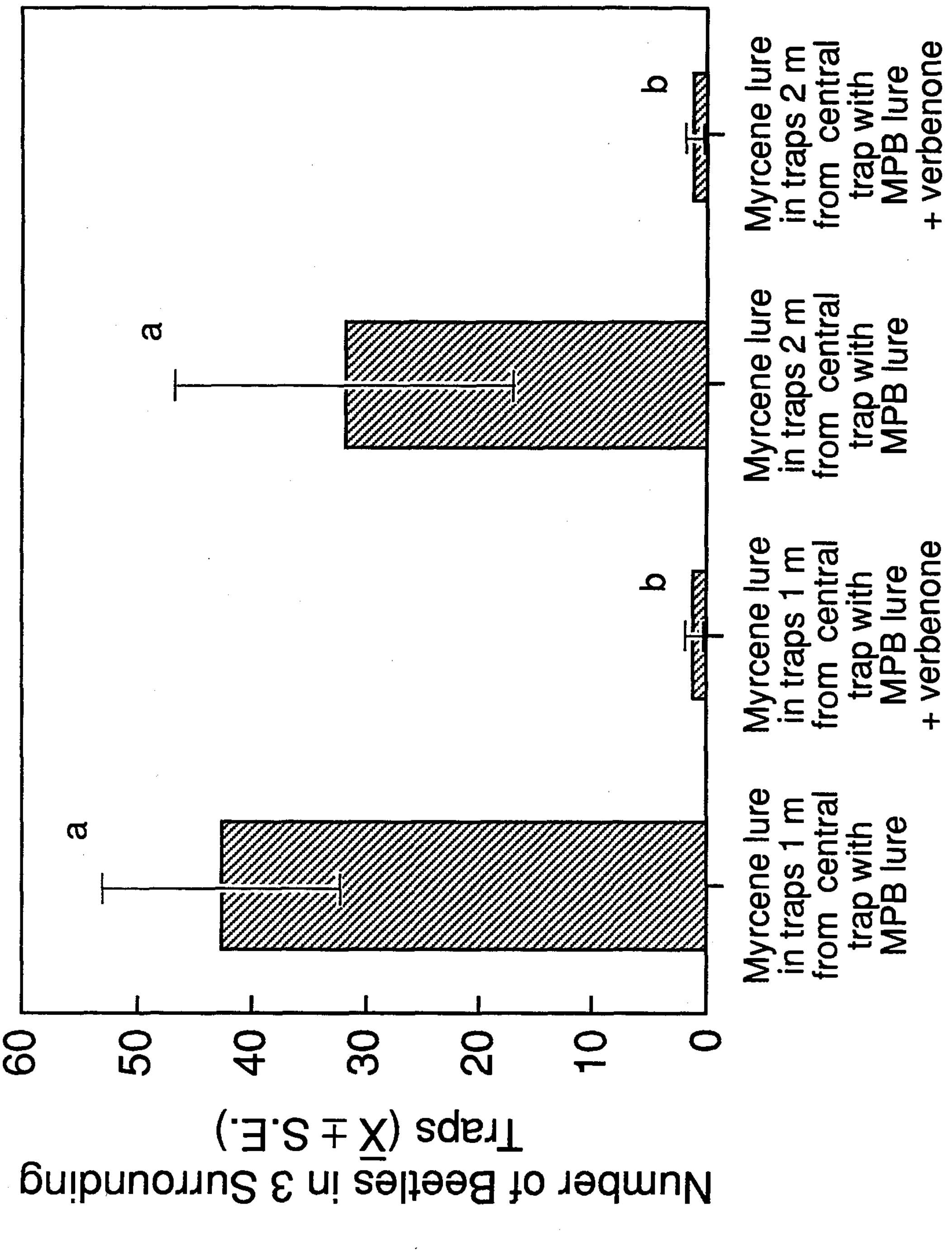
downwind trap. This may be explained in part by the pheromone diffusion model proposed by Fares et. al (1980) who suggest that because MPBs fly in late afternoon, coinciding with periods of little or no air movement, pheromone would be concentrated around the original source. However, before any conclusions can be drawn, more information is needed on the volatility and vapour pressure of the compounds in question, the movement of these compounds in a pheromone plume within the forest (Bossert and Wilson 1963; Aylor 1976; Fares et al. 1980) and the particular way behavioural changes are induced (Murlis and Jones 1981) by such compounds.

It is possible that some semiochemicals that act at close range for the MPB have not been identified. The addition of these unknown semiochemicals to the current baits could increase the response of beetles to the central attractive source.

Although myrcene has been shown to increase trap catches of MPB to single multiple funnel traps baited with *exo*-brevicomin and *trans*-verbenol in a concentration dependent manner (Conn et al. 1983; Borden et al. 1987), this was not evident in this experiment and the apparent effect of myrcene (Table 1) was due to unusually high trap catches in one replicate.

When verbenone was added to the central trap (1.9 mg/day) the response of the MPB to the central trap and the 3 surrounding traps was completely inhibited (Fig. 7). Presumably, verbenone was active at least 2 m from its source at this release rate. It was hypothesized that the stable MPB baits would attract beetles and that verbenone would cause beetles to switch (Geiszler and Gara 1978) to nearby surrounding traps. Furthermore, because of its instability, the effect of verbenone should have decreased with distance from the release point. These hypotheses were not upheld at these close distances. If the verbenone release rate was reduced or if the distance between the traps was increased, an effect might have been seen.

Figure 7. Response by MPBs to a group of 3 multiple funnel traps, baited with myrcene at 1 or 2 m distance from a central trap containing a MPB lure, with or without verbenone. Approx. 20 km east of Penticton B.C., 20 - 25 Aug. 1991. $N=4$, Bars with same letter are not significantly different, Friedman Test, $P< 0.05$. No difference in the response of males or females among treatments, Chi-square test, $P<0.05$. Total population: 48% male, 52% female.


Number of Beetles in 3 Surrounding Traps (X̄ ± S.E.)
0
10
20
30
40
50
60
a
b
a
b
Myrcene lure in traps 1 m from central trap with MPB lure
Myrcene lure in traps 1 m from central trap with MPB lure + verbenone
Myrcene lure in traps 2 m from central trap with MPB lure
Myrcene lure in traps 2 m from central trap with MPB lure + verbenone

When attractive pheromones were added to the surrounding traps (Fig. 8) the verbenone protection broke down in traps 2 m from the verbenone source. Thus pheromone-producing beetles in trees close to attacked trees should be able to override the effect of verbenone, allowing the characteristic clumped distribution of MPB infestations (Safranyik et al. 1974). In this experiment the central traps that contained verbenone caught an average of 8 and 25 beetles at a 1 and 2 m separation from the surrounding traps, respectively. This represents 11.0 and 11.5 % of the beetles responding to traps at 1 and 2 m treatments respectively. The responses to surrounding traps were substantially lower than the results in Table 1. Although the verbenone protection began to break down at 2 m, the central trap still maintained some of its repellent properties.

Bioactivity of Chrysanthenone

The results of both trapping experiments (Table 2) indicated that chysanthenone has no behavioral influence on the response of MPB to the synthetic attractants. This effect was confirmed by the tree baiting experiment (Table 3). Although, the chrysanthenone used had some impurities, it is unlikely that any combination of these contaminents could have caused opposing attractant and repellant effects on the MPB that would have resulted in no apparent behavioural influence. One can therefore conclude that verbenone decomposes to an inert substance that has neither an attractant or repellant effect on the MPB.

Figure 8. Response by MPBs to a group of 3 multiple funnel traps baited with MPB funnel lures at a 1 or 2 m distance from a central trap containing a MPB funnel lure with or without verbenone. Approx. 20 km east of Penticton, B.C. 25 Aug. - 10 Sept. 1991. N=2.

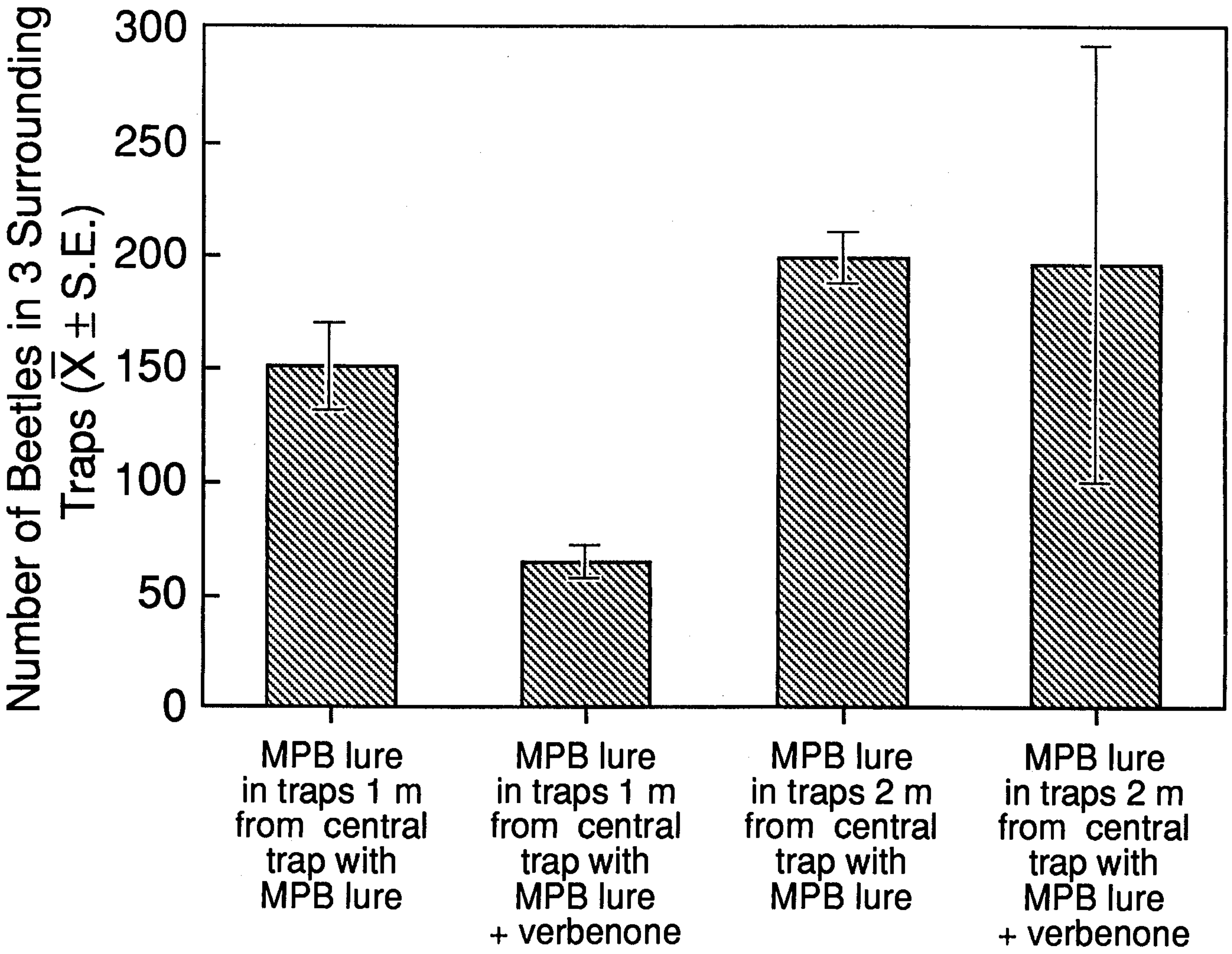

Number of Beetles in 3 Surrounding Traps ($\bar{X} \pm$ S.E.)
300
250
200
150
100
50
0
MPB lure in traps 1 m from central trap with MPB lure
MPB lure in traps 1 m from central trap with MPB lure + verbenone
MPB lure in traps 2 m from central trap with MPB lure
MPB lure in traps 2 m from central trap with MPB lure + verbenone

Table 2. Response of MPB in two 1990 experiments in which multiple funnel traps were baited with MPB funnel lures baits, chrysanthenone, or both together (N=5). Approx. 35 km east of Penticton, B.C.

Date of Experiment	Treatment	Number of MPB/trap (mean ± S.E.)[a]	
		males	females
25 July - 1 Aug. 1990	unbaited control	1.6 ± 0.7a	0.2 ± 0.2a
	MPB funnel lure	158.6 ± 50.6b	83.6 ± 25.0b
	chrysanthenone	1.0 ± 0.4a	0.4 ± 0.3a
	MPB funnel lure + chrysanthenone	181.4 ± 30.8b	94.4 ± 10.6b
1 Aug. - 9 Aug. 1990	unbaited control	2.6 ± 0.9a	2.6 ± 0.9a
	MPB funnel lure	94.4 ± 20.1b	109.4 ± 23.2b
	chrysanthenone	3.4 ± 1.4a	4.0 ± 1.5a
	MPB funnel lure + chrysanthenone	94.8 ± 27.6b	94.2 ± 27.5b

[a] Means within a column and experiment followed by the same letter are not significantly different, Friedman Test, $P < 0.05$.

Table 3. Comparative attack frequency and density by MPB on lodgepole pines treated with MPB tree baits alone and with chrysanthenone, N=10. Approx. 35 km. north-east of Princeton, B.C. 25 July - 16 Sept. 1990.

Treatment	Attack on baited trees		Number of attacked trees within 10 m of a baited tree (mean ± S.E.)[a]	
	% mass attacked	Attack density (mean ± S.E.)[a]	Mass attacked ($>31.25/m^2$)	Lightly attacked ($<31.25/m^2$)
MPB tree bait	100	78.3±4.5a	3.3±0.7a	0.8±0.2a
MPB tree bait + chrysanthenone	100	75.2±6.3a	2.5±0.4a	1.2±0.2a

[a] Means within a column followed by the same letter are not significantly different, Friedman Test, $P<0.05$.

Biological Implications

The inability of the MPB to orient directly to a silhouette releasing semiochemicals in a "forest" of silhouettes (Table 1), may in part explain the seemingly random landings by MPB on host and non-host trees (Hynum and Berryman 1980). A random host search would seem rather inefficient, as demonstrated convincingly for *Ips typographus* L., by computer based simulation of host selection (Gries et al. 1989). Moeck and Simmons (1991) reported an apparent primary attraction of MPB towards bolts of lodgepole pine, although no primary attractants were identified. Gries et al. (1989) argue that landings on non-host trees are rest stops during dispersal. But, they may also occur because the MPB orients towards the general area of an attractant source and then uses visual cues (upright silhouettes) to select a host, determining its suitability after landing. While all landing beetles are caught under the trapping situation (Table 1), they would be free to resume flight if they landed on trees.

This type of host searching and selection may also explain in part, why MPB attacks in a characteristic patch infestation (Safranyik et al. 1974). If many suitable hosts are present in one area, that has an attractant source, all the acceptable trees in close proximity could be selected by the incoming beetles, even though they might not be able to find the initial attractive tree.

The detection of approximately equal amounts of verbenone emanating from the gallery containing only a female and from galleries containing male and female MPBs (Fig. 5), and the finding that verbenone production did not increase in the first 4 days of attack (results not shown), leads one to question how verbenone functions as an antiaggregation pheromone. The role of verbenone was also questioned for the western pine beetle, when Browne et al. (1979) discovered verbenone in the air emanating from logs containing females, and reported that the concentration of verbenone was unchanged when males were added to the system. The MPB has very little control of verbenone production, since verbenone is primarily produced by yeasts within the beetles' galleries (Leufvén et al 1984; Hunt and Borden 1990), with minor contributions made by internal microorganisms (Hunt and Borden 1989, 1990) and the autoxidation of α-pinene (Hunt et al. 1989). Therefore, its release rate would depend on the amount of infected host tissue and not on the presence of mated females in the system. For *I. typographus*, verbenone production does not increase until late in the attack sequence, approximately 5 days after initial attack (Birgersson et al. 1984; Leufvén and Birgersson 1987). However, within 5 days of initial infestation by the MPB, attack is usually terminated (Rasmussen 1974), and the release of volatiles including verbenone from the individual galleries has begun to decline because the beetles have packed the gallery entrances with frass (pers. obs.; Raffa 1988). Raffa and Berryman (1983) have also linked the termination of attack with the reduction of host volatiles resulting from the beetles' ability to overcome the host defense mechanisms. However, results from the volatile capture experiment indicated that volatiles emanating from the galleries containing male-female pairs had been severely depleted by the end of the experiment but volatiles emanating from the single female gallery remained relatively unchanged (results not shown). Raffa and Berryman (1983) conclude that vigorous hosts could prevent mass attack by filling galleries with resin, preventing the release of the beetles' pheromones, indicating that the reduction in attractive compounds (host and beetle-produced) is very important for the cessation of attack. Also, Edson (1978) reported that the presence of stridulating males reduced the attractancy of logs containing female MPBs. Clearly, there is much more involved in the switching of hosts (Geiszler and Gara 1978), than just increased verbenone production.

I propose the hypothesis that verbenone is a general indicator of a poor host. I suggest that verbenone is one of the unknown compounds (Moeck and Simmons 1991), used by the MPB to determine suitable hosts. Verbenone is a known multifunctional pheromone in the southern pine beetle (Rudinsky 1973) and evidence for its role as a host compound may come from verbenones' ability to inhibit the response of many scolytid beetles including *D.brevicomis*, *D.frontalis* (Renwick 1967; Renwick and Vité 1970; Payne et al. 1980), *D. adjunctus* Blandford (Livingston et al. 1983), *I.pini* (Say) (Devlin 1992), *I. typographus* (Bakke 1981; Schlyter et al. 1989), *I. paraconfusus* Lanier (Byers and Wood 1980), and *I. sexdentatus* Boern. (Paiva et al. 1989). It is possible that levels of verbenone high enough to cause a response by MPBs could be evident in dead or stressed trees through the autoxidation of α-pinene and through microbial metabolism, regardless of whether the tree was killed by the MPB or some other agent. If the attack dynamics of MPB are comparable to those of *I. typographus*, and verbenone production does increase later in the attack sequence (Birgersson et al. 1984; Leufvén and Birgersson 1987), it is probable that verbenone prevents the MPB from re-attacking a mass attacked tree (poor host signal) later in the season. However, it is apparently not responsible, at least by itself, for the mechanism of host switching (Geiszler and Gara 1978). Some other factors such as male stridulation (Ryker and Rudinsky 1976; Edson 1978) the release of other beetle-produced multifunctional or antiaggregant pheromones, such as frontalin (Ryker and Libbey 1982), pinocarvone (Libbey et al. 1985) and ipsdienol (Hunt and Borden 1988), and the sealing of galleries with frass causing a decline in the release of the attractive compounds must be involved with this mechanism.

Although verbenone production does not increase on an individual gallery basis, its production throughout the tree would rise with increasing numbers of galleries, causing repellency of beetles at the tree level. However, the continual sealing of galleries by the males (pers. obs.) on subsequent days of attack would compensate for this increase and reduce verbenone output correspondingly. More information and studies are needed to confirm the role and production time of ventilation holes (Reid 1962a,b) in the release of volatile compounds. However, the creation of ventilation holes corresponding to the increase of verbenone production (Birgersson et al. 1984) late in the attack sequence may be important for preventing attack by the competitor *I.pini* (Rankin and Borden 1991) as it is for preventing re-attack by the MPB.

The reduced response of MPBs to the known synthetic attractants by verbenone, may indicate that these baits do not represent the complete mixture occurring in nature. Alternatively, release of verbenone at 1.9 and 3.8 mg/day may be far in excess of that occurring in nature, causing verbenone to over-ride the natural attraction reproduced by the baits.

Importance of Verbenone Decomposition

To determine the presence of occupied hosts, the MPB has apparently evolved to use a repellent semiochemical that will not cause widespread disruption of orientation. The photosensitivity of verbenone may explain in part why and how the beetle switches hosts (Geiszler and Gara 1978). MPBs are drawn by pheromones and kairomones to trees, but at close range and high population densities, they switch to nearby hosts, resulting in small spot infestations, (Safranyik et al. 1974; Geiszler and Gara 1978). A rapid breakdown of verbenone emanating from a mass-attacked tree would allow nearby trees to be attacked without beetles being deterred by verbenone. These spot infestations will provide open areas and material for forest fires (Cole 1978, Peterman 1978) that are important for the regeneration of lodgepole pine.

Technical Implications

MPBs fly at high light intensities and high temperatures that occur in the early to late afternoon (McCambridge 1971; Billings and Gara 1975; Safranyik 1978). Flight is not initiated until temperatures have reached 19°C, and ceases when evening temperatures fall below this level (Safranyik 1978). The breakdown of verbenone to chrysanthenone during this period of high light intensity could effectively reduce the concentration of verbenone below a critical response threshold.

The rapidity of the breakdown of verbenone to chrysanthenone (Fig. 3), clearly justifies the use of ultraviolet absorbers used in commercial formulations and devices (Phero Tech Inc., Delta, B.C.), and also indicates that the placement of verbenone release devices on the north faces of trees (Lindgren et al. 1989) is advisable.

Previous research (Amman et al. 1989; Lindgren et al. 1989; Amman et al. 1991; Shea et al. 1992) and the results contained in this study show that verbenone does have properties that can be exploited to prevent beetle attack in high value stands. An easy and cost-effective method of applying verbenone would be to aerially disperse semiochemical impregnated devices (e.g. beads). However, application technology must compensate for the reduction in efficacy of verbenone when it released from these devices sitting on the ground (Fig. 6). Development of a more persistent release device that would lodge in part in the foliage and would not penetrate the litter layer of the forest floor might greatly improve the efficacy of broadcast applications of antiaggregants. Justification for employing semiochemicals above ground can be seen in the experiments of Amman et al. (1989) and Lindgren et al. (1989) who found consistent reductions in tree mortality when verbenone was released from bubble caps placed approx. 2 m above the ground at 10 m centers. In contrast, inconsistent results were achieved by the verbenone impregnated pellets when they were broadcast aerially (Shea et al. 1992; B.S. Lindgren, Phero Tech Inc., Delta B.C., pers. com.). The effectiveness of the bubble cap system is possibly due to a consistent release rate (Devlin 1992) and a high concentration of verbenone in the MPB flight path. The MPB usually attacks trees in the lower 10 m of the bole (Shepherd 1965). Vité and Baader (1990) also report that the reduction in response by scolytids is highest when inhibitors are placed in the same plume as attractants. Similarly, deployment of verbenone and ipsenol from bubble caps affixed to felled lodgepole pines were more effective in deterring attack by *I. pini*, than when the same two compounds were deployed on the ground in impregnated beads, except when the dose was doubled and deployment occurred no earlier than 2 weeks prior to first attack (Borden et al. 1992; Devlin 1992). However, more information is needed on the volatility and vapour pressure of verbenone, the movement of verbenone within a pheromone plume (Bossert and Wilson 1963; Aylor 1976; Fares et al. 1980) before any firm conclusions can be drawn from these observations.

Ideally any future applied research with verbenone, should also test additional compounds that are known to inhibit response of the MPB, e.g. frontalin (Ryker and Libbey 1982; Libbey et al. 1985), *endo*-brevicomin (Ryker and Rudinsky 1982), ipsdienol (Hunt and Borden 1988), and pinocarvone (Libbey et al. 1985). If any or all of these compounds can increase the deterrent effect that is achieved by verbenone alone, a truly effective tool could be developed. A blend of semiochemicals would be comparable to the combination of verbenone and ipsenol used to reduce the attack of *I. pini* on lodgepole pine slash (Devlin 1992).

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