Antiaggregants for the Mountain Pine Beetle

by

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ANTIAGGREGANTS FOR THE MOUNTAIN PINE BEETLE

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ABSTRACT

Recent research suggests that use of nonhost compounds or interspecific synomones may improve the ability of the antiaggregation pheromone verbenone to protect valuable stands of timber against attack by the mountain pine beetle (MPB), *Dendroctonus ponderosae* Hopkins. Coupled gas chromatographic-electroantennographic detection (GC-EAD) studies indicated that MPB responded to all six-carbon green leaf alcohols tested [1-hexanol, (*E*)-2-hexen-1-ol, (*Z*)-2-hexen-1-ol, (*E*)-3-hexen-1-ol, and (*Z*)-3-hexen-1-ol], and to four compounds in the bark of the nonhost trembling aspen, *Populus tremuloides* Michx. In field trapping studies conducted from 1992 - 1994 near Princeton, B.C., Lanierone, pinocarvone, hexanal, (*E*)-2-hexenal, and trembling aspen bolts did not disrupt response to attractive MPB lures. A combination of ipsdienol, an aggregation pheromone for *Ips pini* (Say), with verbenone reduced catches of females to a level not significantly different ($P<0.05$) from that to blank control traps. A blend of the green leaf alcohols [1-hexanol, (*Z*)-2-hexen-1-ol, (*E*)-2-hexen-1-ol and (*Z*)-3-hexen-1-ol] was a very effective disruptant, and the two best disruptants, (*E*)-3-hexen-1-ol and (*Z*)-3-hexen-1-ol, reduced catches of both sexes to a level not significantly different from that to a blank control trap. Neither of the clerid predators captured, *Enoclerus sphegeus* (F.) nor *Thanasimus undatulus* (Say), was repelled by green leaf volatiles. The striped ambrosia beetle, *Trypodendron lineatum* (Olivier), was significantly attracted to MPB semiochemical treatments in two experiments. Two operational experiments tested the ability of antiaggregant treatments to protect standing trees from attack when affixed in a 10 x 10 m grid surrounding a single attractant-baited tree. In 1993, combinations of high verbenone and either low or high hexanal doses reduced the percentage of mass attack significantly over that in control plots. In 1994, low or high verbenone doses, tested either alone or in combination with green leaf volatiles, yielded no significant differences between treatments by any criterion, possibly due to high initial population levels. While operational trials were unsuccessful overall, the results of GC-EAD and trapping studies suggest that green leaf alcohols and trembling aspen volatiles are promising disruptants which may prove to be effective in protecting single high-value trees as well as carefully selected stands with low initial MPB population levels.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Antiaggregants for the Mountain Pine Beetle

INTRODUCTION

SIGNIFICANCE OF THE MOUNTAIN PINE BEETLE AND LODGEPOLE PINE FORESTS

The mountain pine beetle (MPB), *Dendroctonus ponderosae* Hopkins, is the most destructive bark beetle in western North America (Furniss and Carolin 1977). In British Columbia, the MPB killed approximately 195.7 million pines between 1972 and 1985, with an estimated economic loss, even after salvage harvesting, of $4.1 - 5.4 billion (Borden 1990). It continues to be the most damaging forest insect pest in B.C. The volume lost in 1992 was 2.3 million m^3, which is about 18% of the annual lodgepole pine harvest, and nearly 11 times the area lost to forest fires (Wood and Van Sickle 1993).

The most common host of the MPB is lodgepole pine, *Pinus contorta* Douglas, although ponderosa pine, *P. ponderosa* Lawson, and western white pine, *P. monticola* Douglas, are often attacked (Safranyik et al. 1974). Lodgepole pine is the most abundant conifer species in B.C., accounting for 25% of the available timber volume and 38% of the yearly harvest (Miller et al. 1993). Large, even-aged stands of mature lodgepole pine occur throughout the interior of B.C., largely due to fire suppression efforts over the last 50 years (Maclauchlan and Brooks 1994).

MPB infestations disrupt long-term forest management (Maclauchlan and Brooks 1994). Miller et al. (1993) modeled the impact of MPB in B.C. if current MPB control programs were discontinued, and predicted dramatic volume losses, shortfalls in timber supply, major losses in industry and government revenue, and negative impacts on employment, environmental values, community and social values, and recreation and tourism.

MPB BIOLOGY AND HOST SELECTION

Adult MPBs emerge from infested trees in mid- to late July, usually during periods of high pressure and good weather, and begin searching for suitable hosts (Reid 1962; Raffa 1988). Females initiate attack, landing on trees primarily in response to visual (Shepherd 1965) and olfactory cues (primary attraction) (Moeck and Simmons 1991). When populations are low, beetles tend to select physiologically weakened trees, but almost any host tree will be successfully colonized during severe epidemics (Furniss and Carolin 1977; Raffa 1988).

While boring into suitable trees, females release the aggregation pheromone *trans*-verbenol (Pitman et al. 1968), attracting mostly males as well as other females (Borden et al. 1987a). Arriving males release *exo*-brevicomin, which mainly attracts females (Borden et al. 1987a). Myrcene, a host monoterpene, acts as a kairomone, greatly enhancing the attraction of both pheromones and helping to induce mass-attack on the tree (Conn et al. 1983; Borden et al. 1983, 1987).

MPBs vector symbiotic microorganisms acquired from their brood galleries in specialized maxillary mycangia (Whitney and Farris 1970). These microorganisms are introduced into the new host by colonizing beetles, and overcome the tree's natural defense systems by rapidly shutting down translocation and killing the tree (Raffa 1988).

As colonization progresses, the amount of *trans*-verbenol declines, while the release of an antiaggregation pheromone, verbenone, 4,6,6-trimethylbicyclo[3.1.1]hept-3-en-2-one (Ryker and Yandell 1983; Borden et al. 1987a), progressively increases. Verbenone is apparently produced in small quantities through autoxidation of α-pinene (Hunt et al. 1989), and through metabolism of *trans*- and *cis*-verbenol by microorganisms in the guts of beetles (Hunt and Borden 1989). It is primarily produced, however, through the conversion of *trans*- and *cis*-verbenol by microorganisms in the galleries (Leufvén et al. 1984; Hunt and Borden 1990). This occurs late in the colonization process, deters additional beetles from attacking and overcrowding a mass-attacked tree (Borden et al.

1987a), and causes beetles to 'switch' attack to nearby trees (Geiszler et al. 1980). (–)-Verbenone is biologically active , while the (+) enantiomer is not (Ryker and Yandell 1983).

Mating occurs under the bark. Mated females begin boring vertical galleries in the phloem, cutting egg niches on either side and laying an egg in each (Raffa 1988). Larvae feed on the phloem tissue, mining horizontal galleries outward from the parental gallery as they pass through four instars. MPBs usually overwinter as larvae (Reid 1962). When temperatures increase in the spring, the final instar undergoes a non-feeding prepupal stage and pupates; and the ensuing callow adults usually feed for about a month before emerging. There is usually only one generation per year, but a partial second generation is possible in warm years (Raffa 1988).

MPB MANAGEMENT: THE NEED FOR ALTERNATIVE TACTICS

A number of strategies and tactics have been successfully developed and implemented for integrated MPB management in B.C. (Borden and Lindgren 1988; Maclauchlan and Brooks 1994). Some of the major tactics employed include: survey and assessment techniques for directing control activities, such as hazard or risk rating of stands (Shore and Safranyik 1992), removal or destruction of infested wood through sanitation harvesting or single tree treatments (McMullen et al. 1986; Maclauchlan and Brooks 1994), semiochemical baiting for monitoring, pre-logging containment and concentration of infestations, or post-logging mop-up of residual populations (Borden and Lindgren 1988; Borden 1990), and silvicultural strategies, such as the development of mixed stands with a mosaic of age classes, or reduced rotation times (Safranyik et al. 1974).

While silvicultural methods such as sanitation harvesting can be effective alone in reducing MPB populations, the integration of these methods with attractive semiochemicals in recent years has greatly increased their success (Borden and Lindgren 1988; Hall 1989; Borden 1990).

Many of these tactics, however, involve managing the beetle in a destructive manner (e.g. sanitation harvesting), or are expensive, labour-intensive, and potentially hazardous (e.g. single-tree disposal, "fell and burn"). Environmentally acceptable strategies, such as the use of repellents or antiaggregants, are needed to protect high value commercial timber stands as well as stands in campgrounds, parks, and riparian areas (Amman et al. 1989, 1991; Lindgren et al. 1989; Gibson et al. 1991; Shea et al. 1992; Amman 1994). While single trees may be protected through the use of preventative insecticides (Gibson and Bennett 1985; McMullen et al. 1986) this is not practical for large-scale use and may affect nontarget insects or wildlife, as well as humans (Amman 1994).

With ever-increasing public scrutiny of forest management and the emphasis on integrating values such as tourism, wildlife and fisheries with timber values, the use of tactics such as sanitation harvesting may be politically unpopular, ineffective, or even impossible. The new B.C. Forest Practices Code (Petter 1994) places strict guidelines on maximum allowable clearcut sizes and the management of riparian areas and leave strips. This may lead to the buildup of beetle populations in these areas, as foresters become unable to extract entire infestations. Large scale mortality in infested riparian zones and leave strips may defeat integrated resource plans, leading to increased fire danger or drastic changes in age class or species composition. Under these conditions, antiaggregants may be one of the few options available (or even the only option) for MPB management, and would be a valuable asset to any integrated management plan.

ANTIAGGREGANTS: CURRENT RESEARCH

Three major groups of compounds have shown antiaggregative activity in bark beetles: multifunctional pheromones, interspecific synomones, and antiaggregation pheromones (Borden 1995). *exo*-Brevicomin and frontalin are both multifunctional pheromones in the MPB, enhancing the response to attractant-baited traps at low release rates (0.05 mg per 24 h) but reducing the response at high (5.0 mg per 24 h) rates (Borden et al. 1987a). On baited trees, however, *exo*-brevicomin can induce attack (Borden et al. 1990) even at relatively high rates (2.5 mg per 24 h) (Shore et al. 1992), although McKnight (1979) found antiaggregative effects when *exo*-brevicomin was released on western white pines at high rates.

Interspecific synomones function in resource partitioning and reproductive isolation by causing mutual or unilateral repellency (Borden 1995). For example, ipsdienol, an aggregation pheromone for the pine engraver, *Ips pini* (Say) (Teale et al. 1991), a MPB competitor, reduces the attraction of MPBs to attractant-baited traps (Hunt and Borden 1988; Borden et al. 1992).

Most research with antiaggregants for the MPB has focused on verbenone (Lindgren and Borden 1989, 1993; Amman 1994). (−)-Verbenone was first shown to have antiaggregative properties in the MPB in laboratory and field bioassays performed by Ryker and Yandell (1983). While results from experiments using multiple funnel traps (Lindgren 1983) have shown encouraging repellency (Borden et al. 1987a; Schmitz 1989), operational trials have been inconsistent. Attempts to develop verbenone as a reliable tool for controlling mountain pine beetles have utilized either aerially dispersed verbenone-impregnated pellets (Shea et al. 1992), or bubble-cap release devices affixed to trees at 10 m centres throughout a stand (Amman et al. 1989; Lindgren et al. 1989). While both methods are sometimes effective (Amman et al. 1989; Lindgren et al. 1989; Amman et al. 1991; Shea et al. 1992), results have been inconsistent from year to year in lodgepole pine forests (Gibson et al. 1991; Shea et al. 1992), and none of the trials in ponderosa pine forests has yielded significant results (Bentz et al. 1989; Lister et al. 1990; Gibson et al. 1991). This inconsistency could be caused by differences in population levels, since verbenone seems to be most effective at low population levels where it can interfere effectively with aggregation (Lindgren and Borden 1993). Other possible factors may include variation in micrometeorology on the release rate and dispersion of verbenone (Kostyk et al. 1993), differences in behaviour or genetics of the beetles (Amman 1994), inadequate power of verbenone when used alone (J.H. Borden[1] , pers. comm.), variation in ratios of aggregation and antiaggregation pheromones (Miller et al. 1994), or photoisomerization of verbenone to an inactive substance, chrysanthenone (Kostyk et al. 1993).

Verbenone does appear to have the ability to protect single, high-value trees from attack. Shore et al. (1992), were able to reduce the response of beetles to trees cobaited with *exo*-brevicomin and verbenone to levels not significantly different from the response to unbaited trees.

INTEGRATED STRATEGIES

A semiochemical-mediated decision "tree" developed by Borden (1995) suggests four critical choices for host-seeking beetles. In this pathway, beetles must be able to reject inappropriate host species, unsuitable or resistant hosts, and hosts fully colonized by heterospecific or conspecific competitors. Thus, the ultimate antiaggregant treatment would make the host smell "like a resistant non-host fully colonized by both con- and heterospecifics" (Borden 1995). This could be even more powerful if used in a "push-pull" strategy with attractants (Lindgren and Borden 1993; Borden 1995), protecting valuable trees from attack with antiaggregants ("push") while attracting beetles to nearby traps or trees baited with aggregation pheromones ("pull").

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Recent research has supported the idea that combinations of disruptant semiochemicals can be much more effective than a single disruptant (Borden 1993). By employing a combination of ipsdienol, an aggregation pheromone for the California fivespined ips, *Ips paraconfusus* Lanier, and verbenone, an antiaggregant for the western pine beetle, *Dendroctonus brevicomis* LeConte, Paine and Hanlon (1991) and Bertram and Paine (1994a) were able to reduce trap catches of both species significantly over the use of just one antiaggregant. Except where the populations were very high, Bakke (1987) dramatically reduced attack density of *Ips typographus* L. by treating felled Norway spruce logs with plastic flakes impregnated with verbenone and ipsenol. Ipsenol is produced by *I. typographus* males (Bakke 1981) as well as sympatric *Ips* species (Borden 1985), and may reduce intra- and interspecific competition. Similarly, Borden et al. (1992) and Devlin and Borden (1995) found that a combination of two repellent synomones, ipsenol from *Ips latidens* (LeConte), and verbenone from *D. ponderosae* Hopkins, effectively deterred infestation by pine engravers. Bertram and Paine (1994b) were successful in reducing western pine beetle attack on ponderosa pines baited with two antiaggregants (ipsdienol and *exo*-brevicomin) and attractants, compared to that on control trees with only attractants. Attack densities on treated trees were 34 per m^2, below the hypothesized threshold for tree mortality (Bertram and Paine 1994b).

As suggested by Borden (1995), it may also be possible to integrate nonhost and 'resistant' host kairomones into an antiaggregant blend. Although very little is known about the mechanisms involved in rejecting nonhost tree species in bark beetles, the use of olfactory cues would allow beetles to reject nonhosts quickly, reducing time costs and mortality risks during dispersal (Gries et al. 1989; Schroeder 1992). Gries et al. (1989) modelled host finding in *I. typographus*, predicting a 27 fold increase in host finding and reproductive success with primary attraction and upwind flight over that achieved by random searching alone. Reducing the number of inappropriate hosts sampled also reduces the risk of being killed by resin from such hosts (Moeck et al. 1981; Wood 1982).

One particularly ubiquitous group of chemicals, the "green leaf volatiles" (GLVs), are promising candidates for improved disruptant blends. GLVs are six carbon alcohols, aldehydes, and derivative esters commonly found in green plants (Visser et al. 1979; Whitman and Eller 1990), and occuring across a wide variety of plant families (Visser et al. 1979). Formed through the oxidative degradation of leaf lipids, these chemicals are released continually by the leaves (Visser and Avé 1978). The function, if any, of these compounds in plants is unknown (Whitman and Eller 1990); however, a diverse array of insects in several orders are able to perceive these compounds and respond to them (Visser et al. 1979; Visser 1986). GLVs can function as attractive kairomones (Visser et al. 1979; Guerin et al. 1983; Kamm and Buttery 1983; Katsoyannos and Guerin 1984), synergistically enhance attraction to sex pheromones (Dickens et al. 1990), or act as synomones in "tritrophic interactions" in which a herbivore-damaged plant produces large quantities of these chemicals, attracting natural enemies of the herbivore (Turlings et al. 1990; 1993; Whitman and Eller 1990; Ramachandran and Norris 1991).

GLVs have also shown disruptive activity. Although a mixture of GLVs appears to be the primary source of attraction to host plants for the Colorado potato beetle, none is attractive alone or in the wrong ratio, and even a slight increase in the concentration of one component can decrease attraction (Visser and Avé 1978). Two compounds, not in this attractive blend, were also active in electrophysiological tests and disrupted positive anemotaxis to potato odour; (*Z*)-2-hexen-1-ol, present in potato foliage, was a weak disruptant, whereas a compound absent from potato foliage, (*Z*)-3-hexen-1-ol (Visser et al. 1979), was a strong disruptant (Visser and Avé 1978).

Similarly, Dickens et al. (1992) reported that hexanal and 1-hexanol disrupted the response of three species of coniferous bark beetles, the southern pine beetle, *Dendroctonus frontalis* Zimmerman, the eastern fivespined ips, *Ips grandicollis* (Eichhoff), and the small southern pine engraver, *Ips avulsus* (Eichhoff), to traps baited with attractant semiochemicals. Supporting the deterrent effect of nonhost volatiles, Schroeder (1992) reported reductions in attraction to ethanol by conifer scolytids, *Tomicus piniperda* (L.) and *Hylurgops palliatus* (Gyll.), when flight barrier traps were cobaited with nonhost aspen or birch bolts. Conversely, the response to ethanol by two ambrosia beetles which reproduce in deciduous trees, *Trypodendron domesticum* (L.) and *Xyleborus dispar* (F.), was interrupted when traps were co-baited with α-pinene, a major monoterpene constituent of conifers (Nijholt and Schönherr 1976; Schroeder and Lindelöw 1989).

There is also evidence that beetles are able to detect changes in host resistance through host kairmones such as estragole (also known as methyl chavicol or 4-allylanisol) (Hobson 1995). Stark et al. (1968) reported that a 70% drop in estragole was the largest change detected in volatile consitituents of ozone-damaged ponderosa pine which were preferentially attacked by western pine beetles and MPBs. Estragole has been found to disrupt the response to attractant-baited traps by *D. brevicomis*, *D. ponderosae*, *I. pini*, the red turpentine beetle, *D. valens* LeConte (Hobson 1995), *D. frontalis* (Hayes et al. 1994), the spruce beetle, *D. rufipennis* (Kirby), and the eastern larch beetle, *D. simplex* LeConte (Werner 1994). However, Hayes et al. (1994) reported no further reduction in trap catch when estragole was added to verbenone over that to verbenone alone.

OBJECTIVES

The aim of this investigation was to elucidate a blend of disruptants which would enhance the activity of verbenone as an operational tool against the MPB. Specific objectives were to:

1. test extracts from trembling aspen, *Populus tremuloides* Michx., bark and leaves for antennal activity, as these are the most common deciduous trees in the MPB habitat, and may contain specific volatiles which repel MPB;
2. test the following candidate antiaggregants in the field for their capacity to disrupt response to attractant-baited traps:

   a) Lanierone and ipsdienol, aggregation pheromones for *I. pini*, a competitor of the MPB (Teale et al. 1991),
   b) pinocarvone, a compound isolated from the frass of MPB, and found to halve the response to an attractive bait (Libbey et al. 1985), and
   c) hexanal, a green leaf volatile (GLV) found to repel three other scolytid species (Dickens et al. 1992), as well as other green leaf aldehydes and alcohols;
3. determine the most active blends or components of candidate mixtures from (2) in traps;
4. determine if the most active antiaggregant blend can also enhance the activity of verbenone in traps;
5. test whether aspen volatiles emanating from logs hung on traps disrupt attraction of MPBs to attractant-baited traps; and
6. conduct operational experiments, testing the ability of antiaggregant blends of verbenone and candidate disruptants deployed over wide areas to protect stands of lodgepole pine from MPB attack.

MATERIALS AND METHODS

ELECTROPHYSIOLOGICAL STUDIES

Twenty-one synthetic chemicals, mostly green leaf volatiles (Table 1) were selected for analysis by coupled gas chromatographic-electroantennographic detection (GC-EAD) (Arn et al. 1975; Gries et al. 1993). Chemicals such as (*Z*)-3-hexenal were not tested, as these are extremely unstable and would be impractical to use operationally. Trembling aspen volatiles were obtained from trees felled in February, 1994 near Princeton, B.C. Branches and stems up to 7.0 cm in diameter were immediately cut into 22 cm lengths and placed in an aeration chamber for 5 days. Branches were also cut and placed upright in beakers of distilled water at room temperature to induce bud break. Once leaves had emerged, branch tips were cut off, their cut ends immersed in a small beaker of distilled water to keep them fresh, and also placed in an aeration chamber for 5 days. Volatiles from aerations were captured on Porapak-Q and recovered by extraction with pentane (Pierce et al. 1981).

MPB-infested lodgepole pine bolts were collected in September 1993 and February 1994 near Princeton, B.C., and waxed on both ends. Logs collected in September were allowed to overwinter outside before being placed in cages in the laboratory, whereas logs collected in February were caged promptly. Emerged beetles were removed from cages daily and used immediately in GC-EAD analysis by R. Gries[1] in January and April, 1994. The apparatus was modified for testing scolytids (G. Gries[1], unpublished) and employed a Varian 3400 gas chromatograph equipped with a fused silica column (DB-5, 30 m × 0.32 mm). Electrodes were placed into the head (indifferent electrode) and antennal club (recording electrode) of living beetles (both sexes) with the aid of a micro-manipulator. Both *exo*- and *endo*-brevicomin (10 ng each) were used as control stimuli in all tests involving synthetic chemicals. Beetles observed to respond to brevicomin controls were then tested with synthetic stimuli. Synthetic chemicals were tested at 20-25 ng, and

TABLE 1. Chemicals tested in electrophysiological studies.

Chemical	**Source** [a]	**Purity (%)** [b]
1-propanol	Aldrich	99
1-butanol	Anachemia	99
1-pentanol	Sigma	99
1-hexanol	Sigma	98
(*Z*)-2-hexen-1-ol	Aldrich	96
(*E*)-2-hexen-1-ol	Aldrich	95
(*Z*)-3-hexen-1-ol	Aldrich	98
(*E*)-3-hexen-1-ol	Aldrich	98
1-heptanol	Aldrich	99
1-octanol	Aldrich	99
1-nonanol	Sigma	98
1-decanol	Sigma	98
hexanal	Aldrich	98
(*E*)-2-hexenal	Aldrich	99
heptanal	Aldrich	95
octanal	Aldrich	99
nonanal	Aldrich	95
decanal	Sigma	99
indole [c]	Sigma	99+
linalool [c]	Sigma	95-97
(*Z*)-3-hexenyl acetate [c]	Sigma	98

[a] Chemical sources: Aldrich Chemical Co., Milwaukee, WI; Anachemia Chemical Co., Vancouver, BC; Sigma Chemical Co., St. Louis, MO.

[b] Purity as listed by manufacturer; indole received in crystalline form.

[c] "Tritrophic compounds", synomones produced by herbivore-damaged plants, attracting natural enemies of the herbivore (Turlings et al. 1993).

volatiles recovered from Porapak-Q were diluted in pentane. Antennally active compounds in aspen extracts were identified using coupled GC-mass spectrometry (MS) (Hewlett Packard 5985B) in full-scan and selected ion monitoring (SIM) mode.

Fresh trembling aspen bark was macerated in a blender and the volatile oils extracted using a simultaneous steam distillation-continuous extraction still head (Flath and Forrey 1977). Volatiles were extracted with pentane, which was removed under a stream of nitrogen. Residual solvent was removed by brief vacuum pumping. The final weight of volatile oils per gram of bark was multiplied by the ratio of each antennally active component from GC-analysis, giving gram-equivalents of each component per gram of bark.

FIELD EXPERIMENTS

Nine randomized complete block experiments, including seven trapping experiments (Exp. 1-7) and two tree-baiting experiments (Exp. 8 and 9) were conducted in 1992 through 1994 in stands of lodgepole pine, *Pinus contorta* var. *latifolia* Engelmann, near Princeton, British Columbia. Experiment numbers, dates, locations, and numbers of replicates are listed in Table 2.

Trapping Experiments

All trapping experiments utilized 12-unit multiple funnel traps (Lindgren 1983), hung from ropes or poles. Traps were deployed in lines with 25 m between traps and lines. All chemical names, abbreviations, release devices, and release rates are listed in Table 3. The green leaf volatiles (GLVs) listed were chosen because they appear often in GLV literature, and were cheap and easy to obtain. Release rates of verbenone were lower than optimal to allow the effects of potential adjuvants to be detected.

Except where otherwise stated, three control treatments were used in these experiments to assess the effectiveness of candidate disruptants: an attractive control,

TABLE 2. Numbers, dates, locations, and numbers of replicates for field trapping experiments, 1992-1994.

Exp. No.	Dates	Location [a]	Replicates
1	July 12-July 28, 1992	Whistle Ck.	12
2	July 21-Aug. 7, 1993	McNulty Ck.	20
3	Aug. 22-Aug. 31, 1993	McNulty Ck.	10
4	July 11-23, 1994	Willis Ck.	20
5	July 23-Aug.1, 1994	Willis Ck.	16
6	Aug. 12-16, 1994	Willis Ck.	10
7	Aug. 11-13, 1994	Willis Ck.	20
8	June 28-Aug. 30, 1993	McNulty Ck.	5
9	June 22-Aug. 31, 1994	Willis Ck.	8

[a] Whistle Creek, approximately 25 km east of Princeton, B.C.; McNulty Creek, approximately 30 km east of Princeton, B.C.; and Willis Creek, approximately 20 km south of Princeton, B.C.

TABLE 3. Description of semiochemicals employed in seven randomized-block trapping experiments (Exp. 1-7) for the mountain pine beetle.

Exp.	Semiochemical[a]	Source[b]	Abbreviation	Release Device	Release Rate (mg per 24 h)
1-7	3- component mountain pine beetle lure		MPB	Separated devices as below	
	myrcene	P	M	1 closed polyethylene bottle (15 mL)	18
	trans-verbenol	P	tV	1 bubble cap	1.0
	exo-brevicomin	P	eB	1 flex lure	0.05
1,6	verbenone (low dose)	P	v	1 bubble cap	0.6
2,4	verbenone (high dose)	P	v	2 bubble caps	1.2
1	ipsdienol	P	i	1 bubble cap	0.2
1	Lanierone	P	L	1 bubble cap	0.2
2	pinocarvone	SFU	pino	5 capillary tubes	1.0[c]
2,3	hexanal (low dose)	A	h	1 capillary tube	1.2[c]
1	hexanal (high dose)	A	h	1 closed polyethylene microcentrifuge tube (1.8 mL)	3.0[c]
2	green leaf volatiles, mixture of compounds used in Exp. 3	A	GLV	1 capillary tube for entire mixture	1.3[c]
3	green leaf volatiles, 5 component blend as below		GLV	separated devices as below	
3	1-hexanol	A	1-OH	1 open polyethylene microcentrifuge tube (400 μL)	2.1[c]
	(*E*)-2-hexen-1-ol	A	E-2-OH	1 open polyethylene microcentrifuge tube (400 μL)	1.8[c]
	(*Z*)-3-hexen-1-ol	A	Z-3-OH	1 open polyethylene microcentrifuge tube (400 μL)	1.3[c]
	hexanal	A	1-ALD	1 capillary tube	1.2[c]
	(*E*)-2-hexenal	A	E-2-ALD	1 capillary tube	1.3[c]

TABLE 3. (Continued)

Exp.	Semiochemical[a]	Source[b]	Abbreviation	Release Device	Release Rate (mg per 24 h)
3	green leaf volatiles, 5 component blend as below		GLV	separated devices as below	
3	1-hexanol	A	1-OH	1 open polyethylene microcentrifuge tube (400 μL)	2.1[c]
	(*E*)-2-hexen-1-ol	A	E-2-OH	1 open polyethylene microcentrifuge tube (400 μL)	1.8[c]
	(*Z*)-3-hexen-1-ol	A	Z-3-OH	1 open polyethylene microcentrifuge tube (400 μL)	1.3[c]
	hexanal	A	1-ALD	1 capillary tube	1.2[c]
	(*E*)-2-hexenal	A	E-2-ALD	1 capillary tube	1.3[c]
4,5	green leaf alcohols, 4 component blend as below		OH	separated devices as below	
5	1-hexanol	S	1-OH	1 bubble cap	3.8
5,6	(*E*)-2-hexen-1-ol	B	E-2-OH	1 bubble cap	3.8
5	(*Z*)-2-hexen-1-ol	B	Z-2-OH	1 bubble cap	3.8
5,6	(*Z*)-3-hexen-1-ol	B	Z-3-OH	1 bubble cap	3.8
4	green leaf aldehydes, 2 component blend as below		ALD	separated devices as below	
4	hexanal	A	1-ALD	1 bubble cap	13
	(*E*)-2-hexenal	B	E-2-ALD	1 bubble cap	13

[a] Where a 'mixture' is noted, semiochemicals are released from a single release device; all other semiochemicals and blends are released from separate devices. All green leaf volatiles stabilized with 1.2% (wet weight) Ethanox® 330 antioxidant, Ethyl Chemicals Group, Baton Rouge, LA.

[b] Symbols for sources as follows: P=Phero Tech Inc., Delta, BC; A=Aldrich Chemical Company, Milwaukee, WI; S=Sigma Chemical Company, St. Louis, MO; B=Bedoukian Research Inc., Danbury, CT; SFU=synthesized by H.D. Pierce, Jr., Department of Chemistry, Simon Fraser University, Burnaby, BC, V5A 1S6. Purities as in Table 1, except for pinocarvone (91%), (*E*)-2-hexen-1-ol (95%), (*Z*)-2-hexen-1-ol (92%), (*Z*)-3-hexen-1-ol (97%), and (*E*)-2-hexenal (98%).

[c] Determined in laboratory at 24° C. All other release rates determined by Phero Tech, Inc. at 22° C.

consisting of a three-component MPB lure alone, a disruptive control, consisting of a MPB lure plus verbenone, and a non-attractive unbaited trap.

Exp. 1 tested the addition of three candidate antiaggregants, hexanal, ipsdienol or Lanierone, to verbenone and a MPB lure, compared to all three control treatments. Exp. 2 tested the ability of hexanal, pinocarvone, verbenone, or a mixture of green leaf volatiles (released together) to disrupt MPB response to MPB lures against all three control treatments. Exp. 3 compared the disruptive effect of hexanal alone *versus* hexanal plus a blend of four other green leaf volatiles (released separately) to attractive and non-attractive controls. The aim of Exp. 4 and 5 was to discern the most active components of the GLV blend. Exp. 4 compared the disruptive effect of green leaf aldehydes, alcohols, or both, added to MPB lures, *versus* the disruptive control or a blank trap. Based on the results of this experiment, the green leaf alcohols (the most repellent GLVs), were tested individually in Exp. 5. All individual alcohol components were tested in combination with MPB lures for disruptive ability *versus* blank traps; there was no MPB lure control. In Exp. 6, the best individual GLVs from Exp. 5 were tested alone with a MPB lure, or together with verbenone, to determine if they could enhance the antiaggregant effect of verbenone.

Exp. 7 tested the effect of trembling aspen bolts hung on traps baited with MPB lures *versus* MPB lures alone, in a design similar to that of Schroeder (1992). A living aspen tree with a diameter at breast height (dbh, measured approximately 1.3 m above the ground) of 16 cm was felled approximately 25 km south of Princeton, B.C. early on August 11, 1994 and cut into 30 cm long bolts. Bolts were split in half with an axe to increase the surface area, then placed in mesh bags which were hung on traps. The experiment was run for one day, re-randomized with the same bolts and then run for a second day.

Captured insects were collected within a week and stored in a freezer. MPBs, clerids, scolytids, and striped ambrosia beetles, *Trypodendron lineatum* (Olivier), were counted. Sex of MPBs and *T. lineatum* was determined.

Tree-Baiting Experiments

Two tree-baiting experiments (Exp. 8 and 9) tested candidate antiaggregants alone or in combination with verbenone for the ability to protect standing trees in simulated operational applications. Chemicals names, release devices, and release rates are given in Table 4. Descriptive stand data are tabulated in Table 5.

Experimental plots (50 x 50 m) (Fig. 1), similar to those used by Lindgren et al. (1989), were laid out in a randomized, complete block design, with 75-100 m between blocks. A single tree (≥20 cm dbh) in the centre of each plot was baited with a MPB tree bait (Table 4) 2-3 m high on the north side. In antiaggregant treatment plots, the centre tree was surrounded by a 10 x 10 m grid of antiaggregants (36 per plot), stapled 2-3 m high on the north side of the nearest vertical object, thus challenging beetles to fly through the antiaggregant grid to find and attack the baited tree. Control plots were also 50 x 50 m but contained only the central baited tree.

Exp. 8 compared all possible binary combinations of low or high doses of hexanal with low or high doses of verbenone (Table 4) for operational protection of trees. Exp. 9 compared attack in control plots to four antiaggregant treatments: low verbenone, high verbenone, low verbenone plus GLVs, and high verbenone plus GLVs (Table 4).

Assessment of both experiments was done by examining all trees in September after beetle flight, using a methodology similar to that used by Lindgren and Borden (1993) and Lindgren et al. (1989). Numbers of trees attacked the previous year ('red attack') were noted, as well as numbers of 'mass-attacked' (≥31.25 attacks per m^2), 'lightly attacked' (<31.25 attacks per m^2) and 'unattacked' trees. The mass-attack designation is a conservative estimate of the attack density required to cause host mortality (Raffa and Berryman 1983). Density of attack on the baited centre tree was assessed by counting all attacks in two 20 x 40 cm strips (0.16 m^2 total area) at eye level on the east and west sides of the tree.

TABLE 4. Description of semiochemicals employed in two randomized complete block tree-baiting experiments (Exp. 8 and 9) for the mountain pine beetle.

Exp.	**Semiochemical** [a]	**Abbreviation**	**Release Device**	**Release Rate (mg per 24 h)**
8,9	mountain pine beetle tree bait, 2 component blend as below	Control		
	trans-verbenol	tV	1 bubble cap	1.0
	exo-brevicomin	eB	1 bubble cap	0.05
8,9	verbenone (low dose)	LV	1 bubble cap	0.6
8,9	verbenone (high dose)	HV	1 bubble cap	10
8	hexanal (low dose)	LH	1 closed polyethylene microcentrifuge tube (400 μL)	7.0 [b]
8	hexanal (high dose)	HH	1 closed polyethylene bottle (15 mL)	60 [b]
9	green leaf volatiles, alcohol and aldehyde blend as below	GLV	separate devices as below	
	1-hexanol	1-OH	1 bubble cap	3.8
	(*E*)-2-hexen-1-ol	E-2-OH	1 bubble cap	3.8
	(*Z*)-2-hexen-1-ol	Z-2-OH	1 bubble cap	3.8
	(*Z*)-3-hexen-1-ol	Z-3-OH	1 bubble cap	3.8
	hexanal	1-ALD	1 bubble cap	13
	(*E*)-2-hexenal	E-2-ALD	1 bubble cap	13

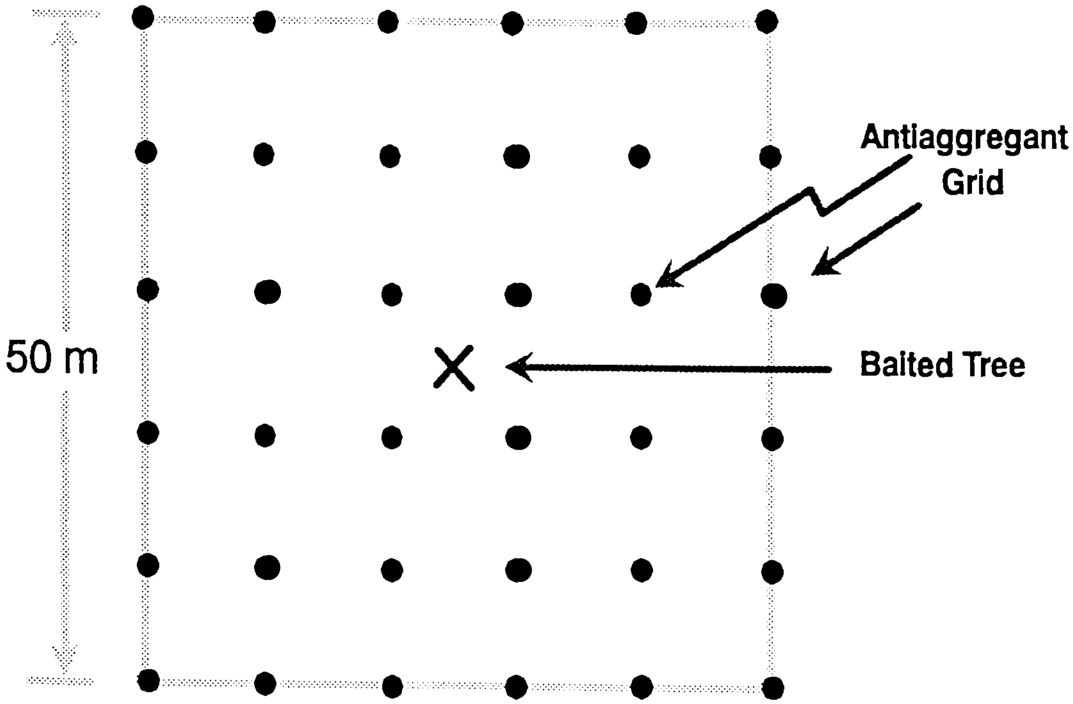
[a] Sources and purities of chemicals as in Table 3. Hexanal and all other green leaf volatiles stabilized with 1.2% (wet weight) Ethanox® 330 antioxidant, Ethyl Chemicals Group, Baton Rouge, LA.

[b] Determined in laboratory at 24° C. All other release rates determined by Phero Tech, Inc. at 22° C.

TABLE 5. Descriptive data provided by Weyerhauser Canada Ltd. for stands used in Exp. 8 and 9 in 1993 and 1994, respectively. Exp. 8 and 9 encompassed two and three stands, respectively.

Exp. no.	Percent lodgepole pine infested in previous year	Stand area (ha)	No. lodgepole pines per ha	Average dbh (cm)
8	0.62%	48.5	709.4	22.8
		14.3	1848.4	19.8
9	6.52%	115.0	1220.8	19.9
		11.8	419.2	26.4
		20.1	1024.7	19.7

FIG. 1. Plot layout for Exp. 8 and 9 showing centre tree with a MPB tree bait, and surrounding 10 x 10 m grid of 36 test antiaggregants, stapled to the nearest vertical object. Control plots were also 50 x 50 m but contained only the central baited tree.


50 m
Antiaggregant Grid
Baited Tree

Data analysis

To satisfy criteria for normality and homoscedasticity, data on trap catches in Exp. 1-7 were transformed by $\log_{10}(x+1)$ and percentage data in Exp. 8 and 9 were transformed by $\arcsin\sqrt{x}$ (Zar 1984). ANOVA (GLM procedure, SAS institute Inc. 1985), and the Ryan-Einot-Gabriel-Welsch Multiple Q-test (α = 0.05) (REGWQ procedure, SAS Institute Inc. 1985; Day and Quinn 1989) were used to determine differences between means in all experiments. Orthogonal contrasts (SAS Institute Inc. 1985) were also used to compare treatment means to the blank trap for low catches of clerid predators in Exp. 4. In Exp. 5, nonparametric Mann-Whitney-Wilcoxon tests (Zar 1984) were used to test the alternative hypothesis that trap catches to two semiochemical treatments containing green leaf alcohols were significantly lower than catches in a nearby MPB monitoring trap containing attractive lures.

RESULTS AND DISCUSSION

ELECTROPHYSIOLOGICAL STUDIES

Of the synthetic chemicals tested (Table 1), analysis by GC-EAD revealed that MPB antennae responded to all six-carbon alcohols tested, including 1-hexanol (Fig. 2), (*E*)-2-hexen-1-ol, (*Z*)-2-hexen-1-ol, (*E*)-3-hexen-1-ol, and (*Z*)-3-hexen-1-ol (Fig. 3). Responses were reproduced in at least two tests. Beetles did not respond to any of the six-carbon aldehydes or other compounds tested.

In three tests with volatiles from trembling aspen bark and stems, MPB antennae responded to 0.4-7 ng of compounds identified through GC-MS as 1-hexanol, benzaldehyde, benzyl alcohol, and nonanal (Fig. 4). These compounds occur naturally at 30.3, 1.6, 22.6, and 4.5μg per gram of fresh bark, respectively (based on volatile oil recovery from steam distillation of trembling aspen bark of 0.0243% by weight). Volatiles from foliage elicited no antennal response (R. Gries, pers. comm.). Since MPBs tend to fly beneath the tree canopy (Safranyik et al. 1992), it may be that they are more sensitive to volatiles in trembling aspen bark than to volatiles in the foliage.

Curiously, nonanal from trembling aspen bark elicited a response, whereas synthetic nonanal did not. This disparity may be due primarily to difficulties in manipulating beetles' antennae. Many insects had to be screened before one would respond to *exo*- and *endo*-brevicomin control stimuli, and the antennae of these insects may have become inactive by the time they were exposed to nonanal, a late-eluting chemical.

All but one of the 6-carbon alcohols tested were incorporated into field experiments in 1994. (*E*)-3-hexen-1-ol was not tested as it is very expensive ($2700 per kg), and would thus be impractical for operational use. The results from the analysis of volatiles from trembling aspen were available too late to incorporate nonanal, benzaldehyde and benzyl alcohol into field experiments.

FIG. 2. Flame ionization detector (FID) and electroantennographic detector (EAD: beetle antenna) responses to nine synthetic test chemicals. Only 1-hexanol (6-OH) shows a positive antennal response on the EAD. 5-OH=1-pentanol; 6-ALD=hexanal; 6-OH=1-hexanol; 7-ALD=heptanal; 7-OH=1-heptanol; 8-ALD=octanal; 8-OH=1-octanol; Lin=linalool; 9-ALD=nonanal.

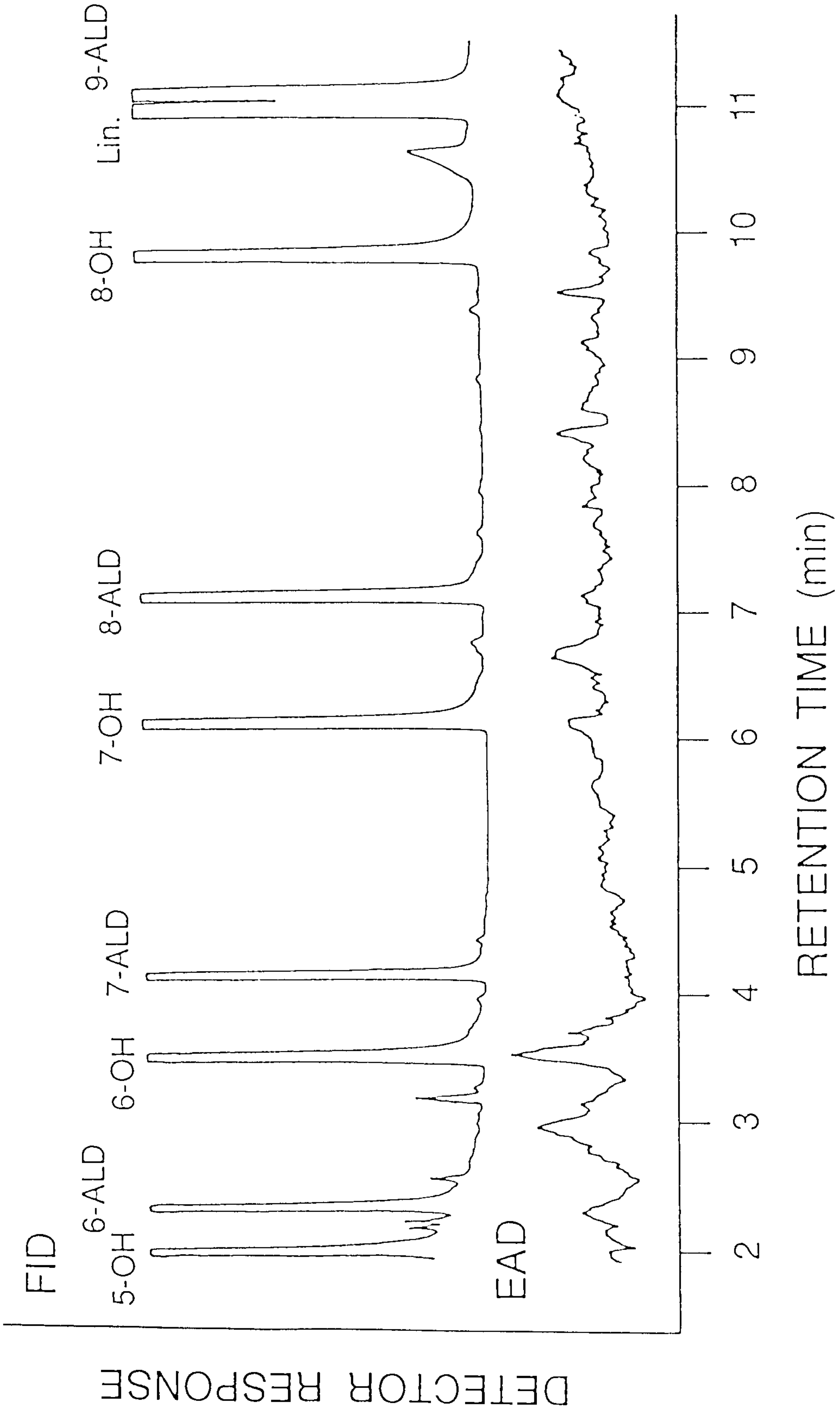

FID
5-OH
6-ALD
6-OH
7-ALD
7-OH
8-ALD
8-OH
Lin.
9-ALD
EAD
2
3
4
5
6
7
8
9
10
11
RETENTION TIME (min)
DETECTOR RESPONSE

FIG. 3. Flame ionization detector (FID) and electroantennographic detector (EAD: beetle antenna) responses to four synthetic test chemicals. All four chemicals elicted positive antennal responses.

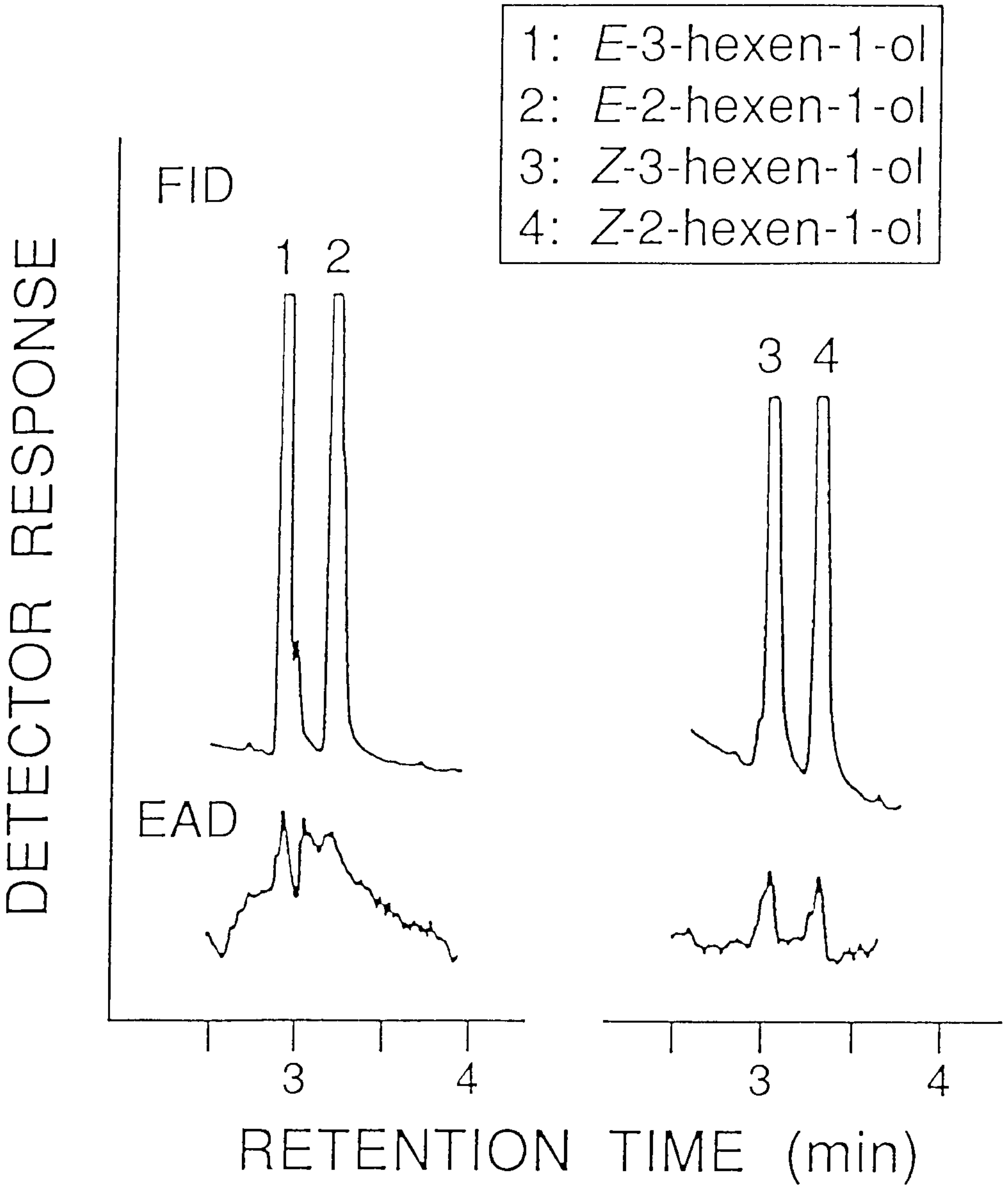
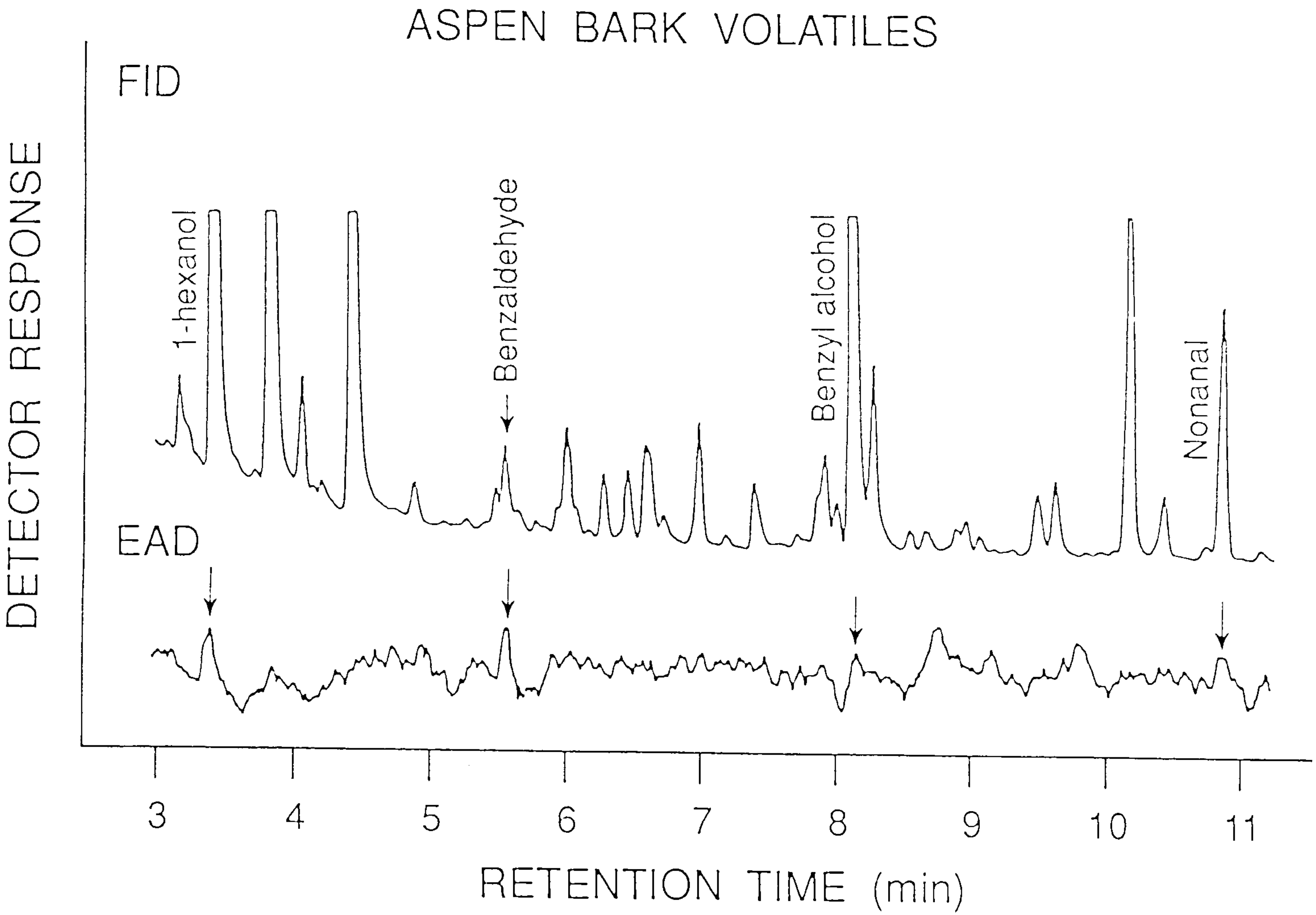

1: *E*-3-hexen-1-ol
2: *E*-2-hexen-1-ol
3: *Z*-3-hexen-1-ol
4: *Z*-2-hexen-1-ol
FID
1
2
3
4
EAD
DETECTOR RESPONSE
3
4
3
4
RETENTION TIME (min)

FIG. 4. Flame ionization detector (FID) and electroantennographic detector (EAD: beetle antenna) responses to aspen bark volatiles. Positive responses to 1-30 nanograms of 1-hexanol, benzaldehyde, benzyl alcohol and nonanal (FID trace) are labelled with arrows on the EAD trace.


ASPEN BARK VOLATILES
FID
EAD
1-hexanol
Benzaldehyde
Benzyl alcohol
Nonanal
DETECTOR RESPONSE
3
4
5
6
7
8
9
10
11
RETENTION TIME (min)

TRAPPING STUDIES

In Exp. 1, Lanierone and hexanal did not significantly improve disruption of beetles of either sex to the MPB lure over that caused by verbenone alone (Fig. 5). When ipsdienol and verbenone were present together, catches of females were reduced to a level not significantly different from that to blank control traps. This result is consistent with the reported repellency of MPB by ipsdienol (Hunt and Borden 1988, Borden et al. 1992).

Pinocarvone did not interrupt the response to MPB lures in Exp. 2 (Fig. 6), even though the release rate, 1.0 mg per 24 h, was twice that found to reduce MPB response significantly by Libbey and Ryker (1985). The attractant control used by Libbey and Ryker (1985), however, did not contain *exo*-brevicomin, and may not have attracted beetles strongly.

Hexanal was an ineffective disruptant when tested alone at 1.2 mg per 24 h (Exp. 2,3; Figs. 6,7), demonstrating that in Exp. 1 (Fig. 5) a weak possible effect was not over-ridden by verbenone. These results differ from those of Dickens (1992) who reported that hexanal was a more effective disruptant than 1-hexanol for three other species of bark beetles. In other experiments (results not shown) hexanal released at 7.0 mg per 24 h again had no significant disruptive effect. The lack of an antennal response to hexanal (Fig. 2) is in agreement with its behavioural inactivity.

In Exp. 2 (Fig. 6) a mixture of GLVs, released from a single device, reduced catches of females, but not to the same extent caused by verbenone. Subsequent GC-analysis of these baits, however, indicated that the release of alcohols was very low from this device. When each component was released from separate devices in the same trap in Exp. 3 (Fig. 7) GLVs caused a strongly significant reduction in catches of both sexes, with catches of females being not significantly different from those in the blank traps.

FIG. 5. Response of *Dendroctonus ponderosae* in Exp. 1 to multiple funnel traps baited with MPB lures alone, and in combination with verbenone or three candidate antiaggregants. Bars associated with the same letter are not significantly different, Ryan-Einot-Gabriel-Welsch Multiple Q-test, $P < 0.05$, n=12. Abbreviations of stimuli as in Table 3.

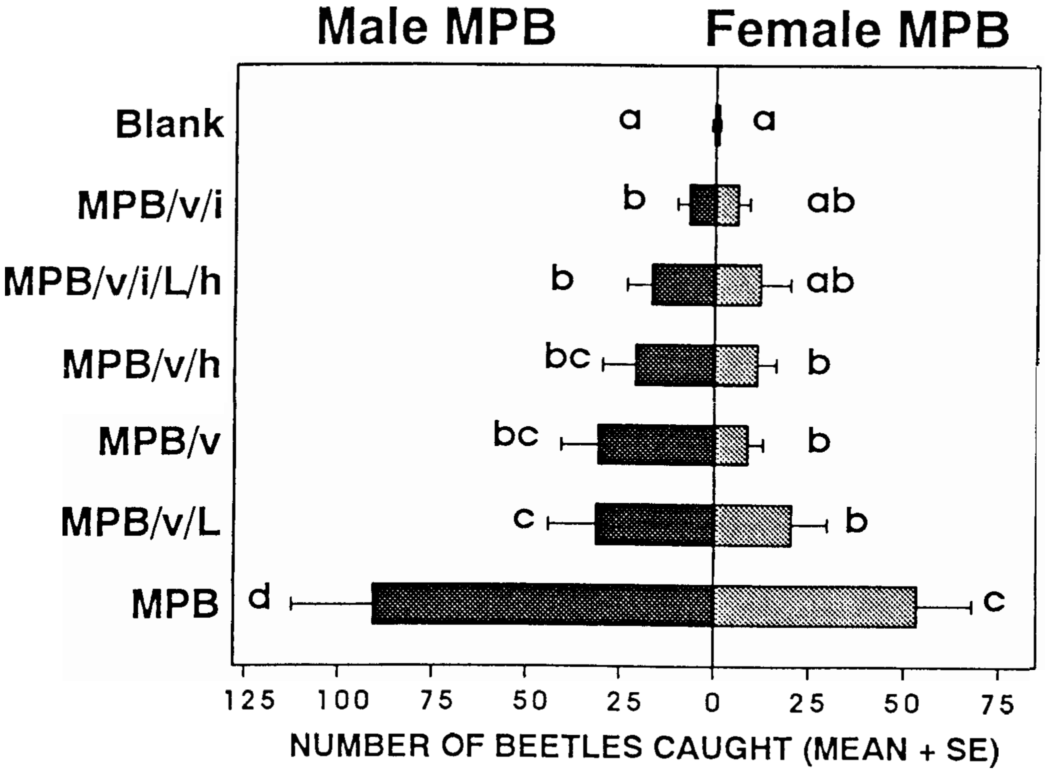

Male MPB
Female MPB
Blank
MPB/v/i
MPB/v/i/L/h
MPB/v/h
MPB/v
MPB/v/L
MPB
a
a
b
ab
b
ab
bc
b
bc
b
c
b
d
c
125
100
75
50
25
0
25
50
75
NUMBER OF BEETLES CAUGHT (MEAN + SE)

FIG. 6. Response of *Dendroctonus ponderosae* in Exp. 2 to multiple funnel traps baited with MPB lures alone, and in combination with verbenone, pinocarvone, hexanal, or a mixture of green leaf volatiles released from a single device (Table 3). Bars associated with the same letter are not significantly different, Ryan-Einot-Gabriel-Welsch Multiple Q-test, $P < 0.05$, n=20. Abbreviations of stimuli as in Table 3.

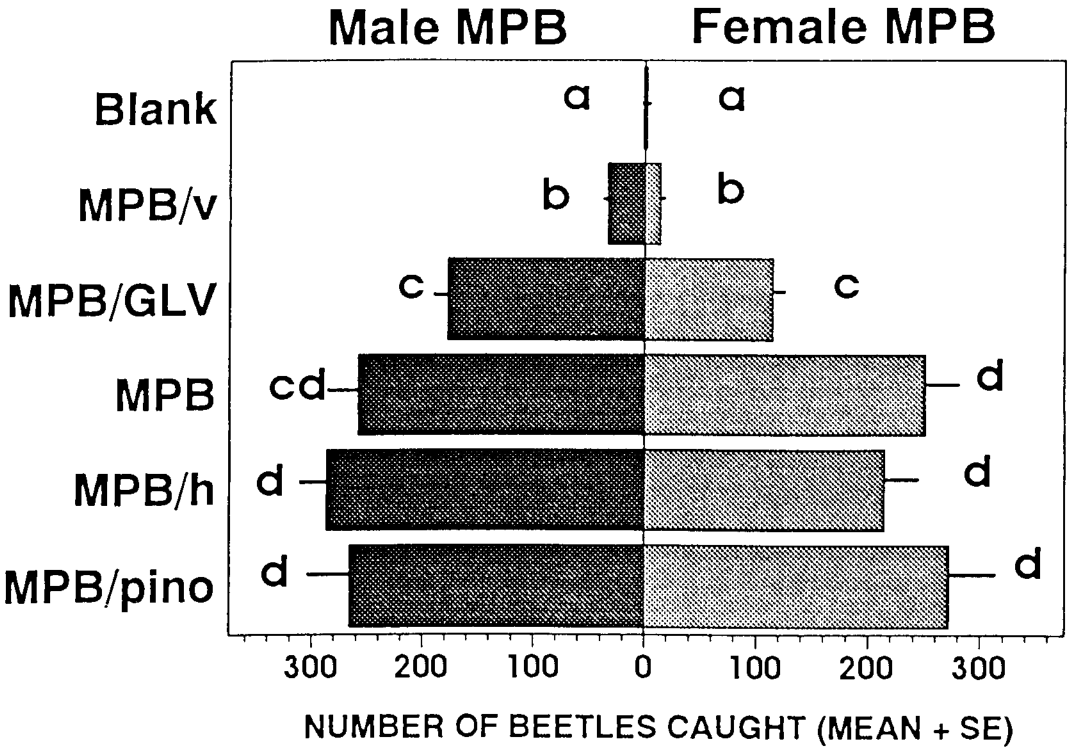
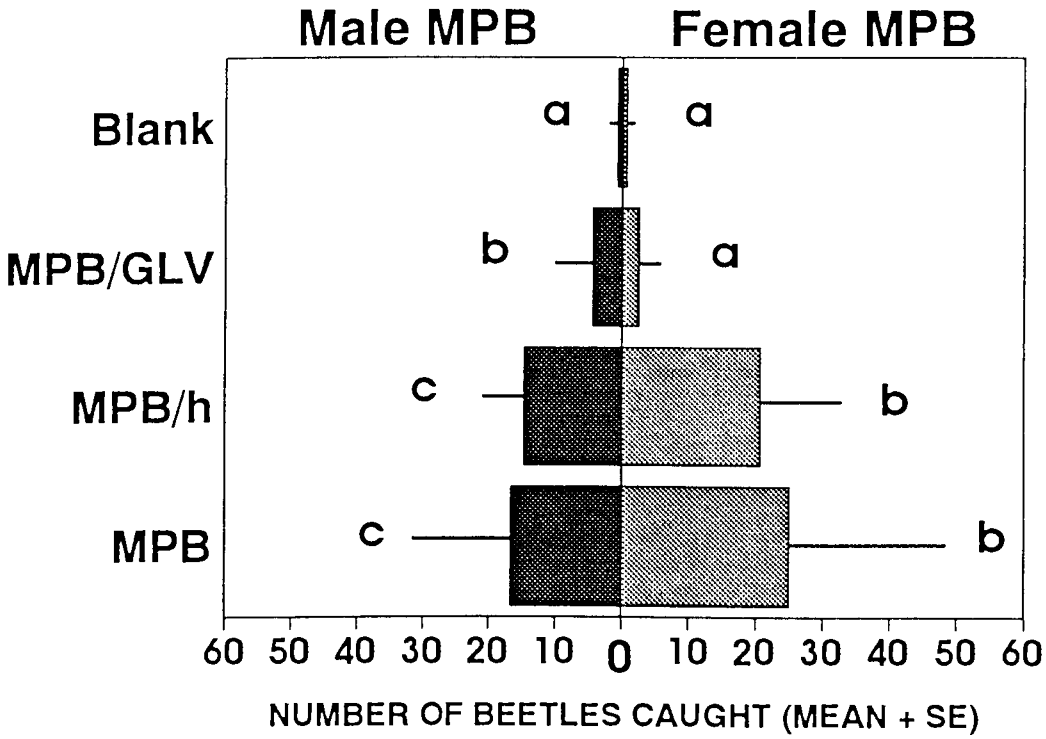

Male MPB
Female MPB
Blank
MPB/v
MPB/GLV
MPB
MPB/h
MPB/pino
a
a
b
b
c
c
cd
d
d
d
d
d
300
200
100
0
100
200
300
NUMBER OF BEETLES CAUGHT (MEAN + SE)

FIG. 7. Response of *Dendroctonus ponderosae* in Exp. 3 to multiple funnel traps baited with MPB lures alone, and in combination with hexanal or hexanal plus four other green leaf volatiles released from separate devices (Table 3). Bars associated with the same letter are not significantly different, Ryan-Einot-Gabriel-Welsch Multiple Q-test, $P< 0.05$, n=10. Abbreviations of stimuli as in Table 3.


Male MPB
Female MPB
Blank
MPB/GLV
MPB/h
MPB
a
a
b
a
c
b
c
b
60 50 40 30 20 10 0 10 20 30 40 50 60
NUMBER OF BEETLES CAUGHT (MEAN + SE)

Exp. 4 demonstrated that a green leaf alcohol blend comprising 1-hexanol, (*Z*)-3-hexen-1-ol, (*E*)-2-hexen-1-ol, and (*Z*)-2-hexen-1-ol (the latter not tested in Exp. 3), was competitive with verbenone as an antiaggregant, whereas the aldehydes, hexanal and (*E*)-2-hexenal clearly were poor disruptants (Fig. 8).

(*Z*)-3-hexen-1-ol and (*E*)-2-hexen-1-ol were the two most potent green leaf alcohol antiaggregant components of the mixture from Exp. 4 (Exp. 5, Fig. 9). Each of these alcohols alone disrupted the response of both sexes of MPB to the same level as a blend of all four alcohols, and reduced female catches to levels not significantly different from that to a blank trap. The highest catches in Exp. 5 were in response to MPB lures in combination with 1-hexanol or (*Z*)-2-hexen-1-ol. Although MPB lure controls were not included in Exp. 5, mean catches (± SE) (n=2) in a monitoring trap baited with a MPB lure in the same area as Exp. 5 were 64.0 ± 13.0 males and 16.5 ± 2.5 females, respectively (Fig. 9). These catches are significantly higher (one-tailed Mann-Whitney tests, $P<0.05$) than male or female catches to either 1-hexanol or (*Z*)-2-hexen-1-ol treatments, indicating that these chemicals also have disruptive properties.

A combination of (*Z*)-3-hexen-1-ol and (*E*)-2-hexen-1-ol in Exp. 6 (Fig. 10) significantly reduced male and female catches by 94% and 96%, respectively, compared to the attractive MPB lure control. This disruptive power was the same as that of verbenone.

Supporting the disruptive effect of GLVs against the MPB (Figs. 6-9), I have also found that a blend of GLVs significantly disrupts the response of *T. lineatum* to its pheromone lineatin (unpublished data). In addition they disrupt the response of *D. rufipennis* to attractive semiochemicals (T.M. Poland[1], pers. comm.).

The reduction in trap catches caused by the GLV blend, ranging from 71% in Exp. 3 to 96% in Exp. 6, compares very favourably with recent results from other investigators, particularly when release rates (Table 3) are considered. When hexanal was released at 0.25 mg per 24 h from funnel traps also containing attractants, Dickens et al. (1992) reported reductions in mean trap catches for *D. frontalis*, *I. grandicollis*, and *I. avulsus* of

FIG. 8. Response of *Dendroctonus ponderosae* in Exp. 4 to multiple funnel traps baited with MPB lures in combination with green leaf alcohols, aldehydes, or both (Table 3). Bars associated with the same letter are not significantly different, Ryan-Einot-Gabriel-Welsch Multiple Q-test, $P < 0.05$, n=20. Abbreviations of stimuli as in Table 3.

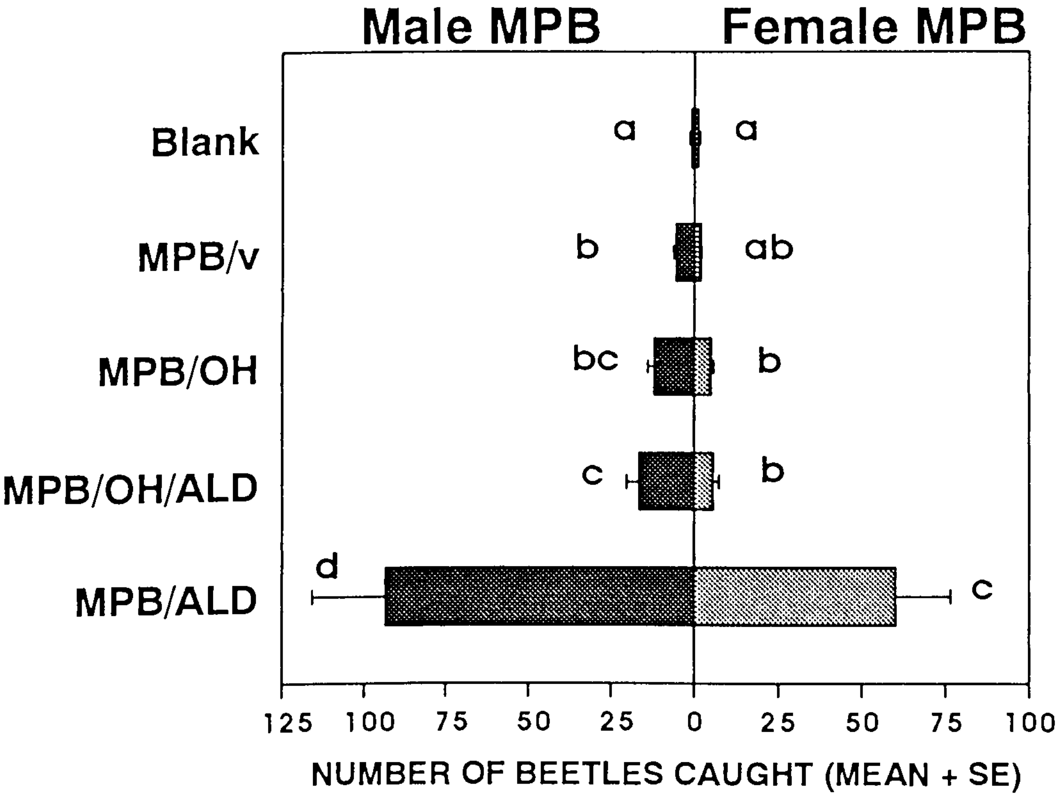

Male MPB
Female MPB
Blank
MPB/v
MPB/OH
MPB/OH/ALD
MPB/ALD
a
a
b
ab
bc
b
c
b
d
c
125
100
75
50
25
0
25
50
75
100
NUMBER OF BEETLES CAUGHT (MEAN + SE)

FIG. 9. Response of *Dendroctonus ponderosae* in Exp. 5 to multiple funnel traps baited with MPB lures in various combinations with green leaf alcohols. Arrows on x-axis indicate mean catches (n=2) in a monitoring trap adjacent to the experiment, serving as a partial attractive control. Male and female responses to 1-hexanol and (*Z*)-2-hexen-1-ol are significantly lower than responses to the monitoring trap (one-tailed Mann-Whitney-Wilcoxon tests, $P< 0.05$). Bars associated with the same letter are not significantly different, Ryan-Einot-Gabriel-Welsch Multiple Q-test, $P< 0.05$, n=16. Abbreviations of stimuli as in Table 3.

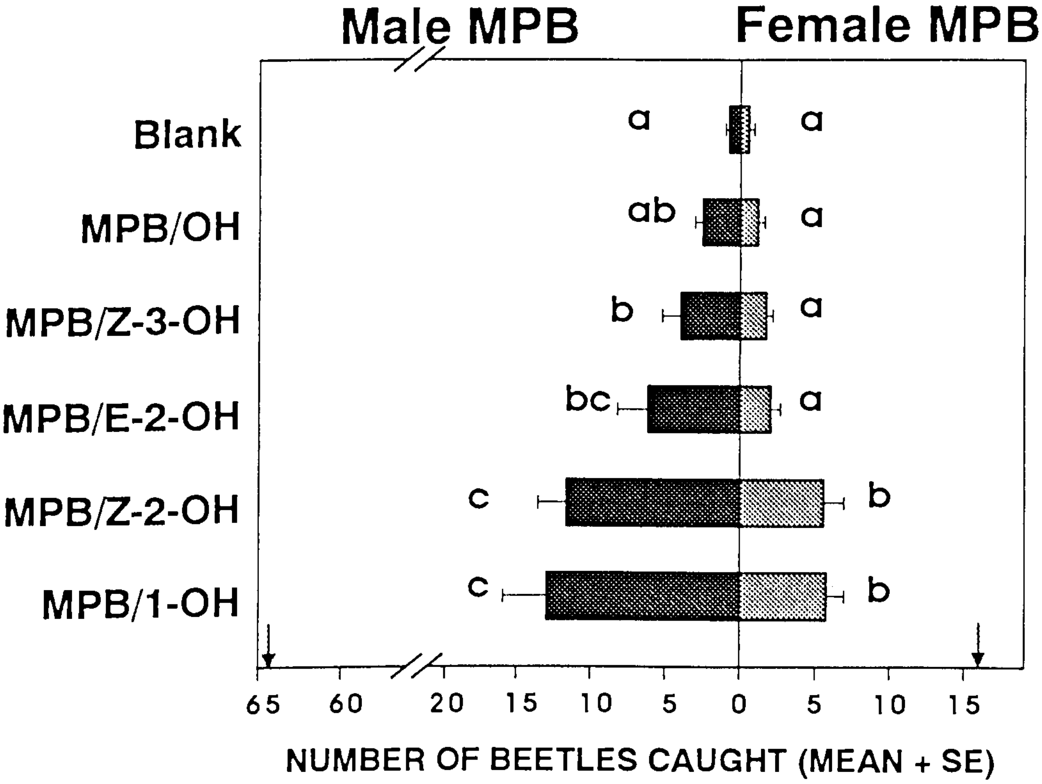
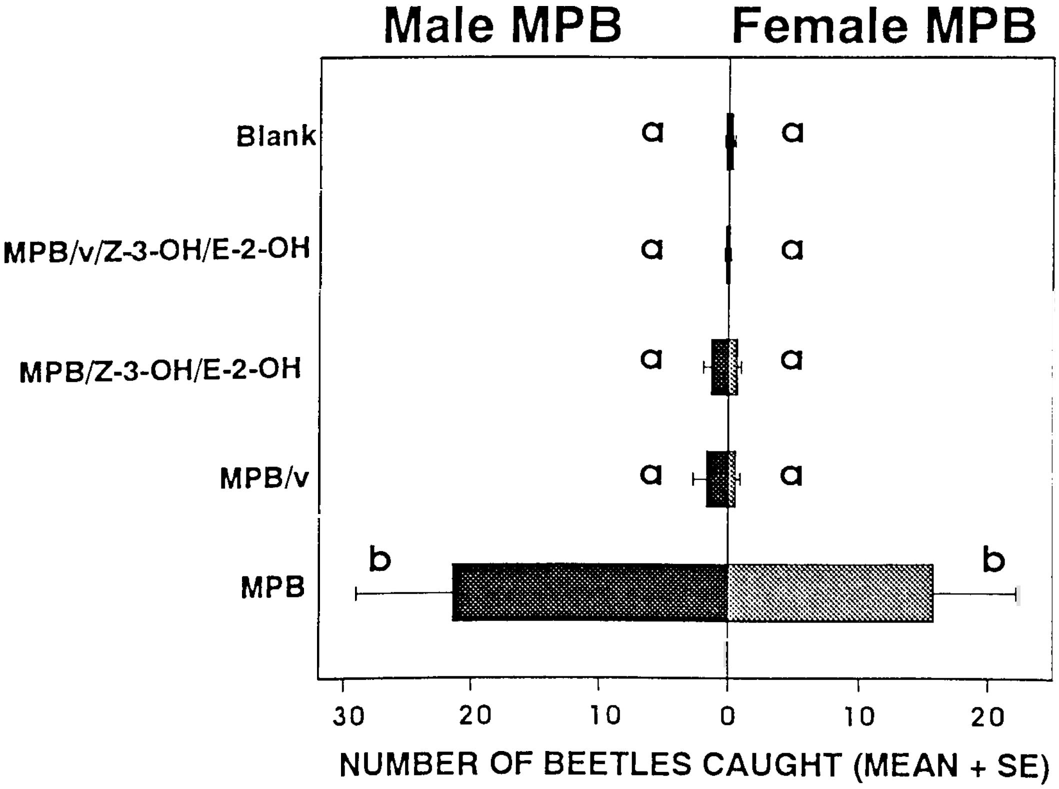

Male MPB
Female MPB
Blank
MPB/OH
MPB/Z-3-OH
MPB/E-2-OH
MPB/Z-2-OH
MPB/1-OH
a
a
ab
a
b
a
bc
a
c
b
c
b
65
60
20
15
10
5
0
5
10
15
NUMBER OF BEETLES CAUGHT (MEAN + SE)

FIG. 10. Response of *Dendroctonus ponderosae* in Exp. 6 to multiple funnel traps baited with MPB lures alone or in combination with two green leaf alcohols, verbenone, or both. Bars associated with the same letter are not significantly different, Ryan-Einot-Gabriel-Welsch Multiple Q-test, $P < 0.05$, n=10. Abbreviations of stimuli as in Table 3.


Male MPB
Female MPB
Blank
MPB/v/Z-3-OH/E-2-OH
MPB/Z-3-OH/E-2-OH
MPB/v
MPB
a
a
a
a
a
a
a
a
b
b
30
20
10
0
10
20
NUMBER OF BEETLES CAUGHT (MEAN + SE)

46, 54, and 69%, respectively (calculated from table in Dickens et al. 1992). Hayes et al. (1994) reported that estragole caused significant reductions (about 25-38%, calculated from Figs. 1 & 2 in Hayes et al. 1994) in response by *D. frontalis* to traps also baited with attractants. However, the release rates ranged from approx. 160-1237 mg per 24 h, and estragole did not further reduce trap catches when added to verbenone (Hayes et al. 1994). More comparable were Hobson's (1995) release rates with estragole released at about 4.8 mg per 24 h causing reductions in response to attractant-baited traps by *D. brevicomis*, *D. ponderosae*, and *I. pini* of 60, 71, and 29%, respectively.

The antennal and behavioural activity of green leaf alcohols found here supports the hypothesis of Dickens et al. (1992) that GLVs are used by scolytids in host selection. GLVs may also help MPBs to fly above the deciduous understorey (Borden et al. 1986; Safranyik et al. 1992). Borden et al. (1986) reported that MPB tree baits placed on lodgepole pines below the level of a dense understorey of Sitka alder, *Alnus sinuata* (Regel) Rydb., were ineffective at inducing mass-attack.

Aspen Volatiles as Disruptants

In Exp. 7, aspen bolts did not significantly interrupt the response of MPB to attractant baited traps. This result contrasts with that of Schroeder (1992) who showed significant reductions in response by *T. piniperda* and *H. palliatus* when bolts of aspen, *Populus tremula* L., or birch, *Betula pendula* Roth, were hung adjacent to traps baited with the weakly-attractive host kairomone ethanol. It may be that the MPB lures are so strong that they overpower any disruptive stimulus.

While steam distillations of quaking aspen bark yielded low amounts of volatile oils (≈243 μg per gram bark, wet weight), aspen is usually found growing in clonal groups which could provide a quite powerful olfactory stimulus. Testing of the four antenally active compounds from trembling aspen (Fig. 3) at various release rates may resolve the question as to whether or not olfactory stimuli are important in recognition of trembling aspen as a non-host for the MPB. Visual (Shepherd 1966), tactile (Shepherd 1965) and gustatory (Raffa and Berryman 1982) cues may also play a part in host specificity by the MPB.

Associated Insects

Trypodendron lineatum was significantly attracted in Exp. 1 and 2 to all semiochemical treatments when compared to the blank trap (Figs. 11,12). This finding adds to the growing body of evidence suggesting that ambrosia beetles use bark beetle pheromones in host selection (Benz et al. 1986; Setter and Borden 1992). Subsequent experiments should determine what components of the semiochemical blends are actively attracting *T. lineatum*.

Both *Enoclerus sphegeus* (F.) and *Thanasimus undatulus* (Say), clerid predators of the MPB (Furniss and Carolin 1977), were captured in Exp. 4 (Fig. 13). *E. sphegeus* responded significantly only to the treatments with MPB lures and GLV alcohols in the traps, whereas all semiochemical treatments caught significantly more *T. undatulus* than blank traps (orthogonal contrasts, P=0.004). Thirty-one *T. undatulus* were also captured in Exp. 5, too few to reveal a difference between treatments. These results suggest that neither *E. sphegeus* nor *T. undatulus* are disrupted by GLVs, and that *E. sphegeus* may even be slightly attracted by six-carbon alcohols. Similarly, Hayes et al. (1994) reported no reduction of the response of *Thanasimus dubius* (F.), a predator of the southern pine beetle, to the attractant pheromone of *D. frontalis* in the presence of the disruptant estragole. In contrast, Schroeder (1992) found that predatory beetles, *Rhizophagus depressus* (F.), were interrupted in their response to ethanol by nonhost volatiles. While *T. undatulus* appeared to be unaffected by GLVs in Exp. 4, I found its response to be interrupted by the presence of GLVs in traps baited with lineatin (unpublished results), an aggregation semiochemical for *T. lineatum*. Both of these discrepancies may be a result of

FIG. 11. Response of *Trypodendron lineatum* in Exp. 1 to multiple funnel traps baited with MPB lures alone, and in combination with verbenone or three candidate antiaggregants. Bars associated with the same letter are not significantly different, Ryan-Einot-Gabriel-Welsch Multiple Q-test, $P < 0.05$, n=12. Abbreviations of stimuli as in Table 3.

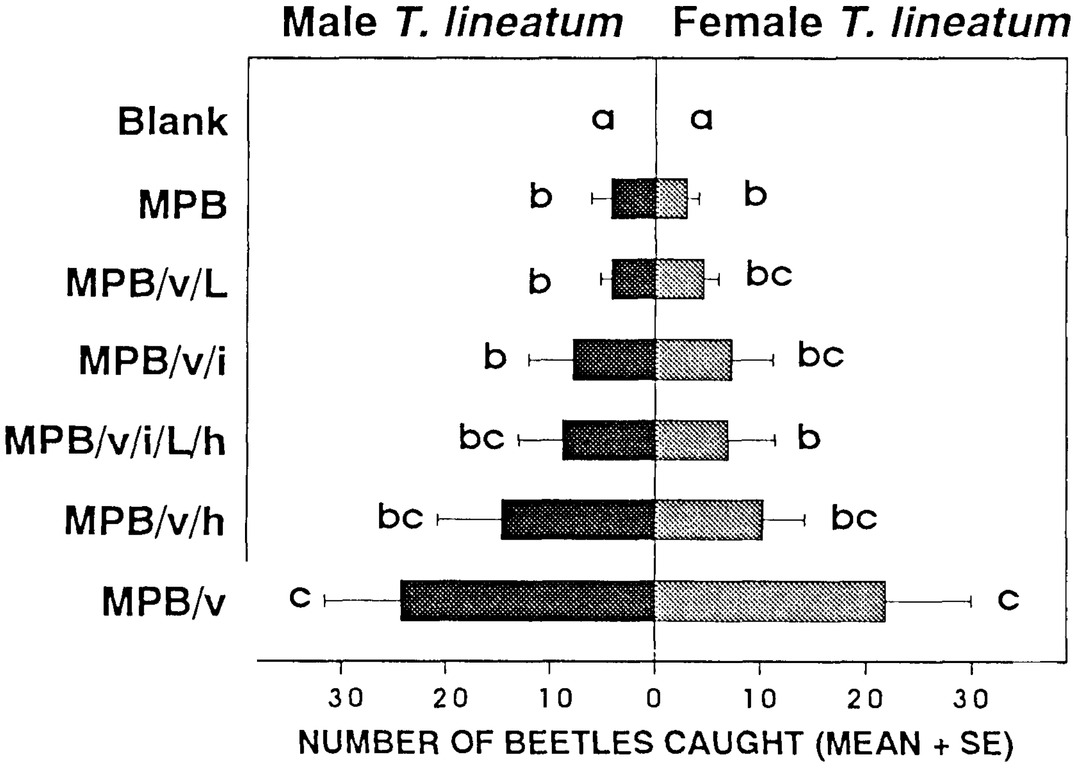

Male T. lineatum
Female T. lineatum
Blank
MPB
MPB/v/L
MPB/v/i
MPB/v/i/L/h
MPB/v/h
MPB/v
a
a
b
b
b
bc
b
bc
bc
b
bc
bc
c
c
30
20
10
0
10
20
30
NUMBER OF BEETLES CAUGHT (MEAN + SE)

FIG. 12. Response of *Trypodendron lineatum* in Exp. 2 to multiple funnel traps baited with MPB lures alone, and in combination with verbenone, pinocarvone, hexanal, or a mixture of green leaf volatiles released from a single device (Table 3). Bars associated with the same letter are not significantly different, Ryan-Einot-Gabriel-Welsch Multiple Q-test, $P < 0.05$, n=20. Abbreviations of stimuli as in Table 3.

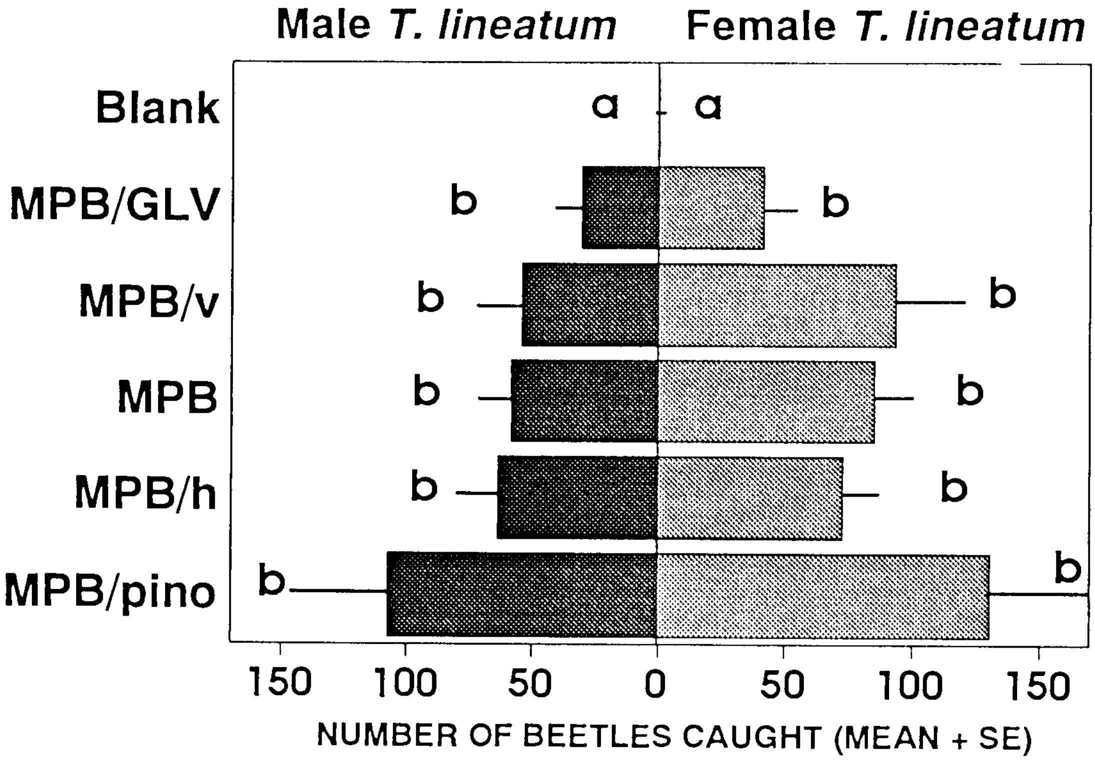
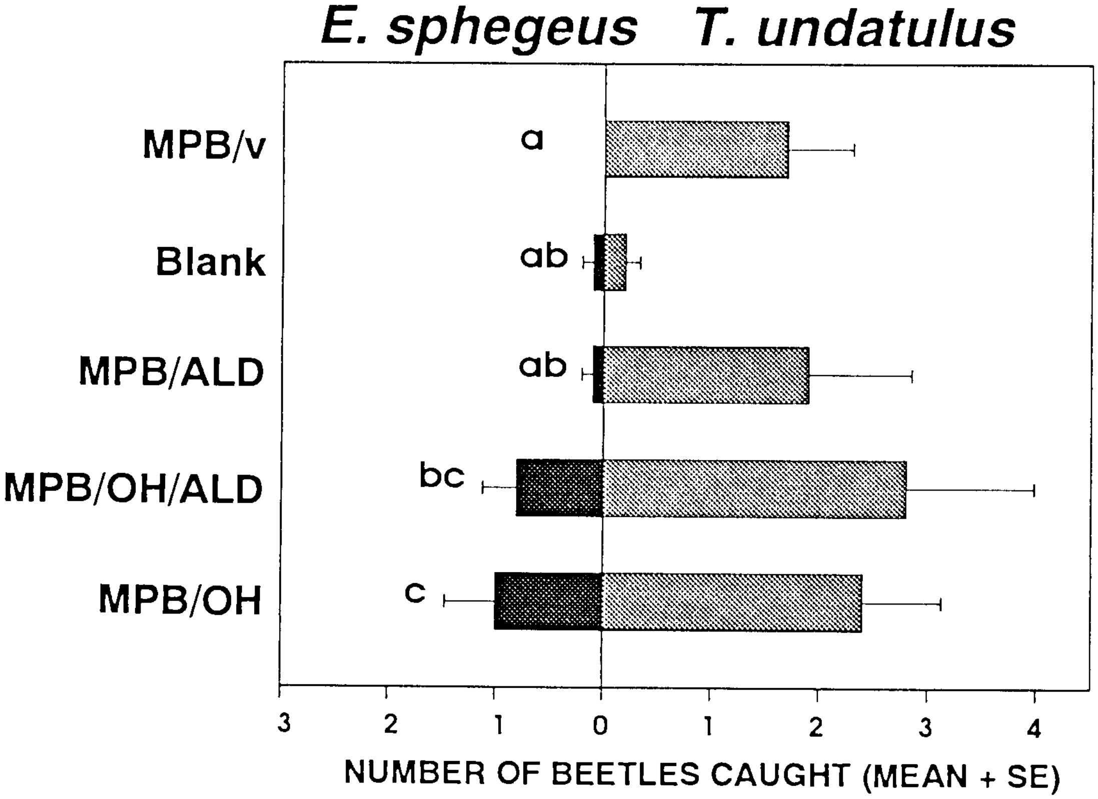

Male T. lineatum
Female T. lineatum
Blank
MPB/GLV
MPB/v
MPB
MPB/h
MPB/pino
a
a
b
b
b
b
b
b
b
b
b
b
150
100
50
0
50
100
150
NUMBER OF BEETLES CAUGHT (MEAN + SE)

FIG. 13. Response of 20 *Enoclerus sphegeus* and 90 *Thanasimus undatulus* in Exp. 4 to multiple funnel traps baited with MPB lures in combination with verbenone, or green leaf alcohols, aldehydes, or both. Bars associated with the same letter are not significantly different, Ryan-Einot-Gabriel-Welsch Multiple Q-test, *P*< 0.05, n=10. Orthogonal contrasts on *T. undatulus* catches indicated that all semiochemical treatments caught significantly more beetles than the blank. Abbreviations of stimuli as in Table 3.


E. sphegeus
T. undatulus
MPB/v
Blank
MPB/ALD
MPB/OH/ALD
MPB/OH
a
ab
ab
bc
c
3
2
1
0
1
2
3
4
NUMBER OF BEETLES CAUGHT (MEAN + SE)

a stronger attraction of predatory beetles to the MPB attractant than to either ethanol or lineatin.

The response of both species of predators to semiochemicals associated with the MPB is consistent with the accepted hypothesis that such semiochemicals are used as host-finding kairomones by entomophagous insects (Borden 1982). *E. sphegeus* was previously shown to respond to *exo*-brevicomin (Borden et al. 1987b), a major component of MPB lures. *T. undatulus* has been recorded to date responding only to the aggregation pheromone frontalin (Borden 1982).

TREE BAITING

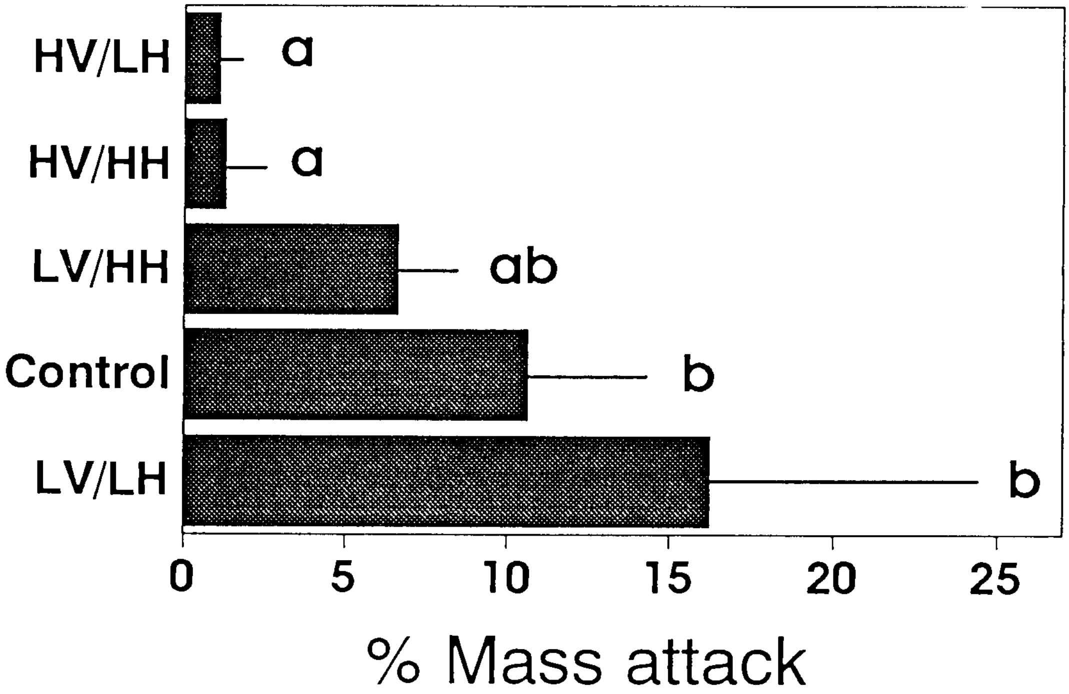
In 1993 (Exp. 8), attack density on centre trees baited with the MPB tree bait was not significantly different among treatments, although both treatments containing the high-verbenone dose prevented attack completely on centre trees in three blocks (Table 6). An analysis of percent mass attack (Fig. 14) indicated significantly lower attack for both high-verbenone treatments when compared to control blocks, with a possible reduced incidence of mass attack with hexanal released at 60 mg per 24 h. This apparent reduction in mass attack with hexanal is puzzling in the light of the inactivity of hexanal in trapping studies.

In Exp. 9 in 1994 there were no significant differences by any criterion. Possible reasons for the failure of Exp. 9 may be: 1) high population pressure from the 6.25% of trees attacked in 1993 (Table 5) that could have overwhelmed the treatments in 1994; and 2) inadequate release rates of GLVs to enhance the activity of verbenone released at a low rate, particularly if green leaf alcohols oxidized to aldehydes (Visser and Avé 1978).

TABLE 6. Summary of attack on centre trees baited with MPB attractants in Exp. 8. Treatments compare combinations of low and high hexanal with low and high verbenone in protecting stands from attack. Attack densities are not significantly different, ANOVA, $P > 0.05$, n=5. Abbreviations of stimuli as in Table 4.

Treatment	**Number of baited centre trees NOT attacked**	**Attack density per m^2 on baited, attacked trees (mean ± SE)**
Control	0	73.8 ± 10.9
LV/LH	0	81.2 ± 10.3
LV/HH	0	102.6 ± 9.4
HV/LH	2	73.3 ± 23.9
HV/HH	1	87.5 ± 13.1

FIG. 14. Percentage of trees mass attacked in an operational tree-baiting experiment in 1993 (Exp. 8). Treatments compare combinations of low and high hexanal with low and high verbenone doses in protecting stands from attack, *versus* an attractant control. Bars associated with the same letter are not significantly different, Ryan-Einot-Gabriel-Welsch Multiple Q-test, $P< 0.05$, n=5. Abbreviations of stimuli as in Table 4.


HV/LH
a
HV/HH
a
LV/HH
ab
Control
b
LV/LH
b
0
5
10
15
20
25
% Mass attack

CONCLUSIONS

Of the candidate antiaggregants tested in trapping experiments, ipsdienol and the green leaf alcohols were the most promising. Ipsdienol is expensive and may not be operationally viable except for protection of single, high-value trees. Green leaf alcohols are very effective disruptants in funnel-traps, and have the advantage of being cheap and easy to obtain, but more work is needed to bring these chemicals to an operational level for use against the MPB.

While the large-scale, operational experiments were not successful, the use of green leaf alcohols and verbenone may still prove to be effective in protecting single, high-value trees, as well as carefully selected stands. These tactics would be most effective in stands which, unlike my experimental stands, have little or no pre-existing attack. Due to the aggressive nature of the MPB, it may be necessary to integrate verbenone and GLVs with other tactics such as "push-pull" (Lindgren and Borden 1993) or competitive displacement (Borden 1992). The discovery of four antennally active chemicals in aspen bark volatiles (one of which, 1-hexanol, is a GLV) also holds promise for the elucidation of blends of non-host volatiles that may further enhance the disruptant effect of known antiaggregants.

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