Synomones of two sympatric species deter attack by the pine engraver, *Ips pini* (Coleoptera: Scolytidae)

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The capture of pine engravers, *Ips pini* (Say), in ipdienol-baited, multiple-funnel traps in British Columbia was significantly reduced when devices releasing ipsenol or verbenone were placed in the traps. These results suggest that ipsenol and verbenone are synomones released by *Ips latidens* (LeC.) and the mountain pine beetle, *Dendroctonus ponderosae* Hopk., respectively. When verbenone and ipsenol were released together from five stations 2 m apart on felled trees, at 50 and 1.5 mg per day per tree, respectively, there was a 66.7% reduction in the number of logs attacked and a 98.8% reduction in attack density. The same treatment caused a 74.1% reduction in attack density on standing trees surrounded by a 4 × 4 grid of 16 release devices at 5-m centres. The antiaggregant composition of verbenone plus ipsenol has considerable operational potential for use in precommercial thinnings and in areas where standing pines are of high value; e.g., in rural subdivisions, shelterbelts, and recreational forests.

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La capacité de capture des scolytes du pin, *Ips pini* (Say), par des pièges à cols multiples utilisant l'ipdiénol comme appât fut significativement réduite lorsque des dispositifs émettant du ipsénol ou de la verbénone étaient placés dans les pièges. Ces résultats semblent indiquer que l'ipsénol et la verbénone sont des synomones produites respectivement par *Ips latidens* (LeC.) et par le dendroctone du pin ponderosa, *Dendroctonus ponderosa* Hopk. Lorsque la verbénone et l'ipsénol étaient émis ensemble à des taux respectifs de 50 et 1,5 mg par jour par arbre, à partir de cinq stations distantes de 2 m et installées sur des arbres abattus, on a pu noter une diminution de 66,7% du nombre de billes attaquées et une baisse de 98,8% de la densité d'attaque. Le même traitement à l'aide de 16 émetteurs chimiques situés chacun à 5 m des centres d'une grille 4 × 4 entraîna une diminution de 74,1% de la densité d'attaque d'un groupe d'arbres sur pied. Les propriétés répulsives du complexe verbénone–ipsénol offre un grand potentiel d'utilisation dans le cas des éclaircies pré-commerciales et dans les zones de pins de grande valeur, par exemple, dans les subdivisions rurales, dans les bandes de protection et dans les forêts de récréation.

[Traduit par la rédaction]

Introduction

The pine engraver, *Ips pini* (Say), infests pine trees of numerous species (Sartwell *et al.* 1971; Furniss and Carolin 1977). Large populations can build up in unused portions of trees killed by other bark beetles, e.g., the mountain pine beetle, *Dendroctonus ponderosae* Hopk., and in slash from windthrow, logging, or silvicultural operations. When populations rise, *I. pini* may kill standing trees.

Outbreaks in standing trees are rapid, and the life cycle of *I. pini* is short, reducing the efficacy of direct control methods (Furniss and Carolin 1977). For example, removal of infested trees by logging may not be feasible prior to emergence of the brood beetles. Conventional, chemical insecticides can be used to protect trees or slash from attack, but their use is often environmentally questionable. Insecticides applied to the bark often do not kill beetles under the bark. Thus management tactics are employed to retain beetles in slash by continually laying down new host material (Livingston 1979), or to prevent outbreaks by disposing of slash, e.g., by piling and burning, and by prompt salvage of windthrown trees or those killed by other bark beetles. Such methods can be costly, time-consuming, logistically difficult, and not wholly effective.

Host selection and aggregation on fresh host trees or logs by *I. pini* is mediated by two semiochemicals: the aggregation pheromone ipsdienol (2-methyl-6-methylene-2,7-octadien-4-ol) and the host tree monoterpene β-phellandrene (3-methylene-6(-1-methylethyl) cyclohexene) (Plummer *et al.* 1976; Birch *et al.* 1980; Lanier *et al.* 1980; Miller and Borden 1990*a*). Similarly, mountain pine beetles mediate host selection and attack with three semiochemicals: myrcene (7-methyl-3-methylene-1,6-octadiene); *trans*-verbenol (*trans*-4,6,-trimethylbicyclo[3.1.1]hept-3-en-2-ol); and *exo*-brevicomin (*exo*-7-ethyl-5-methyl-6,8-dioxabicyclo[3.2.1] octane) (Pitman *et al.* 1968, 1969; Rudinsky *et al.* 1974; Billings *et al.* 1976; Libbey *et al.* 1985; Borden *et al.* 1987). *Ips latidens* (LeC.) utilizes ipsenol (2-methyl-6-methylene-7-octen-4-ol) and β-phellandrene (S.J. Seybold and D.L. Wood,[1] personal communication; Miller and Borden 1990*b*).

The mountain pine beetle employs verbenone (4,6,6-trimethylbicyclo[3.1.1]hept-3-en-2-one) as an antiaggregation pheromone that inhibits the response to myrcene, *trans*-verbenol, and *exo*-brevicomin and thereby regulates attack density (Ryker and Yandell 1983; Borden *et al.* 1987). Similarly, aggregation by the spruce beetle, *Ips typographus* L., in Europe is inhibited by verbenone and ipsenol (Bakke 1981; Schlyter *et al.* 1989). No pheromones are known that terminate the attack of *I. pini* or *I. latidens*.

An aerially applied, bead formulation of MCH (3-methyl-2-cyclohexen-1-one), an antiaggregation pheromone of the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopk., has been developed to protect felled Douglas-fir logs, *Pseudotsuga*

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menziesii (Mirb.) Franco, from attack (Furniss *et al.* 1981, 1982; McGregor *et al.* 1984). Verbenone released from bubble-cap devices affixed to trees can be used operationally to prevent or inhibit infestation by the mountain pine beetle (Amman *et al.* 1989; Lindgren *et al.* 1989*a*; Schmitz 1989). Similarly, MCH in bubble caps can protect felled Douglas-fir and spruce trees from Douglas-fir beetles and spruce beetles, *Dendroctonus rufipennis* (Kby.), respectively (Lindgren *et al.* 1988, 1989*b*).

Several instances of interspecific, semiochemical-based communication by bark beetles have been documented (Borden 1982; Byers 1989). In Californian forests of ponderosa pine, *Pinus ponderosa* Laws., *S*-(−)-ipsenol (Birch and Light 1977; Birch *et al.* 1977) and *S*-(+)-ipsdienol (Birch *et al.* 1980) produced by *Ips paraconfusus* Lanier are inhibitory to *I. pini*. Conversely, *R*-(−)-ipsdienol produced by *I. pini* is inhibitory to *I. paraconfusus* (Light and Birch 1979). This mutual inhibition of response by synomones, semiochemicals that are "adaptively favorable to both the emitter and the receiver" (Nordlund 1981), apparently serves to reserve a host log for the first arriving species (Birch and Wood 1975).

Mutual inhibition of response between *I. paraconfusus* and the western pine beetle, *Dendroctonus brevicomis* LeC., probably segregates each species in distinct areas of the same host tree (Byers and Wood 1980). *S*-(−)ipsenol, *S*-(+)-ipsdienol, and *S*-*cis*-verbenol (*cis*-4,6,6-trimethylbicyclo[3.1.1]hept-3-en-2-ol) produced by *I. paraconfusus* were inhibitory to *D. brevicomis* at high concentrations in a laboratory olfactometer (Byers and Wood 1981), and verbenone released by *D. brevicomis* inhibited the orientation of *I. paraconfusus* to attractive logs (Byers and Wood 1980).

(±)-Ipsenol (hereafter referred to as ipsenol) has some promise in protecting logs from attack by *I. pini*. When released at 2 mg per day in Idaho, it reduced by 68% the response of *I. pini* to traps surrounding ponderosa pine logs containing 25 pheromone-producing males; ipsenol released at 0.3 mg per day was far less inhibitory (Furniss and Livingston 1979). Infestation of ponderosa pine logs containing pheromone-producing male *I. pini* in California was arrested by surrounding the logs with six devices, each releasing 1 mg per day of ipsenol; no protective effect was obtained when the ipsenol release rate was reduced tenfold (Birch and Light 1977).

Our overall objective was to develop a semiochemical-based method of deterring attack by *I. pini*, without promoting attack by its associates, *D. ponderosae* and *I. latidens*. Our specific objectives were to test the following hypotheses; (*i*) that ipsenol has the same deterrent effect on northern populations of *I. pini* in a lodgepole pine ecosystem that it has in ponderosa pine forests in Idaho and California; (*ii*) that verbenone produced by *D. ponderosae* is a synomone that deters attack by *I. pini*; and (*iii*) that verbenone and ipsenol together are a more effective deterrent to *I. pini* than either one alone.

Material and methods

Five experiments were conducted in 1988 and 1989 in forests of lodgepole pine, *Pinus contorta* var. *latifolia* Engelmann, in the interior of British Columbia.

Trapping experiments

Experiments 1 and 2 were conducted near Princeton, British Columbia: from 18 July to 9 August 1988 (expt. 1) and 2–26 September 1989 (expt. 2).

In expt. 1 (±)-ipsdienol (hereafter referred to as ipsdienol) and ipsenol (chemical purities 97%) were obtained from Phero Tech Inc., Vancouver, British Columbia. Resease devices consisted of lengths of C-flex® tubing (i.d. = 1.6 mm; o.d. = 3.2 mm) (Concept Inc., Clearwater, Fla.) filled with solutions of either ipsdienol or ipsenol in ethanol. Lengths of C-flex and concentrations of solutions were varied to obtain a range of release rates determined in the laboratory at 24°C. Eight-unit, multiple-funnel traps (Lindgren 1983) were suspended between trees by rope. They were spaced 10–15 m apart within a replicate, and replicates were at least 100 m apart. There were five replicates of six traps each in a randomized, complete block layout, with six treatments comprising ipsdienol alone released at 0.6 mg per day, or with ipsenol at 0.06, 0.18, 0.6, 1.8, or 6.0 mg per day.

In expt. 2, bubble-cap lures containing either ipsdienol or verbenone (chemical purity 98%) were obtained from Phero Tech Inc. The release rates of ipsdienol and verbenone were approximately 0.3 and 10 mg per day, respectively. Eight replicates of four traps each were deployed as in expt. 1. The treatments in a randomized block layout were as follows: (*i*) unbaited control; (*ii*) verbenone alone; (*iii*) ipsdienol alone; and (*iv*) verbenone with ipsdienol.

Captured beetles were preserved in 70% ethanol, sexed (Lanier and Cameron 1969), and counted. Catch data were transformed by $\ln(y + 1)$ to correct for heteroscedasticity and were then subjected to ANOVA and Duncan's multiple range test ($\alpha = 0.05$) (SAS Institute Inc. 1985).

Host selection experiments

Experiments 3–5 were conducted in 1989 in stands of pure lodgepole pine approximately 90 km west of Williams Lake, British Columbia: from 2 May to 28 June (expt. 3), 25 July to 23 August (expt. 4), and 27 July to 7 October (expt. 5).

In expt. 3, 80 lodgepole pines, 15–20 cm diameter at breast height (DBH, = 1.3 m), at 33-m centres were selected. They were felled on 2–3 May. On 4 May they were marked at 0.5-m intervals, and at 4- and 6-m positions, semiochemical-loaded bubble caps (Phero Tech Inc.) were affixed in eight treatments in a randomized, complete block design as follows: (*i*) ipsdienol released at 0.6 mg per day from two bubble caps; (*ii*) ipsdienol as above, with ipsenol released at 0.6 mg per day from two bubble caps; (*iii*) ipsdienol with verbenone released at 20 mg per day from two bubble caps; (*iv*) ipsdienol, with ipsenol and verbenone; (*v*) untreated controls; (*vi*) ipsenol; (*vii*) verbenone; and (*viii*) ipsenol with verbenone. There were 10 replicates (logs) per treatment.

On 25 May, each log was inspected, and any *I. pini* attack, as evidenced externally by frass was marked by a pin with a colored head. On 26–28 June, a final tally of attacks from the base to 10 m up the logs was done. To assess the accuracy of the pinning procedure, and to determine if there was any effect of treatment on brood production, the two 0.5 m long sections of log on either side of the semiochemical treatment at 4 m were sawn free from five logs for each treatment. If there were <2 attacks visible externally on these sections, samples were taken at 6 m, or failing that, at the closest point at which there were >2 attacks. One of the 0.5 m long cut sections was debarked, and all attacks were tallied according to species. The other section was placed in a sealed, cardboard, rearing box with a 454-mL glass jar emplaced in one wall to capture emergent beetles. The boxes were held outdoors for 60 days at Williams Lake in a partially shaded location. Emergent beetles in the glass jars and in debris in the boxes were separated by species and sex and counted.

Experiment 4 was at the same site as expt. 3 to ensure a large supply of beetles, but no newly felled tree was closer than 15 m to a brood log. Thirty groups of three lodgepole pine trees each were felled (total = 90 trees, DBH 15–20 cm). The trees in each group were felled so that they lay close together on the ground, often crisscrossing. There were three treatments deployed in a randomized block design as follows: (*i*) untreated controls; (*ii*) verbenone; and (*iii*) verbenone with ipsenol. Verbenone was released from bubble caps (Phero Tech Inc.) at 10 mg per day. Ipsenol was released from bubble caps at 0.3 mg per day. One device, containing the appropriate compound, was stapled to the northerly, or most shady, side of each of the three

TABLE 1. Effect of ipsenol on the response of *Ips pini* to ipsdienol-baited multiple-funnel traps near Princeton, British Columbia, 16 July to 9 August 1988 (n = 5)

Treatment	No. of *Ips pini* captured ($\bar{x}$±SE)*
Ipsdienol	83.6±37.0*a*
Ipsdienol + ipsenol	
0.06 mg per day	38.0±14.0*b*
0.18 mg per day	4.2±0.7*c*
0.6 mg per day	6.0±2.3*c*
1.8 mg per day	2.0±1.8*c*
6.0 mg per day	0.8±0.8*c*

*There was no significant difference in sex ratio of beetles captured when ipsdienol alone was used or ipsdienol with ipsenol at 0.06 mg per day (t-test, $P > 0.23$). Too few beetles were captured to allow sex ratio analysis when other baits were used. Means followed by the same letter are not significantly different; $P < 0.05$, Duncan's multiple range test on data transformed by $\ln(y + 1)$.

TABLE 2. Effect of verbenone on the response of *Ips pini* to multiple-funnel traps near Princeton, British Columbia, 2–26 September 1989 (n = 8)

Treatment	No. of *Ips pini* captured ($\bar{x}$±SE)*
Unbaited control	0.8±0.3*a*
Verbenone	0.4±0.2*a*
Ipsdienol	99.4±16.7*c*
Verbenone + ipsdienol	33.3±9.3*b*

*There was no significant difference in sex ratio of beetles captured between treatments with or without verbenone (t-test, $P > 0.39$). Means followed by the same letter are not significantly different; $P < 0.05$, Duncan's multiple range test on data transformed by $\ln(y + 1)$.

logs at 1, 3, 5, 7, and 9 m from the base. Thus verbenone was released at 50 mg per day per log, and ipsenol at 1.5 mg per log. In the approximate geographic centre of each group of three trees, a wooden stake was driven into the ground. A single ipsdienol bait, identical with that used in expt. 3 and releasing ipsdienol at 0.3 mg per day, was stapled to each stake at 1 m above ground. This bait was intended to draw *I. pini* close to the logs, where they would then be faced with a yes–no decision as to their suitability as hosts. On 22–23 August, attacks as evidenced by frass piles were marked with colored pins and counted up to 10 m from the base of each log.

In the final experiment, 30 standing lodgepole pines (DBH 15–20 cm) were selected at 50-m centres. A single ipsdienol bubble cap bait releasing ipsdienol at 0.3 mg per day was affixed 2–2.5 m high on the north side of each tree. This bait ensured that the tree would be attractive to *I. pini*. The 30 trees were divided into 10 replicates of three treatments laid out in a randomized block design. Ten attractive control trees received no further treatment. A 4 × 4 grid was laid out at 5-m centres around each of the remaining trees. At each centre a single verbenone bubble cap releasing verbenone at 10 mg per day, or a verbenone bubble cap plus an ipsenol bubble cap releasing ipsenol at 0.3 mg per day, was stapled to the north side of the nearest available object (usually a lodgepole pine tree) at maximum reach from the ground. Thus each ipsdienol-baited tree, except for the controls, was surrounded by 16 semiochemical stations in a 15 × 15 m block. *Ips pini* were challenged to fly through the semiochemical "blanket" to reach the baited tree. The experiment was evaluated on 7–9 October by counting all *I. pini* attacks on each of the ipsdienol-baited trees.

Attack densities and emergence levels in expt. 3 were transformed by $\sqrt{y + 0.5}$ to correct for heteroscedasticity. Means in expts. 3–5 were subjected to ANOVA and the Newman–Keuls test ($\alpha = 0.05$) (SAS Institute Inc.).

Results and discussions

Trapping experiments

In expt. 1, ipsenol substantially reduced the capture of *I. pini* in ipsdienol-baited traps at all doses >0.18 mg per day (Table 1). This result is consistent with data for California and Idaho populations on ponderosa pine (Birch and Light 1977; Birch *et al.* 1977; Furniss and Livingston 1979). It suggests that wherever *I. pini* competes with a species that produces ipsenol (e.g., *Ips paraconfusus* in California, *I. latidens* in Idaho and British Columbia), there is a good likelihood that ipsenol will act as an inhibitor and could be used to reduce or prevent attacks by *I. pini*.

Verbenone also substantially reduced the capture of *I. pini* in ipsdienol-baited traps (Table 2). Thus verbenone could serve to reserve the major portion of the bole of a tree for *D. ponderosae* and to direct *I. pini* to other parts of the tree, much as would occur between *D. brevicomis* and *I. paraconfusus* (Byers and Wood 1980). Verbenone is also produced by male *I. pini* (Lanier *et al.* 1980), but it is not known if it functions as an antiaggregation pheromone in this species. As for ipsenol, this result suggests that the probable biological role of verbenone in resource partitioning could be exploited by using it to reduce or prevent attacks by *I. pini*.

Host selection experiments

There was a strong relationship between external counts of *I. pini* attack and the number of verified galleries in five 0.5 m long logs debarked for each treatment in expt. 3 ($r^2 = 0.843$, $P < 0.001$, $y = 0.42 + 1.06x$, Minitab Rel. 5.1.1, Minitab, Inc., State College, Penn.). Therefore, counting galleries on the basis of external evidence is a good indicator of actual attack density.

In expt. 3, the combination of ipsenol and verbenone clearly reduced the attack densities on ipsdienol-baited logs (Fig. 1). The effect was verified with debarked logs, for which the attack density on, and emergence from, logs treated with ipsenol plus verbenone were significantly lower than for both ipsdienol-baited and untreated control logs (Table 3). In no case was there a pronounced increase in emergence that might have reflected a differentially greater reproductive success at lower than at higher attack densities.

The results (Fig. 1, Table 3) suggest that verbenone alone might be an effective treatment. However, no protective effect was achieved with ipsenol alone, confirming the results of Birch and Light (1977), but with ipsenol released at a biologically realistic rate of 1.2 mg per day per log. Because the candidate antiaggregants were released only at 4- and 6-m positions on the 10 m long logs, it is not surprising that the logs were colonized, probably beginning at points where the odor of any released compounds was lowest. The results led us to retest the hypotheses that verbenone alone or the combination of verbenone plus ipsenol could effectively deter attack by *I. pini*.

The ipsdienol baits in the centre of each three-log plot in expt. 4 drew beetles into the area, after which they heavily attacked all 30 of the untreated control and verbenone-treated logs (Fig. 2) (note the higher attack densities on control logs than in Fig. 1). Despite the presence of the ipsdienol baits, only a third of the logs treated with verbenone plus ipsenol

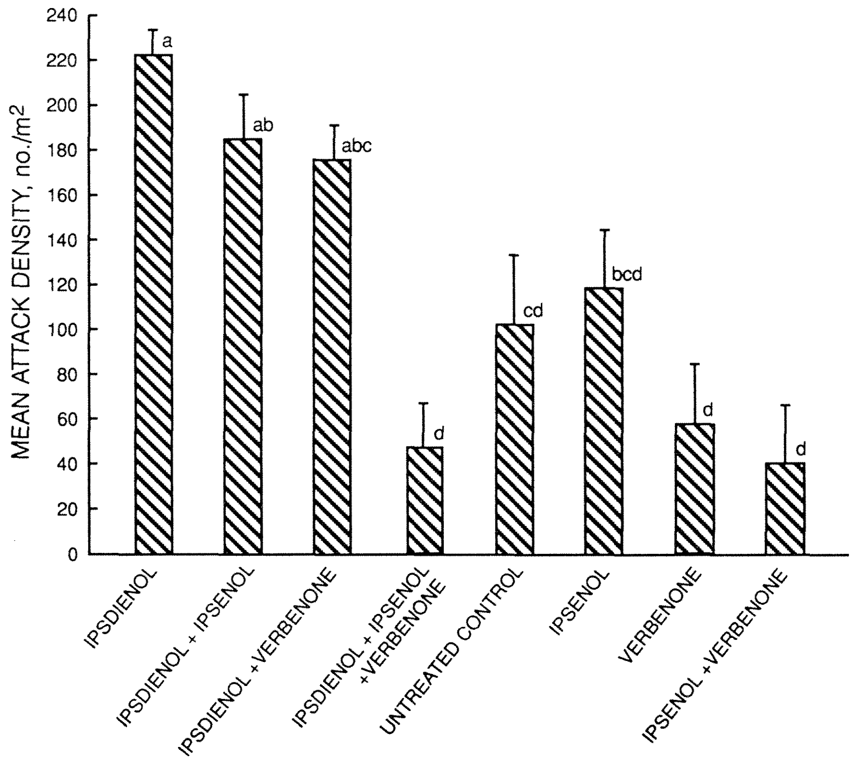

FIG. 1. Ranked attack densities by *Ips pini* on 10 m long lodgepole pine logs bearing bubble-cap devices releasing ipsdienol, ipsenol, verbenone, or combinations thereof, 4 May – 28 June 1989, Williams Lake Forest District, British Columbia (n = 10). Means with the same letter are not significantly different; Newman–Keuls test, $P < 0.05$. One standard error is shown for each mean.

TABLE 3. Density of *Ips pini* attacks counted after debarking, and number of emergent beetles, from adjacent 0.5 m long log sections taken from five trees for each treatment in experiment 3

Treatment	Attack density, no. per m^2 ($\bar{x}$±SE)*	No. of emergent beetles per m^2 ($\bar{x}$±SE)*	
		Males	Females
Ipsdienol	142.6±9.7*a*	74.7±10.1*a*	178.2±33.8*a*
Ipsdienol + ipsenol	96.4±7.3*abc*	62.2±17.9*a*	182.9±47.8*a*
Ipsdienol + verbenone	121.6±42.3*ab*	78.2±31.3*a*	171.5±52.2*a*
Ipsdienol + ipsenol + verbenone	19.5±11.4*cd*	22.4±14.4*ab*	37.0±21.5*ab*
Untreated control	103.4±17.5*abc*	58.3±12.4*a*	165.6±51.9*a*
Ipsenol	105.5±7.8*abc*	69.6±16.6*a*	172.4±44.4*a*
Verbenone	50.6±33.8*bcd*	21.3±13.4*ab*	46.5±37.9*ab*
Ipsenol + verbenone	6.0±4.5*d*	1.1±1.1*b*	0.0±0.0*b*

*Means within a column followed by the same letter are not significantly different; Newman–Keuls test, $P < 0.05$.

were attacked, and these at such low densities that the attack was inconsequential (Fig. 2). The attack would probably have been even less if the ipsdienol bait had been absent, as in an operational treatment.

On standing, control trees in expt. 5, induced attack was low because the trees resisted invasion by *I. pini*. However, they sustained an average of 5.8 attacks, mostly around the ipsdienol baits (Table 4). Grid treatments with verbenone alone, at 5-m centres, or with the combination of verbenone plus ipsenol, reduced the *I. pini* attack by 70.7 or 74.1%, respectively. Either treatment might be used to reduce or prevent attack by *I. pini* on standing pine trees, but it is likely that verbenone with ipsenol would be the most effective treatment in countering any sources of attractive ipsdienol set up by attacking beetles that broke through the antiaggregant grid.

Biological and practical implications

When faced with the bogus semiochemical message that a potential host was infested by either *I. latidens* producing ipsenol, or mountain pine beetles producing verbenone, there was significant inhibition of attack (Tables 1 and 2). These semiochemicals, therefore, could function as synomones (Nordlund 1981) involved in resource partitioning. They

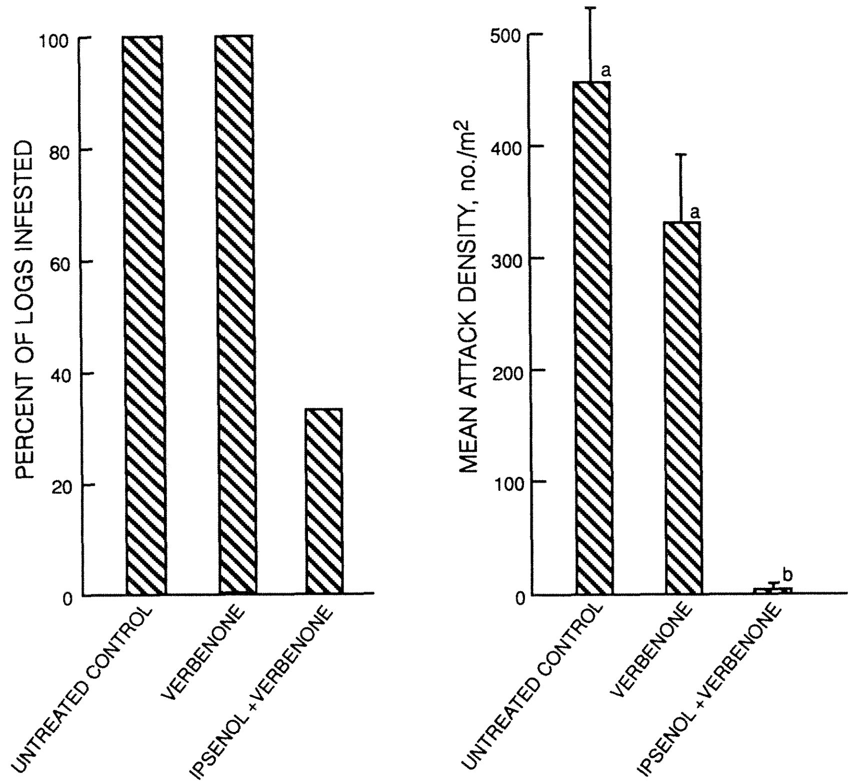

FIG. 2. Attack by *Ips pini* on 10 m long lodgepole pine logs treated with potential antiaggregants, 27 July – 23 August 1989, Williams Lake Forest District, British Columbia. There were 30 logs in 10 replicates of three logs each for each treatment. Means with the same letter are not significantly different; Newman–Keuls test, $P < 0.05$. One standard error is shown for each mean.

TABLE 4. Attack by *Ips pini* on standing lodgepole pine trees treated with ipsdienol and surrounded by 16 stations at 5-m centres, from which potential antiaggregants were released, 27 July – 7 October 1989, Williams Lake Forest District, British Columbia ($n = 10$)

Treatment	No. of attacks on ipsdienol-baited trees ($\bar{x}$±SE)*
Ipsdienol-baited control	5.8±1.0*a*
Ipsdienol-baited tree surrounded by 16 verbenone stations	1.7±0.6*b*
Ipsdienol-baited tree surrounded by 16 verbenone + ipsenol stations	1.5±0.6*b*

*Means followed by the same letter are not significantly different; Newman–Keuls test, $P < 0.05$.

would allow the producer to deter attack by a potential competitor for a host in which the former was already established and would allow the perceiver to avoid competition (Light *et al.* 1983; Rankin and Borden 1991) with an already-established species.

Deployment of a blend of ipsenol and verbenone, which is probably rare in nature, apparently created an unnatural situation, in which *I. pini* must have perceived that a potential host was infested by potential competitors of two species (Figs. 1 and 2; Tables 3 and 4). Thus the strength of the deterrent stimulus was unnaturally high and very effective at deterring attack (Figs. 2 and 3). This double-stimulus effect is different from that on the European *I. typographus*, for which verbenone is an antiaggregation pheromone, and ipsenol is most probably a synomone produced by sympatric *Ips* spp. (Schlyter *et al.* 1989). It is different again from that on *D. brevicomis*, which is deterred from responding to attractive semiochemicals by a blend of verbenone and ipsdienol, both of which may have intra- and inter-specific effects (Paine and Hanlon 1991).

The effective deterrence achieved with verbenone and ipsenol suggests that a blend of these two semiochemicals could be developed for operational use to deter attack by *I. pini* (Borden *et al.* 1990). For example, in a precommerical thinning that left abundant host material on the ground, a broadcast application of pellets releasing verbenone and ipsenol might be used to prevent attack by *I. pini* and consequent buildup of populations large enough to threaten the remaining high-value crop trees. On-tree devices releasing verbenone and ipsenol, similar to those used to release verbenone to deter attack by the mountain pine beetle (Amman *et al.* 1989; Lindgren *et al.* 1989*a*; Schmitz 1989), might also be used to protect standing trees from attack following precommercial thinning.

Such devices might also be used to disperse beetles away from natural outbreaks in standing trees, and also from vulnerable trees in disturbed areas, e.g., recreational forests, rural subdivisions, or unnatural plantings, such as shelterbelts. Of significance is the fact that verbenone is repellent to *I. latidens* (D.R. Miller, unpublished). Therefore, a treatment incorporating verbenone with ipsenol would overcome the risk of inducing unwanted attacks (Borden 1989) by sympatric, ipsenol-responding species like *I. latidens*.

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