Pheromone interruption of pine engraver, *Ips pini*, by pheromones of mountain pine beetle, *Dendroctonus ponderosae* (Coleoptera: Scolytidae)

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ABSTRACT

The effect of pheromones of *Dendroctonus ponderosae* Hopkins on the attraction of *Ips pini* (Say) to its pheromone, ipsdienol, was investigated in stands of lodgepole pine. The mixture of *cis*- and *trans*-verbenol significantly reduced catches of *I. pini* in traps baited with ipsdienol at three locations in British Columbia. *exo*-Brevicomin had no effect on catches of *I. pini*, irrespective of the enantiomeric composition of *exo*-brevicomin. Ipsdienol did not significantly reduce the attraction of *D. ponderosae* to traps baited with *cis*- and *trans*-verbenol, and (±)-*exo*-brevicomin.

Key Words: Coleoptera, Scolytidae, *Ips pini*, *Dendroctonus ponderosae*, pheromone interruption, synomone, *exo*-brevicomin, *cis*-verbenol, *trans*-verbenol, ipsdienol

INTRODUCTION

The pine engraver, *Ips pini* (Say), and the mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae), are common bark beetle species in stands of lodgepole pine, *Pinus contorta* var. *latifolia* Engelmann (Pinaceae), in western North America (Furniss and Carolin 1980). *Ips pini* breeds in the phloem tissue of dead, dying or downed lodgepole pines (Furniss and Carolin 1980). *Dendroctonus ponderosae* breeds in the healthy phloem tissue of live, standing pine trees (Unger 1993). During the past 80 years, *D. ponderosae* has killed more than 500 million pine trees in British Columbia alone (Unger 1993). Densities of *D. ponderosae* galleries on infested material range from 10 – 261/m^2 with optimal brood production densities of 75 – 85/m^2 (Safranyik and Linton 1998). Population levels of *I. pini* can build up during drought conditions, or following catastrophic events such as logging, fire, windthrow, or epidemics of *D. ponderosae*, with attack densities reaching 200-300/m^2 (Safranyik *et al.* 1996). At times, populations of *I. pini* may be sufficiently large that they initiate attacks on live, standing trees. Two years after the 1988 fire in the greater Yellowstone Park area, 44 % of the lodgepole pines were infested by *I. pini* (Amman and Ryan 1991).

In spite of their abundance and similarity in phloem resource requirements, these two species maintain ecological and reproductive isolation by assembling on host material in large non-overlapping, single-species aggregations. *Dendroctonus ponderosae* generally infests the lower bole of standing trees whereas *I. pini* attacks mid- and upper-bole regions, or the entire tree bole in the absence of *D. ponderosae* (Furniss and Carolin 1980). Separation of aggregations seems to be facilitated by semiochemicals. *Ips pini* uses ipsdienol (2-methyl-6-methylene-2,7-octadien-4-ol) as an aggregation pheromone (Birch *et al.* 1980; Lanier *et al.* 1980) with both sexes preferring a racemic blend throughout most

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of British Columbia (Miller *et al.* 1996). *Dendroctonus ponderosae* produces various semiochemicals and responds optimally to the combination of *exo*-brevicomin (*exo*-7-ethyl-5-methyl-6,8-dioxabicyclo[3.2.1]octane) and *cis*- and *trans*-verbenol (*cis*- and *trans*-4,6,6-trimethylbicyclo[3.1.1]hept-3-en-2-ol) (Borden *et al.* 1987; Miller and Lafontaine 1991).

Mutual interruption of pheromone attraction can enhance specificity in bark beetle aggregations (Byers 1989). Ipsdienol, produced by male *I. pini*, interrupts the attraction of *D. ponderosae* to the semiochemical blend of myrcene, (±)-*exo*-brevicomin, and *cis*- and *trans*-verbenol (Hunt and Borden 1988). The pheromone blend of (±)-*exo*-brevicomin and *cis*- and *trans*-verbenol, produced by *D. ponderosae*, interrupts the attraction of *I. pini* to its pheromone ipsdienol (Hunt and Borden 1988). The effects of individual components are not known. Therefore, our study assessed the effects of (+)-, (-)-, and (±)-*exo*-brevicomin, and the mix of *cis*- and *trans*-verbenol, separately and in combination, on the attraction of *I. pini* to ipsdienol. Specifically, we expected that all these compounds would reduce trap catches of male and female *I. pini* to ipsdienol-baited multiple-funnel traps.

MATERIALS AND METHODS

Chemicals and Release Devices. Phero Tech Inc. (Delta, British Columbia) supplied polyethylene bubble-cap lures containing a 13:87 mixture of *trans*- and *cis*-verbenol [both chemical purities 98%; both enantiomeric compositions 83:17 (-):(+)]. The verbenols were released at a combined rate of ca. 1.74 mg/d at 24 °C (determined by weight loss). In 1986, Phero Tech Inc. supplied laminar (±)-*exo*-brevicomin lures (chemical purity 98%). In 1987, each *exo*-brevicomin lure consisted of an open polyethylene microcentrifuge tube (400 mL) (Evergreen Scientific, Los Angeles, California) containing one 3-cm-long glass capillary tube (i.d. 13 mm; o.d. 15 mm) filled with *exo*-brevicomin. Phero Tech Inc. supplied (±)-*exo*-brevicomin (chemical purity 98%) and B.D. Johnston (Department of Chemistry, Simon Fraser University, Burnaby, British Columbia) supplied (+)-*exo*-brevicomin [chemical purity >99%; enantiomeric composition 97:3 (+):(-)] and (-)-*exo*-brevicomin [chemical purity >99%; enantiomeric composition 2:98 (+):(-)]. The release rates of *exo*-brevicomin were approximately 0.12 mg/d at 25 °C in 1986 (determined by collection of volatiles on Porapak-Q) and approximately 0.15 mg/d at 20 °C in 1987 (determined by weight loss).

(±)-Ipsdienol (chemical purity >98%) was obtained from Bedoukian Research Inc. (Danbury, Connecticut). In 1986, each ipsdienol lure consisted of eight Microcap® disposable pipettes (2μL) (Drummond Scientific Co., Broomall, Pennsylvania), each pipette sealed at one end, filled with (±)-ipsdienol and placed in an open polyethylene, microcentrifuge tube (1.8 mL) (Evergreen Scientific). In 1987, each ipsdienol lure consisted of a 10-cm length of C-flex® tubing (i.d. 1.6 mm; o.d. 3.2 mm) (Concept Inc., Clearwater, Florida), filled with an ethanol solution of (±)-ipsdienol, and heat-pressure sealed at both ends. The release rates of ipsdienol were approximately 0.08 mg/day at 24 °C in 1986 (determined by weight loss) and approximately 0.6 mg/day at 24 °C in 1987 (determined by collection of volatiles on Porapak-Q). Ethanol, used in the formulation to reduce the risk of polymerization of ipsdienol, is not attractive to *I. pini* (Miller 1990).

Experiments. Three experiments were conducted in 1986-1987. In all experiments, replicates of 8-unit Lindgren multiple-funnel traps (Phero Tech Inc.) were set in mature stands of lodgepole pine. Replicates were spaced at least 100 m apart, and traps were spaced 10-15 m apart within each replicate. Each trap was suspended by rope between trees such that the top of each trap was 1.3-1.5 m above ground level. No trap was within 2 m of any tree.

Experiment 1 tested the effect of ipsdienol, (±)-*exo*-brevicomin and verbenols on the attraction of *I. pini* and *D. ponderosae*. Ten replicates of five traps/replicate were set on 4 August, 1986, in regular pentagon formations near Princeton, British Columbia. The following treatments were randomly assigned within each replicate: (1) ipsdienol alone; (2) ipsdienol and (±)-*exo*-brevicomin; (3) ipsdienol and verbenols; (4) ipsdienol, (±)-*exo*-brevicomin and verbenols; and (5) (±)-*exo*-brevicomin and verbenols. The experiment was terminated on 3 September, 1986.

In 1987, experiment 2 tested the effect of (±)-*exo*-brevicomin and verbenols on the attraction of *I. pini* to ipsdienol at three sites in British Columbia: Princeton, Williams Lake and Radium. At each site, five replicates of four traps/replicate were set in grids of 2 X 2 on 16 July, 7 September, and 9 September, respectively. The following treatments were randomly assigned within each replicate: (1) ipsdienol alone; (2) ipsdienol and (±)-*exo*-brevicomin; (3) ipsdienol and verbenols; and (4) ipsdienol, (±)-*exo*-brevicomin and verbenols. Trapping was terminated at the three sites on 29 September, 3 October, and 1 October, 1987, respectively.

In 1987, experiment 3 tested the effect of enantiomeric composition of *exo*-brevicomin on the attraction of *I. pini* to ipsdienol. Five replicates of five traps/replicate were set on 20 August, each in a regular pentagon formation near Princeton, British Columbia. The following treatments were randomly assigned within each replicate: (1) ipsdienol alone; (2) ipsdienol and (-)-*exo*-brevicomin; (3) ipsdienol and (+)-*exo*-brevicomin; (4) ipsdienol and (±)-*exo*-brevicomin; and (5) ipsdienol and double (±)-*exo*-brevicomin. The separate release rates of (-)- and (+)-*exo*-brevicomin in treatments 2, 3 and 5 were identical whereas the combined release rate of both enantiomers in treatments 2, 3 and 4 were identical. The total release rate of *exo*-brevicomin in treatment 5 was twice that of *exo*-brevicomin in treatment 4. The experiment was terminated on 29 September, 1987.

Sexes of *I. pini* were determined using declivital characters (Wood 1982) whereas those of *D. ponderosae* were determined by dissection and examination of genitalia. Voucher specimens were deposited at the Entomology Museum, Simon Fraser University.

Statistical Analyses. The data were analyzed with the SYSTAT statistical package (version 8.0) (SPSS 1998). Trap catch data from all experiments were transformed by $\ln(Y+1)$ whereas sex ratio data (for catches > 5) were transformed by arcsine$\sqrt{(Y)}$. All data were analyzed by one-way ANOVA, followed by Fisher's least-significant-difference (LSD) multiple comparison test when $P < 0.05$. In addition, data from experiment 2 were analyzed by full-factorial three-way ANOVA using location, verbenol mix and *exo*-brevicomin as the model factors.

RESULTS

The treatments in experiment 1 had a significant effect on catches of *I. pini* ($F_{4,44}$ = 15.85, $P < 0.001$) and *D. ponderosae* ($F_{4,29}$ = 4.48, P = 0.006). Three replicates were excluded in the analyses for *D. ponderosae* because no beetles were captured in these replicates. The combination of (±)-*exo*-brevicomin and *cis*- and *trans*-verbenol significantly interrupted the attraction of *I. pini* to its pheromone ipsdienol, reducing mean catches of *I. pini* to levels similar to those in traps baited only with (±)-*exo*-brevicomin and *cis*- and *trans*-verbenol (Fig. 1). Mean catches in traps baited with either ipsdienol and (±)-*exo*-brevicomin or ipsdienol and the verbenol mixture were not significantly different from mean catches in traps baited only with ipsdienol. The response of *D. ponderosae* was the converse of *I. pini* with the highest catches in all traps baited with the verbenol mixture (Fig. 1). There was no significant effect of treatment on sex ratios for either *I. pini* ($F_{2,21}$ = 0.36, P = 0.705) or *D. ponderosae* ($F_{3,16}$ = 2.47, P = 0.099). The mean percentages (±SE)

of male *I. pini* and *D. ponderosae* in trap catches were 33 (± 3) % and 47 (± 3) %, respectively.

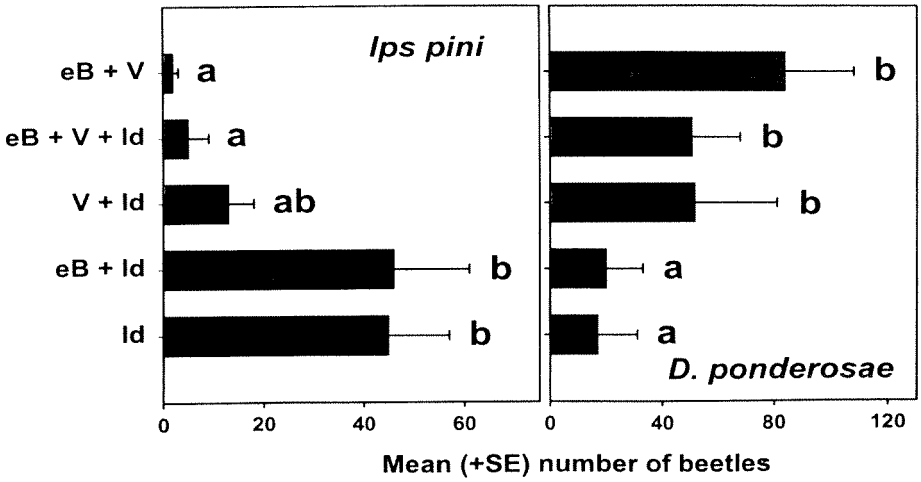

Figure 1. Effect of ipsdienol (Id), (±)-*exo*-brevicomin (eB), and *cis*- and *trans*-verbenol mixture (V) on the attraction of *Ips pini* and *Dendroctonus ponderosae* to multiple-funnel traps in experiment 1 in 1986 (N = 10). Mean trap catches, within the same figure, followed by the same letter are not significantly different at P = 0.05 (Fisher's LSD test).

In experiment 2, the verbenol mixture had a significant effect on catches of *I. pini* (Table 1). The effect was consistent for all three regions since no interaction term was significant. Catches of *I. pini* to ipsdienol-baited traps were significantly reduced by the verbenol mixture, with or without (±)-*exo*-brevicomin (Fig. 2). There was no significant effect of (±)-*exo*-brevicomin on trap catches (Table 1). In all three regions, catches of *I. pini* in traps baited with ipsdienol and (±)-*exo*-brevicomin were not significantly different from those in traps baited with ipsdienol alone (Fig. 2). There was no effect of treatment on sex ratios of *I. pini* in trap catches (Table 1). The mean (±SE) percentage of males in trap catches was 25 (± 1) %.

Table 1

Analysis of variance on effects of location (Princeton, Williams Lake, and Radium, BC), verbenol mixture, and (±)-*exo*-brevicomin on number and sex ratio of *Ips pini* responding to ipsdienol-baited multiple-funnel traps in 1987 (Experiment 2).

	Trap catch [a]			Proportion of males [b]		
Source	df	F	P	df	F	P
Location (A)	2	24.26	<0.001	2	0.63	0.539
Verbenol mix (B)	1	27.73	<0.001	1	0.06	0.809
(±)-*exo*-Brevicomin (C)	1	0.04	0.833	1	0.19	0.669
A * B	2	0.15	0.862	2	0.57	0.567
A * C	2	0.92	0.406	2	0.31	0.733
B * C	1	0.26	0.610	1	1.08	0.304
A * B * C	2	0.35	0.703	2	1.26	0.293
Error	48			47		

[a] Data transformed by ln(Y + 1).
[b] Data transformed by arcsine$\sqrt{(Y)}$.

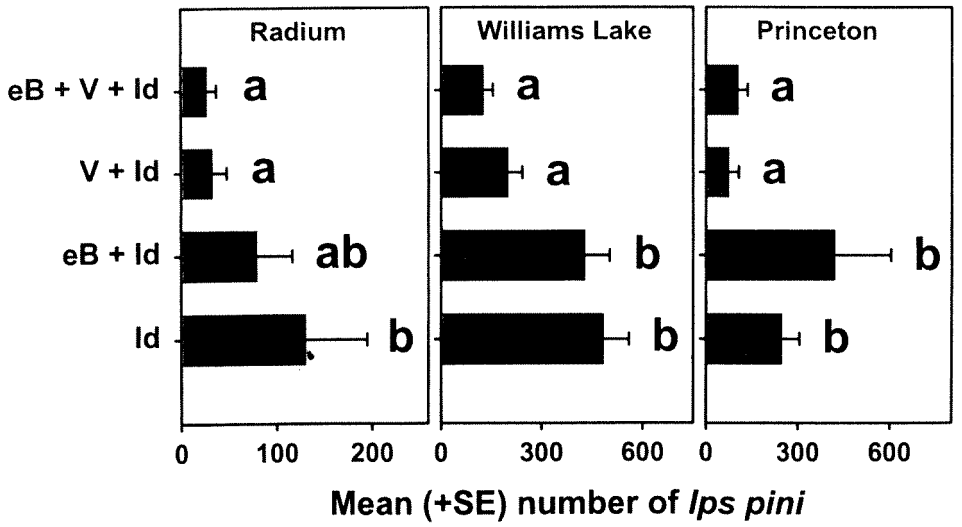

Figure 2. Effect of (±)-*exo*-brevicomin (eB) and *cis*- and *trans*-verbenol mixture (V) on the attraction of *Ips pini* to ipsdienol (Id) - baited multiple-funnel traps in experiment 2 in 1987 (N = 5). Mean trap catches, within the same figure, followed by the same letter are not significantly different at P = 0.05 (Fisher's LSD test).

In experiment 3, the enantiomeric composition of *exo*-brevicomin had no significant effect on trap catches of *I. pini* ($F_{4,20}$ = 0.54, P = 0.707) or sex ratio of captured *I. pini* ($F_{4,20}$ = 1.65, P = 0.202) (Fig. 3). The mean (±SE) percentage of males in trap catches was 27 (± 2) %.

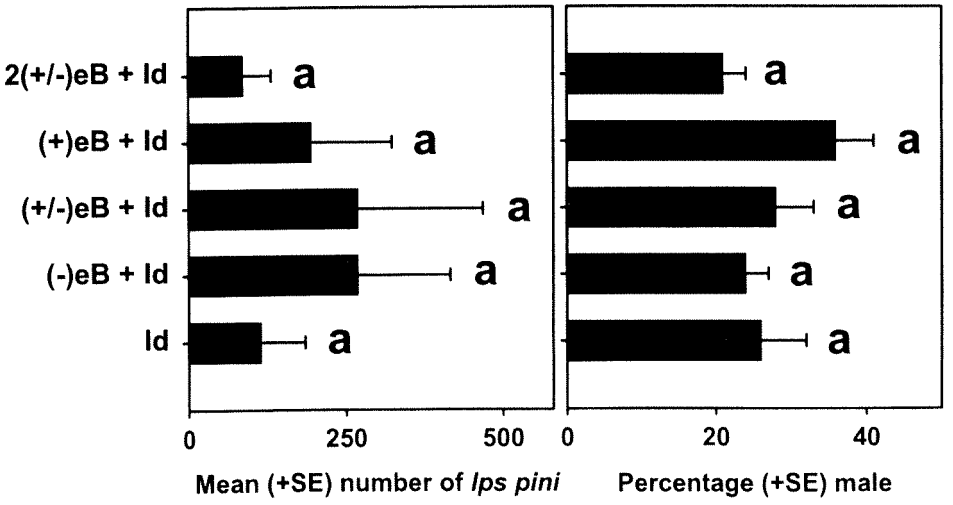

Figure 3. Effect of enantiomeric composition of *exo*-brevicomin (eB) on the attraction of *Ips pini* to ipsdienol (Id) - baited multiple-funnel traps in experiment 3 in 1987 (N = 5). Mean trap catches, within the same figure, followed by the same letter are not significantly different at P = 0.05 (Fisher's LSD test).

DISCUSSION

Bark beetles use semiochemicals to ensure ecological and reproductive isolation (Byers 1989). Host partitioning within the southern pine bark beetle guild of five species occurs through pheromone specificity and mutual interruption of pheromone attraction (Smith *et al.* 1993). The principal pheromones and synomones are ipsenol, ipsdienol, frontalin, verbenone, brevicomins and verbenols (Smith *et al.* 1993). Similarly in Europe, separation among six species of *Ips* DeGeer is maintained by pheromone blends of ipsenol, ipsdienol, amitinol, myrtenol, and verbenols (Kohnle *et al.* 1988, 1993).

The same phenomenon is apparent among western species of bark beetles in North America as well. Mutual interruption of pheromone response occurs between *I. pini* and *D. ponderosae* in stands of lodgepole pine in British Columbia. Our results substantiate prior work by Hunt and Borden (1988) demonstrating that the attraction of *I. pini* to its pheromone is interrupted by pheromones of *D. ponderosae*. Specifically, we found that attraction of *I. pini* to (±)-ipsdienol was clearly interrupted by the combination of *cis*- and *trans*-verbenol (Figs. 1-2).

Additional work is required to separate the effects of *cis*-verbenol and *trans*-verbenol, and their enantiomeric compositions, on the interruption of pheromone attraction by *I. pini*. Our work employed a 13:87 mix of *cis*- and *trans*-verbenol with an overall enantiomeric composition of 83:17 (-):(+), due to the lack of availability of pure compounds. Both *cis*- and *trans*-verbenol are used by *D. ponderosae* as aggregation pheromones (Miller and Lafontaine 1991) and likely have similar effects on the response of *I. pini* to its pheromone.

Exo-brevicomin had no effect on the attraction of *I. pini* to ipsdienol (Figs. 1-2). Pureswaran *et al.* (2000) demonstrated that *exo*-brevicomin significantly decreased catches of male *I. pini* to (±)-ipsdienol-baited multiple-funnel traps near Princeton, BC. There was no significant effect on catches of female *I. pini* (Pureswaran *et al.* 2000). It is possible that our results with *exo*-brevicomin were due to an inappropriate dose range. We used devices, which released *exo*-brevicomin at rates of 0.12-0.15 mg/d at 20-25 °C whereas Pureswaran *et al.* (2000) used devices, which released *exo*-brevicomin at a rate of ca. 3.1 mg/d at 25 °C.

The enantiomeric composition of *exo*-brevicomin had no effect on trap catches of *I. pini* (Fig. 3). Pureswaran *et al.* (2000) demonstrated antennal responses of male and female *I. pini* to (+)-*exo*-brevicomin and (+)-*endo*-brevicomin. The antipodes, (-)-*exo*-brevicomin and (-)-*endo*-brevicomin, elicited no response from *I. pini*. Further trials with *exo*-brevicomin should be conducted with higher release rates of the (+)-enantiomer since the lack of antennal activity with the (-)-enantiomer should correlate with a lack of field activity.

In contrast to Hunt and Borden (1988), ipsdienol had no effect on the attraction of *D. ponderosae* to the female-produced pheromones, *cis*- and *trans*-verbenol (Fig. 1). All our experiments were conducted in late summer (August and September) whereas Hunt and Borden (1988) demonstrated significant interruption in pheromone response in experiments conducted in July. Their experiments conducted in early August failed to demonstrate interruption of attraction of *D. ponderosae* to the blend of myrcene, *exo*-brevicomin, and *cis*- and *trans*-verbenol by ipsdienol. It is possible that discrimination by *D. ponderosae* differs during the season, possibly due to differential costs and benefits related to the onset of colder temperatures (Reid 1962). Since the egg and early larval stages are susceptible to high mortality from cold temperatures, beetles need to ensure that eggs hatch and develop to the cold-tolerant 3-rd and 4-th larval stages prior to the arrival of winter temperatures (Safranyik and Linton 1998). Additional work should be conducted on the effect of another *I. pini* pheromone, lanierone (2-hydroxy-4,4,6-trimethyl-2,5-cyclohexadien1-one), as an interruptant for *D. ponderosae*. Lanierone produced by male

I. pini (Teale *et al.* 1991) significantly increases catches of *I. pini* to ipsdienol-baited traps in British Columbia (Miller *et al.* 1997).

Semiochemical specificity and mutual interruption of pheromones in western pine forests is not limited to *I. pini* and *D. ponderosae*. More than 50 species of bark beetles have been reported on lodgepole pine, many of which are phloeophagous and maintain ecological and reproductive separation (Wood 1982). Attraction of *I. latidens* (LeConte) to its pheromone, ipsenol (2-methyl-6-methylene-7-octen-4-ol), is interrupted by (+)-ipsdienol (Miller and Borden 1992) whereas attraction of *I. pini* is interrupted by the pheromone of *I. latidens*, ipsenol (Borden *et al.* 1992). The attraction of *I. integer* (Eichhoff) to lanierone is interrupted by ipsdienol whereas the attraction of *I. pini* to ipsdienol is enhanced by lanierone (Miller *et al.* 1997). Mutual interruption of pheromone attraction also occurs between *I. pini* and *I. paraconfusus* Lanier (Birch and Wood 1975; Birch *et al.* 1980) and between *I. paraconfusus* and *D. brevicomis* LeConte (Byers and Wood 1980, 1981).

Semiochemical interruptants will play an important role in future integrated pest management programs for bark beetles (Borden *et al.* 1992). For example, interruptants can be used to minimize the likelihood that populations of *I. pini* build up in slash generated by thinning operations to such levels that they successfully attack and kill standing trees (Borden *et al.* 1992). Verbenone (4,6,6-trimethylbicyclo[3.1.1]hept-3-en-2-one), an antiaggregation pheromone produced by *D. ponderosae* (Borden *et al.* 1987), and ipsenol, a pheromone produced by *I. latidens* (Miller *et al.* 1991), interrupt the attraction of *I. pini* to its pheromone (Borden *et al.* 1992). The combination of verbenone and ipsenol resulted in a 67% reduction in the number of downed lodgepole pines attacked by *I. pini* and a 99% reduction in attack density (Borden *et al.* 1992).

A complete understanding of the role and impact of the various pheromones and kairomones is required to develop effective management programs. For example, the combination of the interruptants for *D. frontalis* Zimmermann, verbenone and *endo*- and *exo*-brevicomin, reduced the landings of *D. frontalis* on live loblolly pine by 84% with a 84% reduction in eggs laid (Payne and Richerson 1979). However, the treatment failed to prevent tree mortality due to an increase in attacks by another bark beetle, *I. avulsus* (Eichhoff).

The risks and consequences of interruptants should be carefully considered in management programs that facilitate interspecific competition to reduce the reproductive potential of a pest species. Significant reductions in survivorship of *D. frontalis* can occur by the practice of simply falling infested trees and abandoning them (Billings 1980). This fall-and-leave practice apparently increases levels of competition by secondary bark beetles, predation and parasitism (Billings 1980). Other researchers have used semiochemicals to induce similar levels of competition with bark beetles in western North America. Rankin and Borden (1991) used ipsdienol to induce attacks by *I. pini* on logs previously infested with *D. ponderosae*, resulting in a 73% reduction in progeny of *D. ponderosae*. Safranyik *et al.* (1998) obtained a 49% reduction in progeny of *D. ponderosae* by baiting standing lodgepole pine with *I. pini* pheromones, ipsdienol and lanierone, when baiting was conducted in September. In both studies, the attack densities of *D. ponderosae* between control and treated trees were not significantly different. However, Safranyik *et al.* (1998) found that baiting standing trees with *I. pini* pheromones in August resulted in a 53% reduction in attack density of *D. ponderosae* with no difference in mean progeny production between treated and control trees. Attractants used to initiate competition against a pest species such as *D. ponderosae* should be applied with due consideration to timing of application and appropriate combinations of semiochemicals.

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