VERTICAL DISPLACEMENT OF *IPS LATIDENS* AND *IPS PINI* (COLEOPTERA: SCOLYTIDAE) BY SEMIOCHEMICAL INTERRUPTION

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Abstract

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The effect of semiochemical interruptants was examined for *Ips latidens* (LeConte) and *Ips pini* (Say) using artificial trees (tall-traps) consisting of an array of seven Lindgren multiple-funnel traps suspended vertically on a rope ladder. *S*-(+)-Ipsdienol reduced the numbers of *I. latidens* captured in (±)-ipsenol-baited funnel traps relative to funnel traps immediately above them and to control tall-traps. The combination of (±)-*exo*-brevicomin and *cis*- and *trans*-verbenol reduced the numbers of *I. pini* captured in (±)-ipsdienol-baited funnel traps relative to funnel traps immediately above them and to control tall-traps. These results provide support for semiochemical-based pest-management tactics that utilize a point source of interruptant at the base of a tree while noting limitations in behavioural effects and efficacy.

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Résumé

Nous avons testé les effets d'inhibiteurs sémiochimiques chez *Ips latidens* (LeConte) et *Ips pini* (Say) en utilisant des arbres artificiels (arbres-pièges) composés de sept pièges Lindgren à plusieurs entonnoirs suspendus verticalement sur une échelle de corde. Le *S*-(+)-ipsdiénol a réduit le nombre de *I. latidens* capturés dans des pièges à entonnoirs garnis de (±)-ipsénol comparativement au nombre capturé dans les pièges à entonnoirs installés immédiatement au-dessus et dans les arbres-pièges témoins. La combinaison de (±)-*exo*-brévicomine et de *cis*- et *trans*-verbénol a eu pour effet de réduire le nombre d'*I. pini* capturés dans les pièges à entonnoirs garnis de (±)-ipsdiénol comparativement au nombre capturé dans les pièges témoins situés immédiatement au-dessus et dans les arbres-pièges témoins. Ces résultats justifient le recours à des tactiques d'aménagement sémiochimiques qui utilisent une substance inhibitrice ponctuelle placée à la base d'un arbre, mais soulignent l'importance de tenir compte des limites de l'efficacité de la méthode et de ses effets sur le comportement.

[Traduit par la Rédaction]

Introduction

Ips pini (Say) and *Ips latidens* LeConte (Coleoptera: Scolytidae) are common species of bark beetles that breed in the phloem tissue of dead, dying, or downed lodgepole pine, *Pinus contorta* var. *latifolia* Engelmann (Pinaceae), in western North America (Furniss and Carolin 1980). These species are often present in large numbers during epidemics of the mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae) (Furniss and Carolin 1980). *Ips latidens* generally breeds in the tops and limbs of trees, occasionally infesting dry portions of the main bole in association with either *I. pini* or *D. ponderosae* (Furniss and Carolin 1980; Miller and Borden 1985).

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Both *I. pini* and *I. latidens* assemble on hosts in large, single-species aggregations, facilitated by aggregation pheromones (Borden 1982; Birch 1984; Byers 1989). Male *I. latidens* produce predominantly (*R*)-(+)-ipsenol (2-methyl-6-methylene-7-octen-4-ol), and both male and female *I. latidens* are attracted to racemic blends (Miller *et al.* 1991). *Ips pini* uses ipsdienol (2-methyl-6-methylene-2,7-octadien-4-ol) as an aggregation pheromone (Stewart 1975; Birch *et al.* 1980*a*; Lanier *et al.* 1980), preferring a racemic blend in southwestern British Columbia (Miller *et al.* 1996).

Both species exhibit mutual interruption of attraction through their use of pheromones, a mechanism that could ensure ecological and reproductive isolation (Birch 1984; Miller 1991). Ipsdienol, produced by male *I. pini*, interrupts the attraction of *I. latidens* to its pheromone (Miller and Borden 1992). Ipsenol, produced by male *I. latidens*, interrupts the attraction of *I. pini* to its pheromone, ipsdienol (Borden *et al.* 1992).

The present study examines the effect of vertical distance from a point source at the base of a tree on the interruption of pheromone attraction with *I. latidens* and *I. pini*. The concentration of a semiochemical interruptant from a point source at the base of a tree should diminish with increasing vertical distance along a tree bole due to dilution in a three-dimensional air space. This phenomenon should lead to a reduction in pheromone interruption because both species exhibit a dose-dependent response to interruptants (Miller 1991; Miller and Borden 1992).

The experimental design employed artificial "trees" rather than live trees to avoid the possibility of natural beetle attacks and confoundment from additional pheromone sources. Specifically, this study assessed the effect of semiochemical interruptants in reducing the numbers of *I. latidens* and *I. pini* arriving on an artificial "tree," particularly with respect to a source of interruptant located at the base of the tree. A point release source of interruptant(s) at the base of an artificial tree should (1) reduce numbers of landing beetles relative to the upper portions of the tree, and (2) reduce numbers of landing beetles in the upper portions of the treated tree relative to the same portions in untreated controls.

Materials and Methods

In 1986, two experiments were conducted in mature stands of lodgepole pine near Princeton (49°27′N, 120°31′W), British Columbia. In each experiment, eight tall-traps were set in four replicates of two tall-traps per replicate. Each tall-trap consisted of seven eight-unit multiple-funnel traps (Lindgren 1983) (Phero-Tech Inc., Delta, British Columbia) suspended in a vertical array on rungs of a ladder constructed of polypropylene rope (diameter 6 mm) and metal conduit pipe for rungs (length 70 cm, diameter 16 mm), spaced at intervals of about 1 m. Each tall-trap was positioned between trees by a rope-and-pulley suspension system such that no tall-trap was within 5 m of any tree and the collection cup of the bottom funnel trap was about 0.5 m above ground. Tall-traps were set about 25 m apart within a replicate with a spacing of >5 km between replicates.

The design in Experiment 1 approximated a hypothetical scenario involving attacks on trees by *I. latidens* (Fig. 1). The four lowest funnel traps of each tall-trap were baited with the pheromone for *I. latidens*, (±)-ipsenol, on 24 June. Within each replicate, the two lowest funnel traps of one tall-trap were baited on the same date with the interruptant, (+)-ipsdienol, and the tall-trap was designated as "treated." The three uppermost funnel traps were left blank to assess the accuracy of attraction relative to baited funnel traps. Trap catches were collected at intervals of 2–3 weeks until termination of the experiment on 4 August.

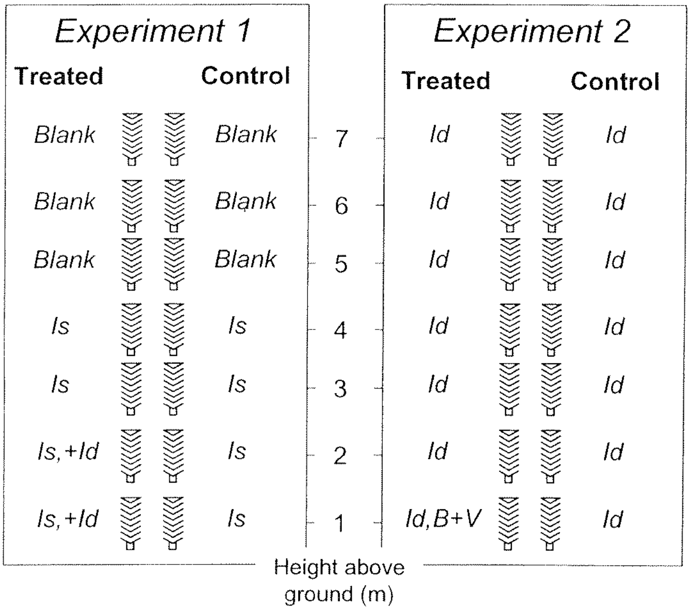

FIGURE 1. Design and baiting scheme for artificial trees (tall-traps) consisting of seven eight-unit Lindgren multiple-funnel traps each. Baits included (±)-ipsenol (Is), (±)-ipsdienol (Id), (+)-ipsdienol (+Id), and (±)-*exo*-brevicomin plus *cis*- and *trans*-verbenol (B + V).

Experiment 2 was designed for *I. pini*, which generally infest entire tree boles (Fig. 1). Because few *I. latidens* were captured in the blank funnel traps in Experiment 1, all funnel traps were baited with the pheromone for *I. pini*, (±)-ipsdienol, on 4 August. Within each replicate, the lowest funnel trap of one tall-trap was baited on the same date with the pheromones for *D. ponderosae*, *exo*-brevicomin and *cis*- and *trans*-verbenol (B + V), and the tall-trap was designated as treated. *exo*-Brevicomin and *cis*- and *trans*-verbenol, produced by *D. ponderosae*, interrupt the attraction of *I. pini* to its pheromone (Miller 1991). Trap catches were collected at intervals of 2–3 weeks until termination of the experiment on 2 September.

(±)-Ipsenol and (±)-ipsdienol (chemical purities > 98%) were obtained from Bedoukian Research Inc. (Danbury, Connecticut). BJ Johnston (Department of Chemistry, Simon Fraser University, Burnaby, British Columbia) supplied *S*-(+)-ipsdienol (optical purity 98%, chemical purity > 98%). Glass capillary (±)-*exo*-brevicomin lures (chemical purity > 98%) and polyethylene bubble-cap lures containing a 13:87 mixture of *cis*- and *trans*-verbenol [chemical purities 98%, enantiomeric compositions 83:17 (–):(+)] were supplied by Phero-Tech Inc.

Each ipsenol and ipsdienol lure consisted of eight Microcap® disposable pipettes (2 µL) (Drummond Scientific Co., Broomall, Pennsylvania), each sealed at one end and filled with (±)-ipsenol, (±)-ipsdienol, or (+)-ipsdienol and placed in an open polyethylene, microcentrifuge tube (1.8 mL) (Evergreen Scientific, Los Angeles, California). The release rate of ipsenol and ipsdienol from lures was about 80 µg/d at 24°C. The release rates of verbenols from bubble-cap lures were about 128 µg/d at 25°C, while the release rate of *exo*-brevicomin was 12–31 µg/d at 27°C. All release rates were determined by gravimetric analysis.

Sexes of *I. pini* were determined using declivital characters (Lanier and Cameron 1969), whereas those of *I. latidens* were determined by dissection and examination of genitalia. Voucher specimens were deposited at the Entomology Museum, Simon Fraser University.

Paired *t* tests were used to compare total catches in selected traps between control and treated tall-traps. For each experiment, trap catch data [transformed by $\ln(Y + 1)$] and sex ratio data (for catches > 5) [transformed by $\arcsin(Y)$] for control and treated tall-traps were subjected separately to two-way analysis of variance (ANOVA), using replicate and trap height as model factors. Fisher's least significant difference (LSD) multiple range test was performed when $P \leq 0.05$. The data were analyzed with the SYSTAT statistical package version 8.0 (SPSS Inc., Chicago, Illinois).

Results

The interruptants significantly reduced trap catches of *I. latidens* and *I. pini*. In Experiment 1, the mean ± SE total catch of 3 ± 1 *I. latidens* in the two bottom traps of the treated tall-traps was less than the mean total catch of 93 ± 38 in the two bottom traps of the control tall-trap ($t_3 = 7.70$, $P = 0.005$). In Experiment 2, the mean ± SE total catch of 8 ± 5 *I. pini* in the bottom trap of the treated tall-traps was less than the mean total catch of 107 ± 50 in the bottom trap of the control tall-trap ($t_3 = 6.52$, $P = 0.007$).

Interruptants in the lower funnel traps also reduced total catches of *I. latidens* and *I. pini* in traps above those treated with interruptants. In Experiment 1, combined total catches of *I. latidens* in ipsenol-baited funnel traps at heights of 3 and 4 m above ground were lower in treated tall-traps than in control tall-traps (mean ± SE total catches of 35 ± 9 and 103 ± 53, respectively) ($t_3 = 3.89$, $P = 0.030$). In Experiment 2, combined total catches of *I. pini* in ipsdienol-baited funnel traps at all heights ≥2 m were lower in treated tall-traps then in control tall-traps (mean ± SE total catches of 338 ± 155 and 642 ± 245, respectively) ($t_3 = 10.19$, $P = 0.002$).

Ips latidens and *I. pini* discriminated between individual pheromone sources within a vertical array of traps. In Experiment 1, the response of *I. latidens* was affected by trap height in both control ($F_{6,18} = 44.71$, $P < 0.001$) and treated ($F_{6,18} = 44.71$, $P < 0.001$) tall-traps, due largely to the unbaited traps at heights of 5–7 m (Fig. 2). As well, catches of beetles in the two lower ipsdienol- and ipsenol-baited funnel traps of the treated tall-trap were lower than catches in the two ipsenol-baited traps immediately above them. Catches in the lower traps were comparable to those in the three uppermost, blank traps. In contrast, there was no difference in trap catches of *I. latidens* among the four ipsenol-baited traps of the control tall-trap. Few *I. latidens* were captured in blank traps at heights of ≥5 m, even though the trap located at a height of 4 m was baited with its pheromone ipsenol.

In Experiment 2, the response of *I. pini* was affected by trap height in both control ($F_{6,18} = 5.00$, $P = 0.004$) and treated ($F_{6,18} = 34.74$, $P < 0.001$) tall-traps (Fig. 3). Catches of *I. pini* in the lower (B + V)- and ipsdienol-baited funnel trap of the treated tall-trap were less than catches in traps baited with ipsdienol alone. There was no difference in mean catches among the traps of the control tall-trap.

In Experiment 1, the sex ratio of *I. latidens* captured in funnel traps was unaffected by trap height in control ($F_{3,8} = 0.56$, $P = 0.655$) or treated ($F_{1,2} = 0.80$, $P = 0.465$) tall-traps. The mean ± SE proportion of male *I. latidens* in trap catches was 0.18 ± 0.02. In Experiment 2, the sex ratio of *I. pini* captured in funnel traps was unaffected by trap height in control ($F_{6,18} = 0.42$, $P = 0.856$) and treated ($F_{6,16} = 1.12$, $P = 0.393$) tall-traps. The mean ± SE proportion of male *I. pini* in trap catches was 0.40 ± 0.01.

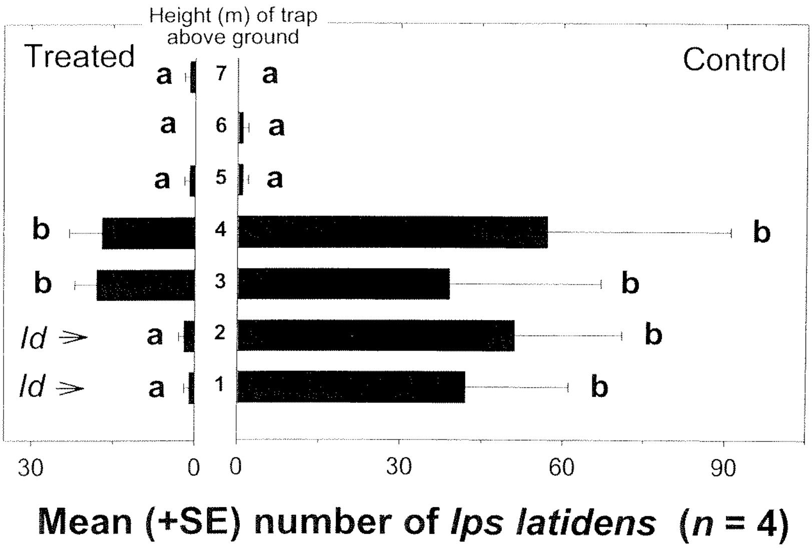

FIGURE 2. Interruptive effect of ipsdienol (Id) on catches of *Ips latidens* in ipsenol-baited (1–4) and blank (5–7) funnel traps within tall-traps. Heights of traps determined at middle of each trap. Means, within a figure of seven trap means, followed by a different letter are significantly different (Fisher's LSD test, $P = 0.05$).

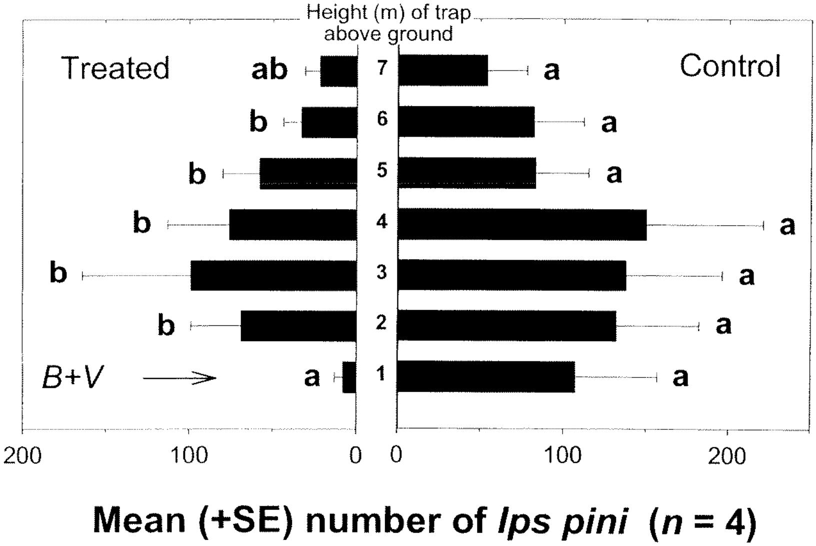

FIGURE 3. Interruptive effect of *exo*-brevicomin and verbenols (B + V) on catches of *Ips pini* in ipsdienol-baited funnel traps within tall-traps. Heights of traps determined at middle of each trap. Means, within a figure of seven trap means, followed by a different letter are significantly different (Fisher's LSD test, $P = 0.05$).

Discussion

These results with *I. latidens* and *I. pini* support the contention that variation in bark beetle behaviours, relative to vertical stratification of attacks and pheromone dispersal, is important in the dynamics of bark beetle populations. The behavioural phenomena involved in vertical segregation of host material by bark beetles have been clearly described for the bark beetle guild in southern pine stands (Smith *et al.* 1993) and likely apply to other pine systems as well (Borden 1982; Birch 1984; Byers 1989). The southern pine beetle, *Dendroctonus frontalis* Zimmerman, generally attacks loblolly pines at heights of 2–6 m above ground (Dixon and Payne 1979; Coster *et al.* 1977). The mid-bole is generally occupied by *Ips calligraphus* (Germar), whereas *Ips grandicollis* (Eichhoff) dominates in lower branches and parts of the mid-bole (Birch and Svihra 1979; Paine *et al.* 1981). *Ips avulsus* (Eichhoff) is found throughout the trunk, dominating in the upper bole, where it stays separate from *I. grandicollis* (Birch and Svihra 1979; Svihra *et al.* 1980; Paine *et al.* 1981).

Host separation of bark beetle species in southern pine forests seems to be facilitated by semiochemicals (Birch *et al.* 1980*b*; Svihra *et al.* 1980; Smith *et al.* 1990). *Dendroctonus frontalis* is attracted by the pheromone frontalin (Vité 1971; Payne *et al.* 1978, 1982; Billings 1985). *Ips avulsus* and *I. calligraphus* are attracted by the pheromone ipsdienol (Vité *et al.* 1978; Smith *et al.* 1990; Kohnle *et al.* 1994), with attraction of *I. calligraphus* enhanced by *cis*-verbenol and host compounds (Renwick and Vité 1972). Attraction of *I. avulsus* is enhanced by (*S*)-(–)-ipsenol (Hedden *et al.* 1976; Kohnle *et al.* 1994) and mixtures of *endo*- and *exo*-brevicomin (Richerson and Payne 1979). *Ips grandicollis* is attracted by (*S*)-(–)-ipsenol and host monoterpenes (Vité *et al.* 1976; Billings 1985; Smith *et al.* 1990; Kohnle *et al.* 1994).

Niche separation is ensured by mutual interruption of pheromone attraction (Birch *et al.* 1980*b*; Svihra *et al.* 1980). The attraction of *I. calligraphus* is interrupted by the pheromone of *I. avulsus*, whereas the attraction of *I. grandicollis* is interrupted by the pheromones of *D. frontalis* and *I. calligraphus* (Birch *et al.* 1980*b*; Svihra *et al.* 1980; Kohnle *et al.* 1994). Attraction of *D. frontalis* is interrupted by the pheromone of *I. grandicollis* (Birch *et al.* 1980*b*).

Vertical stratification in host utilization by semiochemicals has implications for the development of semiochemical-based management tactics. A point source of interruptant at the base of an artificial tree reduced catches of both *I. latidens* and *I. pini* in vertically adjacent traps baited only with their respective pheromones, relative to the same traps in control trees (Figs. 2, 3). These results support the current application of interruptants at the base of a tree in operational tactics designed to prevent attacks by bark beetles over the length of a tree bole. Research trials to reduce infestation levels of *D. ponderosae* have utilized devices releasing the antiaggregation pheromone, verbenone, at heights of 1.5–2 m above ground on boles of lodgepole and ponderosa pine (Amman *et al.* 1989; Lindgren *et al.* 1989; Bentz *et al.* 1989; Gibson *et al.* 1991). A similar approach has been used with interruptants for *Dendroctonus brevicomis* LeConte (Paine and Bertram 1995), *Dendroctonus pseudotsugae* Hopkins (Ross *et al.* 1996), *Dendroctonus rufipennis* (Kirby) (Holsten and Werner 1987), *D. frontalis* (Billings *et al.* 1995), and *Ips paraconfusus* Lanier (Shea and Neustein 1995).

However, such tactics have not gained widespread acceptance due to inconsistent efficacy as exemplified by trials with verbenone on *D. ponderosae* (Borden 1994; Amman and Lindgren 1995). Verbenone significantly reduced infestation levels of *D. ponderosae* in some stands of lodgepole pine but not in others (Lindgren *et al.* 1989; Amman *et al.* 1991; Gibson *et al.* 1991; Shore *et al.* 1992). No significant effect of verbenone on populations of *D. ponderosae* was ever observed in stands of ponderosa pine (Bentz *et al.* 1989; Lister *et al.* 1990; Gibson *et al.* 1991).

The semiochemical ecology of bark beetles is complex, and sophisticated pest-management tactics that specifically address critical factors underlying the variation in beetle behaviour will be needed (Vité and Francke 1992; Borden 1995). Climate, stand structure, and technological limitations affected past trials (Shea *et al.* 1992; Borden 1994; Amman and Lindgren 1995). Vertical stratification in the effect of interruptants may have played a role in past trials with verbenone as well. Catches of *I. latidens* and *I. pini* in traps above those baited with interruptants were significantly higher than those in traps baited with interruptants (Figs. 2, 3). The interruptants reduced catches but did not preclude significant numbers of landings by beetles along the bole of the tree. Similarly, the use of interruptants in operational trials may have been negated by beetle attacks above the location of the interruptants.

A thorough understanding of bark beetle behaviours associated with a range of critical factors should reveal vulnerable life history points to exploit in pest management (Borden 1989). Probability estimates for the various behaviours associated with semiochemical dispersion patterns, particularly as they fluctuate over time and space, will allow us to refine integrated pest-management tactics. Issues such as release rates from semiochemical devices and the density of release points must be considered and evaluated to address the variation in bark beetle behaviours. Additional classes of semiochemicals such as nonhost odours and pheromones from competing species may yield successes in the future by overcoming the constraints of beetle biology relative to spatial parameters (Borden 1994). These may include combinations of antiaggregative pheromones with pheromones of competing species (Borden *et al.* 1992; Paine and Bertram 1995) or the addition of nonhost compounds such as 4-allylanisole (Hayes *et al.* 1994) and green leaf volatiles (Poland *et al.* 1998).

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