Dose-Dependent Pheromone Responses of *Ips pini, Orthotomicus latidens* (Coleoptera: Scolytidae), and Associates in Stands of Lodgepole Pine

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ABSTRACT We conducted four behavioral choice tests in stands of mature lodgepole pine in British Columbia, from 1988 to 1991, to determine the dose-dependent responses of *Orthotomicus latidens* (LeConte) and *Ips pini* (Say) to their respective pheromones. Dose-dependent responses were exhibited by *I. pini* to ($\pm$)-ipsdienol and lanierone, with trap catches directly proportional to pheromone release rates. We found differences in sex ratio of *I. pini* in their responses to ipsdienol but not lanierone. There was no dose-dependent response exhibited by *O. latidens* to its pheromone, ($\pm$)-ipsenol, with or without the presence of the host kairomone, ($-$)-β-phellandrene. The bark beetle predator, *Enoclerus lecontei* (Wolcott), showed a dose-dependent response to lanierone. *Thanasimus undatulus* (Say) was attracted to ipsenol in a dose-dependent fashion only when traps were also baited with β-phellandrene. Neither *T. undatulus* nor *E. sphegeus* (F.) exhibited dose-dependent responses to ipsdienol.

KEY WORDS *Ips pini, Orthotomicus latidens*, ipsenol, ipsdienol, lanierone

MANY BARK BEETLES (COLEOPTERA: Scolytidae) efficiently use their host resource by the phenomenon of single-species mass aggregations, occurring mostly on trunks and large branches (Byers 1989). Male and female beetles aggregate in large numbers on suitable host trees, tunneling and laying eggs within the phloem tissues. The phenomenon is largely directed by pheromones and kairomones (Byers 1989) and may facilitate use of a valuable yet often ephemeral or spatially unpredictable resource (Atkins 1966).

Clear explanations for the mass aggregation phenomenon are still limited to a few species that attack live trees (Alcock 1982). Species such as the mountain pine beetle, *Dendroctonus ponderosae* Hopkins, require a minimum number of attacks or galleries by beetles to overcome the defenses of lodgepole pine, *Pinus contorta* variety *latifolia* Engelm. (Raffa and Berryman 1983). Typically, attacks by bark beetles in such aggregations start with a few beetles and progress to larger assemblages (Byers 1989). It is likely that pheromone production first increases as assemblages grow larger and that beetles show preferences for assemblages with high production of pheromones, thereby facilitating even larger assemblages.

The benefit of cooperation at low densities for bark beetles seems to be offset by the effects of competition

at higher densities (Berryman et al. 1985). Raffa and Berryman (1983) found that reproductive success of *D. ponderosae* decreased after densities reached high levels. Therefore, we would expect pheromone production and responses by beetles to decrease in combination with an increased production of antiaggregation pheromones to further interrupt attraction of beetles (Byers 1989).

The benefits to beetles joining such assemblages when tree defenses are minimal are unclear (Alcock 1982). Common species of pine bark beetles such as the pine engraver, *Ips pini* (Say), exhibit large single species aggregations, but typically only attack downed or dying pine trees (Furniss and Carolin 1980). Rankin and Borden (1991) and Robins and Reid (1997) found a negative effect of beetle density on the reproductive success of *I. pini* allowed to breed in lodgepole pine bolts. Aukema and Raffa (2004) suggested that one benefit of mass aggregations of *I. pini* may be dilution of predation by clerid and histerid bark beetle predators.

In addition to *I. pini, Orthotomicus latidens* (LeConte) (previously *Ips latidens;* Cognato and Vogler 2001) is a common bark beetle species in stands of lodgepole pine (Furniss and Carolin 1980). Like *I. pini*, this species typically attacks dead, dying, or downed pine trees and branches (Furniss and Carolin 1980). In British Columbia, the pheromone used by *O. latidens* is ipsenol (Miller et al. 1991), whereas *I. pini* uses ipsdienol and lanierone (Miller et al. 1996, 1997).

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Table 1.   Descriptions of semiochemical-releasing devices used in pheromone dose experiments for bark beetles in stands of lodgepole pine in British Columbia

Devices	Chemical[a]	Description	Release rates (mg/d at 24°C)
1–2	Ipsdienol (+50/−)	C-Flex; 8 mg/ml; 10 and 30 cm	0.06 and 0.18
3–5	Ipsdienol (+50/−50)	C-Flex; 80 mg/ml; 10, 30, and 100 cm	0.60, 1.80, and 6.00
6	Ipsdienol (+50/−50)	Polyvinyl bubble cap	0.2
7–8	Ipsenol (+50/−50)	C-Flex; 4 mg/ml; 10 and 30 cm	0.03 and 0.09
9–11	Ipsenol (+50/−50)	C-Flex; 40 mg/ml; 10, 30, and100 cm	0.30, 0.90, and 3.00
12–15	Lanierone	Polyvinyl bubble caps	0.0002, 0.002, 0.02, and 0.2
16	(−)-β-Phellandrene	Polyethylene centrifuge tube (1.8 ml)	8

[a]All chemical purities >95%.

If there is a negative consequence to beetles joining large aggregations, as suggested by Robins and Reid (1997), we would expect catches of *I. pini* and *O. latidens* in pheromone-baited traps to decrease with increasing release rates of pheromone. In contrast, if large aggregations confer benefits to responding beetles, as suggested by Aukema and Raffa (2004), we would expect catches of beetles to be directly proportional to release rates of pheromones.

However, if the driving force behind the ecology of bark beetles is truly the rare and ephemeral nature of host resources, as suggested by Atkins (1966), we would expect that trap catches would be independent of pheromone release rates. Beetles would be attracted to any site-releasing pheromones, irrespective of rate. If beetles were too choosy, they might not find another resource patch if demand for such resources exceeds supply. Aggregations of beetles in such a scenario would therefore be a consequence of not having alternative resource opportunities.

Our objective was to determine the effects of release rate (dose) on the attraction of *O. latidens* and *I. pini* to their respective pheromones in stands of lodgepole pine. We also determined the dose–response of the common bark beetle predators, *Enoclerus lecontei* (Wolcott), *E. sphegeus* (F.), and *Thanasimus undatulus* (Say) (Coleoptera: Cleridae) to the same bark beetle pheromones. Clerids respond to bark beetle pheromones and may exert selection pressures on pheromone traits (Raffa and Dahlsten 1995, Dahlsten et al. 2003). *Thanasimus undatulus*, *E. lecontei*, and *E. sphegeus* are attracted to ipsdienol (Miller and Borden 1990b, 2003, Miller et al. 1997) with lanierone increasing attraction of *E. lecontei* to ipsdienol but not *E. sphegeus* or *T. undatulus* (Seybold et al. 1992, Miller et al. 1997). Ipsenol is attractive to *T. undatulus* (Miller et al. 1991).

Materials and Methods

Semiochemical Release Devices. Phero Tech (Delta, Canada) supplied release devices 6 and 12–16 (Table 1), as well as (±)-ipsenol and (±)-ipsdienol (chemical purities >98%). (−)-β-Phellandrene (chemical purity, 98%) was obtained from H. D. Pierce, Jr. (Department of Chemistry, Simon Fraser University, Burnaby, Canada). Release devices 1–5 and 7–11 were manufactured with C-flex tubing (ID,

1.6 mm; OD, 3.2 mm; Concept, Clearwater, FL). Pieces of C-flex tubing (10, 30, and 100 cm long) were filled with ethanol solutions of either ipsenol or ipsdienol and heat-pressure sealed at both ends. In device 6, ipsdienol was formulated in 1,3-butanediol at a concentration of 80 mg/ml. Release rates for devices 1–15 (Table 1) were determined by collection of volatiles on Porapak-Q and quantitative analysis by gas chromatography. The release rate for device 16 was determined by weight loss.

Experiments. Four randomized block experiments were conducted from 1988 to 1994 (Table 2) in an attempt to determine the effect of release rate (dose) on the attraction of *I. pini* to its pheromones, ipsdienol (experiment 1) and lanierone (experiment 2), and *O. latidens* to its pheromone, ipsenol (experiments 3 and 4). All experiments were set in mature stands of lodgepole pine. Experiment 1 was conducted near Williams Lake, British Columbia, Canada, whereas experiment 2 was conducted near Kimberley, British Columbia, Canada, to exploit high population levels of *I. pini*. Experiments 3 and 4 were conducted near Princeton, British Columbia, Canada. The trapping periods for experiments 1–4 were 17 July to 16 August 1998, 11–29 July 1991, 23 June to 10 July 1988, and 10–20 July 1988, respectively.

In all experiments, blocks of four or six eight-unit, multiple-funnel traps (Phero Tech) were set in grids of 2 by 2 or 2 by 3. Replicate grids were placed at least 100 m apart, and traps were spaced 10–15 m apart within each replicate. Each trap was suspended between trees by rope such that the bottom of each trap

Table 2.   Summary of pheromone dose response experiments

Experiment	Pheromone	Release rate class (mg/d at 24°C)					
		Control	1	2	3	4	5
I. pini							
1	Ipsdienol	0	0.06	0.18	0.60	1.80	6.00
2	Lanierone[a]	—	0.0002	0.002	0.02	0.2	—
O. latidens							
3	Ipsenol	0	0.03	0.09	0.30	0.90	3.00
4	Ipsenol[b]	0	0.03	0.09	0.30	0.90	3.00

$n = 5$.

[a]All traps baited with ipsdienol, released at 0.2 mg/d at 24°C (device 6, Table 1).

[b]All traps baited with β-phellandrene, released at 8 mg/d at 24°C (device 16, Table 1).

was 0.2–0.5 m above ground level. No trap was within 2 m of any tree. A small piece (3 by 3 cm) of dichlorvos-impregnated wax bar (No Pest Strip; Loveland Industries, Greeley, CO) was added to each cup to ensure mortality and protect beetles from damage by predators.

We employed a behavioral choice type of design in all our experiments. All treatments within a block were grouped within the same area with traps spaced 10–15 m apart. Because all treatments had the same component pheromones, we would expect that the pheromone plumes from each treatment would blend together, spreading over a single area. Choices by beetles would be based on changes in pheromone concentrations in the air as they approach various traps rather than attraction from separate catchment areas of different sizes.

In experiments 1, 3, and 4, treatments were randomly assigned to traps within each block as follows: (1) a control treatment lacking the pheromone and (2–6) five treatments consisting of the target pheromone released at five different rates (Table 2). Release devices 1–5 (Table 1) were used for ipsdienol in experiment 1, whereas release devices 7–11 were used for ipsenol in experiments 3 and 4, with one device per trap in all three experiments. The control trap in experiment 1 was not baited with either pheromone or kairomone. All traps in experiment 4 were additionally baited with β-phellandrene (device 16), a host compound that synergizes the attraction of O. latidens to ipsenol (Miller and Borden 1990a). In experiment 2, only four rates of lanierone (devices 12–15) were tested (without a control treatment), with only one device per trap. All traps in experiment 2 were baited with ipsdienol bubblecaps (device 6) as well.

Captured beetles were held frozen until counted. Sex ratios of I. pini in experiments 1 and 2 were determined using declivital characters (Lanier and Cameron 1969). Sex ratios of O. latidens and clerid predators were not determined. Voucher specimens were deposited at the Entomology Museum, Simon Fraser University.

Statistical Analyses. Data were analyzed using the SYSTAT statistical package version 10.2 (SYSTAT Software, Richmond, CA). Trap catch data were transformed by $\ln(Y)$ or $\ln(Y + 1)$ to remove heteroscedasticity. Sex ratio data were not transformed. Data in all experiments were subjected to two-way analysis of variance (ANOVA), using replicate and treatment as model factors, followed by Tukey's honestly significant difference (HSD) multiple comparison test when $P < 0.05$. Regression analyses were conducted against the release rate of pheromones, transformed by $\ln(X)$. Controls were not included in regression analyses. For each regression, residuals were examined to ensure the appropriateness of either a linear or curvilinear model and the range of the regression lines.

Results

The total number of I. pini captured in experiment 1 was 635 (range, 0–162 beetles/trap). Catches were

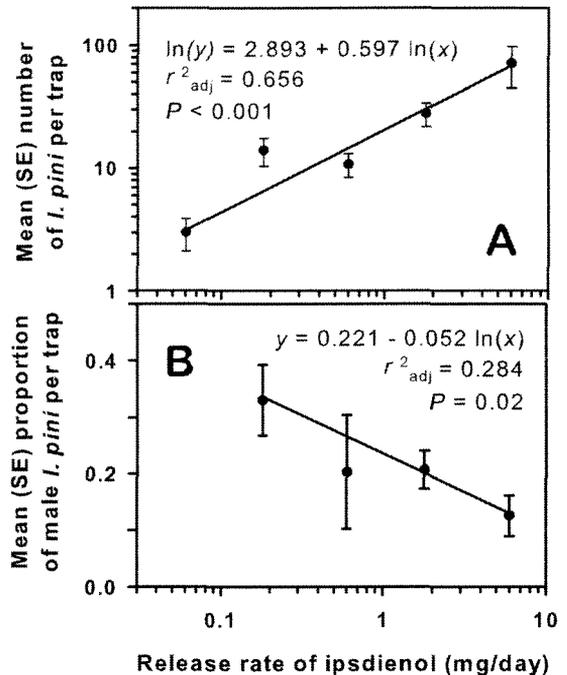
Fig. 1. Effects of ipsdienol, released at various rates, on catches of I. pini (A) and proportion of male I. pini (B) in multiple-funnel traps near Williams Lake, BC, in 1988 (experiment 1). The mean ± SE catch of I. pini in control traps was 0.6 ± 0.6 beetles.

significantly affected by the ipsdienol treatments ($F = 12.388$; df = 5,16; $P < 0.001$), with catches in ipsdienol-baited traps significantly greater than those in control traps (Tukey's HSD test, $P < 0.05$). There was a strong dose-dependent response to ipsdienol, with the highest catches associated with traps baited with lures releasing ipsdienol at the highest rate (Fig. 1A). The regression equation accounted for almost 66% of the variation in trap catches. The proportion of males in trap catches decreased as the rate of ipsdienol increased (Fig. 1B).

The total number of I. pini captured in experiment 2 was 32,356 (range, 345–4,850 beetles/trap). Catches were significantly affected by the lanierone treatments ($F = 31.443$; df = 3,12; $P < 0.001$). Beetles in British Columbia exhibited a strong dose-dependent response to lanierone in traps baited with ipsdienol, with the highest catches associated with traps baited with lures releasing lanierone at the highest rates (Fig. 2A). The regression equation accounted for almost 78% of the variation in trap catches. There was no effect of lanierone release rate on the sex ratio of I. pini in trap catches ($F = 0.762$; df = 3,12; $P = 0.537$; Fig. 2B). The mean ± SE proportion of male beetles in traps was 0.548 ± 0.023.

The total numbers of O. latidens captured in experiments 3 and 4 were 782 and 702, respectively, with maximum trap catches of 94 and 74 beetles, respectively. As expected from Miller et al. (1991), trap catches of O. latidens in experiments 3 and 4 were
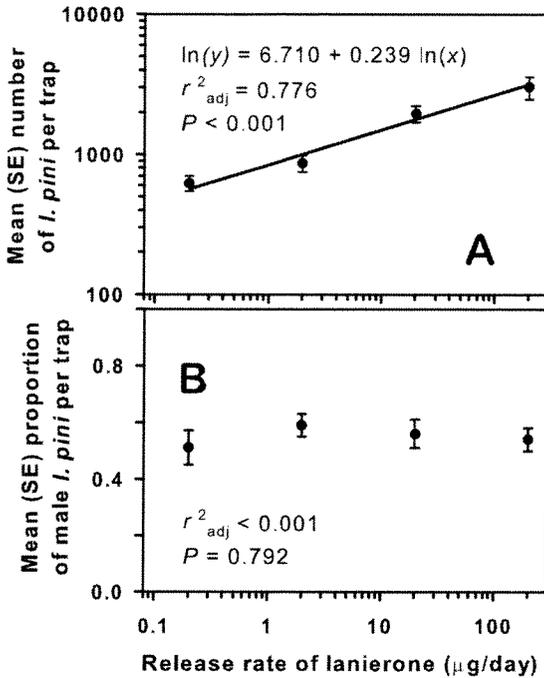
Fig. 2.   Effects of lanierone, released at various rates, on catches of *I. pini* (A) and proportion of male *I. pini* (B) in multiple-funnel traps near Kimberley, BC, in 1991 (experiment 2).
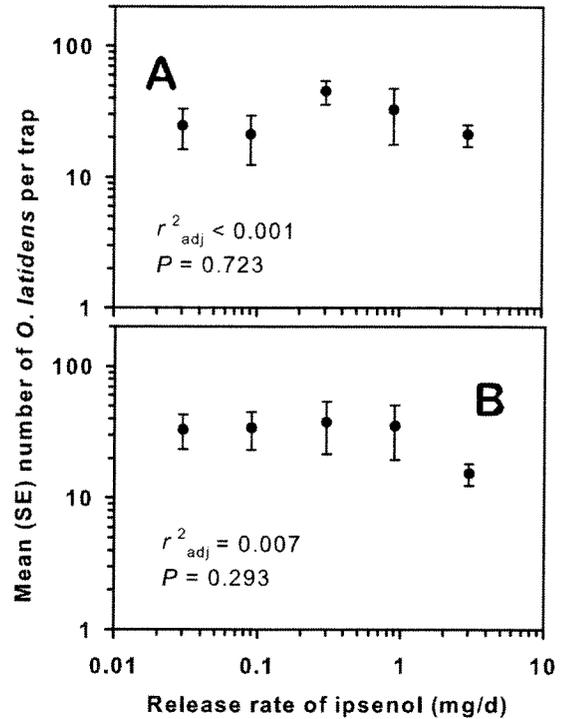

Fig. 3.   Effects of ipsenol, released at various rates, on catches of *O. latidens* in multiple-funnel traps baited (A) without β-phellandrene (experiment 3) and (B) with β-phellandrene (experiment 4) near Princeton, BC, in 1988. The mean $\pm$ SE catches of *O. latidens* in control traps in experiments 3 and 4 were 0.6 $\pm$ 0.4 and 0.4 $\pm$ 0.2 beetles, respectively.

strongly affected by the presence of ipsenol ($F = 13.279$; df $= 5,17$; $P < 0.001$, and $F = 10.307$; df $= 5,16$; $P < 0.001$, respectively). Catches in control traps (not baited with ipsenol) were significantly lower than those in traps baited with ipsenol, regardless of release rate or presence of β-phellandrene (Tukey's HSD test, $P < 0.05$). However, there was no effect of release rate of ipsenol on catches of *O. latidens*, with or without the presence of β-phellandrene (Fig. 3A and B). The mean $\pm$ SE response of *O. latidens* to ipsenol-baited traps in experiments 3 and 4 was 31 $\pm$ 5 and 29 $\pm$ 4, respectively

Total catches of predators did not exceed 265 beetles for any experiment. The total numbers of *T. undatulus* and *E. sphegeus* captured in experiment 1 were 124 and 139 beetles, respectively. There were no significant ipsdienol treatment effects on catches of either species ($F = 1.369$; df $= 5,20$; $P = 0.225$ and $F = 1.627$; df $= 5,20$; $P = 0.145$, respectively). The mean $\pm$ SE catches of *T. undatulus* and *E. sphegeus* in ipsdienol-baited traps in experiment 1 were 4.9 $\pm$ 1.1 and 5.5 $\pm$ 1.4, respectively.

The total numbers of *T. undatulus* and *E. sphegeus* captured in experiment 2 were 73 and 43 beetles, respectively. There were no significant lanierone treatment effects on catches of either species ($F = 0.552$; df $= 3,12$; $P = 0.522$ and $F = 1.011$; df $= 3,12$; $P = 0.422$, respectively). The mean $\pm$ SE catches of *T. undatulus* and *E. sphegeus* in traps baited with ipsdienol and lanierone in experiment 2 were 3.7 $\pm$ 0.5 and 2.2 $\pm$ 0.4, respectively.

There was a significant effect of lanierone treatment on catches of *E. lecontei* in experiment 2 ($F = 8.985$; df $= 3,12$; $P = 0.002$), with catches in traps with lanierone released at the highest rate significantly greater than those in traps with lanierone released at the two lowest rates (Tukey's HSD test, $P < 0.05$). The regression equation explained almost 59% of the variation in trap catches (Fig. 4). The total number of *E. lecontei* captured in experiment 2 was 190 (range, 0–37 beetles/trap).

The total numbers of *T. undatulus* captured in experiments 3 and 4 were 32 and 38 beetles, respectively. There was a significant ipsenol treatment effect on catches in experiment 4 ($F = 6.016$; df $= 5,19$; $P = 0.002$) but not in experiment 3 ($F = 1.009$; df 5,19; $P = 0.438$; Fig. 5A and B). Catches of *T. undatulus* in experiment 4 were directly proportional to the release rate of ipsenol, although the regression equation accounted for only 27% of the variation in trap catches (Fig. 5B). The mean $\pm$ SE catch of *T. undatulus* to traps baited with ipsenol in experiment 3 was 1.2 $\pm$ 0.3 beetles.

Discussion

Our results in experiments 1 and 2 are consistent with the observed behavior of *I. pini*, which typically
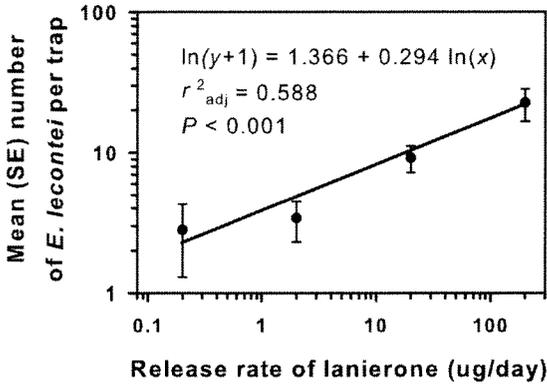
Fig. 4. Effects of lanierone, released at various rates, on catches of *E. lecontei* in multiple-funnel traps near Williams Lake, BC, in 1988 (experiment 2).

exhibits large, ever-growing aggregations on freshly fallen pines and logging slash (Furniss and Carolin 1980). Poland and Borden (1994) measured the density of *I. pini* galleries on windthrown lodgepole pine at ≈ 100 galleries/m^2. Gries et al. (1988) estimated the mean $\pm$ SE rate of ipsdienol production by individual male *I. pini* on lodgepole pine at 0.02 ± 0.004 mg/d.
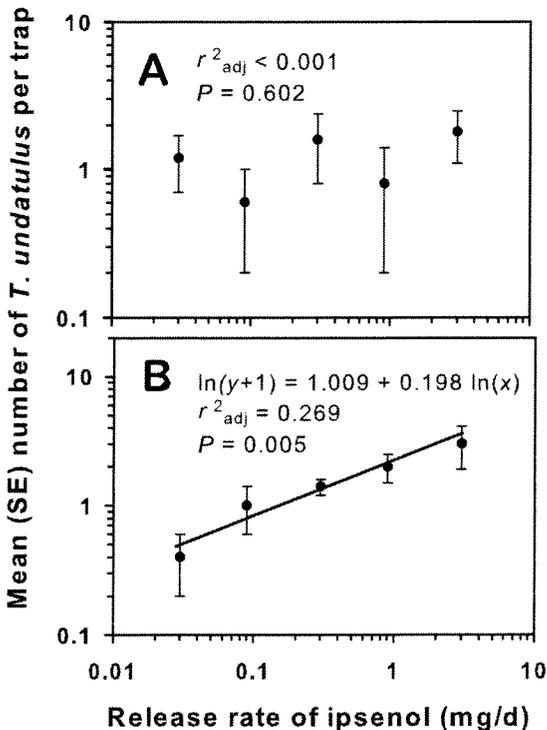

Fig. 5. Effects of ipsenol, released at various rates, on catches of *T. undatulus* in multiple-funnel traps baited (A) without β-phellandrene (experiment 3) and (B) with β-phellandrene (experiment 4) near Princeton, BC, in 1988. The mean $\pm$ SE catches of *T. undatulus* in control traps in experiments 3 and 4 were 0.4 ± 0.2 and 0 ± 0 beetles, respectively.

Therefore, we would expect the rate of ipsdienol to be ≈ 0.8 mg/d over a funnel-trap equivalent area of 0.4 m^2, well within the range used in experiment 1 (Fig. 1A).

The increases in catches of *I. pini* with increasing doses of either ipsdienol or lanierone (Figs. 1A and 2A) suggest that the benefits of aggregation may outweigh the negative effects of density on reproductive fitness (Robins and Reid 1997). Experiment 1 was conducted during an epidemic of *I. pini* attacking live lodgepole pine where beetles undoubtedly would have benefited from aggregative behavior in overcoming tree defenses. Populations of beetles had bred up previously in the tops of trees killed by *D. ponderosae* and in logging slash. Trees attacked by *D. ponderosae* still have intact green crowns and may retain resistance mechanisms to attacks by *I. pini*, albeit less than the lower bole of a live tree. In experiment 2, population levels of *I. pini* had increased dramatically because of an abundance of windthrown pines, many with intact crowns and partially intact root systems.

In the response of *I. pini* to ipsdienol, we found a greater representation by females in catches to traps baited with the higher doses (Fig. 1B). Unlike *O. latidens*, *I. pini* are typically polygamous, with three to four females joining single males in galleries (Reid and Roitberg 1994). If pheromone production by male *I. pini* is related to density of galleries, females may benefit more than males from a dose-dependent pheromone response because each gallery offers opportunities for three to four females. Alternatively, females may be choosing males that produce large amounts of ipsdienol, especially when choosing one gallery over another. There can be considerable variation in the amount of ipsdienol produced by individual male *I. pini* (Gries et al. 1990, Miller et al. 1996). Mate choice by female beetles may be dependent on the rate of pheromone production (Sargent and Reid 1999).

In contrast to *I. pini*, we found no dose-dependent response by *O. latidens* to traps baited with the pheromone ipsenol, even for traps baited with the host compound β-phellandrene (Figs. 3A and B). Typically, *O. latidens* is found in small- to medium-sized aggregations in fairly thin, dry phloem (Miller and Borden 1985), often in tops and limbs of weakened or dying trees such as those attacked by *D. ponderosae*, but also occasionally in small patches on the bole of live mature lodgepole pine (Furniss and Carolin 1980). Unlike the *I. pini* situations described above, there may be little additional benefit to individual *O. latidens* in joining large groups of conspecifics over small groups as there may not be a need to overcome tree defenses. In addition, female *O. latidens* join males in monogamous relationship (Reid 1999), and there is likely little opportunity for late-arriving females to find a mate.

If there was a negative effect on reproductive success from large aggregations in *O. latidens* such as in *I. pini* (Robins and Reid 1997), we might expect interruption of attraction to ipsenol at high rates of release. However, if host material suitable for attacks and breeding by *O. latidens* is relatively rare compared

with that for *I. pini*, the consequence of intraspecific competition may be offset for *O. latidens*. The lack of response supports the hypothesis that pheromone response by *O. latidens* is an adaptive advantage in locating rare and ephemeral habitats. Aggregations would be a consequence of many individuals arriving on a rare commodity rather than selection pressures favoring aggregations such as in *D. ponderosae* (Raffa 2001).

Consideration of the issue of large single species aggregations is further confounded by the high diversity of scolytid species known to occur in stands of lodgepole pine. Bright (1976) stated that >50 species of bark and ambrosia beetles have been recorded on lodgepole pine in Canada and Alaska. Interspecific competition may play a significant role in separating species into single species assemblages, often facilitated by interspecific interruption of pheromone responses (Byers 1989). Reproductive success of *D. ponderosae* can be severely reduced if mass attacks are followed closely by *I. pini* attacks (Rankin and Borden 1991). *Pityogenes knechteli* and *I. pini* show clear spatial separation when found together on the same lodgepole pine (Poland and Borden 1994).

Explanations for the different behaviors exhibited by predators to variation in pheromone doses in our studies are not clear. We found that *T. undatulus* and *E. sphegeus* were not affected by release rates of ipsdienol or lanierone. It is possible that at low predator densities, equal prey opportunities exist, regardless of aggregation size, because gallery density may not change much with increasing aggregation size. Alternatively these beetles may feed on *I. pini* only when alternate prey, such as *D. ponderosae*, are not abundant. Their behavioral responses may be selected for pheromones produced by *D. ponderosae* and not *I. pini*. Experiment 1 was conducted in area with a recent collapse of a large-scale epidemic of *D. ponderosae*.

In our studies, we found that *E. lecontei* exhibited a dose-dependent increase in attraction to lanierone, similar to results obtained by Seybold et al. (1992). Sites with high rates of pheromone production by bark beetles may represent greater feeding opportunities for both adult and larval predators, thereby justifying the dose-dependent relationship. We found that the ratio of *E. lecontei* to *I. pini* captured in lanierone-baited traps continued to increase (Fig. 6). It is also possible that density of predators may increase intraspecific competition for predators, thereby decreasing the relationship. Seybold et al. (1992) offer several other explanations for dose-dependent attraction of *E. lecontei* to lanierone.

Responses of predators may also require additional semiochemicals to elicit maximum attraction. Ipsenol had a dose affect on responses of *T. undatulus* when β-phellandrene was present in the traps but not when it was absent (Fig. 5A and B). It is possible that responses by predators require full contextual information, such as kairomones, especially when the same information relates to other prey.

Understanding trophic interactions in the semiochemical ecology of pine hosts, bark beetles, and pred-
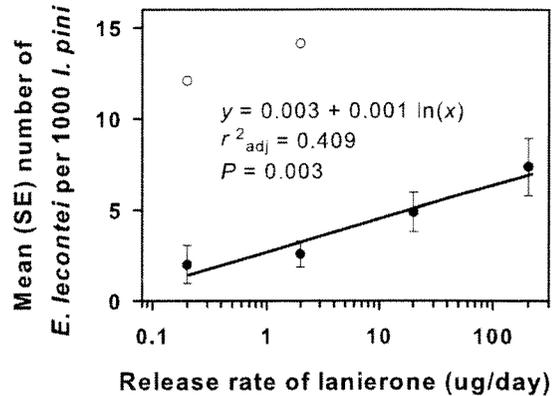

Fig. 6. The effects of lanierone, released at various rates, on catches of *E. lecontei* relative to catches of *I. pini* in multiple-funnel traps near Kimberley, BC, in 1991 (experiment 2).

ators will require studies focused on the various selection pressures (Raffa 2001). Particular attention will have to be paid to micro-evolutionary changes, particularly in the tactics between bark beetles and predators. Extensive variation in the semiochemical ecology of bark beetles has been shown for numerous species including *D. ponderosae* and *I. pini* (Borden et al. 1986, 1990, Schlyter and Birgersson 1989, Miller et al. 1996). There is a strong genetic basis to the use of pheromones and kairomones by *I. pini* (Hager and Teale 1996, Wallin et al. 2002). Predators and competitors can exert significant influences in the use of pheromones by bark beetles (Raffa 2001). Variation in the use of enantiomers of ipsdienol by *I. pini* can be related to responses by predators such as *Thanasimus dubius* (F.) on *I. pini* (Herms et al. 1991, Aukema and Raffa 2000). Because these are likely to be ever changing pressures, it seems likely that populations of some species of bark beetles and their predators may undergo significant changes in their population genetics over short time frames (1–10 yr), with respect to their semiochemical ecology.

Acknowledgments

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