

β -PHELLANDRENE:
KAIROMONE FOR PINE ENGRAVER, *Ips pini* (Say)
(COLEOPTERA: SCOLYTIDAE)

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Abstract—The responses of *Ips pini* (Scolytidae) to multiple-funnel traps baited with the pheromone, ipsdienol, and various monoterpenes were determined in stands of lodgepole pine in southern and central British Columbia. *Ips pini* was attracted to both ipsdienol and β -phellandrene, demonstrating that β -phellandrene is a kairomone for this species. *Lasconotus complex* (Colydiidae) and a *Corticus* sp. (Tenebrionidae) were attracted to both ipsdienol and β -phellandrene. The *Corticus* sp. exhibited a synergistic response to the combination of ipsdienol and β -phellandrene; the responses of the other two species to the combination were additive. The predators, *Thanasimus undatulus*, *Enoclerus sphegeus*, and *E. lecontei* (Cleridae), were attracted to ipsdienol-baited traps, while *Monochamus clamator* (Cerambycidae) and *Dendroctonus ponderosae* (Scolytidae) were attracted to β -phellandrene. Attraction of all eight species increased with increasing release rates of ipsdienol and/or β -phellandrene.

Key Words—Kairomone, β -phellandrene, ipsdienol, monoterpenes, *Ips pini*, Coleoptera, Scolytidae, predators, competition, primary attraction, dose response.

INTRODUCTION

The mass aggregation phenomenon, typical of many subcortical feeding insects, has long been known for the pine engraver, *Ips pini* (Say). Anderson (1948) found that *I. pini* were attracted, in large numbers, to bolts of jackpine, *Pinus banksiana* Lambert, infested with *I. pini*. The principal semiochemical involved in mass aggregation was identified as the male-produced pheromone, ipsdienol

(2-methyl-6-methylene-2,7-octadien-4-ol) (Vité et al., 1972; Stewart, 1975; Birch et al., 1980; Lanier et al., 1980).

Although evidence of the use of pheromones by *I. pini* has been documented, very little has been gleaned on the use of host-produced kairomones in facilitating mass aggregation. Monoterpenes are abundant in the phloem tissue of lodgepole pine, *P. contorta* var. *latifolia* Engelm (Mirov, 1961; Shrimpton, 1972, 1973), a common host for *I. pini* (Furniss and Carolin, 1980), and are used as attractive kairomones by several species of Scolytidae (Borden, 1982; Dickens et al., 1984; Byers et al., 1985, 1988; Schroeder and Eidmann, 1987; Schroeder, 1988; Volz, 1988; Chénier and Philogène, 1989; Schroeder and Lindelöw, 1989; Miller and Borden, 1990). β -Phellandrene is the major constituent monoterpene in the phloem tissue of lodgepole pine (Shrimpton, 1972). Four species of bark beetles that typically breed in lodgepole pine are attracted to β -phellandrene (Miller and Borden, 1990). We hypothesized, therefore, that β -phellandrene should act as a kairomone for *I. pini*, either as an attractant or repellent, and either alone or in synergy with the pheromone, ipsdienol.

METHODS AND MATERIALS

Chemicals. (+)-3-Carene, (+)-limonene, (-)- β -phellandrene, racemic α -pinene, (-)- β -pinene, and terpinolene (chemical purities, all > 95 %) were obtained from H.D. Pierce, Jr. (Department of Chemistry, Simon Fraser University). The chiralities of β -phellandrene and β -pinene are predominantly (-) in lodgepole pine (Mirov, 1961). β -Myrcene and racemic ipsdienol (chemical purities, both 98%) were obtained from Phero Tech Inc. (Vancouver, British Columbia).

Release Devices. In experiment 1, monoterpenes were released from closed, polyethylene microcentrifuge tubes (400 μ l) (Evergreen Scientific, Los Angeles, California), each filled with a single monoterpene. The release rates for α -pinene, β -pinene, myrcene, 3-carene, limonene, β -phellandrene, and terpinolene were approximately 8.9, 9.3, 22.3, 22.9, 25.5, 29.3, and 29.5 mg/day, respectively, at 27°C (determined by weight loss). In experiment 2, β -phellandrene was released in two fashions to obtain two different release rates: (1) two closed, polyethylene microcentrifuge tubes (each 400 μ l) per trap; and (2) one closed, polyethylene screw-cap bottle (15 ml) (Ampak Inc., Richmond, British Columbia) per trap. The release rates were approximately 59 and 450 mg/day, respectively, at 27°C. In experiment 3, β -phellandrene was released in three fashions: (1) one open, polypropylene microcentrifuge tube (1.5 ml) (Quality Scientific Plastics, Petaluma, California) per trap, containing five 2-cm-long glass capillaries (ID 1.5 mm; OD 1.8 mm), each sealed at one end

and filled with β -phellandrene; (2) five closed, polyethylene microcentrifuge tubes (1.8 ml) (Evergreen Scientific) per trap; and (3) one closed, polyethylene screw-cap bottle (15 ml) per trap. The release rates were approximately 3, 40, and 450 mg/day, respectively, at 27°C.

Ipsdienol was released from 10-cm-lengths of C-flex@ tubing (ID 1.6 mm; OD 3.2 mm) (Concept Inc., Clearwater, Florida), filled with a solution of ipsdienol in ethanol (chemical purity, 99%), and pressure-sealed at both ends. In experiments 1-2, the release rate of ipsdienol was approximately 0.6 mg/day at 24°C. The release rates for the devices used in experiment 3 (approximately 6, 60, and 600 μ g/day at 24°C) were obtained by varying the concentration of ipsdienol in ethanol.

Trapping Experiments. In all experiments, grids of multiple-funnel traps (Lindgren, 1983) were set in mature stands of lodgepole pine. 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 top funnel of each trap was 1.3-1.5 m above ground. No trap was within 2 m of any tree. Sexes of captured *I. pini* were determined using declivital characters (Lanier and Cameron, 1969).

The effects of various monoterpenes were tested in experiment 1 in order to distinguish the effect of β -phellandrene relative to other monoterpenes common in lodgepole pine (Shrimpton, 1972). Five replicates of eight 8-unit traps per replicate, were set near Princeton, British Columbia, in grids of 2 X 4, from May 29 to July 2, 1987. The treatments were as follows: (1) ipsdienol alone, (2) ipsdienol with α -pinene, (3) ipsdienol with β -pinene, (4) ipsdienol with 3-carene, (5) ipsdienol with myrcene, (6) ipsdienol with terpinolene, (7) ipsdienol with β -phellandrene, and (8) ipsdienol with limonene.

Experiment 2 tested for effects of β -phellandrene as a kairomone in primary and secondary attraction of *I. pini*, as well as for interactions between ipsdienol, β -phellandrene and locality. Three replicates of six 12-unit traps per replicate were set in grids of 2 X 3 at each of three localities in British Columbia in 1988: (1) near Princeton from August 24 to September 4, (2) near Jaffray from August 25 to September 27, and (3) near Williams Lake from August 27 to 31. The treatments were as follows: (1) blank control, (2) β -phellandrene (59 mg/day), (3) β -phellandrene (450 mg/day), (4) ipsdienol alone, (5) ipsdienol with β -phellandrene (59 mg/day), and (6) ipsdienol with β -phellandrene (450 mg/day).

Experiment 3 tested for response of *I. pini* to different doses of ipsdienol and β -phellandrene, as well as for interaction between ipsdienol, β -phellandrene, and locality. Two replicates of nine 12-unit traps per replicate were set in grids of 3 X 3 at each of three localities in British Columbia in 1988: (1) near Princeton from August 19 to September 1, (2) near Jaffray from August 25 to September 27, and (3) near Williams Lake from August 27 to 31. The

treatments were the nine binary combinations of ipsdienol (6, 60, and 600 $\mu\text{g}/\text{day}$) with β -phellandrene (3, 40, and 450 mg/day), with each of the release rates for a given chemical occurring only once in any row or column of each grid.

Statistical Analyses. The data were analyzed using the SAS statistical package version 5.0 (SAS Institute Inc., Cary, North Carolina). When necessary, trap catch data were transformed to remove heteroscedasticity. In experiment 1, trap catches of *I. pini* were transformed by $\sqrt[3]{Y}$. In experiment 2, catches of all species were transformed by $\ln(Y + 1)$. In experiment 3, catches of (1) *Thanasimus undatulus* Say (Cleridae) and *Lasconotus complex* LeConte (Colydiidae) were transformed by $\sqrt[3]{Y}$, (2) *Dendroctonus ponderosae* Hopkins (Scolytidae) were transformed by $-1/\sqrt{Y}$, and (3) *I. pini* and a *Corticium* sp. (Tenebrionidae) were transformed by $\ln(Y + 1)$. Sex ratio data for *I. pini* were transformed by $\arcsin\sqrt{Y}$. Homoscedastic data were subjected to either one-way, two-way, or three-way full-factorial ANOVA. Block effects were not considered in the analyses. Three orthogonal contrasts were performed for experiment 1 while Duncan's multiple-range tests were used in experiments 2 and 3 when $P < 0.05$.

RESULTS

β -Phellandrene had a significant effect on trap catches of *I. pini* in all three experiments. In experiment 1, catches to traps baited with ipsdienol and β -phellandrene were significantly higher than catches to traps baited with ipsdienol and any other monoterpene (Figure 1). There were no significant differences between the ipsdienol treatment and either the ipsdienol + β -phellandrene treatment (orthogonal contrast, $F(1, 32)$, $P = 0.226$) or the remaining treatments (orthogonal contrast, $F(1, 32)$, $P = 0.488$).

Jaffray data were omitted from analyses in experiments 2 and 3 because only 12 *I. pini* were caught. In experiment 2, β -phellandrene alone significantly increased trap catches (Table 1, Figure 2A,C). In Princeton, traps with baits releasing β -phellandrene at a high rate were preferred over those with a low release rate, while catches in blank control traps were intermediate (Figure 2A). In Williams Lake, traps with baits releasing β -phellandrene at either rate were preferred over blank controls (Figure 2C). There was an additive, not synergistic, interaction between ipsdienol and β -phellandrene on the response of *I. pini* (Table 1). Significant interactions occurred between location and β -phellandrene treatments, and between location, β -phellandrene, and ipsdienol treatments (Table 1).

In experiment 3, responses of *I. pini* increased as the release rates of ips-

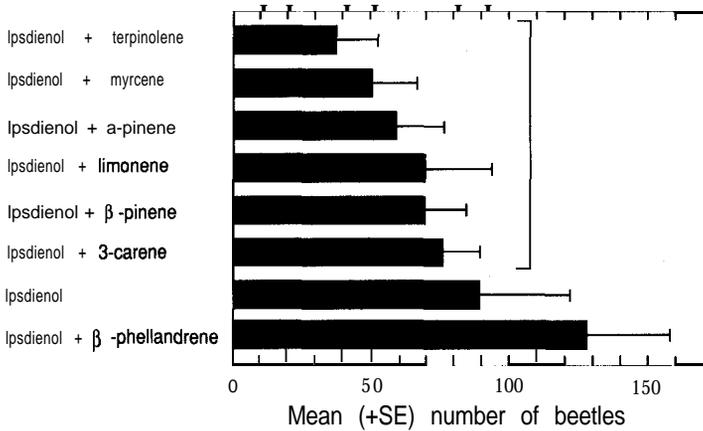


FIG. 1. The effect of various monoterpenes on the attraction of *pini* to ipsdienol-baited multiple-funnel traps in experiment 1 near Princeton, BC, from May 24 to July 2, 1987. Means grouped by a line are significantly different from the treatment of ipsdienol + β -phellandrene at $P = 0.027$ [orthogonal contrast, ANOVA, $F(1, 32)$, on data transformed by $\sqrt[3]{Y}$ ($N = 5$)].

TABLE 1. ANALYSIS OF VARIANCE ON EFFECTS OF LOCATION (PRINCETON AND WILLIAMS LAKE, BC), IPSDIENOL (0.6 mg/day), AND β -PHELLANDRENE (59 and 450 mg/day) ON NUMBER AND SEX RATIO OF *Ips pini* RESPONDING TO MULTIPLE-FUNNEL TRAPS (EXPERIMENT 2, 1988)

| Source | Trap catch ^a | | | Proportion of males ^b | | |
|---------------------------|-------------------------|--------|---------|----------------------------------|-------|-------|
| | df | F | P | df | F | P |
| Location (A) | 1 | 32.34 | < 0.001 | 1 | 0.49 | 0.493 |
| Ipsdienol (B) | 1 | 281.46 | < 0.001 | 1 | 12.17 | 0.003 |
| β -Phellandrene (C) | 2 | 5.66 | 0.010 | 2 | 0.45 | 0.647 |
| A*B | 1 | 1.79 | 0.193 | 1 | 0.02 | 0.896 |
| A*C | 2 | 5.07 | 0.015 | 2 | 0.38 | 0.692 |
| B*C | 2 | 1.71 | 0.203 | 2 | 2.68 | 0.094 |
| A*B*C | 2 | 2.94 | 0.072 | 0 | | |
| Error | 24 | | | 19 | | |

^aData transformed by $\ln(Y + 1)$.

^bData transformed by $\arcsin\sqrt{Y}$.

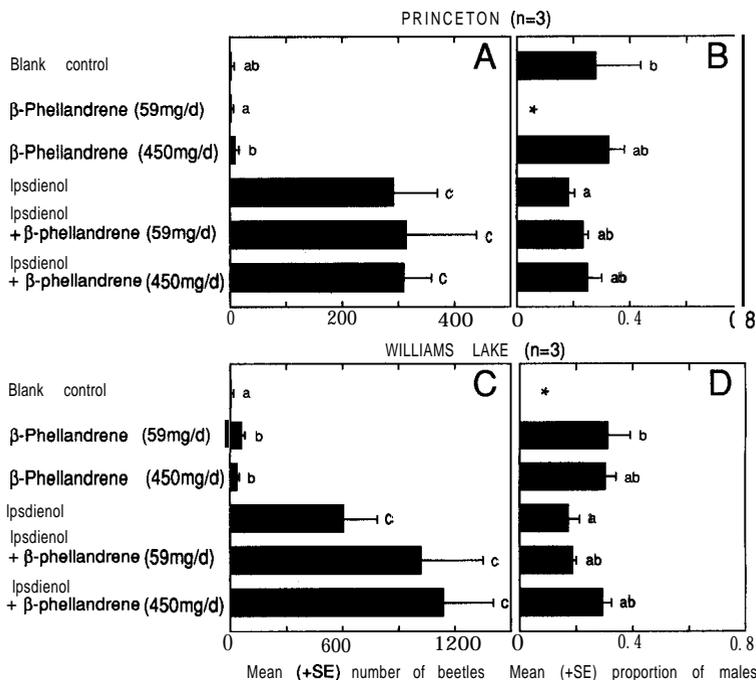


FIG. 2. The effect of β -phellandrene, with or without ipsdienol, on the attraction (A,C) and sex ratio (B,D) of *Ips pini* responding to multiple-funnel traps in experiment 2 near Princeton (A,B) and Williams Lake (C,D) from August 24 to September 4, 1988 and August 27 to 31, 1988, respectively. Mean trap catches from the same location followed by the same letter are not significantly different at $P = 0.05$ [Duncan's multiple-range test on data transformed by $\ln(Y + 1)$]. Mean proportions of males, in traps at the same location, followed by the same letter are not significantly different at $P = 0.05$ (Duncan's multiple-range test on data transformed by $\arcsin\sqrt{Y}$). The proportions of males for treatments with low trap catches (*) were not included in the analyses.

dienol and β -phellandrene increased (Table 2, Figure 3A,B). There were significant differences between Princeton and Williams Lake in the magnitude of the increase (Table 2). However, in both cases the preferred treatments were those with high release rates of ipsdienol and β -phellandrene (Duncan's multiple-range test, $P = 0.05$).

The effect of β -phellandrene on the sex ratio of responding *I. pini* was variable. In experiment 1, the proportion of males in trap catches (mean \pm SE = 0.38 ± 0.013) was not affected by the presence of monoterpenes [ANOVA, $F(7, 32)$, $P = 0.5821$]. In experiment 2, the presence of ipsdienol in traps significantly reduced the proportion of males (Table 1, Figure 2B,D). β -Phellandrene did not affect the sex ratio of beetles caught, although the interaction

TABLE 2. ANALYSIS OF VARIANCE ON EFFECTS OF LOCATION (PRINCETON AND WILLIAMS LAKE, BC), RELEASE RATE OF IPSIDIENOL (6, 60, and 600 $\mu\text{g}/\text{day}$), AND OF β -PHELLANDRENE (3, 40, and 450 mg/day) ON NUMBER AND SEX RATIO OF *Ips pini* RESPONDING TO MULTIPLE-FUNNEL TRAPS (EXPERIMENT 3, 1988)

| Source | Trap catch ^a | | | Proportion of males ^b | | |
|---------------------------|-------------------------|-------|--------|----------------------------------|-------|--------|
| | df | F | P | df | F | P |
| Location (A) | 1 | 15.45 | 0.001 | 1 | 5.18 | 0.035 |
| Ipsdienol (B) | 2 | 48.08 | <0.001 | 2 | 17.79 | <0.001 |
| β -Phellandrene (C) | 2 | 17.57 | <0.001 | 2 | 0.64 | 0.538 |
| A * B | 2 | 4.93 | 0.020 | 2 | 0.16 | 0.857 |
| A * C | 2 | 0.83 | 0.454 | 2 | 0.46 | 0.641 |
| B * C | 4 | 0.73 | 0.582 | 4 | 1.32 | 0.299 |
| A * B * C | 4 | 0.56 | 0.698 | 4 | 0.96 | 0.456 |
| Error | 18 | | | 18 | | |

^aData transformed by $\ln(Y + 1)$.

^bData transformed by $\arcsin\sqrt{Y}$.

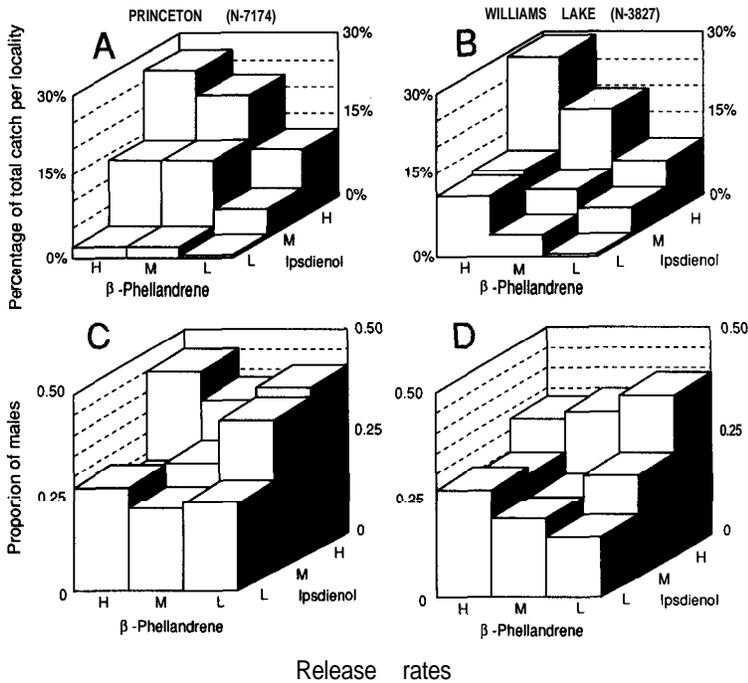


FIG. 3. The interaction between β -phellandrene and ipsdienol on the attraction (A,B) and sex ratio (C,D) of *Ips pini* responding to multiple-funnel traps in experiment 3 near Princeton (A,C) and Williams Lake (B,D) from August 19 to September 1, 1988 and August 27-31, 1988, respectively. Release rates were 3(L), 40(M), and 450(H) mg/day for β -phellandrene and 6(L), 60(M), and 600(H) $\mu\text{g}/\text{day}$ for ipsdienol.

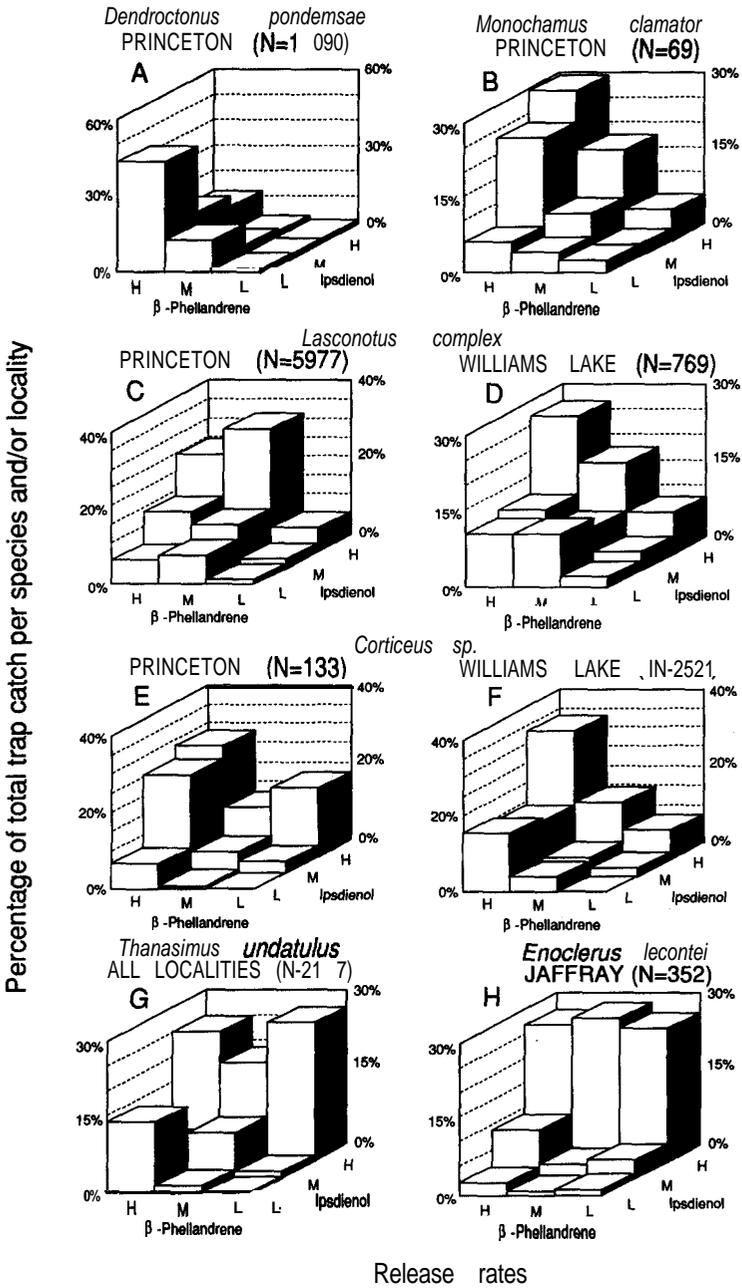


TABLE 3. ANALYSIS OF VARIANCE ON EFFECTS OF RELEASE RATE OF IPSDIENOL (6, 60, and 600 μ g/day) AND OF β -PHELLANDRENE (3, 40, and 450 mg/day) ON ATTRACTION OF *D.* AND *M. clamator* TO MULTIPLE-FUNNEL TRAPS (EXPERIMENT 3, 1988)

| Source | <i>Dendroctonus ponderosae</i> ^a | | | <i>Enoclerus lecontei</i> ^b | | | <i>Monochamus clamator</i> ^a | | |
|---------------------------|---|--------------|--------|--|-------------|--------|---|------|-------|
| | df | F | P | df | F | P | df | F | P |
| Ipsdienol (a) | 2 | 1.92 | 0.208 | 2 | 129.43 | <0.001 | 2 | 2.32 | 0.154 |
| β -Phellandrene (B) | 2 | 28.11 | <0.001 | 2 | 1.28 | 0.325 | 2 | 3.28 | 0.085 |
| A*B | 4 | 0.23 | 0.912 | 4 | 0.95 | 0.478 | 4 | 0.58 | 0.683 |
| Error | 8 | | | 9 | | | 9 | | |

^aPrinceton, BC.

^bJaffray, BC.

between ipsdienol and β -phellandrene was weakly significant. In contrast, the proportion of males caught in traps in experiment 3 increased with an increase in release rate of ipsdienol but showed no effect due to the release rate of β -phellandrene (Table 2, Figure 3C,D).

The mountain pine beetle, *Dendroctonus ponderosae*, was the only other scolytid trapped in large numbers (Figure 4A). In experiment 3, catches of *D. ponderosae* increased as the release rate of β -phellandrene increased (Table 3, Figure 4A). Conn et al. (1983) found that β -phellandrene had no effect on *D. ponderosae*. However, they employed low release rates (7 mg per day), comparable to our lowest release rate which showed little effect.

In experiments 2 and 3, species of Cleridae, Colydiidae, Tenebrionidae, and Cerambycidae (Coleoptera) showed significant responses to the presence of β -phellandrene and/or ipsdienol. Clerids showed a consistent preference for ipsdienol in both experiments. In experiment 2, *T. undatulus*, *Enoclerus sphegeus* F., and *E. Zecontei* Wolcott were caught preferentially in traps baited with ipsdienol (Table 4). In experiment 3, *T. undatulus* and *E. Zecontei* showed increased

FIG. 4. The interaction of β -phellandrene and ipsdienol on the attraction of *D. ponderosae* (Scolytidae), *M. clamator* (Cerambycidae), *L. complex* (Colydiidae), a *Corticeus* sp. (Tenebrionidae), *T. undatulus* (Cleridae), and *E. Zecontei* (Cleridae) to multiple-funnel traps in experiment 3 near Princeton, Jaffray, and/or Williams Lake, BC, from August 19 to September 1, 1988, August 25 to September 27, 1988, and August 27 to 31, 1988, respectively. Release rates were 3(L), 40(M) and 450(H) mg/day for β -phellandrene and 6(L), 60(M), and 600(H) μ g/day for ipsdienol.

TABLE 4. EFFECT OF β -PHELLANDRENE WITH AND WITHOUT IPSIDIENOL ON IPSON ATTRACTION OF *L. complex*, *T. undatulus*, *E. sphegeus*, AND *E. lecontei* TO MULTIPLE-FUNNEL TRAPS (EXPERIMENT 2, 1988)

| | Mean (\pm SE) catch per week ^a | | | |
|--|--|--|--|--|
| | <i>Lasconotus complex</i> ^b | <i>Thanasimus undatulus</i> ^c | <i>Enoclerus sphegeus</i> ^d | <i>Enoclerus lecontei</i> ^e |
| Blank control | 0.4 \pm 0.29 a | 0.3 \pm 0.20 a | 0.0 \pm 0.00 a | 0.1 \pm 0.08 a |
| β -Phellandrene (59 mg/day) | 1.2 \pm 1.17 a | 0.1 \pm 0.14 a | 1.2 \pm 0.58 ab | 0.1 \pm 0.08 a |
| β -Phellandrene (450 mg/day) | 17.5 \pm 7.99 b | 0.7 \pm 0.44 a | 1.2 \pm 0.58 ab | 0.6 \pm 0.46 ab |
| Ipsdienol | 141.1 \pm 69.80 c | 3.7 \pm 0.98 b | 6.4 \pm 3.09 c | 2.8 \pm 0.90 bc |
| Ipsdienol + β -phellandrene (59 mg/day) | 350.9 \pm 129.71 cd | 1.8 \pm 0.47 b | 5.3 \pm 2.02 bc | 5.6 \pm 2.51 c |
| Ipsdienol + β -phellandrene (450 mg/day) | 377.5 \pm 118.31 d | 3.7 \pm 1.49 b | 9.3 \pm 2.92 c | 2.7 \pm 1.34 abc |

^aCatches were standardized for an interval of one week. Means within a column followed by different letters are significantly different at $P = 0.05$ [Duncan's multiple-range test on data transformed by $\ln(Y + 1)$].

^bPooled for Princeton and Williams Lake, BC ($N = 6$).

^cPooled for Princeton, Jaffray, and Williams Lake, BC ($N = 9$).

^dWilliams Lake, BC ($N = 3$).

^eJaffray, BC ($N = 3$).

attraction to traps as the release rate of ipsdienol increased (Tables 3 and 5, Figure 4G,H). There were no significant effects due to locality, β -phellandrene, or interactions.

In contrast, two other potential predators or competitors, *L. complex* (Colydiidae) and a *Corticeus* sp., nr. *strublei* Blaisdell, (Tenebrionidae) were affected by both ipsdienol and β -phellandrene. In experiment 2, significantly more *L. complex* were caught in traps baited with ipsdienol than in traps not baited with ipsdienol (Table 4). More beetles were caught in traps with β -phellandrene released at a high rate than in the blank controls; the most preferred treatment was ipsdienol with a high release rate of β -phellandrene. The interaction between β -phellandrene and ipsdienol was additive, not synergistic or inhibitory [ANOVA, $F(2, 24)$, $P = 0.1911$. In experiment 3, trap catches of both *L. complex* and the *Corticeus* sp. increased as release rates of ipsdienol and β -phellandrene increased (Figure 4C-F). There were significant interactions between location and both ipsdienol and β -phellandrene for *L. complex* (Table 5). As in experiment 2, the interaction between ipsdienol and β -phellandrene was additive for *L. complex*. However, the interaction between ipsdienol and β -phellandrene had a synergistic effect on catches of the *Corticeus* sp. The combination resulted in trap catches greater than the sum of the proportional increases. The increased attraction of *Monochamus clamator* (LeConte) (Cerambycidae) to increasing release rates of β -phellandrene was weakly significant (Table 3, Figure 4B).

TABLE 5. ANALYSIS OF VARIANCE ON EFFECTS OF LOCATION, RELEASE RATE OF IPSDIENOL (6, 60, and 600 $\mu\text{g/day}$) AND OF β -PHELLANDRENE (3, 40, and 450 mg/day) ON ATTRACTION OF *T. undatulus*, *L. complex*, AND *Corticeus* SP. (TENEBRIONIDAE) TO MULTIPLE-FUNNEL TRAPS (Experiment 3, 1988)"

| Source | <i>Thanasimus undatulus</i> ^b | | | <i>Lasconotus complex</i> ^b | | | <i>Corticeus</i> sp. ^c | | |
|---------------------------|--|-------|--------|--|-------|--------|-----------------------------------|--------|--------|
| | df | F | P | df | F | P | df | F | P |
| Location (A) | 2 | 2.87 | 0.074 | 1 | 88.44 | <0.001 | 1 | 131.36 | <0.001 |
| Ipsdienol (B) | 2 | 19.27 | <0.001 | 2 | 18.45 | <0.001 | 2 | 67.61 | <0.001 |
| β -Phellandrene (C) | 2 | 1.08 | 0.353 | 2 | 21.37 | <0.001 | 2 | 127.86 | <0.001 |
| A*B | 4 | 1.37 | 0.270 | 2 | 4.63 | 0.024 | 2 | 5.28 | 0.23 |
| A*C | 4 | 0.60 | 0.663 | 2 | 5.45 | 0.014 | 2 | 3.54 | 0.62 |
| B*C | 4 | 0.82 | 0.525 | 4 | 0.16 | 0.955 | 4 | 11.01 | <0.001 |
| A*B*C | 8 | 0.56 | 0.798 | 4 | 0.35 | 0.841 | 3 | 0.53 | 0.669 |
| Error | 27 | | | 18 | | | 12 | | |

^aLocations were Princeton, Jaffray, and Williams Lake, BC, for *T. undatulus*, and Princeton and Williams Lake, BC, for *L. complex* and *C. strublei*.

^bData transformed by $\sqrt[3]{Y}$.

^cData transformed by $\ln(Y + 1)$.

DISCUSSION

Our results support the hypothesis that β -phellandrene is used as a host kairomone by *I. pini*. Traps with baits releasing β -phellandrene at a high rate were more attractive to *I. pini* than blank control traps (Fig. 2A,B). β -Phellandrene significantly increased catches of *I. pini* to traps baited with ipsdienol (Table 1, Figures 2C, 3A,B) except for one location on one occasion when it failed to substantiate these results (Figure 2A). Conclusive support of this hypothesis requires the determination of the volatiles actually released from host material suitable for *I. pini*.

The effect of the interaction between ipsdienol and β -phellandrene on the response of *I. pini* was additive, according to ANOVA. Similarly, *I. Zatidens* showed an additive effect to the combination of its pheromone, ipsenol, and β -phellandrene (Miller and Borden, 1990). There is no evidence of either synergy or saturation in responses by either species. In both cases, the proportional increase in response due to the presence of β -phellandrene was the same with the respective pheromone as without it.

β -Phellandrene is a general kairomone for many species breeding in lodgepole pine. In addition to *I. pini*, we found that *D. ponderosae*, *L. complex*, a *Corticus* sp., and *M. clamator* also were attracted to β -phellandrene. Miller and Borden (1990) found that *I. latidens*, *I. mexicanus* (Hopkins), *Hylastes longicollis* Swaine, and *Hylurgops porosus* (LeConte) also were attracted to traps baited with β -phellandrene. All nine species breed in lodgepole pine and are attracted by the most abundant monoterpene in its phloem tissue (Shrimpton, 1972). It seems probable that β -phellandrene also should be important for many other species breeding in conifers with high proportions of β -phellandrene in their phloem tissues. β -Phellandrene has the potential of becoming an important and critical component of many commercial baits for bark beetles, particularly since predators such as clerids are not attracted (Tables 3-5). Unfortunately, β -phellandrene is not commercially available.

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