THE USE OF MONOTERPENES AS KAIROMONES BY *IPS LATZDENS* (LECONTE) (COLEOPTERA: SCOLYTIDAE)

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Abstract

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The responses of *Ips lutidens* (LeConte) to multiple-funnel traps baited with various monoterpenes were determined in stands of lodgepole pine in British Columbia. β-Phellandrene was attractive to *I. lutidens* in the absence of the pheromone ipsenol. β-Phellandrene increased the attraction of *I. lutidens* to ipsenol-baited traps while α-pinene, 3-carene, terpinolene, and myrcene reduced trap catches. Differential responses by males and females to sources of ipsenol with or without β-phellandrene suggest that the information conveyed to males differs from that conveyed to females. Species-specific responses to monoterpenes by *I. lutidens* and three sympatric species of scolytids suggest that unique combinations of kairomones could be important in facilitating matings with conspecifics. Pheromones need not be the sole constituent of species-specific chemical messages.

Résumé

La réponse d’*Ips lutidens* (LeConte) à divers monoterpenes places dans des pièges à entonnoirs multiples a été déterminée dans des peuplements de pin lodgepole en Colombie britannique. β-Phellandrène a attire *I. latidens* en absence de la pheromone ipsenol. β-Phellandrène a accru l’attraction de *I. Zutidens* vers des pièges contenant ipsenol alors que α-pinène, 3-carène, terpinolene et myrcbne ont réduit les captures. Des niveaux de réponse différents pour males et femelles à des sources d’ipsénol, avec ou sans β-phellandrène, suggbrent que l’information transmise aux males diffère de celle transmise aux femelles. L’existence de réponses aux monoterpbnes spécifiques à l’espèce, pour *I. lutidens* et trois espbces sympatriques de scolytes, suggèrent que des combinaisons uniques de kairomones pourraient Ctre importantes dans la facilitation de l’accouplement avec des individus con-spécifiques. Les pheromones ne sont pas nécessairement les seules composantes des messages chimiques spécifiques à l’espèce.

Introduction

In British Columbia, the bark beetle, *Ips Zutidens* (LeConte), feeds and breeds in the phloem tissue of lodgepole and ponderosa pines, *Pinus contortu* var. *latifolia* Engelmann and *P. ponderosu* Douglas ex Lawson, respectively (Bright 1976; Fumiss and Carolin 1980; Wood 1982). *Ips lutidens* aggregates on suitable hosts in response to the male-produced pheromone ipsenol (2-methyl-6-methylene-7-octen-4-ol) (Wood *et al.* 1967; Fumiss and Livingston 1979; S.J. Seybold personal communication; unpublished data). As well, primary attraction of *I. lutidens* to lodgepole pine has been demonstrated in British Columbia, although the kairomones were not identified (Miller *et al.* 1986). Beetles preferentially landed on trees stressed by girdling of the phloem tissue at a height of 3.5–4.0 m above ground. Monoterpenes are abundant in phloem tissue of lodgepole pine (Shrimpton 1972, 1973) and are used as kairomones by scolytids in genera other than *Ips* (Borden 1982; Byers *et* al. 1985; Byers *et* al. 1988; Chénier and Philogbne 1989; Dickens *et* al. 1984; Schroeder 1988; Schroeder and Eidmann 1987; Schroeder and Lindelöw 1989; Volz 1988). It seems probable, therefore, that monoterpenes may also play a role as kairomones for *I. Zutidens.* Because β-phellandrene is the most abundant monoterpene in phloem of lodgepole pine, it should be the most likely candidate.

Our objective was to test the hypothesis that in stands of lodgepole pine in British Columbia, monoterpenes found in the phloem tissue of lodgepole pines, particularly β-phellandrene, are used as kairomones by *I. lutidens.*

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Materials and Methods

Chemicals. (+)-3-Carene, (−)-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 (chemical purity, 98%) was obtained from Phero Tech Inc. (Vancouver, B.C.). Racemic ipsenol (chemical purity, 98%) was obtained from Bedoukian Research Inc. (Danbury, CT).

Release Devices. Monoterpenes were released from closed, polyethylene micro-centrifuge tubes (400 μL) (Evergreen Scientific, Los Angeles, CA), each filled with a single monoterpene. The release rates for a-pinene, β-pinene, myrcene, 3-carene, β-phellandrene, and terpinolene were approximately 8.9, 9.3, 22.3, 22.9, 29.3, and 29.5 mg per day, respectively, at 27°C (determined by weight reduction). An ipsenol release device consisted of a 10-cm length of C-flex@ tubing (ID = 1.6 mm; OD = 3.2 mm) (Concept Inc., Clearwater, FL), filled with a solution of ipsenol in ethanol, or plain ethanol (99%) for ethanol controls, and heat-pressure sealed at both ends. The release rate of ipsenol was approximately 0.6 mg per day at 24°C (determined by collection of volatiles on Porapaq-Q).

Trapping Experiments. In all experiments, grids of g-unit, multiple-funnel traps (Lindgren 1983) (Phero Tech Inc., Vancouver, B.C.) were set in mature stands of lodgepole pine near Princeton, B.C. Replicate grids were placed at least 100 m apart, and traps were spaced 10-15 m apart within each replicate grid. Each baited trap was suspended from a metal pole such that the top funnel of each trap was 1.3-l .5 m above ground.

The effects of various monoterpenes in combination with ipsenol were tested in Experiment 1. Ten replicates of nine traps per replicate were set in grids of 3 x 3, from 24 May to 2 July in 1987. The treatments were as follows: (1) blank control; (2) ethanol control; (3) racemic ipsenol; (4) ipsenol with 3-carene; (5) ipsenol with myrcene; (6) ipsenol with β-phellandrene; (7) ipsenol with α-pinene; (8) ipsenol with β-pinene; and (9) ipsenol with terpinolene.

Experiment 2 compared the effect of β-phellandrene with that of the combination of the other five monoterpenes, with and without ipsenol. Ten replicates of eight traps each were set in grids of 2 x 4, from 25 May to 2 July 1987. The treatments were as follows: (1) ethanol control; (2) β-phellandrene alone; (3) combination of 3-carene, myrcene, α-pinene, β-pinene, and terpinolene; (4) all six monoterpenes; (5) racemic ipsenol alone; (6) ipsenol with β-phellandrene; (7) ipsenol with 3-carene, myrcene, a-pinene, β-pinene, and terpinolene; and (8) ipsenol with all six monoterpenes.

Statistical Analyses. The data were analyzed using the SAS statistical package ver. 5.0 (SAS Institute Inc., Cary, NC). When necessary, trap catch data were transformed to remove heteroscedasticity. In Experiment 1, catches of *I. latidens*, *Hylastes longicollis* Swaine, and *I. mexicanus* (Hopkins) were transformed by ln(Y+ 1). In Experiment 2, catches of *I. latidens* were transformed by $\sqrt[3]{Y}$ and those of *I. mexicanus* were transformed by ln(Y + 1). Sex ratio and all remaining catch data were not transformed. Homoscedastic data were subjected to one-way ANOVA and Duncan's multiple range test when $P<0.05$. In Experiment 1, a *priori* multiple contrasts were also performed on the trap catch data for *I. latidens, I. mexicanus, H. longicollis*, and *Hylurgops porosus* LeConte. In Experiment 2, three-way full-factorial ANOVA was performed to determine interaction effects.

Results

Experiment 1. Ipsenol and Monoterpenes. Monoterpenes had a significant effect on the attraction of *I. latidens* to sources of ipsenol (Fig. 1). The combination of β-phellandrene and ipsenol was the preferred treatment, increasing trap catches by >100% relative to ipsenol alone. Multiple contrasts discerned groupings in the data. The catches in traps baited with ipsenol and either 3-carene, myrcene, a-pinene, or terpinolene seemed to be

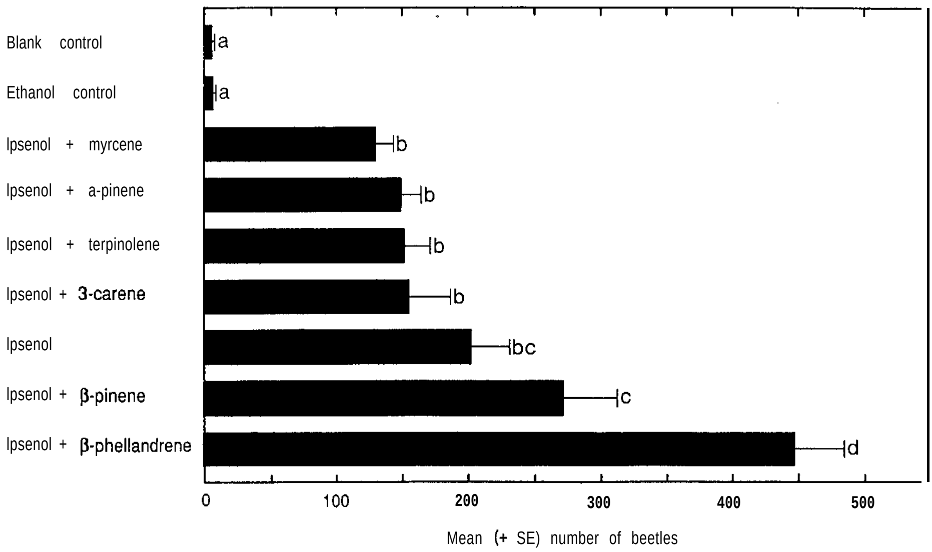

FIG. 1. The effects of various monoterpenes on the attraction of *Ips latidens* to ipsenol-baited multiple-funnel traps near Princeton, B.C., from 24 May to 2 July 1987 ($N = 10$). Means followed by the same letter are not significantly different at $P = 0.05$ [Duncan's multiple range test on data transformed by $\ln(Y + 1)$].

similar. As a group, their trap catches were compared with that of traps baited with ipsenol alone and the reduction was found to be weakly significant (multiple contrast ANOVA, $P = 0.074$). There was no significant difference in the sex ratio of *I. latidens* among the different treatments [ANOVA, $F(7,49)$, $P = 0.9221$. The mean (± SE) proportion of males in traps baited with ipsenol was 0.16 ± 0.010, significantly different from a 1:1 ratio (t-test, $P < 0.001$, df = 69).

Hylurgops porosus, H. longicollis, and ***I. mexicanus*** showed significant differences due to treatments [ANOVA, $F(8,80)$, $P = 0.020$, $P < 0.001$, and $P < 0.001$, respectively]. β-Phellandrene and 3-carene increased catches of all three species (Table 1). *Hylastes longicollis* showed a strong preference for traps baited with 3-carene (Table 1). Terpinolene

Table 1. The effect of monoterpenes on the attraction of ***Ips mexicanus, Hylurgops porosus***, and ***Hylastes longicollis*** to ipsenol-baited multiple-funnel traps, near Princeton, B.C., 25 May to 2 July 1987 ($N = 10$)

	Mean (± SE) number of beetles*			
Treatments	*Ips mexicanus*	*Hylurgops porosus*†		*Hylastes longicollis*
Blank control	0±0.2	11±3.1		6±1.7
Ethanol control	0±0.2	17±4.5		6±0.9
Ipsenol	3±1.1	16±4.6		4±0.9
Ipsenol + a-pinene	5±1.6	15k3.8		3±0.8
Ipsenol + myrcene	2±0.5	15±3.2		7±0.8
Ipsenol + β-pinene	5±1.3	15±3.3		11±1.6
Ipsenol + terpinolene	2±0.5	24k7.5	0.027	10±1.8
Ipsenol + β-phellandrene	23k3.2	37±6.5	(P = ~~0.27~~)	8±1.1
Ipsenol + 3-carene	16±3.1	31±6.7		32±4.9]‡

*Means within a column grouped by a line are significantly different from the ipsenol treatment at $P < 0.001$ unless otherwise noted [multiple contrasts ANOVA, $F(1,71)$ on data transformed by $\ln(Y + 1)$].

†Data not transformed for analyses.

‡Significantly different from the group of ipsenol + myrcene, ipsenol + β-pinene, ipsenol + terpinolene, and ipsenol + β-phellandrene ($P < 0.001$).

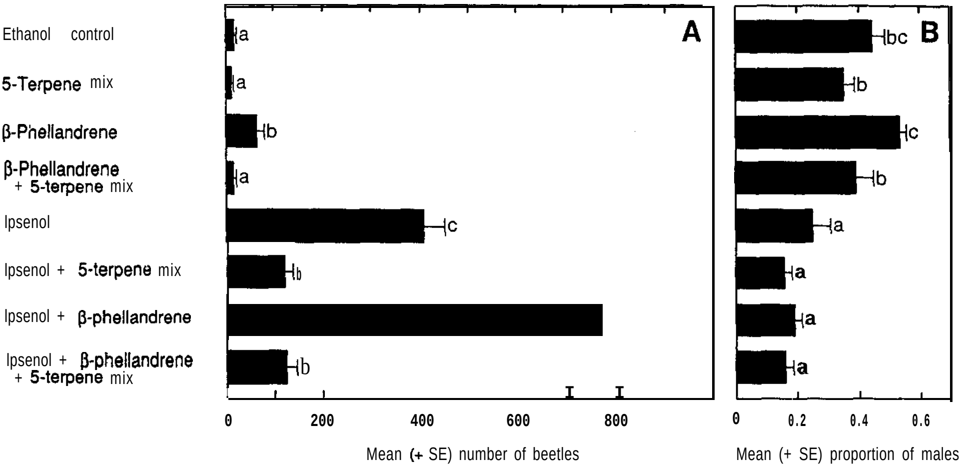

FIG. 2. The interaction between β-phellandrene, a five-terpene mix of 3-carene, a-pinene, β-pinene, terpinolene, and myrcene, and racemic ipsenol on the attraction (A) and sex ratio (B) of *Ips latidens* responding to multiple-funnel traps near Princeton, B.C., from 25 May to 2 July 1987 ($N = 10$). Means followed by the same letter are not significantly different at $P = 0.05$ (Duncan's multiple range test). Catch numbers were transformed by $\sqrt[3]{Y}$ for analyses.

increased catches of ***H. porosus*** and ***H. longicollis*** relative to traps baited with ipsenol alone; the later species showed attraction to sources of myrcene and β-pinene as well. Only ***I. mexicanus*** showed any attraction to sources of ipsenol alone.

Experiment 2. Ipsenol and β-Phellandrene. *Ips latidens* was attracted to traps baited with β-phellandrene, even without ipsenol. β-Phellandrene with ipsenol was significantly more attractive than all other treatments (Fig. 2A). The interaction between ipsenol and β-phellandrene appears to be additive and not synergistic [ANOVA, $F(1,71)$, $P = 0.937$]. The relative increase in trap catches between the ethanol control and β-phellandrene is similar to the relative increase between ipsenol and ipsenol with β-phellandrene. Similarly, the relative increase in trap catches due to ipsenol was the same whether β-phellandrene was absent or present. Sources of the five-terpene mix of 3-carene, myrcene, α-pinene, β-pinene, and terpinolene were not attractive and inhibited responses of ***I. latidens*** to ipsenol, β-phellandrene, and the combination of ipsenol with β-phellandrene. Inhibition by the five-terpene mix is consistent with the weak inhibition demonstrated by four of the five monoterpenes in Experiment 1 (Fig. 1).

The proportions of male ***I. Zatidens*** responding to traps baited with only monoterpenes were not significantly different from that to the ethanol control, although proportionally fewer males responded to the five-terpene mix than to β-phellandrene (Fig. 2B). Whenever ipsenol was present, the sex ratio became strongly female biased, regardless of the monoterpene additives. There were weakly significant interactions between ipsenol and β-phellandrene, and between ipsenol and the five-terpene mix [ANOVA, $F(1,54)$, $P = 0.090$ and $P = 0.038$, respectively]. In both cases, the proportion of females tended to increase when ipsenol was presented with monoterpenes.

Zps mexicanus was attracted, ***albeit*** in low numbers (all trap catches <10), to sources of β-phellandrene and ipsenol [ANOVA, $F(1,71)$, ***P-CO.001*** and $P<0.001$, respectively]; the preferred treatment was the combination of β-phellandrene and ipsenol (mean ± SE = 26 ± 13.0) (Duncan's multiple range test, $P<0.05$). The interaction between ipsenol and β-phellandrene was additive, not synergistic [ANOVA, $F(1,71)$, ***P = 0.1961.***

Discussion

Our results support the hypothesis that host kairomones are used by *I.* ***lutidens*** (Fig. 1). β-Phellandrene was attractive alone and increased attraction to sources of ipsenol (Fig. 2A). In contrast, the four other monoterpenes negated the effects of β-phellandrene (Fig. 2A). The combination of all six monoterpenes with ipsenol significantly reduced trap catches relative to traps baited with ipsenol alone. These results are the clearest demonstration that monoterpenes are used as kairomones by a species of *Ips* since monoterpenes were implicated as attractants for *I. typographus* L. (Rudinsky ***et*** al. 1971*a*, 1971*b*; Tomescu *et* al. 1979) and *I.* ***grundicollis*** (Eichhoff) (Werner 1972*a*, 1972*c*). Conclusive support of this hypothesis requires the determination of the volatiles actually released from host material suitable for *I.* ***lutidens.***

Ips lutidens seems to prefer phloem drier than that used by *I. pini* (Miller and Borden 1985). β-Phellandrene is the major monoterpene in phloem of lodgepole pine (Shrimpton 1972, 1973). As phloem dries, therefore, it would be the most likely to remain above the threshold level required for perception at some distance from a potential host. In fresh hosts, other monoterpenes may be present at levels above thresholds and may indicate non-preferred phloem conditions.

Zps lutidens does not show a sex-specific response to sources of monoterpenes (Fig. 2B). The sex ratio of *I.* ***lutidens*** emerging from infested lodgepole pine is approximately 1: 1 (Miller and Borden 1985). The sex ratio of *I.* ***lutidens*** caught in control traps was not significantly different from 1: 1 (t-test, $P = 0.26$, df = 3). Similarly, ***D.*** *pseudotsugae* Hopkins (Furniss and Schmitz 1971) and ***Tomicus piniperdu*** (L.) (Byers ***et al.*** 1985) do not show sexual specificity in their responses to monoterpenes. Kairomones probably convey contextual information about the environment and therefore should not necessarily be expected to be sex-specific.

In contrast, *I.* ***lutidens*** did exhibit a strong female bias in response to ipsenol-baited traps (Fig. 2B). This sex-specificity in responses to ipsenol does reflect differential benefits to females and males, as in the six-spined spruce bark beetle, *Pityogenes* ***chulcogruphus*** L., in Europe (Byers ***et al.*** 1988).

In polygynous species of bark beetles, such as ***I. lutidens*** and ***P. chulcogruphus,*** the production of pheromone by males, particularly in the presence of monoterpenes, signifies to females that there are galleries available for breeding. As long as pheromone is produced, females should have galleries to enter, particularly since several females can join the same male (Kirkendall 1983). Males, on the other hand, are looking for access to suitable breeding material in order to gain access to females. Sources of pheromone are attractive because males can usually establish galleries in adjacent phloem on the same log or tree. However, the number of available sites is limited and the relative benefits to males should decrease as the available sites are taken; benefits to females should not be expected to decrease. The production of pheromone should increase as more males establish galleries. Increases in the attraction of males may still occur but not to the same extent as increases in the attraction of females, as occurs in *I. paraconfusus* Lanier and *P. chalcographus* (Byers 1983; Byers ***et al.*** 1988). Schlyter ***et al.*** (1987) found that significantly more female than male *I.* ***typogruphus*** (L.) landed on pheromone-baited traps, even though both sexes showed equal long-distance attraction to the same pheromone sources.

When all sites are occupied by males, then males will no longer benefit by responding to pheromone sources. However, females will still benefit as the continued production of pheromones probably signifies that some males are still looking for females. Pheromone production by males of three polygynous species, ***I.*** *paraconfusus,* ***I. grundicollis*** (Eichhoff), and *I. calligraphus* (Germar), seems to decrease as males acquire females, and apparently ceases as harems are filled (Borden 1967; Werner 1972b; Svihra 1982).

Table 2. The relative effects of monoterpenes on the attraction of four sympatric species of Scolytidae in stands of lodgepole pine near Princeton, B.C. Repellency signified by − ; no effect by 0; mild attraction by + ; and strong attraction by + +

Monoterpene	*Ips latidens*	*Ips mexicanus*	*Hylurgops porosus*	*Hylastes longicollis*
a-Pinene	−	0	0	0
β-Pinene	0	0	0	+
Myrcene	−	0	0	+
Terpinolene	−	0	+	+
3-Carene		+	+	+ +
β-Phellandrene	+ +	+	+	+

Primary attraction to high-girdled lodgepole pine has been demonstrated for *H. longicollis* (misidentified as *H. gracilis*) (Miller *et* al. 1986). Harrington (1983) found that ***H. longicollis*** and ***H. porosus*** were preferentially attracted to stumps and wounded stems of ponderosa pine. The response of these species to monoterpenes, particularly 3-carene (Table 1), could provide the basis for primary attraction. Furthermore, our results strongly suggest that responses to kairomones can be species-specific. Of four species examined, specific preferences were found in all four on the basis of monoterpenes alone (Table 2). Pheromones need not be the sole constituent of species-specific chemical messages.

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