DOSE-DEPENDENT AND SPECIES-SPECIFIC RESPONSES OF PINE BARK BEETLES (COLEOPTERA: SCOLYTIDAE) TO MONOTERPENES IN ASSOCIATION WITH PHEROMONES

DANIEL R MILLER' and JOHN H BORDEN

Centre for Environmental Biology, Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia, Canada V5A lS6

Abstract

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Monoterpenes affected the attraction of three sympatric species of bark beetles (Coleoptera: Scolytidae) to pheromone-baited multiple-funnel traps in stands of lodgepole pine. Catches of *Ips pini* (Say) in traps baited with its pheromone, ipsdienol, were directly related to the release rates of 3-carene, pphellandrene, and β-pinene. Catches of *Dendroctonus ponderosae* Hopkins in traps baited with exo-brevicomin and cis- and trans-verbenol were directly related to the release rates of 3-carene, myrcene, and β-phellandrene. *Ips Zatidens* (LeConte) exhibited preferences for traps baited with ipsenol and β-phellandrene or β-pinene but not in a dose-dependent fashion. Catches of *I. latidens* in traps baited with its pheromone, ipsenol, were inversely proportional to the release rates of 3-carene, myrcene, and terpinolene. Similarly, catches of *I. pini* in traps baited with its pheromone, ipsdienol, were inversely proportional to the release rates of myrcene and terpinolene. These results demonstrate a degree of species specificity among three phloeophagous species with respect to preferred host odours. The bark beetle predators-associates *Lusconotus complex* LeConte (Coleoptera: Colydiidae) and *Corticeus* Piller and Mitterpacher sp. (Coleoptera: Tenebrionidae) demonstrated some measure of specificity to monoterpenes in their responses to ipsdienol-baited funnel traps. y-Terpinene increased attraction of *L. complex* but had no effect on *Corticeus* sp., whereas a- and β-pinene increased attraction of *Corticeus* sp. but had no effect on *L. complex.*

Miller DR, Borden JH. 2000. Réactions spécifiques à la dose et à l'espèce chez des scolytes des pins (Coleoptera; Scolytidae) mis en présence de monoterpènes combinés à des phéromones. *The Canadian Entomologist* 132 : 183–195.

Résumé

La presence de monoterpbnes a modifié l'attirance de pièges à entonnoirs multiples garnis de pheromones pour trois espbces sympatriques de scolytes des pins (Coleoptera : Scolytidae) dans une for&t de pins à feuilles tordues. Les récoltes d'*Ips pini* (Say) dans les pièges garnis de la pheromone même de l'insecte, l'ipsdienol, Ctaient reliées directement aux taux de liberation de 3-carène, de β-pheilandrène et de β-pinène. Les récoltes de *Dendroctonus ponderosae* Hopkins dans les pièges garnis d'*exo*-brévicomine et de *cis*- et trans-verbenol Ctaient en correlation avec les taux de liberation de 3-carène, de myrcene et de β-pheilandrène. *Ips latidens* (LeConte) a manifesté une preference pour les pibges garnis d'ipsénol et de β-pheilandrène ou β-pinène, mais indépendamment de la dose. Les récoltes d'*I. latidens* dans les pièges garnis de la pheromone de cet insecte, l'ipsénol, se sont avérées inversement proportionnelles aux taux de liberation de 3-carène, de myrcene et de terpinolene. De même, les captures d'*I. pini* dans les pièges garnis de sa pheromone, l'ipsdiénol, étaient inversement proportionnelles aux taux de liberation de myrcene et de terpinolène. Ces résultats démontrent l'existence d'une certaine spécificité chez chacune de ces trois espèces phloéophages quant aux odeurs d'hôtes qu'elles préfèrent. Les

[1] Author to whom all correspondence should be sent at the following address: Forestry Sciences Laboratory, Southern Research Station, USDA Forest Service, 320 Green Street, Athens, Georgia 30602.2044, United States (E-mail: dmiller/srs_athens@fs.fed.us).

prédateurs/associés des scolytes *Lasconotus complex* LeConte (Coleoptera : Colydiidae) et *Corticeus* Piller et Mitterpacher sp. (Coleoptera : Tenebrionidae) ont démontré un certain degré de spécificité aux monoterpenes dans leurs reactions aux pièges à entonnoirs garnis d'ipsdiénol. L'y-terpinbne a augmenté l'attirance des pièges pour *L. complex* mais n'a pas eu d'effet sur *Corticeus* sp., alors que l'α-pinène et la β-pinène ont augmenté l'attirance des pibges pour *Corticeus* sp., mais pas pour *L. complex*.

[Traduit par la Redaction]

Introduction

Bark beetles (Coleoptera: Scolytidae) continue to be primary pests of coniferous forests throughout British Columbia (Maclauchlan and Brooks 1994). Losses of spruce to spruce beetles, *Dendroctonus rufipennis* (Kirby), have amounted to 10% of all spruce volumes harvested in British Columbia (Humphreys and Safranyik 1993); losses of Douglas-fir to the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins, have exceeded 2.5 million cubic metres over the past 20 years (Humphreys 1995). The most dramatic impact on forested lands has been caused by the mountain pine beetle, *Dendroctonus ponderosae* Hopkins, which has killed over 500 million pines trees in British Columbia during the past 80 years (Unger 1993).

Mortality of trees is conditional upon the success of bark beetles in overcoming the various defenses that trees employ for protection against fungi, bacteria, bark beetles, and other insects (Berryman 1969; Shrimpton and Watson 1971; Shrimpton 1978; Cates and Alexander 1982; Payne 1983; Raffa and Berryman 1987). In addition to primary resinosus from severed resin ducts, trees attempt to flood wounded areas with traumatic resin (induced resinosus), defining the boundaries of such areas with necrotic tissue. Compounds such as monoterpenes, particularly in traumatic resin, may be toxic to bark beetles (Smith 1963; Reid and Gates 1970; Coyne and Lott 1976; Cates and Alexander 1982; Payne 1983; Raffa and Berryman 1983; Raffa *et al.* 1985).

Several species of bark beetles use monoterpenes as attractive kairomones (Wood 1982; Volz 1988; Borden 1989; Byers 1989). Monoterpenes may be released at higher rates than normal when phloem tissue is stressed (Madden 1977) or when physical damage occurs to the tissue (e.g., lightning strikes, wind damage, or mass attacks by bark beetles) (Wood 1982; Byers 1989). Furthermore, various species use monoterpenes as precursors for pheromones, having developed mechanisms to detoxify low concentrations of selected monoterpenes (Francke and Vité 1983; Pierce *et al.* 1987; Vanderwel and Oehlschlager 1987; Byers 1989; Gijzen *et al.* 1993).

In southern British Columbia, three species of bark beetles commonly attack lodgepole pine, *Pinus contorta* var. *latifolia* Engelmann (Pinaceae): *Ips latidens* (LeConte), *Ips pini* (Say), and *Dendroctonus ponderosae*. β-Phellandrene is attractive to both *I. latidens* and *I. pini*, alone or in combination with their pheromones (Miller and Borden 1990*a*, 1990b). Attraction of *D. ponderosae* to its pheromones is increased by myrcene (Billings *et al.* 1976; Borden *et al.* 1987) and 3-carene (Conn *et al.* 1983), and possibly by a-pinene, camphene, and terpinolene (Pitman 1971; Billings *et al.* 1976). Both *I. pini* and *D. ponderosae* have receptor cells on their antennae keyed to various monoterpenes. Myrcene and a-pinene activate cells in antennae of *I. pini* (Angst and Lanier 1979; Mustaparta *et al.* 1979). Antennae of *D. ponderosae* respond to a-pinene, β-pinene, camphene, 3-carene, myrcene, and limonene (Whitehead 1986).

Our objective was to determine the effects of seven major pine monoterpenes (Mirov 1961; Shrimpton 1972, 1973) on the attraction of *I. latidens*, *I. pini*, and *D. ponderosae* to their respective pheromones in stands of lodgepole pine. We tested two hypotheses: (1) all three species would show dose-dependent responses (responses

that are directly or inversely proportional to release rates of monoterpenes); and (2) evidence of species specificity would be revealed by differing combinations of attractive or interruptive kairomones.

Materials and Methods

Twenty-one experiments were conducted in 1988 and 1989. The experiments attempted to determine the effects of 3-carene, myrcene, β-phellandrene, a-pinene, β-pinene, y-terpinene, and terpinolene on the responses of (1) to its pheromone, ipsenol (Exps. l-7); (2) *I. pini* to its pheromone, ipsdienol (Exps. 8-14); and (3) ***D. ponderosae*** to its pheromones exo-brevicomin and ***cis***- and trans-verbenol (Exps. 15-21). Experiments 1-7 and 15-21 were conducted near Princeton (49°27′N, 120°31′W), British Columbia, where population levels of *I.* ***latidens*** and ***D. ponderosae*** were high. In 1988, Experiments 8-14 were conducted near Williams Lake (52°08′N, 122°09′W), British Columbia, to exploit high population levels of ***I.*** *pini*. All experiments were set in mature stands of lodgepole pine.

In all experiments, replicates of six eight-unit, multiple-funnel traps (Lindgren 1983) (Phero Tech Inc., Delta, British Columbia) were set in grids of 2 x 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 top funnel of each trap was 1.3-1.5 m above ground. No trap was within 2 m of any tree.

Five replicate grids per experiment were set for Experiments l-5 and 7 during the periods of 13 June – 19 July 1989, 3 l May – 21 June 1989, 23 June – 22 July 1988, 10 May 3 June 1989, 10 May 13 June 1989, and 9-28 June 1989, respectively. Six replicate grids were set for Experiment 6 from 28 June to 19 July 1989. Treatments, randomly assigned within each replicate, were as follows: (1) a control treatment of ipsenol alone; and (2-6) five treatments consisting of ipsenol and one monoterpene. The monoterpene treatments within a replicate differed only in release rates (Table 1). In Experiments l-2 and 4-7, ipsenol was released from bubble-cap lures at 0.2-0.3 mg/d at 24°C (Phero Tech Inc.). In Experiment 3, ipsenol was released at about 0.6 mg/d at 24°C from 10-cm lengths of C-flex@ tubing (i.d. 1.6 mm, o.d. 3.2 mm) (Concept Inc., Clearwater, Florida), filled with an ethanol solution of ipsenol, and heat-pressure sealed at both ends (Phero Tech Inc.).

In 1988, five replicate grids per experiment were set for Experiments 8-14 during the periods of 29 August 7 September, 17-27 August, 9-18 August, 31 August – 7 September, 28 August – 7 September, 27-29 August, and 7-18 September, respectively. Treatments were as in Experiments l-7 (monoterpene release rates listed in Table 1) and ipsdienol replaced ipsenol. As with ipsenol in Experiment 3, ipsdienol was released from C-flex® lures at about 0.6 mg/d (Phero Tech Inc.).

Five replicate grids per experiment were set for Experiments 15-21 during the periods of 25 July – 10 August 1989, 14-24 August 1988, 4-14 August 1988, 19 July 10 August 1989, 19 July – 1 August 1989, 6 August – 2 September 1989, and 24 August – 1 September 1988, respectively. Treatments were as in Experiments 1-14 (monoterpene release rates listed in Table 1) and ipsenol and ipsdienol replaced with exo-brevicomin, and ***cis***- and trans-verbenol. The mix of ***cis***- and trans-verbenol was released from bubble-cap lures at a combined rate of about 1.74 mg/d at 24°C (determined by weight loss). In Experiments 16, 17, and 21, exo-brevicomin was released from glass capillary tube lures at about 0.15 mg/d at 20°C (determined by weight loss). In Experiments 15 and 18-20, exo-brevicomin was released from laminar lures at about 0.1 mg/d at 24°C (Phero Tech Inc.).

TABLE 1. Release rates of monoterpenes (mg/d at 27-30°C) targeted for *Zps latidens, Zps pini*, and *Dendroctonus ponderosae.*

Release rate class	3-Carene	Myrcene	β-Phellandrene	α-Pinene	β-Pinene	y-Terpinene	Terpinolene
				Ips latidens			
	Exp. 1	Exp. 2	Exp. 3	Exp. 4	Exp. 5	Exp. 6	Exp. 7
1	0.7	2.6	0.1	2.5	1.2	0.6	0.2
2	14.6	12.3	4.8	14.7	6.7	28.6	25.7
3	34.9	62.6	8.8	26.9	23.1	51.7	47.1
4	184	136	187	286	243	294	343
5	1217	1293	2084	1239	1199	2172	2065
				Ips pini			
	Exp. 8	Exp. 9	Exp. 10	Exp. 11	Exp. 12	Exp. 13	Exp. 14
1	0.7	2.6	2.1	2.5	1.2	0.6	0.2
2	4.8	9.4	4.8	14.7	6.7	2.3	0.6
3	17.4	47	8.8	26.9	23.1	25.8	23.6
4	184	136	44	286	243	294	343
5	1217	646	1042	1239	1199	2172	2065
				Dendroctonus uonderosae			
	Exp. 15	Exp. 16	Exp. 17	Exp. 18	Exp. 19	Exp. 20	Exp. 21
1	0.7	5.2	2.1	2.5	1.2	0.6	0.2
2	14.6	18.8	4.8	14.7	6.7	28.6	0.6
3	34.9	135.5	8.8	26.9	23.1	51.7	23.6
4	183	917	44	143	121	294	343
5	609	6463	1042	826	799	1086	2065

In 1988, (+)-3-carene, (–)-β-phellandrene, (–)-α-pinene, (–)-β-pinene, y-terpinene, and terpinolene (all chemical purities > 95%) were obtained from HD Pierce, Jr (Department of Chemistry, Simon Fraser University). In 1989, (+)-3-carene, (-)-a-pinene, (–)-β-pinene, and y-terpinene (all chemical purities > 95%) were obtained from Aldrich Chemical Co. (Milwaukee, Wisconsin) and terpinolene (chemical purity 94%) was obtained from D Vanderwel (Department of Chemistry, Simon Fraser University). Phero Tech Inc. supplied the following: (1) β-myrcene (chemical purity 98%); (2) (+)-ipsenol (chemical purity 98%); (3) (+)-ipsdienol (chemical purity 98%); (4) polyethylene bubble-cap lures containing (+)-ipsenol (chemical purity 98%) in 3-butanediol; (5) polyethylene bubble-cap lures containing a 13:87 mixture of *cis*- and *trans*-verbenol [both chemical purities 98%; both enantiomeric compositions 83:17 (-):(+)I; (6) laminar *exo*-brevicomin lures (chemical purity 98%); and (7) open polyethylene microcentrifuge tubes (400 mL) (Evergreen Scientific, Los Angeles, California), each containing a 3-cm-long glass capillary tube (i.d. 13 mm, o.d. 15 mm) filled with *exo*-brevicomin (chemical purity 98%).

The following devices were used to release monoterpenes: (1) open polypropylene microcentrifuge tubes (1.5 mL) (Quality Scientific Plastics, Petaluma, California), each containing one 2-cm-long glass capillary tube (i.d. 1.5 mm, o.d. 1.8 mm), sealed at one end and filled with a monoterpene; (2) open polypropylene microcentrifuge tubes (1.5 mL) (Quality Scientific Plastics), each containing live 2-cm-long glass capillary tubes (i.d. 1.5 mm, o.d. 1.8 mm), sealed at one end and filled with a monoterpene; (3) closed polyethylene microcentrifuge tubes (0.25 mL) (Evergreen Scientific) filled

with a monoterpene; (4) closed polyethylene microcentrifuge tubes (0.4 mL) (Evergreen Scientific) filled with a monoterpene; (5) closed polyethylene microcentrifuge tubes (1.8 mL) (Evergreen Scientific) filled with a monoterpene; (6) polyethylene transfer pipettes (3.5 mL) (Saint-Amand Mfg. Co., San Fernando, California) filled with a monoterpene and heat-pressure sealed; and (7) closed polyethylene screw-cap bottles (1.5 mL) (Ampak Inc., Richmond, British Columbia) filled with a monoterpene. The ranges of release rates (Table 1) were obtained through different numbers and combinations of lures to achieve an even distribution along a logarithmic scale. Some lure combinations were changed in 1989 because the rates determined concurrently with the experiments did not achieve this distribution.

For determinations of sex ratio in trap catches, subsamples (n = 30-50) of captured beetles from each experiment were taken at random from catches in traps baited with monoterpene rate classes 1, 3, and 5 (Table 1). Sexes of *I. pini* were determined using declivital characters (Lanier and Cameron 1969), whereas those of ***I. latidens*** and ***D. ponderosae*** were determined by dissection and examination of genitalia. Voucher specimens were deposited at the Entomology Museum, Simon Fraser University.

Trap catch data were analyzed using the SAS statistical package version 5.0 (SAS Institute Inc., Cary, North Carolina). One replicate in Experiment 19 was excluded from analyses because only 12 beetles were captured. Data were transformed by $\ln(Y)$ to remove heteroscedasticity and regressed against the release rate of monoterpene, transformed by $\ln(X)$, using a general linear model. Residuals were examined to ensure the appropriateness of a linear model and the range of the regression lines. The transformed data for each experiment were subjected to two-way analysis of variance (ANOVA) using replicate and treatment as model factors. In each experiment, five orthogonal comparisons were performed using protocols in Sokal and Rohlf (1981, pp. 233-242). Sex ratio data were analyzed by χ^2 tests of independence using the Minitab statistical package (Department of Statistics, Pennsylvania State University, University Park, Pennsylvania). Trap catch data for non-scolytid beetle species were analyzed by Fisher's least significant difference (LSD) test using the SYSTAT statistical package version 7.0 (SPSS Inc., Chicago, Illinois).

Results

All three species showed dose-dependent responses to 3-carene and myrcene (Figs. l-3). Catches of ***I. latidens*** were inversely proportional to the release rate of 3-carene (Fig. 1A), whereas those of *I. pini* and ***D. ponderosae*** were directly proportional (Figs. 2A, 3A). Catches of ***I. latidens*** in traps baited with 3-carene at the highest release rates were lower than those in the control traps ($F_{1,18}$ = 13.3 1, P = 0.002). Relative to control traps, traps baited with 3-carene at the two highest release rates caught more *I. pini* ($F_{1,24}$ = 38.22, $P < 0.001$; and $F_{1,24}$ = 49.01, $P < 0.001$, respectively). Traps baited with 3-carene at the highest rate caught more ***D. ponderosae*** than control traps ($F_{1,24}$ = **4.80, P = 0.040).**

Trap catches of both ***I. latidens*** and *I. pini* were inversely proportional to the release rate of myrcene (Figs. 1 B, 2B), whereas those of ***D. ponderosae*** were directly proportional (Fig. 3B). Relative to controls, traps baited with myrcene at the three highest release rates caught fewer ***I. latidens*** ($F_{1,18}$ = ***5.40, P = 0.035;*** $F_{1,18}$ = ***8.72, P =*** 0.010; and $F_{1,18}$ = 7.24, P = 0.017, respectively) and *I. pini* ($F_{1,23}$ = 12.35, ***P = 0.002;*** $F_{1,23}$ = 10.23, P = 0.005; and $F_{1,23}$ = 15.59, $P < 0.001$, respectively). Catches of ***D. ponderosae*** were higher in traps baited with myrcene at the two highest release rates than those in control traps ($F_{1,23}$ = 4.11, P = 0.042; and $F_{1,23}$ = 12.42, P = 0.002, respectively).

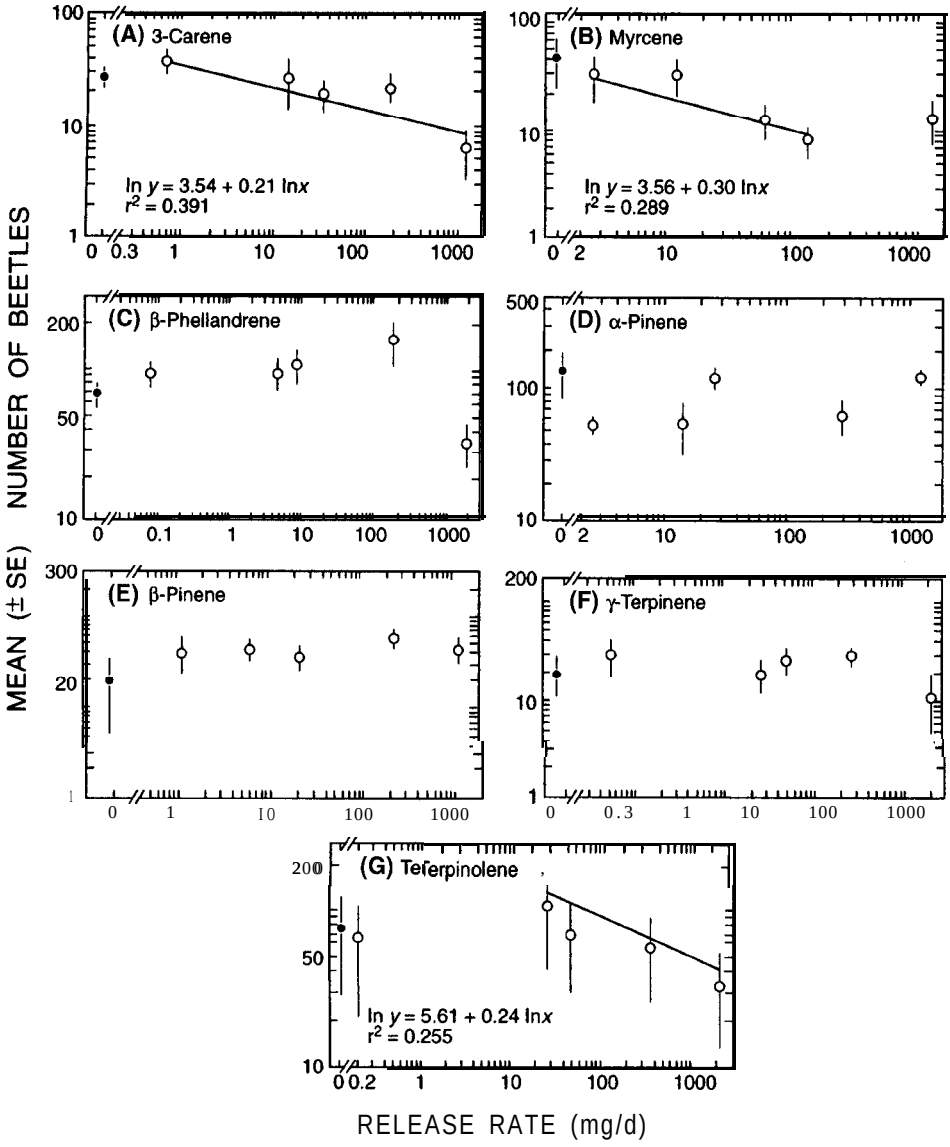

FIGURE 1. Effects of 3-carene (A), myrcene (B), β-phellandrene (C), a-pinene (D), β-pinene (E), γ-terpinene (F), and terpinolene (G) on the attraction of *Zps latidens* to multiple-funnel traps baited with ipsenol. Slopes of regression lines are significantly different from zero (*t* test, *P* = 0.003, 0.032, and 0.054, respectively). Solid circles represent data for traps without monoterpene devices.

All three species showed attraction to β-phellandrene. Catches of *I. latidens* in traps baited with ipsenol and β-phellandrene released at the second highest rate were greater than those in control traps ($F_{1,24}$ = 5.70, P = 0.027), even though there was no evidence of a dose-dependent response (Fig. 1C). However, catches of *I. latidens* in traps with β-phellandrene at the highest release rate were lower than those in control traps ($F_{1,24}$ = 10.97, P = 0.004). *Ips pini* and *D. ponderosae* exhibited dose-dependent attraction to β-phellandrene (Figs. 2C, 3C). Catches of both species were directly proportional to the release rate of β-phellandrene. Catches of *I. pini* in traps baited with

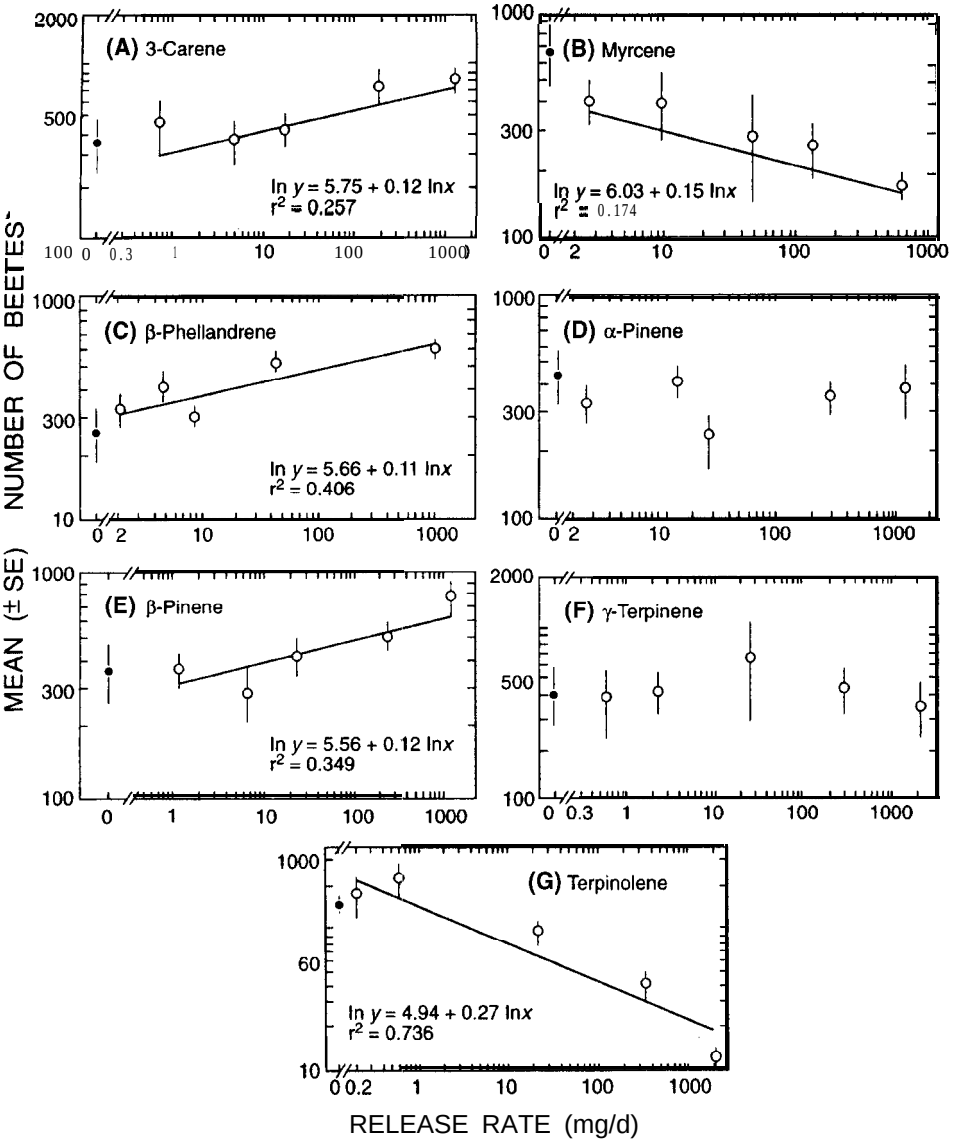

FIGURE 2. Effects of 3-carene (A), myrcene (B), β-phellandrene (C), a-pinene (D), β-pinene (E), γ-terpinene (F), and terpinolene (G) on the attraction of *Ips pini* to multiple-funnel traps baited with ipsdienol. Slopes of regression lines are significantly different from zero (*t* test, *P* = 0.01, 0.038, < 0.001, 0.002, and < 0.001, respectively). Solid circles represent data for traps without monoterpene devices.

treatments 2, 4, and 5 were greater than those in the control traps (F, $_{24}$ = 11.47, *P* = *0.003;* $F_{1,24}$ = 25.57, *P* < 0.001; and $F_{1,24}$ = 34.49, *P* < 0.001, respectively).

There was no discernible effect of a-pinene on catches of *I. latidens, I. pini*, and *D. ponderosae* (Figs. 1D, 2D, and 3D). In contrast, β-pinene affected the pheromone responses of two of the three species. *Ips pini* exhibited dose-dependent attraction to β-pinene (Fig. 2E). Catches in traps baited with β-pinene at the two highest release rates were greater than those in the control traps ($F_{1,24}$ = 5.94, *P* = 0.024; and $F_{1,23}$ = 21.57, *P* < 0.001, respectively). Catches of *I. latidens* in traps baited with β-pinene were not

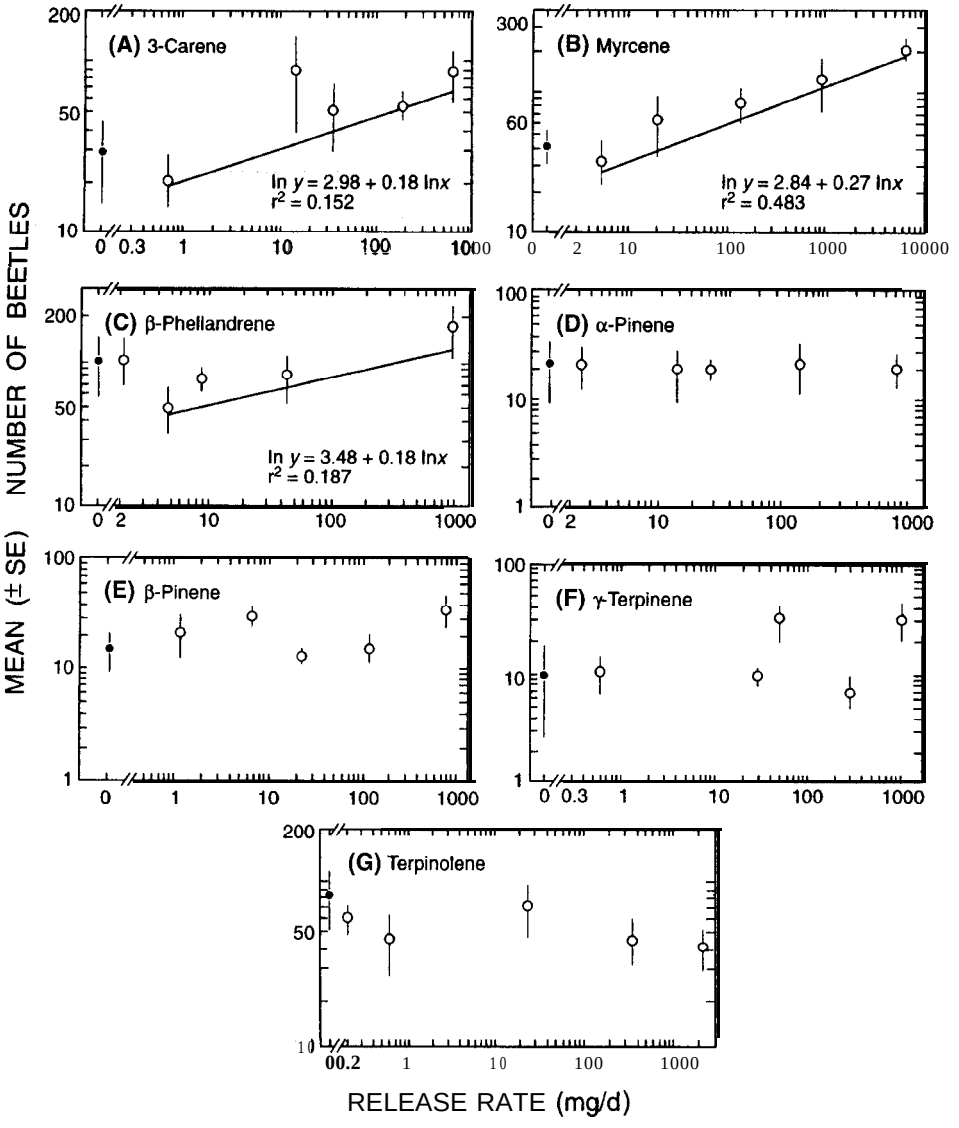

FIGURE 3. Effects of 3-carene (A), myrcene (B), β-phellandrene (C), α-pinene (D), β-pinene (E), γ-terpinene (F), and terpinolene (G) on the attraction of *Dendroctonus ponderosae* to multiple-funnel traps baited with *exo*-brevicomin and *trans*- and *cis*-verbenol. Slopes of regression lines are significantly different from zero (*t* test, $P = 0.054$, < 0.001, and 0.057, respectively). Solid circles represent data for traps without monoterpene devices.

affected in a dose-dependent fashion, although catches in traps with the two highest rates were greater than those in the control traps ($F_{1,23} = 7.57$, $P = 0.013$; and $F_{1,23} = 4.88$, $P = 0.040$, respectively) (Fig. 1E).

None of the species showed dose-dependent responses to y-terpinene (Figs. 1F, 2F, and 3F). Catches of *D. ponderosae* in traps baited with y-terpinene at two of the three highest release rates were greater than those in the control traps ($F_{1,12} = 6.22$, $P = 0.032$; and $F_{1,12} = 6.56$, $P = 0.028$, respectively).

TABLE 2. Mean (± SE) number of *Corticeus* sp. (Coleoptera: Tenebrionidae) captured in multiple-funnel traps (n = 5) baited with ipsdienol and various monoterpenes.

Release rate class*	α-Pinene	β-Pinene	3-Carene	γ-Terpinene	β-Phellandrene
Control	17.2±2.7*ab*	26.6±9.7*ab*	19.0±1.7*b*	14.0±6.0*a*	2.4±1.1*a*
1	16.0±1.6*a*	26.0±10.3*a*	10.8±2.5*a*	19.4±7.9*a*	3.6±0.9*a*
2	23.5±4.0*ab*	27.4±4.1*ab*	16.6±1.8*b*	12.4±5.4*a*	1.6±0.6*a*
3	29.0±4.0*b*	44.2±10.2*b*	41.6±5.4*c*	12.0±1.9*a*	2.4±1.0*a*
4	61.6±10.6*c*	114.0±26.0*c*	76.6±7.1*d*	9.8±1.8*a*	4.6±1.9*a*
5	105.0±25.7*c*	200.0±56.9*c*	102.2±11.5*d*	9.4±2.0*a*	13.0±3.3*b*

NOTE: Means within a column followed by a different letter are significantly different (Fisher's least significant difference test, $P = 0.05$).

* Monoterpene release rates as listed in Table I.

Terpinolene significantly reduced trap catches of all three species. Catches of *I. latidens* and *I. pini* were inversely proportional to the release rate of terpinolene (Figs. 1G, 2G). Catches of *I. pini* in traps baited with terpinolene at the two highest release rates were lower than those in the control traps ($F_{1,24} = 25.06$, $P < 0.001$; and $F_{1,24} = 69.30$, $P < 0.001$, respectively). Catches of *D. ponderosae* were lower in traps baited with terpinolene at the highest release rate than in the control traps ($F_{1,24} = 4.50$, $P = 0.047$).

Evidence of sex-specific responses of the three species to different release rates of monoterpenes was found in only two experiments. The proportion of male *I. pini* caught in traps baited with β-phellandrene increased as the release rate of β-phellandrene increased ($\chi^2 = 5.46$, $P < 0.025$). The proportion of male *D. ponderosae* in traps baited with γ-terpinene decreased as the release rate of γ-terpinene increased ($\chi^2 = 7.99$, $P < 0.01$). The mean ± SE proportion of male *I. latidens* and *I. pini*, in experiments lacking any association between sex ratio and release rates of monoterpenes, was 0.20 ± 0.02 in both cases. The mean ± SE proportion of male *D. ponderosae* caught in experiments lacking any association between sex ratio and release rate of monoterpenes was 0.51 ± 0.04.

Two beetle species associated with bark beetles were captured in large numbers. Catches of *Corticeus* Piller and Mitterpacker sp. (Coleoptera: Tenebrionidae) to traps baited with ipsdienol were affected by a-pinene, β-pinene, 3-carene, and β-phellandrene (Table 2). The highest catches were found in traps with the highest release rates of monoterpenes. γ-Terpinene had no effect on trap catches. Similarly, catches of *Lasconotus complex* LeConte (Coleoptera: Colydiidae) in ipsdienol-baited traps were highest in those baited with 3-carene and β-phellandrene, released at the highest rates (Table 3). a-Pinene and β-pinene had no effect on catches, and catches to traps baited with γ-terpinene seemed highest in the intermediate range of release rates.

Discussion

Species specificity in host location by *I. latidens*, *I. pini*, and *D. ponderosae* can be achieved by the use of the pheromones ipsenol, ipsdienol, and *exo*-brevicomin with *cis*- and trans-verbenol. Our results indicate that responses to monoterpenes can enhance separation among these three species (Table 4).

Attraction of all three species is enhanced by β-phellandrene, the principal constituent of gum turpentine from lodgepole pine (Mirov 1961). Increasing release rates of 3-carene and myrcene reduces the attraction of *I. latidens* but increases the attraction of *D. ponderosae*. Attraction of *I. pini* is increased by 3-carene but reduced by myrcene.

TABLE 3. Mean (± SE) number of *Lasconotus complex* (Coleoptera: Colydiidae) captured in multiple-funnel (n = 5) traps baited with ipsdienol and various monoterpenes.

Release rate class*	a-Pinene	β-Pinene	3-Carene	y-Terpinene	β-Phellandrene
Control	90±40.5*a*	50±12.8*a*	101±53.6*a*	46±18.6*a*	10±2.5*a*
1	68±27.4*a*	50±17.9*a*	40±9.4*a*	79±24.9*a*	36±6.7*b*
2	77±25.5*a*	41±6.3*a*	98±30.6*a*	127±28.2*ab*	39±7.4*b*
3	92±28.8*a*	68±12.8*a*	304±72.1*b*	157±36.3*b*	67±16.9*b*
4	110±39.1*a*	52±12.7*a*	666±223.4*b*	126±16.8*b*	112±20.0*c*
5	105±38.6*a*	64±14.1*a*	572.2±170.1*b*	109±31.4*b*	181±25.1*c*

NOTE: Means within a column followed by a different letter are significantly different (Fisher's least significant difference test, $P = 0.05$).
* Monoterpene release rates as listed in Table 1.

TABLE 4. Summary of positive (+), neutral (0), and negative (–) effects of monoterpenes on the responses of three sympatric pine bark beetles to pheromone-baited funnel traps.

Monoterpene	*Ips latidens*	*Ips pini*	*Dendroctonus ponderosae*
3-Carene	–	+	+
Myrcene		–	+
β-Phellandrene	+	+	+
a-Pinene	0	0	0
β-Pinene	+	+	+/○
y-Terpinene	0	0	+/○
Terpinolene		–	–/○

The attraction of *D. ponderosae* to 3-carene and myrcene (Figs. 3A, 3B) is consistent with Billings *et* al. (1976), Conn *et* al. (1983), and Borden *et al.* (1987). Conn *et al.* found that β-phellandrene had no effect on *D. ponderosue;* however, they employed low release rates (7 mg/d), comparable to our lowest release rate, which showed little effect. The attraction of *I. lutidens* and I. *pini* to monoterpenes is consistent with Miller and Borden (1990*a*, 1990*b*).

Some evidence of multifunctionality in the responses of beetles to monoterpenes was apparent. β-Phellandrene at the highest release rate inhibited the response of *I. lutidens* to ipsenol-baited traps, whereas at the second-highest release rate it resulted in trap catches greater than those in the controls. In contrast, trap catches of *D. ponderosae* were reduced with the second-lowest release rate of β-phellandrene but then increased in direct proportion to the release rate of β-phellandrene. *Dendroctonus ponderosue* may prefer hosts releasing large amounts of β-phellandrene, whereas *I. lutidens* may prefer hosts releasing only low amounts. This hypothesis is consistent with the observation that *I. lutidens* seems to prefer drier phloem tissue than that preferred by *D. ponderosue* (Miller and Borden 1985), which attacks mature lodgepole pines (Safranyik *et al.* 1974) that produce copious amounts of resin (Shrimpton 1978; Cates and Alexander 1982; Raffa and Berryman 1987), presumably with a high β-phellandrene content. Species specificity in the use of kairomones suggests that beetles may respond best to stimuli that convey information regarding the presence of preferred host qualities, indicating hosts in which they would have a competitive advantage.

Dose-dependent functions were noted in 11 of the 21 experiments conducted on these three species (Figs. 1-3). This type of behavioral response may reflect variation in host availability and quality, even in the absence of pheromones. Each species may be able to breed in lodgepole pine phloem with various compositions of monoterpenes, although there may be an optimal blend. Alternatively, variation in responses may reflect abilities of beetles to invade phloem of other pine species. 3-Carene and β-pinene are the major constituents of gum turpentine from ponderosa pine, *Pinus ponderosa* P. Laws. ex C. Laws. (Mirov 1961). Resin of western white pine, *Pinus monticola* Dougl. ex D. Don, contains primarily α- and β-pinene (Mirov 1961). 3-Carene is also a major constituent of gum turpentine from whitebark pine, *Pinus albicaulis* Engelmann (Mirov 1961). All four hosts are found in southern British Columbia. Habitats used by bark beetles tend to be patchy and ephemeral (Atkins 1968; Alcock 1982). Beetles may not have the luxury of waiting for an optimal host patch. Even when a host is found, the optimal areas for breeding may already be taken by conspecifics, thereby forcing the newcomer into suboptimal phloem conditions.

Predators may also exhibit specificity in responses to host compounds, possibly relating to the abundance of preferred prey items associated with various combinations of monoterpenes. *Lasconotus* and *Corticeus* species have been implicated as predators of bark beetle eggs and larvae (Parker and Davis 1971; Hackwell 1973; Furniss and Carolin 1980; Triplehorn 1990), possibly gaining benefits by responding to both host odors and beetle-produced pheromones. Attraction of both *L. complex* and *Corticeus* sp. was increased by β-phellandrene and 3-carene. Attraction of *L. complex* was also increased by y-terpinene, which had no effect on *Corticeus* sp. In contrast, attraction of *Corticeus* sp. was increased by both α- and β-pinene which had no effect on *L. complex.*

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