

Nadir Erbilgin · Kenneth F. Raffa

Modulation of predator attraction to pheromones of two prey species by stereochemistry of plant volatiles

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Abstract Predators and parasitoids are known to exploit both plant volatiles and herbivore pheromones to locate their insect prey. However, the interaction of these chemical cues in prey location, and the implications of multiple sources of chemical cues to predator feeding breadth and tracking of herbivore counter adaptations, are less well understood. We evaluated the responses of three coleopteran predators to the pheromones and plant signals associated with two species of common bark beetle prey. *Thanasimus dubius*, *Platysoma cylindrica*, and *Corticus parallelus* feed exclusively on the fauna within trees colonized by bark beetles. The predominant bark beetles in conifer forests of central Wisconsin are *Ips pini* and *Ips grandicollis*. The aggregation pheromone of Wisconsin *I. pini* contains ipsdienol, which occurs as (+) and (-) enantiomers, and lanierone, and the pheromone of *I. grandicollis* contains ipsenol. The major hosts of these bark beetles are *Pinus resinosa*, *Pinus banksiana*, and *Pinus strobus*, which contain monoterpenes as their predominant phytochemical volatiles. Monoterpenes by themselves did not attract predators. However, some monoterpenes significantly affected predator attraction to aggregation pheromones. Myrcene, and to a lesser extent 3-carene, reduced predator attraction. By contrast, α -pinene consistently enhanced attraction by all three predators to the pheromones of their *Ips* prey. However, the predators' responses were modulated by the stereochemistry of α -pinene, and these responses differed when confronted with the different pheromones of the two prey species. (+)- α -Pinene synergized predator responses to the pheromone of *I. pini*, whereas (-)- α -pinene synergized responses to the pheromone of *I. grandicollis*. This pattern occurred for all three predator species. Interactions between herbivore pheromones and host plant compounds may provide an important source of behavioral plasticity in predators, and facilitate their

ability to track several cryptic species that are distributed across multiple plant species and that show semiochemical variation in space and time.

Keywords Enemy free space · Pheromones · Phenotypic plasticity · Scolytidae · Predation

Introduction

Entomophagous insects exploit a diverse array of chemical cues to locate their prey (Sabelis and Van de Baan 1983; Price 1986; Dicke 1988; Vet and Groenewold 1990; Dicke et al. 1990a; Turlings et al. 1990; English-Loeb et al. 1993; Agrawal 1999). Many parasitoids, and some predators, orient towards plant odors, including specific chemical signals released following feeding by herbivores (Turlings et al. 1990, 1998; Dicke et al. 1993; Rose et al. 1998; Thaler 1999). Similarly, the frass or pheromones produced by herbivorous insects can provide predators and parasitoids with chemical signals that orient them to suitable habitats and hosts. Despite the recognized importance of both plant volatiles and insect pheromones in prey finding behaviors by entomophagous insects, interactions between these sources have been studied less, particularly among predators attacking several prey species (Price et al. 1980; Vinson 1981; Barbosa and Saunders 1985). Some exceptions include the predatory mite, *Phytoseiulus persimilis* Athias-Henriot, which uses both volatiles from plants infested with the spider mite, *Tetranychus ureticae* Koch, and their pheromones (Sabelis et al. 1984; Dicke 1986), and some natural enemies of bark beetles that use conifer monoterpenes to modulate responses to aggregation pheromones (Miller and Borden 1990; Erbilgin and Raffa, 2000a).

Bark beetles (Coleoptera: Scolytidae) are cryptic, endophytic insects that develop within the subcortical tissues of trees, in which they spend all but a few days of their life cycles. Once they have selected potential hosts, adult bark beetles release aggregation pheromones that

N. Erbilgin (✉) · K.F. Raffa
345 Russell Laboratories, Department of Entomology,
University of Wisconsin, Madison, WI 53706, USA
e-mail: erbilgin@entomology.wisc.edu
Fax: +1-608-2623322

attract both males and females (Wood 1982; Miller 1990; Miller et al. 1990; Seybold 1992; Vanderwel 1994). These aggregation pheromones may be oxidized derivatives of, or be synergized by, host conifer monoterpenes (Wood 1982). Within scolytid species, there is often geographic variation in the stereochemistry of pheromones (Lanier et al. 1980; Raffa and Klepzig 1989; Berisford et al. 1990; Seybold et al. 1992, 1995; Miller et al. 1997).

Coleopteran predators are important mortality agents of bark beetles and can be closely linked to their population dynamics (Reeve 1997; Turchin et al. 1999). Evidence for their impact comes from exclusion experiments, laboratory assays, life tables, and time-series analyses of field populations (Miller 1986; Riley and Goyer 1986; Turchin et al. 1991; Weslien and Regnander 1992; Schroeder and Weslien 1994; Weslien 1994; Schroeder 1996; Reeve 1997; Turchin et al. 1999). Predators exploit both host tree odors and bark beetle pheromones as kairomones (Wood et al. 1968; Stephen and Dahlsten 1976; Mizell et al. 1984; Grégoire et al. 1992). Most, if not all, coleopteran predators attack several species of scolytids, and thus may exploit a broad set of chemical signals. The interactions between host volatiles and pheromones, and the role of host plants in the behavioral plasticity of attraction to prey pheromones, are not well understood.

Raffa and Klepzig (1989) proposed that the chiral specificity of bark beetle pheromones may evolve partially as a response to predator recognition. Subsequent work demonstrated that disparities between the relative preferences of predators versus prey for specific stereoisomers and additional components may facilitate escape from predators, yet retain intraspecific functionality (Raffa and Dahlsten 1995; Aukema et al. 2000a,b). It is not known how the stereochemistry of host plant compounds affects these predator-prey relationships. However, the attractiveness of tunneling *Ips pini* (Say) to flying conspecifics and their insect predators varies with host tree species (Erbilgin and Raffa 2000a).

The pine engraver, *I. pini*, colonizes *Pinus* trees throughout much of North America, and is the most common bark beetle species associated with conifers in the Great Lakes region (Schenk and Benjamin 1969; Miller et al. 1989; Klepzig et al. 1991). During establishment within a suitable tree, adult males emit ipsdienol (2-methyl-6-methylene-2,7-octadien-4-ol) and lanierone (2-hydroxy-4,4,6-trimethyl-2,5-cyclohexadien-1-one) (Birch et al. 1980; Lanier et al. 1980; Seybold et al. 1992, 1995; Miller et al. 1996). In Wisconsin, *Ips grandicollis* (Eichhoff) is a frequent associate and competitor of *I. pini* (Klepzig et al. 1991; Raffa 1991; Wallin and Raffa 2001). Male *I. grandicollis* produce the aggregation pheromone ipsenol (Vité et al. 1972; Werner 1972). A third species, *Ips perroti* Swaine, is sometimes present and responds to the pheromone of *I. pini*, but occurs in very low numbers. For example in a 3-year study of five sites in Wisconsin, only 1.5% of over 160,000 *Ips* were *I. perroti*, and in a 2-year study of six sites, only 0.6% of over 26,000 *Ips* were *I. perroti* (Hobson and Raffa 1996; Aukema 1999; Aukema et al. 2000a, b).

The flight periods of *I. pini* and *I. grandicollis* coincide in the Great Lakes region (Raffa 1991), and both species colonize *Pinus resinosa* (Aiton), *Pinus banksiana* Lamb. and *Pinus strobus* L. (Drooz 1985). *I. pini*, however, is more commonly associated with *P. resinosa*, whereas *I. grandicollis* is more commonly associated with *P. banksiana* (Klepzig et al. 1991; Wallin and Raffa 2001). Erbilgin and Raffa (2000b) found that some host monoterpenes inhibited the flight response of *I. pini* to ipsdienol plus lanierone. In contrast, (-)- α -pinene enhanced the attraction of *I. grandicollis* to its pheromone, ipsenol. Similar to *I. pini*, *I. grandicollis* showed reduced attraction to ipsenol in the presence of most other host monoterpenes.

Thanasimus dubius (F.) (Coleoptera: Cleridae) and *Platysoma cylindrica* (Paykull) (Histeridae) are the most abundant predators of *I. pini* and *I. grandicollis* in the Great Lakes region (Raffa and Klepzig 1989; Raffa 1991; Raffa and Dahlsten 1995). Adults and larvae of *T. dubius* feed on adult and larval bark beetles, respectively, and *P. cylindrica* are egg predators. *Corticus parallelus* Melsh (Tenebrionidae), and *Tenebroides collaris* (Sturm) (Trogositidae) are also predators of *Ips* spp., but their biologies are less well known (Raffa 1991; Aukema et al. 2000a). Each of these predators is attracted to both ipsdienol and ipsenol, and is attracted to *I. pini* boring in different tree species in the same order as their prey (Erbilgin and Raffa 2000a). Our objective in this study was to evaluate how host plant compounds influence the responses of these predators to sources of pheromones from two prey species.

Materials and methods

Study sites, treatments, and experimental design

The field sites consisted of three *P. resinosa* forests in Wisconsin, USA. They are located near Spring Green, Sauk Co. (latitude N43° 11.78', longitude W90° 11.15'), Lake Delton, Juneau Co. (latitude N43° 58.28', longitude W90° 07.35'), and Necedah, Jackson Co. (latitude N44° 22.24', longitude W90° 43.80'). We conducted experiments in 1998 and 1999, during the major flight period of *I. pini* and *I. grandicollis*. Synthetic lures and blank controls were assigned to multiple funnel traps (Lindgren 1983) in a randomized block design, as described in Erbilgin and Raffa (2000b). Traps were spaced a minimum of 10 m apart within blocks, and blocks were separated by 50–60 m. Unbaited control traps were used in all experiments. We sampled treatments every 4 days, and re-randomized treatments at each collection to minimize potential spurious effects due to trap positions within a block or block locations within a site.

We tested the major monoterpenes present in the phloem tissue of *P. resinosa*, *P. banksiana*, and *P. strobus* in Wisconsin (Bridgen et al. 1979; Klepzig et al. 1995, 1996; Raffa and Smalley 1995; Wallin and Raffa 1999), and the pheromones of *I. pini* and *I. grandicollis*. The test chemicals were from Phero Tech, (Delta, British Columbia). The monoterpenes were: racemic- α -pinene, [chemical purity (cp)=99%, enantiomeric purity (ep)=95%] (-)- β -pinene (cp =99%, ep =97.5%), myrcene (cp =97%), 3-carene (cp =97%). The pheromones were: racemic ipsdienol (98%), lanierone (98%), and racemic ipsenol (98%). Monoterpenes and pheromones were released from closed polyethylene micro-centrifuge tubes (15 ml), and from 20 mg bubblecaps, respectively. These

synthetic lures maintain constant emission rates for approximately 3 months. We chose release rates of monoterpenes and pheromones to emulate release rates associated with pine trees following entry by bark beetles (Browne et al. 1979; Ikeda et al. 1980; Lanier et al. 1980; Byers et al. 1985; Strömvalld and Petersson 1991; Teale et al. 1991; Erbilgin and Raffa 2000b). The release rates of (+)- α -pinene, (-)- α -pinene, (-)- β -pinene, myrcene, and 3-carene were 227.9 mg/day, 339 mg/day, 211.2 mg/day, 335.6 mg/day, 457.2 mg/day at 27°C, respectively. The pheromones ipsdienol, lanierone, and ipsenol were released at 110 μ g/day, 100 μ g/day, and 110 μ g/day at 25°C, respectively.

Field assays

We tested a total of 24 combinations of monoterpenes and pheromones in nine experiments over 2 years. Simultaneous comparison of this many choices could violate the underlying assumption of independence that is implicit in behavioral choice tests (Peterson and Renaud 1989; Lockwood 1998), create spurious spatial effects in the field, and potentially mask the activity of weakly attractive compounds by drawing insects to highly attractive compounds. Therefore, we approached the problem sequentially, by first testing monoterpenes alone to determine whether they are attractive (or repellent), and then proceeding to combinations of monoterpene with pheromone (Fig. 1). We included both negative controls (blanks) to provide a baseline arrival rate to traps containing no attractant, and positive controls (pheromones) to validate that adequate populations were available to generate a statistically significant effect when an attractant was present. In the latter experiments, a treatment of monoterpene alone could be excluded where prior assays showed it has no effect. Because of the theoretical possibility that weak levels of attraction could be masked by highly attractive monoterpenes or by the positive controls, we (1) conducted two sets of assays, in which all monoterpenes were tested simultaneously, and again in which the same monoterpenes were tested in smaller groups, and (2) conducted separate experiments in which we deployed positive checks in two experimental fashions: true positive controls within the treatment blocks (to validate that local populations are high enough to respond to an attractant under these conditions), and stand monitoring controls outside treatment blocks (to assure that adequate populations are present within the stand, but mitigate the risk of directing populations away from weakly attractive compounds).

The questions we addressed are listed below. A flow diagram of the overall series of experiments, and the decision tree by which our results guided subsequent experimental design, are shown in Fig. 1.

1. Are the major predators of bark beetles attracted to monoterpenes present in phloem of host pines in the Great Lakes region?

A. Experiment 1.1. Simultaneous evaluation of the predominant monoterpenes in Great Lakes region pine phloem

The major monoterpene constituents in the phloem of *P. resinosa*, *P. banksiana*, and *P. strobes* were simultaneously presented to field populations of flying insects. The treatments were: (1) myrcene, (2) (+)- α -pinene, (3) (-)- α -pinene, (4) (-)- β -pinene, (5) Δ -3-carene, (6) ipsdienol plus lanierone, and (7) blank control. Both negative and positive controls were positioned within treatment blocks. There were 14 replicates. This experiment was conducted from 6 to 14 May 1998.

B. Experiment 1.2. Simultaneous evaluations of small groups of monoterpenes present in Great Lakes region pine phloem

In order to verify the lack of attraction by predators to plant monoterpenes we observed in experiment 1.1 (see Results), we conducted a more sensitive assay, in which the same monoterpenes were tested in two smaller groups, and we deployed pheromone-baited

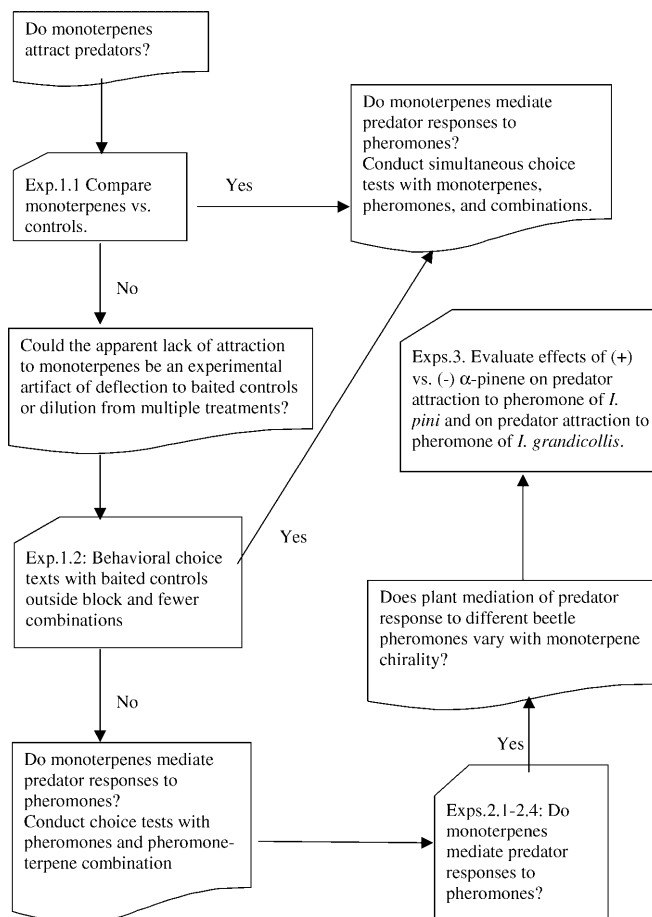


Fig. 1 Flow diagram of the sequence and decision tree of experimental procedures. Questions are illustrated in boxes with rounded bottoms, and the experiment (s) to address them are shown in the boxes with angular edges. The answers to each question (yes or no) determined by each experiment lead to the next question. See text for details

monitoring traps within the site but outside the treatment blocks (Fig. 1). In the first assay, we included monoterpenes that display substantial variation in enantiomeric composition in midwestern pines. There were 20 replicates of: (1) (+)- α -pinene, (2) (-)- α -pinene, and (3) blank control. In the second assay, we included monoterpenes that do not display substantial variation in enantiomeric composition in midwestern pines. There were 20 replicates of: (1) (-)- β -pinene, (2) 3-carene, (3) myrcene, and (4) blank control. In addition, 20 replicates of pheromone-baited and unbaited traps were located within the stand but outside of the blocks: (1) ipsdienol with lanierone, (2) ipsenol, and (3) blank control. These experiments were conducted from 1 to 21 May 1999.

2. Are predator responses to bark beetle pheromones mediated by host plant monoterpenes?

A. Experiment 2.1. Effects of host plant monoterpenes on predator responses to ipsdienol

This experiment tested whether the responses of insect predators to the primary pheromone component of *I. pini* are affected by the presence of host plant monoterpenes. There were 35 replicates of each treatment: (1) (+)- α -pinene with ipsdienol, (2) (-)- α -pinene with ipsdienol, (3) (-)- β -pinene with ipsdienol, (4) myrcene with ipsdienol, (5) 3-carene with ipsdienol, (6) ipsdienol, and (7) blank control. This experiment was conducted from 30 May to 19 June 1998.

B. Experiment 2.2. Effects of host monoterpenes on predator response to ipsdienol plus lanierone

This experiment tested whether the responses of insect predators to the complete pheromone (ipsdienol plus lanierone) of *I. pini* are affected by the presence of monoterpenes. There were 28 replicates of seven treatments: (1) (+)- α -pinene with ipsdienol plus lanierone, (2) (-)- α -pinene with ipsdienol plus lanierone, (3) (-)- β -pinene with ipsdienol plus lanierone, (4) myrcene with ipsdienol plus lanierone, (5) 3-carene with ipsdienol plus lanierone, (6) ipsdienol plus lanierone, and (7) blank control. This experiment was conducted from 21 June to 7 July 1998.

C. Experiment 2.3. Effects of host plant monoterpenes on predator response to ipsenol

This experiment tested whether the responses of insect predators to the pheromone of *I. grandicollis* are affected by the presence of monoterpenes. There were 20 replicates of seven treatments: (1) (+)- α -pinene with ipsenol, (2) (-)- α -pinene with ipsenol, (3) (-)- β -pinene with ipsenol, (4) myrcene with ipsenol, (5) 3-carene with ipsenol, (6) ipsenol, and (7) blank control. This experiment was conducted from 5 June to 25 June 1999.

D. Experiment 2.4. Effects of (-)- α -pinene on predator response to ipsenol

Based on earlier work in which we observed attraction by *I. grandicollis* to (-)- α -pinene (Erbilgin and Raffa 2000b), we conducted a separate test of this monoterpene alone and with ipsenol, in addition to the more complete design described in experiment 2.3. This experiment consisted of 14 replicates of four treatments: (1) ipsenol, (2) (-)- α -pinene, and (3) ipsenol with (-)- α -pinene, and (4) blank control. This experiment was conducted from 7 to 15 July 1998.

3. Does host plant mediation of predator attraction to the pheromones of different prey species vary with monoterpene enantiomeric composition?

Based on results from the above experiments (see Results), we conducted two assays to compare how different stereoisomers of α -pinene interact with the pheromones of *I. pini* or *I. grandicollis* to affect responses by predators that can exploit both species. In the first assay, we included both enantiomers of α -pinene in the presence or absence of ipsenol. There were 20 replicates of six treatments (1) (+)- α -pinene, (2) (+)- α -pinene with ipsenol, (3) ipsenol, (4) (-)- α -pinene, (5) (-)- α -pinene with ipsenol, (6) blank control. In the second assay, there were also 20 replicates of 6 treatments: (1) (+)- α -pinene, (2) (+)- α -pinene with ipsdienol plus lanierone, (3) ipsdienol plus lanierone, (4) (-)- α -pinene, (5) (-)- α -pinene with ipsdienol plus lanierone, and (6) blank control. Both experiments were conducted from 1 to 21 June 1999.

Statistical analyses

Data were analyzed using analysis of variance. Each variable was tested to satisfy assumptions of normality and homogeneity of variance (Zar 1996) by graphical analysis of residuals (Neter et al. 1983). If the variance was non-homogeneous, variables were transformed to $\log_{10}(x+1)$, which provided distributions that satisfied these assumptions in all cases. Dependent variables were analyzed in a split-plot design, with randomized block design treating sites as blocks (PROC MIXED; SAS 1996). Covariance parameter estimates (REML) for block and block \times treatment were calculated for each variable. If the covariance parameter of a block was equal to '0', then the block term was eliminated from the random statement in the model. If it was different from 0, the '-2 Residual Log Likelihood' values of the model with and without random block were compared by chi-square analysis ($df=1$) at the $P<0.05$ level. If chi-square analysis revealed any significance, then block

was included in the random statement. An additional blocking factor for collection time was included for all experiments with over 2 collection periods. A protected LSD test ($P<0.05$) was used for multiple comparison of means.

Because the numbers of insects were not distributed normally, a Poisson distribution was used where appropriate. These data were analyzed using the GLIMMIX module within SAS. We replaced 0s by a small constant, as suggested in Wolfinger and O'Connell (1993): The statistical inference varied very little when we varied this constant from 0.001 to 0.02, so we used 0.01.

Results

We captured a total of 3,383 predators. As in previous work with this system (Raffa and Klepzig 1989; Raffa 1991; Raffa and Dahlsten 1995; Miller et al. 1997; Aukema et al. 2000a, b; Erbilgin and Raffa 2000a, b), the most abundant predators in our traps were *T. dubius* ($n=1,314$), *P. cylindrica* ($n=1,256$), and *C. parallelus* ($n=210$). Together these species accounted for 82.2% of all predators. Other predators captured in lower numbers were *Platysoma parallelum* (Say) (Coleoptera: Histeridae) ($n=180$), *Tenebroides* sp. (Coleoptera: Tenebrionidae) ($n=128$), *Thanasimus undatulus* (Say) (Coleoptera: Cleridae) ($n=124$), *E. nigrifrons* (Say) (Coleoptera: Cleridae) ($n=64$), *Grynocharis quadrilineata* (Melsheimer) ($n=37$), *Zenodosus* sp. ($n=37$), *Enoclerus nigripes* (Say) (Coleoptera: Cleridae) ($n=33$). Because of small sample sizes, these less abundant species were excluded from further analysis.

1. Are the major predators of bark beetles attracted to monoterpenes present in phloem of host pines in the Great Lakes region?

Predators were not attracted to host pine monoterpenes. In experiment 1.1, they were attracted only to traps baited with the pheromone of *I. pini*, ipsdienol plus lanierone, relative to unbaited controls (*T. dubius*: $df=13$, $F=5.773$, $P<0.0001$; *P. cylindrica*: $df=13$, $F=3.409$, $P<0.0044$). Experiment 1.2 supported these results. No predators were caught at any of the monoterpene treatments. However, predators were significantly attracted to monitor traps baited with the pheromones of *I. pini* (ipsdienol plus lanierone), and *I. grandicollis* (ipsenol) relative to blank controls that were likewise positioned outside of the treatment blocks (*T. dubius*: $df=19$, $F=4.36$; $P<0.02$; *P. cylindrica*: $df=19$, $F=3.147$, $P<0.041$). *T. dubius* and *P. cylindrica* showed no difference in their preference for the pheromones of *I. pini* versus *I. grandicollis*.

2. Are predator responses to bark beetle pheromones mediated by host plant monoterpenes?

Several monoterpenes had significant effects on the attraction of predators to bark beetle pheromones. These effects varied with predator species, pheromone, mono-

terpene, and pheromone-monoterpene combination. *Thanasimus dubius* were significantly more attracted to traps baited with (+)- α -pinene plus ipsdienol than traps baited with ipsdienol alone, or ipsdienol combined with other monoterpenes (Fig. 2A) (except perhaps 3-carene). Attraction of *T. dubius* to ipsdienol was also enhanced by the release of (-)- α -pinene and 3-carene. The presence of myrcene significantly reduced attraction of *T. dubius* to ipsdienol. Attraction of *P. cylindrica* to ipsdienol was not affected by the release of these monoterpenes. Attraction of *C. parallelus* was enhanced by 5.5 \times when ipsdienol was combined with (+)- α -pinene (Fig. 2A). No other monoterpene had a statistically significant effect on the attraction of *C. parallelus* to ipsdienol.

The effects of plant monoterpenes on the attraction of bark beetle predators to the complete *I. pini* pheromone, ipsdienol plus lanierone, were generally similar to their effects on attraction to ipsdienol alone (Fig. 2B). Synergism of the attraction by *T. dubius* to ipsdienol plus lanierone was again strongest for (+)- α -pinene and 3-carene. Also, *T. dubius* were significantly more attracted to ipsdienol plus lanierone when they were combined with (-)- α -pinene than to ipsdienol plus lanierone alone. Addition of myrcene to ipsdienol plus lanierone reduced the numbers of *T. dubius* captured to the level of the unbaited control. (+)- α -Pinene also increased the attraction of *P. cylindrica* to ipsdienol plus lanierone. Myrcene inhibited attraction of *P. cylindrica* to ipsdienol plus lanierone by 27% (Fig. 2B). Synergism of responses by *C. parallelus* to beetle pheromones was again evident when (+)- α -pinene was released along with ipsdienol plus lanierone. Other host compounds did not significantly affect attraction to ipsdienol plus lanierone (Fig. 2B).

The effects of host plant monoterpenes on the same predator species were different when they were combined with the pheromone of *I. grandicollis*. (-)- α -Pinene increased the attraction of *T. dubius*, *P. cylindrica*, and *C. parallelus* to ipsenol (Fig. 3). The attraction of *T. dubius* to ipsenol was not affected by any other monoterpene. Myrcene plus ipsdienol attracted the fewest *T. dubius* of any chemical treatment, and was the only treatment that did not differ from the unbaited controls. As with *T. dubius*, (-)- α -pinene was the most potent synergist of attraction to ipsenol by *P. cylindrica* (Fig. 3). (-)- β -Pinene also enhanced attraction to ipsenol by *P. cylindrica*. All of the remaining treatments attracted significantly higher numbers of *P. cylindrica* than did unbaited controls, but there was no variation among baited treatments. A similar pattern was observed for *C. parallelus*. Attraction to the combination of (-)- α -pinene and ipsenol was significantly higher than to the other treatments. Attraction of *C. parallelus* to the other combinations of ipsenol-monoterpene was not different from controls.

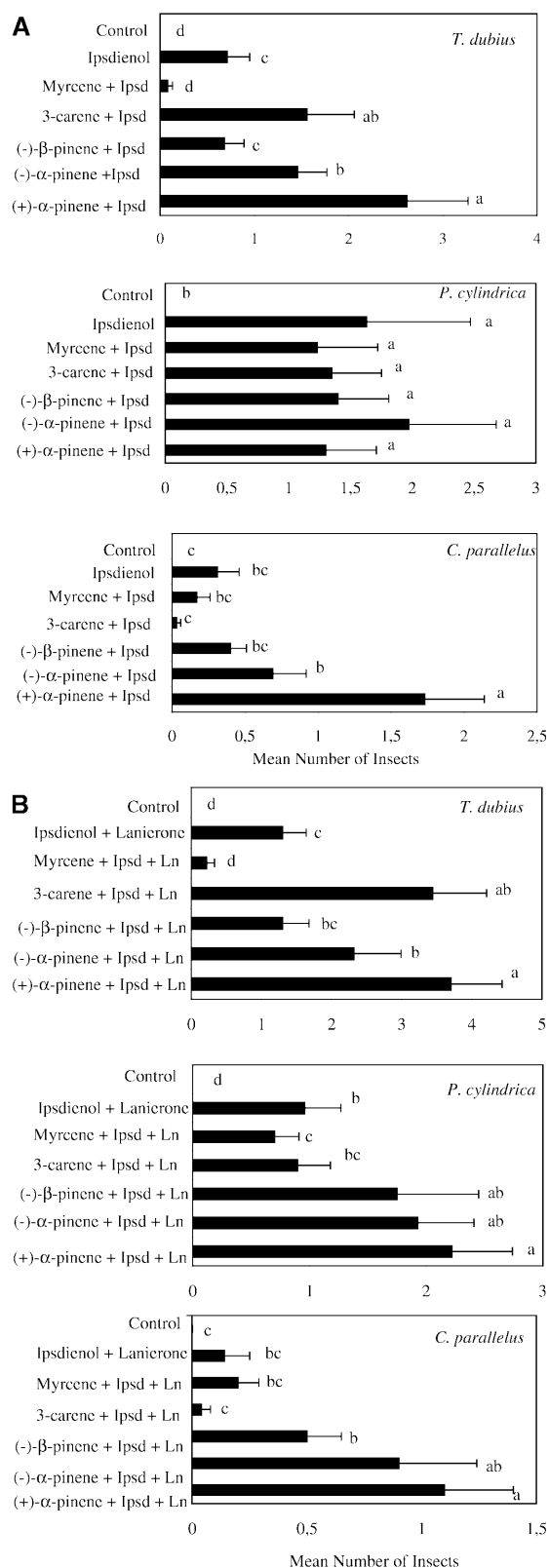


Fig. 2 Responses of bark beetle predators to pine monoterpenes alone or combined with bark beetle pheromones (A) ipsdienol: *T. dubius*: $F_{6,35}=9.751$, $P<0.0001$; *P. cylindrica*: $F_{6,35}=3.229$, $P<0.0046$; *C. parallelus* $F_{6,35}=11.73$, $P<0.0001$, (B) ipsdienol plus lanierone: *T. dubius*: $F_{6,28}=14.22$, $P<0.0001$; *P. cylindrica*:

$F_{6,28}=5.133$, $P<0.0046$; *C. parallelus* $F_{6,28}=6.305$, $P<0.0001$. Bars with the same letter within each species are not significantly different, PROX-MIX and Tukey's Protected LSD test on data transformed by $y'=\log(x+1)$, $P<0.05$

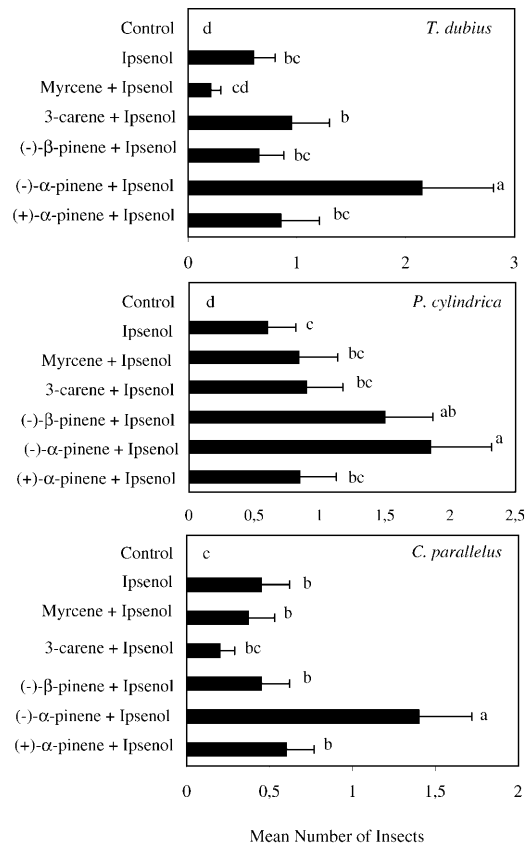


Fig. 3 Responses of bark beetle predators to the bark beetle pheromone ipsenol, alone or combined with various host pine monoterpenes. Bars with the same letter within each species are not significantly different, PROX-MIX and Tukey's Protected LSD test on data transformed by $y' = \log(x+1)$, $P < 0.05$. *T. dubius*: $F_{3,20}=4.211$, $P < 0.0007$; *P. cylindrica*: $F_{3,20}=3.907$, $P < 0.0013$; *C. parallelus* $F_{3,20}=6.152$, $P < 0.0001$

When the potential synergism of ipsenol by (-)-α-pinene was tested in the absence of other monoterpenes, the results were consistent with those of previous experiments. The attraction of *T. dubius* and *P. cylindrica* to ipsenol was synergized by (-)-α-pinene (Fig. 4). As before, there was no attraction to (-)-α-pinene alone, and predators were significantly attracted to ipsenol.

3. Does host plant mediation of predator attraction to the pheromones of different prey species vary with monoterpene stereochemistry?

The stereochemistry of α-pinene affected predator responses to the pheromones of different prey species. The response of *T. dubius* to ipsenol was strongly synergized by the presence of (-)-α-pinene, but only weakly by (+)-α-pinene (Fig. 5A). This pattern was the same for all three species. The attraction of both *P. cylindrica* and *C. parallelus* to ipsenol was synergized by (-)-α-pinene, but not by (+)-α-pinene (Fig. 5B, C). Conversely, (+)-α-pinene synergized the attraction of *T. dubius* to the

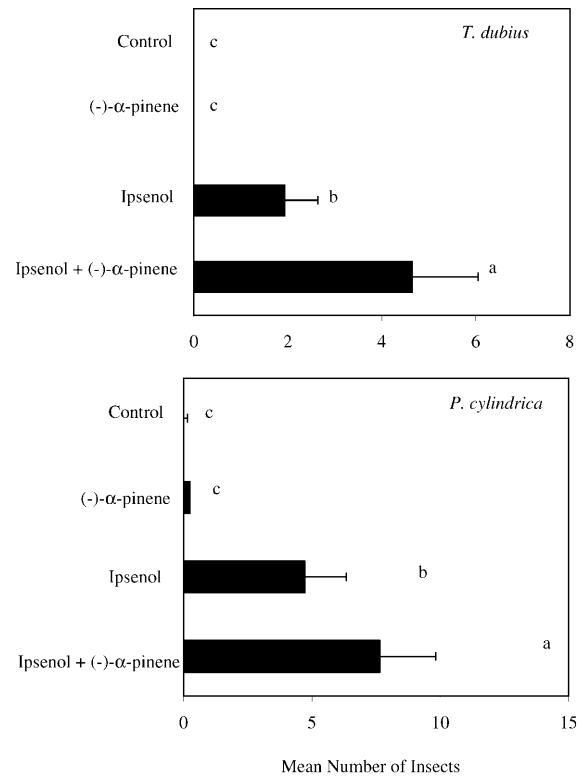


Fig. 4 Responses of bark beetle predators to (-)-α-pinene and ipsenol alone and in combination. Bars with the same letter within each species are not significantly different, PROX-MIX and Tukey's Protected LSD test on data transformed by $y' = \log(x+1)$, $P < 0.05$. *T. dubius*: $F_{3,14}=6.541$, $P < 0.0036$; *P. cylindrica*: $F_{3,14}=5.653$, $P < 0.007$

pheromone of *I. pini*, ipsdienol plus lanierone (Fig. 5D). (-)-α-Pinene did not increase attraction of *T. dubius* to ipsdienol. (+)-α-Pinene also synergized the attraction of *P. cylindrica* and *C. parallelus* to ipsdienol plus lanierone (Fig. 5E, F). (-)-α-Pinene did not affect attraction of *T. dubius* to ipsdienol plus lanierone. It significantly increased attraction of *P. cylindrica* and *C. parallelus* to ipsdienol plus lanierone, but this increase was slight (Fig. 5D–F).

Overall, attraction to ipsenol was strongly synergized by (-)-α-pinene. In contrast, attraction to ipsdienol plus lanierone was most strongly enhanced by (+)-α-pinene.

Discussion

These results demonstrate that the stereochemistry of host plant compounds can differentially influence the responses of predators to pheromones of various prey species. (-)-α-Pinene strongly synergizes the response of each predator tested to the pheromone of *I. grandicollis*, ipsenol. Conversely, (+)-α-pinene synergizes the attraction of the same predators to the pheromone of *I. pini*, ipsdienol plus lanierone. Predators are not attracted to monoterpenes in the absence of bark beetle pheromones.

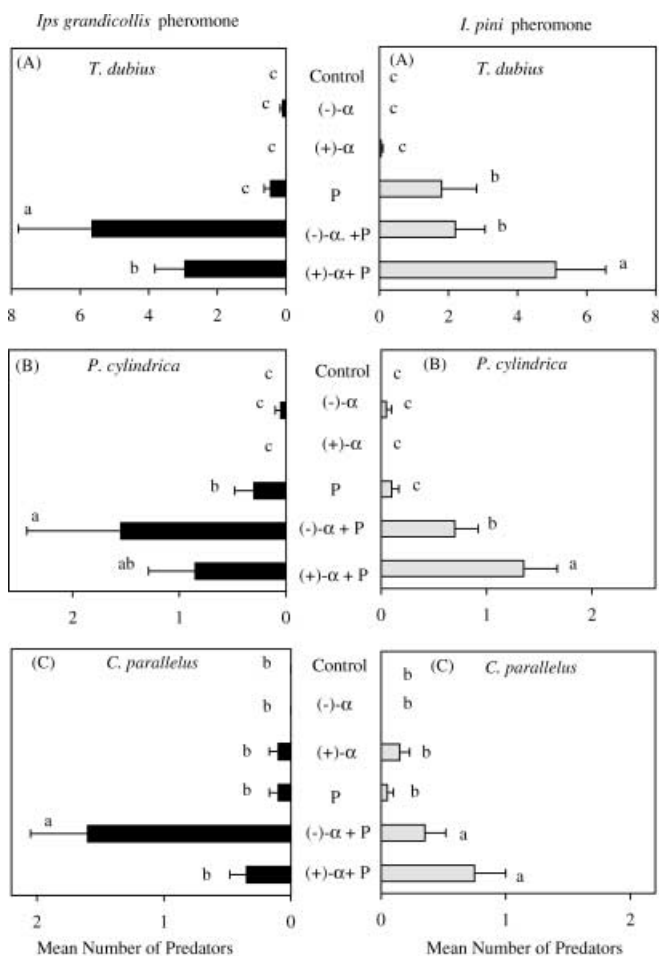


Fig. 5 Responses of bark beetle predators to two enantiomers of α -pinene alone or combined with the pheromone of either *Ips grandicollis* (ipsenol) or *Ips pini* (ipsdienol plus lanierone). Bars with the same letter within each species and within each pheromone category are not significantly different, PROX-MIX and Tukey's Protected LSD test on data transformed by $y' = \log(x + 1)$, $P < 0.05$. Treatment of *I. pini* pheromone: *T. dubius*: $F_{3,20} = 7.85$, $P < 0.0001$; *P. cylindrica*: $F_{3,20} = 7.892$, $P < 0.0001$; *C. parallelus*: $F_{3,20} = 5.76$, $P < 0.008$; treatment of *I. grandicollis* pheromone: *T. dubius*: $F_{3,20} = 6.62$, $P < 0.0047$; *P. cylindrica*: $F_{3,20} = 4.43$, $P < 0.0171$; *C. parallelus*: $F_{3,20} = 2.797$, $P < 0.0202$. Abbreviations: (-)- α : (-)- α -pinene; (+)- α : (+)- α -pinene; P pheromone

Modulation of predator exploitation of kairomones by plant volatiles could facilitate counter adaptation to semiochemical shifts within bark beetle populations that might otherwise allow prey to avoid predators. Scolytid species exhibit substantial variation in the enantiomeric ratios and additional components of their pheromones, both over broad scales of space and time (Lanier et al. 1980; Miller et al. 1989), and also within regions and over brief time periods (Raffa and Klepzig 1989; Herms et al. 1991; Raffa 1995; Aukema 2000a, b). This dynamic variation in space and time may represent a coevolving system among bark beetles and their predators (Raffa and Dahlsten 1995), as has been suggested in other systems involving chemical and acoustical communication (Aldrich et al. 1989; Zuk et al. 1993).

Flexible prey searching strategies that incorporate plant stereochemistry may also facilitate the ability of predators to detect several prey species. α -Pinene occurs as a significant component of the oleoresin of the Pinaceae (Kurth 1952; Mirov 1961), and has previously been shown to synergize the attraction of several conifer-infesting scolytids and natural enemies to pheromones (Chénier and Philogène 1989; Schroeder and Lindelöw 1989; Erbilgin and Raffa 2000b). Although *I. pini* and *I. grandicollis* can colonize the same host trees, *I. pini* is more commonly associated with *P. resinosa*, while *I. grandicollis* is more commonly associated with *P. banksiana* (Klepzig et al. 1991; Wallin and Raffa 2001). The oleoresin of *P. banksiana* contains more (-)- α -pinene than that of *P. resinosa* (Erbilgin, unpublished data). Several studies have shown that natural enemies can distinguish between odors from closely related plant cultivars (Elzen et al. 1985, 1986; Ding et al. 1989). Our results suggest that predator exploitation of plant kairomones may vary depending upon the pheromone signal of the prey species that is most commonly associated with various plants.

Stereochemically based chemodiversity is prevalent among the terpenoids, which represent a large family of natural products (Connolly and Hill 1991). For example, *Ips paraconfusus* Lanier transforms (-)- α -pinene from *Pinus ponderosa* Dougl. ex Laws, to *cis*-verbenol, an active constituent of its aggregation pheromone (Renwick et al. 1976). However, when these insects are exposed to (+)- α -pinene, they form *trans*-verbenol, which is not attractive and, when combined with verbenone, inhibits aggregation (Renwick et al. 1976; Byers 1989). To the best of our knowledge, there are no previous examples of predator responses to herbivore pheromones being differentially mediated by various stereoisomers of plant compounds.

Modulation of predator behaviors through environmental signals in addition to prey kairomones may function as a mechanism for contending with the spatial and temporal variation in the densities of multiple prey species (Meyer 1987; Scheiner 1993). Variation in responses by predators and parasitoids has been shown to be influenced by both genetic and environmental factors (Via 1987; Stearns 1989; Vet et al. 1990; Turlings et al. 1993). For example, Prévost and Lewis (1990) demonstrated heritable responses by *Microplitis croceipes* (Cresol) (Hymenoptera: Braconidae) to specific odor blends. Likewise, learning is common among natural enemies that respond to specific odors associated with their hosts (Lewis and Tumlinson 1988; Papaj and Vet 1990; Vet and Groenewold 1990; Vet et al. 1990; Turlings et al. 1992; Vet and Papaj 1992; Godfray 1993). Learning of olfactory cues has been explored more extensively in parasitoids, but also has been reported for ant, wasp, and mite predators (Carlin and Hölldobler 1983; Isingrini et al. 1985; Chang et al. 1988; Dicke et al. 1990a, b). The potential roles of learning and heredity in the foraging behavior of coleopteran predators of bark beetles have not been examined.

Several studies have shown that herbivores can gain partial escape from predators and parasites by colonizing "enemy free space", including plant species less conducive to searching by natural enemies (Bernays and Graham 1988; Bernays and Minkenberg 1997). Our results suggest that plasticity in predator responses to plant volatiles associated with prey colonization may enable natural enemies to partially overcome this difficulty, and that the stereochemistry of host compounds may provide an important signal.

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