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DOSE AND ENANTIOSPECIFIC RESPONSES OF WHITE PINE CONE BEETLES, *Conophthorus coniperda,* TO a-PINENE IN AN EASTERN WHITE PINE SEED ORCHARD

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Abstract-The white pine cone beetle, *Conophthorus coniperda,* exhibited dose and enantiospecific responses to a-pinene in stands of mature eastern white pine, *Pinus strobus*, in a seed orchard near Murphy, North Carolina, USA. (−)-α-Pinene significantly increased catches of cone beetles to traps baited with (±)-*trans*-pityol. (+)-a-Pinene did not increase catches of beetles to pityol-baited traps and interrupted the response of beetles to traps baited with (±)-*trans*-pityol and (−)-α-pinene. Maximal attraction of cone beetles to pityol-baited traps was obtained with lures releasing (−)-α-pinene at a rate of 103 mg/day at 23°C. Lures releasing (−)-α-pinene at rates lower or higher than 103 mg/day resulted in reduced catches to traps baited with (±)-*trans*-pityol. The sex ratio in all catches was heavily male biased. Attraction of the clerid predator, *Thanasimus dubius,* to traps baited with (±)-*trans*-pityol increased significantly with the presence of α-pinene, irrespective of enantiomeric composition. Maxima1 attraction of *T. dubius* to pityol-baited traps occurred with devices releasing (-)-a-pinene at the highest rate tested, 579 mg/d at 23°C, a sub optima1 rate for cone beetles.

Key Words-Scolytidae, *Conophthorus coniperdu,* kairomones, enantiospecificity, α-pinene, chirality, Cleridae, *Thanasimus dubius.*

INTRODUCTION

The white pine cone beetle, ***Conophthorus coniperdu*** (Schwas-z) (Coleoptera: Scolytidae). breeds in the cones of eastern white pine, *Pinus* **strobus** L. (Godwin and ODell, 1965; Ebel et al., 1980). Adult beetles emerge from aborted cones in the

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spring and fly to cones in the upper crowns of white pines. Initially, female beetles attack the base of second-year cones, girdling the stem, and tunneling along the cone axis. Eggs are laid along an egg gallery within a cone. Larvae hatch and feed indiscriminately within the cone, consuming most of the seeds. At times, beetles may also attack first-year conelets and new shoots (Godwin and ODell, 1965).

Eastern white pine is a dominant and valuable tree species throughout northeastern North America (Farrar, 1995). Cone damage by beetles can have a significant impact on natural regeneration of eastern white pine following forest fires (Godwin and ODell, 1965) and on seed production in white pine seed orchards, with losses of 60–100% at times (Graber, 1964; Odera. 1968; Morgan and Mailu, 1976). Prescribed fire can be used to control populations within seed orchards, consuming beetles while beetles are still in aborted cones on the forest floor (Wade et al., 1989).

Semiochemicals may provide a valuable tool in mitigating the impacts of cone beetles through their use in monitoring and mass-trapping programs, as well as in mating disruption or push-pull strategies (Rappaport et al., 2000). Males are attracted to infested cones (de Groot et al., 1991) by the sex pheromone, (+)-*trans*-pityol (2*R*,5*S*)-2-(1-hydroxy-1-methylethyl)-5-methyltetrahydrofuran], produced by females (Birgersson et al., 1995). Attractants for females have not been identified. (f)-a-Pinene synergizes the attraction of males to pityol-baited traps (de Groot and DeBarr, 1998; de Groot et al., 1998; Rappaport et al., 2000).

w-Pinene is a common monoterpene in eastern white pine with an enantiomeric composition dominated by the (−) enantiomer (Mirov, 1961). Hobson et al. (1993) demonstrated enantiospecificity in attraction of the red turpentine beetle, *Dendroctonus valens* LeConte (Scolytidae), to α-pinene in stands of ponderosa pine, *Pinus ponderosa* P. Laws. ex C. Laws. Cone beetles may show similar enantiospecific responses to host kairomones. All previous work with cone beetles dealt with racemic α-pinene only (de Groot and DeBarr, 1998; de Groot et al., 1998; Rappaport et al., 2000). In addition, the issue of release rates has not been examined and should be investigated. Miller and Borden (2000) demonstrated dose-dependent relationships with host monoterpenes for three species of bark beetles. Our objective was to determine the effect of dose and enantiomeric composition of a-pinene on the response of male cone beetles to the pheromone, (±)-*trans*-pityol. Specifically, we hypothesized that males would show enantiospecificity to (−)-α-pinene and that trap catches would increase with release rate of α-pinene.

METHODS AND MATERIALS

Chemicals and Release Devices. Phero Tech Inc. (Delta, British Columbia) supplied polyethylene bubblecap lures containing (±)-*trans*-pityol (hereafter referred to as simply pityol) (chemical purity >98%), released at about 0.14 mg/day at 23°C. Previous studies have demonstrated that (−)-*trans*-pityol has no effect on the response of cone beetles to (+)-*trans*-pityol (Birgersson et al., 1995). Sigma-Aldrich Co. (Milwaukee, Wisconsin, USA) supplied (-)-, (+)- and (f)-a-pinene and (−)-β-pinene (chemical purities >98%). The enantiomeric composition of (-)-a-pinene and (−)-β-pinene was 98% (−), whereas the enantiomeric composition of (+)-a-pinene was 95% (+). Pinenes were released from the following types of sealed low-density polyethylene devices: (l-2) 250- and 400-μl centrifuge tubes (Fisher Scientific, Pittsburgh, Pennsylvania); (3) 8-ml Nalgene wide-mouth screw-cap bottles (Cole-Parmer Instrument Co., Vernon Hills, Illinois, USA); (4) 15-ml Boston round screw-cap bottles (0. Berk Co., Union, New Jersey, USA); and (5) 15-ml cylinder screw-cap bottles (PheroTech Inc.). The release rates (at 23°C in still air) from these devices were the same for all pinenes at about 5, 10, 47, 107, and 193 mg/day, respectively.

Experimental Design. Four experiments were conducted at the Beech Creek Seed Orchard (USDA Forest Service, Nantahala National Forest) near Murphy, North Carolina, USA in 1999–2001. In each experiment, Japanese beetle traps (Trécé Inc., Salinas, California, USA) were baited with pityol and suspended by rope and pulley in the crowns of mature eastern white pines (15-20 m height), adjacent to cones, with only one trap per tree. The distance between trees varied from 15 to 30 m. Beetles were collected in 500-ml plastic Mason jars, filled with approximately 200 ml of plumber's antifreeze (pink propylene glycol solution) as a killing and preservation agent. Trap catches were collected at 3-week intervals with the glycol solution replaced on each occasion. Sexes of captured beetles were determined by examination of the 7th and 8th abdominal tergites (Kinzer and Ridgill, 1972).

Experiments l-3 tested the effects of enantiomeric composition of α-pinene on the attraction of cone beetles to pityol-baited traps. In each experiment, 40 traps were set in 10 replicate blocks of 4 traps/block. The trapping periods for experiments l-3 were March 1 l-May 15, 1999, March 14–May 10, 2000, and March 28-May 30, 200 1, respectively. In experiment 1, the following treatments were randomly assigned to pityol-baited traps within each block: (1) control; (2) (f)-a-pinene [50:50 mix of (−)- and (+)-a-pinene); (3) (-)-a-pinene; and (4) (It)-a-pinene + β-pinene. Each pinene was released separately by using release device 5. β-Pinene is a common monoterpene in eastern white pine (Mirov, 1961) and may affect attraction of cone beetles to α-pinene.

Experiment 2 was designed to separate the effect of enantiomeric composition from that of dose (release rate). The following treatments were randomly assigned to pityol-baited traps within each block: (1) (±)-α-pinene (about 193 mg/day at 23°C); (2) (-)-a-pinene (about 193 mg/day at 23°C); (3) (±)-α-pinene (about 384 mg/day at 23°C); and (4) (-)-a-pinene (about 384 mg/day at 23°C). The two release rates of a-pinene were obtained by using either one or two of release device 5. The release rate of (-)-a-pinene is the same in treatment 2 as in treatment 3, whereas the release rate of α-pinene (irrespective of enantiomeric composition) is the same in treatment 1 as in treatment 2, and the same in treatment 3 as in treatment 4.

In experiment 3, the following treatments were randomly assigned to pityol-baited traps within each block: (1) control; (2) (-)-a-pinene; (3) (+)-a-pinene; and (4) (−)-α-pinene and (+)-α-pinene. Each pinene was released from a separate release device 5 with one device used in treatments 2 and 3, and two devices used in treatment 4.

Experiment 4 determined the dose-dependent effect of (-)-a-pinene on the attraction of beetles to baited traps. Forty-two traps were set in seven replicate blocks of 6 traps/block for the period March 28-May 30, 2001. The following treatments, differing only in the release rate of (−)-α-pinene (at 23°C), were assigned randomly to pityol-baited traps within each block: (1) about 5 mg/day; (2) about 20 mg/day; (3) about 47 mg/day; (4) about 107 mg/day; (5) about 193 mg/day; and (6) about 579 mg/day. Release rates 1, 3, 4, and 5 were obtained with one of device 1, 3, 4, and 5, respectively. Release rate 2 was obtained with two of device 2, whereas release rate 6 was obtained with three of device 5. Release rates from devices are not expected to be constant under field conditions. These data for rates at 23°C serve primarily as an index series (or set of reference values) that we expect lie within the range of rates experienced under field conditions.

GC-MS Analysis of Cone Volatiles. Second-year eastern white pine cones were collected in the spring of 2001 at the USDA Forest Service Beech Creek Seed Orchard near Murphy, North Carolina. Ten cones from each of three randomly selected trees were collected in early March and 10 cones from each of five randomly selected trees in late May different from those selected in March. Each set of 10 cones was sealed in a separate Mylar bag and stored at −10°C.

Each set of cones was aerated in a sealed glass collection chamber (10 liter) (Analytical Research Systems Inc., Gainesville, Florida, USA) with a flow of charcoal-filtered air introduced to the bottom of the chamber at approximately 1 liter/min. Volatiles were collected on 72-mm Super-Q columns (5 mm OD) (Analytical Research Systems Inc.). The columns were rinsed with pentane (1 ml), and the extract was analyzed on an Hewlett-Packard G1800C coupled gas chromatograph and mass spectrometer (GC-MS) with electron ionization detection and a chiral fused-silica capillary column (J&W Cyclodex-B, 30 m x 0.250 mm, 0.25 μm film thickness; J&W Scientific, Folsom, California, USA). Following a splitless injection, the temperature was held constant at 50°C for 2 min, then increased to 100°C at a rate of 8°C/min, held constant at 100°C for 2 min, then increased to 210°C at a rate of 12°C/min. Inlet and detector temperatures were held at 190°C. Helium was used as the carrier gas at a flow rate of 0.9 ml/min. All peaks were identified by comparing mass spectra, recorded at 70 eV and intervals of 1.0 sec, and retention times to the mass spectra and retention times of analytical standards.

Statistical Analyses. The data were analyzed with the Systat statistical package version 9.01 for Windows (SPSS Inc, Chicago, Illinois, USA). Trap catch data were transformed by $\ln(y + 1)$ or $\ln(y)$, as required, to remove heteroscedasticity. Sex ratio data were transformed by $\text{arcsine}(y)$. Data from experiments 1-3 were subjected to either one- or two-way ANOVA, whereas data from experiment 4 were regressed on release rates, transformed by $\ln(x)$. Differences in mean catches among treatments in experiments 1-3 were determined by Fisher's least significant difference (LSD) multiple-comparison test when $P = 0.05$. Differences in sex ratios were determined by 1 -way ANOVA or t tests.

RESULTS

Trap catches in experiment 1 were affected by treatments ($F_{3,16} = 5.074$, $P =$ 0.0 12). Catches of cone beetles were highest in traps with (-)-a-pinene and pityol (Figure 1). Although male beetles dominated all catches, there was a difference in sex ratio in catches among the treatments ($F_{3,14} = 4.201$, $P = 0.026$). The proportion (mean ± SE) of males caught in traps baited with pityol, (±)-α-pinene, and β- pinene was 0.905 ± 0.017, significantly lower than the proportion of males caught in the remaining treatments (0.973 ± 0.012) (LSD multiple comparison test, $P < 0.05$).

In experiment 2, catches of cone beetles were affected by the enantiomeric composition of α-pinene ($F_{1,36} = 22.119$, $P < 0.001$). Catches were greater in traps baited with pityol and (−)-α-pinene than in those baited with pityol and

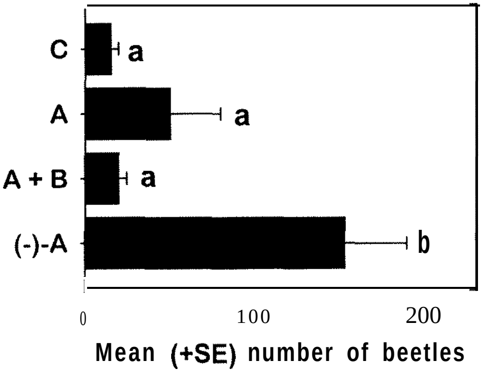

FIG. 1. Comparison of mean (+SE) total catches of *C. coniperdu* in pityol-baited traps with (±)-α-pinene (A), (f)-a-pinene and (−)-β-pinene (A + B), and (-)-a-pinene [(-)-A] to pityol-baited control traps (C) from March 11 to May 15, 1999, in experiment I ($n = 10$). Means followed by different letters are significantly different at $P = 0.05$ (LSD multiple comparison test).

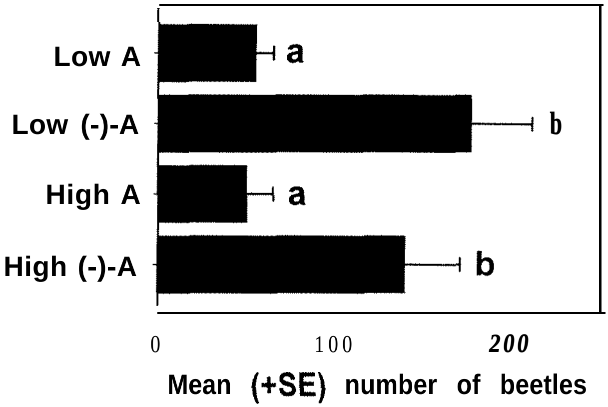

FIG. 2. Effects of (-)-a-pinene [(-)-A] and (±)-α-pinene (A), released at two different rates (low and high), on mean (+SE) total catches of C. *coniperda* in pityol-baited traps from March 14 to May 10, 2000, in experiment 2 (N = 10). Means followed by different letters are significantly different at $P = 0.05$ (LSD multiple comparison test).

(I(c)-a-pinene (Figure 2). Trap catches were unaffected by dose ($F_{1,36} = 0.545$, $P = 0.465$) or the interaction between dose and enantiomeric composition ($F_{1,36} = 0.014$, $P = 0.908$). There was no effect of treatment on sex ratios of beetles in trap catches ($F_{3,35}$, $P = 0.396$). The proportion of males in trap catches was 0.860 ± 0.013.

Catches of beetles to pityol-baited traps in experiment 3 were increased by (-)-a-pinene ($F_{1,39} = 46.998$, $P < 0.001$) but not by (+)-a-pinenealone ($F_{1,39} = 2.454$, $P = 0.125$) (Figure 3). (+)-a-Pinene interrupted the response of beetles to traps baited with (-)-a-pinene and pityol. There was no difference in sex ratio in catches for traps baited with pityol and (−)-α-pinene and those baited with pityol, (−)- and (+)-α-pinene ($t_{16} = 0.199$, $P = 0.844$). Data on sex ratio for the remaining treatments were not obtained due to low catches.

In experiment4, catches of beetles to traps baited with pityol and (-)-a-pinene increased as the release rate of (-)-a-pinene increased up to the rate associated with device 4 (107 mg/day at 23°C) and then decreased with higher rates (Figure 4). Catches in traps baited with (−)-α-pinene released at 107 mg/day at 23°C were higher than those in traps baited with (−)-α-pinene released at the highest and lowest rates (LSD multiple comparison test, $P = 0.05$). There was no difference in catches of traps with the highest and lowest release rates of (−)-α-pinene (LSD multiple comparison test, $P = 0.05$). There was an effect of treatments on the sex ratio of beetles in trap catches ($F_{5,36} = 2.487$, $P = 0.049$). The proportion (mean ± SE) of males caught in traps baited with pityol and (−)-α-pinene released at the highest rate was 0.986 ± 0.007, significantly higher than the proportion of males

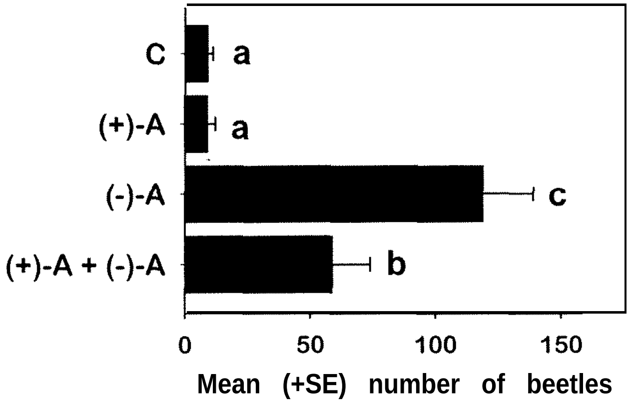

FIG. 3. Comparison of mean (+SE) total catches of C. *coniperda* in pityol-baited traps with (−)-α-pinene [(-)-A], (+)-α-pinene [(+)-A], and (+)-a-pinene and (−)-α-pinene [(+)-A + (-)-A], to pityol-baited control traps (C) from March 28 to May 30, 2001, in experiment 3 (N = 10). Means followed by different letters are significantly different at $P = 0.05$ (LSD multiple comparison test).

caught in the remaining treatments (0.942 ± 0.008) (LSD multiple comparison test, $P < 0.05$).

The dominant monoterpenes in cone volatiles were a-pinene, β-pinene, limonene, and myrcene (Figure 5). Myrcene seemed to be more prevalent in

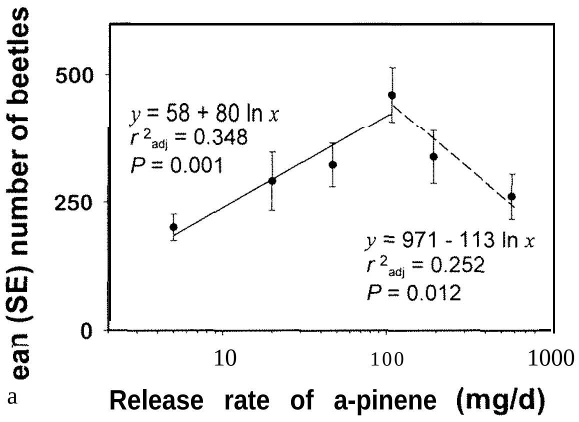

FIG. 4. Dose-dependent attraction and interruption of *C. coniperda* by (-)-a-pinene to traps baited with pityol from March 28 to May 30, 2001, in experiment 4 (N = 7). Slopes of regression lines are significantly different from zero (*t* test, $P < 0.05$). Release rates were determined in still air at 23°C.

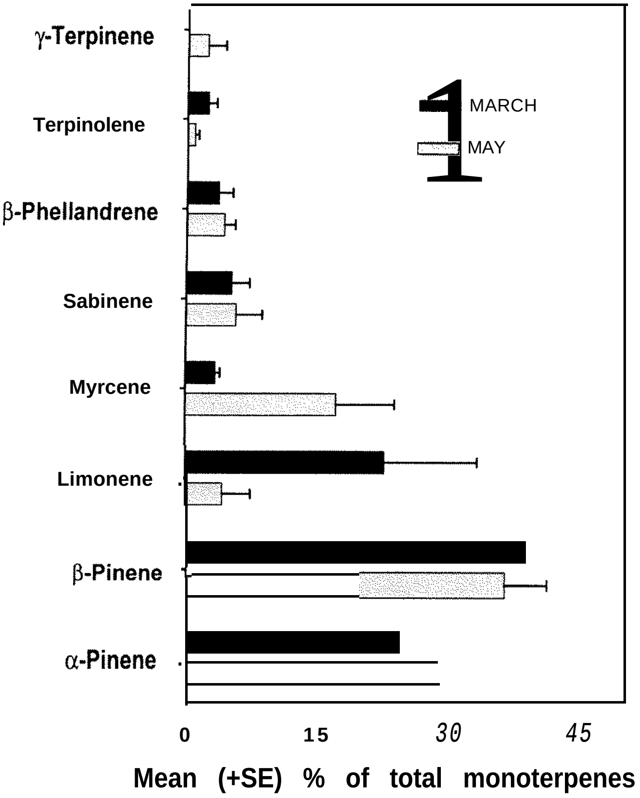

FIG. 5. Composition of volatile monoterpenes from eastern white pine cones collected in March (N = 3) and May 2001 (N = 5) from the Beech Creek Seed Orchard in Nantahala National Forest, North Carolina.

volatiles emitted from cones collected in May than in March, whereas limonene seemed to be prevalent in volatiles emitted from cones collected in March than in May. The enantiomeric composition of a-pinene in volatiles from cones collected in March was (mean ±SE) 80.9 ± 3.0% (−), significantly lower than the enantiomeric composition of 93.2 ± 1.7% (−) emitted by cones collected in May ($t_6 = 3.863$, $P = 0.008$).

The bark beetle predator, *Thanasimus dubius* (F.) (Coleoptera: Cleridae) was affected by treatments in three of the four experiments. In experiment 1, all traps baited with pityol and α-pinene caught twice as many clerid beetles as those baited with pityol alone ($F_{5,24} = 7.256$, $P < 0.001$) (Figure 6). The same result was obtained in experiment 3, where catches in traps baited with pityol alone were lower than those baited with pityol and either (+)- or (-)-a-pinene ($F_{3,39} =$

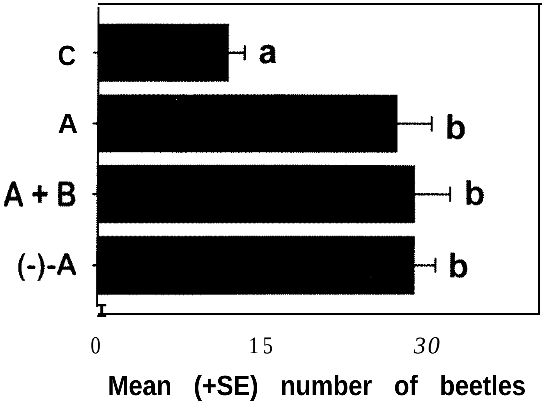

FIG. 6. Comparison of mean (+SE) total catches of the clerid, *T. dubius*, in pity&baited traps with ($\pm$)-α-pinene (A), (It)-a-pinene and ($-$)-β-pinene (A + B), and ($-$)-α-pinene [(-)-A] to pityol-baited control traps (C) from March 11 to May 15, 1999, in experiment 1 (N = 10). Means followed by different letters are significantly different at $P = 0.05$ (LSD multiple comparison test).

6.639, $P = 0.001$) (Figure 7). There was no effect of treatments on catches of *T. dubius* in experiment 2, where all treatments contained pityol and a-pinene ($F_{3,35} = 0.766$, $P = 0.521$). The catch of *T. dubius* in experiment 2 was 24.3 ± 2.3 (mean ±SE). In experiment 4, the responses of *T. dubius* were affected by the release rate of ($-$)-α-pinene ($F_{5,36} = 3.473$, $P = 0.012$). Traps baited with pityol and ($-$)-α-pinene, released at the highest rate, caught significantly more clerid beetles than any other treatment (Figure 8). There was no difference among the other treatments (LSD multiple comparison test, $P = 0.05$).

DISCUSSION

Male white pine cone beetles exhibited enantiospecific responses to α-pinene. Attraction of beetles to pityol was increased by (-)-a-pinene (Figures 1-3). (+)-a-Pinene did not increase attraction of beetles to pityol (Figure 3). In fact, (+)-a-pinene interrupted the attraction of beetles to traps baited with pityol and (-)-a-pinene (Figures 2 and 3). Our results are consistent with the enantiomeric composition of α-pinene emitted by cones in the same orchard, which was primarily (-)-a-pinene. (f)-a-Pinene [SO: 50 mix of ($-$)- and (+)] increased attraction of beetles to pityol albeit less than (-)-cl-pinene alone (Figure 3). This is consistent with previous trials that demonstrated a synergistic effect of ($\pm$)-α-pinene on the attraction of white pine cone beetles to pityol in stands of eastern white pine (de Groot et al., 1998; Rappaport et al., 2000).

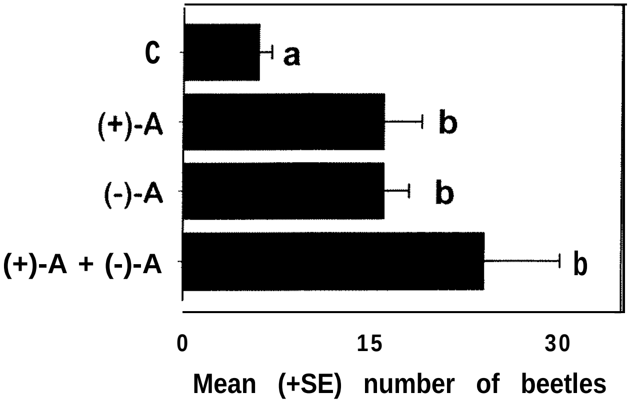

FIG. 7. Comparison of mean (+SE) total catches of the clerid, *T. dubius*, in pityol-baited traps with (−)-α-pinene [(-)-A], (+)-α-pinene](+)-A], and (+)-α-pinene and (-)-α-pinene [(+)-A + (-)-A], to pityol-baited control traps (C) from March 28 to May 30, 2001, in experiment 3 (N = 10). Means followed by different letters are significantly different at $P = 0.05$ (LSD multiple comparison test).

Enantiospecific behavioral responses to α-pinene occur with a western species of cone beetles as well. In western North America, attraction of the cone beetle, *C. ponderosae* Hopkins, to pityol-baited traps was strongly increased by (−)-α-pinene in a coastal stand of western white pine, *P. monticola* Dougl. ex D. Don

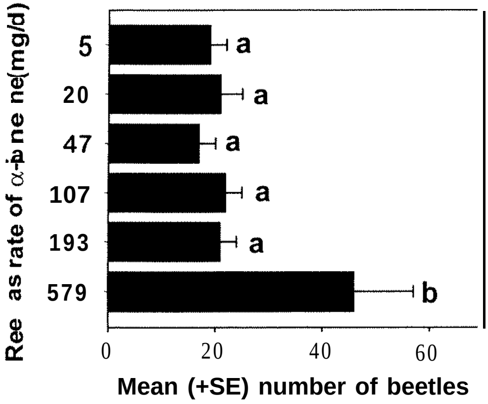

FIG. 8. Effect of (−)-α-pinene, released at six different rates (at 23°C), on mean (+SE) total catches of the clerid, *T. dubius*, in pityol-baited traps from March 14 to May 10, 2000, in experiment 4 (N = 10). Means followed by different letters are significantly different at $P = 0.05$ (LSD multiple comparison test).

(Miller et al., 2000) and (±)- and (−)-α-pinene in stands of western white pine in Idaho (Rappaport et al., 2000, 2002). However, Rappaport et al. (2002) found that in Idaho, traps baited with pityol and (+)-a-pinene caught more cone beetles than those baited with pityol and (-)-a-pinene, even though the mean enantiomeric composition of a-pinene emitted by cones of western white pine in the study was 96% (−). Neither (±)-α-pinene nor (+)-α-pinene was tested in the coastal stand of western white pine (Miller et al., 2000).

In contrast, de Groot et al. (2002) found that attraction of male red pine cone beetles, *Conophthorus resinosae* Hopkins, to traps baited with pityol in plantations of red pine, *Pinus resinosa* Ait., in eastern North America was interrupted by α-pinene, irrespective of enantiomeric composition. These results are surprising as de Groot et al. (2002) found that α-pinene was the predominant volatile collected from cones of red pine, accounting for >40% of the total volatiles on average. They found that attraction of red pine cone beetles was interrupted more by a-pinene with enantiomeric compositions of 12% (-) to 69% (−) than with cr-pinene with an enantiomeric composition of 86% (−), the mean enantiomeric composition of α-pinene in volatiles from red pine cones.

Variation in responses among species is not surprising nor is geographic variation within a species, as numerous examples are known within the family Scolytidae (Borden, 1982; Byers, 1989). However, we should expect some correlation between odors emitted by a host and the responses of beetles to those hosts that they infest, or at least they should not interrupt attraction.

One confounding issue in previous trials may have been the release rate characteristics of devices used for a-pinene. de Groot et al. (2002) used devices that released a-pinene at 150–450 mg/day at 24°C. Rappaport et al. (2002) used devices that released α-pinene at 100–330 mglday. In our study, we found that maximal attraction of cone beetles to pityol occurred with a lure releasing a-pinene at a rate of 107 mg/day at 23°C (Figure 4). Traps with devices releasing cr-pinene at rates higher or lower than 107 mg/day (at 23°C) resulted in a reduction in beetle catches relative to those with lures releasing a-pinene at 107 mg/day. These results may be due to a mixed-functional response to (-)-a-pinene, requiring a very specific dose for maximal attraction. An alternate explanation may be that at high release rates, the interruptive effect of the antipode, (+)-α-pinene, may play a significant role. In our study, the enantiomeric composition of cr-pinene was 98% (−). Release rates of 100–400 mg/day (at 23°C), therefore, would result in release rates of (+)-α-pinene of 2-8 mg/day (at 23°C), which may be above threshold levels.

Another possible explanation for these various results may relate to host preferences (Rappaport et al., 2002; de Groot et al., 2002). The cone beetle, C. *ponderosae*, attacks cones of 12 species of western pines (Wood, 1982). The predominant enantiomer of α-pinene in the resin of western white pine is (−)-α-pinene in the Pacific Northwest, whereas (+)-a-pinene is more abundant than (−)-α-pinene in other species such as limber pine (I? *flexilis* James) and ponderosa pine (*P. ponderosa* P. Laws. ex C. Laws.) (Mirov, 1961). In some species such as lodgepole pine (*P. contorta* var. *latifolia* Engelm.), whitebark pine (*P. albicaulis* Engelm.), and ponderosa pine, the quantity of α-pinene in the resin may be low or nonexistent (Mirov, 1961). The preference for (+)-α-pinene may be a consequence of past competition rather than current host preferences (Rappaport, 2002).

In eastern North America, the cones of jack pine, *P. banksiana* Lamb., a species sympatric with red pine, are not attacked by C. *resinosue* (= *C. banksianae* McPherson), although the twigs are attacked (Mattson, 1989; de Groot and Fleming, 1994). de Groot et al. (2002) found that the emission of cr-pinene from cones of jack pine was high, accounting for 41% of the total volatiles on average. However, the mean enantiomeric composition of cr-pinene was 66% (-) in jack pine as opposed to a mean of 86% (-) in eastern white pine (de Groot et al., 2002). The resin of the exotic, yet abundant, Scots pine *(I? sylvestris* L.) contains primarily (+)-a-pinene (Mirov, 1961). The predominant enantiomer of α-pinene in southeastern pine species, in or near the range of white pine cone beetles, such as shortleaf pine (*P. echinata* Mill.), loblolly pine (*P. taeda* L.), and longleaf pine *(I? palustris* Mill.) is (+)-a-pinene, although in others such as Virginia pine (*P. Virginia* Mill.) and pitch pine (*P. rigida* Mill.) it is (-)-a-pinene (Mirov, 1961).

Host selection may be based on monoterpene blends rather than merely the presence of cr-pinene and its enantiomeric composition. In our study, we found that β-pinene was as abundant as a-pinene (Figure 4), yet we did not find any effect of β-pinene on catches of beetles to traps baited with pityol and ($\pm$)-α-pinene) (Figure 1). Limonene was initially quite abundant in March, but seemed to decrease by May (Figure 4). In contrast, the abundance of myrcene seemed to have increased over the same time period. de Groot et al. (1998) tested β-pinene, limonene, and myrcene in traps baited with pityol and a-pinene for attraction to C. *coniperda*. However, limonene and myrcene were never tested alone. Interactions between monoterpenes on the responses of cone beetles in previous studies may have masked behaviors to individual compounds. Furthermore, we should not be surprised to find variation in host volatile preferences based on local abundance of host species given the variation of hosts in some species such as *C. ponderosae*. Similarly, responses of red pine cone beetles may depend on the presence of other monoterpenes, not the dominant cr-pinene.

We need to examine responses of beetles to host odors and blends for possible attractants as well as indicators of susceptibility, tolerance, and resistance of cones to attacks by cone beetles. Henson (1960,196 1) found that both male and female white pine cone beetles formed aggregations when confined in open arenas in the laboratory. Morgan and Mailu (1976) reported aggregations of up to 12 beetles/site during early feeding attacks on twigs and cones. Currently, only attractants for males have been identified, namely the combination of (+)-*trans*-pityol and

(−)-α-pinene (Birgersson et al., 1995; de Groot et al., 1998). As the attacking sex, females seem to be able to find suitable hosts prior to the appearance of males. There is no evidence that females are attracted by volatiles produced by other females such as aggregation pheromones. In laboratory assays, de Groot et al. (1991) found that both male and female white pine cone beetles were attracted to host compounds. Some trees in seed orchards of eastern white pine seem to be preferred by white pine cone beetles, whereas others are left untouched (personal observations, D. R. Miller and G. L. DeBarr). Therefore, it seems plausible that, if females use chemical attractants at all, host odors may play a significant role in host location by female cone beetles.

Predators may play a role in the semiochemical ecology of cone beetles as well. Attraction of the clerid predator, *T. dubius*, to (±)-*trans*-pityol is increased by the kairomone, a-pinene, irrespective of enantiomeric composition (Figures 6 and 7). Previously, de Groot and DeBarr (2000) found that ***T. dubius*** was attracted to the combination of pityol and c-u-pinene, but they did not test the binary combination against pityol alone. Unlike the cone beetles (Figure 4), ***T. dubius*** showed a strong preference for traps baited with (±)-*trans*-pityol and devices releasing α-pinene at the highest rate (Figure 8). Our observations on ***T. dubius*** may relate to a general predator strategy and not a specific one for cone beetles. Other potential prey, such as the twig beetles ***Pityophthorus carinicep****s* LeConte and ***P. puberulus*** (LeConte) (Scolytidae), are also attracted to the combination of pityol and a-pinene (de Groot and DeBarr, 2000). High release rates of monoterpenes are often associated with attacks by the southern pine beetle, ***Dendroctonus frontalis*** Zimmermann (Scolytidae), and associated bark beetles, on southern pines (Thatcher et al., 1980). The predator, ***T. dubius,*** is a common and abundant predator of species in the southern pine bark beetle guild (Thatcher et al., 1980).

The phenomenon of enantiospecificity is not new for the bark beetle family. Numerous species exhibit enantiospecificity to pheromones, particularly with respect to the pheromones ipsenol and ipsdienol (Borden, 1982; Byers, 1989). However, our results and those of Rappaport et al. (2002) and de Groot et al. (2002) with cone beetles are only the second demonstration of enantiospecificity to host compounds by bark beetles. Previously, Hobson et al. (1993) found that attraction of ***D. valens*** to (+)-a-pinene was interrupted by (−)-α-pinene. Our results with ***C. coniperda*** showing dose-dependent attraction to (-)-a-pinene over a low range of release rates and dose-dependent interruption over a higher range are unique. Previous results with host compounds and bark beetles, such as these of Miller and Borden (2000), have typically demonstrated one or the other, never both.

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