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CHIRAL SPECIFICITY IN RESPONSES BY THE BARK BEETLE *Dendroctonus valens* TO HOST KAIROMONES

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Abstract—The attraction of the red turpentine beetle, *Dendroctonus valens*, to the resin volatiles of its host, *Pinus ponderosa*, is elicited by three chiral monoterpenes. In field assays response was greatest to (*S*)-(−)-β-pinene; 92% (*S*)-(−)-α-pinene found in *P ponderosa* resin was not attractive. However, 75% (*R*)-(+)-α-pinene, which occurs in *Pinus lambertiana*, a sympatric host of *D. valens*, was attractive. (*S*)-(−)-α-Pinene interrupted response to (*R*)-(+)-α-pinene. (*S*)-(+)-3-Carene from both hosts was attractive at the (*R*)-(+)-α-pinene level. Three sympatric coniferous nonhosts each have the same attractive monoterpenes but produce less resin. These studies demonstrate the importance of chirality of host compounds in the host finding behavior of this bark beetle.

Key Words—*Dendroctonus valens*, coleoptera, Scolytidae, host selection, chiral, enantiomer, kairomone, *Pinus ponderosa*, α-pinene, β-pinene, monoterpene, olfaction.

INTRODUCTION

Several genera of bark beetles (e.g., *Dendroctonus*, *Ips*, *Scolytus*) aggregate on their hosts, which results in the death of the tree. Through this aggregation behavior these insects are able to reproduce and secure food for their progeny

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(D.L. Wood, 1982). Although considerable progress has been made in understanding pheromone-mediated aggregation of bark beetles (Borden, 1985; D.L. Wood, 1982; Lewis, 1984), little is known about how these insects find their hosts prior to the production of attractant pheromones. Chénier and Philogène (1989) list five scolytids (*Ips grandicollis* Eichoff, *Tomicus minor* Hartig, *Tomicus piniperda* L., *Hylastes ater* Paykull, and *Dryocetes autographus* Ratzeburg) that are attracted to pure conifer monoterpenes. The odor of oleoresin or pure turpentine, a variable mixture of mostly monoterpenes, is attractive to several scolytid species, including *Dendroctonus terebrans* Olivier (Fatzinger, 1985; Payne et al., 1987; Phillips et al., 1988) and *Dendroctonus valens* Leconte (Vité and Gara, 1962). Turpentine or pure monoterpenes increase attraction of seven species of *Dendroctonus* (*D. adjunctus* Blanford, *D. brevicomis* Leconte, *D. ponderosae* Hopkins, *D. rufipennis* Kirby, *D. pseudotsugae* Hopkins, *D. frontalis* Zimmerman, *D. terebrans*) to their respective pheromones (Borden, 1985; Phillips et al., 1990). Many conifer monoterpenes are optically active but chiral specificity to kairomones has not been previously tested in any scolytid species and is not generally known among insect herbivores (E. Bernays, personal communication). Our recent investigation shows that *D. valens* is attracted to two sympatric host species, *Pinus ponderosa* Lawson and *P. lambertiana* Dougl., by three chiral monoterpene hydrocarbons.

Female *D. valens* select host trees in the genus *Pinus* in which to excavate egg galleries. Males and females are attracted to resin exuding from wounded and/or diseased hosts (Vité and Gara, 1962; Owen, 1985; Moeck et al., 1981; Goheen et al., 1985). No pheromone has been identified for *D. valens*, in contrast to several of its congeners (D.L. Wood, 1982; Borden, 1985). *D. valens* rarely mass attacks *P. ponderosa* or *P. lambertiana* and is not an aggressive killer of these species (Smith, 1971). It is often found colonizing the base of trees that are being mass attacked by other scolytids (e.g., *D. brevicomis* and *D. ponderosae* in California) although Owen et al. (in preparation) did not find attraction of *D. valens* to the pheromone of *D. brevicomis*. The objective of our study was to identify which volatile compounds in the resin of ponderosa pine were attractive to *D. valens*, and to explain the mechanism of *D. valens* host selection.

METHODS AND MATERIALS

We analyzed the attraction of *D. valens* to the resin of *P. ponderosa* using resin distillates and individual compounds in field tests using methods described in Birch et al. (1980). Initially, attractive compounds were isolated through steam distillation to produce an attractive volatile fraction. Resin was collected by wounding trees with a V-notch cut into the xylem, which was allowed to

flow into open 100-ml containers overnight. The resin was distilled with steam for 2 hr and collected using a Liebig condenser. Water was removed from the distillate by adding methylene chloride to the mixture and isolating the nonpolar compounds in a separatory funnel. Methylene chloride was removed from the distillate using a rotary evaporator. Responses to distillate and residue were assayed singly and in combination by placing baits on flight traps (Lindgren, 1983) in a complete randomized block design. Eight-funnel Lindgren traps were placed a minimum of 20 m apart in blocks separated by a minimum 100 m. Treatments were placed randomly each day in each block. One-milliliter quantities of test compounds were released from four 1.5-ml, 9-mm ID, plastic Eppendorf centrifuge tubes (West Coast Scientific, Emeryville California) for each compound on each trap. Beetles were collected and sexed each day.

The monoterpene concentrations of the distillate were determined by gas chromatography (GC) on two capillary columns as described below: a 54-m × 0.5-mm-ID OV-17 and a 43-m × 0.5-mm-ID Carbowax 20 M support-coated (SCOT). After diluting the distillate in *n*-pentane, split injection (20:1) was used, with injectors at 220°C. The carrier gas was helium (25 cm/sec flow rate) and both columns were run at 70°C for 5 min, then programmed at 6°C/min to the upper limit (220°C). Detection was by flame ionization (FID); detectors were at 250°C. The monoterpenes were identified by comparison of retention times with those of the authentic substances analyzed under the same conditions. The composition was calculated from the peak areas, normalizing all detected compounds to 100%. The stereochemistry of chiral monoterpenes was determined by analysis on a 30-m × 0.25-mm-ID Cyclodex B chiral column (J&W Scientific, Folsom, California), carrier gas helium (25 cm/sec), temperature 75°C. Whole oleoresin was analyzed for each of five trees (except for *Libocedrus decurrens* Torr., which was from three trees).

The five principal monoterpenes comprising 91% of the steam distillate were tested in two field assays. All five compounds were tested against blank controls in a six-choice test. A subtractive field assay was conducted with five mixtures of the monoterpenes using the concentrations found in the distillate of the initial resin. Each combination of monoterpenes was mixed in a single vial. In the subtractive assay, each compound was successively replaced by a solvent, decane, and tested against blank controls and a complete mixture of the five compounds. The release rate, determined gravimetrically, was approximately 0.8 ml/hr at 23°C for all test compounds but varied in the field with changes in ambient temperature, air pressure, isolation etc.. Chemicals were obtained from Aldrich Chemical Co. (Milwaukee, Wisconsin). Their chemical purity was: (*R*)-(+)-α-pinene 98%, (*S*)-(−)-α-pinene 98%, (*S*)-(+)-3-carene 95%, myrcene 85%, (*R*)-(+)-limonene 97%, (*S*)-(−)-limonene 97%, and (*S*)-(−)-β-pinene 99%. In tests 2 and 3 the natural concentration of enantiomers present in *P. ponderosa* resin was mixed with the solvent decane. (For example, in test

2 the α-pinene treatment was 14.3% (*S*)-(−)-α-pinene, 0.9% (*R*)-(+)-α-pinene, and 84.8% decane. In test 3 the XB treatment had the complete mix of compounds shown for ponderosa pine in the concentrations given in Table 5 (below) with 35.8% decane substituted for (*S*)-(−)-β-pinene).

Because α-pinene was the only monoterpene in which both enantiomers were present in greater than 0.1% of resin volatiles, the attractiveness of each isomer was tested individually. We tested (*R*)-(+)- and (*S*)-(−)-α-pinene (optical purity > 96%) and varying mixtures of the two enantiomers by substituting decane for one of the enantiomers. In addition to ponderosa pine resin, the results of the α-pinene test prompted our analysis of the resin of the only other host species of *D. valens* in our test area, sugar pine (*P. lambertiana*), and of all three coniferous nonhosts: white fir, *Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.; incense cedar, *Libocedrus decurrens*, and Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco.

A dose–response test was conducted for (*S*)-(−)-β-pinene using release rates of 0.0, 0.7, 7, and 70 ml/day. (*S*)-(−)-β-Pinene was released from open glass tubes attached to flight traps and treatments were assigned each day in a randomized block with a total of 10 replicates for each treatment.

Results from the six field assays were tested with Friedman's two-way analysis for block designs with correction for multiple comparisons setting the experiment-wise type I error rate at the 0.05 level. If significant differences existed among all treatments, then treatments were compared with a Wilcoxon test with α set at 0.05 (SAS Institute, Cary, North Carolina).

RESULTS

The distillate of *P. ponderosa* resin was about 40 times more attractive to *D. valens* than the residue. The residue was not significantly different from the blank control (Table 1). Treatments caught equal numbers of males and females, and the responses of both sexes were pooled for analysis. Chemical analysis of the distillate revealed that the principal monoterpenes of the resin of *P. ponderosa* were: β-pinene [>98% (*S*)-(−)], 3-carene [>99% (*S*)-(+)] and limonene [>98% (*S*)-(−)]. In contrast to the relatively pure enantiomeric composition of these compounds, α-pinene was present in the *P. ponderosa* resin as a mixture with mean 95% (*S*)-(−) and 5% (*R*)-(+) (range of 10 trees sampled: 92%/8%–97%/3%).

Field tests 2 and 3 revealed a strong attraction of both sexes to (*S*)-(−)-β-pinene (Table 2). The dose test shows an increase in response with increasing dose of (*S*)-(−)-β-pinene. Catch at each dose was significantly different from the next highest dose (Table 3). There was a reduced but still significant attraction to (*S*)-(+)-3-carene (Table 2, tests 2 and 3). The catch at the two less

TABLE 1. CATCH OF *D. valens* IN TRAPS BAITED WITH *P. ponderosa* RESIN DISTILLATE OR RESIDUE (BLODGETT FOREST, EL DORADO COUNTY, CALIFORNIA, MAY 1988, TEST 1)[a]

Treatment	Mean catch	SE
Distillate	18.09a	4.42
Residue	0.45b	0.24
Recombination	18.63a	4.67
Control	0.36b	0.36

[a] Distillate ≠ residue; Friedman's test $\alpha = 0.05$, Wilcoxon test $\alpha = 0.05$, means followed by the same letter are not significantly different; 11 replicates/treatment

TABLE 2. CATCH OF *D. valens* IN TRAPS BAITED WITH TEST MONOTERPENES (BLODGETT FOREST, EL DORADO COUNTY, CALIFORNIA, APRIL 1990, TESTS 2 AND 3)[a]

Test 2			Test 3		
Monoterpene treatment	Mean catch/trap/day[b]	SE	Mixture minus one monoterpene	Mean catch/trap/day[b]	SE
(*S*)-(−)-β-Pinene	61.1a	10.44	XB [no (*S*)-(−)-β-pinene]	0.9a	0.27
(*S*)-(+)-3-Carene	11.2b	3.47	XC [no *S*-(+)-3-carene]	14.9b	2.98
Myrcene	2.5c	0.62	XM (no myrcene)	20.8c	3.79
α-Pinene	0.7d	0.27	XA (no α-pinene)	25.0c	4.01
Limonene	0.8d	0.36	XL (no limonene)	13.5bc	2.58
Blank control	0.4d	0.28	Complete mixture	20.2c	2.76
			Blank control	0.1d	0.08

[a] Chiral monoterpenes were tested using the natural blend of enantiomers found in ponderosa pine resin, 16 replicates/treatment in test 2; 22 replicates/treatment in test 3.
[b] Friedman's test $\alpha = 0.05$, Wilcoxon test $\alpha = 0.05$, means followed by the same letter are not significantly different.

abundant monoterpenes in *P. ponderosa* resin, α-pinene and limonene, were not significantly different from the blank control. A third less abundant monoterpene, myrcene, showed statistically significant but minor attraction in our initial test (Table 2, test 2) but was not significantly attractive in the subtractive assay (Table 2, test 3). In both tests 4 and 5 (Table 4) the (*R*)-(+) enantiomer of α-pinene was found to be significantly attractive to *D. valens*. A mixture of decane and the (*R*)-(+) enantiomer was more attractive than a similar mixture

TABLE 3. DOSE RESPONSE OF *D. valens* TO INCREASING DOSE OF (*S*)-(−)-β-PINENE (BLODGETT FOREST, EL DORADO COUNTY CALIFORNIA, JUNE 1990, TEST 6)[a]

Release rate of (*S*)-(−)-β-pinene	Mean catch/trap/day*	SE
70 ml/day	68.7a	26.53
7.0 ml/day	27.5b	15.32
0.7 ml/day	2.2c	0.73
Control	2.2c	1.56

[a]Friedman's test $\alpha = 0.05$, Wilcoxon test $\alpha = 0.05$, means followed by the same letter are not significantly different.

containing the (*R*)-(+) and (*S*)-(−) enantiomers (Table 4, test 4), thus proving that the (*S*)-(−) enantiomer interrupts attraction.

Resin of sugar pine, like ponderosa pine, had a large proportion of the most attractive monoterpene, (*S*)-(−)-β-pinene. However, the largest proportion of its resin volatiles was composed of α-pinene (48%), of which, two thirds was the attractive (*R*)-(+) enantiomer (Table 5). The three nonhosts also each contain large amounts of attractive monoterpenes: (*S*)-(−)-β-pinene in white fir and (*R*)-(+)-α-pinene in all three species. Very little (*S*)-(+)-3-carene was found in these nonhost conifers.

DISCUSSION

The remarkable stereospecificity of *D. valens*' attraction to (*R*)-(+)-α-pinene suggests that enantioselectivity of host compounds may be a significant component of bark beetle host selection behavior. Renwick et al. (1976) found that exposure of *Ips paraconfusus* Lanier to the two optical isomers of α-pinene led to the production of different verbenols, (+)-*trans*-verbenol from (*R*)-(+)-α-pinene and (+-*cis*-verbenol from (*S*)-(−)-α-pinene. If pheromone production by other species of scolytids is similarly influenced by the chirality of host compounds, then stereospecificity in response of beetles to optically active kairomones may be a key element in species-isolating mechanisms and host race (biotype) formation. White et al. (in preparation) studied the antennal response of *D. valens* to resin fractions and to individual components from the resin of *P. ponderosa* using the electroantennogram (EAG) technique (Schneider, 1957; White and Birch, 1987). They concluded that there was a clear difference between the responses to (*R*)-(+)-α-pinene and (*S*)-(−)-α-pinene.

Our field results parallel those of Birch et al. (1980), who found that the response of *Ips pini* Say to its pheromone, (−)-ipsdienol, is interrupted by the

TABLE 4. CATCH OF *D. valens* IN TRAPS BAITED WITH ENANTIOMERS OF α-PINENE [BLODGETT FOREST, EL DORADO COUNTY CALIFORNIA, JUNE 1990 (TEST 4) AND JUNE 1991 (TEST 5)]

Test 4			Test 5		
Treatment	Mean catch/trap/day[a]	SE	Treatment	Mean catch/trap/day[a]	SE
96% (*R*)-(+)	8.8a	2.99	(*S*)-(−)-β-Pinene	27.8a	5.25
75% (*R*)-(+)/25% solvent	6.8a	1.88	(*S*)-(+)-3-Carene	2.6b	0.88
75% (*R*)-(+)/25% (*S*)-(−)	1.5b	0.92	(*R*)-(+)-α-Pinene	2.2b	0.63
Control	0.2b	0.12	(*S*)-(−)-α-Pinene	0.1c	0.08
			Control	0.6c	0.32

[a] Friedman's test $\alpha = 0.05$, Wilcoxon test $\alpha = 0.05$, means followed by the same letter are not significantly different; 9 replicates/treatment in test 4; 20 replicates/treatment in test 5.

TABLE 5. MONOTERPENES PRESENT AS >1% OF RESIN VOLATILES OF 5 TREES FOR EACH SPECIES COLLECTED AT BLODGETT FOREST, EL DORADO COUNTY, CALIFORNIA

	Percent of total volatiles, mean (SD)				
Monoterpene	*Pinus ponderosa*	*Pinus lambertiana*	*Pseudotsuga menziesii*	*Libocedrus decurrens*[a]	*Abies concolor*
(*S*)-(−)-β-Pinene	35.8(4.3)	20.3(9.7)	12.1(3.6)	0.7(0.3)	39.9(16)
(*S*)-(+)-3-Carene	34.4(4.2)	4.7(2.3)	<0.1(0.1)	0(0)	0.2(0.1)
Myrcene	7.0(2.1)	4.5(2.4)	1.1(0.4)	2.0(1.3)	2.3(1.7)
(*S*)-(−)-Limonene	5.5(4.2)	0.1(0.2)	1.8(1.1)	1.0(0.3)	3.7(4.8)
(*R*)-(+)-Limonene	<0.1(0.1)	0.1(0.1)	0.2(0.2)	0.2(0.3)	0.1(0.1)
(*S*)-(−)-α-Pinene	14.3(2.3)	21.1(7.1)	25.6(3.4)	37.3(7.3)	14.3(3.4)
(*R*)-(+)-α-Pinene	0.9(0.4)	47.9(19.2)	55.2(6.5)	55.7(10.8)	30.3(9.9)
(*S*)-(−)-β-Phellandrene	0.6(0.1)	0.3(0.1)	1.9(0.6)	0.9(1.3)	7.9(3.3)

[a] Only three trees sampled.

antipode of this terpene alcohol. Chiral specificity of *Dendroctonus spp.* to their pheromones is summarized by Phillips et al. (1990). *D. terebrans* and *D. brevicomis* respond to (+)-*exo*-brevicomin and (−)-frontalin. Antipodes of these compounds do not interrupt response. *D. ponderosae* produces frontalin and *exo*-brevicomin and responds to both enantiomers of each compound. The response can be aggregation or antiaggregation, depending on release rate (see synopsis in Phillips et al., 1990, p. 256). Although we have shown that (*S*)-(−)-α-pinene interrupts response only to (*R*)-(+)-α-pinene, there is an indica-

tion that it also interrupts attraction to the complete mixture of volatiles from the host. When α-pinene [94% (*S*)-(−)] was removed from the complete mixture, the mean catch increased, although not significantly (Table 2, test 3). The strong attraction to (*R*)-(+)-α-pinene and the interruption of attraction exhibited by its antipode are particularly interesting when the relative proportions of these enantiomers in the resin of *P. lambertiana* and *P. ponderosa* are considered.

The response of the beetles parallels the distribution of the major resin components of their two host species in this forest type, i.e. (*S*)-(−)-β-pinene in *P. ponderosa* and (*R*)-(+)-α-pinene in *P. lambertiana* (Table 5). The second most abundant monoterpene in the volatiles of each host species was also attractive to *D. valens*, i.e. (*S*)-(+)-3-carene in *P. ponderosa* and (*S*)-(−)-β-pinene in *P. lambertiana*. Neither myrcene nor limonene was abundant in either host, and the beetle response to them was weak or not significantly different from controls (Table 2, tests 2 and 3). No discrimination was evident between the two enantiomers of limonene in EAG studies (White et al., in preparation). While attractive compounds may be present among the 49 present in the untested 9% of the volatiles, none of these was greater than 1% of the total volatiles present in the resin (Cool, unpublished).

The broad host and geographic range of *D. valens* (most North American pines; S.L. Wood, 1982) raises intriguing possibilities of host and regional specialization. However, it remains to be established whether or not local adaptation to host kairomones occurs for *D. valens*. EAG, behavioral, and genetic tests with beetles emerging from known sympatric hosts would be required to prove host race formation.

The possibility that beetles may be attracted by widely distributed compounds such as (*S*)-(−)-β-pinene and interrupted by inhibitory compounds such as (*S*)-(−)-α-pinene in the same mixture would be an example of the complex signal discussed by Dethier (1954). Other authors (Renwick and Radke, 1983; Thorsteinson, 1960) have suggested that host selection in generalist herbivores may rely upon deterrent compounds to avoid nonhosts, while specialists search for key stimuli found only in the correct combination in their host. Quantitative differences in resin production might partially explain the lack of colonization of nonhosts. Incense cedar produces very little wound resin. White fir produces and exudes cortical resins, especially in its mid- and upper bole, but very little resin is typically present in the lower bole and root collar where *D. valens* would be expected to feed (Hobson, unpublished). Douglas fir xylem resin is released with breakage, but it is not as abundant as the resin of the two host pines (Hobson, unpublished). In addition to the quantitative differences in host versus nonhost resin production, it seems likely that nonhost status might be assessed by other cues such as olfactory interruptants and/or visual information or, after landing, by gustatory antifeedants and/or tactile cues (Visser, 1986; Lewis, 1984; Elkinton and Wood, 1980). Further research is needed to determine

whether or not compounds that interrupt attraction are present in nonhost conifers that occur in forests with the hosts of *D. valens*.

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