

SHORT COMMUNICATION

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Strategies of a bark beetle, *Pityogenes bidentatus*, in an olfactory landscape

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Abstract Volatiles from leaves or bark of nonhost birch (*Betula pendula*) and Norway spruce (*Picea abies*) dramatically reduced the attraction of the bark beetle, *Pityogenes bidentatus* (Coleoptera: Scolytidae), to their aggregation pheromone components (*cis*-verbenol and grandisol) in the field. In addition, odors from both the needles and bark of the host Scots pine (*Pinus sylvestris*) similarly inhibited attraction. Monoterpenes of pine and spruce (α -pinene, β -pinene, terpinolene, and 3-carene) as well as ethanol, chalcogran and some non-host green leaf alcohols [(*Z*)-3-hexen-1-ol, (*E*)-2-hexen-1-ol, and 1-hexanol], also reduced catches. Collections of volatiles from the field-tested plant tissues indicated they released monoterpenes in amounts similar to the synthetics that inhibited responses. The various plant and insect sources of these inhibitory compounds indicate that *P. bidentatus* bark beetles have evolved several strategies to increase their fitness by avoiding non-host and unsuitable host trees in a complex olfactory landscape.

Introduction

Bark beetles of the genus *Pityogenes* are relatively small (2–3 mm long) and attack conifers, usually the limbs, tops, or smaller diameter trunks of weakened hosts (Lekander et al. 1977). *Pityogenes bidentatus* (Herbst) and *Pityogenes quadridens* (Hartig) are common in conifer forests of northern Europe and colonize

Scots pine, *Pinus sylvestris* L. Another common species, *Pityogenes chalcographus* (L.), feeds on Norway spruce, *Picea abies* (L.). One of the most common non-host trees of these bark beetles is birch, *Betula pendula* (Lekander et al. 1977). In these and most other bark beetle species, a “pioneer” individual finds a susceptible host tree that allows the beetle to release a species-specific aggregation pheromone (Byers 1995). Conifers such as pines and spruce usually produce resin, consisting of mildly toxic monoterpenes, in order to defend against the penetrations of the attacking beetles (Byers 1995). Therefore, bark beetles may have evolved olfactory mechanisms and behaviors for the avoidance of specific volatile monoterpenes in tree resins. However, several studies have found that certain monoterpenes enhance the attraction to pheromone components in some of the more “aggressive” bark beetles that kill standing trees (Bedard et al. 1969; Rudinsky et al. 1972; Werner 1972; Byers et al. 1988).

The pioneer bark beetles of the most “aggressive” tree-killing species probably find suitable host trees by landing at random, since there is no evidence of attraction to uncolonized hosts (Moeck et al. 1981; Byers 1995). As the tree becomes colonized and begins to degrade, higher rates of verbenone and ethanol are released that reduce attraction of most of these bark beetles to pheromone or host monoterpenes (Bakke 1981; Klimetzek et al. 1986; Byers et al. 1989, 1998; Byers 1992, 1993, 1995). There also is increasing evidence that aggregation responses to semiochemicals by conifer-infesting bark beetles in several genera are reduced by volatiles from nonhost angiosperm trees (e.g. *Betula*, *Populus*, *Acer*) (Dickens et al. 1992; Schroeder 1992; Schlyter et al. 1995; Wilson et al. 1996; Borden et al. 1997, 1998; Guerrero et al. 1997; Byers et al. 1998; Deglow and Borden 1998; Huber et al. 1999; Zhang et al. 1999a, b; Poland and Haack 2000). These studies have found that some of the most important nonhost compounds are (*Z*)-3-hexen-1-ol, (*E*)-2-hexen-1-ol, and 1-hexanol, mostly from leaves, as well as *trans*-conophthorin from bark.

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Materials and methods

To investigate whether *P. bidentatus* has several strategies for quickly avoiding nonhosts and unsuitable host trees during host-finding, we tested the effects of volatiles from leaves or bark from appropriate trees on the attraction of *P. bidentatus* to its aggregation pheromone components, grandisol and *cis*-verbenol (Baader 1989; J.A. Byers et al., unpublished) in the field. The pheromone baits were placed inside a pair of traps, each trap consisting of plastic cylinders (18 cm diameter × 28 cm high) covered at the top but open at the bottom and suspended over a funnel (31 cm diameter) that collected beetles striking the cylinder (Fig. 1). Inside each cylinder was a fine screen cage, either empty (control) or containing freshly cut bark chips or twigs with leaves/needles of either nonhost birch (*B. pendula*), nonhost Norway spruce (*P. abies*), or host Scots pine (*P. sylvestris*) (Fig. 1). The pair of traps were separated 6 m apart at 1.2 m height and revolved at 2 rph (Byers et al. 1990a). The plant materials were divided into equal portions, one for use in the traps and one for collecting their volatiles, at the same time as the field test occurred.

Volatiles from the twigs and leaves/needles or bark chips were collected for chemical analysis by enclosing them in plastic cooking bags (Meny Toppits, 35 × 43 cm) through which activated-carbon filtered air was sucked at 300 ml/min. The effluent volatiles were adsorbed on 30 mg Porapak Q (50–80 mesh, Supelco) in a 3 mm ID Teflon tube for 1.5 h. Diethyl ether washings (300 µl) of the Porapak Q were kept at –20°C until chemical analysis on a combined HP 5890 series II gas chromatograph and HP 5972 mass selective detector (GC-MSD). Columns, conditions, and quantification procedures were as described by Zhang et al. (1999a).

Results

Volatiles from birch bark chips or leaves/twigs (*B. pendula*) reduced the response of *P. bidentatus* to aggregation pheromone down to only 16% or 17%, respectively, compared with aggregation pheromone alone in the revolving trap pair (Fig. 1). The inhibition of response was nearly complete for spruce bark at only 2%, while spruce needles/twigs reduced response to 28% (Fig. 1). Surprisingly, both host Scots pine bark and needles/twigs were effective in reducing attraction of the beetles to 22% and 40%, respectively, of those attracted to pheromone alone (Fig. 1). Due to the hundreds of beetles attracted per hour, it was possible to observe their orientation behavior in the late afternoon sun. Beetles flew upwind against a slight breeze (<0.5 m/s) for at least 20 m while converging toward the pheromone source. However, when the beetles approached to within about 0.5–1 m of the trap with the spruce bark, they were repelled and turned away.

Analysis of the Porapak Q-entrapped volatiles revealed, as expected, that high quantities of monoterpenes were released from the conifer materials compared to lesser but still significant amounts from the birch leaves/twigs (Table 1). Background air from the study area (mostly pines with some spruce) contained 7.4, 3.7, and 3.7 ng/l of α -pinene, β -pinene, and 3-carene, respectively. This indicates that when beetles flew toward the conifer bark samples the monoterpene concentration increased about 2,000-fold (Table 1). Some of the monoterpenes in the rotating pair of traps were

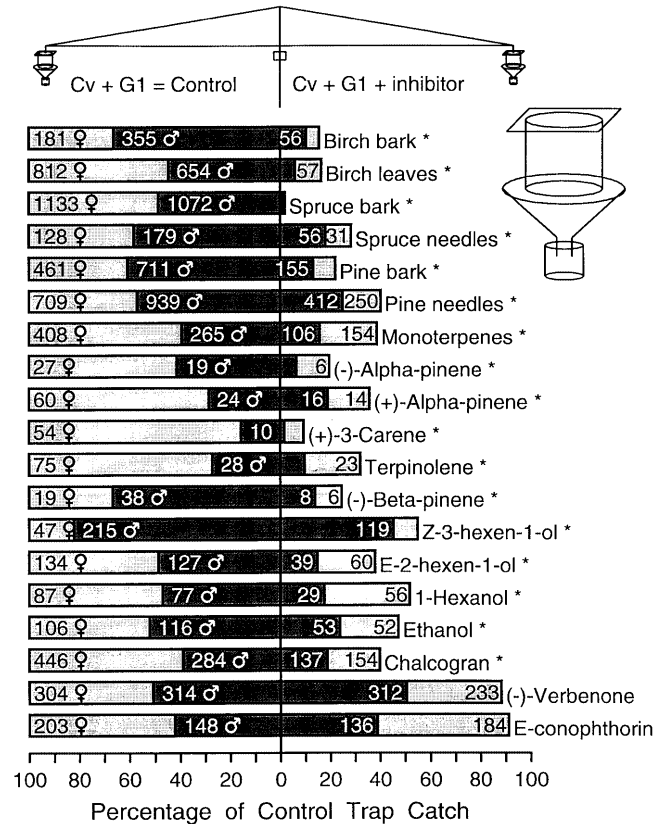


Fig. 1 Reduced catches of *Pityogenes bidentatus* on traps releasing pheromone plus inhibitor volatiles compared with control traps containing pheromone alone. The trap pairs were mechanically rotated at 2 rph to minimize catch variation due to trap position. Test replicates were conducted for at least 1 h, and after each replicate the inhibitory source, but not the attractant, was switched to the other trap. Replicate catches were summed, and the paired control and treatment were compared, using a χ^2 goodness of fit test, to an expected catch if there were no differences based on the average for both traps. Tests used 100, 200, and 220 g bark chips and 80, 160, and 220 g leaves/twigs of pine, birch, and spruce, respectively (2 May 1998), and the chemicals as indicated (April–May 1998–2000) near Sjöbo, Sweden. *P. bidentatus* pheromone components, cV [(*S*)-*cis*-verbenol, 96%, Borregaard] and G1 [racemic *cis*-configured grandisol, (1*R**,2*S**)-1-(2-hydroxyethyl)-1-methyl-2-(1-methylethenyl)cyclobutane, Frank Enterprises, Columbus, Ohio], were released from small tubes at 21 and 0.5–2 µg/h, respectively. (*Z*)-3-hexen-1-ol, (*E*)-2-hexen-1-ol, 1-hexanol (each >98%, Aldrich), (-)-verbenone ($[\alpha]^{20D} = -246^\circ$, 99.2% e.e., Bedoukian), *trans*-conophthorin (85%, Pherotech), and ethanol were released at 260, 210, 170, 40, 210, and 50,000 µg/h, respectively. The “monoterpenes” (\pm)- α -pinene (>98%, Aldrich), (+)-3-carene ($[\alpha]^{20D} = +15^\circ$, 95%, Aldrich) and terpinolene (97%, Carl Roth) were released in a mixture at 2,500 µg/h. (-)- α -Pinene ($[\alpha]^{20D} = -50^\circ$, >99.5%, Fluka), (+)- α -pinene ($[\alpha]^{20D} = +57^\circ$, 99%, Fluka), (-)- β -pinene ($[\alpha]^{20D} = -21^\circ$, 99%, Aldrich), (+)-3-carene, and terpinolene were released alone at about 1,400, 1,400, 980, 2,130, and 780 µg/h, respectively, from various combinations of tubes. Chalcogran (46% *E*: 54% *Z*, >98%; from W. Francke), was released at 66 µg/h. Catches with asterisks were significantly lower than the pheromone controls in the same test at $P < 0.01$ (χ^2 goodness of fit)

released at quantities similar to total amounts emitted from the plant materials in the field test (Table 1, Fig. 1). Monoterpenes from host Scots pine [(+)- and (-)- α -pinene, (+)-3-carene, and terpinolene], individu-

Table 1 Release rates of volatiles ($\mu\text{g/h}$) from plant materials (leaves, needles, and bark of nonhosts birch, *Betula pendula*, and Norway spruce, *Picea abies*, and host Scots pine, *Pinus sylvestris*)

used in the field test of *Pityogenes bidentatus* inhibition to aggregation pheromone (2 May 1998, Fig. 1). The volatiles were collected on Porapak Q and identified by GC-MSD^a

Compound	Birch: <i>B. pendula</i>		Spruce: <i>P. abies</i>		Pine: <i>P. sylvestris</i>	
	Leaves	Bark ^b	Needles	Bark	Needles	Bark
α -Pinene	0.1	0.2	7	260	200	110
Camphene	2.9		0.6	14	5	2
β -Pinene	105	0.1	6	260	16	4.2
Sabinene	7		0.1	15	35	3.2
3-Carene	3.9	0.05	1.1	12	315	160
Myrcene	25	0.01	0.3	100	32	25
2-Carene	0.5			1.7	5.7	4.8
Limonene	26	0.01	1.1	140	6.8	11.2
β -Phellandrene	42	0.02	1.2	81	31	9.3
τ -Terpinene	0.4		0.03	3.7	7.4	11.3
Terpinolene	1.3		0.03	22	34	70
1-Hexanol	0.01	0.01				
(<i>Z</i>)-3-Hexen-1-ol	0.06	0.01				
Terpinen-4-ol				1.8		0.1
α -Cedrene				3.2		
Copaenene	1.9			0.2	0.4	0.6
β -Bourbonene + (isomers)	0.1 + (1.2)					
Camphor					0.2	0.8
Bornyl acetate			0.03		0.5	1.2
α -Santalene		0.5				
α -Zingiberene		0.8				
β -Caryophyllene	0.5			15	1	
α -Terpinyl acetate						2.7
Germacrene-D					0.7	2.1
α -Muuroolene	0.2				0.4	1.4
δ -Cadinene	0.9			0.2	2.3	0.2
Myrtenol				0.1		0.1
<i>trans</i> -Carveol						0.04

^a Chemicals were identified by comparison of retention times and mass spectra to those of authentic compounds and computer data libraries (NBS75K and additions)

^b Only a trace of *trans*-conophthorin was detected

ally or together, reduced responses significantly and comparable to the plant materials (Fig. 1). These monoterpenes and ($-$)- β -pinene (from spruce), and probably others as well, appear to be largely responsible for the inhibition by the nonhost Norway spruce and host Scots pine twigs/needles and bark. 1-Hexanol and (*Z*)-3-hexen-1-ol were released from birch leaves and bark; and higher quantities of these green leaf alcohols reduced responses to pheromone (Fig. 1). Ethanol, at an apparently high release rate, as well as chalcogran (a pheromone component of competing bark beetles) were also inhibitory (Fig. 1). However, inhibitor candidates ($-$)-verbenone and *trans*-conophthorin did not have any appreciable activity (Fig. 1).

The catches on a rotor trap baited with only aggregation pheromone components were compared at three sites 80–110 m apart during 4-hourly collections (2 May 1998). *P. bidentatus* flies later in the afternoon than *Ips typographus* or *P. chalcographus*, which fly when the temperatures raise above 17–18°C (Byers 1995). The first collection at 1600 hours took beetles that were attracted for the previous 2 h, since few fly before 1400 hours. The sex ratios within a site did not change significantly during the afternoon; however, between these relatively close sites, the sex ratios were significantly

different (Fig. 2). Although the baits were the same, the numbers caught were much lower at site 3 than at the other two sites (Fig. 2). These results show that there can be a difference not only in flight densities but even in sex ratios in nearby areas of the forest. The sex ratios on the control pheromone baits do not appear significantly different from those on the baits with inhibitory plant materials or synthetic compounds (Fig. 1).

Discussion

Many of the studies cited above have theorized that conifer bark beetles avoid nonhost angiosperm volatiles as an aid in selecting the appropriate host; our results suggest that *P. bidentatus* avoid volatiles from nonhosts birch and Norway spruce (Fig. 1) for the same reasons. However, it is surprising that these beetles also avoid volatiles from their host tree, Scots pine, at seemingly natural rates of release (Fig. 1). In contrast, *Toxomicus piniperda*, which also colonizes Scots pine, is strongly attracted to volatiles from host bark, and this is due to the same monoterpenes, α -pinene, 3-carene, and terpinolene (Byers et al. 1985) that are avoided by *P. bidentatus* (Fig. 1). Other reports on bark beetles sug-

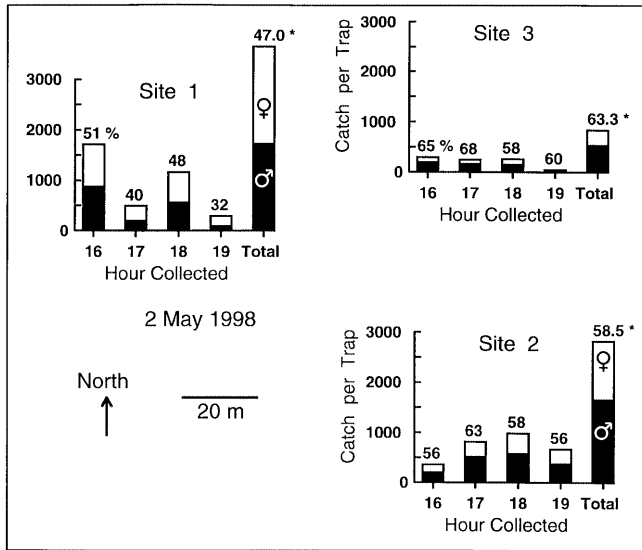


Fig. 2 Catch of *Pityogenes bidentatus* on grandisol and *cis*-verbenol on 2 May 1998 at three sites (drawn to scale, Sjöbo, Sweden). Numbers above bars are the percentage males; asterisks indicate total proportions were significantly different in comparisons with other sites (χ^2 , $P < 0.01$)

gest that host monoterpenes should enhance *P. bidentatus* response to aggregation pheromone. For example, monoterpenes (e.g. myrcene) enhance or synergize the attraction of several “aggressive”, tree-killing bark beetle species in the genera *Dendroctonus* and *Ips* to aggregation pheromone components (Bedard et al. 1969; Rudinsky et al. 1972; Werner 1972). The six-spined spruce engraver, *P. chalcographus*, is an aggressive sibling species that prefers smaller diameter Norway spruce, but can be found attacking trees of any size (Byers 1995; personal observations). Monoterpenes from the host, α -pinene, (-)- β -pinene, and camphene slightly increased the response of walking *P. chalcographus* to aggregation pheromone components (Byers et al. 1990b). Also, monoterpenes increase the frequency of beetles entering holes in plastic “logs” releasing pheromone (Byers et al. 1988). The view that host monoterpenes are attractive or enhance aggregation to pheromone is probably a useful paradigm, but not in the case of *P. bidentatus*, as reported here.

Further work is needed to clarify the precise roles of monoterpenes, not only for *P. bidentatus* but also for other bark beetles. Nevertheless, several of the host and nonhost monoterpenes appear to be largely responsible for the avoidance of nonhost spruce and pine (and maybe birch leaves) by *P. bidentatus* (Fig. 1, Table 1). Other, unidentified, volatiles seem important for the avoidance of birch bark. However, one likely suspect, *trans*-conophthorin (released from birch bark, Byers et al. 1998; Zhang et al. 2000) and known to inhibit some other bark beetles (Huber et al. 1999; Q.-H. Zhang et al., unpublished) did not significantly affect response to pheromone (Fig. 1). On the other hand, three green leaf volatiles from birch, (*Z*)-3-hexen-1-ol

and (*E*)-2-hexen-1-ol, and 1-hexanol did reduce attraction (Fig. 1). These compounds also are known to reduce aggregation of other bark beetles, as mentioned earlier.

The olfactory “landscape” becomes even more complex when several other compounds are considered. (-)-Verbenone, a known inhibitor of *P. chalcographus* (Byers 1993) and many other bark beetles, did not have a significant effect on the response of *P. bidentatus* to aggregation pheromone (Fig. 1). Verbenone appears to reduce aggregation response in those bark beetles that bore into living trees (Byers et al. 1989; Byers 1993, 1995), but has not been effective in reducing the response of *Hylurgops palliatus* to ethanol (Byers 1992). *H. palliatus* is considered a “secondary” species since it feeds in decaying pine that would have microorganisms producing ethanol as well as verbenone (Byers et al. 1989). Ethanol, at a relatively high release rate, reduced the attraction of *P. bidentatus* to pheromone (Fig. 1), an effect also shown for *P. chalcographus* (Byers et al. 1998). This is in accordance with the theory that ethanol from decadent hosts reduces response of “primary” bark beetles such as *Ips typographus* (Klimek et al. 1986) which colonize living trees that release little or no ethanol (Moock 1970; Kimmerer and Kozłowski 1982). Finally, *P. bidentatus* were inhibited by the release of chalcogran (Fig. 1), released as a pheromone component of *P. chalcographus* (sympatric), and more importantly by *P. quadridens*, which competes for similar bark areas on Scots pine (Francke et al. 1977, 1995; Byers et al. 1988, 1990b).

P. bidentatus appears to be a “nonaggressive” species, rarely attacking living trees, but specializing in colonizing diseased and dying branches. In this role, the beetle would want to avoid host monoterpenes that indicate bark areas exuding fresh oleoresin. It is well known that conifer trees resist bark beetle attack with a quantitative resinosis (Byers 1995). Also, beetles colonizing dying branches might need to tolerate some verbenone, which may increase with ageing (Byers et al. 1989). The branches must still be living so the presence of ethanol, which was inhibitory, may indicate tissues overly decayed and unsuitable. To test these theories, a bait releasing the aggregation pheromone components (as used in the tests) was placed on each of three trees (15 cm DBH, spaced 30 m apart): birch, *B. pendula*, Norway spruce, and Scots pine (2 May 1998). Interestingly, the birch tree incurred some attacks (22 holes penetrating 1–5 mm into the phloem) which were all abandoned by 17 May 1998, except for two holes with dead beetles and four holes with living beetles (17 May 1998). None of the short galleries had brood. The mortality and unsuccessful attacks indicate that there is a selective advantage in avoiding birch. Attractive pheromone baits placed on birch could not induce spruce-infesting *P. chalcographus* to attack (Byers et al. 1998). The Scots pine tree was not attacked by *P. bidentatus*, but a cut branch (6 cm diameter \times 40 cm long), hung on the tree on 9 May, received 30 attacks and all were suc-

cessful. The baited Norway spruce tree was not attacked. These results confirm the view that *P. bidentatus* avoids nonhost trees and healthy hosts, preferring cut limbs of low resistance potential.

The complexity of the olfactory landscape has provided opportunities for *P. bidentatus* bark beetles to evolve multiple strategies for finding suitable hosts from among unsuitable hosts and nonhosts and for avoiding competitive interactions with stochastic occurrences of other species. This complexity provides new insights into the design and testing of control strategies in pest management with semiochemicals.

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