

NOTE

Host odour *alpha*-pinene increases or reduces response of *Ips avulsus* (Coleoptera: Curculionidae: Scolytinae) to its aggregation pheromone, depending on separation of release points

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Abstract

Monoterpenes in the resin of host trees are important host-location and -selection signals for conifer-infesting bark beetles and can increase or reduce responses to aggregation pheromones. Research on this interaction has been largely limited to collocated release points of the semiochemicals; however, sources are often separated in nature. I performed a trapping experiment to investigate whether distance between semiochemical release points influences how host monoterpene *alpha*-pinene affects *Ips avulsus* (Eichhoff) (Coleoptera: Curculionidae) response to its aggregation pheromone (ipsdienol and lanierone). High release (8 g/day) of *alpha*-pinene from a pheromone-baited trap caused a reduction in catches, but the same release of *alpha*-pinene from 4 m away significantly increased catches relative to pheromone alone. A low release (0.06 g/day) of *alpha*-pinene with either arrangement had no effect. Hence, a host odour released at rates sufficient to deter *I. avulsus* responses to its pheromone may nevertheless enhance attraction if the release point is sufficiently displaced from the pheromone source. The result suggests that, for *I. avulsus*, the semiochemical *alpha*-pinene may influence host finding and close-range assessment of host suitability in different ways. Operational lure formulations for some species of bark beetle might be improved by separating pheromone and host odour components or by adding a displaced host odour device.

In conifer-infesting bark beetles (Coleoptera: Curculionidae: Scolytinae), it is common for dispersing, host-seeking individuals to respond to odours produced by host trees either when these compounds are alone or present with beetle pheromone components (Miller and Borden 2000; Pureswaran and Borden 2005; Hofstetter *et al.* 2012). These odours include various monoterpenes present in the host's defensive resin that are released copiously following a breach of the tree's inner bark or sapwood (Ruel *et al.* 1998; Tisdale *et al.* 2003; Seybold *et al.* 2006). Mechanical injury (*e.g.*, windthrow, lightning strike, harvesting operations) and insect attacks can result in release of large quantities of host volatiles (Coulson *et al.* 1986; Strömwall and Petersson 1991; Pureswaran and Sullivan 2012). Presumably, these odours are attractive because they signal the location of trees of a suitable taxon that have been damaged and potentially weakened, rendering them more susceptible to colonisation (Schroeder and Lindelow 1989; Tunset *et al.* 1993; Pureswaran and Borden 2005).

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Evidence also suggests that concentrations of airborne resin volatiles may provide information on susceptibility and suitability of an individual host tree (Byers *et al.* 1985; Liu *et al.* 2011; Burke and Carroll 2016). High levels could signify a strong defensive response and resin production in quantities that might prove lethal to invading bark beetles (Erbilgin and Raffa 2000; Raffa *et al.* 2005; Byers 2012). Hence, relatively nonaggressive bark beetles that are less tolerant of resin defences may be attracted to low concentrations of host monoterpenes but repelled by high concentrations (Miller and Borden 2000; Erbilgin *et al.* 2003), resulting in a peaked, biphasic dose response to these compounds (Erbilgin *et al.* 2003; Raffa *et al.* 2005).

The bark beetle *Ips avulsus* (Eichhoff) is native to the southeastern United States of America and can be a consequential killer of pines (Pinaceae) when population numbers are high (Nebeker 2011). Pioneering males initiate galleries in the trees' phloem and release a two-component pheromone (ipsdienol and lanierone) that attracts mates as well as other males that initiate attacks (Vité *et al.* 1972; Birgersson *et al.* 2012). Sufficient attacks can deplete resin defences of living hosts and render them suitable for colonisation. *Ips avulsus* is considered a bark beetle of intermediate aggressiveness, typically attacking weakened, wind-thrown, broken, or other trees with compromised defences, and this species only occasionally colonises healthy trees (Coulson *et al.* 1986; Flamm *et al.* 1993). Evidence for a role of host monoterpenes in the chemical ecology of *I. avulsus* is limited. High (1–6 g/day) release of turpentine (the monoterpene-dominated distillate of pine resin) or the primary monoterpene of *I. avulsus* hosts, *alpha*-pinene (Mirov 1961; Bookwalter *et al.* 2019), either alone or with ethanol, reduces response of *I. avulsus* to traps baited with *Ips* pheromone components (Billings 1985; Miller *et al.* 2011; Miller 2020). There is no evidence of attractiveness of host odours, including *alpha*-pinene, to *I. avulsus*, either alone or with pheromones (Vité *et al.* 1964; Birch *et al.* 1980; Svihra 1982; Billings 1985; Smith *et al.* 1990; Miller *et al.* 2011).

In the above-mentioned tests indicating that *alpha*-pinene reduces attraction of *I. avulsus*, the pheromone and *alpha*-pinene were released from the same point in space (a trap). However, in nature, host odours and bark beetle pheromones may differ in their points of origin, and it is possible that, under these circumstances, the semiochemicals may interact differently and produce altered behavioural responses by the beetles. When its release point is displaced, *alpha*-pinene might provide an attractive cue for presence of host material while not signalling host unsuitability and mortality risk at the pheromone source. As such, one might expect enhanced, rather than reduced, catches of *I. avulsus* by pheromone lures when displaced, high-release devices of *alpha*-pinene are present. The following study tested this hypothesis.

Three lines of five 12-unit multiple funnel traps (Lindgren 1983) were established within mature pine forest (predominantly *Pinus taeda* Linnaeus) in central Louisiana, United States of America (within 2 km of 31.447° N, 92.286° W). Traps were more than 20 m from a road, more than 5 m from the nearest pine, and 100–200 m apart within the lines. More than 1 km separated the lines. Collection cups of the traps were 1–2 m above the ground and contained several centimetres of diluted propylene glycol. Traps were uniformly baited with “bubble” type lures releasing *I. avulsus* pheromone components ipsdienol (racemic, 0.6–0.8 mg/day at 25 °C; > 95% purity) and lanierone (0.05 mg/day at 25 °C; > 95% purity) attached to the trap midway vertically (Synergy Semiochemicals Corp., Delta, British Columbia, Canada; release and purity data provided by manufacturer). Treatments (factor TRTMT) were (1) no additional lure, (2) a low-rate release device of *alpha*-pinene attached to the trap, (3) a low-rate *alpha*-pinene device suspended approximately 1.5 m above the ground from a plastic pole positioned 4 m from the trap, and (4) and (5) similar to treatments 2 and 3, respectively, but each with a high-rate *alpha*-pinene device. *alpha*-Pinene devices were attached to traps at the same height as the pheromone components but on the opposite side of the trap. The pole supporting the displaced *alpha*-pinene device was positioned randomly relative to the trap at either 0°, 72°, 144°, 216°, or 288° from north within each line. The low-rate *alpha*-pinene device was a completely filled (4-mL), low-density polyethylene transfer pipette with a heat-sealed tip (Samco, San Francisco,

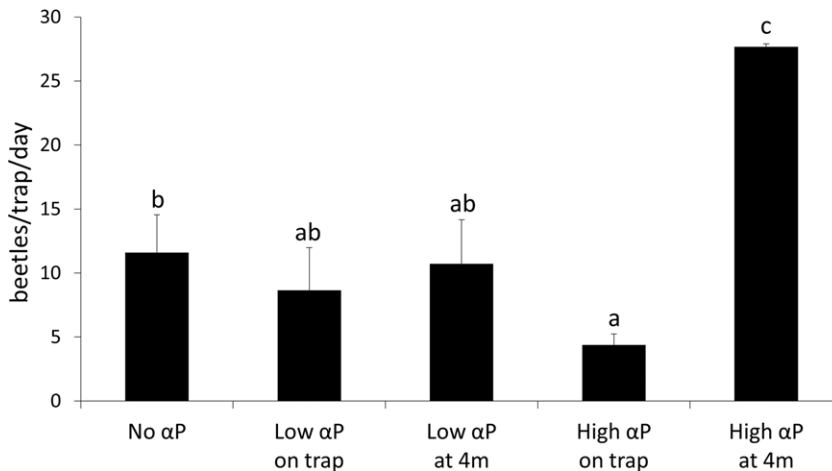


Fig. 1. Mean ($\pm$ standard error) responses of bark beetle *Ips avulsus* to multiple-funnel traps baited with devices releasing *Ips avulsus* aggregation pheromone (ipsdienol and lanierone) and host odour *alpha*-pinene (α P) at two different rates (low = 0.06 g/day; high = 8 g/day; at $\sim 23^\circ\text{C}$) either from the trap itself or a point 4 m away. Means associated with same letter were not significantly different (Tukey's test, $\alpha = 0.05$). Raw means are shown; statistical analyses were performed with cube-root transformed data.

California, United States of America; 0.06 g/day release); the high-rate device was a sealed low-density polyethylene enclosure (15 cm $\times$ 18 cm; 0.069 mm barrier thickness; 200 mL *alpha*-pinene; a 15 $\times$ 15-cm piece of burlap inside the enclosure wicked liquid throughout the interior; 8 g/day release) constructed with an impulse sealer. The *alpha*-pinene was 27% (+)enantiomer and at least 98% purity (Sigma-Aldrich, Milwaukee, Wisconsin, United States of America). Release rates for *alpha*-pinene devices were measured gravimetrically in a fume hood at mean 23°C . Treatments initially were assigned randomly to traps within each line. Catches were collected at 3- to 5-day intervals, at which time treatments were re-randomised among traps within lines without replacement to a previous position. Rotations and collections occurred until every treatment had been at a trap position once (75 samples). The experiment was conducted from 2 to 20 September 2010.

Data (catches of *I. avulsus*, cube-root transformed) were analysed as a multiple Latin-squares design, with each trap line representing a square (factor SQUARE), and, within each square, each collection date (factor DATE) representing a row and each trap (factor TRAP) representing a column. Generalised linear model factors were SQUARE, TRTMT, DATE, SQUARE $\times$ TRTMT, DATE $\times$ TRTMT, and TRAP(SQUARE). The error term for tests was SQUARE $\times$ TRTMT. Suitability of the transformation was determined through examination of residuals plots. Tukey's tests were used for all-pairwise comparisons ($\alpha = 0.05$). Statistical analysis was performed with SAS 9.4 (SAS Institute, Cary, North Carolina, United States of America).

A total of 3606 *I. avulsus* (identified according to Wood (1982)) was trapped. Catches were influenced by treatment ($F = 16.7$; $df = 4, 8$; $P < 0.001$; Fig. 1). Catches with the low-rate *alpha*-pinene device, either on or off the trap, did not differ from the control (no *alpha*-pinene). High-rate devices of *alpha*-pinene reduced catches of *I. avulsus* below the level of the control (approximately half) when placed on the trap but increased catches above the control (approximately double) when placed 4 m away.

The results indicate that high-release sources of *alpha*-pinene may either enhance or reduce *I. avulsus* response to its aggregation pheromone depending on proximity of the release points of the semiochemicals. This result is consistent with that of Miller and Crowe (2018) who

found that *I. avulsus* catches were greater in a pheromone-baited trap if it was located 6 m rather than 2 m from a trap releasing ethanol and a high rate of *alpha*-pinene (0.5 and 1–6 g/day, respectively); however, their test did not determine whether the effects were the result of attraction or inhibition. Hence, *alpha*-pinene could have distinct functions for *I. avulsus* at different spatial scales. The attraction-enhancing effect of the high-rate *alpha*-pinene device in the present experiment occurred at 4 m and thus presumably would influence beetle behaviour within a space encompassing multiple potential host trees and a substantial portion of the host bole. The antagonistic effects of *alpha*-pinene occurred at a smaller distance (15–20 cm separated the *alpha*-pinene and pheromone devices on the trap). This antagonism may divert beetles from portions of the host where high concentrations of *alpha*-pinene indicate a vigorous and potentially lethal defensive response. Thus, for *I. avulsus*, *alpha*-pinene may function both as (a) a host patch or “host habitat” location cue (Payne 1983), enhancing location of sites with trees potentially suitable for colonisation, and as (b) a short-range indicator of insufficient susceptibility and suitability of a particular host or a portion thereof. However, because the experiment used a pheromone lure, conclusions must be confined to the context of an ongoing beetle attack; the possible role of *alpha*-pinene in “pioneer” attacks requires further study. Furthermore, it is unknown how often host-seeking *I. avulsus* in nature might encounter airborne *alpha*-pinene concentrations comparable to those produced by the high-release devices.

The alternatively enhancing or reducing effects of *alpha*-pinene on *I. avulsus* responses are potentially attributable to an undiscovered biphasic dose response (*i.e.*, with attractive or repellent effects produced by either low or high concentrations, respectively (Rudinsky 1973; Sullivan and Brownie 2021), a phenomenon often termed “multifunctionality” in the bark beetle literature) to *alpha*-pinene. *Ips avulsus*’ sibling species, *Ips pini* (Say), has a biphasic dose response to *alpha*-pinene released from traps baited with aggregation pheromone (Erbilgin *et al.* 2003), as does the white pine cone beetle, *Conophthorus coniperda* (Schwarz) (Coleoptera: Curculionidae) (Miller *et al.* 2003). Average airborne concentration of a semiochemical is influenced by both the rate of release and the distance from the release point (Strand *et al.* 2009; Cardé 2021). Because of this, a biphasic dose response may coincide with a biphasic “distance-response” (Sullivan and Mori 2009; Sullivan 2016). The experiment tested only two release rates of *alpha*-pinene (0.06 and 8 g/day), and response to traps was not altered by the low-rate device whether it was located on or off the trap. Whether an intermediate or lower rate of *alpha*-pinene from the trap can enhance attraction remains to be tested. Also, future research should address whether distances of host odour release greater than 4 m from the pheromone source can enhance *I. avulsus* attraction.

These results and interpretation provide further evidence that operational lures for *Ips avulsus* and perhaps other species of less aggressive bark beetles might be improved by deploying host odour devices away from pheromone-baited traps (Miller and Crowe 2018).

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