Semiochemical Disruption of the Pine Shoot Beetle, *Tomicus piniperda* (Coleoptera: Scolytidae)

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ABSTRACT The pine shoot beetle, *Tomicus piniperda* (Coleoptera: Scolytidae), is an exotic pest of pine in North America. We evaluated blends of semiochemical disruptants, which included nonhost volatiles and verbenone, for their ability to disrupt attraction of *T. piniperda* to traps baited with the attractant α-pinene and to Scots pine, *Pinus sylvestris* L., trap logs. In Michigan and in Ontario, Canada, a single blend of nonhost volatiles alone [comprised of 1-hexanol, (Z)-3-hexen-1-ol, (*E*)-2-hexen-1-ol, 3-octanol, and 1-octen-3-ol] or the nonhost volatile blend combined with verbenone significantly reduced attraction of *T. piniperda* to attractant-baited traps by 68–77%. Similarly, verbenone plus the nonhost volatile blend or a similar blend without 1-octen-3-ol also significantly reduced attack density of *T. piniperda* on pine trap logs by 56–74% in both Michigan and Ontario. Although relative responses between the different blends were slightly different between Michigan and Ontario, the recommended operational disruptant consisted of 1-hexanol, (Z)-3-hexen-1-ol, (*E*)-2-hexen-1-ol, 3-octanol, and verbenone.

KEY WORDS *Tomicus piniperda*, nonhost volatiles, verbenone, disruptants

THE PINE SHOOT BEETLE, *Tomicus piniperda* (L.) (Coleoptera: Scolytidae), is a native pest in pine-growing regions of Europe, Asia, and northern Africa (Schroeder and Eidmann 1987, Långström and Hellqvist 1991, Ye 1997). Overwintering adults become active in the early spring (Bakke 1968). They orient to host volatiles, including α-pinene, to locate and attack brood material such as stumps, slash, or severely stressed, weakened, or freshly killed pines (Byers et al. 1985). Adult females bore individually into the bark of suitable hosts and excavate a nuptial chamber where each female is joined by a single male. Females excavate a gallery and lay eggs in the phloem. Larvae tunnel in the phloem and pupate at the ends of their larval galleries. Most adults emerge in the early summer and feed in the shoots of healthy pine trees. Maturation feeding within shoots continues until temperatures cool in autumn when beetles move down the trunk and construct niches in the outer bark at the base of trees to overwinter (Långström 1983, Petrice et al. 2002).

T. piniperda was first discovered in the Great Lakes region of North America in 1992 (Haack and Poland 2001). Many native North American pine species provide suitable habitat for breeding and for maturation feeding (Lawrence and Haack 1995, Siegert and McCullough 2001). Pine Christmas tree plantations are especially susceptible to infestations of *T. piniperda* because fresh stumps and piles of unsold or culled trees are usually available for colonization each year. Semiochemical disruptants may prove useful in protecting susceptible brood material from attack and thus prevent population buildup and large infestations.

A number of semiochemicals have been found to inhibit responses of *T. piniperda*. Kangas et al. (1970) and Perttunen et al. (1970) found that *T. piniperda* responded negatively to *cis*-verbenol and verbenone in laboratory trials. Byers et al. (1989) found that verbenone served as an olfactory cue of progressive host degradation and unsuitability and that it inhibited attraction of *T. piniperda* to host monoterpenes, including α-pinene, 3-carene, and terpinolene. The presence of bolts from nonhost deciduous trees (*Populus* and *Betula*) decreased attraction of *T. piniperda* to attractant-baited traps (Schroeder 1992). Poland and Haack (2000) evaluated responses of *T. piniperda* to common green leaf volatiles and found that a blend of four green leaf alcohols [1-hexanol, (Z)-3-hexenol, (Z)-2-hexenol, and (*E*)-2-hexenol] significantly reduced attraction of *T. piniperda* to α-pinene-baited funnel traps. Similarly, Schlyter et al. (2000) found that attraction of *T. piniperda* to baited traps was

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Table 1. Semiochemicals tested for disruption of attraction of *T. piniperda* to attractant-baited multiple funnel traps and to Scots pine trap logs in Michigan and Ontario

Code	Contents[a] (chemical purity)	Ratio	Release device and rate[b]
5-OH-blend	1-Hexanol (99.6%) Z3-Hexenol (98.3%) E2-Hexenol (99.8%) (±)-3-Octanol (99.4%) (±)-1-Octen-3-ol (99.6%)	2:1:1:1:1	15-ml Polyethylene vial 10 mg/day
5-OH+V-blend	1-Hexanol (99.6%) Z3-Hexenol (98.3%) E2-Hexenol (99.8%) (±)-3-Octanol (99.4%) (±)-1-Octen-3-ol (99.6%) (84%−)-Verbenone (98%)	2:1:1:1:1	15-ml Polyethylene vial 10 mg/day Bubble cap 2 mg/day
4-OH-blend	1-Hexanol (99.6%) Z3-Hexenol (98.3%) E2-Hexenol (99.8%) (±)-3-Octanol (99.4%)	2:1:1:1	15-ml Polyethylene vial 10 mg/day
4-OH+V-blend	1-Hexanol (99.6%) Z3-Hexenol (98.3%) E2-Hexenol (99.8%) (±)-3-Octanol (99.4%) (84%−) Verbenone (98%)	2:1:1:1	15-ml Polyethylene 10 mg/day Bubble cap 2 mg/day

[a] All semiochemicals and release devices were supplied by Phero Tech, Inc., Delta, BC, Canada.
[b] Release rates given are for the total combined release rate of each blend.

inhibited by verbenone or by several nonhost leaf and bark volatiles, including C6 and C8 alcohols.

Our overall goal was to develop an operational disruptant blend that could be used for *T. piniperda* population management by reducing attacks and population buildup in suitable breeding material. We selected blends of nonhost alcohols and verbenone based on the most promising disruptants reported in the literature (Poland and Haack 2000, Schlyter et al. 2000). Our specific objectives were 1) to determine whether combining verbenone with nonhost volatiles would enhance disruption of flying *T. piniperda* to attractant-baited traps, and 2) to evaluate combinations of disruptant nonhost volatiles and verbenone in reducing *T. piniperda* attacks on trap logs.

Materials and Methods

Two field experiments were conducted to determine whether semiochemicals could inhibit the attraction of *T. piniperda* to α-pinene or to pine breeding material. The field experiments were conducted in southern Michigan and in southern Ontario, Canada. Field sites in both Michigan and Ontario consisted of Scots pine, *Pinus sylvestris* L., Christmas tree plantations infested with *T. piniperda*. Trees were 1.5–2.5 m in height and 7–12 yr old. The Michigan site for both the trapping experiment and the trap log experiment was located in Mason, Ingham County (42° 58′ N, 84° 44′ W). The Ontario sites were located in Mulmur Township (44° 14′ N, 80° 13′ W) (trapping experiment) and in Maryborough Township (43° 42′ N, 80° 42′ W) (trap log experiment).

The trapping experiment was conducted from 22 March to 2 May 2001 in Michigan and was replicated in an identical manner on the same dates in Ontario. We deployed 12-unit multiple funnel traps (Lindgren 1983) in randomized complete blocks with at least 15 m between traps. Each experiment consisted of 10 replicates (i.e., blocks) separated by at least 25 m. Traps were baited with α-pinene alone or in combination with two different disruptant blends. An unbaited control trap was also included. In 2001, the 5-OH-blend consisted of five nonhost alcohols, including 1-hexanol, (*Z*)-3-hexen-1-ol, (*E*)-2-hexen-1-ol, 3-octanol, and 1-octen-3-ol (Table 1). The 5-OH+V-blend was identical to the 5-OH-blend except that it included verbenone (Table 1). Insects were collected from traps biweekly and stored frozen until counted and sexed. The total number of beetles captured in each trap was transformed by $\log(x + 1)$ to satisfy assumptions of normality and homoscedasticity and was then analyzed by two-way analysis of variance (ANOVA) with model factors for block and treatment. Differences among treatments were compared using the Ryan–Einot–Gabriel–Welch multiple comparison procedure (SAS Institute 1996) at $\alpha = 0.05$.

The trap log experiment was conducted from 22 March to 30 April 2002 in Michigan and replicated on the same dates in Ontario. It compared attack density by *T. piniperda* on untreated trap logs and on trap logs treated with four different disruptant blends. Healthy Scots pine trees were felled in late January 2002, and the lower portions of the boles, where bark was thick and rough, were cut into trap logs ≈15–20 cm in diameter and 60 cm in length. The cut ends of the logs were waxed and they were held in cool indoor conditions until placed in the field on 22 March. Individual trap logs were placed horizontally on wire (Michigan) or wooden (Ontario) supports just above the ground with at least 20 m between trap logs. The logs were laid out in randomized complete blocks with 10 replicates (i.e., blocks) of each treatment. Blocks were separated by at least 25 m. Release devices containing disruptant

Table 2. Mean number (± SE) of *T. piniperda* captured in 12-unit multiple funnel traps baited with α-pinene alone or combined with various semiochemical disruptants, 22 March–2 May 2001 (*n* = 10 traps/treatment)

Treatment	Mean no. of *T. piniperda* captured[a]	
	males	females
Michigan		
Unbaited	1.3 ± 0.4c	1.4 ± 0.3c
α-Pinene	76.8 ± 9.9a	90.5 ± 12.2a
α-Pinene + 5-OH-blend	24.9 ± 4.9b	23.5 ± 5.2b
α-Pinene + 5-OH+V-blend	21.0 ± 4.5b	18.2 ± 3.6b
Ontario		
Unbaited	0.2 ± 0.1c	0.3 ± 0.2c
α-Pinene	21.8 ± 2.6a	21.3 ± 3.5a
α-Pinene + 5-OH-blend	6.8 ± 2.5b	7.5 ± 2.4b
α-Pinene + 5-OH+V-blend	4.9 ± 0.9b	5.7 ± 0.8b

[a] Different letters within a column and field site indicate significant differences between treatments, Ryan–Einot–Gabriel–Welch multiple comparison test on data transformed by log $(x + 1)$, $P > 0.05$. ANOVA results for Michigan (treatment: $F = 60.66$, df = 3, $P = 0.0001$; block: $F = 1.73$, df = 9, $P = 0.13$) and for Ontario (treatment: $F = 83.57$, df = 3, $P = 0.0001$; block: $F = 1.10$, df = 9, $P = 0.39$).

Table 3. *T. piniperda* attack density (± SE) on *P. sylvestris* trap logs treated with various semiochemical disruptants, 22 March–30 April 2002 (*n* = 10 trap logs/treatment)

Treatment	No. of parental galleries/m^2[a]	
	Michigan	Ontario
Control	89.9 ± 9.8a	68.5 ± 13.8a
5-OH-blend	65.3 ± 10.4a	18.3 ± 5.2bc
4-OH-blend	55.4 ± 9.3a	41.3 ± 12.5ab
5-OH+V-blend	22.7 ± 4.4b	13.3 ± 7.3c
4-OH+V-blend	30.9 ± 8.7b	30.7 ± 13.5bc

[a] Different letters within a column indicate significant differences between treatments, Ryan–Einot–Gabriel–Welch multiple comparison test on data transformed by log $(x + 1)$, $P > 0.05$. ANOVA results for Michigan (treatment: $F = 10.57$, df = 4, $P = 0.0001$; block: $F = 2.14$, df = 9, $P = 0.06$) and for Ontario (treatment: $F = 6.52$, df = 4, $P = 0.0005$; block: $F = 2.04$, df = 9, $P = 0.06$).

blends were attached to the bark on the upper surface at the midpoint of the logs. The four disruptant blends consisted of the same blends as tested in 2001 (5-OH-blend and 5-OH+V-blend) as well as similar blends without 1-octen-3-ol (4-OH-blend and 4-OH+V-blend; Table 1), which was omitted because of concerns about toxicity. On 30 April, all trap logs were retrieved and brought into the laboratory where they were held frozen for up to 6 wk and then debarked to determine the number of *T. piniperda* parental galleries. Attack density for each log was calculated as the number of *T. piniperda* galleries divided by the outside-bark log surface area. Attack density was transformed by log $(x + 1)$ and then analyzed as described above.

Results and Discussion

In the trapping experiment, in both Michigan and Ontario, there were significant differences in the number of *T. piniperda* captured between treatments (Michigan: $F = 60.66$, df = 3, $P = 0.0001$; Ontario: $F = 83.57$, df = 3, $P = 0.0001$) but not between blocks (Michigan: $F = 1.73$, df = 9, $P = 0.13$; Ontario: $F = 1.10$, df = 9, $P = 0.39$). The response to α-pinene-baited traps was significantly greater than the response to unbaited traps for both sexes (Table 2). Both disruptant blends significantly reduced attraction of *T. piniperda* to α-pinene baited traps in Michigan and Ontario (Table 2). The 5-OH-blend reduced attraction to α-pinene by 71% in Michigan and 68% in Ontario. The 5-OH+V-blend reduced attraction by 77% in Michigan and 75% in Ontario. There were no significant differences between the two blends, indicating that adding verbenone (5-OH+V-blend) to the nonhost volatiles in the 5-OH-blend did not further reduce attraction to α-pinene-baited traps.

Similarly, in the trap log experiment, in both Michigan and Ontario there were significant differences in the density of *T. piniperda* attacks on trap logs between treatments (Michigan: $F = 10.57$, df = 4, $P = 0.0001$; Ontario: $F = 6.52$, df = 4, $P = 0.0005$) but not between blocks (Michigan: $F = 2.14$, df = 9, $P = 0.06$; Ontario: $F = 2.04$, df = 9, $P = 0.06$). Treatment responses were slightly different between Michigan and Ontario (Table 3). In Michigan, neither of the blends that omitted verbenone (5-OH-blend and 4-OH-blend) significantly reduced attack density of *T. piniperda* on trap logs. However, the blends that included verbenone (5-OH+V-blend and 4-OH+V-blend) significantly reduced attack densities by 74 and 66%, respectively, relative to the untreated *P. sylvestris* trap logs. There was no significant difference between attack densities on logs treated with the 5-OH+V-blend and the 4-OH+V-blend, indicating that 1-octen-3-ol is not necessary for a disruptant effect (Table 3). Overall, the results for Michigan suggest that including verbenone with the nonhost volatiles is more important than including 1-octen-3-ol for ensuring effective disruption of *T. piniperda*.

In Ontario, in contrast to Michigan, all of the disruptant blends significantly reduced *T. piniperda* attack densities relative to untreated *P. sylvestris* logs except for the 4-OH-blend, which lacked both verbenone and 1-octen-3-ol (Table 3). The omission of 1-octen-3-ol in Ontario seemed to reduce the efficacy of both the 5-OH-blend and the 5-OH+V-blend. There were no significant differences between the 5-OH-blend and the 5-OH+V-blend or between the 4-OH-blend and the 4-OH+V-blend, indicating that including verbenone did not significantly improve the disruptant effect in Ontario. Including verbenone in the 4-OH+V-blend partially offset the omission of 1-octen-3-ol and resulted in 56% reduction in attack density, which was intermediate between the reduction for the 4-OH-blend (40%) and the 5-OH-blend (73%). The results for Ontario suggest that 1-octen-3-ol contributed more to the disruptant effect of the blends than did verbenone.

The results of the trapping experiment (Table 2) support previous findings that blends of nonhost volatiles (C6 and C8 alcohols) inhibit attraction of *T. piniperda* to attractant-baited traps (Poland and Haack 2000, Schlyter et al. 2000). These results are similar to observations made for other species in which various green leaf volatiles or angiosperm-derived nonhost volatiles inhibited attraction of conifer-attacking bark beetles to attractant-baited traps or reduced attacks on suitable host material (Dickens et al. 1992, Wilson et al. 1996, Borden et al. 1997, Deglow and Borden 1998, Poland et al. 1998, de Groot and MacDonald 1999, Huber and Borden 2001).

Verbenone is an antiaggregant for several species of bark beetles (Payne et al. 1978, Ryker and Yandell 1983, Byers et al. 1989, Devlin and Borden 1995, McPheron et al. 1997, Holsten et al. 2001, Rappaport et al. 2001). Verbenone is produced primarily through metabolism of *trans*- and *cis*-verbenol by microorganisms in the guts of beetles (Hunt and Borden 1989) and in their galleries (Leufvén et al. 1984, Hunt and Borden 1990). It is also produced through autoxidation of α-pinene (Hunt et al. 1989). As host colonization progresses, the amount of verbenone increases and deters additional beetles from overcrowding fully colonized host material (Ryker and Yandell 1983). It has been identified in the hindguts of *T. piniperda* (Francke and Heemann 1976).

Verbenone did not significantly enhance the disruptant effect of the nonhost volatile blend in either Michigan or Ontario in the trapping experiment in 2001 (Table 2), or in Ontario in the trap log experiment in 2002 (Table 3). However, there were significantly fewer *T. piniperda* attacks on logs with verbenone added to the nonhost volatile blends in Michigan in the trap log experiment conducted in 2002 (Table 3). The effect of verbenone in interrupting host colonization may be more variable than its effect in interrupting trap catch due to the complex nature of colonization behavior and host-insect interactions compared with flight behavior.

Results of operational trials using verbenone to deter attacks on trees by mountain pine beetle, *Dendroctonus ponderosae* Hopkins, have also been inconsistent with some trials indicating a disruptant effect for verbenone (Shea et al. 1992, Lindgren and Borden 1993) and other trials indicating no significant treatment effect (Bentz et al. 1989, Lister et al. 1990, Shore et al. 1992). Results for the southern pine beetle, *Dendroctonus frontalis* Zimmermann, by using much higher release rates of verbenone, have been more consistent. Standardized operational tactics involving application of high release rates of verbenone alone or with tree felling have been successfully developed for the southern pine beetle (Clarke et al. 1999). Inconsistencies in efficacy of verbenone may be due in part to differences in release rate and dispersion (Kostyk et al. 1993), in beetle behavior and beetle genetics (Amman 1994), or in beetle population levels (Lindgren and Borden 1993). Verbenone also breaks down, under UV light, to the behaviorally inactive compound chrysanthenone (Kostyk et al. 1993), although stabilizers can be added to prevent decomposition of verbenone. Verbenone seems to be most effective as a potential operational control at low population levels where it can interfere effectively with beetle aggregation (Lindgren and Borden 1993). Attack densities on unbaited control trap logs were similar between Michigan and Ontario (Table 3; t value = 1.26, $P > 0.225$, PROC t-test; SAS Institute 1996), indicating that population levels were also likely very similar and were fairly high at both sites. Because identical release devices were used at both sites and site and weather conditions were similar, differences in release rates and dispersion could not explain the inconsistent effect of verbenone. Differences in responses in the trap log experiment between Michigan and Ontario were most likely due to behavioral responses to the complex and variable cues associated with trap logs. Disruption of colonization of host material involves numerous behavioral steps including host location, landing, walking, and feeding stimulation. Verbenone has been found to inhibit the feeding behavior of the pine weevil, *Hylobius abietis* L. (Coleoptera: Curculionidae) (Lindgren et al. 1996) and the walking behavior of California fivespined ips, *Ips paraconfusus* Lanier (McPheron et al. 1997).

Our results support the hypothesis that combinations of disruptant semiochemicals may be more effective than single disruptants on their own (Borden 1997). This result is similar to that found with the mountain pine beetle where combinations of nonhost volatiles and verbenone significantly reduced the number of mass-attacked trees (Huber and Borden 2001).

Reduction of attack density on natural brood material would reduce population buildup and could potentially prevent the development of large infestations. In Christmas tree plantations, removing stumps and burning piles of culled trees is not always feasible. Treatment with disruptants could help prevent populations from building up within these breeding sites. Disruptants may also be useful for protecting managed forest stands, perhaps as part of a push-pull strategy by using disruptants within a managed stand and attractive traps and trap logs along the edge to capture *T. piniperda* that are disrupted and disperse from the stand (Borden 1997).

Although relative responses to the particular disruptant blends differed slightly between Ontario and Michigan, the blends that we tested consistently and significantly reduced attraction and attacks by *T. piniperda*. In Michigan, inclusion of verbenone increased the disruptant effect of the nonhost volatiles, whereas 1-octen-3-ol did not; in Ontario 1-octen-3-ol contributed more to the disruptant effect of the blends than did verbenone. Nevertheless, inclusion of verbenone in Ontario partially offset the effect of omitting 1-octen-3ol. The blend including verbenone and nonhost volatiles with 1-octen-3-ol omitted would be preferred because of toxicity concerns regarding 1-octen-3-ol. In both Michigan and Ontario, the 4-OH+V-blend composed of hexanol, (*Z*)-3-hexen-1-ol, (*E*)-2-hexen-1-ol, 3-octanol, and verbenone is the recommended operational disruptant blend among those tested for use against *T. piniperda.*

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