DISRUPTANT EFFECTS OF 4-ALLYLANISOLE AND VERBENONE ON *TOMICUS PINIPERDA* (COLEOPTERA: SCOLYTIDAE) RESPONSE TO BAITED TRAPS AND LOGS

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ABSTRACT

We assessed the inhibitory effects of the host compound 4-allylanisole (release rates = 1 and 2 mg/d in 1994, and 1 and 10 mg/d in 2001) on the response of the pine shoot beetle, *Tomicus piniperda* (L.), adults to funnel traps baited with the attractant host compound α-pinene (release rate = 150 mg/d) in two pine Christmas tree plantations in Michigan in spring 1994 and two other plantations in spring 2001. In three of the four plantations, all doses of 4-allylanisole significantly reduced *T. piniperda* attraction to α-pinene-baited traps by 46 to 76%. We also tested the inhibitory effect of the antiaggregation pheromone verbenone (release rates = 2 and 4 mg/d) on *T. piniperda* attack density on pine bolts (average bolt length was 62 cm and diameter was 19 cm) at three sites (two pine forest stands and one Christmas tree plantation) in Michigan in 1994. Verbenone significantly reduced *T. piniperda* attack density by 37 to 60% at the two pine stands, but not at the Christmas tree plantation.

Bark beetles (Coleoptera: Scolytidae) are among the first subcortical insects to colonize weakened host trees (Haack and Slansky 1987). Timing of host colonization is an important factor determining the reproductive success of bark beetles. In situations where bark beetles attempt to colonize trees that are still relatively vigorous, the first to arrive commonly encounter high levels of host resistance, which often leads to high rates of colonization failure. On the other hand, for bark beetles that are among the last to arrive at a tree undergoing colonization, host resources are often limited and the remaining phloem tissue may be insufficient to sustain their progeny. Many conifer-infesting bark beetles exploit host- and insect-produced semiochemicals to aid in judging host vigor and the degree to which a tree has been colonized (Borden 1982). Two semiochemicals that have been implicated in bark beetle assessment of host suitability are 4-allylanisole and verbenone. 4-Allylanisole is associated with high host vigor, whereas verbenone is associated with hosts in which colonization is well underway (see references below). If 4-allylanisole and verbenone cause a strong inhibitory response in bark beetles, then such compounds could theoretically be used to protect logs and trees from bark beetle attack.

4-Allylanisole is an aromatic ether or phenylpropanoid and is commonly called estragole or methyl chavicol. 4-Allylanisole is a natural compound found in a variety of plant species, including the oleoresin of many North American (Mirov 1961) and Eurasian species of hard pines, *Pinus* spp., such as Scots pine, *Pinus sylvestris* L. (Bardysav et al. 1970). In a study by Cobb et al. (1972), foliar concentrations of 4-allylanisole in ponderosa pine, *Pinus ponderosa* Laws, were significantly lower in trees suffering pollution damage, and the authors speculated that the lower levels of 4-allylanisole may partially explain why these trees were preferentially attacked by *Dendroctonus* bark beetles (Stark et al. 1968). Similarly, 4-allylanisole levels were reported to be significantly lower in

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diseased compared with healthy pine trees (Nebeker et al. 1995) and in chemically-treated compared with untreated control pines (Hayes et al. 1994a); moreover, the diseased and chemically-treated pines suffered more intense *Dendroctonus* attack in both studies. In addition, Bridges (1987) noted that 4-allylanisole was the most effective host compound tested in retarding growth of the symbiotic fungi associated with *Dendroctonus frontalis* Zimmermann. In field studies, 4-allylanisole has been shown to inhibit bark beetle attraction to pheromone-baited traps (Hayes and Strom 1994, Hayes et al. 1994b, Strom et al. 1999, Werner 1995), and lightning-struck pines (Hayes and Strom 1994). However, in two recent field studies by Strom et al. (2002, 2004), 4-allylanisole concentrations in oleoresin were found not to be significantly higher in pines that escaped *D. frontalis* attack compared with trees from the general population, and that 4-allylanisole when applied to the trunks of individual pine trees was not able to protect them from *D. frontalis* attack.

Verbenone acts like an antiaggregation pheromone in several conifer-infesting scolytid bark beetles, e.g., species of *Dendroctonus*, *Ips*, and *Tomicus* (Byers et al. 1989, Holsten et al. 2001, Poland et al. 2004a, Sun et al. 2003). Verbenone is produced by microorganisms in the guts of adult bark beetles and in bark beetle galleries (Hunt et al. 1989, Hunt and Borden 1990, Leufven et al. 1984). Typically, as host colonization proceeds, concentrations of verbenone increase and eventually reach levels that inhibit further colonization. In this way, verbenone limits overcrowding of host trees (Ryker and Yandell 1983). Several studies have shown that verbenone limits attraction of certain scolytid species to traps baited with attractive host compounds or pheromones (Bertram and Paine 1994, Holsten et al. 2001, Lindgren and Miller 2002, Miller et al. 1995, Paiva et al. 1988, Rappaport et al. 2001, Salom et al. 1992, Strom et al. 2001, Sun et al. 2003, Zhang et al. 2001). In addition, several other studies have been conducted to test verbenone as a protectant for logs (Bakke 1987, Kohnle et al. 1992), individual trees (Bertram and Paine 1994, Huber and Borden 2001, Sun et al. 2003, Watterson et al. 1982) and stands of trees (Borden et al. 2003, Clarke et al. 1999, Devlin and Borden 1994, Jakus et al. 2003, Lindgren and Borden 1993, Progar 2003, Shea et al. 1992). Although verbenone was shown to inhibit bark beetle attraction in the above studies, it had little effect in field studies conducted by Bentz et al. (1989) and Shore et al. (1992).

The pine shoot beetle, *Tomicus piniperda* (L.) (Coleoptera: Scolytidae), is a major pest of pines in its native range of Eurasia and North Africa (Långström 1983, Ye 1991). Established populations of *T. piniperda* were first discovered in North America in 1992 (Haack 2001, Haack and Poland 2001), and as of March 2005, it was known to occur in 14 US states and 2 Canadian provinces. In the northern parts of its range, *T. piniperda* overwinters in the outer bark at the base of live pine trees (Långström 1983, Kauffman et al. 1998, Petrice et al. 2002). In early spring, as temperatures begin to exceed 10-12°C, adults initiate flight and search for suitable host material, such as recently cut or fallen pine trees or severely weakened pine trees (Salonen 1973, Poland et al. 2002). The host monoterpene α-pinene is one of the key attractants for *T. piniperda* (Byers et al. 1985, Poland et al. 2003), and typically has been the only attractant used in *T. piniperda* trapping programs in the United States and Canada (Haack and Poland 2001, Lindgren 1997). In this study, we tested the inhibitory effect of 4-allylanisole on *T. piniperda*'s response to traps baited with α-pinene, and the inhibitory effect of verbenone on *T. piniperda* attack density of pine logs.

MATERIALS AND METHODS

1994 4-Allylanisole Study. A trapping study was conducted at two Scots pine Christmas tree plantations in southern Michigan. One plantation was near Eaton Rapids, Eaton County (42°33'N, 84°37 W) and the other was about 25 km north near DeWitt, Clinton County (42°47'N, 84°31 W). We set out 12-unit multiple funnel traps (PheroTech Inc., Delta, BC, Canada) in early March 1994, which was before initiation of *T. piniperda* spring flight that started in the area on 22 March 1994 (Haack et al. 2000). The experiment included four treatments, with four replicates per plantation: (1) α-pinene (150 mg/d at 23°C), (2) α-pinene and a low dose of 4-allylanisole (1 mg/d at 22-24°C), (3) α-pinene and a 2×-dose of 4-allylanisole (2 mg/d), and (4) unbaited control. α-Pinene lures were obtained from PheroTech Inc. and were reported by the company to have more than a 98% purity, and a 93%(-):7%(+) enantiomeric ratio. 4-Allylanisole (Aldrich Chemical Co., Milwaukee, Wisconsin) was dispensed from closed 1.5-ml plastic Eppendorf microcentrifuge tubes, each with a single 2-mm hole in the lid. We determined the release rate of 4-allylanisole gravimetrically. A single tube was used per trap for the low dose of 4-allylanisole and two tubes were used for the high dose. Traps were laid out in randomized complete blocks and were placed a minimum of 15 m apart. Adults were collected and the tubes were refilled with 4-allylanisole at 2 to 3 week intervals throughout the trapping period from March through early June 1994. The α-pinene lures did not require replacement during the study period. This trapping period was sufficiently long to collect parent adults during both their initial spring flight and their later re-emergence flight from brood material. The sum of all *T. piniperda* adults collected from each trap was calculated for the entire collection period.

2001 4-Allylanisole Study. A second trapping study was conducted at two Scots pine Christmas tree plantations in southern Michigan. One plantation was near Mason, Ingham County (42°37'N, 84°22 W) and the other was about 110 km north near Shepherd, Isabella County (43°35'N, 84°41 W). As in 1994, we set out 12-unit multiple funnel traps in March 2001 before initiation of *T. piniperda* spring flight. The experiment comprised four treatments with 10 replicates per plantation: (1) α-pinene (150 mg/d), (2) α-pinene and a low dose of 4-allylanisole (1 mg/d), (3) α-pinene and a 10×-dose of 4-allylanisole (10 mg/d), and (4) unbaited control. Again, we used standard α-pinene lures from PheroTech Inc. However, in 2001, the release device for 4-allylanisole consisted of "flex-rope" impregnated with 4-allylanisole (PheroTech, Inc.). The release rate from the flex-rope was ca. 1 mg/d for every 2-cm length of rope. Therefore, to obtain release rates of 1 mg/d and 10 mg/d, we used lengths of 2 cm and 20 cm, respectively. The trap contents were emptied at 1-2 week intervals during March and April. The study was terminated after *T. piniperda* peak flight had occurred. The sum of all *T. piniperda* adults collected during the trapping period was calculated for each trap.

1994 Verbenone Study. A trap-log study was conducted at three sites in southern Michigan that were known to be infested with *T. piniperda*. The sites included a Scots pine stand near Augusta, Kalamazoo County (42°21'N, 85°20'W), a red pine (*Pinus resinosa* Ait) stand about 85 km to the east of Augusta near Dansville, Ingham County (42°32'N, 84°19'W), and a Scots pine Christmas tree plantation about 8 km north Dansville near Mason, Ingham County (the same site that was used for the 4-allylanisole study in 2001). We felled healthy Scots pine trees in February 1994 and cut bolt sections from the trunks. The bolts were cut between branch whorls and measured 59-67 cm long and 15-27 cm in diameter (outside bark). There were three treatments and six replicates per site. The treatments were (1) one verbenone dispenser per bolt (2 mg/d), (2) two verbenone dispensers per bolt (4 mg/d), and (3) untreated control bolts. We used verbenone bubble-cap dispensers from PheroTech that were reported to have a 98% purity and an 84%(-):16%(+) enantiomeric ratio. The bolts were positioned horizontally and supported a few centimeters above the ground by wire supports. Elevating the bolts allowed bark beetles to completely colonize the entire bolt surface area. The verbenone dispensers were attached near the center of each bolt along the upper surface. Replicates were spaced a minimum of 20 m apart. Within each replicate, bolts were spaced 4-5 m apart. All bolts were recovered in mid-April after initial *T. piniperda* spring flight had occurred, and were held frozen until dissected. We recorded the length of each bolt as well as diameter inside-bark at each cut end. After removal of the outside bark, we recorded the number of *T. piniperda* galleries. Using the values for bolt length and average diameter inside-bark, we calculated the surface area of each bolt as a cylinder. *Tomicus piniperda* attack density was calculated for each bolt by dividing the number of *T. piniperda* galleries on a given bolt by the surface area for that bolt.

Statistical Analyses. The data sets for each study were initially analyzed by two-way analysis of variance (ANOVA) to test for significant effects of treatment and site (PROC GLM; SAS Institute 1988). If site was not significant, the data were pooled with respect to site and a one-way ANOVA was performed to test for significant treatment effects. When treatments varied significantly at $P = 0.05$, a means separation test was conducted with the Student-Newman-Keuls multiple range test.

RESULTS

1994 4-Allylanisole Study. Attraction of *T. piniperda* to α-pinene-baited traps was significantly reduced by both doses of 4-allylanisole. An initial two-way analysis of variance ($F = 3.01$; df = 7, 24; $P < 0.021$) indicated the mean number of *T. piniperda* collected per trap varied significantly with respect to treatment ($F = 6.09$; df = 3; $P < 0.004$), but not site ($F = 0.79$; df = 1; $P > 0.38$) or their interaction term ($F = 0.66$; df = 3; $P > 0.58$). After pooling the data with respect to site, a one-way ANOVA indicated both 4-allylanisole treatments significantly reduced attraction to α-pinene-baited traps (Table 1). Of the original eight replicates, only seven were used in the final analyses because two collection cups within the same replicate had fallen during part of the study.

Overall, for the entire March to June flight season, 922 *T. piniperda* adults were collected in the 28 funnel traps, with 560 adults collected in the 7 traps baited with only α-pinene, 211 in the 7 traps baited with α-pinene and low dose of 4-allylanisole (1 mg/d), 137 in the 7 traps baited with α-pinene and the high dose of 4-allylanisole (2 mg/d), and 14 in the 7 unbaited control traps. On average, the low dose of 4-allylanisole significantly reduced *T. piniperda* attraction to α-pinene-baited traps by 62%, while the high dose of 4-allylanisole significantly reduced attraction by 76% (Table 1). There was no significant difference in trap catch between the low dose and high dose of 4-allylanisole (Table 1).

2001 4-Allylanisole Study. An initial two-way analysis of variance ($F = 22.5$; df = 7,72; $P < 0.0001$) indicated the mean number of *T. piniperda* collected per trap varied significantly with respect to treatment ($F = 49.0$; df = 3; $P < 0.0001$) and site ($F = 7.6$; df = 1; $P < 0.0074$), but not their interaction term ($F = 1.02$; df = 3; $P > 0.38$). Considering the above, we performed a separate one-way ANOVA for each site. Attraction of *T. piniperda* to α-pinene-baited traps was significantly reduced by both doses of 4-allylanisole at the Shepherd site, but by neither dose at the Mason site in 2001 (Table1).

At the Shepherd site, 6598 *T. piniperda* adults were collected in the 40 funnel traps, with 3296 adults collected in the 10 traps baited with only α-pinene, 1769 in the 10 traps baited with α-pinene and low dose of 4-allylanisole (1 mg/d), 1503 in the 10 traps baited with α-pinene and the high dose of 4-allylanisole (10 mg/d), and 30 in the 10 unbaited control traps. On average, the low dose of 4-allylanisole significantly reduced *T. piniperda* attraction to α-pinene-baited traps by 46%, while the high dose of 4-allylanisole significantly reduced attraction by 55% (Table 1). There was no significant difference in trap catch between the low dose and high dose of 4-allylanisole at Shepherd (Table 1). At the Mason site, 8856 *T. piniperda* adults were collected in the 40 funnel traps, with 3759 adults collected in the 10 traps baited with only α-pinene, 2594 in the 10 traps baited with α-pinene and low dose of 4-allylanisole (1 mg/d), 2448 in the 10 traps baited with α-pinene and the high dose of 4-allylanisole (10 mg/d), and 55 in the 10 unbaited control traps. Although not significantly different, the mean number of

Table 1. Mean (±SEM) number of *Tomicus piniperda* adults collected in baited multiple funnel traps in 1994 (March - June) and 2001 (March - April) at two pine Christmas tree field sites per year in Michigan.

	Mean (+SEM) number of adults per trap		
		2001 study sites	
Treatment[1]	**1994 study**	**Shepherd**	**Mason**
α-pinene, no 4-allylanisole	80.0 ± 27 a[2]	329 ± 29 a	376 ± 53 a
α-pinene, low 4-allylanisole	30.1 ± 5 b	177 ± 18 b	259 ± 28 a
α-pinene, high 4-allylanisole	19.6 ± 5 b	150 ± 22 b	244 ± 39 a
Blank control	2.0 ± 1 c	3 ± 1 c	6 ± 1 b
F, df, $P <$	25, (3,24), 0.001	43, (3,36), 0.0001	19, (3,36), 0.0001
No. reps (no. adults)[3]	7 (922)	10 (6598)	10 (8856)

[1]Twelve-unit funnel traps were baited with α-pinene (150 mg/d in both years); low 4-allylanisole (1 mg/d in both years), or high 4-allylanisole (2 mg/d in 1994 and 10 mg/d in 2001).
[2]Means followed by the same letter (within columns) are not significantly different at the $P = 0.05$ level (SNK mean separation test).
[3]There were 4 replicates per site (= reps) in 1994; however, 2 traps in one replicate were disturbed during one trapping period and thus, after pooling, only 7 replicates were analyzed. There were 10 replicates per site in 2001.

T. piniperda captured was reduced by 31% in traps with the low dose of 4-allylanisole, and by 35% in traps with the high dose of 4-allylanisole compared to the control traps (Table 1).

1994 Verbenone Study. Attack density of *T. piniperda* was significantly reduced on Scots pine bolts treated with verbenone compared to untreated bolts at two of the three study sites. An initial two-way analysis of variance ($F = 3.50$; df = 8, 45; $P < 0.003$) indicated that mean *T. piniperda* attack density varied significantly with respect to treatment ($F = 8.59$; df = 2; $P < 0.007$), and site ($F = 3.35$; df = 2; $P > 0.045$), but not their interaction term ($F = 1.04$; df = 4; $P > 0.39$). Given the above, we performed a separate one-way ANOVA for each of the three sites and found verbenone reduced significantly attack density at two of three sites (Table 2). Bolts averaged (± sem) 62.4 ± 0.3 cm in length and 19.0 ± 0.4 cm in diameter (inside bark). Bolt size did not vary significantly among sites ($F = 0.35$; df = 2,51; $P > 0.70$ for length, $F = 0.31$; df = 2,51; $P > 0.73$ for diameter). Similarly, bolt surface area did not vary significantly among treatments ($F = 0.44$; df = 2,51; $P > 0.64$).

Overall, we counted 2540 *T. piniperda* attacks (egg galleries) on the 54 bolts used in this study, 1113 attacks on the 18 control bolts, 824 attacks on the 18 bolts with 1 verbenone bubble-cap per bolt, and 632 attacks on the 18 bolts with 2 verbenone bubble-caps per bolt. At the two forested sites, Augusta and Dansville, the addition of verbenone at either rate significantly decreased *T. piniperda* attack density; however, verbenone did not reduce attack density at the Christmas tree site near Mason (Table 2). At the two forested sites, addition of a single verbenone dispenser decreased attack density on average by 37 to 53%, whereas addition of two dispensers decreased attack density by 49 to 60%. At the Christmas tree site, addition of a single verbenone dispenser per bolt had virtually no effect on attack density when compared to the control bolts, whereas average attack density was lowered by 25% when two verbenone dispensers were added per bolt, although this difference was not significant (Table 2).

Table 2. Mean (±SEM) *Tomicus piniperda* attack density (attacks per square meter of bark surface area) on red pine bolts treated with 0, 1, or 2 verbenone dispensers each at two forested sites (Augusta and Dansville) and one Christmas tree plantation (Mason) in Michigan in spring 1994.

	Study site		
Treatment [1]	**Augusta**	**Dansville**	**Mason**
Control, no verbenone	197.5 ± 29 a	159 ± 24 a[2]	155.8 ± 31 a
One verbenone dispenser	123.5 ± 15 b	75 ± 26 b	155.4 ± 24 a
Two verbenone dispensers	99.7 ± 21 b	63 ± 18 b	117.5 ± 15 a
F, (df), *P* >	5.0, (2,15), 0.021	5.2, (2,15), 0.019	0.8, (2,15), 0.46
No. bolts (no. attacks)	18 (824)	18 (745)	18 (973)

[1]Pine bolts were treated with 0, 1, or 2, verbenone release devices (2 mg/d per device).

[2]Means followed by the same letter (within columns) are not signioficantly different at the *P* = 0.05 level (SNK mean separation test).

DISCUSSION

The current study demonstrates *T. piniperda* responds negatively to both 4-allylanisole and verbenone. The overall level of reduction (46 to 76%) in number of *T. piniperda* captured in traps baited with α-pinene and various release rates of 4-allylanisole (Table 1) is similar to reductions published for other conifer-attacking bark beetles. For example, 4-allylanisole was reported to decrease attraction to pheromone-baited traps by 35% in *Dendroctonus brevicomis* LeConte (Hayes and Strom 1994); 37-56% in *Dendroctonus frontalis* (Hayes et al. 1994b, Strom et al. 1999), 77% in *Dendroctonus ponderosae* Hopkins (Hayes and Strom 1994); 82% in *Dendroctonus rufipennis* (Kirby) (Werner 1995), 73% in *Dendroctonus simplex* LeConte (Werner 1995), and 43% in *Ips pini* (Hayes and Strom 1994). In another field study, Joseph et al. (2001) reported 4-allylanisole significantly reduced attraction to baited traps for seven scolytids species: *Gnathotrichus retusus* (LeConte), *Hylastes longicollis* Swaine, *Hylastes macer* LeConte, *Hylastes nigrinus* (Mannerheim), *Hylurgops porosus* (LeConte), *Hylurgops reticulates* Wood, and *Ips latidens* LeConte.

Although 4-allylanisole has been shown frequently to reduce bark beetle attraction to baited traps, there have been two field trials where 4-allylanisole failed to protect pine stumps in one case and live trees in another. In the first study, McCullough et al. (1998) found no difference in *T. piniperda* attack density on freshly cut pine stumps that had one 4-allylanisole dispenser attached to each stump during the March-April *T. piniperda* flight season compared with control stumps that had no 4-allylanisole dispensers. Similarly, Strom et al. (2004) reported that all formulations of 4-allylanisole that they tested failed to protect individual loblolly pine, *Pinus taeda* L., trees from *D. frontalis* attack in a large-scale field trial. In the above two studies, it is possible that 4-allylanisole slowed the rate of colonization, but over time the adult bark beetles fully colonized the host material. Alternatively, it is possible that the 4-allylanisole release rates used in the above two studies were too low to significantly reduce colonization of trees and stumps, because brood material is generally much more attractive than traps.

Verbenone, a recognized antiaggregation pheromone for many species of bark beetles, has been shown to reduce bark beetle attack in some field studies (Clarke et al. 1999, Lindgren and Borden 1993, Shea et al. 1992), but not others

(Bentz et al. 1989, Shore et al. 1992). In the case of *T. piniperda*, Kohnle et al. (1992) reported lower attack density on bolts sprayed with an emulsion of verbenone, and Baader and Vité (1990) noted lower attack densities on trees that had their lower trunk wrapped with a slow-release, verbenone-impregnated strip. In addition, Schlyter et al. (1988) reported that verbenone reduced *T. piniperda* attack on pine logs in forest stands. In our study, verbenone lowered *T. piniperda* attack density on pine bolts in the two forest stands but not at the Christmas tree plantation. Our observations could be related to local *T. piniperda* population levels or to UV inactivation of verbenone. For example, Lindgren and Borden (1993) noted that verbenone was most effective when bark beetle populations were low. Considering our three study sites, the overall number of attacks was highest at the Christmas tree plantation (973 *T. piniperda* attacks on 18 bolts) compared with the two forest sites (824 attacks at Augusta, and 745 attacks at Dansville). It is interesting to note that it was at the same Christmas tree site near Mason, Michigan, where verbenone failed to reduce *T. piniperda* attack density in 1994 and 4-allylanisole failed to reduce *T. piniperda* trap-catch in 2001. Given that verbenone is known to break down under UV light (Kostyk et al. 1993), it is possible that more verbenone was inactivated by UV light in the open Christmas tree plantation compared with the shaded forested sites. PheroTech now adds a UV stabilizer in their verbenone products, but this was not the case in early 1994.

Considering the findings of the present study, and those by others that dealt with *T. piniperda* (Baader and Vité 1990, Kohnle et al. 1992, McCullough et al. 1998, Schlyter et al. 1988), it appears that *T. piniperda* adults are more strongly inhibited by verbenone than 4-allylanisole. However, in no study has *T. piniperda* attraction been reduced to zero. This is an important factor, considering that the current US federal quarantine regulates the movement of pine host material that can potentially harbor any life stage of *T. piniperda*. Nursery and Christmas tree managers within the infested portion of the US must pass inspection prior to shipping pine trees to uninfested portions of the US. The presence of a single *T. piniperda* adult results in a failed inspection and shipment is prohibited (Haack and Poland 2001). Given these circumstances, semiochemicals may not prove useful to fully protect host material from *T. piniperda* attack, which is essential to growers who ship out of quarantined areas and who must meet the current requirements for pest–free host material. Nevertheless, semiochemical-based management may be effective in reducing *T. piniperda* attack to levels below an aesthetic damage threshold for local growers who do not ship trees out of quarantined areas. Furthermore, integrated pest management programs that combine both semiochemical deterrents and attractants as a push-pull tactic (Borden et al. 2003, Lindgren and Borden 1993, Poland et al. 2003, 2004a, 2004b, Sun et al. 2003) may be useful in reducing overall *T. piniperda* populations in managed areas.

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