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Pine shoot beetle, *Tomicus piniperda* (Col., Scolytidae), responses to common green leaf volatiles

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Abstract: We tested the hypothesis that green leaf volatiles (GLVs) disrupt the response of overwintered pine shoot beetles, *Tomicus piniperda* (L.) to multiple-funnel traps baited with the attractive host volatile α-pinene. A combination of four GLV alcohols, 1-hexanol (*E*)-2-hexen-1-ol (*Z*)-2-hexen-1-ol, and (*Z*)-3-hexen-1-ol, caused 54 and 36% reduction in the number of pine shoot beetles captured in two separate trapping experiments. Similarly, a combination of the four alcohols plus two GLV aldehydes, hexanal and (*E*)-2-hexenal, caused 38% reduction in the number of pine shoot beetles captured compared with α-pinene alone. A blend of the two GLV aldehydes was not disruptive. None of the four GLV alcohols nor the two GLV aldehydes were disruptive when tested individually. The finding that the blend of four GLV alcohols reduced attraction of *T. piniperda* supports the general hypothesis that GLVs common to nonhost angiosperms are disruptive to conifer-attacking bark beetles (Scolytidae).

1 Introduction

The larger pine shoot beetle, *Tomicus piniperda* (L.), is one of the most important forest insect pests of pine, *Pinus* spp., in Europe, Asia, and parts of northern Africa (SCHROEDER and EIDMANN, 1987; LÅNGSTRÖM and HELLQVIST, 1991; YE, 1994; HUI and LIEUTIER, 1997). *Tomicus piniperda* was discovered in North America in 1992 (HAACK et al., 1997) and as of December 1998 is found in 243 counties in nine US states and 23 counties in Canada (NAPIS, 1998).

Like other wood-and bark-boring beetles, *T. piniperda* has a restricted range of suitable hosts. It attacks primarily pines, and although living trees may occasionally be killed (CZOKAJLO et al., 1997; HUI and LIEUTIER, 1997), it generally reproduces in recently fallen or dead trees (LÅNGSTRÖM, 1984). Suitable host material is typically widely scattered throughout the forest each year. Behavioral responses to volatile plant chemicals are critical in locating suitable hosts in which reproduction can occur. Long range primary attraction by *T. piniperda* has been demonstrated to the host monoterpenes (±)-α-pinene (+)-3-carene, and terpinolene and to ethanol (BYERS et al., 1985; SCHROEDER and EIDMANN, 1987; BYERS, 1992).

In seeking suitable hosts, many unsuitable hosts and nonhost trees are probably encountered and rejected by bark beetles. Avoidance of nonhosts has also been demonstrated for *T. piniperda*. In central Sweden, attraction of *T. piniperda* and *Hylurgops palliatus* (Gyll.) (Col., Scolytidae) to ethanol-baited traps was disrupted by the presence of bolts from *Populus tremula* L. or *Betula pendula* Roth (SCHROEDER, 1992). The mechanisms of nonhost avoidance are not understood. Rejection can be based on a lack of host characteristics or the presence of repellent or deterrent stimuli. Some of the latter stimuli may be green leaf volatiles (GLVs), which are six carbon alcohols, aldehydes, and derivative esters that are general odour components commonly found in many plants (VISSER et al., 1979; WHITMAN and ELLER, 1990). Although GLVs occur across a wide variety of plant families, they are especially abundant in herbaceous plants and deciduous shrubs and trees (VISSER et al., 1979).

There is increasing evidence that GLVs may represent a key semiochemical signal in the discrimination between host and nonhost species by conifer-infesting bark beetles (BORDEN, 1996). In Sweden, attraction of both *T. piniperda* and *Ips typographus* (L.) (Scolytidae), the European spruce bark beetle, to attractant-baited traps was reduced by a blend of six GLVs including hexanol (*E*)-2-hexen-1-ol (*Z*)-3-hexen-1-ol, linalool, hexanal and (*E*)-2-hexenal, especially in synergism with verbenone (SCHLYTER et al., 1995). Hexanal and 1-hexanol disrupted attraction of the scolytids, *Dendroctonus frontalis* Zimmermann, the southern pine beetle, *Ips grandicollis* (Eichhoff), the eastern five-spined ips, and *Ips avulsus* (Eichhoff), the small southern pine engraver, to traps baited with attractant semiochemicals in the southern United States (DICKENS et al., 1992). In British Columbia, Canada, a blend of four GLV alcohols disrupted attraction by *Dendroctonus ponderosae* Hopkins, the mountain pine beetle, to semiochemical-baited traps, whereas, a blend of two GLV aldehydes was inactive (WILSON et al., 1996). The two most disruptive alcohols (*E*)-2-hexen-1-ol and (*Z*)-3-hexen-1-ol, reduced the number of *D. ponderosae* captured in attractant-baited traps to levels found in unbaited control traps and also reduced attacks on attractant-baited trees. A blend of two GLV aldehydes and four GLV alcohols disrupted attraction of *Dendroctonus rufipennis* Kirby, the spruce beetle, in British Columbia (POLAND et al., 1998). The GLV aldehyde, (*E*)-2-hexenal, and two

GLV alcohols (*E*)-2-hexen-1-ol and (*Z*)-2-hexen-1-ol were disruptive to male *Dendroctonus brevicomis* LeConte, western pine beetles, while (*Z*)-2-hexen-1-ol was disruptive to female western pine beetles (POLAND et al., 1998). GLV alcohols have also been shown in field experiments to disrupt the response to aggregation pheromones by conifer-infesting ambrosia beetles (Scolytidae) in British Columbia, including *Trypodendron lineatum* (Olivier), the striped ambrosia beetle (BORDEN et al., 1997), *Gnathotrichus sulcatus* (LeConte), and *Gnathotrichus retusus* (LeConte) (DEGLOW and BORDEN, 1998a,b). For *T. lineatum* and *G. sulcatus* the two aldehydes, hexanal and (*E*)-2-hexenal, enhanced the response to the pheromone baits (BORDEN et al., 1997; DEGLOW and BORDEN, 1998a).

The mounting evidence for the disruptive effects of common GLVs for several species of conifer-attacking scolytids, coupled with the promising results of disruption of *T. piniperda* by bolts of nonhost trees in Europe, suggest that common GLVs may also be disruptive to *T. piniperda*. Our objectives were to test common GLVs, alone and combined, as potential disruptants for *T. piniperda*.

2 Materials and methods

Three field trapping experiments were conducted in 1998 in Scotch pine, *Pinus sylvestris* L., Christmas tree plantations with high *T. piniperda* populations. All experiments employed 12-unit multiple funnel traps (Phero-Tech, Inc., Delta, BC, Canada) laid out between rows of Christmas trees in randomized complete blocks with at least 15 m between traps. Experiments 1 and 2 were conducted in a 30 acre plantation near Hesston, LaPorte County, Indiana, in an area that was surrounded by agricultural fields. The trees were approximately 14-year-old, 2.5–3 m tall, and were no longer being managed for Christmas tree sales, i.e. trees were not pruned. Relatively little suitable breeding material (i.e. stumps, slash, culled trees) was available in the stand. Experiment 3 was conducted in a 36 acre plantation near Mason, Ingham County, Michigan. Traps were laid out in a 24 acre area of the plantation. Most of the plantation was under active management for Christmas tree sales. The trees ranged from new seedlings to approximately 15 years of age; however, the area where the traps were laid out was composed of approximately 7-year-old Scotch pine trees that were approximately 1.7 m tall. Stumps, slash and culled trees were abundan throughout the plantation. However, within 10 m of eac funnel trap in the experimental area, all stumps were cut t less than 5 cm in height and buried with dirt and all slash wa removed prior to initial spring flight by *T. piniperda* in 199 This sanitation was conducted to avoid any influence of hos material on *T. piniperda* responses to the baited funnel traps The plantation was surrounded by stands of deciduous tree or open fields. In both plantations, all traps were set up a least 20 m from the end of a row and at least 30 m from th edge of the plantation.

Attractant *T. piniperda* lures (Phero Tech Inc.) consiste of the host kairomone component α-pinene (2,6,6-trimethyl bycyclo[3.1.1]hept-2-ene), released as stated in table 1. The si GLVs that were tested consisted of two aldehydes, hexanal and (*E*)-2-hexenal, and four alcohols, 1-hexanol (*E*)-2-hexen 1-ol (*Z*)-2-hexen-1-ol, and (*Z*)-3-hexen-1-ol. The release rate for the six GLVs are given in table 1. These six GLVs were chosen because they are often reported in the literature a being disruptive to conifer-attacking scolytids (DICKENS et al. 1992; WILSON et al., 1996; BORDEN et al., 1997; DEGLOW an BORDEN, 1998a,b; POLAND et al., 1998). They are also inex pensive and readily available, and thus would be amenable t commercial development and cost-effective operationa implementation.

In each experiment, α-pinene-baited and unbaited contro traps served as positive and negative control treatments, respectively, against which the bioactivity of GLV treatments added to α-pinene could be assessed. Experiment 1 tested a blend of the four alcohols, a blend of the two aldehydes, and a blend of all six GLVs. Experiment 2 tested each of the two aldehydes individually and both combined, and Experiment 3 tested each of the four alcohols individually and all four combined. All GLVs were released individually from bubble cap dispensers (Phero Tech, Inc.). For treatments in which GLVs were combined, individual dispensers were used for each compound. Therefore, the overall release rate was higher when GLVs were combined than when tested individually. Initially, four to 10 replicates of each treatment were set up per experiment. Every 3–4 weeks, the treatments were reposi tioned providing new replicates. The dates of the collection periods and numbers of replicates (*n*) laid out during each collection period for each experiment are presented in table 2. During each collection period, a few traps were found to have been disturbed (i.e. the trap had fallen down or the collection cup had fallen off). Therefore, the number of replicates (*n*) of each treatment varied slightly in the analyses.

All captured *T. piniperda* adults in each experiment were collected at regular intervals and held at −18°C until counted. The numbers of insects captured were transformed by log

Table 1. *Description of semiochemicals employed in trapping experiments for* Tomicus piniperda

Semiochemical	Source[1]	Release device[2]	Release rate (mg/24 h)
α-pinene	Phero-Tech	15 ml polyethylene bottle	300
hexanal	Aldrich	bubble cap	13
(*E*)-2-hexenal	Aldrich	bubble cap	13
1-hexanol	Aldrich	bubble cap	3.8
(*E*)-2-hexen-1-ol	Aldrich	bubble cap	3.8
(*Z*)-2-hexen-1-ol	Bedoukian	bubble cap	3.8
(*Z*)-3-hexen-1-ol	Aldrich	bubble cap	3.8

[1] Aldrich = Aldrich Chemical Company, Milwaukee, WI, USA; Bedoukian = Bedoukian Research Inc., Danbury, CT, USA.
[2] Release devices prepared by Phero-Tech, Inc. with semiochemicals stabilized with 1.2% (wet weight) Ethanox® 330 antioxidant, Ethyl Chemicals Group, Baton Rouge, LA, USA. Release rates determined in the laboratory at 20°C by Phero-Tech, Inc.

ble 2. Experimental ·ations, treatments, llection periods, d number of ɔlicates for field ıpping experiments for ɔmicus piniperda in diana and Michigan

Experiment no. and location	Treatments	Collection period	Number of replicates (*n*)
1	unbaited control	Feb. 20–Mar. 30	10
Laporte County	α-pinene	Mar. 30–Apr. 22	10
Indiana	α-pinene + aldehydes	Apr. 22–June 23	10
	α-pinene + alcohols		
	α-pinene + all GLVs		
2	unbaited control	Feb. 20–Mar. 30	4
Laporte County	α-pinene	Mar. 30–Apr. 22	8
Indiana	α-pinene + hexanal	Apr. 22–June 23	8
	α-pinene + (*E*)-2-hexenal		
	α-pinene + both aldehydes		
3	unbaited control	Feb. 13–Mar. 28	7
Ingham County	α-pinene	Mar. 28–Apr. 3	7
Michigan	α-pinene + hexanol	Apr. 3–June 4	7
	α-pinene + (*E*)-2-hexen-1-ol		
	α-pinene + (*E*)-3-hexen-1-ol		
	α-pinene + (*Z*)-2-hexen-1-ol		
	α-pinene + all alcohols		

able 3. Results of ANOVA for experiments 1, 2, and 3 for Tomicus piniperda *in Indiana and Michigan*

	Collection period			
Factor in model	1 (Feb 20–Mar 30) (*F*, d.f., P)	2 (Mar 30–Apr 22) (*F*, d.f., P)	3 (Apr 22–Jun 23) (*F*, d.f., P)	Total (Collection 1–3) (*F*, d.f., P)
Experiment 1				
whole model	5.44, 13, 0.0001	4.81, 12, 0.0004	5.23, 13, 0.0001	6.87, 32, 0.0001
treatment	9.36, 4, 0.0001	9.18, 4, 0.0001	9.83, 4, 0.0001	16.15, 4, 0.0001
replicate	3.70, 9, 0.0037	2.62, 8, 0.0298	3.18, 9, 0.0063	2.85, 26, 0.0001
collection period	–	–	–	40.47, 2, 0.0001
Experiment 2				
whole model	3.44, 7, 0.0443	3.32, 11, 0.0050	2.95, 11, 0.0107	3.88, 23, 0.0001
treatment	3.06, 4, 0.0751	5.89, 4, 0.0014	2.80, 4, 0.0458	6.18, 4, 0.0002
replicate	3.94, 3, 0.0476	1.85, 7, 0.1173	3.04, 7, 0.0171	2.35, 17, 0.0064
collection period	–	–	–	12.28, 2, 0.0001
Experiment 3				
whole model	4.96, 12, 0.0001	2.51, 12, 0.0162	8.49, 12, 0.0001	11.38, 24, 0.0001
treatment	4.35, 6, 0.0021	3.51, 6, 0.0078	15.01, 6, 0.0001	14.25, 6, 0.0001
replicate	5.57, 6, 0.0004	1.52, 6, 0.1996	1.98, 6, 0.0950	1.12, 16, 0.3408
collection period	–	–	–	84.78, 2, 0.0001

$(x + 1)$ to satisfy assumptions of normality and homoscedasticity (ZAR, 1984). The transformed data were analysed by analysis of variance (ANOVA) (GLM procedure, SAS Institute Inc. 1989) for a randomized complete block design. For each collection period, a two-way ANOVA was employed treating replicate as the blocking factor. For all three collection periods combined, a three-way ANOVA was employed with blocking factors for both replicate and collection period. The Ryan–Einot–Gabriel–Welsh (REGW) multiple comparison procedure (SAS INSTITUTE INC., 1989; DAY and QUINN, 1989) was used to determine differences between treatment means in all experiments.

3 Results and discussion

In experiment 1, 3103 *T. piniperda* adults were captured. Results of the three-way ANOVA for data from all three collection periods combined showed a significant effect for treatment ($F = 16.15$, d.f. $= 4$, $P < 0.0001$), collection period ($F = 40.47$, d.f. $= 2$, $P < 0.0001$), and replicate ($F = 2.85$, d.f. $= 26$, $P < 0.0001$) (table 3). The blend of four GLV alcohols resulted in a 54% reduction in the number of *T. piniperda* captured compared with attractant-baited traps (table 4). Similarly, the complete six-component alcohol–aldehyde blend significantly reduced trap catches; however, the blend of the two aldehydes did not significantly reduce trap catches. The highest numbers of *T. piniperda* were captured during the initial peak flight and declined with successive collections. However, within each collection period, the pattern of responses was similar (table 4).

In experiment 2, 1491 *T. piniperda* adults were captured. As in experiment 1, the GLV aldehydes were

Table 4. *Mean number of* T. piniperda *adults collected per trap in experiment 1 in multiple-funnel traps baited wi α-pinene (ap) alone or with blends of two green leaf aldehydes (aldehydes) and four alcohols (alcohols) released in Table 1*

	Collection 1 Feb 20–Mar 30		Collection 2 Mar 30–Apr 22		Collection 3 Apr 22–June 23		Total Collection 1–3	
Treatment	*n*	Mean ± SE	*n*	Mean ± SE	*n*	Mean ± SE	*n*	Mean ± SE
unbaited control	9	3.7 ± 1.1 c	8	0.38 ± 0.18 b	10	0.2 ± 0.13 c	27	1.4 ± 0.49 d
ap	10	66.8 ± 14.5 ab	9	42.3 ± 7.3 a	10	11.4 ± 1.9 a	29	40.1 ± 6.9 a
ap + aldehydes	7	67.4 ± 9.8 a	8	32.1 ± 4.9 a	10	8.0 ± 2.2 ab	25	32.4 ± 5.8 ab
ap + alcohols	7	27.6 ± 8.5 b	7	27.7 ± 9.1 a	10	5.4 ± 0.99 b	24	18.4 ± 4.1 c
ap + aldehydes and alcohols	9	36.4 ± 7.7 ab	7	34.0 ± 8.6 a	10	8.5 ± 1.8 ab	26	25.0 ± 4.3 bc
T. piniperda		1694		1073		336		3103

Number of replicates (*n*) of each treatment are given for each collection period.
Means followed by the same letter (within columns) are not significantly different, REGW test, $P < 0.05$.

Table 5. *Mean number of* T. piniperda *adults collected per trap in experiment 2 in multiple-funnel traps baited wit α-pinene (ap) alone or with two green leaf aldehydes alone or together released as in Table 1*

	Collection 1 Feb 20–Mar 30		Collection 2 Mar 30–Apr 22		Collection 3 Apr 22–June 23		Total Collection 1–3	
Treatment	*n*	Mean ± SE	*n*	Mean ± SE	*n*	Mean ± SE	*n*	Mean ± SE
unbaited control	3	2.0 ± 2.0 b	8	0.3 ± 0.2 b	8	1.6 ± 1.1 b	19	1.1 ± 0.6 b
ap	3	54.7 ± 23.3 a	8	16.1 ± 3.1 a	7	9.1 ± 3.7 a	18	19.8 ± 5.4 a
ap + hexanal	4	37.0 ± 15.9 a	8	20.3 ± 4.3 a	8	7.3 ± 2.0 a	20	18.4 ± 4.2 a
ap + (*E*)-2-hexenal	3	6.7 ± 2.8 a	8	31.5 ± 8.5 a	8	10.8 ± 2.1 a	19	18.8 ± 4.4 a
ap + both aldehydes	4	31.5 ± 15.1 a	8	23.9 ± 6.2 a	8	8.6 ± 3.2 a	20	19.3 ± 4.3 a
T. piniperda		464		737		290		1491

Number of replicates (*n*) of each treatment are given for each collection period.
Means followed by the same letter (within columns) are not significantly different, REGW test, $P < 0.05$.

Table 6. *Mean number of* T. piniperda *adults collected per trap in experiment 3 in multiple-funnel traps baited wit α-pinene (ap) alone or with four green leaf alcohols alone or together released as in Table 1*

	Collection 1 Feb 20–Mar 30		Collection 2 Mar 30–Apr 22		Collection 3 Apr 22–June 23		Total Collection 1–3	
Treatment	*n*	Mean ± SE	*n*	Mean ± SE	*n*	Mean ± SE	*n*	Mean ± SE
unbaited control	7	0.14 ± 0.14 b	7	0.43 ± 0.43 b	7	0.28 ± 0.18 c	21	0.28 ± 0.16 c
ap	7	24.0 ± 4.7 a	7	37.9 ± 7.5 a	7	96.0 ± 11.0 a	21	52.7 ± 8.3 a
ap + hexanol	7	18.1 ± 6.4 a	7	30.6 ± 7.2 a	7	82.4 ± 5.9 ab	21	43.7 ± 7.2 ab
ap + (*E*)-2-hexenol	7	14.3 ± 4.6 a	7	30.6 ± 9.1 a	7	60.6 ± 7.4 b	21	35.1 ± 5.8 ab
ap + (*Z*)-2-hexenol	7	13.9 ± 3.1 a	7	25.4 ± 3.4 a	7	82.4 ± 11.3 ab	21	40.6 ± 7.7 ab
ap + (*Z*)-3-hexenol	7	13.9 ± 3.5 a	7	32.7 ± 9.8 a	7	77.7 ± 13.5 ab	21	41.4 ± 8.1 ab
ap + all four alcohols	7	16.6 ± 5.8 a	7	27.3 ± 3.5 a	7	56.7 ± 3.7 b	21	33.5 ± 4.5 b
T. piniperda		707		1293		3193		5194

Number of replicates (*n*) of each treatment are given for each collection period.
Means followed by the same letter (within columns) are not significantly different, REGW test, $P < 0.05$.

not disruptive; trap catches were not reduced by either of the two aldehydes alone or by both together (table 5). For all three collection periods combined, the three-way ANOVA again showed significant effects for treatment ($F = 6.18$, d.f. = 4, $P < 0.0002$), collection period ($F = 12.28$, d.f. = 2, $P < 0.0001$), and replicat ($F = 2.35$, d.f. = 17, $P < 0.007$) (table 3). Although tra catches again declined over time after the initial emerg ence flight, responses to the different treatment remained similar across collection periods.

n experiment 3, 5194 *T. piniperda* adults were tured. None of the four individual alcohols were uptive on their own; however, as in experiment 1, four component alcohol blend caused a significant uction of 36% in the number of *T. piniperda* captured ble 6). For all three collection periods combined, the ee-way ANOVA showed significant effects for treatnt ($F = 14.25$, d.f. = 6, $P < 0.0001$) and collection iod ($F = 84.78$, d.f. = 2, $P < 0.0001$), but not for ication ($F = 1.12$, d.f. = 16, $P = 0.34$) (table 3). ike experiments 1 and 2, the number of *T. piniperda* tured increased over time in experiment 3. During first collection period, many beetles emerging from rwintering sites probably colonized the abundant od material available elsewhere in the plantation d for experiment 3. Later on, the higher trap catches bably resulted from re-emerging parental adults that e dispersing from brood material that had become y occupied.

Overall, the results of these three experiments are ilar to those for *D. ponderosae*. Neither of the aldees was disruptive for *D. ponderosae*, and all of the ohols were disruptive, with the two most effective ng (*E*)-2-hexen-1-ol and (*Z*)-3-hexen-1-ol (WILSON l., 1996). These results provide further evidence that mon GLVs may allow conifer-attacking scolytids discriminate nonhost deciduous trees from suitable t trees.

The deterrence of the blend of four GLV alcohols in eriment 1 (table 4) and experiment 3 (table 6) may icate an additive or dose-dependent effect of the indiual components. DEGLOW and BORDEN (1998a) nd an increasing degree of repellency of GLV alcos as additional components were included for *G. atus*, suggesting an additive rather than synergistic ct of combined stimuli. Therefore, higher doses or nbinations of deterrent compounds may produce nger repellency.

The disruptive effect of the common GLV alcohol nd suggests that nonhost volatiles may be promising managing populations of *T. piniperda*. Disruption *T. piniperda* attraction in Europe to bolts of aspen birch (SCHROEDER, 1992) and preliminary results ing specific antennally active volatiles from aspen es in North America (POLAND et al., unpublished a), suggest that specific volatiles from particular nont trees would be even more effective than common Vs.

Long-range primary attraction to host volatiles is portant for *T. piniperda* in locating suitable breeding terial. In the Great Lakes region of North America, ial spring flight and colonization by *T. piniperda* ally occurs in late February or early March, which uch earlier than first flight for most sympatric pinecking bark beetles (HAACK and LAWRENCE, 1997; ACK et al., 1998). During March in the Great Lakes ion, buds of deciduous nonhost trees are still dornt and thus no foliage is present. The blend of bark l foliar volatiles vary considerably with phenology host and nonhost trees (ZOU and CATES, 1995). erefore, the common GLVs tested in the present dy may not reflect naturally occurring nonhost nds of bark volatiles that would be prevalent in the Palearctic (European) natural ecosystem during the initial period when *T. piniperda* is seeking brood material.

Unlike most conifer-attacking scolytids, *T. piniperda* has a second dispersal period in which the beetles fly to the crowns of healthy trees to complete maturation by feeding in shoots. Emergence of brood adults and the shoot feeding dispersal flight usually occurs in late May or early June in the Great Lakes region. During this phase of *T. piniperda*'s life cycle, visual and olfactory cues may be important in locating suitable hosts for shoot feeding. Evidence of shoot-feeding aggregations in Yunnan, China (HUI and LIEUTIER, 1997) suggests that *T. piniperda* responds to some type of attractant before being sexually mature. Avoidance of nonhost volatiles would be adaptive during shoot location, which occurs when deciduous trees have abundant foliage and are actively photosynthesizing. Further research is required to determine if GLVs are disruptive to *T. piniperda* F_1 adults when locating hosts for shoot feeding.

In developing and implementing a semiochemical-based management programme for *T. piniperda*, GLVs may have considerable potential for disrupting the beetle's ability to locate suitable brood material and shoots. Infestations and subsequent damage might be reduced through (1) increased mortality during dispersal of parent adults seeking brood material and subsequently decreased brood production; and (2) increased mortality when locating hosts for shoot-feeding and reduced shoot-feeding damage.

Although the pheromone-positive responses of several conifer-attacking scolytids are now known to be disrupted by GLVs in general, the particular responses to individual GLV components varies among scolytid species. It would be adaptive for conifer-attacking bark beetles to recognize and avoid general volatile compounds that are commonly found in a wide variety of nonhost deciduous and herbaceous species rather than recognizing precise tree-specific volatiles for each nonhost species (BORDEN et al., 1998). In this way, several species of nonhost trees with partially overlapping blends of common volatile compounds could be perceived and avoided during host location. On the other hand, certain specific compounds found in host trees, and other compounds found in the most prevalent nonhost species, could be important for close range host selection. Precise blends of specific host and pheromone components would mediate specificity in host selection and maintain breeding isolation between sympatric species of bark beetles.

Trembling aspen, *Populus tremuloides* Michx., is the most common nonhost angiosperm in the range of *D. ponderosae* which attacks lodgepole pine trees, *Pinus contorta* var. *latifolia* Engelmann. 1-Hexanol was one of four GLVs collected from trembling aspen bark that were disruptive for *D. ponderosae* (BORDEN et al., 1998). It was the only component that was disruptive on its own.

Further research on the responses of *T. piniperda* to specific host and nonhost volatiles during different phases of its life cycle is required to determine the role of primary attraction and nonhost avoidance when

locating breeding sites and shoots. A greater understanding of host location will aid in the development of semiochemical-based management strategies so that damage from *T. piniperda* is minimized.

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