ELECTROPHYSIOLOGICAL AND BEHAVIOURAL RESPONSES OF *TOMICUS PINIPERDA* AND *TOMICUS MINOR* (COLEOPTERA: SCOLYTIDAE) TO NON-HOST LEAF AND BARK VOLATILES

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Abstract

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Leaf and bark volatiles from non-host birches, *Betula pendula* Roth. and *Betula pubescens* Ehrh. (Betulaceae), and aspen, *Populus tremula* L. (Salicaceae), were tested on spring-dispersing *Tomicus piniperda* (L.) and *Tomicus minor* (Hart.) by gas chromatographic – electroantennographic detection (GC–EAD) and by attractant-baited traps in southern Sweden. GC–EAD analysis of the head-space volatiles from fresh bark chips of *B. pendula* revealed two green leaf alcohols, 1-hexanol and (Z)-3-hexen-1-ol, that consistently elicited antennal responses by *T. piniperda* and *T. minor.* Further analyses with synthetic mixtures showed that the antennae of these two *Tomicus* species also responded to other green leaf alcohols, such as (E)-2-hexen-1-ol found from the non-host leaves, and C$_8$-alcohols, 3-octanol and 1-octen-3-ol, from bark of non-host birches and aspen. No antennal responses of the *Tomicus* species were observed to green leaf C$_6$-aldehydes and C$_6$-acetate or to non-host bark volatiles like *trans*-conophthorin, benzaldehyde, salicylaldehyde, and benzyl alcohol. In field trapping experiments, blends of electrophysiologically active green leaf alcohols or C$_8$-alcohols resulted in reductions (>60%) in the number of *T. piniperda* captured compared with that for the kairomone-baited trap. When these two blends were combined, trap catch was further reduced (90%), which was not significantly different from that for the blank control. Neither the blend of two green leaf aldehydes plus the acetate nor the bark compounds *trans*-conophthorin or benzyl alcohol reduced trap catches. *Tomicus minor* had a response pattern similar to that of *T. piniperda.* *Hylurgops palliatus* (Gyll.) (Coleoptera: Scolytidae) was attracted to the combination of kairomone and verbenone but not to kairomone and was not affected by the blends of green leaf volatiles. Our results suggest that selected leaf–bark C$_6$-alcohols and the bark C$_8$-alcohols may have potential in developing semiochemical-based management programs against both pine shoot beetles by repelling them from suitable breeding and feeding sites.

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Résumé

Les substances volatiles émanant d'arbres non hôtes, les bouleaux *Betula pendula* Roth. et *Betula pubescens* Ehrh. (Betulaceae) et le peuplier tremble *Populus tremula* L. (Salicaceae), ont été testées sur les scolytes *Tomicus piniperda* (L.) et *Tomicus minor* (Hart.) par un système de détection combiné, chromatographie au gaz – électroantennographie (GC–EAD), au moment de la dispersion de printemps; de plus, nous avons installé des pièges garnis d'une substance attirante dans le sud de la Suède. L'analyse par GC–EAD des substances volatiles émanant de morceaux d'écorce frais de *B. pendula* a révélé la présence de deux alcools des feuilles vertes le 1-hexanol et le (*Z*)-3-hexen-1-ol qui provoquent constamment des réactions antennaires chez les deux scolytes. Des analyses plus poussées avec des mélanges synthétiques ont démontré que les deux espèces de *Tomicus* réagissent également à d'autres alcools des feuilles vertes, tels le (*E*)-2-hexen-1-ol trouvé dans les feuilles d'arbres non hôtes et les alcools C_8, le 3-octanol et le 1-octen-3-ol trouvé dans l'écorce des arbres non hôtes, les deux bouleaux et le peuplier tremble. Les espèces de *Tomicus* n'ont manifesté aucune réaction antennaire aux aldéhydes et à l'acétate des feuilles vertes ou aux substances volatiles des écorces d'arbres non hôtes comme la *trans*-conophthorine, la benzaldéhyde, la salicylaldéhyde et l'alcool benzylique. Dans des expériences de piégeage en nature, des mélanges d'alcools de feuilles vertes qui provoquent des réactions électrophysiologiques ou d'alcools C_8 ont entraîné des réductions (>60%) des nombres de *T. piniperda* capturés comparativement aux nombres récoltés dans les pièges garnis de kairomones. En combinant les deux mélanges, le nombre d'insectes attrapés a diminué encore davantage (90%), nombre qui ne différait pas significativement du nombre obtenu dans les pièges témoins non garnis. Ni le mélange des deux aldéhydes des feuilles vertes avec l'acétate, ni les composés de l'écorce, la *trans*-conophthorine ou l'alcool benzylique, n'ont diminué les captures. *Tomicus minor* a eu le même type de réaction que *T. piniperda. Hylurgops palliatus* (Gyll.) (Coleoptera : Scolytidae) est attiré par la combinaison kairomone–verbénone, mais pas par la kairomone seule, et il n'est pas affecté par les mélanges de substances volatiles émanant des feuilles vertes. Nos résultats indiquent que certains alcools C_6 des feuilles et de l'écorce, de même que les alcools C_8 de l'écorce peuvent s'avérer d'une grande utilité dans les programmes de lutte sémiochimique contre les scolytes des pins en les repoussant de leurs sites de reproduction ou d'alimentation.

[Traduit par la Rédaction]

Introduction

Tomicus piniperda (L.) (Coleoptera: Scolytidae) and *Tomicus minor* (Hart.) are major insect pests of pines, *Pinus* spp. (Pinaceae), in Europe and Asia (Postner 1974; Schroeder and Eidmann 1987; Långström and Hellqvist 1991; Ye 1991; Ye and Lieutier 1997). Recently, the larger pine shoot beetle *T. piniperda*, was discovered in North America and has caused serious problems for the Christmas tree industry (Haack *et al.* 1997). Suitability of host trunks or logs for *T. piniperda* is recognised over the long range by olfaction (Byers *et al.* 1985) and over the short range by preference for a coarse bark structure (Schlyter and Löfqvist 1990). *Tomicus piniperda* utilises a kairomone blend of four host monoterpenes [(+)- and (–)-α-pinene, Δ3-carene, and terpinolene] as the long-range signal to locate its mate and host (Byers *et al.* 1985), whereas *T. minor* has a female-produced pheromone with (–)-*trans*-verbenol as a main component (Lanne *et al.* 1987).

When searching for suitable hosts in flight, bark beetles will encounter not only suitable host trees and their odours but also unsuitable hosts and non-host trees. Rejection of these trees could be based on an imbalance of certain host characteristics and (or) a negative response to some non-host stimuli (Schlyter and Birgersson 1999).

Schroeder (1992) showed that the weak attraction to ethanol by *T. piniperda* and *Hylurgops palliatus* (Gyll.) (Coleoptera: Scolytidae) was reduced by the presence of non-host bark from birch, *Betula pendula* Roth. (Betulaceae), or aspen, *Populus tremula* L. (Salicaceae). Unsuitable, fully colonised hosts release verbenone, which inhibits attraction to kairomone-baited traps (Byers *et al.* 1989) or host logs (Schlyter *et al.* 1988). The mechanisms of non-host avoidance in *T. piniperda* and *T. minor* are not fully understood; however, volatiles from leaves (Schlyter *et al.* 1995; Poland and Haack 2000) and (or) bark of non-host trees are most likely involved.

The pheromone–kairomone positive responses of over 15 species of conifer-infesting scolytids have been shown to be inhibited by green leaf volatiles (mostly six carbon alcohols, aldehydes, and derivative esters) (Dickens *et al.* 1991, 1992; Schlyter *et al.* 1995; Deglow and Borden 1998*a*, 1998*b*; Zhang *et al.* 1999*a*, 1999*b* and references therein). These volatiles have been confirmed in Sweden to be produced by the leaves of non-host taiga angiosperms (Byers *et al.* 1998; Zhang *et al.* 1999*a*, 1999*b*). The response of spring-dispersing *T. piniperda* to host kairomone has been shown to be inhibited by a blend of six green leaf volatiles in Sweden (Schlyter *et al.* 1995) and four green leaf alcohols, 1-hexanol, (*E*)-2-hexen-1-ol, (*Z*)-2-hexen-1-ol, and (*Z*)-3-hexen-1-ol, in the United States (Poland and Haack 2000).

There is also evidence that volatiles from non-host bark might play an important role in the host selection of conifer bark beetles (Borden et al. 1998). Guerrero *et al.* (1997) showed that benzyl alcohol, identified in the callus of *Eucalyptus radiata* var. *australiana* (Baker and Smith) Blakely (Myrtaceae), was detected by a specific olfactory cell and can at high doses (about 700 mg/d) reduce attraction to host logs in *Tomicus destruens* (Woll.). Gas chromatographic – electroantennographic detection (GC–EAD) analysis of the head-space volatiles from fresh bark chips of three Scandinavian non-host species (*B. pendula*, *Betula pubescens* Ehrh., and *P. tremula*) revealed five compounds that consistently elicited antennal responses by *Ips typographus* (L.) (Coleoptera: Scolytidae) (Zhang *et al.* 2000). Inhibition of attraction by these electrophysiologically active non-host bark volatiles (in combination or alone), including *trans*-conophthorin and C_8-alcohols, in *I. typographus* has been shown in the field (Q-H Zhang *et al.*, unpublished data). In Canada, Borden *et al.* (1998) and Huber *et al.* (1999) found four bark volatile compounds from non-host angiosperm trees, *Populus* spp., *Betula papyrifera* Marsh, and *Acer macrophyllum* Pursh, which elicited antennal responses from five conifer-attacking species of Scolytidae, including three species of the genus *Dendroctonus* Erichson, one of *Ips* DeGeer, and one of *Dryocoetes* Eichhoff. The disruptive effect of these non-host bark volatiles on the response of *Dendroctonus* spp. to a pheromone–kairomone blend also has been observed in the field (Borden *et al.* 1998; Huber *et al.* 1999). In addition, single cell responses to unknown compounds from bark of non-host birch (*B. pendula*) have been demonstrated in Scandinavian *Trypodendron lineatum* (Oliver) (Coleoptera: Scolytidae) and *I. typographus* (Tømmerås 1989; Tømmerås and Mustaparta 1989).

Our objectives were to (*i*) determine if the green leaf and bark volatiles from non-host birches and aspen are detected by the antennae of spring-dispersing *T. piniperda* and *T. minor*; and (*ii*) test the antennally active volatiles, if any, and other candidates from non-hosts active in other bark beetle species for their ability to inhibit the kairomone–pheromone response of the pine shoot beetles in the field.

Materials and Methods

Volatiles from fresh bark chips of non-host *B. pendula* were collected by head-space sampling in June 1998 in Asa (57°12′N, 14°56′E), Småland, southern Sweden,

and analysed by gas chromatography – mass spectroscopy (GC–MS) as described by Zhang *et al.* (2000). The air-entrainment extracts were stored at –18°C before GC–EAD analysis.

Spring-dispersing beetles of both species were collected from attractant-baited traps deployed in March and April 1998 and 1999 in a plantation of *Pinus sylvestris* L. (Pinaceae) located near Veberöd (55°39'N, 14°27'E) and Sjöbo (55°38'N, 14°40'E), 20 km east of Lund, in southern Sweden. Adults were separated by sex and kept alive at 4°C for GC–EAD analysis. The cut antennae of both sexes and species were tested using an HP 6890 gas chromatograph containing a fused silica column (HP-Innowax; 30 mm × 0.25 mm × 0.25 mm) as described by Zhang *et al.* (1999*b*, 2000). The antennal signal was stored and analysed on a personal computer equipped with an Intelligent Data Acquisition Card and the program EAD (version 2.3, Syntech, Hilversum, The Netherlands). Aeration extracts (3 μL) of fresh *B. pendula* bark chips were injected. In addition, three synthetic mixtures (1–5 mL/injection) were studied with the antennae of both species to confirm compound identity and obtain replicates of electrophysiological activity (Table 1; Figs. 1, 2): (*i*) green leaf volatiles (10 ng/mL for each compound) commonly found from intact leaves of the non-hosts birches and aspen (Zhang *et al.* 1999*a*); (*ii*) non-host bark compounds (100 ng/mL for each compound), reportedly active in other conifer bark beetles species (Guerrero *et al.* 1997; Borden *et al.* 1998; Huber *et al.* 1999; Zhang *et al.* 2000); and (*iii*) *Tomicus*-related compounds, including a pheromone component of *T. minor*, (–)-*trans*-verbenol, and a known inhibitor from old hosts, verbenone, plus two host kairomone monoterpenes, α-pinene and Δ3-carene (100 ng/mL for each). For each sample (both bark aerations and synthetic mixtures), antennae from two females and one male of each species were tested. The antennae of female *T. piniperda* were also tested with an aeration sample of a fresh *P. sylvestris* log (25 cm long, 12 cm in diameter) containing large amounts of kairomone components, α-pinene, Δ3-carene, and terpinolene.

Four field trapping experiments (Exps. 1–4) were carried out in March and April 1993 and 1998–1999 in Scots pine, *P. sylvestris*, plantations at Fjälkinge (56°04'N, 14°18'E) and Veberöd–Sjöbo, Skåne, southern Sweden. In Experiments 1–3, 12-unit Lindgren funnel traps (Phero Tech Inc., Delta, British Columbia) were set up in lines with at least 10 m between traps. In Experiment 4, window-type traps formed by combining two polycarbonate landing traps (Anderbrant *et al.* 1988) back to back were placed 1 m high in equilateral triangles (10-m sides), with 20 m between triangles. Dispensers were put under an inverted 250-mL plastic cup painted light grey. The initial bait positions were randomised and rotated after each replicate (when ≥10 beetles were caught in the best trap). In each experiment, attractant-baited and unbaited traps served as *positive* and *blank control* treatments, respectively, against which the behavioural activity of green leaf volatiles and other non-host volatile treatments added to the attractants could be assessed. Verbenone was also included in Experiments 1 and 3 as a *negative control*.

Experiment 1 tested the effect of different groups of green leaf volatiles on *T. piniperda* in the spring of 1998. The green leaf volatiles tested were grouped based on the results of a pilot GC–EAD test and compared with verbenone. For each compound, individual dispensers were used (see Table 2 for release rates).

Experiment 2 was conducted in the spring of 1999 and tested the capacity of the electrophysiologically active volatiles from non-host bark in different combinations to inhibit response of both *T. piniperda* and *T. minor*. *trans*-Conophthorin, although not showing electrophysiological activity, was also included in the experiment because it is strongly inhibiting to attraction of *I. typographus* (Zhang *et al.* 2000) and several North American conifer bark beetle species (Huber *et al.* 1999). The attractant lure included both *T. piniperda* kairomone (as in Exp. 1) and the *T. minor* pheromone component,

TABLE 1. Sources and purity of synthetic compounds tested.

Chemical	Source of synthetics	Purity (%)*	Field experiment No.
Bark beetle compounds			
Tomicus minor pheromone component			
(−)-*trans*-Verbenol	Valterova, IOCB, Czech Republic	>98	2, 3
Antiaggregant from old host bark			
Verbenone	Aldrich, United States	99	1, 3
Host monoterpenes			
α-Pinene	Aldrich, United States	98	1–4
Δ3-Carene	Aldrich, United States	95	1–4
Terpinolene	C. Roth, Germany	85	1–4
Non-host volatiles			
Mainly from green leaves			
Hexanal	Aldrich, United States	98	1
(E)-2-Hexenal	Aldrich, United States	99	1
(Z)-3-Hexenyl acetate	Lancaster, United Kingdom	99	1
1-Hexanol[†]	Aldrich, United States	98	1–3
(Z)-3-Hexen-1-ol[†]	Aldrich, United States	98	1–3
(E)-2-Hexen-1-ol	Aldrich, United States	97	1–3
(E)-3-Hexen-1-ol	Aldrich, United States	98	1
(Z)-2-Hexen-1-ol	Acros, United States	95	1
(±)-Linalool	Aldrich, United States	97	1
From non-host bark			
(±)-3-Octanol	Acros, United States	99	2, 3
(±)-1-Octen-3-ol	Acros, United States	98	2, 3
Benzaldehyde	Aldrich, United States	99	
Salicylaldehyde	Sigma-Aldrich, United States	98	
Geranyl acetone	Sigma-Aldrich, United States	95	
Benzyl alcohol	Aldrich, United States	99	4
trans-Conophthorin	Phero Tech Inc., Canada	87	2, 3

NOTE: All compounds were used in GC-EAD tests.
* Label information.
[†] Also found from bark (Zhang *et al.* 2000).

(−)-*trans*-verbenol. Experiment 3, carried out in the spring of 1999, was similar to Experiment 2, but tested whether a ternary blend (green leaf alcohols, C_8-alcohols, and *trans*-conophthorin) and verbenone alone, or in combination, could reduce captures of the pine shoot beetles in attractant-baited traps. The *trans*-conophthorin alone and its combination with verbenone were also included to gain more data on its bioactivity.

In Experiment 4, conducted in 1993, one of the bark volatiles from non-host *P. tremula*, benzyl alcohol, was tested on *T. piniperda* because single cell electrophysiological data suggested this compound was active in a closely related (possibly conspecific) taxon, *T. destruens* (Guerrero *et al.* 1997). The attractant used was the same kairomone as that used in Experiment 1 (Table 2).

All insects caught were kept alive at 4°C until the determination of species and sexes. Considerable variation in the numbers of beetles captured between replicates and experiments occurred, thus the counts displayed in graphs were converted to proportion (*p*) of total captured beetles within each replicate. For analysis, the data were
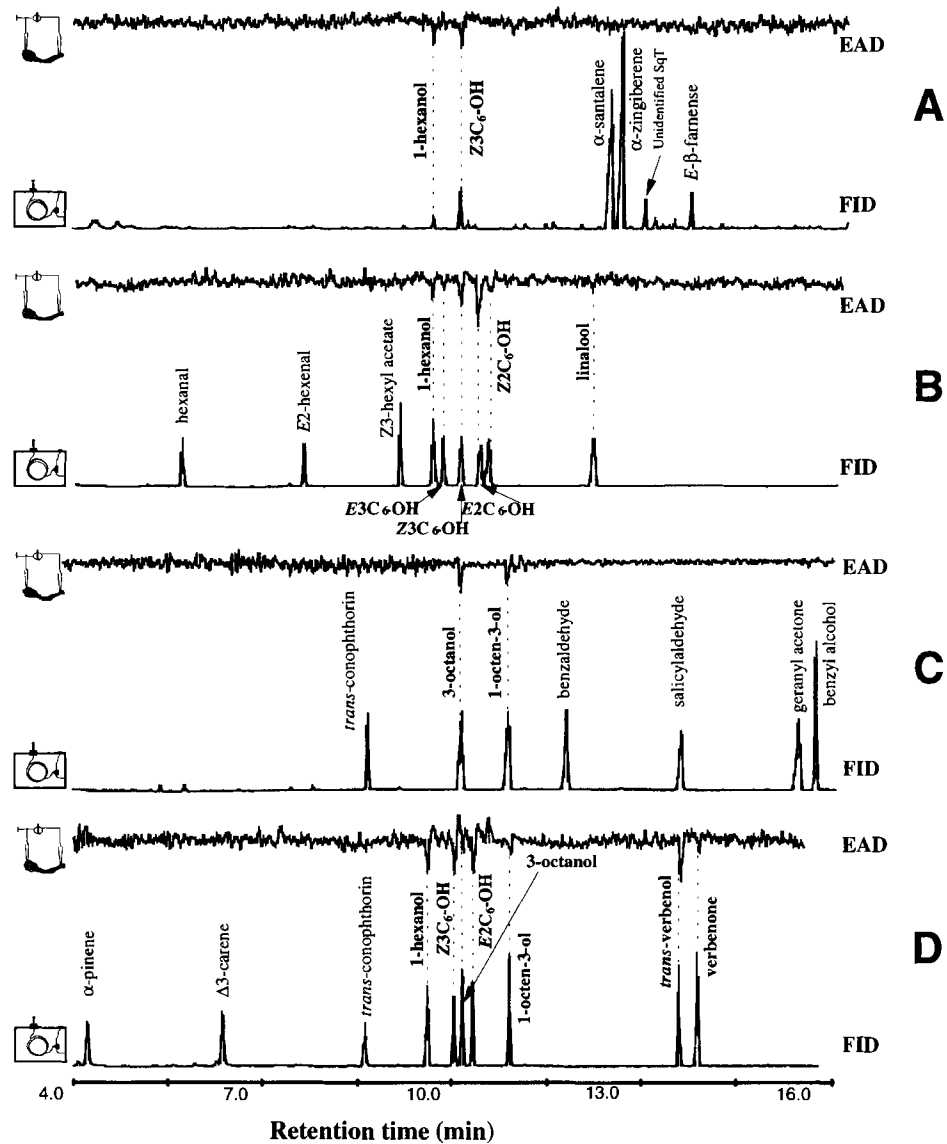
FIGURE 1. GC–EAD responses of *Tomicus piniperda* antennae to non-host volatiles: (A) head-space volatiles from fresh bark chips of the non-host taiga angiosperm *Betula pendula*; (B) a synthetic mixture of nine green leaf volatiles (20 ng/compound); (C) a synthetic mixture of seven compounds identified from non-host bark (60 ng/compound); and (D) a synthetic "*Tomicus*" mixture of 10 compounds containing host kairomone (monoterpenes), the *T. minor* pheromone component, and non-host volatiles (60 ng/compound). EAD, electroantennographic detector; FID, flame ionization detector. SqT, sesquiterpene.

transformed by $\arcsin(p)^{1/2}$ or $\log(x + 1)$, depending on the best fit to the assumption of homogeneity of variances for ANOVA. The means were compared by ANOVA followed by the Duncan multiple range test (SPSS 8.0 for Windows) at $\alpha = 0.05$. The sex ratios for the treatments within each experiment were compared with 95% binomial confidence intervals (Byers and Wood 1980).
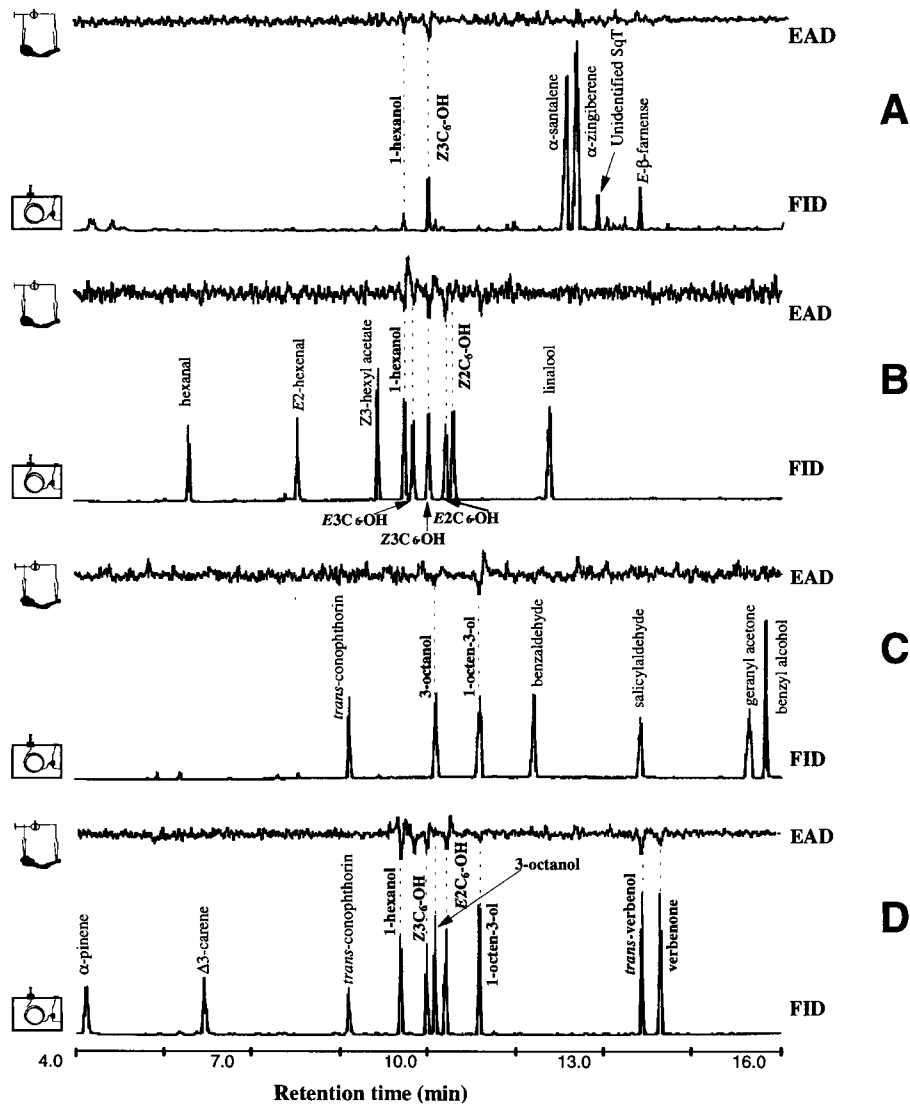
FIGURE 2. GC–EAD responses of *Tomicus minor* antennae to non-host volatiles: (A) volatiles from bark of *Betula pendula*; (B) synthetic mixture of green leaf volatiles; (C) synthetic mixture from non-host bark; and (D) synthetic "*Tomicus*" mixture (for details see Fig. 1).

Results

GC–EAD Analyses. In GC–EAD analysis of volatiles from *B. pendula* fresh bark chips, antennae of both species and sexes consistently responded to two green leaf alcohols, 1-hexanol (2–3 ng) and (Z)-3-hexen-1-ol (7–10 ng) (Figs. 1A, 2A). No antennal responses were recorded to any other compounds in the bark aeration extracts, including the dominant components, α-santalene (150 ng) and α-zingiberene (200 ng). From the first synthetic mixture of green leaf volatiles, all five of the C_6-alcohols elicited repeatable antennal responses by both species (Figs. 1B, 2B). A weak antennal response to (±)-linalool was only found by *T. piniperda* (Fig. 1B). 1-Hexanol and (Z)-3-hexen-1-ol emitted from both leaves and bark and (E)-2-hexen-1-ol from leaves of birches and aspen

TABLE 2. Chemicals, acronyms, release rates, and dispensers used in the field trapping experiments.

Chemical (acronym)	Release rate (mg/24 h)[*]	Dispenser	Field experiment No.			
			1	2	3	4
Attractants						
Kairomone blend (K)						
α-Pinene	31 ⎤		✓	✓	✓	✓
Δ3-Carene	15.4 ⎬ 600 µL of a 2:1:1 mix of α-pinene–Δ3-carene–terpinolene in a closed No. 733[†] PE-vial with 6 mm diam. hole in the lid		✓	✓	✓	✓
Terpinolene	15.4 ⎦		✓	✓	✓	✓
Pheromone component (P)						
(–)-*trans*-Verbenol	0.3	50 µL in an glass tube vial[‡]		✓	✓	
Non-host green leaf and bark volatiles[§]						
Green leaf volatiles combination with high GC–EAD response (3OH-A)						
1-Hexanol	4	200 µL in an open No. 730 PE-vial[∥]	✓			
(Z)-3-Hexen-1-ol	6	200 µL in an open No. 730 PE-vial	✓			
(E)-2-Hexen-1-ol	5	200 µL in an open No. 730 PE-vial	✓			
Green leaf volatiles combination with low GC–EAD response (3OH-B)						
(E)-3-Hexen-1-ol	6	200 µL in an open No. 730 PE-vial	✓			
(Z)-2-Hexen-1-ol	5	200 µL in an open No. 730 PE-vial	✓			
(±)-Linalool	1.3	200 µL in an open No. 730 PE-vial	✓			
Green leaf volatiles combination with no GC–EAD response (2Ald-Ac)						
1-Hexanal	14	200 µL in No. 730 PE-vial with 2 mm diam. hole in the lid	✓			
(E)-2-Hexenal	7	200 µL in No. 730 PE-vial with 2 mm diam. hole in the lid	✓			
(Z)-3-Hexenyl acetate	9	200 µL in an open No. 730 PE-vial	✓			

TABLE 2 (*concluded*).

Chemical (acronym)	Release rate (mg/24 h)[*]	Dispenser	Field experiment No.			
			1	2	3	4
Mix of high-response green leaf volatiles in one dispenser (GLV)						
1-Hexanol	2			✓	✓	
(Z)-3-Hexen-1-ol	2	200 µL of a 1:1:1 mix in an open No. 730 PE-vial		✓	✓	
(E)-2-Hexen-1-ol	2			✓	✓	
Bark alcohols combination (C$_8$-OHs)						
(±)-3-Octanol	1.2			✓	✓	
(±)-1-Octen-3-ol	1.6	200 µL of a 1:1 mix in an open No.730 PE-vial		✓	✓	
trans-Conophthorin (from non-host bark) (tC)	5	Two open 250-µL PE microcentrifuge tubes (RD0249)		✓	✓	
Benzyl alcohol (from non-host bark) (BA)	5	600 µL in a No. 731 PE-vial[¶]				✓
Old host signal[**]						
Verbenone (Vn)	0.5	200 µL in an open No. 730 PE-vial	✓		✓	
No. of replicates (trap rotations)			6	3	3	7

[*] Measured at 20–21°C in 0.7 m/s for 7–10 d.

[†] PE-vial (Kartell, Italy) with 20 mm inner diameter and 29 mm inner height.

[‡] Glass vial with 3.5 mm opening and 25 mm inner height.

[§] Based on results of preliminary GC–EAD.

[|] PE-vial (Kartell, Italy) with 6 mm opening and 29 mm inner height.

[¶] PE-vial (Kartell, Italy) with 12.5 mm opening and 29 mm inner height.
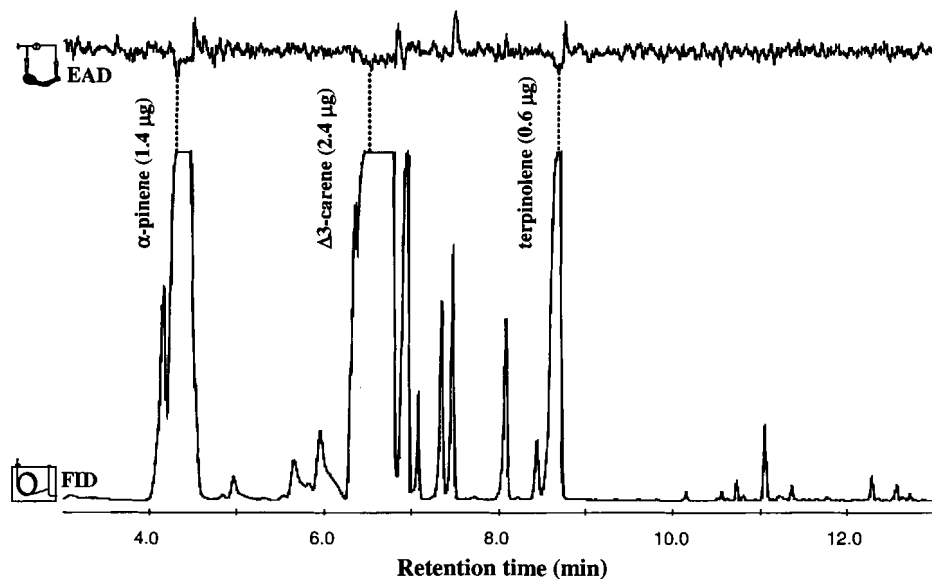
[**] Served as negative control.

FIGURE 3. GC–EAD responses of *Tomicus piniperda* antennae to high doses of monoterpenes from an aeration sample of host *Pinus sylvestris* log (25 cm long, 12 cm in diameter; aerated for 1 h with airflow of 300 mL/min).

elicited stronger antennal responses than those to (*E*)-3-hexen-1-ol and (*Z*)-2-hexen-1-ol, which were not found in the non-host trees. The green leaf aldehydes, hexanal and (*E*)-2-hexenal, and the green leaf acetate, (*Z*)-3-hexyl acetate, were not electrophysiologically active.

When testing the second synthetic mixture of seven non-host bark volatiles we found earlier in either *Betula* spp. or aspen, or reported active, both species showed electrophysiological activity only to the two C_8-alcohols, 3-octanol and 1-octen-3-ol. The response of *T. minor* to 3-octanol seems to be weaker than that to 1-octen-3-ol (Figs. 1C, 2C). No antennal responses to other bark volatiles, including *trans*-conophthorin and benzyl alcohol, were recorded (Figs. 1C, 2C). The antennal activity of the green leaf alcohols and C_8-alcohols, but not *trans*-conophthorin, was again shown in GC–EAD runs with a third synthetic blend. This third "*Tomicus*" blend" included two host monoterpenes, three green leaf alcohols, two C_8-alcohols, *trans*-conophthorin, (–)-*trans*-verbenol, and verbenone (Figs. 1D, 2D). The magnitude of antennal responses to the active non-host alcohols was similar to those of the *T. minor* pheromone component (–)-*trans*-verbenol and the well-known inhibitor verbenone. No GC–EAD responses were found to any of the host kairomone monoterpenes in the *Tomicus* blend at the dose tested (Figs. 1D, 2D); however, EAD responses of female *T. piniperda* to α-pinene (1.4 μg), Δ3-carene (2.4 μg), and terpinolene (0.6 μg) from an aeration sample of a *P. sylvestris* log were observed (Fig. 3). Antennae of *T. piniperda* responded to (–)-*trans*-verbenol as strongly as did *T. minor* antennae (Figs. 1D, 2D).

Field Trapping Experiments. A total of 127 *T. piniperda* and 67 *H. palliatus* were captured in Experiment 1. Analysis of catch data showed catches of the two species to be homoscedastic (homogeneous variances) after transformation by $\log(x + 1)$ (Levene statistics $f_{8,45} = 1.1$, $P = 0.39$ and $f_{8,45} = 1.2$, $P = 0.29$, respectively). The blend 2Ald-Ac did not reduce trap catches compared with the positive control; however, the negative
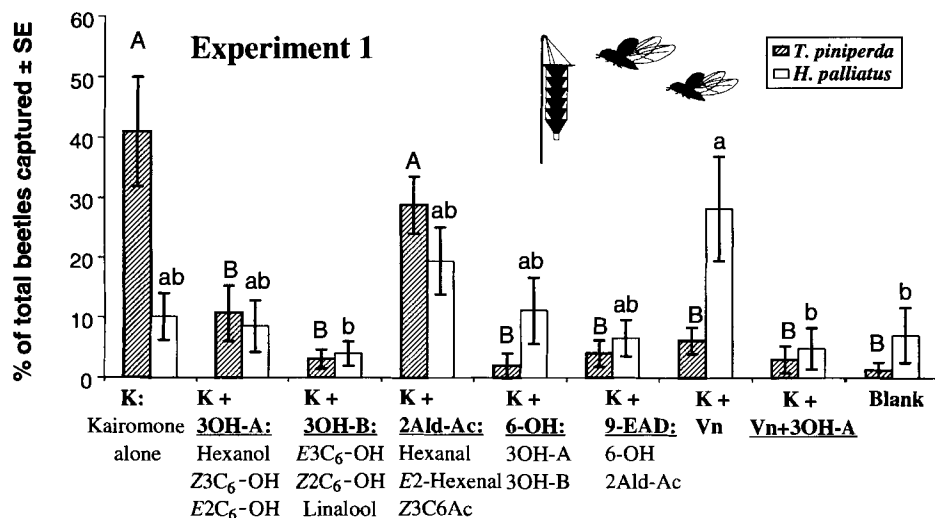
FIGURE 4. Field behavioural responses of *Tomicus piniperda* and *Hylurgops palliatus* to non-host leaf odours (green leaf volatiles) and verbenone (Vn: old host signal) added to the attractant source, Veberöd, southern Sweden, March–April 1998. Bars with the same letter are not different [ANOVA on log(x + 1), Duncan multiple range test, P > 0.05]. K, kairomone blend, active control. For other acronyms see Table 2.

control (kairomone + verbenone) and all other combinations of electrophysiologically active green leaf alcohols resulted in significant reductions in the number of *T. piniperda* captured compared with the trap baited with kairomone (Fig. 4). These reductions ranged from 62 to 96%, with no significant differences among these alcohol treatments. There were no effects on the *T. piniperda* sex ratio, which was around 55–60% males for all the treatments (P > 0.1). In contrast to *T. piniperda*, *H. palliatus* was not attracted to the positive control (kairomone) but was attracted to the negative control (kairomone + verbenone) (Fig. 4). Neither positive nor negative effects of the green leaf volatiles blends tested were observed on *H. palliatus*, as no significant differences in trap catches were found compared with the blank control.

In Experiment 2, 195 *T. piniperda* and 62 *T. minor* were captured. For both species catch data were strongly heteroscedastic (Levene statistics $f_{8,18}$ > 3.5, P < 0.01 for both species), and the same was true for Experiment 3 because of the strong inhibitory effects of several treatments that had zero catch and consequently zero variance. For comparison with the other experiments, the same parametric ANOVA approach is used for Experiments 2 and 3, but significance levels must be conservatively interpreted, as not all assumptions for ANOVA are fulfilled. The *trans*-conophthorin was inactive in both species (Fig. 5). For *T. piniperda*, the blend of green leaf volatiles and the mixture of C_8-OHs reduced the trap catches by 60–61%. When these two blends were combined, further trap catch reductions (up to 90%) were achieved, which was not different from the blank control. Addition of *trans*-conophthorin did not increase the inhibitory effects of green leaf volatiles or C_8-OHs blends alone, or both (Fig. 5).

Although the total number of *T. minor* caught was low, the treatments including the non-host volatiles caught less beetles than the attractants alone, except for *trans*-conophthorin which appeared to have no effect or may have slightly increased trap catches. A reduction in number of lesser pine shoot beetles captured was only found for the treatment combining the two blends, green leaf volatiles and C_8-OHs (Fig. 5), which did not catch any beetles. No effects on sex ratio were found in either pine shoot beetle species (about 60% males in all treatments, P > 0.1).
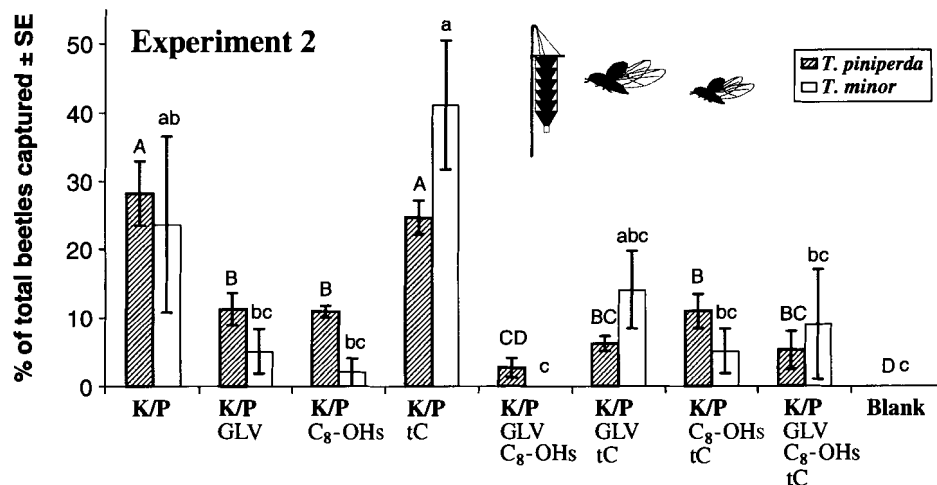
FIGURE 5. Field behavioural responses of *Tomicus piniperda* and *Tomicus minor* to all combinations of the blends of non-host leaf and bark volatiles added to the attractant source, Sjöbo, southern Sweden, March–April 1999. Bars with the same letter are not different [ANOVA on $\arcsin(p)^{1/2}$, Duncan multiple range test, $P > 0.05$]. K/P, kairomone blend with pheromone component of *T. minor*, active control. For other acronyms see Table 2.
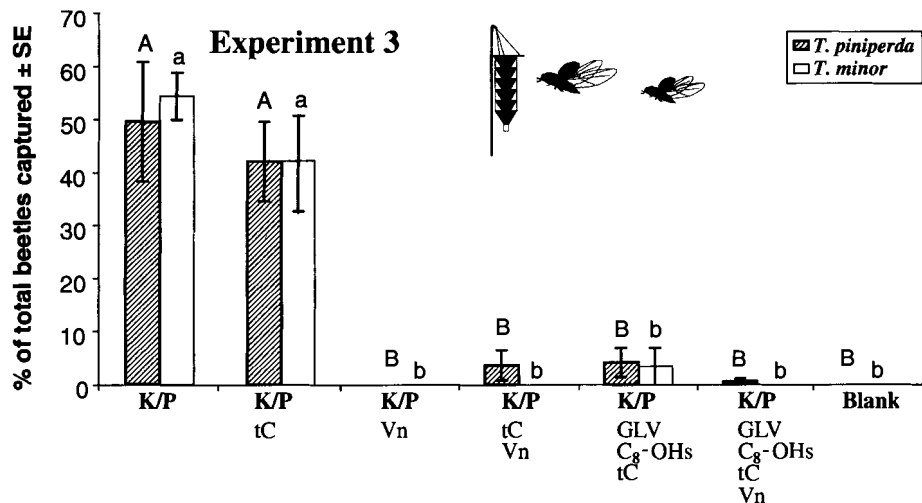

FIGURE 6. Field behavioural responses of *Tomicus piniperda* and *Tomicus minor* to verbenone (Vn: old host signal) and the blends of non-host leaf and bark volatiles added to the attractant source, Sjöbo, southern Sweden, March–April 1999. Bars with the same letter are not different [ANOVA on $\arcsin(p)^{1/2}$, Duncan multiple range test, $P > 0.05$]. K/P, kairomone blend with pheromone component of *T. minor*, active control. For other acronyms see Table 2.

In Experiment 3, similar numbers of the two species were caught (77 *T. piniperda* and 57 *T. minor*) but catch data were clearly heteroscedastic (Levene statistics $f_{8,18} > 3$, $P < 0.05$ for both species). As in Experiment 2, *trans*-conophthorin was apparently inactive for both species (Fig. 6); however, all other treatments with green leaf volatiles or verbenone resulted in lower numbers of *T. piniperda* and *T. minor* caught than for the attractants alone, and they were not different from the blank control (Fig. 6). Because of the overall low catches and the zero catches with verbenone alone, no synergistic effects between verbenone and *trans*-conophthorin and (or) the ternary blend of non-host

TABLE 3. Catch of *Tomicus piniperda* and *Hylurgops palliatus* in Experiment 4, in which 5 mg benzyl alcohol/d was added to bait of monoterpene kairomone blend, Fjälkinge, Sweden, April 1993.

Data transformation	Treatment	Mean	SD	95% CI	
				Lower bound	Upper bound
		Tomicus piniperda			
x	Blank	0.4	0.5	−0.1	0.9
	Kairomone	5.9	4.0	2.1	9.6
	Benzyl alcohol	5.6	3.8	2.0	9.1
arcsin$(p)^{1/2}$	Blank	0.1	0.2	0.0	0.3
	Kairomone	0.8	0.4	0.5	1.2
	Benzyl alcohol	0.7	0.3	0.4	1
		Hylurgops palliatus			
x	Blank	2.4	3.2	−0.5	5.3
	Kairomone	3.6	4.5	−0.6	7.7
	Benzyl alcohol	2.4	2.6	0	4.8

volatiles could be determined. There were again no effects on sex ratios of each species (around 60–65% males, $P > 0.1$).

In Experiment 4, 83 *T. piniperda* and 59 *H. palliatus* were caught. Analysis of *T. piniperda* trap catches showed that both absolute and relative catches were homoscedastic, but arcsin$(p)^{1/2}$ transformed data showed better homogeneity of variances (Levene statistic $f_{2,18} = 0.24$, $P = 0.79$). Conversely, for *H. palliatus*, only the absolute data were homoscedastic (Levene statistic $f_{2,18} = 2.93$, $P = 0.08$). The mean captures of *T. piniperda* differed ($F_{2,18} = 11.8$, $P < 0.001$), but only between the blank and the two treatments (Table 3). Thus, the addition of benzyl alcohol to the kairomone-baited traps did not reduce attraction of the larger pine shoot beetle (Table 3). There were no effects on *T. piniperda* sex ratio, which was around 70% males for both treatments. For *H. palliatus*, all mean values, including the blank trap, were similar (Table 3, $F_{2,18} = 2.4$, $P > 0.1$).

Discussion

Our results show that five non-host alcohols are detected by antennae of *T. piniperda* and *T. minor* from *Betula* spp. and *P. tremula*: 1-hexanol and (Z)-3-hexen-1-ol from both leaves and bark, (E)-2-hexen-1-ol from the leaves, and 3-octanol and 1-octen-3-ol from the bark (Zhang *et al.* 1999*a*, 2000). In contrast, no antennal responses were observed to the green leaf aldehydes and the acetate. A similar GC–EAD response pattern has been found for *I. typographus* (Zhang *et al.* 1999*a*, 1999*b*, 2000). In *Dendroctonus ponderosae* Hopkins, Wilson *et al.* (1996) also reported antennal responses to the green leaf alcohols, but not to the green leaf aldehydes. However, some other non-host bark volatiles such as *trans*-conophthorin, benzaldehyde, salicylaldehyde, and benzyl alcohol, which are electrophysiologically active in several other conifer bark beetle species (Guerrero *et al.* 1997; Borden *et al.* 1998; Huber *et al.* 1999; Zhang *et al.* 2000), did not elicit any GC–EAD responses in *T. piniperda* and *T. minor*. Antennal sensitivity of both *Tomicus* species to the active non-host green leaf alcohols and C_8-alcohols was similar to that of the *T. minor* major pheromone component, (−)-*trans*-verbenol (Lanne *et al.* 1987), and the well-known inhibitor, verbenone (Schlyter *et al.* 1988, 1995; Byers *et al.* 1989). No GC–EAD responses were found to any of the host kairomone monoterpenes in the synthetic mixture at the doses tested, which might

be due to the high response thresholds to the monoterpenes (Lanne *et al.* 1987). At a much higher dose from the air-entrainment sample of a host log, the kairomone monoterpenes elicited strong antennal responses (Fig. 3). In addition, a similar antennal response pattern was found when the newly emergent F_1 adults of both species (without maturation feeding) were tested (Q-H Zhang *et al.*, unpublished data).

In agreement with our GC–EAD results, the blend of the green leaf aldehydes and acetate did not significantly reduce trap catches of *T. piniperda* (Fig. 4), whereas all the other blends with antennally active green leaf alcohols significantly reduced trap captures (Figs. 4–6). This is consistent with the finding of Poland and Haack (2000) that their blends of four green leaf alcohols reduced attraction of *T. piniperda*, whereas the green leaf aldehydes, hexanal and (*E*)-2-hexenal, were inactive in the North American population.

Our field trapping experiments also disclosed the inhibitory effects of a blend of the two electrophysiologically active C_8-alcohols, 3-octanol and 1-octen-3-ol, on *T. piniperda* and *T. minor*. Recently, 3-octanol and 1-octen-3-ol were identified from the head-space samples of fresh bark chips of *B. pendula*, *B. pubescens*, and *P. tremula* (Zhang *et al.* 2000). Their GC–EAD activity and inhibitory effect on *I. typographus* and *I. duplicatus* have been shown (Zhang *et al.* 2000, 2001). When combining green leaf alcohol and C_8-alcohol blends, a significant reduction of trap catches was achieved in *T. piniperda*. This may indicate either an additive or a synergistic (multiplicative) effect of combined stimuli (Deglow and Borden 1998a; Poland and Haack 2000).

The inhibition effect on the attraction of *T. piniperda* to ethanol-baited traps by the presence of *B. pendula* or *P. tremula* bark and xylem was reported from biological experiments by Schroeder (1992). In the light of our new data, his results can be explained by a combination of the emission of the two green leaf alcohols, 1-hexanol and (Z)-3-hexen-1-ol, and the two C_8-alcohols, 3-octanol and 1-octen-3-ol, from his split non-host bolts.

Huber *et al.* (1999) suggested that *trans*-conophthorin may represent a general warning odour analogous to aposematic warning colours such as red and orange. The results of our GC–EAD and field trapping experiments on the two *Tomicus* species are inconsistent with this hypothesis. A similar lack of effects of *trans*-conophthorin has been found in *T. lineatum* (Kohnle *et al.* 1992) and two conifer-infesting species of *Pityogenes* (Byers *et al.* 2000).

Benzyl alcohol, a non-host volatile from *Eucalyptus*, inhibited attacks by the closely related (possibly conspecific) *T. destruens* at release rates of about 700 mg/d per log in a field host log experiment (Guerrero *et al.* 1997). This compound was also found from bark of non-host angiosperms present in taiga forest, such as *P. tremuloides* (Borden *et al.* 1998) and *P. tremula* (Zhang *et al.* 2000), and showed a disruptive effect on aggregation of *D. ponderosae* when tested in binary or ternary combinations with other non-host volatiles, but was inactive on its own (Borden *et al.* 1998). Our results clearly indicate that benzyl alcohol was inactive on *T. piniperda* not only at the antennal level but also at the behavioural level, as shown in the GC–EAD and the field trapping experiments (Fig. 1; Table 3). A dose effect may explain the different findings. The release rate in the current trapping study was around 100 times less than that used on logs by Guerrero *et al.* (1997) and about one half of that used by Borden *et al.* (1998), but was similar to those of the active non-host volatiles in our experiments (Table 2). Alternatively, the lack of recognition of benzyl alcohol by *T. piniperda* might be because this compound is not emitted by common non-host angiosperms, *B. pendula* and *B. pubescens*, associated with its host Scots pine in Scandinavian natural habitats (Zhang *et al.* 2000).

In Experiments 1 and 4, *H. palliatus* was not attracted to the monoterpene bait, but in Experiment 1 *H. palliatus* was attracted to the negative control (kairomone + verbenone), which is in agreement with the finding of Schlyter *et al.* (1995). These

monoterpenes have been shown to increase entry of *H. palliatus* into artificial holes releasing ethanol (Byers 1992). None of the treatments containing green leaf volatiles differed from the blank control (Fig. 4). On the other hand, the blend of 1-hexanol, (*Z*)-3-hexen-1-ol, and (*E*)-2-hexen-1-ol in combination with verbenone caught significantly lower numbers of *H. palliatus* than the verbenone, which might indicate an inhibitory effect of the green leaf alcohols alone.

In Scandinavia, the initial spring flight and colonisation by *T. piniperda* and *T. minor* usually occurs at the end of March and beginning of April, which is much earlier than the first flights for most sympatric bark beetles (Långström 1984). During their short flight period in the early spring, the majority of buds of non-host deciduous trees, such as *B. pendula*, *B. pubescens*, and *P. tremula*, remain unopened and little or no foliage is present. Meanwhile, the temperature during the flight is usually about 12–15°C, which may not be high enough to cause intact non-host bark to emit sufficient amounts of behaviourally active volatiles. The green leaf alcohols and C_8-alcohols tested in the present study were mainly based on the analyses of the aeration samples of non-host leaves and cut bark taken in mid-June. Therefore, they may not be ecologically relevant when the *Tomicus* species are searching for their brood materials in the early spring. The shoot-feeding dispersal flight normally occurs in the summer, when the non-host leaf and bark volatiles, such as green leaf alcohols and C_8-alcohols, appear to be more abundant (Zhang *et al.* 1999*a*, 2000). Avoidance of non-host volatiles would be beneficial to the young adults during the relatively short flights to locate pine shoots (Poland and Haack 2000). Further study is needed to determine if the antennally active green leaf alcohols and C_8-alcohols are behaviourally informative and relevant to the F_1 adults of the two *Tomicus* species when locating host pines for shoot feeding in summer.

Our results in Europe and the findings by Poland and Haack (2000) from the United States suggest that green leaf alcohols from non-host leaves and (or) bark and C_8-alcohols from the bark have potential for semiochemical-based management programs by keeping the beetles away from suitable breeding sites (logs and trunks) and feeding sites (shoots).

Acknowledgements

References

Anderbrant O, Schlyter F, and Löfqvist J. 1988. Dynamics of tree attack in the bark beetle *Ips typographus* under semi-epidemic conditions. pp. 35–52 *in* TL Payne, H Saarenmaa (Eds), *Integrated Control of Scolytid Bark Beetles, Proceedings of the IUFRO Working Party on Bark Beetles Symposium*, Vancouver, 3–10 July 1988. Blacksburg: Virginia Tech Press
Borden JH 1989. Semiochemicals and bark beetle populations exploitation of natural phenomena by pest management strategists. *Holarctic Ecology* **12**: 501–10

Borden JH, Wilson IM, Gries R, Chong LJ, Pierce HD, Jr, Gries G. 1998. Volatiles from the bark of trembling aspen, *Populus tremuloides* Michx. (Salicaceae), disrupt secondary attraction by the mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae). *Chemoecology* **8**: 69–75

Byers JA. 1992. Attraction of bark beetles, *Tomicus piniperda*, *Hylurgops palliatus*, and *Trypodendron domesticum*, and other insects to short-chain alcohols and monoterpenes. *Journal of Chemical Ecology* **18**: 2385–402

Byers JA, Wood DL. 1980. Interspecific inhibition of the response of the bark beetles, *Dendroctonus brevicomis* and *Ips paraconfusus*, to their pheromones in the field. *Journal of Chemical Ecology* **6**: 149–64

Byers JA, Lanne BS, Löfqvist J, Schlyter F, Bergström G. 1985. Olfactory recognition of host-tree susceptibility by pine shoot beetles. *Naturwissenschaften* **72**: 324–6

Byers JA, Lanne BS, Löfqvist J. 1989. Host-tree unsuitability recognized by pine shoot beetles in flight. *Experientia* **45**: 489–92

Byers JA, Zhang Q-H, Schlyter F, Birgersson G. 1998. Volatiles from non-host birch trees inhibit pheromone response in spruce bark beetles. *Naturwissenschaften* **85**: 557–61

Byers JA, Zhang Q-H, Birgersson G. 2000. Strategies of a bark beetle, *Pityogenes bidentatus*, in an olfactory landscape. *Naturwissenschaften*. In press.

Deglow EK, Borden JH. 1998a. Green leaf volatiles disrupt and enhance response to aggregation pheromones by the ambrosia beetle, *Gnathotrichus sulcatus* (LeConte) (Coleoptera: Scolytidae). *Canadian Journal of Forest Research* **28**: 1697–705

——— 1998b. Green leaf volatiles disrupt and enhance response by the ambrosia beetle, *Gnathotrichus retusus* (LeConte) (Coleoptera: Scolytidae), to pheromone-baited traps. *Journal of the Entomological Society of British Columbia* **95**: 9–15

Dickens JC, Billings RF, Payne TL. 1991. Green leaf volatiles: a ubiquitous chemical signal modifies insect pheromone responses. pp. 277–80 *in* I Hrdy (Ed), *Insect chemical ecology*. Prague: Acadamia Praha

——— 1992. Green leaf volatiles interrupt aggregation pheromone response in bark beetles infecting pines. *Experientia* **48**: 523–4

Guerrero A, Feixas J, Pajares J, Wadhams LJ, Pickett JA, Woodcock CM. 1997. Semiochemically induced inhibition of behaviour of *Tomicus destruens* (Woll.) (Coleoptera: Scolytidae). *Naturwissenschaften* **84**: 155–7

Haack RA, Lawrence RK, Mccullough DG, Sadof CS. 1997. *Tomicus piniperda* in North America: an integrated response to a new exotic scolytid. pp. 62–72 *in* JC Gregoire, AM Leibhold, FM Stephen, KR Day, SM Salom (Eds), Proceedings: Integrating Cultural Tactics into the Management of Bark Beetles and Reforestation Pests. *US Forest Service General Technical Report* **NE-236**

Huber DPW, Gries R, Borden JH, Pierce HD, Jr. 1999. Two pheromones of coniferophagous bark beetles found in the bark of non-host angiosperms. *Journal of Chemical Ecology* **25**: 805–16

Kohnle U, Densborn S, Kölsch P, Meyer H, Francke W. 1992. *E*-7-methyl-1,6-dioxaspiro [4.5]decane in the chemical communication of European Scolytidae and Nitidulidae (Coleoptera). *Journal of Applied Entomology* **114**: 187–92

Lanne BS, Schlyter F, Byers JA, Löfqvist J, Leufvén A, Bergström G, Van Der Pers JNC, Unelius R, Bæckström P, Norin T. 1987. Differences in attraction to semiochemicals present in sympatric pine shoot beetles, *Tomicus minor* and *T. piniperda*. *Journal of Chemical Ecology* **13**: 1045–67

Långström B. 1984. Windthrown Scots pines as brood material for *Tomicus piniperda* and *T. minor*. *Silva Fennica* **18**: 187–98

Långström B, Hellqvist C. 1991. Shoot damage and growth losses following three years of *Tomicus* attacks in Scots pine stands close to a timber storage site. *Silva Fennica* **25**: 133–45

Poland TM, Haack RA. 2000. Pine shoot beetle, *Tomicus piniperda* (Coleoptera: Scolytidae), responses to common green leaf volatiles. *Journal of Applied Entomology* **124**: 63–9

Postner M. 1974. Scolytidae, Borkenkäfer, *Blastophagus*. pp. 397–400 *in* W Schwenke (Ed), *Die Forstschädlinge Europas*. Hamburg: Verlag Paul Parey

Schlyter F, Birgersson G. 1999. Forest beetles. pp. 113–48 *in* RJ Hardie, A Minks (Eds), *Pheromones of non-lepidopteran insects associated with agricultural plants*. Wallingford: CAB International

Schlyter, F, Löfqvist, J. 1990. Colonisation patterns in the pine shoot beetle, *Tomicus piniperda*: effects of host declination, structure and presence of conspecifics. *Entomologia Experimentalis et Applicata* **54**: 163–72

Schlyter F, Byers JA, Löfqvist J, Leufvén A, Birgersson G. 1988. Reduction of attack density of the bark beetles *Ips typographus* and *Tomicus piniperda* on host bark by verbenone inhibition of attraction to pheromone and host kairomone. pp. 53–68 *in* TL Payne, H Saarenmaa (Eds), *Integrated Control of Scolytid Bark Beetles, Proceedings of the IUFRO Working Party on Bark Beetles Symposium*, Vancouver, 3–10 July 1988. Blacksburg: Virginia Tech Press

Schlyter F, Löfqvist J, Jakus R. 1995. Green leaf volatiles and verbenone modify attraction of European *Tomicus*, *Hylurgops*, and *Ips* bark beetles. pp. 29–44 *in* FP Hain, SM Salom, WF Ravlin, TL Payne, KF Raffa (Eds), *Behavior, Population Dynamics, and Control of Forest Insects, Proceedings of a Joint*

IUFRO Working Party Conference, February 1994. Wooster: Ohio Agricultural Research and Development Center

Schroeder LM. 1992. Olfactory recognition of non-hosts aspen and birch by conifer bark beetles *Tomicus piniperda* and *Hylurgops palliatus*. *Journal of Chemical Ecology* **18**: 1583–93

Schroeder LM, Eidmann HH. 1987. Gallery initiation by *Tomicus piniperda* (Coleoptera: Scolytidae) on Scots pine trees baited with host volatiles. *Journal of Chemical Ecology* **13**: 1591–9

Tømmerås BÅ. 1989. Host selection by odorous compounds from host and non-host trees in bark beetles. *Fauna Norvegica Series B* **36**: 75–9

Tømmerås BÅ, Mustaparta H. 1989. Single cell responses to pheromones, host and non-host volatiles in the ambrosia beetle *Trypodendron lineatum*. *Entomologia Experimentalis et Applicata* **52**: 141–8

Wilson IM, Borden JH, Gries R, Gries G. 1996. Green leaf volatiles as antiaggregants for the mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae). *Journal of Chemical Ecology* **22**: 1861–75

Ye H. 1991. On the bionomy of *Tomicus piniperda* (L.) (Coleoptera: Scolytidae) in the Kunming region of China. *Journal of Applied Entomology* **112**: 366–9

Ye H, Lieutier F. 1997. Shoot aggregation by *Tomicus piniperda* (L.) (Col: Scolytidae) in Yunnan, southwestern China. *Annales des Sciences Forestieres (Paris)* **54**: 635–41

Zhang Q-H, Birgersson G, Zhu J-W, Löfstedt C, Löfqvist J, Schlyter F. 1999*a*. Leaf volatiles from nonhost deciduous trees: variation by tree species, season, and temperature and electrophysiological activity in *Ips typographus*. *Journal of Chemical Ecology* **25**: 1923–43

Zhang Q-H, Schlyter F, Anderson P. 1999*b*. Green leaf volatiles interrupt pheromone response of spruce bark beetle, *Ips typographus*. *Journal of Chemical Ecology* **25**: 2847–61

Zhang Q-H, Schlyter F, Birgersson G. 2000. Bark volatiles from non-host angiosperm trees of spruce bark beetle, *Ips typographus* L. (Coleoptera: Scolytidae): chemical and electrophysiological analysis. *Chemoecology*. **10**: 69–80

Zhang Q-H, Liu G-T, Schlyter F, Birgersson G, Anderson P, Valeur P 2001. Olfactory responses of *Ips duplicatus* from Inner Mongolia, China to nonhost leaf and bark volatiles. *J. Chem. Ecol.* In press.