

Enhancement of attraction and trap catches of the old-house borer, *Hylotrupes bajulus* (Coleoptera: Cerambycidae), by combination of male sex pheromone and monoterpenes

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Abstract: Monoterpenoid compounds extracted from wood of Scots pine, *Pinus sylvestris* L, synergized the attraction of the old-house borer, *Hylotrupes bajulus* (L), to the male pheromone (3*R*)-3-hydroxy-2-hexanone ((3*R*)-ketol) + 1-butanol. Glasshouse experiments using ground traps baited with extracts derived from Scots pine wood or the monoterpenes (+)- α -pinene, (-)-verbenone, (-)-*trans*-pinocarveol and (+)-terpinen-4-ol attracted significantly more *H bajulus* females, but caught fewer of them, than the synthetic pheromone mixture alone. Traps baited with higher concentrations of the monoterpene mixture attracted fewer females than those baited with lower dosages, whilst very high concentrations of the mixture (6–10 vials) caught no insects. However, a combination of (3*R*)-ketol + 1-butanol or (\pm)-3-ketol + 1-butanol with monoterpenes resulted in the capture of significantly more females than either the sex pheromone or the monoterpene mixture alone. Traps baited with a blend of the male's sex pheromone or the monoterpenes attracted significantly more, but caught fewer, males than females. Here again, a combination of the above blends enhanced the attraction of males significantly when compared with the attractancy of either of the compounds/mixtures used alone.

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Keywords: *Hylotrupes bajulus*; Coleoptera; Cerambycidae; sex pheromones; monoterpenes; trap catches; attraction; synergism

1 INTRODUCTION

Longhorned beetles have received significant research attention in recent years because of the serious economic damage that some species can cause to timber.^{1–3} The old-house borer, *Hylotrupes bajulus* (L) (Coleoptera: Cerambycidae), is an important pest of coniferous wood that causes serious damage to the structural timbers of buildings. Female beetles lay their eggs on structural wood and the resulting larvae subsequently bore into the softwood that is frequently used in residential buildings, sometimes causing the collapse of infested houses. Spray application of toxic insecticides to control the beetle in residences is undesirable and alternative control methods, such as biological control, need to be investigated.

Higgs and Evans⁴ first reported that the pheromone components (-)-verbenone and *p*-cymen-8-ol produced in the frass of the wood-boring larvae of *H bajulus* mediated the oviposition behaviour of adults.

Schröder *et al*⁵ showed that adult male *H bajulus* produced a sex pheromone attractive to female beetles, and identified the major component of the pheromone as (3*R*)-3-hydroxy-2-hexanone [(3*R*)-ketol]. Noldt *et al*⁶ reported that the pheromone is produced by exocrine glands in the prothorax of the male *H bajulus*. Chemical analysis of hexane extracts obtained by surface extraction of dissected prothoracic glands and headspace samples revealed the male-specific compounds (3*R*)-ketol and 2-hydroxy-3-hexanone, the diastereomeric diols (2*R*, 3*R*)-2,3-hexanediol, (2*S*, 3*R*)-2,3-hexanediol and 2,3-hexanedione, as well as 1-butanol.⁷ Fettköther *et al*⁷ found that unmated females were attracted to pheromone blends (headspace extracts of males and synthetic blends of other major glandular compounds) and also to the compound (3*R*)-ketol in wind-tunnel experiments. Ground traps baited with synthetic (3*R*)-ketol + 1-butanol were the most efficient compounds in capturing *H bajulus* in

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both greenhouse and field tests (Reddy, GVP, unpublished results). Fekkötter *et al*⁸ reported that female *H bajulus* were also attracted to a blend of (–)-verbenone, (+)- α -pinene, (+)-terpinen-4-ol and (–)-*trans*-pinocarveol, whereas male beetles were attracted to a mixture of (+)-terpinen-4-ol, (+)- α -pinene and (–)-*trans*-pinocarveol in wind-tunnel experiments. In the present study we have investigated the effectiveness of several lures against *H bajulus* adults and report that both attraction and trap catches of the beetle were increased by a combination of the male's sex pheromone and monoterpene mixtures.

2 EXPERIMENTAL

2.1 Insects

Hylotrupes bajulus adults were obtained from a laboratory culture maintained at the Institute for Wood Biology and Wood Protection, Hamburg (Germany).⁶ Newly emerged beetles were kept individually in Bellaplast™ boxes (Bellaplast AG, Altstätten, Switzerland) lined with moistened filter paper. Male and female beetles were kept in separate rooms under 20 °C and a 12:12h light:dark photoperiod until used in experiments.⁷

2.2 Pheromones, monoterpenes and pine wood extract

The synthetic pheromone mixtures, (3*R*)-ketol + 1-butanol (purity \geq 98.5%) and (\pm)-3-ketol + 1-butanol (purity \geq 98.5%) were obtained from the Department of Chemistry, Cornell University.

The monoterpenes (+)- α -pinene, (–)-verbenone, (–)-*trans*-pinocarveol and (+)-terpinen-4-ol (purity \geq 99%) were obtained from Fluka Chemika, and hexane (HPLC grade) was obtained from Merck.

A 23-g portion of sawdust was obtained from culture blocks of pine wood (*Pinus sylvestris* L) and Soxhlet extracted for 8 h with hexane (>99.5% purity). After evaporation of the solvent, the resulting yellow oil was resuspended in the original solvent. For the experiments, the crude wood extract was tested at a concentration of 1:100 (by volume), representing 8.6 μ g wood extracted per microlitre of solvent.⁸

The test compounds were kept in the refrigerator and allowed to warm to room temperature (22 °C) before dilution to the required concentration with hexane. The pheromone compounds (3*R*)-ketol + 1-butanol (3 mg day⁻¹) and (\pm)-3-ketol + 1-butanol (2.8 mg day⁻¹) were diluted in 100 ml of hexane to give a ratio of 1:1:100 (by volume). The blend of the four monoterpenes (9.5 mg day⁻¹) was diluted in hexane to give a ratio of 1:1:1:100 (by volume), while pine wood extracts (12.5 mg day⁻¹) were diluted at the ratio of 1:100.

2.3 Dispensers

Pheromone dispensers were made from glass screw-top vials, (N 8-1 brown, 23 \times 5.5 \times 1.0 mm, capacity 1 ml; Macherey-Nagel, Duren, Germany) with the

straight end capped with a rubber septum (15 \times 8 mm, Thomas Scientific®, Swedesboro, New Jersey, USA). Each vial was filled with 1000 μ l of the test compound diluted in hexane. Known numbers of vials were used per trap. Each treatment was replicated eight times.

2.4 Greenhouse conditions

All experiments were conducted in a nylon screen cage measuring 450 cm long \times 230 cm wide \times 100 cm high. The average temperature, relative humidity and wind speed were measured with a Meteo Digit III instrument (Lambrecht, Klimatologische Messtechnik, Göttingen, Germany) while light intensity was recorded using a Lux-Meter (Testo GmbH & Co, Lenzkirch, Germany).

2.5 Trapping method

A ground trap was used for all tests, as this apparatus had previously been found to be the most efficient design for capturing *H bajulus* (Reddy GVP, unpublished results). The ground trap (Fig 1) measured 120 \times 60 cm with a baffle (50 \times 8 cm) fitted in the top that served to prevent beetles that fell through the slit from escaping. The trap, when baited with the pheromone or monoterpene mixture, was placed on the ground in the greenhouse screen cage 2 h prior to the release of the beetles, which allowed the pheromone or monoterpene mixture vapours to spread throughout the cage. A running fan was installed behind the trap, with several tightened gauze layers over its downwind opening, in order to produce a uniform airflow through the screen cage. Contaminated air from the screen cage was removed by a downwind exhaust system.

2.6 Attraction and capture efficiency of traps baited with wood extract and monoterpene mixtures

The tests were carried out from April 25 to June 30, 1999 between 12:00 and 17:00 h, since these are typical conditions under which insects are likely to be producing and responding to pheromones.⁸ Ground traps baited with two vials of the pine wood extract or with 1, 2, 4, 6, 8 or 10 vials of the monoterpene mixture were tested in the greenhouse to determine their attractive and capture efficiency for female *H bajulus*. Ten recently emerged females (5–15 days old) were released at a distance of 3 m downwind from the trap. An unbaited trap was used for control

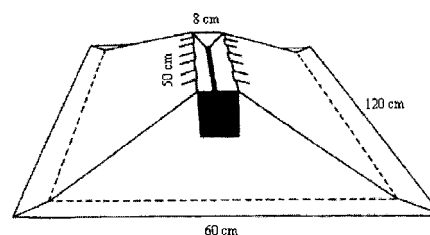


Figure 1. Schematic illustration of the ground trap used in the present study.

experiments. Counts were made of the number of beetles within 1 m of the trap and of the number of beetles that entered the trap during a 3-h (12.30 to 15.30 h) experimental period. The criterion of within 1 m of the trap includes those that were on, but not in, the trap. Captured beetles were immediately removed from the trap and placed in individual containers in order to remove them from the experiment.

2.7 Capture efficiency of females using traps baited with pheromone and/or a mixture of monoterpenes with and without males

Ten unmated females (5–15 days old) were released 3 m downwind from a ground trap baited with two vials of the pheromone mixture (3*R*)-ketol + 1-butanol, or two vials of the monoterpene blend, or two vials of pheromone blend together with two vials of monoterpene blend. In addition, ground traps baited with two vials of (±)-3-ketol + 1-butanol, two vials of the monoterpene blend, or two vials of (±)-3-ketol + 1-butanol and two vials of monoterpene blend were also tested. These experiments were conducted between 12.30 and 15.30 h.

In a second series of experiments, the tests were repeated with the additional presence of two virgin male *H bajulus* (5–15 days old), which were housed in a small nylon screen cage (30 × 20 × 20 cm). The edges of the nylon cage were stapled to prevent the beetles escaping and the apparatus placed 50 cm away from the trap. The male beetles were replaced every 2 days. Observations were made on the number of females approaching and entering the trap or coming into contact with the nylon gauze cage. Females that came to rest on the nylon screen cage for 5 min were considered trapped. Trapped beetles were removed and placed in individual containers to remove them from the experiment. Data for both those attracted or trapped by the cage and by the ground trap were recorded.

2.8 Attraction of male *Hylotrupes bajulus* to traps baited with pheromone, monoterpene mixture and their combination

The attraction of males to their own pheromone, and the monoterpene mixtures, was determined in greenhouse tests as described above. Because male beetles release pheromone in the afternoon (our own observation from preliminary investigations), this experiment was conducted from 9.30 to 12.30 h to avoid contamination. Ten unmated males (5–15 days old) were released 3 m downwind from a ground trap baited with either two vials of the pheromone blend (3*R*)-ketol + 1-butanol, two vials of the monoterpene blend or a trap baited with a combination of two vials of pheromone and two vials of the monoterpene blend. An unbaited trap served as a control. The number of beetles trapped over the 3-h interval was recorded. Trapped beetles were removed following the experiment and placed in individual containers to remove them from the experiment. The numbers

of untrapped beetles at the end of the experiment, and their respective distances from the trap were recorded. A total of eight of replicates was used for each treatment.

2.8 Statistical analysis

Data were analyzed using one-way analysis of variance (ANOVA). Fishers LSD *post hoc* tests were used to determine significant differences between the treatments. All statistical procedures were conducted using SPSS 12.0 for Windows software and, in all cases, the accepted level of significance was 5%.

3 RESULTS

The temperature, relative humidity, light intensity and wind speed that prevailed during the experimental period were 30.2 °C, 31.0%, 79 lux and 2.5 m s⁻¹.

3.1 Attraction and capture efficiency of wood extracts and monoterpene mixtures

Ground traps baited with two vials of the monoterpene mixture or two vials of wood extract attracted similar numbers of female beetles to within 1 m of the trap and also trapped similar numbers, in both cases approximately 20% of the total number attracted (Table 1). Traps baited with one vial of monoterpene mixture attracted significantly fewer beetles ($F_{1,7} = 12.41, P < 0.05$) and also trapped fewer beetles, although the latter difference was not significant ($P > 0.05$). Increasing the monoterpene dosage to four vials had no significant effect on the numbers of beetles attracted or trapped, whilst 8–10 vials resulted in significantly fewer beetles attracted, and no insects were trapped.

3.2 Increase in trap catches by addition of monoterpene blend with and without the presence of males

Ground traps baited with two vials of (3*R*)-ketol + 1-butanol plus two vials of the monoterpene blend

Table 1. Effect of wood extracts and synthetic monoterpenes on the attraction and capture of female *Hylotrupes bajulus*

Treatment	Dosage	Number attracted near to the trap ^a (± SEM)	Number captured by trap ^a (± SEM)
Wood extract	2 vials	7.0 (±0.2) a	2.0 (±0.4) a
Blend of synthetic monoterpenes	1 vial	4.0 (±0.1) b	1.0 (±0.2) a
	2 vials	8.0 (±0.5) a	2.0 (±1.0) a
	4 vials	8.0 (±0.6) a	2.0 (±0.1) a
	6 vials	7.0 (±0.2) a	0
	8 vials	4.0 (±0.3) b	0
	10 vials	2.0 (±0.1) b	0
Unbaited trap	—	0	0

^a Means followed by different letters within the same column are significantly different (one-way ANOVA followed by Fisher's LSD *post hoc* tests, $P \leq 0.05$). The means were generated from eight tests each using 10 insects.

Table 2. Number of *Hylotrupes bajulus* females captured by ground trap or nylon screen cage with two virgin males

Lure	Ground trap ^a (± SEM) (trapped)	Nylon screen cage with virgin males ^a (± SEM)	
		Attracted	Trapped
(3 <i>R</i>)-Ketol + 1-butanol	7.0 (±0.2) b	6.0 (±1.2) b	4.0 (±0.2) a
Monoterpenoid blend	1.0 (±0.6) d	9.0 (±0.2) a	0.0 (±0.1) c
(3 <i>R</i>)-Ketol + 1-butanol plus monoterpenoid blend	9.0 (±1.0) a	8.0 (±0.2) a	2.0 (±0.4) b
(±)-3-Ketol + 1-butanol	4.0 (±0.1) c	3.0 (±0.6) c	5.0 (±0.4) a
Monoterpenoid blend	0.0 (±0.3) d	8.0 (±0.3) a	0.0 (±0.3) c
(±)-3-Ketol + 1-butanol plus monoterpenoid blend	7.0 (±0.2) b	6.0 (±0.1) b	2.0 (±0.1) b

^a Means followed by the different letters within the same column are significantly different (one-way ANOVA followed by Fisher's LSD *post-hoc* tests, $P \leq 0.05$). The means were generated from eight tests each using 10 insects.

yielded significantly higher catches than traps baited with two vials of the pheromone blend or with the monoterpene blend alone ($F_{1,7} = 14.22$, $P < 0.05$) (Table 2). When a nylon screen cage containing two virgin males was tested alongside a trap containing the synthetic pheromone blend, fewer females were trapped. The screen cage (plus males) attracted an average of 8.0 and captured 2.0 females when tested with the synthetic pheromone blend plus the monoterpene blend. However, when a trap baited with the synthetic pheromone blend alone was tested in the presence of males, it attracted an average of 6.0 and caught 4.0 beetles. A 20% increase in trap catches was obtained by adding the monoterpene blend to the synthetic pheromone mixture, but only in the absence of males. The trap baited with (±)-3-ketol + 1-butanol plus the monoterpene blend captured significantly higher numbers of females than a screen cage trap with two virgin males (Fisher's LSD test, $P < 0.05$). A mean of 4.0 beetles per trap was caught by traps baited with (±)-3-ketol + 1-butanol alone. A nylon screen cage trap attracted 3.0 and captured 5.0 beetles per trap. Here again, an increase (30%) in trap catch was obtained by adding the monoterpene blend to (±)-3-ketol + 1-butanol, but only in the absence of males. When baited with the monoterpene blend only, whilst traps attracted *H. bajulus* females, the beetles were unable to locate and enter the trap.

3.3 Response of male *Hylotrupes bajulus* to a trap baited with synthetic pheromone and monoterpene mixtures

Although traps baited with the synthetic pheromone and monoterpene mixtures were less efficient than

Table 3. Attraction of male *Hylotrupes bajulus* beetles towards different lures

Final distance from trap (m)	Percentage of male beetles within the specified distance from the odour source ^a			
	Control	(3 <i>R</i>)-Ketol + 1-butanol	Monoterpenes	(3 <i>R</i>)-Ketol + 1-butanol plus monoterpenes
<1	10.0 d	55.0 a	37.5 a	85.0 a
1–2	15.0 c	31.0 b	30.0 b	12.5 b
2–3	27.5 b	10.0 c	22.5 c	2.5 c
3–4	47.5 a	4.0 d	10.0 d	0.0 d

^a Means followed by different letters within the same column are significantly different (one-way ANOVA followed by Fisher's LSD *post-hoc* tests, $P \leq 0.05$). The means were generated from eight tests each using 10 insects.

females in capturing released males in the greenhouse, they attracted significantly more males to within 1 m of the trap ($F_{1,7} = 8.11$, $P < 0.05$) (Table 3). In the unbaited control traps, only 10% of the released males approached within 1 m and 47.5% remained 4 m from the trap. Furthermore, unbaited traps did not capture any male beetles. Traps baited with two vials of (3*R*)-ketol + 1-butanol attracted significantly higher numbers of males to within 1 m of the trap (55%) than were present at 2, 3 and 4 m (Fisher's LSD test, $P < 0.05$). Thirty-eight per cent of males were attracted to within 1 m distance by the trap baited with two vials of the monoterpene blend. Traps baited with two vials of (3*R*)-ketol + 1-butanol plus two vials of monoterpene blend proved to be the most attractive, and 85% of males were attracted to within 1 m of the release point with the remaining insects remaining at 2 or 3 m.

4 DISCUSSION

Our earlier study⁸ suggested that unmated male and female *H. bajulus* were strongly activated to run and fly in the wind tunnel by extracts of pine wood, larval frass and most of the synthetic monoterpenes that we have used in the current experiments. It is clear from the present study that ground traps baited with either the pine wood extract or the monoterpene mixture attracted higher numbers of females than unbaited traps, but captured very few insects. Evans and Higgs⁹ and Higgs and Evans⁴ reported that the oviposition behaviour in *H. bajulus* is mediated by *p*-cymen-8-ol, (-)-verbenone, myrtenol, (+)- α -terpineol, *trans*-pinocarveol, terpinen-4-ol, chrysanthonone, 3,6,6-trimethyl-cyclohepta-2,4-dienone and an unidentified alcohol that is present in the larval frass. However, these authors did not study the attraction of the beetles to the chemicals present in the frass of their larvae. Becker¹⁰ found that α -pinene acted as the strongest attractant and oviposition stimulant for mated females among 36 essential oil-derived terpenes extracted from coniferous trees. Although we did not use mated females in our study, we found that unmated females

were strongly attracted to the pine wood extract and the monoterpene mixture. Our findings concur with those of Borden,¹¹ Tilles *et al.*,¹² Vitè *et al.*¹³ and Phillips *et al.*¹⁴ who similarly reported that mixtures of monoterpenes could, in some cases, elicit greater catches of other Coleopteran beetles than other lures, such as pheromones.

The present study demonstrated that traps baited with a higher concentration of monoterpene mixtures are less attractive than traps baited at a lower dose, and caught no female beetles. In this respect, our findings are somewhat different from those of Becker¹⁰ who reported that lures containing 36 monoterpenes, including the compounds we have used in the present study, are not effective in capturing *H. bajulus* in their natural habitat. Higgs and Evans⁴ disproved the supposed inactive or repelling effect of terpenoid alcohols and ketones by demonstrating that oviposition in females was mediated by (–)-verbenone and *p*-cymene-8-ol. Discrepancies between studies may result from differences in lure concentration effects, because Becker¹⁰ used higher dosages of substances which, as we have shown, may be critical in their effectiveness as lures for this insect. Fettköther *et al.*⁸ suggested that the beetles might be attracted to lower release rates of monoterpenes than species attracted to stressed or decaying wood due to the fact that this beetle typically oviposits on intact wood, before the onset of decay.

Traps baited with either synthetic (3*R*)-ketol + 1-butanol, or (±)-3-ketol + 1-butanol combined with the monoterpene mixture captured 20–30% more females than traps baited with the sex pheromone or (±)-3-ketol or with the monoterpene mixture alone. Host plant volatiles can evoke a positive effect on the behaviour of insects responding to sex pheromones released in association with the host plant.¹⁵ The increase in attraction to synthetic pheromones when exposure was concurrent with host-plant odours has been reported for both bean and pea leaf weevils,¹⁶ the Mediterranean fruit fly and the smaller European elm bark beetle,¹⁷ the corn earworm and codling moth,^{18,19} Japanese beetle,²⁰ and diamondback moth²¹ and its natural enemies.²² As far as we know, there are only two reports concerning cerambycids that demonstrate a synergistic action of a synthetic sex pheromone combined with host volatiles. Nakamura *et al.*²³ reported that a combination of the synthetic sex pheromone of *Anaglyptus subfasciatus* Pic combined with a floral attractant, methyl phenylacetate, captured significantly more females than traps baited with the individual substances.²³ Similarly, Pajares *et al.*²⁴ observed *Monochamus galloprovincialis* (Olivier) beetles were more attracted to host blends (turpentine or α -pinene and ethanol) supplemented with bark beetle pheromones than to host volatiles alone.

We found that females were attracted to traps baited with the monoterpene mixture alone, but were not captured. That is, the beetles were strongly stimulated to run and fly when they sensed host volatiles, and

orientated upwind towards the baits. However, we believe that *H. bajulus* cannot locate the host in the absence of the pheromone. These results are in agreement with Nakamura *et al.*²³ who reported that traps baited with floral attractants attracted *A. subfasciatus* females, but did not capture them. They suggested that the addition of the male synthetic pheromone to the attractant might guide the beetles to the exact location. We have also observed in this study that the addition of male synthetic pheromone to the monoterpene mixture resulted in the highest numbers of females captured in the greenhouse.

It has been long argued for many insect species that host orientation and location do not exclusively rely upon olfaction of host volatiles.²⁵ Visual cues are likely to be important as insect approach the source of host volatiles, followed by contact reception.²⁶ It could be argued that the low capture rates obtained in the present study were due to the absence of visual cues that were not allowed for in the experimental design. It is, therefore, speculative to assume that host location is solely reliant on the presence of sex pheromones, as we have suggested. It is important, therefore, to recognize that the evidence presented here does not necessarily lead to the conclusion that the sex pheromone (which should perhaps be called an aggregation pheromone as it attracts both sexes) is an absolute requirement for host location. As with many other timber insects, it should not be surprising that a male that has found a suitable host subsequently produces an attractant to lure females and, inadvertently, other males. However, as both sexes appear to orientate to host volatiles (and it is unknown whether male pheromone production is switched on by external cues), it would be difficult to argue that host location is entirely random (as occurs, for example, with *Prostephanus truncatus* (Horn) (Coleoptera: Bostrichidae)).²⁷ Some house borer species may, therefore, locate suitable hosts without the presence of insect-produced compounds. This could be further verified by combining olfactory and visual cues within traps to assess their impact on long-range and short-range host-finding behaviours. This would ultimately help in the design of traps of appropriate colour, contrast and other physical characteristics.

The response of unmated male *H. bajulus* to their own pheromone was first reported by Fettköther *et al.*⁸ in wind-tunnel tests. These workers observed a slight activation and orientation towards the pheromone source, but with insignificant induction of courtship behaviour. In the present study, we observed that males were activated and attracted to traps baited with the sex pheromone, monoterpenes or a combination of both. However, they were not captured in significant numbers. The addition of male synthetic sex pheromone to the monoterpene mixture attracted significantly more male beetles than traps baited with the individual compounds. Furthermore, we observed that females responded more strongly than males to

traps baited with the sex pheromone, the monoterpene mixtures and a combination of both factors.

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REFERENCES

- Hanks LM, Influence of the larval host plant on reproductive strategies of cerambycid beetles. *Annu Rev Entomol* 44:483–505 (1999).
- Allison JD, Borden JH and Seybold SJ, A review of the chemical ecology of the Cerambycidae (Coleoptera). *Chemoecology* 14:123–150 (2004).
- Nerg A-M, Heijari J, Noldt U, Viitanen H, Vuorinen M, Kainulainen P and Holopainen JK, Significance of wood terpenoids in the resistance of Scots pine provenances against the old-house borer, *Hylotrupes bajulus*, and brown-rot fungus, *Coniophora puteana*. *J Chem Ecol* 30:125–141 (2004).
- Higgs MD and Evans DA, Chemical mediators in the oviposition behaviour of the house longhorn beetle, *Hylotrupes bajulus*. *Experientia* 34:46–47 (1978).
- Schröder F, Fettköther R, Noldt U, Dettner K, König WA and Francke W, Synthesis of (3R)-3-hydroxy-2-hexanone, (2R, 3R)-2, 3-hexanediol and (2S, 3R)-2,3-hexanediol, the male sex pheromone of *Hylotrupes bajulus* and *Pyrrhidium sanguineum* (Cerambycidae). *Liebigs Ann Chem* 12:1211–1218 (1994).
- Noldt U, Fettköther R and Dettner K, Structure of the sex pheromone-producing prothoracic glands of the male old-house borer, *Hylotrupes bajulus* (L) (Coleoptera: Cerambycidae). *Int J Insect Morphol Embryol* 24:223–234 (1995).
- Fettköther R, Dettner K, Schröder F, Meyer H, Francke W and Noldt U, The male pheromone of the old-house borer *Hylotrupes bajulus* (L) (Coleoptera: Cerambycidae): identification and female response. *Experientia* 51:270–277 (1995).
- Fettköther R, Reddy GVP, Noldt U and Dettner K, Effect of host and larval frass volatiles on behavioural response of the old-house borer *Hylotrupes bajulus* (L) (Coleoptera: Cerambycidae), in a wind tunnel bioassay. *Chemoecology* 10:1–10 (2000).
- Evans DA and Higgs MD, Mono-oxygenated monoterpenes from the frass of the wood-boring beetle *Hylotrupes bajulus* (L). *Tetrahedron Lett* 41:3585–3586 (1975).
- Becker G, Sinnesphysiologische Untersuchungen über die Eiablage des ausbockkäfers. *Z Vergl Physiol* 30:253–299 (1944).
- Borden JH, Aggregation pheromones, in *Comprehensive Insect Physiology, Biochemistry and Pharmacology*, ed by Kerkurt GA and Gilbert LI, Vol 9, Pergamon Press, Oxford, pp 257–285 (1985).
- Tilles DA, Sjodin K, Nordlander G and Eidman H, Synergism between ethanol and conifer host volatiles as attractant for the pine weevil, *Hyllobius abietis* (L) (Coleoptera: Curculionidae). *J Econ Entomol* 79:970–973 (1986).
- Vité JP, Volz HA and Paiva MR, Semio-chemicals in host selection and colonization of pine trees by the pine shoot beetle, *Tomicus piniperda*. *Naturwissenschaften* 73:39–40 (1986).
- Phillips TW, Wilkening AJ, Atkinson TH, Nation JL, Wilkinson RC and Foltz JL, Synergism of turpentine and ethanol as attractants for certain pine-infesting beetles (Coleoptera). *Environ Entomol* 17:456–462 (1988).
- Reddy GVP and Guerrero A, Interactions of insect pheromones and plant semiochemicals. *Trends Plant Sci* 9:253–261 (2004).
- Blight MM, Pickett JA, Smith MC and Wadhams LJ, An aggregation pheromone of *Sitona lineatus*. *Naturwissenschaften* 71:480 (1984).
- Dickens JC, Jang EB, Light DM and Alford AR, Enhancement of insect pheromone responses by green leaf volatiles. *Naturwissenschaften* 77:29–31 (1990).
- Light DM, Flath RA, Buttery RG, Alom FG, Rice RE, Dickens JC and Jang EB, Host-plant green volatiles synergize the synthetic sex pheromones of the corn earworm and codling moth (Lepidoptera). *Chemoecology* 4:145–152 (1993).
- Yang Z, Bengtsson M and Witzgall P, Host plant volatiles synergize response to sex pheromone in codling moth, *Cydia pomonella*. *J Chem Ecol* 30:619–629 (2004).
- Klein MG, Tumlinson JH, Ladd TL and Doolittle RE, Japanese beetle (Coleoptera: Scarabaeidae): Response to synthetic sex attractant plus phenethyl propionate: Eugenol. *J Chem Ecol* 7:1–7 (1981).
- Reddy GVP and Guerrero A, Behavioral responses of the diamondbackmoth, *Plutella xylostella*, to green leaf volatiles of *Brassica oleracea* subsp *capitata*. *J Agric Food Chem* 48:6025–6029 (2000).
- Reddy GVP, Holopainen JK and Guerrero A, Olfactory responses of *Plutella xylostella* natural enemies to host pheromone, larval frass, and cabbage green leaf volatiles. *J Chem Ecol* 28:131–143 (2002).
- Nakamura K, Leal WS, Nakashima T, Tokoro M, Ono M and Nakanishi M, Increase of trap catches by a combination of male sex pheromones and floral attractant in longhorn beetle, *Anaglyptus subfasciatus*. *J Chem Ecol* 23:1635–1640 (1997).
- Pajares JA, Ibeas F, Diez JJ and Gallego D, Attractive responses by *Monochamus galloprovincialis* (Col., Cerambycidae) to host and bark beetle semiochemicals. *J Appl Entomol* 128:633–638 (2004).
- Giurfa M and Menzel R, Insect visual perception: complex abilities of simple nervous systems. *Curr Opin Neurobiol* 7:505–513 (1997).
- Wehner R, Spatial vision in arthropods, in *Handbook of sensory physiology, Vol VII, 6C Vision in invertebrates*, ed by Autrum H, Springer-Verlag, New York (1981).
- Borgemeister C, Goergen G, Tchabi A, Awande S, Markham RH and Scholz D, Exploitation of a woody host plant and cerambycid-associated volatiles as host finding cues by the larger grain borer (Coleoptera: Bostrichidae). *Ann Entomol Soc Am* 91:741–747 (1988).