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REVIEW PAPER

The semiochemically mediated interactions between bacteria and insects

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Abstract In natural environment, semiochemicals are involved in many interactions between the different trophic levels involving insects, plants and hosts for parasitoids or prey for predators. These volatile compounds act as messengers within or between insect species, inducing particular behaviours, such as the localisation of a source of food, the orientation to an adequate oviposition site, the selection of a suitable breeding site and the localisation of hosts or prey. In this sense, bacteria have been shown to play an important role in the production of volatile compounds which ones act as semiochemicals. This review, focusing on the semiochemically mediated interactions between bacteria and insects, highlights that bacterial semiochemicals act as important messengers for insects. Indeed, in most of the studies reported here, insects respond to specific volatiles emitted by specific bacteria hosted by the insect itself (gut, mouthparts, etc.) or present in the natural environment where the insect evolves. Particularly, bacteria from the families Enterobacteriaceae, Pseudomonaceae and Bacillaceae are involved in many interactions with insects. Because semiochemicals naturally produced by bacteria could be a very interesting option for pest management, advances in this field are discussed in the context of biological control against insect pests.

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Introduction

Bacteria are a large group of single-celled prokaryote microorganisms and are ubiquitous in every habitat on Earth, growing in soil, water as well as in organic matter, plants and animals. There are approximately five nonillion (5.10^{30}) bacteria on Earth, forming much of the world's biomass (Whitman et al. 1998; Fredrickson et al. 2004). For these reasons and like other organisms, insects are continuously in contact with an extremely large variety of bacteria found both in their natural environments as well as in their diets. Different types of interaction can be distinguished between insects and bacteria: the symbiotic, the pathogenic and the semiochemically mediated interactions, these later being in some cases part of the symbiotic relationship. There is an increasing body of examples for symbiotic interactions between insects and bacteria with the associated microorganisms providing nutrients or defensive compounds for their hosts (e.g. Oliver et al. 2003, 2005, 2008, 2010; Scarborough et al. 2005; Douglas 2006; Nakabachi et al. 2006; Thao and Baumann 2004; Baumann et al. 2002; Kaltenpoth 2009; Schoenian et al. 2011; Oh et al. 2009a, b, 2011; Brachmann et al. 2006; Piel et al. 2004; Barke et al. 2010; Haeder et al. 2009; Scott et al. 2008; Leroy et al. 2011; Sabri et al. 2010) and several examples illustrate pathogenic interactions (e.g. Grenier et al. 2006; Harada and Ishikawa 1997; Ffrench-Constant et al. 2007; Herbert and Goodrich-Blair 2007; Harada et al. 1997; Lecadet et al. 1999; Schnepf et al. 1998; de Maagd et al. 2003) while the semiochemically mediated interactions are more rarely described. However, plenty of bacteria have been

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shown to play an important role in the production of volatile compounds which ones may act as semiochemicals. Semiochemicals act as messengers within or between species. These volatile compounds encompass pheromones, allomones, kairomones, attractants and repellents (Nordlund and Lewis 1976). Pheromones are intraspecific signals that aid in finding mates, food and habitat resources, warning of enemies, and avoiding competition (Noorman 2001). Interspecific signals known as allomones and kairomones have similar functions, but the first ones are beneficial to the emitters while the second ones are beneficial to the receptors (Arnaud et al. 2003). Semiochemicals are used in pest management to monitor pest populations and to alter the behaviours of the pest or the behaviours of natural enemies of the pest (Riba and Silvy 1989). In general, the advantages of using semiochemicals in pest control are that they have adverse effects only on target pests, that they are relatively nontoxic and required in low amounts, that they are non-persistent and environmentally safe and that they appear difficult for insects to develop resistance against (Riba and Silvy 1989). Volatile organic molecules acting as semiochemicals are notably formed by the modification of products like fatty acids, aromatic amino acids (L-phenylalanine, L-tyrosine and L-tryptophan) or carbohydrates (shikimate pathway) by bacteria (Schulz and Dickschat 2007). These authors have recorded more than 300 volatile compounds from various bacteria amongst which 75 fatty acid derivatives, 50 aromatic compounds, 74 nitrogen-containing compounds, 30 sulphur compounds, 96 terpenoids and 18 halogenated compounds.

The aim of this review is to provide an inventory of the semiochemically mediated interactions between insects and bacteria. This review also aims to highlight the key roles of bacterial semiochemicals in multitrophic interactions, showing that these volatile compounds mediate the interactions between insects and their other associated trophic levels. Advances in this field are discussed in the context of biological control against insect pests.

The semiochemically mediated interactions between insects and bacteria

Only some studies have focused on the relations between bacterial semiochemicals and insects from the orders of Diptera (Tephritidae, Culicidae and Muscidae), Hymenoptera, Coleoptera and Orthoptera.

Diptera

Tephritidae

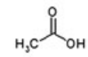
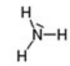
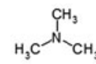
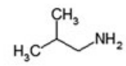
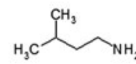
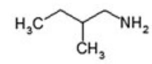
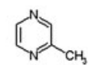
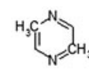
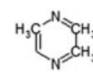
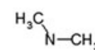
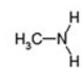
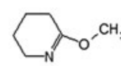
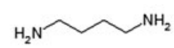
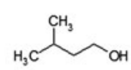
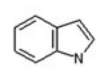
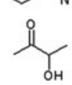
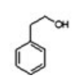
Anastrepha ludens (Diptera: Tephritidae), a serious pest of fruit cultures (Martinez et al. 1994), was shown to be strongly attracted by many bacteria derived chemical cues (Tables 1, 2). Robacker et al. have identified several bacterial volatiles affecting the behaviours of *A. ludens*. For example, low-molecular weight amines produced by a *Staphylococcus* bacterium (RGM-1) in tryptic soy culture were shown to attract protein-hungry adult *A. ludens* under laboratory conditions (Robacker et al. 1993). In the same way, volatiles from tryptic soy broth cultures of *Staphylococcus aureus* were identified and determined as attractants for *A. ludens*, the most effective chemical being dimethylamine (Robacker and Flath 1995; Robacker and Moreno 1995). Robacker et al. (1997) also identified volatiles from tryptic soy broth culture filtrates of *Klebsiella pneumoniae* and *Citrobacter freundii* isolated from the *A. ludens* alimentary tract. Ammonia, methylamine, 3-methylbutanamine, 1-pyrroline, 2,3,4,5-tetrahydropyridine and several pyrazines were identified as attractants to the fruit flies. In another study, Robacker et al. (1998) tested filtrates of 11 bacteria that produced attractive volatiles identified as ammonia, aliphatic amines, pyrazines, imines and acetic acid. Two strains of *Enterobacter agglomerans* were also investigated for attractiveness to sugar-fed fruit flies demonstrating that 3-hydroxy-2-butanone, 2-phenylethanol, ammonia, indole and trimethylpyrazine were attractive (Robacker and Lauzon 2002; Robacker et al. 2004).

Martinez et al. (1994) isolated several bacteria (*Citrobacter freundii*, *Klebsiella pneumoniae*, *Erwinia herbicola*, etc.) from the Mexican fruit fly *A. ludens* alimentary tract and mouthparts and demonstrated that they all attracted this species. Also, these authors reported that two strains of *Bacillus thuringiensis* (subsp. finitimus and subsp. kurstaki) were attractive to *A. ludens* and demonstrated, in field studies, that metabolites from bacterial fermentation of *Citrobacter freundii* and *Klebsiella pneumoniae* captured many *A. ludens* adults.

Lee et al. (1995) analysed the volatile components of the *Klebsiella pneumoniae* bacterial fermentation of a trypticase soy broth that was attractive to *A. ludens* and identified a total of 21 compounds including alcohols, pyrazines, ketones, acids and phenols, the most abundant being 3-methyl-1-butanol, 2-phenylethanol, 2,5-dimethylpyrazine, 2-methyl-1-propanol and 3-(methylthio)-1-propanol. In the same way, DeMilo et al. (1996) identified 22 volatile compounds derived from *Citrobacter freundii* fermentation of a trypticase soy broth. The most abundant volatiles were 3-methyl-1-butanol, phenol, 2,5-dimethylpyrazine, 2-phenylethanol and 2-methyl-1-propanol and were shown to attract *A. ludens*.

The Caribbean fruit fly *Anastrepha suspensa* (Diptera: Tephritidae), another pest of fruit cultures, is also known to be attracted by microbial volatiles from *Enterobacter agglomerans* and other Enterobacteriaceae isolated and

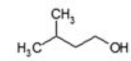
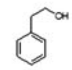
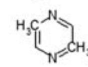
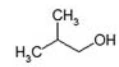
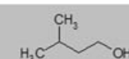
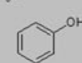
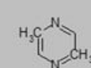
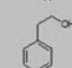
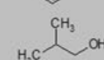
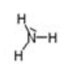
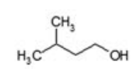
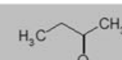
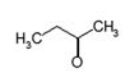
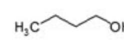
Table 1 Semiochemically mediated interactions between bacteria and Diptera (Tephritidae) (part 1)

Bacteria	Bacterial family	Bacteria origins	Insects	Effects	Active semiochemicals	Structural formula	References
Staphylococcus (RGM-1) *Staphylococcus aureus* *Klebsiella pneumoniae* *Citrobacter freundii* *Enterobacter agglomerans*	Micrococcaceae Micrococcaceae Enterobacteriaceae Enterobacteriaceae Enterobacteriaceae	mouthparts	*Anastrepha ludens*	attraction	acetic acid		Robacker et al (1991) Robacker et al (1993) Robacker and Garcia (1993) Robacker and Flat (1995) Robacker and Moreno (1995) Robacker and Barlet (1997) Robacker et al (1997) Robacker et al (1998) Robacker and Lauzon (2002) Robacker et al (2004)
					ammonia		
					trimethylamine		
					2-methylpropylamine		
					3-methylbutanamine		
					2-methylbutanamine		
					methylpyrazine		
					2,5-dimethylpyrazine		
					trimethylpyrazine		
					dimethylamine		
					methylamine		
					1-pyrroline		
					2,3,4,5-tetrahydropyridine		
					putrescine		
					3-methyl-1-butanol		
					indole		
					3-hydroxy-2-butanone		
					2-phenylethanol		

identified from the insect surfaces and from fruits attacked by larvae (Table 2). Epsky et al. (1998) demonstrated that volatile chemicals emitted from *Enterobacter agglomerans*, a bacterium that has been isolated from adults as well as from fruits infested with larvae, were attractive to females of *A. suspensa* in laboratory bioassays. 3-methyl-1-butanol and ammonia were identified as the two primary volatile chemicals released from cultures of *E. agglomerans*. The combination of 3-methyl-1-butanol and ammonia was more attractive than ammonia alone.

In a study of Jang and Nishijima (1990), bacteria isolated from the crop and stomach of laboratory-reared and wild oriental fruit flies, *Dacus dorsalis*, were identified and positively tested as attractants to this species in a laboratory olfactometer. These bacteria were identified to belong to the family Enterobacteriaceae (*Enterobacter cloacae*,

Table 2 Semiochemically mediated interactions between bacteria and Diptera (Tephritidae) (part 2)

Bacteria	Bacterial family	Bacteria origins	Insects	Effects	Active semiochemicals	Structural formula	References
Bacillus thuringiensis *Citrobacter freundii* *Klebsiella pneumoniae* *Erwinia herbicola* …	Bacillaceae Enterobacteriaceae Enterobacteriaceae Enterobacteriaceae	alimentary tracts	*Anastrepha ludens*	attraction	not identified		Matinez et al (1994)
Klebsiella pneumoniae	Enterobacteriaceae	bacteria strain (fermentation)	*Anastrepha ludens*	attraction	3-methyl-1-butanol 2-phenylethanol 2,5-dimethylpyrazine 2-methyl-1-propanol 3-(methylthio)-1-propanol	    	Lee et al (1995)
Citrobacter freundii	Enterobacteriaceae	bacteria strain (fermentation)	*Anastrepha ludens*	attraction	3-methyl-1-butanol phenol 2,5-dimethylpyrazine 2-phenylethanol 2-methyl-1-propanol	    	DeMilo et al (1996)
Enterobacter agglomerans	Enterobacteriaceae	insects surfaces fruits with pest larvae	*Anastrepha suspensa*	attraction	ammonia 3-methyl-1-butanol	 	Epsky et al (1998)
Plant surfaces bacteria (not identified)		on the host plant	*Dactrocera tryoni* *Dactrocera cacuminatus*	attraction	butanone 1-butanol	 	Drew (1987)
Proteus species bacteria		bacteria strain	*Dactrocera tryoni*	attraction	butanone 1-butanol	 	Drew and Fay (1988)
Enterobacter agglomerans	Enterobacteriaceae	leaves and fruit surfaces	*Rhagoletis pomonella*	attraction	not identified		Lauzon et al (1998)
Citrobacter freundii *Klebsiella pneumoniae* *Enterobacter cloacae*	Enterobacteriaceae Enterobacteriaceae Enterobacteriaceae	in crops alimentary tracts (stomach)	*Dacus dorsalis*	attraction	not identified		Jang and Nishijima (1990)
Enterobacter agglomerans	Enterobacteriaceae	apple foliages	*Rhagoletis pomonella*	attraction	not identified		McCollum et al (1992)

E. agglomerans, *Klebsiella oxytoca* and *Citrobacter freundii*). Lauzon et al. (1998) and MacCollum et al. (1992) isolated bacteria from leaves and fruits and tested these microorganisms as attractants to apple maggot flies, *Rhagoletis pomonella*, showing a distinct preference for odours emitted by certain members of the Enterobacteriaceae.

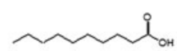
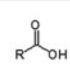
Bacteria isolated from leaves (host plants), fruit surfaces, but also from the alimentary tract (*Enterobacter agglomerans*, *Klebsiella pneumoniae*, *Citrobacter freundii*), were also shown to produce active semiochemicals (amongst which butanone and 1-butanol) attracting the Tephritidae *Dactrocera tryoni* and *Dactrocera cacuminatus* (Drew 1987; Drew and Fay 1988). These authors proposed that butanone is an important stimulant for these species in nature, bringing mature male flies into the feeding sites of the developing females for mating encounters.

In all these studies, the majority of identified bacteria are advantageous to the Tephritidae since these microorganisms produce attractive semiochemicals helping the fruit flies to locate a source of food. Indeed, these bacteria producing volatiles were mainly isolated from fruits and host plant leaves. Bacteria isolated from the alimentary tract and/or from the mouthparts may be partially acquired during probing on the host leaf surfaces or during feeding.

Culicidae

The dipteran Culicidae (*Culex quinquefasciatus*, *Culex restuans*, *Culex pipiens*, *Aedes aegypti*, *Aedes albopictus*, *Anopheles gambiae*) is the second most important insect family showed to be affected by semiochemicals produced by bacteria (Table 3). Trexler et al. (2003) evaluated the

Table 3 Semiochemically mediated interactions between bacteria and Diptera (Culicidae)

Bacteria	Bacterial family	Bacteria origins	Insects	Effects	Active semiochemicals	Structural formula	References
Psychrobacter immobilis *Sphingobacterium multivorum* undetermined *Bacillus* species	Neisseriaceae Sphingobacteriaceae Bacillaceae	water soil	*Aedes albopictus*	attraction oviposition	not identified		Trexel et al (2003)
Enterobacter agglomerans *Pseudomonas maltophilia* *Bacillus cereus*	Enterobacteriaceae Xanthomonadaceae Bacillaceae	not specified	*Culex quinquefasciatus*	oviposition	not identified		Rockett (1987)
Pseudomonaceae	Pseudomonaceae	not specified	*Culex restuans*	attraction	decanoic acid		Maw (1970)
Pseudomonas aeruginosa	Pseudomonadaceae	fatty acid substrates	*Aedes aegypti* *Culex pipiens*	attraction oviposition	decanoic acid		Ikeshoji et al (1975)
Bacillus cereus	Bacillaceae	from the environment	*Aedes aegypti*	attraction oviposition	not identified		Hasselschwert and Rockett (1988)
Environmental bacteria (not identified)		from the environment	*Aedes aegypti* *Aedes albopictus*	attraction oviposition	not identified		Pavlovich and Rockett (2000)
Pseudomonas strains	Pseudomonaceae	soil and water substrates	*Anopheles gambiae*	repellent	not identified		Huang et al (2006)
Bacillus cereus *Pseudomonas fluorescens* *Bacillus thuringiensis*	Bacillaceae Pseudomonaceae Bacillaceae	detritus from the environment	*Culex quinquefascitus*	attraction oviposition	not identified		Poonam et al (2002)
Bacillus sp. *Enterobacter sp.* *Klebsiella sp.* *Pseudomonas sp.*	Bacillaceae Enterobacteriaceae Enterobacteriaceae Pseudomonaceae	water larval habitat	*Aedes aegypti*	oviposition	carboxylic acid		Ponnusamy et al (2008)

responses of *Aedes albopictus* to sources of oviposition attractants and stimulants on gravid mosquitoes attracted to volatiles from larval-rearing water and soil-contaminated cotton towels. Bacteria were isolated from these substrates and from organic infusion made with oak leaves. Water containing *Psychrobacter immobilis* (from larval-rearing water), *Sphingobacterium multivorum* (from soil-contaminated cotton towels), and an undetermined *Bacillus* species (from oak leaf infusion) elicited significantly higher attraction and oviposition than control water without bacteria. In the same way, Pavlovich and Rockett (2000) and Hasselschwert and Rockett (1988) determined that the presence of bacteria (Bacillaceae) elicited the attraction and the oviposition for *Aedes aegypti* and *Aedes albopictus*. According to these authors, even if they did not identify the active semiochemicals, the bacterial content of the breeding water was the most important factor in oviposition site selection.

Rockett (1987) screened a variety of bacterial strains against gravid *Culex quinquefasciatus* and noted that more eggs were laid in water containing *Enterobacter agglomerans*, *Pseudomonas maltophilia* or *Bacillus cereus* than in water without bacteria (control).

Poonam et al. (2002) tested culture filtrates of several bacterial species for their attractive properties against gravid females of *Culex quinquefasciatus* and showed that the culture filtrates of *Bacillus* cereus, *Bacillus thuringiensis* and *Pseudomonas fluorescens* exhibited oviposition stimulation. In binary choice assays, Ponnusamy et al. (2008) demonstrated that microorganisms in leaf infusions produced oviposition-stimulating kairomones, but also that bacteria-associated carboxylic acids and methyl esters serve as potent oviposition stimulants for gravid *Aedes aegypti*. In contrast, the results obtained by Huang et al. (2006) suggested that some bacterial odours may be repellent for *Anopheles gambiae* since a mixture of cultured bacteria (*Pseudomonas* strains) originating from the natural larval habitat (soil and water surfaces) significantly reduced the oviposition.

Maw (1970) reported that bacteria of the family Pseudomonaceae produced decanoic acid and rendered rearing water attractive to *Culex restuans*. Based on this study, Ikeshoji et al. (1975) reported that *Pseudomonas aeruginosa* produced an oviposition attractant/stimulant for *Aedes aegypti* and *Culex pipiens*. This oviposition attractant/stimulant was also identified as decanoic acid.

Since bacteria affecting the Culicidae behaviours were isolated from water, soil or environmental detritus, they can be considered as advantageous for the mosquitoes, guiding these later to an adequate oviposition site and so ensuring an adequate breeding site.

Muscidae

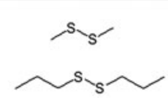
The muscid fly *Musca domestica* was shown to be attracted by alkyl disulphides produced by the bacterium *Klebsiella oxytoca* isolated from eggs and insect surfaces (Lam et al. 2007) (Table 4). This study showed that cues from *Klebsiella oxytoca*, which originates with female *M. domestica* and which proliferates over time on the surface of deposited eggs, first attracted the flies before to inhibit the oviposition at a threshold density. By deploying such evolving cues, females can visit an oviposition site just once and deposit cues that will mediate immediate oviposition induction followed by delayed inhibition, thereby insuring optimal conditions for offspring development.

Romero et al. (2006) isolated and identified nine bacteria from the natural *Stomoxys calcitrans* oviposition/development habitat and evaluated their effects on the stable fly oviposition and on the larval development. Of the nine bacterial strains, *Citrobacter freundii* stimulated oviposition to the greatest extent (similar to that of the natural larval substrate) and also sustained stable fly development (Table 4). These authors also suggested that stable fly development depends on a live microbial community in the natural habitat and that fly females are capable of selecting an oviposition site based on the microbially derived stimuli that indicate the suitability of the substrate for larval development.

Hymenoptera

Thibout et al. (1993, 1995) have identified sulphur containing volatiles such as alkyl disulphides (dimethyl

Table 4 Semiochemically mediated interactions between bacteria and Diptera (Muscidae)

Bacteria	Bacterial family	Bacteria origins	Insects	Effects	Active semiochemicals	Structural formula	References
Klebsiella oxytoca	Enterobacteriaceae	eggs and insect surfaces	*Musca domestica*	oviposition	alkyl disulphides		Lam et al (2007)
Citrobacter freundii	Enterobacteriaceae	larval habitat	*Stomoxys calcitrans*	oviposition development	not identified		Romero et al (2006)

disulphide and dipropyl disulphide) from bacteria (*Bacillus* sp. and *Klebsiella oxytoca*) which attract and help the parasitoid *Diadromus pulchellus* (Hymenoptera: Ichneumonidae) to locate its hosts *Acrolepiopsis assectella* (Table 5). These authors showed that the locomotry activity of this parasitoid is strongly influenced by the dialkyl disulphides emitted by the larval frass of *A. assectella* containing bacteria at the origin of the sulphur volatiles. Locating hosts through specific bacterial volatiles from the larval host frass enhances the efficiency of this parasitoid which spends less energy looking for hosts.

Coleoptera

The Pineapple beetle *Carpophilus humeralis*, damaging a wide variety of agricultural products, was shown to be attracted by the semiochemicals 4-ethyl-2-methoxyphenol, 2,5-diisopropylpyrazine and 2-phenylethanol (Zilkowski et al. 1999) (Table 6). Furthermore, these authors depicted the mass spectra of two unidentified compounds. These compounds were later identified by Dickschat et al. (2005) as 3-methoxy-2-(1-methylpropyl)-5-(2-methylpropyl)pyrazine and 3-methoxy-2,5-*bis*(1-methylpropyl)pyrazine by chemical synthesis. These volatiles were determined to be produced by bacteria present on the host fruits (pineapples) and were tested in field trials showing that these odours drastically increased trap catches for this species. Semiochemicals emitted from these bacteria (growing on fruit surfaces) are advantageous for the Pineapple beetle to locate a source of food, but their attractiveness could play an important role in developing traps for the control of this pest.

Orthoptera

Nolte et al. (1973) suggested that bacteria from the *Locusta migratoria* (Orthoptera: Acrididae) digestive tract convert lignin to locustol (5-ethylguaiacol), an aggregative pheromone. More recently, Dillon et al. (2000) demonstrated a bacterial origin for the phenolic compounds guaiacol and phenol, two components of the locust *Schistocerca gregaria* aggregation pheromone. They demonstrated that guaiacol, a key component of a pheromone derived from locust faecal pellets that promotes the aggregation, was produced by the bacterium *Pantoea agglomerans* in the locust gut. These authors showed that locusts have adapted to use a pheromonal component that is derived from its digestive waste products by the action of bacteria acquired with its food. Dillon and Charnley (2002) also determined that the same species *S. gregaria* contains an abundant gut microflora (*Pantoea agglomerans*, *Klebsiella pneumoniae*, *Enterobacter cloacae*,…) which originated from the insect's diet and that microbial metabolism produced phenolics. These compounds were determined to be useful for the locust host since some products are antimicrobial and contribute to host defense against pathogens while others are employed by the host as components of the aggregation pheromone (Table 7).

Table 5 Semiochemically mediated interactions between bacteria and Hymenoptera

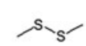
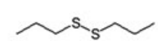
Bacteria	Bacterial family	Bacteria origins	Insects	Effects	Active semiochemicals	Structural formula	References
Klebsiella oxytoca *Bacillus sp.*	Enterobacteriaceae Bacillaceae	gut of host larvae larval host frass	*Diadromus pulchellus*	attraction host finding	dimethyl disulphide		Thibout et al (1995)
					dipropyl disulphide		

Table 6 Semiochemically mediated interactions between bacteria and Coleoptera

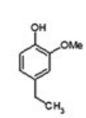
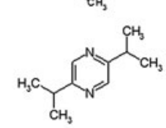
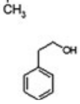
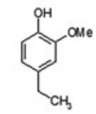
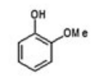
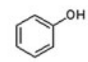
Bacteria	Bacterial family	Bacteria origins	Insects	Effects	Active semiochemicals	Structural formula	References
Fruit surfaces bacteria (not identified)		fruit surfaces	*Carpophilus humeralis*	attraction	4-ethyl-2-methoxyphenol		Zilkowski et al (1999)
					2,5-diisopropylpyrazine		
					2-phenylethanol		

Table 7 Semiochemically mediated interactions between bacteria and Orthoptera

Bacteria	Bacterial family	Bacteria origins	Insects	Effects	Active semiochemicals	Structural formula	References
Pantoea agglomerans *Klebsiella pneumoniae* *Enterobacter cloacae*	Enterobacteriaceae Enterobacteriaceae Enterobacteriaceae	insect gut	*Locusta migratoria*	aggregative pheromone defense	5-ethylguaiacol		Nolte et al (1973) Dillon et al (2000) Dillon and Charnley (2002)
					guaiacol		
					phenol		

The potential use of bacterial semiochemicals in biological control against insect pests

This review, focusing on the semiochemically mediated interactions between bacteria and insects, highlights that bacterial semiochemicals act as important messengers for insects. Indeed, in most of the studies reported here, insects respond to specific volatiles emitted by specific bacteria hosted by the insect itself (gut, mouthparts, etc.) or present in the natural environment where the insect evolves. Particularly, bacteria from the families Enterobacteriaceae, Pseudomonaceae and Bacillaceae were shown to be involved in the interactions with insects by producing semiochemicals. Indeed, insects select sites with particular microorganisms for example for oviposition: in an advantageous way, females of different insect orders are capable of rapidly selecting an oviposition site based on the microbially derived stimuli that indicate the suitability of the substrate for larval development.

Many members of these bacterial families are a normal part of the gut flora found in the intestines of animals, while others are found in water or soil (Schulz and Dickschat 2007). In all cases, bacterial volatiles induce particular behaviours: localisation of a source of food, orientation to and selection of an adequate oviposition site, selection of a suitable breeding site, oviposition regulation (induction or inhibition) according to the relative occurrence of semiochemicals released by bacteria, orientation of males to encounter females into the feeding sites, localisation of hosts or prey and aggregation of individuals in response to specific bacterial volatiles. This strongly suggests that insects can evolve the ability to associate the presence of bacterial volatiles produce by bacteria with different behaviours and such studies certainly lead to a better understanding of the role of bacteria in the ecology of insects but a lack in this field is certainly that only few assays have been performed under natural conditions to evaluate the effects of the bacterial volatiles, separately or in mixtures. Indeed, only few field trials were conducted (Martinez et al. 1994; Drew 1987; Drew and Fay 1988; Zilkowski et al. 1999) to really assess the efficacy of bacterial volatiles for a biological control against insect pests in field crops or orchards.

To our knowledge, trapping systems do not use bacteria as a source of volatiles to attract insect pests even if these microorganisms present a high potential for the production of semiochemicals that could be used in pest management. Degradation and/or modifications of sugars and amino acids by bacteria but also volatiles own biosynthetic pathways based on precursors of the primary metabolism could explain the volatile compounds identified in the studies reported here: for example, the volatiles 3-methyl-1-butanol and 2-methyl-1-propanol are known to be produced by bacteria modifying the amino acid derived starter units while acetic acid, ammonia, butanone, 3-hydroxy-2-butanone, 2-phenylethanol and amines are typical bacterial fermentation-associated substances (Schulz and Dickschat 2007). The mass production of bacteria at a low cost could be envisaged to use these microorganisms as a source of semiochemicals to attract and trap insects in field crops. Another option could be based on the use of bacterial semiochemicals to enhance the presence of auxiliaries in crops to protect: semiochemicals emitted by specific bacteria associated with the insect pests can, for example, increase the effectiveness of parasitoids and predators (Thibout et al. 1993).

The production of chemical attractants by bacteria certainly provides means for detecting and monitoring pests: attractants produced by bacteria could be helpful to trap pests but also to attract beneficial insects. Faced with the challenge to reduce drastically the use of chemical compounds and even banning the use of certain insecticides, biological control against pests using semiochemicals naturally produced by bacteria could be a very interesting option.

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