CHAPTER

10

Applied Chemical Ecology to Enhance Insect Parasitoid Efficacy in the Biological Control of Crop Pests

Ezio Peri[1]*, Rihem Moujahed[1], Eric Wajnberg[2] and Stefano Colazza[1]

[1] Dipartimento di Scienze Agrarie, Alimentari e Forestali, Università degli Studi di Palermo, Viale delle Scienze, 90128 Palermo, Italy
E-mail: ezio.peri@unipa.it (EP)
E-mail: rihem.moujahed@unipa.it (RM)
E-mail: stefano.colazza@unipa.it (SC)
[2] INRIA, Projet Hephaistos, 2004 Route des Lucioles, BP 93, 06902 Sophia Antipolis Cedex, France
E-mail: eric.wajnberg@inra.fr

Abstract

The field application of semiochemicals, used by parasitoids to find mates and to locate their hosts, is a promising environmentally sustainable and highly specific pest control strategy and an attractive alternative to the use of pesticides. In this chapter, we first examine research progress dealing with the effect of semiochemical cues on parasitoid foraging strategy. In the second part, we review the possible field applications of these chemical cues to enhance pest control strategies, either through direct pest control or by manipulating parasitoid behaviour. We then consider novel approaches, such as the "attract and reward" strategy, combining semiochemical application and habitat management to improve the success of pest management. Even if semiochemical-based tactics are promising in pest control, they still are developing and may face several constraints leading to different challenges. Therefore, in the last part of this chapter, we draw attention to the potential

---

*Corresponding author

limitations and risks of semiochemical applications in the field. Then, we propose potential solutions to overcome these different constraints.

1. Introduction

In recent years, scientists, farmers and citizens have been seeking more sustainable agricultural systems that can combine the production of healthy crops along with the greatest possible protection of the agro-ecosystems. One possible approach is the use of a combination of strategies, such as resistant plants, biological control of pests, habitat manipulation, or modification of cultural practices that allow synergy with the long-term prevention of pests and a reduction in risks to human health and the environment. In this view, the use of semiochemicals appears to be an ecologically sustainable strategy that can reduce the use of pesticides. As a consequence, many studies have been conducted to identify, synthesise and produce semiochemical compounds and to investigate their possible use. Some of these have now been commercialised and become tools in Integrated Pest Management (IPM) strategies (Suckling and Karg 2000, Witzgall et al. 2010).

Semiochemical-based manipulation strategies include either "pheromone-based tactics" or "allelochemical-based tactics". The former are well known and represent successful strategies in IPM programs, mainly in orchards, for both direct and indirect control of pests. In contrast, allelochemical-based tactics represent a relatively new approach and few successful applications have been reported thus far.

In recent years, many researchers have investigated the chemical ecology of parasitoids and predators in order to understand the chemical cues that mediate their host location process. Several studies have demonstrated that the use of semiochemicals can modify the behaviour of insect natural enemies, opening new perspectives in using semiochemicals to conserve and/or improve the efficiency of natural enemies in crop systems (Pickett et al. 1997, Khan et al. 2008). However, despite the several researches conducted, mainly under laboratory conditions, to elucidate the interactions between semiochemicals and natural enemies in multitrophic contexts, the application of semiochemicals in the field is still limited (Blassioli-Moares et al. 2013, Colazza et al. 2013, Kaiser et al. 2016).

In this chapter, we review important advances in research concerning chemical compounds that mediate relationships between parasitoids and their host-plant complex and the possible field applications of these compounds for improving pest control efficiency. We first address basic aspects of parasitoid chemical ecology, focusing on the main chemical cues exploited by wasps during both intra-specific and inter-specific relationships leading them to find a mate or hosts. Then, we review studies on chemical compounds that can be applied in the field to improve insect pest control, addressing both "pheromone-based" tactics and "allelochemical-based" tactics as well as other strategies used to manipulate parasitoid behaviour in order to conserve or augment pest control efficiency. Finally, we highlight the limitations and provide our perspective on the application of these chemical compounds in cropping systems to improve parasitoid efficiency in biological control of insect pests.

2. Semiochemicals and their Effect on Parasitoids: How to Cope with a Complex World

As soon as they emerge in a new environment, adult parasitoid females have to face many challenges in order to search for and find a mate and hosts, which are usually both small and inconspicuous, to produce progeny (Godfray 1994). Female parasitoids live in environments that are highly complex (Ode 2013, Wäschke et al. 2013), in which they are continuously flooded with information involving simultaneously visual, auditory, physical, gustative and olfactory cues and only a small part of these are relevant stimuli to find a mate and then hosts (Vet and Dicke 1992). In the course of evolution and thanks to important evolutionary constraints, females of parasitoid species have progressively developed remarkable and sharp capabilities to recognise, from long and/or short distance, reliable and detectable information about where they are, where potential mates and hosts are and even sometimes, where other competing conspecific or heterospecific females are (Hilker and McNeil 2008). Even if such capabilities are necessarily associated with several morphologic, metabolic and physiologic costs, females are constrained to do so in order to produce progeny. For this, they develop a rich arsenal of different types of receptors (Quicke 1997), leading them to discriminate, at each step of their foraging process, what information to take into account versus stimuli that are not relevant. Several decades of work have led to an understanding that, among all stimuli that can be perceived by parasitic wasp females in their foraging environments, olfactory cues play the most important role (Bernal and Luck 2007). Semiochemicals are chemical cues involved in interactions between two organisms. They are classified into two broad groups, pheromones and allelochemicals. Pheromones mediate interactions between organisms of the same species and are subdivided according to their function, such as sex pheromones, alarm pheromones, aggregation pheromones or host marking pheromones. Allelochemicals, on the other hand, mediate interactions between organisms belonging to different species. They are classified into different categories depending on whether the benefit is for the emitter or the receiver: allomones are favourable to the organism that emits the substance; synomones are favourable to both the emitter and the receiver; and kairomones are favourable to the receiver only.

All these terms are context-specific rather than chemical-specific. For example, the sex pheromone emitted by *Sesamia nonagrioides* (Lepidoptera: Noctuidae) acts as a kairomone for adult females of the egg parasitoid *Telenomus busseolae* (Hymenoptera: Scelionidae), which exploits this cue in their host location process (Colazza et al. 1997). The following paragraphs describe the importance of pheromones, synomones and kairomones in the ability of parasitoid females to locate and attack their hosts. The corresponding sections below will describe, for each of these two types of compounds, the use of long- and short-range semiochemicals cues used by parasitoid females in their foraging behaviour.

2.1 Parasitoid Pheromones

In the last fifteen years, several studies have highlighted pheromonal communication in insect parasitoids, mainly belonging to the Hymenoptera. The identified compounds were classified into four groups (Ruther 2013): (1) sex pheromones that can be released by either sex and are involved in three levels of sexual communication, i.e., attraction to the site of release (emitter individual), mate recognition and elicitation of female receptiveness (i.e., aphrodisiac pheromones released by males); (2) marking pheromones that are released by females, e.g., to avoid superparasitism and competition among larvae inside the host, or to optimise clutch size and offspring sex ratio; (3) putative alarm pheromones identified in some bethylid wasp species and (4) aggregation and anti-aggregation pheromones. Although pheromones have been characterised in parasitoids from numerous families, information about the chemistry involved is still scarce (Li 2006, Ruther 2013). For example, a number of studies demonstrated that Dufour's gland is a source of marking pheromone in some parasitoid species (e.g., Guillot and Vinson 1972, Jaloux et al. 2005). Chemical compounds in this gland often match the cuticular hydrocarbon profiles in the parasitoid species studied, suggesting that these cuticular hydrocarbon compounds play a role (Jaloux et al. 2005).

2.2 Synomones

Upon herbivore attack, plants emit complex mixtures of organic compounds, called synomones that recruit natural enemies of the attacking herbivores. From the plant side, these are an indirect defense mechanism (e.g., "cry for help", see Dicke and Baldwin 2010), induced either by the feeding activities of insect herbivores, i.e., herbivore-induced plant volatiles (HIPVs) and/or by their egg-laying behaviour, i.e., oviposition-induced plant volatiles (OIPVs) (Kessler and Heil 2011, Hilker and Fatouros 2015). Depending on the attacking herbivore species, OIPVs can occur with or without plant wounding caused by females during oviposition (Hilker and Fatouros 2015). Interestingly, plants under insect herbivore attack not only emit volatile defensive compounds to attract parasitoid females, but doing so, they can inform other non-attacked plants. Indeed, volatile cues emitted by plants damaged by herbivores have been showed to be selectively detected by healthy plants that are then induced to also release defensive compounds (Guerrieri 2016, Pickett and Khan 2016).

The emission of HIPVs and OIPVs, which are perceived by parasitoids at long distance (i.e., long-range cues) is a widespread ecological phenomenon that has been recorded for at least 49 plant species belonging to 25 different families (Mumm and Dicke 2010, Meiners and Peri 2013, Hilker and Fatouros 2015, Fatouros et al. 2016). However, parasitoids can also perceive synomones after landing on the host plant (i.e., contact or short-range cues). Some recent studies showed that some plants, such as maize and brassicaceous plants, when they are attacked by insect pests, emit substrate-borne chemical cues (i.e., alteration of leaf chemistry composition), which are exploited by insect parasitoids to increase their ability to find hosts to attack (Fatouros et al. 2005, Conti et al. 2010, Blenn et al. 2012, Salerno et al. 2013). For example, oviposition by *Pieris brassicae* and *P. rapae* (Lepidoptera: Pieridae) on *Brassica oleracea* induces changes in the chemistry of the leaf surface that induce an arrestment response in females of the egg parasitoids *Trichogramma brassicae* and *T. evanescens* (Hymenoptera: Trichogrammatidae) (Fatouros et al. 2009, Pashalidou et al. 2010).

Most of these studies have been conducted in tri-trophic systems, including a host plant, an herbivore and a parasitoid species. These systems differ considerably from field conditions, where plants are often attacked by multiple herbivore species, even sometimes simultaneously, leading to alterations in the synomone blends modifying the response of natural enemies (Soler et al. 2013).

In fact, during the last decade studies on parasitoid foraging behaviour has switched from tri-trophic to multi-trophic interaction investigations (De Rijk et al. 2013, Gols 2014). For example, in multi-herbivores communities, some studies demonstrated that the presence of non-host species could have a strong effect on parasitoid foraging behaviour. Non-host herbivores may either share the same plant with the host herbivores of a parasitoid or be present on neighbouring plants (Dicke et al. 2009). On shared plants, herbivores may all feed on a single plant organ or on different plant organs located either above- or below-ground (van Dam and Heil 2011). Using a system including *Vicia faba* plants, two herbivorous insects, the above-ground herbivore *Nezara viridula* (Hemiptera: Pentatomidae) and the above- and below-ground herbivore *Sitona lineatus* (Coleoptera: Curculionidae), at adult and larval stages, respectively and *Trissolcus basalis* (Hymenoptera: Scelionidae), an egg parasitoid of *N. viridula*, Moujahed et al. (2014) demonstrated that induced plant responses caused by the concurrent infestation of non-host beetle *S. lineatus* reduced the attraction of the egg parasitoid toward OIPVs emitted by plants infested by *N. viridula*. Non-host beetle chewing damage from both adults feeding on leaves and larvae feeding on roots significantly changed the composition of the OIPV blend, resulting in a disruptive effect on *T. basalis* host location (Fig. 1).

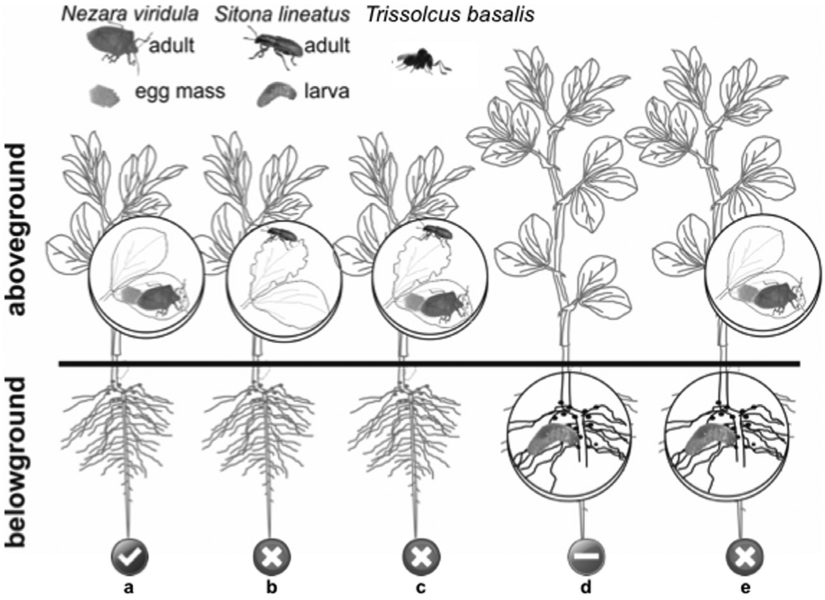

Fig. 1. Effect of non-host herbivore presence (*Sitona lineatus*) on egg parasitoid (*Trissolcus basalis*) attraction towards *Vicia faba* plant attacked by the host, *Nezara viridula*. Above-ground treatment: (a) *Nezara viridula* feeding and oviposition, (b) *Sitona lineatus* adult leaf-feeding, (c) *N. viridula* feeding and oviposition and *S. lineatus* adult leaf-feeding; below-ground treatment: (d) *S. lineatus* larvae root-nodules feeding; above- and below-ground treatment: (e) *N. viridula* feeding and oviposition and *S. lineatus* larvae root-nodules feeding.

Symbols: ✓: positive effect; ×: disruptive effect; –: neutral effect (modified from Moujahed et al. 2014)

Different factors for non-host herbivore attack may induce changes in synomones emission such as the composition of the insect feeding guild (Cusumano et al. 2015), the density of the pest population (Ponzio et al. 2016) or the co-evolutionary history of the plant–insect interaction (Cusumano et al. 2015, Martorana et al. 2017).

The situation is sometimes even more complex than this. In a recent intriguing study, Poelman et al. (2012) demonstrated that cabbage plants attacked by *P. rapae* release volatile compounds that attract primary parasitoids of the genus *Cotesia* (Hymenoptera: Braconidae), e.g., *C. glomerata*, enabling them to find their hosts and to attack and kill them (i.e., a "cry for help" strategy). However, as the authors discovered, volatile compounds released by the plants were also attractive for a hyperparasitoid species, *Lysibia nana* (Hymenoptera: Ichneumonidae) that is then able to find primary parasitoids and kill them. Furthermore, hyperparasitoid females were much more attracted by the volatiles produced by plants attacked by *P. rapae* caterpillars that were previously attacked by their primary parasitoids than by the volatiles produced by plants attacked by unparasitised herbivorous hosts. The difference was due to changes in the oral secretion of the caterpillar hosts when they were parasitised and such changes in oral secretion induced changes in plant volatile emission. Hence, plants that play a "cry for help" strategy attracting natural enemies to protect them actually attract hyperparasitoids that are killing these natural enemies. As a consequence, the overall output is that plant fitness might decrease.

Finally, the response of parasitoids to plant synomones can also be affected by abiotic stresses. For example, *V. faba* plants that were simultaneously in detrimental abiotic conditions (i.e., water stress) and biotic stress (i.e., *N. viridula* attack) showed an alteration in volatile blend emission, resulting in enhanced attraction of the egg parasitoid *T. basalis* (Salerno et al. 2017).

2.3 Kairomones

The ability of parasitoid females to eavesdrop on chemical cues emitted by their hosts and to use them as kairomones in their host location process is a well-documented phenomenon (Powell 1999, Fatouros et al. 2008). Over long distances, parasitoid females can exploit different types of pheromone cues emitted by their hosts to locate their habitat, such as sex (Boo and Yang 2000) or aggregation pheromones (Noldus 1989). Eavesdropping on sex pheromone signals emitted by females to attract males has been demonstrated as a key ability allowing many parasitoid species to find and attack their hosts (Huigens and Fatouros 2013). For example, the egg parasitoid *Telenomus euproctidis* (Hymenoptera: Scelionidae) is attracted by the sex pheromone [(*Z*)-16-methyl-9-heptadecenyl isobutyrate] emitted by females of its nocturnal host, *Orvasca taiwana* (Lepidoptera: Lymantriidae), before mating occurs (Arakaki et al. 2011). The wasp actually remains able to detect traces of the host sex pheromone even 48 hours after the release. Such pheromone traces are retained on host scale hairs of the anal tufts until female moths start laying their egg clutch on a plant. By doing so, female wasps can extend their host searching time and remain active during the temporal gap between nocturnal host mating and oviposition activities and their diurnal foraging time. Some authors even demonstrated a potential synergism between compounds originating from host plants and host sex pheromones, which may create another "bridge-in-time" strategy improving the overall efficacy of their chemical espionage. Whether the detection of adsorbed pheromones is influenced by variation in the epicuticular wax composition of the plant is still unknown (Wäschke et al. 2013).

Other chemical compounds, for example anti-sex pheromone and aggregation pheromone, can act as kairomone signals for parasitoids in their host searching behaviour. For example, some egg parasitoid species are able to exploit host anti-aphrodisiac compounds transferred post-mating from males to female hosts to render them less attractive to conspecific mates, such as benzyl cyanide, indole and/or methyl salicylate (Fatouros et al. 2005, 2009, Huigens et al. 2009). In addition, several species of tachinid parasitoids use the aggregation pheromone produced by pentatomid bugs as a host-finding kairomone (Nakamura et al. 2013). Finally, parasitoids are also able to spy on allomones. For example, defensive compounds such as (*E*)-2-decenal emitted from the metathoracic gland of *N. viridula* adults acts as a long-range kairomone orienting *T. basalis* females to their hosts (Mattiacci et al. 1993)After landing on a host plant, parasitoids mainly perceive contact and/or short-range kairomones to find their hosts, such as, for example, alarm pheromone or host marking pheromones (Hoffmeister et al. 2000, Francis et al. 2005). In this phase of parasitoid foraging, a role is played by chemical footprints left by the hosts. For instance, footprints left on the substrate by the southern green stink bug *N. viridula* are involved in the arrestment responses of the parasitoid *T. basalis* (Colazza et al. 1999). Wölfling and Rostás (2009) revealed that the chemical footprints left by caterpillar *Spodoptera frugiperda* (Lepidoptera: Noctuidae), while walking over a plant surface, are detected by female wasps *Cotesia marginiventris* for up to two days after their hosts have left the site.

Footprints left by herbivores consist of chemicals that probably originate from the insect cuticle, such as (mostly linear) alkanes, diglycerides, triglycerides of high molecular weight, long-chain alcohols and fatty acids (Rostás and Wölfling 2009, Geiselhardt et al. 2011, Lo Giudice et al. 2011). These compounds are not only signals used by parasitoids to find their hosts, but also allow them to fine-tune their host searching behaviour. Indeed, Colazza et al. (2007) revealed that *n*-nonadecane (nC19), which is only present in footprints of *N. viridula* males, acts as a "host sex recognition" cue for *T. basalis*, allowing the wasps to discriminate between the chemical traces of females and males host. Such an ability to discriminate host sex through host chemical footprints was later confirmed with other egg parasitoids attacking pentatomid host bugs (Peri et al. 2013). The ability of parasitoid females to discriminate between male and female adults of their hosts helps them to find potential host eggs more efficiently (Puente et al. 2008a). In this respect, some parasitic wasp species were demonstrated to use associative learning. For instance, rewarded experience (i.e., successful oviposition) occurring after host footprints exploitation increased the arrestment response of *T. basalis* and *Trissolcus brochymenae* females to footprints of their hosts (Peri et al. 2006, 2016). Finally, other contact host-derived by-products (e.g., frass, honeydew, exuviae, mandibular gland secretions, scales) have also been demonstrated to be potential sources of host location kairomones (Fatouros et al. 2008, Colazza et al. 2010, Conti and Colazza 2012, Meiners and Peri 2013). For example, the wasp *Psyllaephagus pistaciae* (Hymenoptera: Encyrtidae) exploits, as both volatile and contact kairomones, cues from honeydew released by the common pistachio psylla, *Agonoscena pistaciae* (Hemiptera: Psyllidae) (Mehrnejad and Copland 2006). Obonyo et al. (2010) showed the importance of frass produced by the hosts *Busseola fusca* (Lepidoptera: Noctuidae) and *Chilo partellus* (Lepidoptera: Crambidae) in short-range host recognition by parasitoids, *Cotesia sesamiae* and *C. flavipes*, respectively. Cues from frass can even be used by female parasitoids to discriminate host from non-host species, hosts of different ages/instars and even hosts feeding on different host plants (e.g., Mattiacci and Dicke 1995, Chuche et al. 2006). The capacity to discriminate between host and non-host species, based on host by-product kairomones, was also reported for cues emitted by cocoons (Bekkaoui and Thibout 1993) or exuviae (Battaglia et al. 2000).

3. Use of Semiochemicals for Agricultural Pest Management

Since the first discovery of semiochemicals, scientists have investigated the possibility of applying these compounds to increase the efficacy of biological control or IPM programs (Suckling and Karg 2000). The potential of semiochemicals to manipulate parasitoid behaviour has opened up new possibilities in pest control, with the promise of environmentally sustainable and highly specific pest control tactics. The use of semiochemicals to improve pest control efficacy represents a relatively new approach that mainly uses plant volatiles. The most promising application involves the use of HIPVs to manipulate the natural enemies of pest species in order to attract and conserve them in the vicinity of the crops to be protected. The following sections describe the different tactics used so far.

3.1 Pheromones-based Tactics

In recent years, the identification of pheromones for a number of parasitoid species has opened up new opportunities to apply pheromone-based tactics for a direct manipulation of parasitoid behaviour. Indeed, studies have proved that parasitoid sex pheromones can be applied for monitoring parasitoid populations. For instance, in apple orchards in New Zealand, Suckling et al. (2002) used the sex pheromone of the female wasp *Ascogaster quadridentata* (Hymenoptera: Braconidae) to assess parasitoid establishment, abundance and phenology synchronisation with the host, the codling moth *Cydia pomonella* (Lepidoptera: Tortricidae). The authors concluded that pheromone trapping of insect biological control agents is a valuable tool that can help to determine and improve parasitoid success. In another study, Hardy and Goubault (2007) suggested application of female bethylid wasp sex pheromones to improve their efficiency as biological control agents. Although parasitoid pheromones have been proved to be promising tools in the manipulation of parasitoids, further field and laboratory tests are required to properly develop this tactic in biological control programs.

3.2 Allelochemicals-based Tactics

3.2.1 Host-Associated Volatiles (Kairomones)

Several studies tested the application of host-associated volatiles (HAVs) to enhance the efficacy of natural enemies. Among these, field studies mainly focused on two kinds of long-range HAVs, host sex and aggregation pheromones, due to their greater potential for parasitoid behavioural manipulation. Table 1 summarises current information about their field applications in different agriculture crops. In fact, host sex and aggregation pheromones have been applied either as tools for monitoring parasitoid populations or for enhancing parasitism rate in the field. An initial experiment on the use of host sex pheromone to monitor parasitoid population density was conducted in the UK by Hardie et al. (1991), who reported the attraction of three parasitoid species, *Praon abjectum*, *P. dorsal* and *P. volucre* (Hymenoptera: Braconidae), to water traps baited with synthetic sex pheromone of *Aphis fabae* (Hemiptera: Aphididae), a blend of (4a*S*,7*S*,7a*R*)-(+)-nepetalactone and (1*R*,4a*S*,7*S*,7a*R*)-(−)-nepetalactol.

In subsequent years, tests in cereal fields, in the UK and Germany, showed that (4a*S*,7*S*,7a*R*)-(+)-nepetalactone was the most effective lure with strongest attraction in autumn (Powell et al. 1993). On the basis of these promising results, the authors proposed to use sex pheromone-baited traps in autumn to manipulate parasitoid populations attacking aphids, a strategy that was later tested on commercial farms in the UK (Powell and Pickett 2003). The role of host sex pheromones in recruiting

Table 1. Host-associated volatile (HAV) candidates for improving parasitoid efficacy in agricultural systems

Crop	HAVs			Effect	References
	Chemicals	Origin/Function	Aim		
Apple	Methyl (2*E*,4*Z*)-decadienoate	Aggregation pheromone of *Euschistus conspersus*	Monitoring adult parasitoid populations	No effect	Krupke and Brunner (2003)
			Test for increased egg parasitism rates	Increase in *Gymnoclytia occidentalis* recruitment by host pheromone-baited traps	
Cereals	(4a*S*,7*S*,7a*R*)-Nepetalactone	Sex pheromone of aphids	Test for increased parasitism rates	Attraction of *Praon volucre*, *P. dorsale*, and *P. abjectum*	Powell et al. (1993)
				Increase in *P. volucre* parasitism	Glinwood et al. (1998)
Citrus	(1*R*,3*R*)-(2,2-Dimethyl-3-isopropenylcyclobutyl) methyl acetate (planococcyl acetate)	Sex pheromone of *Planococcus citri*	Monitoring parasitoid populations	No effect on *Anagyrus* sp. *nov.* near *pseudococci*	Franco et al. (2008)
	(*S*)-Lavandulyl senecioate (LS)	Sex pheromone of *P. ficus*		Attraction of *Anagyrus* sp. *nov.* near *pseudococci*	
	Planococcyl acetate	Sex pheromone *of P. citri*	Test for increased parasitism rates	Increase in *Anagyrus* sp. *nov.* near *pseudococci* parasitism for an Italian population	Franco et al. (2011)

(*Contd.*)

	(*S*)-Lavandulyl senecioate	Sex pheromone of *P. ficus*		Increase in *Anagyrus* sp. *nov.* near *pseudococci* parasitism	
Fig and grapevine	(*S*)-Lavandulyl senecioate	Sex pheromone of *P. ficus*	Monitoring parasitoid populations	More attraction of *Anagyrus* sp. *nov.* near *pseudococci* by LS-baited traps than by LI-baited traps	Franco et al. (2008)
	(*S*)-Lavandulyl isovalerate (LI)	Compound produced by *P. ficus* in mass-rearing conditions			
Grapevine	(*S*)-Lavandulyl senecioate	Sex pheromone of *P. ficus*	Test for increased parasitism rates Test for combined effect of parasitoid inundative release + LS application on parasitism rate	Increase in *Anagyrus sp. nov.* near *pseudococci* recruitment	Mansour et al. (2011)
Soybean	Methyl 2,6,10-trimethyltridecanoate	Sex pheromone of *Euschistus heros*	Monitoring egg parasitoids	Attraction of *Telenomus podisi*, *Trissolcus teretis*, *Tr. urichi* and *Tr. brochymenae*	Borges et al. (1998)
	(*E*)-2-Hexenyl (*Z*)-3-hexanoate	Aggregation pheromone of *Riptortus clavatus*	Test for increased parasitism rates	Early attraction of *Ooencyrtus nezarae* and increase in sentinel eggs parasitism	Mizutani (2006)
	(*E*)-2-Hexenyl (*E*)-2-hexenaoate, (*E*)-2-hexenyl (*Z*)-3-hexenoate, tetradecyl isobutyrate	Aggregation pheromone of *Riptortus pedestris*	Test for increased parasitism rates	Attraction of *O. nezarae*, increase of egg parasitism and reduction of stink bug damage on pods	Alim and Lim (2011)

(*Contd.*)

Table 1. (*Contd.*)

Crop	HAVs			Effect	References
	Chemicals	Origin/Function	Aim		
			Test for distribution and guild composition of egg parasitoids	Increase in *O. nezarae* and *Gryon japonicum* abundance. No effect on parasitoid species relative abundance	Lim and Mainali (2013)
Spindle tree	Mixture of (4a*S*,7*S*,7a*R*)-nepetalactone and (1*R*,4a*S*,7*S*,7a*R*)-nepetalactol	Sex pheromone of *Aphis fabae*	Monitoring parasitoid populations	Increase in parasitoid recruitment by host pheromone-baited traps	Hardie et al. (1991)
Mixed crops	(*Z*)-3,9-Dimethy-6-isopropenyl-3,9-decadienyl propionate	Sex pheromone of *Pseudaulacaspis pentagona*	Monitoring parasitoid populations	Attraction of *Thomsonisca amathus* by host pheromone-baited traps	Bayoumy et al. (2011)
	Mixture of (*Z*)-3,7-dimethy1-2,7-octadienyl propionate and 7-methyl-3-methylene-7-octenyl propionate	Sex pheromone of *Diaspidiotus perniciosus*		Attraction of *Encarsia perniciosi* by host pheromone-baited traps	
	Methyl (*E*,*E*,*Z*)-2,4,6-decatrienoate	Aggregation pheromone of *Plautia stali*	Monitoring parasitoid populations	Attraction of *Gymnosoma rotundatum* by host pheromone-baited traps	Jang and Park (2010), Jang et al. (2011)

parasitoids and enhancing their activities has also been evaluated in vineyards, citrus and fig orchards in the Mediterranean basin. The system studied includes two mealybug species, citrus mealybug *Planococcus citri* and vine mealybug *P. ficus* (Hemiptera: Pseudococcidae) and the parasitoid *Anagyrus* sp. *nov*. near *pseudococci* (Hymenoptera: Encyrtidae) (Franco et al. 2008, 2011, Mansour et al. 2011). In all the experiments conducted, regardless of the cropping systems used, a significant increase in mealybug parasitism was observed when the sex pheromone of *P. ficus*, (*S*)-(+)-lavandulyl senecioate, was applied in the field. Hence, it was suggested that this new HAV-based strategy could be used efficiently in the control of vine mealybug in vineyards and citrus orchards (Franco et al. 2011, Mansour et al. 2011).

Examples of the use of host aggregation pheromone to manipulate parasitoid behaviour were provided by Jang and Park (2010) and Jang et al. (2011). They obtained successful results in monitoring *Gymnosoma rotundatum* (Diptera: Tachinidae) populations in Korean persimmon orchards, by placing sticky traps baited with methyl (*E*,*E*,*Z*)-2,4,6-decatrienoate, the aggregation pheromone of one of its hosts, the brown-winged green stink bug, *Plautia stali* (Hemiptera: Pentatomidae). Considering that the aggregation pheromone of the brown-winged green stink bug is used to attract both sexes of *P. stali* (Park et al. 2010), the use of appropriate pheromone traps was proposed, with the purpose of both reducing pest population densities and increasing parasitism rates (Jang et al. 2011). In Korean soybeans crop, the use of traps baited with the aggregation pheromone from *Riptortus pedestris* (=*clavatus*) (Hemiptera: Alydidae) has become common practice to monitor and reduce the pest population (Alim and Lim 2011, Mainali and Lim 2012). This host pheromone not only attracts conspecific adults in the field but it also has a kairomonal effect on its egg parasitoids, *Ooencyrtus nezarae* (Hymenoptera: Encyrtidae) and *Gryon japonicum* (Hymenoptera: Scelionidae), increasing the abundance of parasitoids up to 18 m from pheromone locations (Lim and Mainali 2013). Recent research also identified the possibility of developing allelochemical-based tactics with "non-natural" chemical compounds. For example, in persimmon orchards, the synthetic compound (2,4,4-trimethyl-2-cyclohexenyl) methyl butyrate, also known as cyclolavandulyl butyrate (CLB), have been shown to attract two parasitoids, *Anagyrus sawadai* and *Leptomastix dactylopii* (Hymenoptera: Encyrtidae), in order to control the Japanese mealybug *Planococcus kraunhiae* (Hemiptera: Pseudococcidae) (Teshiba et al. 2012, Teshiba and Tabata 2017).

3.2.2 Herbivore-Induced Plant Volatiles (Synomones)

The discovery of the crucial role of HIPVs in indirect plant defense triggered ideas to use them to increase pest control efficacy by manipulating the behaviour of natural enemies (Khan et al. 2008). HIPVs can be applied directly onto plants, by spraying, or as plant hormones, inducing the production of defensive chemical volatiles, which attract parasitoids, or even by using a slow-release dispenser that releases chemical compounds attracting natural enemies directly. Additionally, plants may be genetically engineered to increase their emission of HIPVs (Rodriguez-Saona et al. 2012, Stenberg et al. 2015, Guerrieri 2016).

A potential way to manipulate the behaviours of natural enemies is to identify the natural HIPVs, produce them synthetically and then release them, either separately or in a mixture. One of the early studies that demonstrated the potential of synthetic HIPV lures as direct field attractants for parasitoids was performed by James and Grasswitz (2005). In this study, sticky traps, placed in blocks of grape plants baited with controlled-release dispensers of methyl salicylate (MeSA), methyl jasmonate (MeJA) and (Z)-3-hexenyl acetate, captured more parasitic wasps from the families Encyrtidae and Mymaridae than blocks with unbaited traps. Subsequently, the past decade has witnessed many other laboratory and field studies that demonstrated the capability of synthetic HIPVs to increase the diversity or density of parasitoids within various crop systems (Blassioli-Moraes et al. 2013, Colazza et al. 2013, Simpson et al. 2013). For instance, in *Brassica rapa* crops, the use of dispensers of a synthetic mixture of (Z)-3-hexenyl acetate, n-heptanal, α-pinene and sabinene [i.e., volatile compounds induced by larvae feeding activity of the diamondback moth, *Plutella xylostella* (Lepidoptera: Plutellidae)], is able to recruit the parasitoid *Cotesia vestalis* to uninfested plants and to increase its attack on host larvae on infested plants (Uefune et al. 2012).

Treatment with synthetic HIPVs not only directly attracts natural enemies but also likely elicits the treated plant to produce endogenous HIPVs blends that recruit predator and parasitoid arthropods (Simpson et al. 2011a). In maize fields in Mexico, Von Mérey et al. (2011) demonstrated that, in the presence of glass vial dispensers releasing a mixture of four synthetic green leaf volatiles, maize plants released higher amount of sesquiterpenes than non-exposed plants, but this did not influence the impact of parasitoids on *S. frugiperda*. These encouraging results obtained in terms of parasitoid attraction to synthetic HIPVs need to take into account the effect of these volatiles on all the protagonists involved because the use of synthetic HIPVs may have negative effects, such as increasing the likelihood of intraguild predation on natural enemies, followed by a reduction in the top-down control of pests (Poelman and Kos 2016).

Herbivory-induced changes in plant volatiles are known to be regulated by jasmonic acid (JA), salicylic acid (SA) and ethylene (ET) hormonal signaling pathways (Takabayashi 2006, Ode 2013). In general, SA is triggered by phloem-feeding herbivores, whereas JA/ET are activated by biting/chewing herbivores and these pathways act antagonistically

(Stam et al. 2014). Hence, as an alternative to the use of synthetic HIPVs, plants could be sprayed with plant hormones, such as jasmonates [e.g., JA, MeJA, or *cis*-jasmone (CJ)], which play the role of plant elicitors (=inducers) triggering the production and emissions of their own blend of volatiles and leading to the attraction of natural enemies (Rohwer and Erwin 2008). The effects of jasmonates on the enhancement of parasitoids attraction have been demonstrated within various crops systems (e.g., van Poecke and Dicke 2002, Ozawa et al. 2004). For example, van Poecke and Dicke (2002) showed that *Arabidopsis thaliana* treated with JA increased the attraction of *Cotesia rubecula* compared with untreated plants, whereas treatment with SA did not. Moreover, Lou et al. (2005) reported that JA application on rice plants enhanced more than two-fold the parasitisation of brown planthopper' eggs, *Nilaparvata lugens* (Hemiptera: Delphacidae), by its parasitoid *Anagrus nilaparvatae* (Hymenoptera: Mymaridae). Similarly, treatments with CJ enhanced the foraging behaviour of *Telenomus podisi*, an egg parasitoid of soybean stink bug pests (Moraes et al. 2009) and of *Aphidius ervi* (Hymenoptera: Braconidae), a parasitoid of sweet pepper aphids (Dewhirst et al. 2012). However, recent studies showed no effect of jasmonates in enhancing the parasitism rate in a system composed of soybean/cotton crops, stink bug and egg parasitoids. For instance, CJ application on soybean attracted Platygastridae parasitoids but did not affect the parasitisation rate of eggs of the stink bug *Euschistus heros* (Hemiptera: Pentatomidae) (Vieira et al. 2013).

Apart from jasmonates, SA and its analogues also act as phytohormone elicitors and stimulate the biosynthesis and release of endogenous HIPVs. The effect of SA on parasitoids attraction has been well studied within maize crops (e.g., Rostás and Turlings, 2008, Sobhy et al. 2012, 2014). For instance, treating maize plants with BTH (*S*-methyl 1, 2, 3-benzothiadiazole-7-carbothioate), a mimic of SA, reduced the emission rates of two volatile compounds [indole and (*E*)-caryophyllene] from treated plants. This reduction was expected because of the well-known antagonism between SA and JA pathways (Thaler et al. 2002). Despite this reduction, Rostás and Turlings (2008) recorded a higher attractiveness to the parasitoid *Microplitis rufiventris* (Hymenoptera: Braconidae). This result was confirmed by subsequent tests including another elicitor, laminarin, and was explained by a subtractive hypothesis where the suppression of some volatiles not directly involved in parasitoid attraction may results in a higher attractiveness (Sobhy et al. 2012).

So far, there are no commercial products available using phytohormones. One of the reasons that could prevent the production of these products is the multiple role of these plant hormones, which are also responsible for the regulation of other physiological responses in plants. Therefore, the multifunctionality of potential HIPVs needs to be considered to avoid counter-productive results and to develop cost–

benefit analysis of the products for an efficient manipulation of natural enemies in crops.

3.2.3 Engineering of HIPVs in Crop Plants by Genetic Modification

Genetic modification appeared as an alternative way to increase biological control efficacy. The goal is to manipulate plants traits to produce and release specific volatiles (Åhman et al. 2010, Stenberg et al. 2015). Although plant breeding practices have historically ignored the effects of HIPVs on the third trophic level, this is expected to change with recent advances in molecular technologies (Gurr and You 2016, Pickett and Khan 2016). Generally, variation in the composition of HIPVs can be related to plant species, cultivars, phenological stages, host developmental stage and several other factors (McCormick et al. 2012). In this respect, the first approach that can be applied is selective breeding, which consists in selecting cultivars that can naturally enhance the foraging efficiency of natural enemies in field conditions (Michereff et al. 2015, Tamiru et al. 2015, Mitchell et al. 2016). Michereff et al. (2015) demonstrated that the ability to recruit parasitoids can be cultivar-dependent. Indeed, two pest-resistant soybean cultivars (Dowling and IAC 100) attracted a higher number of Platygastridae wasps compared with a susceptible one (Silvânia), with sufficient abundance to control the stink bug *E. heros*. Therefore, the authors suggested that traits in the resistant cultivars could be useful in breeding programs to obtain new cultivars more resistant to stink bugs and more attractive to natural enemies. The second approach is the use of transgenic plants where specific genes are inserted to prime plants for enhanced HIPV responses (Turlings and Ton 2006, Kos et al. 2009). Most research on transgenic plants has been conducted with arable crops such as maize and cotton, or model organisms such as *Arabidopsis* (Blassioli-Moraes et al. 2013, 2016). For instance, Schnee et al. (2006) transferred a sesquiterpene synthase gene that produces (*E*)-β-farnesene, (*E*)-α-bergamotene and other herbivory-induced sesquiterpenes from maize into *Arabidopsis*, resulting in greater emissions of several sesquiterpenes and enhanced attraction of *C. marginiventris* after wasps learned to associate the presence of hosts with the emissions of these sesquiterpenes.

Genetic engineering research has mainly focused on basic aspects of plant signaling pathways from a tri-tropic perspective, but extension of these laboratory studies to practical field applications remains limited. According to Gurr and You (2016), the new gene-editing tool, CRISPR/Cas9, will offer great power to elucidate and manipulate plant defence mechanisms, including HIPVs that involve natural enemy attraction to attacked plants. Therefore, CRISPR/Cas9 will allow highly accurate changes in genomes, which may reduce potential barriers to regulation and adoption (Voytas and Gao 2014).

3.3 Attract and Reward Strategy

Parasitoid recruitment with semiochemicals can be further improved when combined with habitat management, which involves, for example, the provision of flowering companion plants or wildflower strips in managed landscapes with low biodiversity (Gurr et al. 2004). These plants, by supplying beneficial insects with suitable sugars, increase their lifespan and fecundity and thus improve ecosystem services such as pest suppression. The combination between habitat management and semiochemical-based tactics, as a method to manage natural enemies, has been examined extensively and proved to be efficient (Rodriguez-Saona et al. 2012, Simpson et al. 2013). The ecological basis of such strategy relies on the possibility that crops treated with semiochemicals attract natural enemies that might find other plants in the same field, which provide them with food resources as a reward. To date, the application of the "attract and reward" (A&R) strategy is limited to a few cases, where beneficial insects are "attracted" by synthetically produced HIPVs and are then "rewarded" by providing them with floral resources. Simpson et al. (2011b, c) tested A&R strategy in maize, broccoli and grapevine crops, using some HIPVs, such as methyl anthranilate, MeJA, MeSA, (Z)-3-hexenyl acetate, benzaldehyde and their mixtures, as attractants and plants of buckwheat *Fagopyrum esculentum*, as reward. Indeed, this annual plant induces benefits to parasitoids, because its nectar and pollen resources increase the abundance, fitness and parasitism rates of natural enemies (Lee and Heimpel 2005, Irvin et al. 2006, Foti et al. 2017) (Fig. 2).

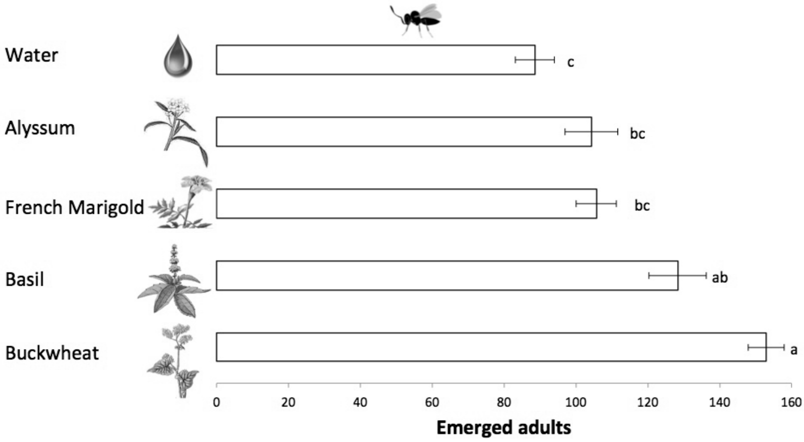

Fig. 2. Effect of floral resources on progeny of the egg parasitoid *Trissolcus basalis*. Significantly more adults emerged from host egg masses parasitised by wasps that had access to buckwheat flowers than to other resources. Means ± SE are reported; different letters indicate where differences among treatments are significant ($P < 0.05$; Based on data from Foti et al. 2017).

Although in some cases parasitoid density significantly increased in treatments with rewards (Simpson et al. 2011b, c), outcomes of these field experiments provided only limited evidence of a positive effect of the A&R strategy, because only one species of scelionids was more abundant in plots with MeSA-treated broccoli and buckwheat plants compared with either MeSA-treated broccoli plots or reward alone (Simpson et al. 2011b). Such non-consistent results obtained so far demonstrate the complexity of the A&R approach and highlight the need for further research to determine the efficacy of such combined strategy in cropping systems. In fact, previous studies showed that A&R could modify the population levels of both herbivorous and carnivorous insects, because each of the two components can determine an unintended recruitment of additional herbivores (Turlings and Ton 2006, Orre et al. 2010) or hyperparasitoids (Baggen et al. 1999, Lavandero et al. 2006, Jonsson et al. 2009), or even a counter-action, as was observed where the reward component may inhibit the attractive one (Orre Gordon et al. 2013). To limit potential negative effects, Orre Gordon et al. (2013) suggested a possible way to improve the A&R strategy and thus the efficacy of biological control of insect pests, by searching for a combination of HIPVs and companion plants that selectively recruit parasitoids, but not herbivorous and/or hyperparasitoid species, because it was demonstrated that there are some HIPVs and food plants that can selectively attract different natural enemy species (Baggen et al. 1999, Begum et al. 2006, Lavandero et al. 2006, Simpson et al. 2011a).

4. Constraints and Challenges of Semiochemical Applications for Biological Control of Crop Pests

As has been discussed in the sections above, the use of semiochemicals to monitor pest density in the field or to disrupt their mating efficiency using pheromones, or to attract natural enemies to control them, has opened up new opportunities leading to efficient, environmentally sustainable pest control strategies. However, the methods and techniques that were – and are still being – developed for this are not necessarily easy and such pest control strategies have always been a subject to controversy regarding the potential limits and risks of using these compounds in the field (Turlings and Ton 2006, Hilker and McNeil 2008, Kaplan 2012, Rodriguez-Saona et al. 2012, Meiners and Peri 2013). More accurately, developing a sound pest control strategy based on the use of semiochemical comes up against several constraints leading to different challenges that are not necessarily easy to solve. The main reason for this is that the use of semiochemicals to manipulate parasitoids' behaviour is done in environments that are, by definition, highly complex, as this has been discussed above (Schröder and Hilker 2008, Wäschke et al. 2013). The processes involved act at the individual, population and ecosystem levels simultaneously and are essentially limitless (Takken and Dicke 2006, Meinwald and Eisner 2008, Colazza and Wajnberg 2013) and, at each level, a handful of both intra- and inter-specific interactions are involved.

Several constraints have been identified and discussed. The most important one is based on the fact that the production and characterisation of the signal molecules used represent a long-lasting and then expensive research effort involving different, and most of the time difficult, steps. Processes involved in the emission and transmission mechanisms of these chemical compounds, the way they are detected by the recipient organisms and the associated neuroendocrine-mediated behavioural and/or physiological changes they trigger must all be accurately understood (Meinwald and Eisner 2008) no matter how these compounds are used in field conditions. It appears that, in order to make increasing strides in our understanding, this entire research effort cannot be done without involving both the genomic and proteomic tools that are now available (Kessler and Baldwin 2002), leading usually to additional costs and the need to solve several technical barriers (Colazza and Wajnberg 2013). Besides this, the consequences of using such chemical compounds in the field at the population level must also be studied, for example in terms of population dynamics, both in time and in space (Meinwald and Eisner 2008). In a nutshell, all of this means that strongly multidisciplinary cooperative partnerships must be developed, essentially between chemical ecologists and genomicists (Meinwald and Eisner 2008), but also involving population and behavioural ecologists (Colazza and Wajnberg 2013). Another constraint is based on the fact that most studies conducted so far have been done under laboratory conditions, which differ considerably from field conditions (Meiners and Peri 2013). The complexity of real field situations and/or the large variation due to unpredicted and fluctuating biotic and abiotic conditions might hamper the efficacy of the chemical compounds used to modify correctly parasitoids' behaviour, even if this has been clearly demonstrated in the laboratory. Hence, the most accurate way to use semiochemicals in different real situations still remains to be discovered in most of the cases.

As a consequence, several attempts at using semiochemicals to improve biological control of crops pest actually led to ineffective pest control or were sometimes even counterproductive (Meiners and Peri 2013). For example, although Roland et al. (1995) demonstrated that releasing borneol in apple orchards can increase the density of *Cyzenis albicans* (Diptera: Tachinidae), a parasitoid of the winter moth *Operophtera brumata* (Lepidoptera: Geometridae), the parasitism rate actually did not increase. One of the possible reasons of such failures might be that semiochemicals could actually decrease parasitoid foraging efficiency because they can attract them to locations without potential hosts to attack, hence leading them to waste time and energy and decreasing their overall pest-killing activity (Powell and Pickett 2003, Puente et al. 2008a). In addition, parasitoid females responding to semiochemicals without finding hosts to attack can rapidly change their foraging behaviour through mechanisms such as habituation (Peri et al. 2006, Abram et al. 2015, Peri et al. 2016), leading also to an overall decrease in their pest control ability.

Indirect negative effects of using semiochemicals with the goal to increase the efficacy of biological control programs can also be observed. Using a semiochemical locally can, for example, attract parasitoids females from remote locations, potentially leading to pest outbreaks in uncontrolled areas with dramatic demographic consequences at larger scales. Additionally, semiochemicals such as plant volatiles that are used to attract parasitoid females can sometimes also attract pests, enhancing overall herbivory levels, for example as shown by Meiners et al. (2005) for the elm leaf beetle *Xanthogaleruca luteola* (Coleoptera: Chrysomelidae). More subtle negative effects can also be observed, for example when semiochemicals attract the primary parasitoid species, which can potentially control the targeted hosts, but also attract hyperparasitoids that can kill the pests' natural enemies, leading to overall greater damage to the plants (Poelman et al. 2012, 2016; see above for a more detailed discussion).

Another challenge might happen when the goal is to use semiochemicals in organic crops, which are becoming more popular nowadays, in order to reduce the use of synthetic pesticides. By definition, with such crops the use of synthetic compounds is prohibited (Simpson et al. 2013). However, the majority of studies involving semiochemicals have been based on synthetic compounds that can be used within conventional agricultural systems only. Such constraints might induce the need to look for products specifically derived from natural sources rather than being synthetically manufactured (Simpson et al. 2013).

Finally, some ecological situations are actually more challenging than others. This is the case, for example, in forest ecosystems in which enhancing pest control by means of using semiochemicals faces very serious constraints. In such ecosystems, the critical pests to control are essentially episodic, complicating the decision about when the treatment must be applied. Additionally, forests are usually grown based on very long rotational harvest cycles (decades or even sometimes centuries) with usual small annual returns, hence limiting the implementation of high-cost pest control strategies. Furthermore, many forest ecosystems are spread over large areas with limited accessibility, further limiting potential pest management decisions (Paine 2013).

Thus, there are still important questions remaining to be solved before an efficient and stable increase in pest control efficacy of insect parasitoids can be achieved by means of using semiochemicals in field conditions

(Meinwald and Eisner 2008, Colazza and Wajnberg 2013). More research is definitely needed into the use of such chemical compounds for pest management (Kaplan 2012), particularly in converting the ever-expanding body of biological knowledge into practicable applications (Simpson et al. 2013). Although quite a lot is already known (see other sections above), the ecological and evolutionary meaning of chemical communication networks, for example, needs to be unraveled more accurately if we want to improve field application. The goal of the end on this section is to propose potential ideas to overcome the different constraints and challenges briefly listed above.

Several ideas have been discussed in the literature. For example, it has been proposed to produce crop varieties, by means of breeding selection or even genetic engineering, with an enhanced ability to emit chemical signals for attracting parasitoids (i.e., synomones) when they are attacked by herbivores (Bottrell et al. 1998), overall leading to a more efficient pest control strategy (see above). In addition, because insect parasitoids are known to change their behaviour according to previous experiences (i.e., learning ability, see above), it has been proposed on several occasions to prime them with semiochemicals prior to release (Hare et al. 1997) in order to enhance their search activity or to retain them in certain areas (Mills and Wajnberg 2008). Insect parasitoids could also potentially be improved by means of breeding selection (Wajnberg 2004), leading them to react more rapidly and more efficiently to semiochemicals when they are released in the field (see above).

There is, however, now a need to address this issue in a more global and formal way, because, as described above, the situation is essentially complex, potentially involving an important number of interacting species both in time and in space. In this respect, the idea here is to make a plea for the development of a modeling framework that is clearly needed if we really want to improve the efficacy of biological control agents to control crop pests with the use of semiochemicals (Mills and Kean 2010, Wajnberg et al. 2016). This is especially true in this case because insects are generally highly time-limited, are also able to modify their behaviour through learning and have to respond to cues that are essentially embedded in a highly complex array of other signals, leading them to experience both costs and benefits. Hence, understanding of the consequences for evolutionary and population dynamics of such features cannot be done without a sound and formal modeling approach (Mills and Wajnberg 2008, Wajnberg et al. 2016). Such modeling work will then provide precious information regarding, for example, how semiochemical compounds can be optimally used, how insect will react (evolve), etc.

Several theoretical works have been published on this topic. For example, Puente et al. (2008a) developed a deterministic model showing that the lag time between herbivory and the emission of plant volatiles in the tri-trophic system *Brassica oleracea–Pieris rapae–Cotesia rubecula* eliminates the benefit for the parasitoids to respond to such chemical compounds. In addition, in the same system, Puente et al. (2008b), using a simulation model, showed that parasitoids do not benefit from responding to plant volatile compounds when their emission continues for a long period of time. These two models demonstrated the importance of both temporal and spatial aspects, likely giving cues about how things should be optimally done. Developing a sound and accurate modeling framework to understand how semiochemicals must ideally be used in field conditions to enhance the efficacy of biological control programs against crop pest is certainly a challenging task. Such a scientific effort needs to be done urgently if we want to obtain efficient, stable and environmentally sustainable pest control strategies without the use of chemical pesticides.

5. Conclusion

Because of the increased use of pesticides worldwide in response to growing human populations and crop production, research on strategies to moderate the negative effects that existing pesticide practices have on human health and the environment is a global challenge in agriculture. One approach to overcome this challenge is to use applied chemical ecology. In recent years, semiochemical-based tactics have emerged as promising tools to enhance the efficacy of natural enemies in the biological control of crop pests. As a consequence, research on the manipulation of insect behaviour by using semiochemicals has increased greatly in the context of pest management. Examples of applications in crop ecosystems of allelochemical-based tactics to reduce insect pest populations by direct (e.g., use of synthetic HIPVs and/or HAVs) or indirect (e.g., use of phytohormonal elicitors or crop varieties, by breeding selection or genetic engineering, enhancing ability to emit attractive chemicals signals) recruitment of natural enemies have increased in number around the world, opening up new opportunities leading to efficient, environmentally sustainable pest control strategies. However, these techniques are often difficult to apply in the field and are subject of controversy regarding the potential limits and risks and the results in terms of enhancing parasitoid efficacy in the biological control of crop pests are sometimes inconsistent. The main reason is that the semiochemical-based tactics aim to manipulate parasitoids behaviour and, therefore, their outcomes can be conditioned by different factors such as, for example, the experience of the parasitoids or the lack of hosts. Moreover, such manipulation is done in highly complex environments, and as a consequence, can act simultaneously at different trophic levels, involving both intra- and inter-specific interactions. Additional comparative studies should be conducted to understand how to limit any negative effects and to investigate, e.g., the effect of landscape complexity on biological control.

For example, the synergy obtained by merging semiochemical-based manipulations and habitat manipulations could be promising, because parasitoids attracted to an allelochemical-treated crop might find some rewards (e.g., food sources such as nectar and pollen or alternative hosts), limiting the possible negative effects of parasitoid recruitment in the absence of hosts. Therefore, an interdisciplinary approach involving different research fields, such as chemical ecology, biological control, insect physiology and behaviour, plant ecology and plant breeding, is needed to open the "chemical ecological toolbox" for developing effective and successful biological control programs.

REFERENCES

Abram, P.K., A. Cusumano, E. Peri, J. Brodeur, G. Boivin and S. Colazza. 2015. Thermal stress affects patch time allocation by preventing forgetting in a parasitoid wasp. Behav. Ecol. 26: 1326–1334.

Åhman, I., G. Robert and N. Velemir. 2010. The potential for modifying plant volatile composition to enhance resistance to arthropod pests. CAB Reviews 5: 1–10.

Alim, M.A. and U.T. Lim. 2011. Refrigerated eggs of *Riptortus pedestris* (Hemiptera: Alydidae) added to aggregation pheromone traps increase field parasitism in soybean. J. Econ. Entomol. 104: 1833–1839.

Arakaki, N., H. Yamazawa and S. Wakamura. 2011. The egg parasitoid *Telenomus euproctidis* (Hymenoptera: Scelionidae) uses sex pheromone released by immobile female tussock moth *Orgyia postica* (Lepidoptera: Lymantriidae) as kairomone. Appl. Entomol. Zool. 46: 195–200.

Atanassov, A., P.W. Shearer and G.C. Hamilton. 2003. Peach pest management programs impact beneficial fauna abundance and *Grapholita molesta* (Lepidoptera: Tortricidae) egg parasitism and predation. Environ. Entomol. 32: 780–788.

Baggen, L.R., G.M. Gurr and A. Meats. 1999. Flowers in tri-trophic systems: mechanisms allowing selective exploitation by insect natural enemies for conservation biological control. Entomol. Exp. Appl. 91: 155–161.

Battaglia, D., G. Poppy, W. Powell, A. Romano, A. Tranfaglia and F. Pennacchio. 2000. Physical and chemical cues influencing the oviposition behaviour of *Aphidius ervi*. Entomol. Exp. Appl. 94: 219–227.

Bayoumy, M.H., B.A. Kaydan and F. Kozár. 2011. Are synthetic pheromone captures predictive of parasitoid densities as a kairomonal attracted tool? J. Entomol. Acarol. Res. 43: 23–31.

Begum, M., G.M. Gurr, S.D. Wratten, P.R. Hedberg and H.I. Nicol. 2006. Using selective food plants to maximise biological control of vineyard pests. J. Appl. Ecol. 43: 547–554.

Bekkaoui, A. and E. Thibout. 1993. Role of the cocoon of *Acrolepiopsis assectella* (Lep., Yponomeutoidae) in host recognition by the parasitoid *Diadromus pulchellus* (Hym., Ichneumonidae). Entomophaga 38: 101–113.

Bernal, J.S. and R.F. Luck. 2007. Mate finding via a trail sex pheromone by *Aphytis melinus* DeBach (Hymenoptera: Aphelinidae) males. J. Insect Behav. 20: 515–525.

Blassioli-Moraes, M.C., M. Borges and R.A. Laumann. 2013. The application of chemical cues in arthropod pest management for arable crops. pp. 225–244. *In*: E. Wajnberg and S. Colazza [eds.]. Chemical Ecology of Insect Parasitoids. Wiley-Blackwell, Oxford, UK.

Blassioli-Moraes, M.C., M. Borges, M.F.F. Michereff, D.A. Magalhães and R.A. Laumann. 2016. Semiochemicals from plants and insects on the foraging behaviour of Platygastridae egg parasitoids. Pesq. Agropec. Bras. 51: 454–464.

Blenn, B., M. Bandoly, A. Kueffner, T. Otte, S. Geiselhardt, N.E. Fatouros et al. 2012. Insect egg deposition induces indirect defense and epicuticular wax changes in *Arabidopsis thaliana*. J. Chem. Ecol. 38: 882–892.

Boo, K.S. and J.P. Yang. 2000. Kairomones used by *Trichogramma chilonis* to find *Helicoverpa assulta* eggs. J. Chem. Ecol. 26: 359–375.

Borges, M., F.G.V. Schmidt, E.R. Sujii, M.A. Medeiros, K. Mori, P.H.G. Zarbin et al. 1998. Field responses of stink bugs to the natural and synthetic pheromone of the Neotropical brown stink bug, *Euschistus heros* (Heteroptera: Pentatomidae). Physiol. Entomol. 23: 202–207.

Bottrell, D.G., P. Barbosa and F. Gould. 1998. Manipulating natural enemies by plant variety selection and modification: a realistic strategy? Annu. Rev. Entomol. 43: 347–367.

Chuche, J., A. Xuéreb and D. Thiéry. 2006. Attraction of *Dibrachys cavus* (Hymenoptera: Pteromalidae) to its host frass volatiles. J. Chem. Ecol. 32: 2721–2731.

Colazza, S., G. Aquila, C. De Pasquale, E. Peri and J. Millar. 2007. The egg parasitoid *Trissolcus basalis* uses n-nonadecane, a cuticular hydrocarbon from its stink bug host *Nezara viridula*, to discriminate between female and male hosts. J. Chem. Ecol. 33: 1405–1420.

Colazza, S., E. Peri and A. Cusumano. 2013. Application of chemical cues in arthropod pest management for orchards and vineyards. pp. 245–265. *In*: E. Wajnberg and S. Colazza [eds.]. Chemical Ecology of Insect Parasitoids. Wiley-Blackwell, Oxford, UK.

Colazza, S., E. Peri, G. Salerno and E. Conti. 2010. Host searching by egg parasitoids: exploitation of host chemical cues. pp. 97-147. *In*: F.L. Cônsoli, J.R.P. Parra and R.A. Zucchi [eds.]. Egg Parasitoids in Agroecosystems with Emphasis on *Trichogramma*. Springer Science and Business Media, Dordrecht, Netherlands.

Colazza, S., C.M. Rosi and A. Clemente. 1997. Response of egg parasitoid *Telenomus busseolae* to sex pheromone of *Sesamia nonagrioides*. J. Chem. Ecol. 23: 2437–2444.

Colazza, S., G. Salerno and E. Wajnberg. 1999. Volatile and contact chemicals released by *Nezara viridula* (Heteroptera: Pentatomidae) have a kairomonal effect on the egg parasitoid *Trissolcus basalis* (Hymenoptera: Scelionidae). Biol. Control 16: 310–317.

Colazza, S. and E. Wajnberg. 2013. Chemical ecology of insect parasitoids: towards a new era. pp. 1–8. *In*: E. Wajnberg and S. Colazza [eds.]. Chemical Ecology of Insect Parasitoids. Wiley-Blackwell, Oxford, UK.

Conti, E. and S. Colazza. 2012. Chemical ecology of egg parasitoids associated with true bugs. Psyche 2012: 1–11.

Conti, E., G. Salerno, B. Leombruni, F. Frati and F. Bin. 2010. Short-range allelochemicals from a plant-herbivore association: a singular case of oviposition-induced synomone for an egg parasitoid. J. Exp. Biol. 213: 3911–3919.

Cusumano, A., B.T. Weldegergis, S. Colazza, M. Dicke and N.E. Fatouros. 2015. Attraction of egg-killing parasitoids toward induced plant volatiles in a multi-herbivore context. Oecologia 179: 163–174.

De Rijk, M., M. Dicke and E.H. Poelman. 2013. Foraging behaviour by parasitoids in multiherbivore communities. Anim. Behav. 85: 1517–1528.

Dewhirst, S.Y., M.A. Birkett, E. Loza-Reyes, J.L. Martin, B.J. Pye, L.E. Smart et al. 2012. Activation of defence in sweet pepper, *Capsicum annuum*, by *cis*-jasmone, and its impact on aphid and aphid parasitoid behaviour. Pest Manag. Sci. 68: 1419–1429.

Dicke, M. and I.T. Baldwin. 2010. The evolutionary context for herbivore-induced plant volatiles: beyond the 'cry for help'. Trend. Plant Sci. 15: 167–175.

Dicke, M. and M.W. Sabelis. 1988. Infochemical terminology: based on cost benefit analysis rather than origin of compounds? Funct. Ecol. 2: 131–139.

Dicke, M., J.J.A. van Loon and R. Soler. 2009. Chemical complexity of volatiles from plants induced by multiple attacks. Nature Chem. Biol. 5: 317–324.

Fatouros, N.E., G. Bukovinszkine'Kiss, L.A. Kalkers, G.R. Soler, M. Dicke and M. Hilker. 2005. Oviposition-induced plant cues: do they arrest *Trichogramma* wasps during host location? Entomol. Exp. Appl. 115: 207–215.

Fatouros, N.E., A. Cusumano, E.G. Danchin and S. Colazza. 2016. Prospects of herbivore egg-killing plant defenses for sustainable crop protection. Ecol. Evol. 6: 6906–6918.

Fatouros, N.E., M. Dicke, R. Mumm, T. Meiners and M. Hilker. 2008. Foraging behaviour of egg parasitoids exploiting chemical information. Behav. Ecol. 19: 677–689.

Fatouros, N.E., F.G. Pashalidou, W.V.A. Cordero, J.J.A. van Loon, R. Mumm, M. Dicke et al. 2009. Anti-aphrodisiac compounds of male butterflies increase the risk of egg parasitoid attack by inducing plant synomone production. J. Chem. Ecol. 35: 1373–1381.

Foti, M.C., M. Rostás, E. Peri, K.C. Park, T. Slimani, S.D. Wratten and S. Colazza. 2017. Chemical ecology meets conservation biological control: identifying plant volatiles as predictors of floral resource suitability for an egg parasitoid of stink bugs. J. Pest Sci. 90: 299–310.

Francis, F., S. Vandermoten, F. Verheggen, G. Lognay and E. Haubruge. 2005. Is the (E)-ß-farnesene only volatile terpenoid in aphids? J. Appl. Entomol. 129: 6–11.

Franco, J.C., E.B. Silva, E. Cortegano, L. Campos, M. Branco, A. Zada et al. 2008. Kairomonal response of the parasitoid *Anagyrus* spec. *nov* near *pseudococci* to the sex pheromone of the vine mealybug. Entomol. Exp. Appl. 126: 122–130.

Franco, J.C., E.B. Silva, T. Fortuna, E. Cortegano, M. Branco, P. Suma et al. 2011. Vine mealybug sex pheromone increases citrus mealybug parasitism by *Anagyrus* sp. near *pseudococci* (Girault). Biol. Control 58: 230–238.

Geiselhardt, S.F., S. Geiselhardt and K. Peschke. 2011. Congruence of epicuticular hydrocarbons and tarsal secretions as a principle in beetles. Chemoecology 21: 181–186.

Glinwood, R.T., W. Powell and C.P.M. Tripathi. 1998. Increased parasitisation of aphids on trap plants alongside vials releasing synthetic aphid sex pheromone and effective range of the pheromone. Biocontrol Sci. Technol. 8: 607–614.

Godfray, H.C.J. 1994. Parasitoids - Behavioural and Evolutionary Ecology. Princeton University Press, Princeton, NJ, USA.

Gols, R. 2014. Direct and indirect chemical defences against insects in a multitrophic framework. Plant Cell Environ. 37: 1741–1752.

Guerrieri, E. 2016. Who's listening to talking plants? pp. 117–136. *In*: J.D. Blande and R. Glinwood [eds.]. Deciphering Chemical Language of Plant Communication, Signaling and Communication in Plants. Springer International Publishing, Gewerbestrasse, Switzerland.

Guillot, F.S. and S.B. Vinson. 1972. Sources of substances which elicit a behavioural response from insect parasitoid, *Campoletis perdistinctus*. Nature 235: 169–170.

Gurr, G.M., S.D. Wratten and M.A. Altieri. 2004. Ecological engineering: a new direction for agricultural pest management. Aust. Farm Bus. Manag. J. 1: 28–35.

Gurr, G.M. and M. You. 2016. Conservation biological control of pests in the molecular era: new opportunities to address old constraints. Front. Plant Sci. 6: 1255.

Hardie, J., S.F. Nottingham, W. Powell and L.J. Wadhams. 1991. Synthetic aphid sex pheromone lures female parasitoids. Entomol. Exp. Appl. 61: 97–99.

Hare, J.D., D.J.W. Morgan and T. Nguyun. 1997. Increased parasitisation of California red scale in the field after exposing its parasitoid, *Aphytis melinus*, to a synthetic kairomone. Entomol. Exp. Appl. 82: 73–81.

Hardy, I.C.W. and M. Goubault. 2007. Wasp fights: understanding and utilising agonistic bethylid behaviour. Biocontrol News Inform. 28: 11–15.

Heil, M. 2014. Herbivore-induced plant volatiles: targets, perception and unanswered questions. New Phytol. 204: 297–306.

Hilker, M. and N.E. Fatouros. 2015. Plant responses to insect egg deposition. Annu. Rev. Entomol. 60: 493–515.

Hilker, M. and J. McNeil. 2008. Chemical and behavioural ecology in insect parasitoids: how to behave optimally in a complex odourous environment? pp. 92–112. *In*: E. Wajnberg, C. Bernstein and J.J.M. van Alphen [eds.]. Behavioural Ecology of Insect Parasitoids: From Theoretical Approaches to Field Applications. Blackwell, Oxford, UK.

Hoffmeister, T.S., B.D. Roitberg and G. Lalonde. 2000. Catching Ariadne by the thread: how a parasitoid exploits the herbivores's marking trails to locate its host. Entomol. Exp. Appl. 95: 77–85.

Huigens, M.E. and N.E. Fatouros. 2013. A hitchhiker's guide to parasitism: chemical ecology of phoretic insect parasitoids. pp. 86–111. *In*: E. Wajnberg and

S. Colazza [eds.]. Chemical Ecology of Insect Parasitoids. Wiley-Blackwell, Oxford, UK.

Huigens, M.E., F.G. Pashalidou, M.H. Qian, T. Bukovinszky, H.M. Smid, J.J.A. van Loon et al. 2009. Hitch-hiking parasitic wasp learns to exploit butterfly antiaphrodisiac. Proc. Natl. Acad. Sci. USA 106: 820–825.

Irvin, N.A., S.L. Scarratt, S.D. Wratten, C.M. Frampton, R.B. Chapman and J.M. Tylianakis. 2006. The effects of floral understoreys on parasitism of leafrollers (Lepidoptera: Tortricidae) on apples in New Zealand. Agric. Forest Entomol. 8: 25–34.

Jaloux, B., C. Errard, N. Mondy, F. Vannier and J.P. Monge. 2005. Sources of chemical signals which enhance multiparasitism preference by a cleptoparasitoid. J. Chem. Ecol. 31: 1325–1337.

James, D.G. and T.R. Grasswitz. 2005. Synthetic herbivore-induced plant volatiles increase field captures of parasitic wasps. BioControl 50: 871–880.

Jang, S.A., J.H. Cho, G.M. Park, H.Y. Choo and C.G. Park. 2011. Attraction of *Gymnosoma rotundatum* (Diptera: Tachinidae) to different amounts of *Plautia stali* (Hemiptera: Pentatomidae) aggregation pheromone and the effect of different pheromone dispensers. J. Asia Pac. Entomol. 14: 119–121.

Jang, S.A. and C.G. Park. 2010. *Gymnosoma rotundatum* (Diptera: Tachinidae) attracted to the aggregation pheromone of *Plautia stali* (Hemiptera: Pentatomidae). J. Asia Pac. Entomol.13: 73–75.

Jonsson, M., S. Wratten, K.A. Robinson and S. Sam. 2009. The impact of floral resources and omnivory on a four trophic level food web. Bull. Entomol. Res. 99: 275–285.

Kaiser, L., P. Ode, S. van Nouhuys, P.-A. Calatayud, S. Colazza, A.-M. Cortesero et al. 2016. The plant as a habitat for entomophagous insects. Adv. Bot. Res. 81: 179–223.

Kaplan, I. 2012. Attracting carnivorous arthropods with plant volatiles: the future of biocontrol or playing with fire? Biol. Control 60: 77–89.

Kessler, A. and I.T. Baldwin. 2002. Plant responses to insect herbivory: the emerging molecular analysis. Annu. Rev. Plant Biol. 53: 299–328.

Kessler, A. and M. Heil. 2011. Evolutionary ecology of plant defences. The multiple faces of indirect defences and their agents of natural selection. Funct. Ecol. 25: 348–357.

Khan, Z.R., C.A.O. Midega, E.M. Njuguna, D.M. Amudavi, J.M. Wanyama and J.A. Pickett. 2008. Economic performance of 'push–pull' technology for stemborer and *Striga* control in smallholder farming systems in western Kenya. Crop Prot. 27: 1084–1097.

Kos, M., J.J.A. van Loon, M. Dicke and L.E.M. Vet. 2009. Transgenic plants as vital components of integrated pest management. Trend. Biotechnol. 27: 621–627.

Krupke, C.H. and J.F. Brunner. 2003. Parasitoids of the consperse stink bug (Hemiptera: Pentatomidae) in North Central Washington and attractiveness of a host-produced pheromone component. J. Entomol. Sci. 38: 84–92.

Lavandero, I.B., S.D. Wratten, R.K. Didham and G. Gurr. 2006. Increasing floral diversity for selective enhancement of biological control agents: a double-edged sward? Basic Appl. Ecol. 7: 236–243.

Lee, J.C. and G.E. Heimpel. 2005. Impact of flowering buckwheat on lepidopteran cabbage pests and their parasitoids at two spatial scales. Biol. Control 34: 290–301.

Li, G. 2006. Host-marking in hymenopterous parasitoids. Acta Entomol. Sinica 49: 504–512.

Lim, U.T. and B.P. Mainali. 2013. Effect of aggregation pheromone trap of *Riptortus pedestris* (Hemiptera: Alydidae) on the distribution and composition of its egg parasitoids. J. Econ. Entomol. 106:1973–1978.

Lo Giudice, D., M. Riedel, M. Rostás, E. Peri and S. Colazza. 2011. Host sex discrimination by an egg parasitoid on brassica leaves. J. Chem. Ecol. 37: 622–628.

Lou, Y.G., M.H. Du, T.C. Turlings, J.A. Cheng and W.F. Shan. 2005. Exogenous application of jasmonic acid induces volatile emissions in rice and enhances parasitism of *Nilaparvata lugens* eggs by the parasitoid *Anagrus nilaparvatae*. J. Chem. Ecol. 31: 1985–2002.

Mainali, B.P. and U.T. Lim. 2012. Annual pattern of occurrence of *Riptortus pedestris* (Hemiptera: Alydidae) and its egg parasitoids *Ooencyrtus nezarae* Ishii and *Gryon japonicum* (Ashmead) in Andong, Korea. Crop Prot. 36: 37–42.

Mansour, R., P. Suma, G. Mazzeo, E. Buonocore, G.K. Lebdi and A. Russo. 2011. Using a kairomone-based attracting system to enhance biological control of mealybugs (Hemiptera: Pseudococcidae) by *Anagyrus* sp. near *pseudococci* (Hymenoptera: Encyrtidae) in Sicilian vineyards. J. Entomol. Acarol. Res. 42: 161–170.

Martorana, L., M.C. Foti, G. Rondoni, E. Conti, S. Colazza and E. Peri. 2017. An invasive insect herbivore disrupts plant volatile-mediated tritrophic signalling. J. Pest Sci. doi:10.1007/s10340-017-0877-5.

Mattiacci, L. and M. Dicke. 1995. The parasitoid *Cotesia glomerata* (Hymenoptera: Braconidae) discriminates between first and fifth larval instars of its host *Pieris brassicae*, on the basis of contact cues from frass, silk, and herbivore-damaged leaf tissue. J. Insect Behav. 8: 485–498.

Mattiacci, L., S.B. Vinson and H.J. Williams. 1993. A long-range attractant kairomone for egg parasitoid *Trissolcus basalis*, isolated from defensive secretion of its host, *Nezara viridula*. J. Chem. Ecol. 19: 1167–1181.

McCormick, A.C., S.B. Unsicker and J. Gershenzon. 2012. The specificity of herbivore-induced plant volatiles in attracting herbivore enemies. Trend. Plant Sci. 17: 303–310.

Mehrnejad, M.R. and M.J.W. Copland. 2006. Behavioural responses of the parasitoid *Psyllaephagus pistaciae* (Hymenoptera: Encyrtidae) to host plant volatiles and honeydew. Entomol. Sci. 9: 31–37.

Meiners, T., N. Hacker, P. Anderson and M. Hilker. 2005. Response of the elm leaf beetle to host plants induced by oviposition and feeding: the infestation rate matters. Entomol. Exp. Appl. 115: 171–177.

Meiners, T. and E. Peri. 2013. Chemical ecology of insect parasitoids: essential elements for developing effective biological control programmes. pp. 193–224. *In*: E. Wajnberg and S. Colazza [eds.]. Chemical Ecology of Insect Parasitoids. Wiley-Blackwell, Oxford, UK.

Meinwald, J. and T. Eisner. 2008. Chemical ecology in retrospect. Proc. Natl. Acad. Sci. USA 105: 4539–4540.

Michereff, M.F.F., M. Michereff-Filho, M.C. Blassioli-Moraes, R.A. Laumann, I.R. Diniz and M. Borges. 2015. Effect of resistant and susceptible soybean cultivars on the attraction of egg parasitoids under field conditions. J. Appl. Entomol. 139: 207–216.

Mills, N.J. and J.M. Kean. 2010. Behavioural studies, molecular approaches, and modeling: Methodological contributions to biological control success. Biol. Control 52: 255–262.

Mills, N.J. and E. Wajnberg. 2008. Optimal foraging behaviour and efficient biological control methods. pp. 3–30. *In*: E. Wajnberg, C. Bernstein and J. van Alphen [eds.]. Behavioural Ecology of Insect Parasitoids: From Theoretical Approaches to Field Application. Blackwell, Oxford, UK.

Mitchell, C., R.M. Brennan, J. Graham and A.J. Karley. 2016. Plant defense against herbivorous pests: Exploiting resistance and tolerance traits for sustainable crop protection. Front. Plant Sci. 7: 1132.

Mizutani, N. 2006. Pheromones of male stink bugs and their attractiveness to their parasitoids. Jpn. J. Appl. Entomol. Zool. 50: 87–99.

Moraes, M.C.B., R.A. Laumann, M. Pareja, F.T.P.S. Sereno, M.F. Michereff, M.A. Birkett et al. 2009. Attraction of the stink bug egg parasitoid, *Telenomus podisi* to defence signals from soybean activated by treatment with *cis*-jasmone. Entomol. Exp. Appl. 131: 178–188.

Moujahed, R., F. Frati, A. Cusumano, G. Salerno, E. Conti, E. Peri et al. 2014. Egg parasitoid attraction toward induced plant volatiles is disrupted by a non-host herbivore attacking above or belowground plant organs. Front. Plant Sci. 5: 601.

Mumm, R. and M. Dicke. 2010. Variation in natural plant products and the attraction of bodyguards involved in direct plant defense. Can. J. Zool. 88: 628–667.

Müller, C. and M. Riederer. 2005. Plant surface properties in chemical ecology. J. Chem. Ecol. 31: 2621–2651.

Nakamura, S., R.T. Ichiki and Y. Kainoh. 2013. Chemical ecology of tachinid parasitoids. pp. 145–167. *In*: E. Wajnberg and S. Colazza [eds.]. Chemical Ecology of Insect Parasitoids. Wiley-Blackwell, Oxford, UK.

Noldus, L.P.J.J. 1989. Semiochemicals, foraging behaviour and quality of entomophagous insects for biological control. J. Appl. Entomol. 108: 425–451.

Obonyo, M., F. Schulthess, B. Le Ru, J. van den Berg, J.F. Silvain and P.A. Calatayud. 2010. Importance of contact chemical cues in host recognition and acceptance by the braconid larval endoparasitoids *Cotesia sesamiae* and *Cotesia flavipes*. Biol. Control 54: 270–275.

Ode, P.J. 2013. Plant defences and parasitoid chemical ecology. pp. 11–36. *In*: E. Wajnberg and S. Colazza [eds.]. Chemical Ecology of Insect Parasitoids. Wiley-Blackwell, Oxford, UK.

Orre, G.U.S., S.D. Wratten, M. Jonsson and R.J. Hale. 2010. Effects of an herbivore-induced plant volatile on arthropods from three trophic levels in brassicas. Biol. Control 53: 62–67.

Orre Gordon, G.U.S., S.D. Wratten, M. Jonsson, M. Simpson and R. Hale. 2013. 'Attract and reward': combining a herbivore-induced plant volatile with floral resource supplementation - multi-trophic level effects. Biol. Control 64: 106–115.

Ozawa, R., K. Shiojiri, M.W. Sabelis, G. Arimura, T. Nishioka and J. Takabayashi. 2004. Corn plants treated with jasmonic acid attract more specialist parasitoids, thereby increasing parasitisation of the common armyworm. J. Chem. Ecol. 30: 1797–1808.

Paine, T.D. 2013. Application of chemical cues in arthropod pest management for forest trees. pp. 282–295. *In*: E. Wajnberg and S. Colazza [eds.]. Chemical Ecology of Insect Parasitoids. Wiley-Blackwell, Oxford, UK.

Park, G.M., S.A. Jang, S.H. Choi and C.G. Park. 2010. Attraction of *Plautia stali* (Hemiptera: Pentatomidae) to different amounts and dispensers of its aggregation pheromone. Korean J. Appl. Entomol. 49: 123–127.

Pashalidou, F.G., M.E. Huigens, M. Dicke and N.E. Fatouros. 2010. The use of oviposition-induced plant cues by *Trichogramma* egg parasitoids. Ecol. Entomol. 35: 748–753.

Peri, E., F. Frati, G. Salerno, E. Conti and S. Colazza. 2013. Host chemical footprints induce host sex discrimination ability in egg parasitoids. PLoS ONE 8: e79054.

Peri, E., G. Salerno, T. Slimani, F. Frati, E. Conti, S. Colazza et al. 2016. The response of an egg parasitoid to substrate-borne semiochemicals is affected by previous experience. Sci. Rep. 6: 27098.

Peri, E., M.A. Sole, E. Wajnberg and S. Colazza. 2006. Effect of host kairomones and oviposition experience on the arrestment behaviour of an egg parasitoid. J. Exp. Biol. 209: 3629–3635.

Pickett, J.A., L.J. Wadhams and C.M. Woodcock. 1997. Developing sustainable pest control from chemical ecology. Agric. Ecosyst. Environ. 64: 149–156.

Pickett, J.A. and Z.R. Khan. 2016. Plant volatile-mediated signalling and its application in agriculture: successes and challenges. New Phytol. 212: 856–870.

Poelman, E.H., M. Bruinsma, F. Zhu, B.T. Weldegergis, A.E. Boursault, Y. Jongema et al. 2012. Hyperparasitoids use herbivore-induced plant volatiles to locate their parasitoid host. PLoS Biol. 10: e1001435.

Poelman, E.H. and M. Kos. 2016. Complexity of plant volatile-mediated interactions beyond the third trophic level. pp. 211–225. *In*: J.D. Blande and R. Glinwood [eds.]. Deciphering Chemical Language of Plant Communication. Springer International Publishing, Gewerbestrasse, Switzerland.

Ponzio, C., P. Cascone, A. Cusumano, B.T. Weldegergis, N.E. Fatouros, E. Guerrieri et al. 2016. Volatile-mediated foraging behaviour of three parasitoid species under conditions of dual insect herbivore attack. Anim. Behav. 111: 197–206.

Powell, W. 1999. Parasitoid hosts. pp. 405–427. *In*: J. Hardie and A.K. Minks [eds.]. Pheromones of Non-Lepidopteran Insects Associated with Agricultural Plants. CABI Publishing, Wallingford, UK.

Powell, W., J. Hardie, A.J. Hick, C. Holler, J. Mann, L. Merritt et al. 1993. Responses of the parasitoid *Praon volucre* (Hymenoptera, Braconidae) to aphid sex-pheromone lures in cereal fields in autumn: implications for parasitoid manipulation. Eur. J. Entomol. 90: 435–438.

Powell, W. and J.A. Pickett. 2003. Manipulation of parasitoids for aphid pest management: progress and prospects. Pest Manag. Sci. 59: 149–155.

Puente, M.E., G.G. Kennedy and F. Gould. 2008a. The impact of herbivore-induced plant volatiles on parasitoid foraging success: a general deterministic model. J. Chem. Ecol. 34: 945–958.

Puente, M., K. Magori, G.G. Kennedy and F. Gould. 2008b. Impact of herbivore induced plant volatiles on parasitoid foraging success: a spatial simulation of the *Cotesia rubecula*, *Pieris rapae*, and *Brassica oleracea* system. J. Chem. Ecol. 34: 959–970.

Quicke, D.L.J. 1997. Parasitic Wasps. Chapman and Hall, London, UK.

Reisenman, C.E., H. Lei and P.G. Guerenstein. 2016. Neuroethology of olfactory-guided behaviour and its potential application in the control of harmful insects. Front. Physiol. 7: 271.

Rodriguez-Saona, C., B.R. Blaauw and R. Isaacs. 2012. Manipulation of natural enemies in agroecosystems: habitat and semiochemicals for sustainable insect pest control. pp. 89–126. *In*: M.L. Larramendy and S. Soloneski [eds.]. Integrated Pest Management and Pest Control: Current and Future Tactics. InTech, Rijeka, Croatia.

Rohwer, C.L. and J.E. Erwin. 2008. Horticultural applications of jasmonates: a review. J. Hortic. Sci. Biotechnol. 83: 283–304.

Roland, J., K.E. Denford and L. Jiminez. 1995. Borneol as an attractant for *Cyzenis albicans*, a tachinid parasitoid of the winter moth, *Operophtera brumata* L. (Lepidoptera, Geometridae). Can. Entomol. 127: 413–421.

Rostás, M. and T.C.J. Turlings. 2008. Induction of systemic acquired resistance in *Zea mays* also enhances the plant's attractiveness to parasitoids. Biol. Control 46: 178–186.

Rostás, M. and M. Wölfling. 2009. Caterpillar footprints as host location kairomones for *Cotesia marginiventris*: persistence and chemical nature. J. Chem. Ecol. 35: 20–27.

Ruther, J. 2013. Novel insights into pheromone-mediated communication in parasitic hymenopterans. pp. 112–144. *In*: E. Wajnberg and S. Colazza [eds.]. Chemical Ecology of Insect Parasitoids. Wiley-Blackwell, Oxford, UK.

Salerno, G., F. De Santis, A. Iacovone, F. Bin and E. Conti. 2013. Short-range cues mediate parasitoid searching behaviour on maize: the role of oviposition-induced plant synomones. Biol. Control 64: 247–254.

Salerno, G., F. Frati, G. Marino, L. Ederli, S. Pasqualini, F. Loreto et al. 2017. Effects of water stress on emission of volatile organic compounds by *Vicia faba*, and consequences for attraction of the egg parasitoid *Trissolcus basalis*. J. Pest Sci. 90: 635–647.

Schnee, C., T.G. Köllner, M. Held, T.C.J. Turlings, J. Gershenzon and J. Degenhardt. 2006. The products of a single maize sesquiterpene synthase form a volatile defense signal that attracts natural enemies of maize herbivores. Proc. Natl. Acad. Sci. USA 103: 1129–1134.

Schröder, R. and M. Hilker.2008. The relevance of background odour in resource location by insects: a behavioural approach. BioScience 58: 308–316.

Simpson, M., G.M. Gurr, A.T. Simmons, S.D. Wratten, D.G. James, G. Leeson et al. 2011a. Insect attraction to synthetic herbivore-induced plant volatile treated field crops. Agric. Forest Entomol. 13: 45–57.

Simpson, M., G.M. Gurr, A.T. Simmons, S.D. Wratten, D.G. James, G. Leeson et al. 2011b. Field evaluation of the 'attract and reward' biological control approach in vineyards. Ann. Appl. Biol. 159: 69–78.

Simpson, M., G.M. Gurr, A.T. Simmons, S.D. Wratten, D.G. James, G. Leeson et al. 2011c. Attract and reward: combining chemical ecology and habitat manipulation to enhance biological control in field crops. J. Appl. Ecol. 48: 580–590.

Simpson, M., D.M.Y. Read and G.M. Gurr. 2013. Application of chemical cues in arthropod pest management for organic crops. pp 266–281. *In*: E. Wajnberg and S. Colazza [eds.]. Chemical Ecology of Insect Parasitoids. Wiley-Blackwell, Oxford, UK.

Sobhy, I.S., M. Erb, A.A. Sarhan, M.M. El-Husseini, N.S. Mandour and T.C.J. Turlings. 2012. Less is more: treatment with BTH and laminarin reduces herbivore-induced volatile emissions in maize but increases parasitoid attraction. J. Chem. Ecol. 38: 348–360.

Sobhy, I.S., M. Erb, Y. Lou and T.C.J. Turlings. 2014. The prospect of applying chemical elicitors and plant strengtheners to enhance the biological control of crop pests. Phil. Trans. Roy. Soc. B 369: 20120283.

Soler, R., T.M. Bezemer and J.A. Harvey. 2013. Chemical ecology of insect parasitoids in a multitrophic above and belowground context. pp 64–85. *In*: E. Wajnberg and S. Colazza [eds.]. Chemical Ecology of Insect Parasitoids. Wiley-Blackwell, Oxford, UK.

Stam, J.M., A. Kroes, Y. Li, R. Gols, J.J.A. van Loon, E.H.I. Poelman et al. 2014. Plant interactions with multiple insect herbivores: from community to genes. Annu. Rev. Plant Biol. 65: 689–713.

Steiner, L.F. 1952. Methyl eugenol as an attractant for oriental fruit fly. J. Econ. Entomol. 45: 241–248.

Stenberg, J.A., M. Heil, I. Ahman and C. Bjorkman. 2015. Optimising crops for biocontrol of pests and disease. Trend. Plant Sci. 20: 698–712.

Suckling, D.M. and G. Karg. 2000. Pheromones and semiochemicals. pp. 63–99. *In*: J. Rechcigl and N. Rechcigl [eds.]. Biological and Biotechnical Control of Insect Pests. CRC Press, Boca Raton, FL, USA.

Suckling, D.M., A.R. Gibb, G.M. Burnip and N.C. Delury. 2002. Can parasitoid sex pheromones help in insect biocontrol? A case study of codling moth (Lepidoptera: Tortricidae) and its parasitoid *Ascogaster quadridentata* (Hymenoptera: Braconidae). Environ. Entomol. 31: 947–952.

Takabayashi, J. 2006. Role of the lipoxygenase/lyase pathway of host-food plants in the host searching behaviour of two parasitoid species, *Cotesia glomerata* and *Cotesia plutellae*. J. Chem. Ecol. 32: 969–979.

Takken, W. and M. Dicke. 2006. Chemical ecology: a multidisciplinary approach. pp. 1–8. *In*: M. Dicke and W. Takken [eds.]. Chemical Ecology: From Gene to Ecosystem. Springer, Dordrecht, Netherlands.

Tamiru, A., Z.R. Khan and T.J.A. Bruce. 2015. New direction for improving resistance to insects by breeding for egg induced defense. J. Insect Sci. 9: 51–55.

Teshiba, M. and J. Tabata. 2017. Suppression of population growth of the Japanese mealybug, *Planococcus kraunhiae* (Hemiptera: Pseudococcidae), by using an attractant for indigenous parasitoids in persimmon orchards. Appl. Entomol. Zool. 52: 153–158.

Teshiba, M., H. Sugie, T. Tsutsumi and J. Tabata. 2012. A new approach for mealybug management: recruiting an indigenous, but 'non-natural' enemy for biological control using an attractant. Entomol. Exp. Appl. 142: 211–215.

Thaler, J.S., M.A. Farag, P.W. Paré and M. Dicke. 2002. Jasmonate-deficient plants have reduced direct and indirect defences against herbivores. Ecol. Lett. 5: 764–774.

Turlings, T.C.J. and J. Ton. 2006. Exploiting scents of distress: the prospect of manipulating herbivore-induced plant odours to enhance the control of agricultural pests. Curr. Opin. Plant Biol. 9: 421–427.

Uefune, M., Y. Choh, J. Abe, K. Shiojiri, K. Sano and J. Takabayashi. 2012. Application of synthetic herbivore-induced plant volatiles causes increased parasitism of herbivores in the field. J. Appl. Entomol. 136: 561–567.

van Dam, N.M. and M. Heil. 2011. Multitrophic interactions below and above ground: en route to the next level. J. Ecol. 99: 77–88.

van Poecke, R.M.P. and M. Dicke. 2002. Induced parasitoid attraction by *Arabidopsis thaliana*: involvement of the octadecanoid and the salicylic acid pathway. J. Exp. Bot. 53: 1793–1799.

Vet, L.E.M. and M. Dicke. 1992. Ecology of infochemical use by natural enemies in a tritrophic context. Annu. Rev. Entomol. 37: 141–172.

Vieira, C.R, M.C.B. Moraes, M. Borges, E.R. Sujii and R.A. Laumann. 2013. cis-Jasmone indirect action on egg parasitoids (Hymenoptera: Scelionidae) and its application in biological control of soybean stink bugs (Hemiptera: Pentatomidae). Biol. Control 64: 75–82.

Von Mérey, G., N. Veyrat, G. Mahuku, R.L. Valdez. T.C.J. Turlings and M. D'Alessandro. 2011. Dispensing synthetic green leaf volatiles in maize fields increases the release of sesquiterpenes by the plants, but has little effect on the attraction of pest and beneficial insects. Phytochemistry 72: 1838–1847.

Voytas, D.F. and C. Gao. 2014. Precision genome engineering and agriculture: opportunities and regulatory challenges. PLoS Biol. 12: e1001877.

Wajnberg, E. 2004. Measuring genetic variation in natural enemies used for biological control: Why and how? pp. 19–37. *In*: L. Ehler, R. Sforza and Th. Mateille [eds.]. Genetics, Evolution and Biological Control. CAB International, Wallingford, UK.

Wajnberg, E., B.D. Roitberg and G. Boivin. 2016. Using optimality models to improve the efficacy of parasitoids in biological control programmes. Entomol. Exp. Appl. 158: 2–16.

Wäschke, N., T. Meiners and M. Rostás. 2013. Foraging strategies of parasitoids in complex chemical environments. pp. 37–63. *In*: E. Wajnberg and S. Colazza [eds.]. Chemical Ecology of Insect Parasitoids. Wiley-Blackwell, Oxford, UK.

Witzgall, P., P. Kirsch and A. Cork. 2010. Sex pheromones and their impact on pest management. J. Chem. Ecol. 36: 80–100.

Wölfling, M. and M. Rostás. 2009. Parasitoids use chemical footprints to track down caterpillars. Commun. Integr. Biol. 2: 353–355.