Semiochemicals from plants and insects on the foraging behavior of Platygastridae egg parasitoids

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Abstract – The objective of this review was to summarize the current information about semiochemicals with potential to be applied in insect pest management in agroecosystems. One of the great challenges to Neotropical agriculture is to reduce the indiscriminate use of pesticides, which can be minimized by using semiochemicals, a tool that can be applied in the field to manage pests and their natural enemies. In addition, small lipophilic molecules from insects and from the secondary metabolism of plants play a fundamental role in the chemical communication of different species that are present in important crops.

Index terms: chemical communication, herbivore-induced plant volatiles (HIPVs), oviposition-induced plant volatiles (OIPVs), pest control, pheromone, synomone.

Semioquímicos de plantas e insetos no comportamento de busca de parasitoides de ovos Platygastridae

Resumo – O objetivo deste artigo de revisão foi reunir informações atuais sobre semioquímicos com potencial para serem aplicados no manejo de insetos-praga em agroecossistemas. Um dos grandes desafios para a agricultura Neotropical é reduzir o uso indiscriminado de pesticidas, que pode ser minimizado pelo uso de semioquímicos, uma ferramenta que pode ser aplicada no campo para o manejo de pragas e de seus inimigos naturais. Além disso, pequenas moléculas lipofílicas dos insetos e do metabolismo secundário de plantas desempenham papel fundamental na comunicação química das diferentes espécies que estão presentes em importantes culturas.

Termos para indexação: comunicação química, voláteis de planta induzidos pela herbivoria (HIPVs), voláteis de planta induzidos pela oviposição (OIPVs), controle de pragas, feromônios, sinomônios.

Introduction

Increasing plant diversity in agroecosystems reduces herbivorous populations and increases the abundance of natural enemies and, consequently, their impact on pests (Schoonhoven et al., 2005). This shows that plant biodiversity could be better explored. An alternative is intercropping or multiple cropping systems using sentinel plants that release volatiles attractive to natural enemies and repellent to herbivores, pushing them away from the target crop, as in a push-pull system (Cook et al., 2007). Another, not yet used but not novel approach, is the adoption of herbivore- and oviposition-induced plant volatiles (HIPVs and OIPVs, respectively) in crop systems. HIPVs and OIPVs are used by plants in their defense against herbivores, to attract and retain their natural enemies (Vet & Dicke, 1992). Besides plant volatiles, semiochemicals from other sources, such as insects, are also used by natural enemies when foraging for hosts and, therefore, might also be used to manipulate their behavior (Vet & Dicke, 1992).

Semiochemicals from plants and insects may be a valuable tool because they can be used for behavioral manipulation of parasitoids, improving their impact on pest populations in agroecosystems. Foraging behavior of parasitoids includes several sequential steps: habitat location, host location and suitability, and oviposition (Godfray, 1994). During these steps, parasitoids can use physical, biochemical, and, mainly, semiochemical cues (Vinson, 1985; Godfray, 1994). The knowledge of the different steps and of the identification of the cues used by the parasitoids in each maneuver could be

relevant to select and obtain semiochemicals that can be used for behavior manipulation.

Egg parasitoids from the Platygastridae family have been shown to be very efficient to control herbivorous pests, especially from the Pentatomidae family (Corrêa-Ferreira, 2000). In Brazil, one of the main soybean (*Glycine max* L.) pests, the brown stink bug *Euschistus heros* (Fabricius) (Hemiptera: Pentatomidae) might be controlled by these parasitoids, which include *Telenomus podisi* Ashmead and *Trissolcus basalis* (Wollaston) (Hymenoptera: Platygastridae) (Michereff et al., 2015). The occurrence of these parasitoids together with *Trissolcus teretis* (Johnson), *Trissolcus urichi* (Crawford), and *Trissolcus brochymenae* (Ashmead) has been widely reported in soybean crops in the country, and *T. podisi* is the most abundant natural enemy of *E. heros* in soybean crops, with >80% parasitism of host eggs (Pacheco & Corrêa-Ferreira, 2000; Michereff et al., 2015).

Since 1950, the negative effect of insecticide application to natural enemies has been observed, and studies have shown that the reestablishment of the parasitoid population takes a long time (Pickett, 1959). Nowadays, due to the intense use of pesticides, natural enemies have a restrict action in the field (Cônsoli et al., 1998).

This review will highlight: plant defense mechanisms and their interaction with natural enemies; important studies conducted in the laboratory and the field, using arable crops, as well as HIPVs and OIPVs; host semiochemicals used to attract natural enemies and for eavesdropping by parasitoids; and the main gaps to efficiently use HIPVs on field conditions to attract natural enemies.

Plant defense mechanisms against herbivores and oviposition

Plants are equipped with several mechanisms to defend themselves against herbivores, microbial pathogens, or abiotic stress, such as hydro or mechanical damage. Plant resistance against insects can be physical, morphological, or chemical. Chemical defenses in plants are derived from the secondary metabolism and can be constitutive or induced (Chen, 2008; Heil, 2008). The constitutive defense is expressed continuously, independently of biotic or abiotic stress, and it is related to the production of different types of compounds, such as proteins, amino acids, sugar, and secondary metabolites (Schoonhoven et al., 2005; Chen, 2008; Heil, 2008). Induced defense is a plant response to damage or stress, which can result in an increase in the production of volatile organic compounds, for example (War et al., 2012; Heil, 2014).

Herbivore-induced plant volatiles are released in greater amounts than constitutive volatiles. Therefore, HIPVs are more easily detectable at long distances by parasitoids, when compared, for example, to volatiles emitted by herbivores themselves or host eggs, carrying on important information to natural enemies about the location of their hosts (Vet & Dicke, 1992; Dicke, 1999) (Figure 1). Both types of defense can be classified as direct, when directly affecting herbivores; or as indirect, when attracting and retaining natural enemies. Direct defense can involve: the reduction of vegetal tissue nutritional quality, in which the plants reduce the supply of essential metabolites to the herbivore; and the production of compounds that minimize herbivore performance or the production of deleterious (toxic) substances to the herbivore (Chen, 2008; War et al., 2012). In indirect defense, plants can 'cry for help', attracting the natural enemies of herbivores, through the release of HIPVs or OIPVs that are used by natural enemies as cues to find their host (Kessler & Baldwin, 2002; Heil, 2008; Hilker & Fatouros, 2015).

Constitutive indirect plant defense chiefly involves the interaction among extrafloral nectaries, food bodies, and domatia with natural enemies. These secretions and structures are used by natural enemies, mainly ants, as food and housing (Schoonhoven et al., 2005; Heil, 2008), but also by other insects, such as ladybird beetles (Pemberton & Vandenberg, 1993), and predatory (Cuautle & Rico-Gray, 2003) and parasitoid wasps (Heil, 2008). Chemical and morphological plant attributes can directly influence the survival, fecundity, and foraging success of natural enemies. These traits can also have indirect effects on the quality of the herbivores that feed on these plants, which, in turn, alters the physiology, behavior, or development of their natural enemies (Cortesero et al., 2000; Chen et al., 2015).

The indirectly-induced plant defense in insect-plant relationships can be elicited by herbivory and/or oviposition injury, which induces the production of volatile organic compounds and also of extrafloral nectaries (Price, 1997; Heil, 2004, 2008; Chen, 2008;

Moraes et al., 2008). The HIPVs and OIPVs vary depending on plant species and cultivars, and influence in different ways the foraging behavior of parasitoids, such as *T. podisi* that is attracted differently to HIPVs released by three different plant species (Dias, 2015) and soybean cultivars (Michereff et al., 2011). The HIPVs emitted by the resistant soybean cultivars Dowling and IAC 100, in laboratory bioassays, attracted *T. podisi*, whereas the HIPVs emitted by the susceptible cultivar Silvânia did not (Michereff et al., 2011); a similar result was observed when these cultivars were evaluated in field conditions (Michereff et al., 2015). Therefore, the effect on the third trophic level might be taken into consideration in the development of resistant plant cultivars. These issues have been proposed since the first studies with HIPVs and natural enemies in the late 1980's, but until now there are only few examples of the role played by genetic engineering crops on the third trophic level, and none of their commercial use (Vet & Dicke, 1992; Schnee et al., 2006).

Plants change the blend of volatile organic compounds in response to damage, either qualitatively or quantitatively (Dicke, 1999), which depends mostly on plant traits that vary among species or genotypes,

and also on the different herbivore species causing the damage (Lin et al., 2008; Rasmann & Turlings, 2008). Furthermore, the chemical profile emitted by herbivore- or oviposition-damaged plants can be markedly different from those of undamaged and mechanically-damaged ones (Moraes et al., 2005, 2008; Michereff et al., 2011). This change can be responsible for the differential attraction of parasitoids and predators (Hoballah & Turlings, 2001). Several works have proposed the use of the plant strategy 'cry for help' in crop systems to manage pests and natural enemies. In addition, these studies suggest that these volatile compounds could increase the effect of natural enemies on herbivores, promoting a cascading effect on the lower trophic levels, leading to a reduction in feeding damage and enhancing plant fitness. However, herbivore-induced volatiles do not always play a role in the 'cry for help' strategy and can present a negative effect on plant fitness. The predator *Thanasimus dubius* (Fabricius) (Coleoptera: Cleridae) feeds on bark beetle adults and eggs; however, its attraction occurs when there is no way to save the plant anymore, meaning that without tree death this predator does not have its source of food (Erbilgin & Raffa et al., 2001).
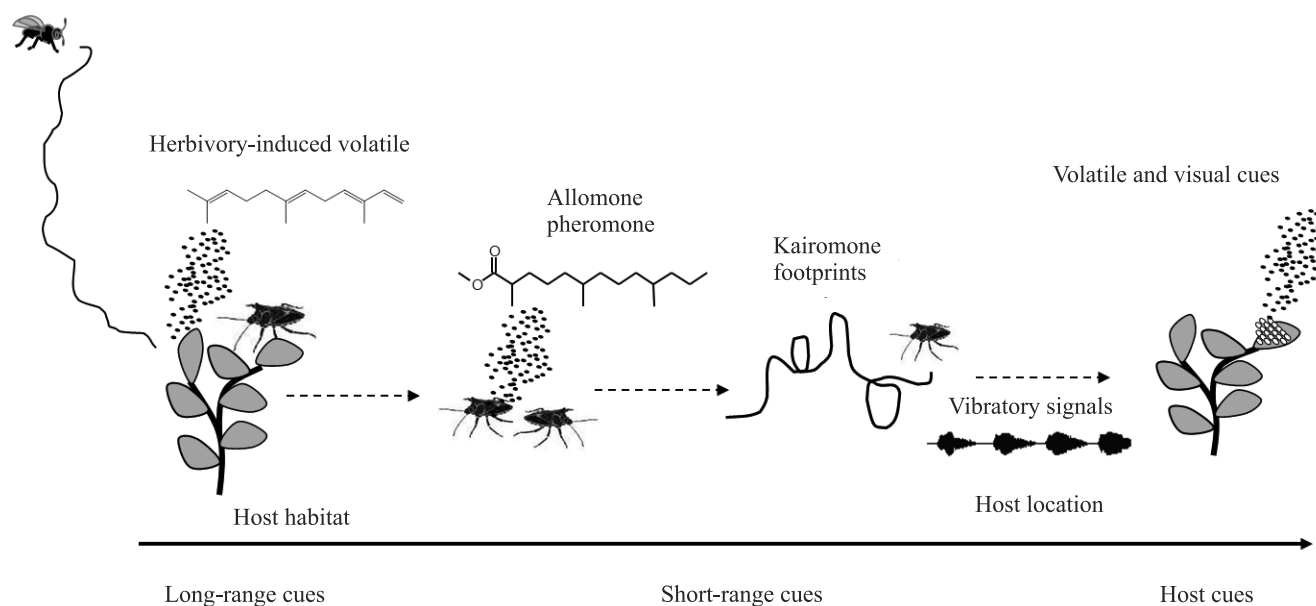

Figure 1. Main cues used by *Telenomus podisi* when searching for hosts, i.e., eggs of Pentatomidae. Long-range cues involve volatiles from plants, constitutive and herbivory-induced volatiles; and short-range cues involve volatile compounds, such as sex pheromones and volatiles from eggs, as well as less volatile or non-volatile compounds, including kairomone footprints, compounds from the host, vibratory signals, and visual cues.

HIPVs/OIPVs and their potential to manage parasitoids in arable crops

The HIPV and OIPV compounds from different plants are well studied and identified. These compounds, in general, are derived from the terpenoid, shikimic, and lipoxygenase pathways (Dudareva & Pichersky, 2008). However, there are still several questions about the importance of these compounds and how they affect the attraction of natural enemies. Most of the pioneering works on HIPVs and their effects on parasitoid behavior were conducted on arable crops, such as maize (*Zea mays* L.), by Turlings et al. (1991) and Takabayashi et al. (1995); cotton (*Gossypium hirsutum* L.), by Turlings et al. (1995) and Cortesero et al. (1997); rice (*Oryza sativa* L.), by Lou et al. (2005) and Melo Machado et al. (2014); soybean, by Moraes et al. (2005, 2008) and Michereff et al. (2011, 2013); and bean (*Phaseolus vulgaris* L.), by Colazza et al. (2004).

Soybean plants and pigeon pea [*Cajanus cajan* (L.) Millsp. (Fabales: Fabaceae)] herbivored by *E. heros* release a similar volatile profile that attracts the egg parasitoid *T. podisi*. However, when soybean is feeding-damaged by *Anticarsia gemmatalis* Hübner (Lepidoptera: Noctuidae) larvae, the chemical profile becomes different and does not attract *T. podisi* (Moraes et al., 2005). Colazza et al. (2004) reported that *T. basalis* is attracted by synomones released by two different legume species, when the plants are damaged by herbivores and oviposition. Different soybean cultivars damaged by *E. heros* herbivory release a similar chemical profile between them and, in comparison to undamaged soybean plants, produce higher amounts of several compounds, such as (*E,E*)-α-farnesene, methyl salicylate, (*Z*)-3-hexenyl acetate, and (*E*)-2-octen-1-ol (Moraes et al., 2008; Michereff et al., 2011). Olfactometer bioassays conducted with *T. podisi* and these compounds, in different mixtures and concentrations, showed that this parasitoid responds only to (*E,E*)-α-farnesene, as a single compound. However, when (*E,E*)-α-farnesene is compared to HIPVs, *T. podisi* responds preferentially to HIPVs, showing that there are other important compounds in host recognition for this parasitoid (Michereff et al., 2013). Parasitoids can also perceive HIPVs and OIPVs after landing on the host plants (Conti et al., 2010). For example, cabbage (*Brassica oleracea* L.) plants respond to oviposition of *Murgantia histrionica* (Hahn) (Hemiptera: Pentatomidae), releasing volatiles that are explored by *T. brochymenae* after they have landed on the plant (Conti et al., 2010).

The identification of HIPV or OIPV key compounds to which parasitoids are attracted to is a very complex task. Egg parasitoids are able to recognize and respond to HIPVs from different plant species that were herbivore-damaged by a common herbivore, as described by Dias (2015), who found that *T. podisi* recognized the volatiles emitted by maize, pigeon pea, and sunflower [*Helianthus annuus* L. (Asterales: Asteraceae)] damaged by its preferred host, *E. heros*; these three plants present a different chemical profile of volatiles. The described studies represent well the complexity of the interactions between plants, herbivores, and natural enemies.

This complexity is spread to other parasitoid families as well. Another example of it occurs in maize, in which studies have shown that different maize cultivars release typical blends, containing: green leaf volatiles, such as (*Z*)-3-hexenal, (*E*)-2-hexenal, (*Z*)-hexen-1-ol, and (Z)-3-hexen-1-yl-acetate; terpenoid compounds like linalool, (*E*)-4,8-dimethyl-1,3,7-nonatriene (DMNT), (3*E*,7*E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene (TMTT), α-bergamotene, (*E,E*)-α-farnesene, (*E*)-β-farnesene, and nerolidol; and compounds from the shikimic acid pathway, including benzyl, phenethyl acetate, and indole (Gouinguené et al., 2003). When maize plants are injured by *Spodoptera* spp. (Lepidoptera: Noctuidae) feeding, the chemical profile changes quantitatively and attracts natural enemies, such as *Cotesia marginiventris* Cresson and *Microplitis rufiventris* Kokujev (Hymenoptera: Braconidae) (Turlings et al., 1991, 2004). When maize plants suffer herbivore damage by *Spodoptera* spp., the main compound released is indole, but bioassays showed that this compound apparently does not influence the response of *C. marginiventris* (D'Alessandro et al., 2006). However, when the minor compounds of the blend released by maize plants are removed, this parasitoid does not respond anymore (D'Alessandro et al., 2009). Recently, Erb et al. (2015) reported that the herbivore-induced indole is used as a signal of danger by other plants, inducing a priming effect on maize plants.

In this scenario, HIPVs can serve as indirect cues for egg parasitoids, providing information about

the presence of eggs, for example, that are more inconspicuous, leading parasitoids to use these volatiles to locate plants with potential hosts (Blassioli-Moraes et al., 2011; Michereff et al., 2011; Peñaflor et al., 2011). The egg parasitoid *Telenomus remus* Nixon (Hymenoptera: Platygastridae) is attracted to HIPVs from maize plants damaged by *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae), after associating these volatiles with oviposition (Peñaflor et al., 2011). Soybean plants herbivore-damaged by *E. heros* also attract *T. podisi*, but soybean plant volatiles induced by oviposisiton do not (Moraes et al., 2008; Michereff et al., 2011). However, the combination HIPVs + OIPVs results in different profiles of chemical volatiles, attracting the parasitoid (Moraes et al., 2008; Michereff et al., 2011). Similar behavior was observed for *T. basalis*, in which bean plant OIPVs induced by *Nezara viridula* L. (Hemiptera: Pentatomidae) were not attractive to this parasitoid, but the combination HIPVs + OIPVs was (Colaza et al., 2004), suggesting that herbivore damage and oviposition appear to act synergistically.

Studies with other parasitoid families have shown that the laid egg can also induce indirect plant defense, releasing chemical volatiles that attract egg parasitoids in the laboratory and in the field (Hilker & Meiners, 2006, 2010). The possibility of using these OIPVs was shown in a non-arable crop, the European field elm *Ulmus minor* Mill. (Rosales: Ulmaceae). When *U. minor* is damaged by the eggs laid by the beetle *Xanthogaleruca luteola* Müler (Coleoptera: Chrysomelidae), it releases a blend of OIPVs that attracts the specialist egg parasitoid *Oomyzus gallerucae* Fonscolombe (Hymenoptera: Eulophidae). This study showed that the homoterpene DMNT is an important component in the attraction of this egg parasitoid. In field tests, plants with DMNT-baited traps attracted more *O. gallerucae* than plants with unbaited ones (Büchel et al., 2011). It should be highlighted that there are no studies showing the attraction of Platygastridae parasitoids to OIPVs without the association of other volatiles. However, in a study to evaluate the influence of volatiles released by egg extracts of the stink bug *E. heros* and of soybean plants treated with them on the foraging behavior of *T. podisi*, this parasitoid was attracted to: volatiles emitted by one egg cluster compared to air; the acetonic extract of one egg cluster compared to acetone; and the acetonic extract of one egg cluster compared to the acetonic extract of 100 egg clusters. These results suggest that one egg cluster and its acetonic extract have volatile compounds that change *T. podisi* foraging behavior, and that the amounts and surroundings of these compounds are important for their recognition by this parasitoid.

Semiochemicals from host or host-associated to manage parasitoids

For plant volatiles, there is a large amount of information about chemicals from host or host-associated cues that parasitoids exploit when foraging. These cues can include: sex, alarm, or other pheromones; host-derivative products, as feces/ frass, debris, scale, honeydew, or host footprints; or habitat or microhabitat components (Godfray, 1994; Fatouros et al., 2008; Colazza et al., 2010). According to Aldrich (1985), an egg parasitoid can use chemical information produced by stink bugs to locate females and, indirectly, stink bug eggs.

Differently from HIPVs and OIPVs, host or host-associated cues are used by parasitoids during different steps of host searching and selection behavior, as in habitat location, host location, or host selection (Godfray, 1994; Fatouros et al., 2008). Furthermore, cues associated to host location and host selection present a more diverse nature than cues used for habitat location, and could stimulate other behaviors than taxis or kinesis locomotor responses, which are typically recorded when parasitoids are stimulated with HIPVs and OIPVs (Laumann et al., 2011; Michereff et al., 2011, 2013).

In general, information from plants, such as herbivore- or oviposition-induced volatiles, is used as long-range cues to locate the host (Kessler & Baldwin, 2002; Moraes et al., 2005, 2008). For short-range cues, when close to the host, parasitoids may use defensive compounds, sex pheromones, and cuticular hydrocarbons (Borges et al., 1998, 2003; Laumann et al., 2009). When parasitoids are close to the host or have physical contact with it, semi- or non-volatile compounds, such as footprints and egg composition, become important for host final recognition, as well as other physical or visual factors, such as texture, color, and vibratory information (Borges et al., 2003; Aquino et al., 2012) (Figure 1).

Telenomus podisi is an egg parasitoid of pentatomid bugs that prefers egg masses of the Neotropical brown stink bug, *E. heros*, whereas *T. basalis* shows preference for egg masses of the Southern green stink bug, *N. viridula* (Corrêa-Ferreira, 2000; Sujii et al., 2002). Despite this preference, Tognon et al. (2014), while studying the influence of original hosts on the chemotaxic behavior and parasitism of *T. podisi*, observed that when *Tibraca limbativentris* Stål (Hemiptera: Pentatomidae) was the original host, the females parasitized this species over *E. heros*, whereas those emerging from *E. heros* exclusively parasitized *E. heros*' eggs, suggesting that the original host can exert influence on their choice. It is important to note that the parasitoid's host searching begins with an innate behavior; however, this can be modified by successive exposure to a particular host, which can result in learning behavior during the development of the immature stage, remaining as an olfactory memory in the adult stage (Vet & Dicke, 1992; Tognon et al., 2013).

Studies have shown that the parasitoid species *T. podisi* and *T. basalis*, besides HIPVs, use semiochemicals from stink bugs and also from their egg masses. Several arena bioassays have been carried out using single and/or simultaneous stimuli, such as egg masses; live virgin *E. heros* males and females; volatile extracts of sexually mature *E. heros* males and females; 2,6,10-methyl-trimethyltridecanoate, a component of the *E. heros* sex pheromone; (*E*)-2-hexenal, a component of the *E. heros* metathoracic gland; and hexane or air as a control. In these assays, *T. podisi* females responded to the *E. heros* male extracts, to 2,6,10-methyl-trimethyltridecanoate, and to (*E*)-2-hexenal, showing that they use chemical cues from *E. heros* to find their host egg masses (Borges & Aldrich, 1992; Silva et al., 2006). *Trissolcus basalis* responds positively to 4-oxo-(*E*)-2-hexenal and (*E*)-2-decenal, two major components present in *N. viridula* glandular secretion, whereas *T. podisi* is attracted to crude gland extracts of the preferred host, *E. heros*, and has its walking pattern altered when stimulated with 4-oxo-(*E*)-2-hexenal (Silva et al., 2006). Besides that, *T. podisi* also responds positively to two major components of *E. heros* glands: (*E*)-2-hexenal and tridecane. These results indicate some degree of specialization in the response of two generalist parasitoid species towards defensive secretions of stink bugs (Laumann et al.,

2009). *Telenomus calvus* (Ashmead) uses pheromones produced by male *Podisus maculiventris* and *Podisus neglectus* (Westwood) (Hemiptera: Pentatomidae) as an indirect mechanism to locate *Podisus* eggs (Aldrich, 1995). This parasitoid requires eggs less than 12 hours old to successfully develop, and so it needs a reliable method of locating fresh eggs. All pheromone blends of male *Podisus* sp. contain (*E*)-2-hexenal, benzyl alcohol, and α-terpineol, providing a reliable cue for the wasp.

At short-range foraging behavior, *T. podisi* recognizes volatile footprints from *E. heros* males (Borges et al., 2003; Silva et al., 2006). Two different strains of *T. podisi*, one from Brazil and the other from the USA, show different foraging behavior when stimulated by *E. heros* footprints. The Brazilian strain recognizes *E. heros* footprints, whereas the North American one does not show the same behavior and ignores the footprints of *E. heros* females, despite the fact that these parasitoids were reared from *E. heros* eggs (Borges et al., 2003). The obtained results indicate a high degree of specialization of natural enemies to recognize the adequate host. The North American strain used as host mainly eggs from *N. viridula* and from other North American species of the genus *Euschistus* (Borges et al., 2003). The same was observed for *T. basalis*, which could differentiate footprints from females and males of its host *N. viridula* (Colazza et al., 2007). The chemical footprints of *N. viridula* left on leaves change the foraging behavior of *T. basalis*; and the chemical footprints induce arrestment behavior on this egg parasitoid (Colazza et al., 2009). In another study, Salerno et al. (2009) showed that *T. brochymenae* prefers the traces left by mated females of *M. histrionica*, when compared to traces from virgin females, males, or parous host females.

In a multisensory condition, *T. podisi* uses olfactory signals to find its host at long distance. This corroborates previous studies that showed that host location is oriented primarily by olfactory cues released directly from the nontarget host egg, which is more detectable and reliable (Vet & Dicke, 1992; Borges et al., 1998). However, in this case, visual information from the substrate could be relevant (Aquino et al., 2012). Once on the plant, the parasitoid probably passes through different steps of searching behavior. The initial searching behavior could be random or may show directionality mediated by the stink bug's vibratory signals, visual cues, or even chemicals with low

volatility, such as cuticular hydrocarbon or volatiles from egg masses and footprints (Borges et al., 2003; Conti et al., 2010; Laumann et al., 2011; Tognon et al., 2014), followed by the final recognition of the host through chemical and physical contact traits, including visual cues (Figure 1).

The potential to apply semiochemicals in arable crops to attract parasitoids

Semiochemicals can be applied directly on plants, as spray, inducing the production of defensive chemical volatiles, which attract parasitoids, or by using a slow release dispenser, which releases the semiochemical, attracting directly natural enemies (Simpson et al., 2011; Vieira et al., 2013). The use of semiochemicals as a strategy to improve biological control has potential to work by itself, but, if combined with other strategies, its success could probably be enhanced. In general, parasitoids follow chemical cues to find their host, but if they do not find the host or a reward, i.e., food or any factor that retains them in the area, they can associate this chemical cue to the absence of host or food, and, by learning this new information, change their response by ignoring this cue (Vet & Dicke, 1992; Blassioli-Moraes et al., 2013). Therefore, semiochemicals could be applied together with habitat manipulation, using a diversity of plants containing nectar or using push-pull systems, combining different stimuli to manipulate natural enemies and pest behavior (Cook et al., 2007; Simpson et al., 2011).

In Brazil, there are few examples of field experiments using semiochemicals to attract and retain parasitoids in field conditions. Two compounds have been evaluated in soybean fields using different approaches: (E)-2-hexenal, with slow release dispensers (rubber septa) distributed randomly on the plots (Vieira et al., 2014); and cis-jasmone, a natural phytohormone that induces the indirect defense of soybean plants (Moraes et al., 2009), sprayed directly on soybean plots, inducing them to produce volatiles (Vieira et al., 2013). Both strategies attracted Platygastridae egg parasitoids. According to Vieira et al. (2013), the richness of parasitoids was higher in soybean areas with greater plant diversity than in soybean areas only with Crotalaria juncea L. (Fabales: Fabaceae) matrix plots.

The number of studies conducted in field conditions using semiochemicals increased in the last few years, but information is still scarce (Blassioli-Moraes et al.,

2013). This is mainly due to the difficulties in knowing which compound is attractive to parasitoids in laboratory bioassays. Besides this, there are several other questions that need to be answered before field tests are placed: what amount of compounds should be used? how should they be applied? and what is the release rate necessary to attract these parasitoids? (Simpson et al., 2011; Blassioli-Moraes et al., 2013; Colazza et al., 2013). Considering these issues, one alternative is to manipulate the plants to produce and release specific volatiles, which can be done by classical breeding or genetic engineering (Schnee et al., 2006; Kunert et al., 2010; Michereff et al., 2011; Bruce et al., 2015). There is no example in the literature on this subject for transgenic transformed arable crops. However, maize transformed with a (E)-β-caryophyllene synthase gene from oregano (Origanum vulgare L.), resulting in constitutive emissions of this sesquiterpene, attracts more entomopathogenic nematodes, minimizing the damage provoked by Diabrotica spp. (Coleoptera: Chrysomelidae) root larvae (Degenhardt et al., 2009). One of the major questions concerning the continuous release of volatiles by modified plants, which, in a natural context, would only occur when the plants are disturbed, is if this difference on release timing will have the same effect on natural enemies (Kunert et al., 2010). An alternative to this problem is to identify genes that prime the chemical defense of the plants.

An easy way to manipulate natural enemies in the field is to detect cultivars and plants that can naturally attract natural enemies and keep off herbivores. Recently, Michereff et al. (2015) showed that three different soybean cultivars – two resistant (Dowling and IAC 100) and one susceptible (Silvânia) – attracted differently the egg parasitoids T. podisi and T. basalis, from the Platygastridae family, in field conditions. The authors suggest that volatiles released by the Dowling cultivar, which attracted more parasitoids, might be involved in this differential attraction.

Parasitoids can be highly specialized in relation to the chemical cues used for host searching. Moreover, in several plant-herbivore-parasitoid systems, this specificity could be related to plant genotypes, plant physiology, phenological stages, host developmental stage, among others (Turlings et al., 1995; Moraes et al., 2005). This suggests that the use of semiochemicals for parasitoid management needs to be studied

case-by-case, and adaptations should be introduced in each particular situation.

Concluding remarks

These and other studies show that the interaction plant-natural enemies mediated by HIPVs and OIPVs has a decisive role on parasitoid host-searching behavior, and that plant biology, genetic and phenotypic characteristics also have a determinant role on community dynamics and biodiversity, with evolutionary consequences for both plant and natural enemies (Hare, 2011).

To summarize, plants have developed sophisticated defense strategies against biotic stressors (pests) using a variety of inducible defense mechanisms that can be exploited in crop protection. Besides their effect against herbivores and their attraction of natural enemies, the small lipophilic molecules released by plants also affect neighboring plants, which can respond to stress signaling by elicitation or augmentation (priming) of the defense response (Kim & Felton, 2013; Erb et al., 2015). The ability to elicit or prime crop plants for defense upon detection of plant stress signaling provides an opportunity to develop new mixed cropping systems, and the identified stress signals associated with pest damage in the sentinel (guard crops) can be used for the activation of defense responses in the main crop.

Therefore, plant volatiles can be used in the field with different approaches: to apply synthetic plant semiochemicals to induce plant defense or attract natural enemies; in intercropping or multiple cropping systems, using plants that release volatiles that attract natural enemies and repel herbivores, pushing away the pests from the target crop; and to provide trap crops that are cultivated around the target crop to attract the pests.

Although there is a considerable amount of studies on the use of semiochemicals by natural enemies, the knowledge of how these semiochemicals can be applied in field conditions to favor the action of these parasitoids is still limited. Research on the learning ability of Platygastridae parasitoids and on how they recognize odor blends will provide information about the right doses and the right time for the application of semiochemicals, greatly helping in their correct application in the field.

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