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Herbivore-Induced Plant Volatiles to Enhance Biological Control in Agriculture

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Abstract

Plants under herbivore attack synthetize defensive organic compounds that directly or indirectly affect herbivore performance and mediate other interactions with the community. The so-called herbivore-induced plant volatiles (HIPVs) consist of odors released by attacked plants that serve as important cues for parasitoids and predators to locate their host/prey. The understanding that has been gained on the ecological role and mechanisms of HIPV emission opens up paths for developing novel strategies integrated with biological control programs with the aim of enhancing the efficacy of natural enemies in suppressing pest populations in crops. Tactics using synthetic HIPVs or chemically/genetically manipulating plant defenses have been suggested in order to recruit natural enemies to plantations or help guiding them to their host more quickly, working as a "synergistic" agent of biological control. This review discusses strategies using HIPVs to enhance biological control that have been proposed in the literature and were categorized here as: (a) exogenous application of elicitors on plants, (b) use of plant varieties that emit attractive HIPVs to natural enemies, (c) release of synthetic HIPVs, and (d) genetic manipulation targeting genes that optimize HIPV emission. We discuss the feasibility, benefits, and downsides of each strategy by considering not only field studies but also comprehensive laboratory assays that present an applied approach for HIPVs or show the potential of employing them in the field.

Introduction

Plants constitutively emit volatile organic compounds (VOCs) that herbivores exploit for host location (Jolivet 1998). Under herbivore attack, plants will emit a much larger diversity and amount of VOCs, which consist of specific and detectable cues for a wide range of natural enemies to locate their host/prey (Paré & Tumlinson 1999, Howe & Jander 2008). In the past, scientists believed that natural enemies were mainly guided by olfactory cues derived from hosts, such as scales (Beevers *et al* 1981), frass (Auger *et al* 1989), and pheromones (Colazza *et al* 1997), until the early 1990s when studies revealed a more sophisticated communication between plants and natural enemies (Turlings *et al* 1990, 1991, Vet & Dicke 1992), the so-called cry for help (Dicke *et al* 1990a), an induced and indirect plant defense mechanism (Turlings & Wäckers 2004). The connotation behind "cry for help" was that plants release odor blends signaling to specific natural enemies in order to help in their defense against herbivore attack. The idea that plants purposely emit herbivore-induced volatiles to recruit natural enemies has been largely discussed (Holopainen 2004, Dicke & Baldwin 2010), and some believe that emission of induced volatiles has not a primordial role in plant defense against herbivores (Peñuelas & Llusià 2004). In this context, herbivore-induced plant volatiles (HIPVs) consist of cues exploited by natural enemies rather than a "cry for help" from plants.

Volatiles emitted by herbivore-damaged plants are complex blends basically made of green leaf volatiles (GLVs—C_6 aldehydes, alcohols, and their esters), terpenoids, aromatics, and amino acid volatile derivatives (Dudareva *et al* 2006). The release of these compounds generally follows a temporal pattern, being GLVs emitted first since they are released from damaged cell membranes (Hatanaka *et al* 1987), and the others volatiles, which are *de novo* synthetized, emitted latter (Paré & Tumlinson 1997, Turlings *et al* 1998a). Other plant organs besides photosynthetic plant tissues also release HIPVs, which is the case of plant roots (Rasmann *et al* 2005).

The composition of HIPV blend is quite variable, and natural enemies seem to exploit the encoded information to infer host suitability. For example, parasitoids are able to discriminate plant volatile blends resulted from damage of their specific hosts (De Moraes *et al* 1998), host developmental stage (Takabayashi *et al* 1995), and even if hosts are parasitized or not (Fatouros *et al* 2005a). However, parasitoids need to cope with variable HIPV blends which are not directly informative about host parameters, such as the plant variety (Geervliet *et al* 1997), the plant developmental stage (Köllner *et al* 2004), co-occurrence with pathogens or non-host herbivores (Rodriguez-Saona *et al* 2005, Rostás *et al* 2006), insect oviposition followed by herbivory (Peñaflor *et al* 2011), and abiotic factors (Gouinguené & Turlings 2002). Because of their great capacity of associative learning (ability of associating chemicals with the presence of host), parasitoids can overcome this issue (Molck *et al* 2000, De Boer & Dicke 2006, Takabayashi *et al* 2006).

Plant induced response is triggered by a combination of cell damage (Heil 2009) and contact with elicitors—two main groups: fatty acid–amino acid conjugates and lytic enzymes—present in the herbivore oral secretions (Mattiacci *et al* 1995, Halitschke *et al* 2001, Truitt *et al* 2004), which activate signaling pathways (lipoxygenase, shikimate, and isoprenoid) coordinated by three main plant hormones: jasmonic acid (JA), salicylic acid (SA), and ethylene (Walling 2000).

Plants detect not only herbivory as a threat but also herbivore oviposition. Analogously to herbivore-induced responses, oviposition triggers the release of oviposition-induced volatiles or chemical changes of leaf surface which function as attractant/arrestant to egg parasitoids (Hilker *et al* 2002, Fatouros *et al* 2005b, Salerno *et al* 2013). In this case, the elicitor is derived from the secretion attaching the eggs to the plant and will contact inner plant tissue through wounding inflicted by female before depositing eggs (Hilker *et al* 2005). Up to now, only few tritrophic systems have been reported in which this interaction occurs, indicating that this type of defense may not be widespread in plant kingdom as volatiles triggered by herbivory (Hilker & Meiners 2002, Colazza *et al* 2004) or this topic should be further investigated.

Besides attracting natural enemies, HIPVs mediate interactions with other trophic levels (Dicke & van Loon 2000). For example, HIPVs can either repel or attract herbivores (De Moraes *et al* 2001, Signoretti *et al* 2012) and also play a role in communication among plants by alerting neighbor plants about herbivory, a phenomenon called "priming" (Engelberth *et al* 2004, Runyon *et al* 2006). Recently, HIPVs have been shown to mediate interactions with the fourth trophic level, the hyperparasitoids (parasitoid of the parasitoid) that are guided by them to find their host, the parasitoids (Poelman *et al* 2012).

The attraction of a wide range of herbivore enemies by HIPVs has been largely documented (see review by Mumm & Dicke 2010), including many carnivorous arthropods (parasitoids and predators) and other entomopathogenic agents, such as nematodes and fungi (Baverstock *et al* 2005, Rasmann *et al* 2005). Nevertheless, isolation and identification of key compounds from the HIPV blend to which natural enemies are attracted is a complex task. It has been attempted by means of gas chromatography–electroantennographic detection (Wei & Kang 2006), blend fractioning combined with bioassays (D'Alessandro & Turlings 2005), mutant plants (Shiojiri *et al* 2006), or use of inhibitors of specific plant biosynthetic pathways (Mumm *et al* 2008). In few cases, identifying key-compounds of attraction is a straightforward task (Rasmann *et al* 2005). But, in general, natural enemy attraction depends on the blend composition (Meiners *et al* 2003, D'Alessandro *et al* 2006), which sometimes is difficult to be determined because it occurs only in trace quantities (D'Alessandro *et al* 2009).

Biological control agents have a great potential to control serious pests in agriculture by inundative and conservative biological control (Botelho *et al* 1999). In order to increment biological control efficacy in the field, manipulation of natural enemy behavior in the field has been suggested (Eilenberg *et al* 2001). Since odors are the most important cues in host search by carnivorous arthropod (Vet & Groenewold 1990), the use of semiochemicals that play a role in host finding can enhance natural enemy efficacy by recruiting them to the crops or facilitating host finding what may lead to high parasitism and predation in the field. Originally, this idea was based on attractants derived from herbivorous insects, known as kairomones (Vinson 1992). However, over the years, it has been shown that most of the host-derived attractants, specifically from the target host stage (eggs and larvae), are difficult to be incorporated in IPM strategies as they are generally of low volatility and consequently low detectability at long distances for parasitoids and predators (Vet & Dicke 1992). Besides, kairomones are generally molecules difficult to be synthesized (Renou *et al* 1992).

The understanding of plant-induced defenses that has been gained in the last years opens up paths for developing novel strategies following integrated pest management (IPM) principles. The main strategy is optimizing herbivory-induced responses on crop plants or to deceivably recruit biological control agents to the field. If natural enemies are attracted and retained in the crops and plants signalize herbivore attack more efficiently in terms of volatiles, host/prey finding efficiency might be enhanced as well as parasitism and predation, as a consequence. Within this context, tactics using synthetic HIPVs or chemically/genetically manipulating plant defenses have been suggested in order to recruit natural enemies to plantations or help guiding them to their host more quickly, working as a "synergistic" agent of biological control. Other strategies by manipulating plant defenses or plant volatile emission directly targeting the herbivore have also been proposed, such as use of repellent volatile for stopping herbivore colonization, or attracting them to specific sites to be trapped or killed (Loughrin *et al* 1995, Bernasconi *et al* 1998, Camelo *et al* 2007). The "push–pull" system, which is the most succeeded pest control method based on chemical ecology, works well in small-sized sorghum and corn areas. It consists of repelling cereal stemborers ("push") by sowing a secondary plant species, which is at the same time attractive to parasitoids, and also a third plant species that emit attractants volatiles for moth oviposition ("pull") (Khan *et al* 1997, see review by Khan *et al* 2008). Although there are valid methods of using VOCs to manipulate herbivore behavior, this will not be the focus of this review.

Developing strategies for attracting natural enemies to crops based on attractive plant volatiles have many advantages over host-derived attractants for the following reasons: Induced plant volatile emission is a widespread mechanism in plants, so exploring HIPVs will embrace a wide range of biological control agents; plant volatiles present high volatility, enabling recruitment of natural enemies at long distances (Vet & Dicke 1992); many synthetic HIPVs are commercially available (e.g., Sigma-Aldrich®); HIPVs can trigger defense mechanisms in neighbor plants (priming) (Kessler *et al* 2006), and lastly, many genes that express enzymes associated to terpenoid biosynthesis have been identified (Degenhardt *et al* 2003).

Nevertheless, exploring induced plant volatile emission in tactics to manipulate natural enemies can present some limitations. Since HIPVs mediate multiple functions in ecosystems, they can represent cues for parasitic plants (Runyon *et al* 2006) or herbivores, which are in most of cases attracted by them (Bolter *et al* 1997, Kalberer *et al* 2001, Carroll *et al* 2006, Halitschke *et al* 2008), though this is not a generalized behavior as some herbivores are repelled by them (De Moraes *et al* 2001, Bruinsma *et al* 2007, Szendrei & Rodriguez-Saona 2010). Therefore, to successfully implement tactics based on HIPVs, it is important to investigate the interactions and particularities mediated by induced defenses of each crop species with the agroecosystem community and avoid that non-target organisms are also attracted.

This review discusses strategies using HIPVs to enhance biological control efficacy that have been proposed in the literature and were categorized here as: (a) exogenous application of elicitors in the plants (Thaler 1999a), (b) use of plant varieties that emit attractive HIPVs to natural enemies (Hoballah *et al* 2002), (c) release of synthetic HIPVs (James & Price 2004, Yu *et al* 2008), and (d) genetic manipulation targeting genes that optimize HIPV emission (Cortesero *et al* 2000) (Fig 1). We highlight not only field studies but also comprehensive laboratory assays that present an applied approach for HIPVs or show the potential of employing them in the field.

Strategies Employing HIPVs to Enhance Biological Control

Exogenous application of elicitors

The use of chemicals that elicit induced resistance in plants against herbivory has been widely suggested (Stout *et al* 2002). This method works as a fake signal of herbivory on the plant activating induced defenses without being actually damaged by herbivores. Theoretically, by applying elicitors, undamaged crop plants will become more resistant because of induced defense mechanisms, such as the synthesis of toxins and release of HIPVs, as it happens when it is damaged. HIPV emission of elicitor-treated plants will attract and maybe retain natural enemies in the area, although natural enemies may not necessarily find their host/prey unless they are able to distinguish between artificially induced and host-damaged plants.

The most studied elicitors are JA (jasmonic acid) and SA (salicylic acid), important plant hormones associated to induced defenses. The intermediates and catabolites belonging to their respective pathways have been studied lately in order to unravel the mechanisms that underlie HIPV synthesis and function (Arimura *et al* 2009, Wu & Baldwin 2009).

JA is a product of the octadecanoid signaling pathway, which is usually associated with herbivore resistance (Vick & Zimmerman 1984, Wasternack *et al* 2006). JA-deficient mutant plants are much more susceptible to herbivores, showing the important role of this molecule on induced resistance (McConn *et al* 1997, Thaler *et al* 2002). On the other hand, SA, derived from shikimic pathway, was most often thought to function in pathogen resistance, called systemic acquired resistance (Kessmann *et al* 1994), which is a type of resistance induced in systemic tissues when a plant is locally infected by pathogens.

Even though SA is associated with plant pathogen resistance, many studies have pointed out that both SA and JA pathways are involved in herbivore-induced response (Heidel & Baldwin 2004). In general, chewing herbivores induce JA pathway (Ozawa *et al* 2000) whereas both SA and

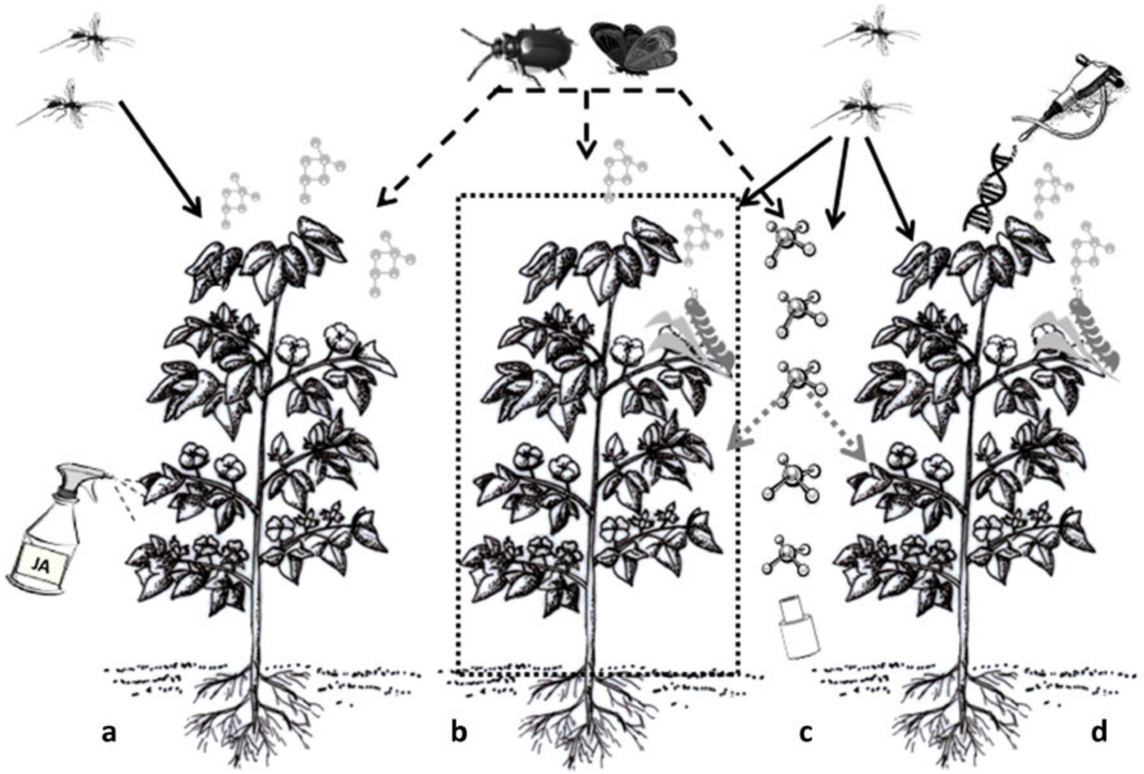

Fig 1 Proposals of strategies to recruit and retain natural enemies using herbivore-induced plant volatiles (HIPVs) in the field. *A* Exogenous application of jasmonic acid (*JA*) as elicitor of herbivore-induced defenses on crops—note that no herbivore damage is necessary for triggering HIPV emission, *B* selection of plant cultivars that have high defense response and emit attractive HIPVs to natural enemies, *C* release of synthetic HIPVs to directly recruit natural enemies to crops, and *D* genetic manipulation of crop plants in order to increase HIPV release and accelerate the induced defense response—as it is possible to manipulate the emission of a couple or single HIPV, herbivore attraction can be avoided. *Full arrow* starting from parasitoid toward plants indicates attraction of natural enemies. *Dotted black arrow* indicates unintended attraction of herbivores to HIPVs, which can occur in some systems. *Dotted gray arrow* indicates that synthetic HIPVs may also act as priming agents of plants exposed to them.

JA are associated to damage inflicted by sucking arthropods, such as mites (De Boer & Dicke 2004) and aphids (Moran & Thompson 2001).

JA has been extensively studied in the context of crop protection as it is involved in both direct and indirect induced defenses against herbivores (Thaler *et al* 2002). Exogenous application of JA triggers emission of a volatile blend similar to the one released by herbivore-damaged plants (Hopke *et al* 1994, Boland *et al* 1995) and at the same time induces direct defenses that affect herbivore performance (Thaler *et al* 1996, Bruinsma *et al* 2007) and behavior (Birkett *et al* 2000, Bruce *et al* 2003). Although JA-induced volatile blend is not identical, and differs in quality and quantity from herbivore-induced plants, it has been shown that JA-induced plants are also attractive to natural enemies (Gols *et al* 1999). The primary difference between the JA- and herbivore-induced blend is the absence, or presence in low amounts, of methyl salicylate (MeSA) (Dicke *et al* 1999), which is a derivative from the shikimate pathway. By contrast, methyl jasmonate (MeJA) is always present in the blend emitted by JA-treated plants, even though it is not always detectable in herbivore-induced plants (Hopke *et al* 1994). Furthermore, JA does not induce the biosynthesis of homoterpenoid compounds, but it is highly effective at triggering mono- and sesquiterpenes, which are generally important compounds for natural enemy attraction (Koch *et al* 1999). The differences in volatile blends emitted by herbivore-infested plant and the JA treatment demonstrate that additional plant hormones, such as ethylene and SA, play a role in HIPV emission and are responsible for triggering other pathways (Kahl *et al* 2000).

Uniform JA application on the crop will recruit natural enemies toward herbivore-infested and non-infested plants what can hamper host/prey finding. Although both JA-treated and herbivore-infested plants are attractive to natural enemies, they are able to perceive subtle differences between blends and usually prefer odors from herbivore-infested over artificially induced plants (Dicke *et al* 1999, Bruinsma *et al* 2009). Nevertheless, in some cases, JA treatment can make undamaged plants more attractive than untreated plants under herbivore attack (Ozawa *et al* 2004). Considering those facts, JA application can mislead natural enemies to non-infested areas, but once hosts are present in JA-treated plots, natural enemies are likely able to find their host/prey.

Most studies demonstrated that JA treatment does cause increased predation and parasitism in the field, leading to reduced herbivory on crops (Heil 2004, Lou *et al* 2005). It has been discussed if higher parasitism in JA-treated plots results from extended larval development period, since herbivores are affected by plant induced direct defenses, or from differential attractiveness of JA-treated areas to natural enemies (Thaler 1999a). Furthermore, JA-treated plants produce more extrafloral nectar (Heil *et al* 2001, Heil 2004), an indirect defense mechanism, which is important as an energy source for natural enemies to improve their survivorship and extend their period of parasitism. Thus, use of JA enhances biological control efficacy likely as a consequence of eliciting a complex of both direct and indirect induced plant defenses.

Another method found to induce plants via JA pathway is based on air exposure or application of JA–catabolites, such as MeJA and *cis*-jasmone. Similarly to the plant hormone, they will activate HIPV emission on undamaged plants and consequently attract natural enemies (Birkett *et al* 2000, Bruce *et al* 2003, Degenhardt & Lincoln 2006). However, compared to JA treatment, plants exposed to JA–catabolites show delayed HIPV emission, likely because they are not directly eliciting JA-related defenses (Moraes *et al* 2009). By contrast, induced terpene emission can last longer using this method (Martin *et al* 2003).

Apart from induced defenses, JA and its catabolites are also modulators of other physiological mechanisms, for example fruit ripening, pollen production, root growth, and tendril coiling (Creelman & Mullet 1997). Thus, as consequence of JA treatment, plants become more resistant to herbivores, but they can also have reduced number of flowers (Thaler 1999b), fruits, and seeds (Redman *et al* 2001). These effects can impact crop yields, and further studies are needed to assess if JA treatment provides greater biological control that compensates yield losses.

As already mentioned earlier, JA-derived blend commonly lacks, or presents, little amounts of MeSA, which is partly SA-dependent pathway (Ament *et al* 2004). Since this compound can be one of the key components in the attraction of predatory mites (De Boer & Dicke 2004, Ishiwari *et al* 2007), the plant hormone SA can represent an important elicitor to recruit natural enemies in the field. Still, predatory mites can be responsive to odors emitted by JA-treated plants, containing little amounts of MeSA (Gols *et al* 1999). In some cases, JA alone does not work as an elicitor of attractive blend for predatory mites, and additional eliciting using SA or its derivatives is necessary (Ozawa *et al* 2000, Shimoda *et al* 2002). However, treatment with SA alone generally does not induce attractive HIPVs to natural enemies (van Poecke & Dicke 2002), but it is more often used as an elicitor for inducing pathogen resistance in plants (Jayaraj *et al* 2009).

Because of interacting effects between SA and JA pathways, the use of JA or SA as elicitors in agriculture can be detrimental to pathogen or herbivore plant resistance, respectively, a phenomenon called “negative cross-talk.” For example, JA application on plants will elicit herbivore resistance, but, at the same time, SA-signaling pathway may be suppressed and plants become more susceptible to pathogen attack (Stout *et al* 1998, Thaler 1999a). On the other hand, if plants are sprayed with SA, plant immune system against pathogens is enhanced, while JA levels might be reduced leading to herbivore susceptibility (Doares *et al* 1995, Felton *et al* 1999, Preston *et al* 1999). This trade-off between signaling pathways likely modulates plant defenses against only one attacker in order to survive. Nevertheless, a negative cross-talk is not a rule, and neutral or positive cross-talk may occur depending on the system (Felton & Korth 2000). Therefore, use of JA or SA as elicitors in crops should be managed in a precautions way to avoid unproductive interactions (Bostock *et al* 2001). For further understanding in “cross-talk” complexity and effects in JA- and SA-related defenses, see review by Smith *et al* (2009).

A second class of elicitors comprises substances present in the herbivore oral secretions. Compared to JA, herbivore-derived elicitors may not be as effective because terpenoid blends emitted by plants rapidly declines over time, whereas JA-treated plants sustainably release terpenoids (Schmelz *et al* 2001). However, Liu *et al* (2009) obtained some successful results testing exogenous application of pectinase, a salivary enzyme from the English green aphid *Sitobion avenae* (F.) (Hemiptera: Aphididae), on wheat that resulted in higher aphid parasitism in greenhouses. The studies using herbivore-derived elicitors in the field are rare probably because they are generally complex molecules (Halitschke *et al* 2001) and also require wounding on plant tissue to induce defensive response.

There are other promising elicitors that have not yet been studied under field conditions, such as alamethicin (Engelberth *et al* 2001), derived from the fungus *Trichoderma viride*, and benzo-(1,2,3)-thiadiazole-7-carbothioic acid *S*-methyl ester (BTH), a mimic of SA, that promote resistance against pathogens (Friedrich *et al* 1996) and herbivores (Shobhy *et al* 2012). BTH has been tested once on corn, but no significant effect was found (von Mérey *et al* 2012).

Stout *et al* (2002) stated that a successful elicitor should show a proper degree of specificity, induce direct and indirect resistance at the stage of plant growth that is vulnerable to pest attack, and induce resistance that is long-lasting and effective against a broad-spectrum of herbivores. Considering these characteristics, JA and its catabolites are strong candidates for being used in the field to recruit natural enemy populations.

Plant cultivars that emit attractive HIPVs to natural enemies

Crop plants generally present a wide range of genotypes resulted from plant breeding that mainly worked toward increasing yield. Consequently, resistance traits against pathogens and herbivores, especially in terms of induced defenses, may have been deteriorated in cultivated plants what can potentially interfere in tritrophic interactions. Indeed, variability in HIPV production seems to naturally occur among different plant genotypes, and it has been confirmed that inbreeding negatively affect HIPV emission in a way that alter recruitment of natural enemies (Delphia *et al* 2009, Kariyat *et al* 2012).

Loughrin *et al* (1995) showed that naturalized variety of cotton emits almost sevenfold more HIPVs than commercial varieties. In contrast, HIPVs emitted by corn plants seem to not be affected by breeding in terms of quality and rates, but there are clear differences in terms of total amount (Gouinguené *et al* 2001). Subsequently, Degen *et al* (2004) studying a broader range of corn inbred lines revealed great differences in HIPV emission among corn cultivars especially in regard to emission of the sesquiterpene (*E*)-β-caryophyllene. This compound is found in most of European lines, but it is absent in blends released by American corn lines.

Variability in terms of quality and/or quantity in HIPV blend among varieties or cultivars does affect natural enemy foraging (Rapusas *et al* 1996, Yong-gen & Jia-an 2001, Hoballah *et al* 2002, Ibrahim *et al* 2005, Kappers *et al* 2011). Wild cultivars are usually more attractive than the cultivated ones (Gols *et al* 2011). Assessment of the attractiveness of cultivars in a laboratory setup can reflect the higher parasitism rates of the same cultivars in the field (Poelman *et al* 2009). So, the use of attractive cultivars in the field is a promising strategy in enhancing biological control efficacy.

Interestingly, Rasmann *et al* (2005) found that (*E*)-β-caryophyllene is produced only by corn roots of European lines attacked by the western corn rootworm *Diabrotica virgifera virgifera* LeConte (Coleoptera: Chrysomelidae), and it plays an important role in host finding by entomopathogenic nematodes. As North American corn lines do not release (*E*)-β-caryophyllene from damaged roots, their use is incompatible with biological control of western corn rootworm with nematodes, which are unable to find their hosts in belowground. American lines likely lost the capacity of producing (*E*)-β-caryophyllene as a result of plant breeding (Köllner *et al* 2008).

It has been theorized that cultivars more susceptible to herbivores (low direct defenses) would allocate more energy in HIPV emission to attract natural enemies (Ballhorn *et al* 2008). Findings of Kännaste *et al* (2008) showed that the most preferred pine clone by herbivores was the ones that emitted the largest amounts of linalool, farnesene, and MeSA, although attractiveness to natural enemies was not demonstrated in this study. Moreover, this hypothesis has not been confirmed for other plant species (van den Boom *et al* 2004).

Nowadays, new crop varieties have been developed by means of genetic engineering with special attention to insect resistance (e.g., *Bt*-crops). The incorporation of a foreign gene can result in pleiotropic changes, such as altering the capacity of the plant to produce HIPVs and, consequently, alter the interactions with the third trophic level (Schuler *et al* 1999a). Studies have shown that *Bt*-plants release less volatiles than non-*Bt* not as a consequence of *Bt* gene, but because herbivores consume less plant tissue on *Bt*-plants (Schuler *et al* 1999b). Studying *Bt*-corn, Dean & De Moraes (2006) suggested that feeding pattern of caterpillars as well as damage amount caused lower release of HIPVs by *Bt*-plants. When damage was standardized, both *Bt* and non-*Bt* plants emitted volatiles at the same ratios and amounts (Himanen *et al* 2009).

Plant variety can indirectly influence parasitoid performance if host is affected by plant resistance. For example, small hosts will affect size or fecundity of parasitoids (van Emden 1995). Interestingly, a recent study conducted by Gols *et al* (2009) showed that parasitoids are able to discriminate plant cultivars that provide optimal progeny development by HIPV emission. However, the same parasitoid is not able to distinguish good cultivars for its development in another plant species, likely because of their evolutionary history (Poelman *et al* 2009).

Considering all these evidences of how plant varieties can influence tritrophic interactions, selecting varieties that signal herbivore attack in a way that optimize host finding by natural enemies is a potential strategy for improving biological control. In order to select a variety, behavioral tests should focus on one or few natural enemies that are important in the location in terms of abundance and potential of suppressing pest population. Because of the high variability in HIPV blends released among varieties, it is possible that different varieties are better for attracting different species of natural enemies and therefore the decision should be compatible with biological control program or the important agents of the particular location. Lastly, it is extremely important that the variety selected is not attractive to herbivores.

Release of synthetic HIPVs

Synthetic versions of HIPVs have been employed in the field with the aim of monitoring abundance and, most importantly, recruitment of populations of natural enemies to crops. Most part of the studies were done by incorporating synthetic HIPVs, individually or in mixture, in controlled-release dispensers in baited traps, and recruitment was measured based on the number of parasitoids/predators trapped on sticky cards (James 2003a, b, 2005).

Nevertheless, using this strategy, the recruitment of natural enemies can be equivocally associated with enhanced biological control. The release of HIPVs may recruit natural enemy populations, but it does not necessarily mean that it will improve foraging efficiency. If natural enemies are guided by synthetic HIPVs, they may be misled to non-infested areas, for example. Alternatively, as some parasitoids species rely on associative learning (Meiners *et al* 2003) to orient toward HIPVs, they might be attracted to synthetic volatiles and not “rewarded” with a host what can be detrimental to their foraging success (Turlings & Ton 2006, Khan *et al* 2008).

To overcome these issues, a new method has been recently proposed by combining synthetic HIPVs with nectar sources, an “attract and reward” strategy, in order to recruit and retain natural enemy populations in crops (Simpson *et al* 2011). In this way, they can feed on nectar if host population is low, or absent; hence, it would avoid negative associations of HIPVs with food resources. The studies testing “attract and reward” showed that there was no synergistic effect on natural enemy abundance, and use of synthetic HIPVs with floral resources at short distances can be detrimental in attracting natural enemies (Orre-Gordon *et al* 2013). According to the authors, synthetics and nectar sources attract different guilds of natural enemies if they are used spatially separated of each other. Because some HIPVs mediate interactions not only with the third trophic level but also with second and fourth levels, using synthetic versions can attract non-target organisms, such as herbivores and hyperparasitoids, to the crops and therefore undermine biological control (Orre *et al* 2010).

Despite all these issues, a couple of studies demonstrated that synthetic HIPVs provide suppression of herbivore populations in the field attributed to the recruitment of natural enemies (James & Price 2004, Mallinger *et al* 2011). It is possible that such effect is partly related to priming of neighbor plants by exposure to HIPVs released from dispensers, i.e., synthetics can “alert” undamaged plants enhancing their ability to trigger defenses against herbivores (Fig 1). So, if the exposed plant is attacked, HIPVs will be produced and release much faster and in higher amounts (Engelberth *et al* 2004).

Up to now, MeSA is the strongest candidate to attract a wide range of natural enemies in the field. This compound is released by several plant species under herbivore attack (Scutareanu *et al* 1997, Dicke *et al* 1998, van Poecke *et al* 2001). The first test carried out by James (2003a) found that traps baited with synthetic MeSA in hop yards had higher catches of the green lacewing *Chrysopa nigricornis* Burmeister (Neuroptera: Chrysopidae) than baited with other HIPVs, such as dimethyl nonatriene and hexenyl acetate. In this study, the author observed that even when aphids were virtually absent in the yard, a great number of the green lacewing were caught, suggesting that the attractive effect was not due to the natural emission of MeSA by aphid-attacked plants.

In a similar setup, James (2003b) verified that MeSA also attracted other predators belonging to Geocoridae, Syrphidae, and Coccinellidae in a hop yard. The follow-up work showed that MeSA actually enhanced biological control agents of the main pests in the yards, spider mites and aphids, which were dramatically reduced in treated areas (James & Price 2004). Despite functioning as an attractant to a wide diversity of natural enemies, MeSA can be repellent or its presence in the blend can negatively affect attractiveness to other species of natural enemies (Snoeren *et al* 2010, Braasch *et al* 2012).

Another promising group of HIPV for manipulating natural enemy populations in the field are the GLVs. It has been shown that a wide range of natural enemies are caught on traps baited with synthetic GLVs (Yu *et al* 2008, James 2003b, 2005). Moreover, GLVs are also an important group of HIPVs mediating plant–plant interactions, acting mainly as priming agents (Paré *et al* 2005). Although exposure to synthetic GLVs primes plants in the field, the effect is not enough to recruit natural enemies and enhance biological control (von Mérey *et al* 2011).

In respect to all these studies, they clearly show that individual HIPVs, in combination with floral nectar or not, can augment natural enemy density in the field. Differently from resistance induced by elicitors, the use of attractive HIPVs to natural enemies would not demand energy costs from plants unless the synthetics intensively primed nearby plants (Ruther & Furstenau 2005). Nevertheless, better methods on how to employ synthetic HIPVs in order to attract natural enemies in a way that higher parasitism and predation compensate attraction of herbivores and/or hyperparasitoids need to be further studied (Kaplan 2012).

Genetic manipulation of genes responsible for volatile emission

Genetic engineering of cultivated plants has been suggested as a mean to unravel biochemical pathways associated with HIPV production (Dicke & van Loon 2000) as well as to identify key volatiles (Xiao *et al* 2012) and enhance plant attractiveness to natural enemies (Degenhardt *et al* 2003). As terpenoids are the most prominent group in HIPV blend and play an important role in natural enemy attraction (Mumm *et al* 2008), genetic engineering has focused on manipulating plant metabolism through mevalonate and methylerythritol-4-phosphate pathways, which are responsible for mono- and sesquiterpene formation (C_{10} and C_{15} skeletons) (Aharoni *et al* 2005). In summary, their syntheses are divided into three steps: formation of C_5 units, condensation of these units, and conversion to end terpenoids. Each step is regulated by specific enzymes of each step which will produce the C_5 basic units, condensate those, and convert to mono- and sesquiterpenes. Details on the plant terpenoid biosynthesis can be found in reviews by Dudareva *et al* (2004) and Nagegowda (2010).

The current understanding on plant biochemistry pathways and molecular changes followed by herbivory allows some manipulation of metabolic routes by inserting genes from other plant species, overexpressing or knocking-down genes that express enzymes involved in terpenoid metabolism (Dudareva & Pichersky 2008). Strategies used for manipulating plant metabolism to enhance HIPV emission can target one or multiple steps of terpenoid synthesis through expression of genes mediating supply of precursors or the enzymes involved in the different steps (Wu *et al* 2006, Houshyani *et al* 2013). Insertion or overexpression of genes mediating enzymes required on the last step of terpenoid synthesis pathways, such as terpene synthases (TPs), seems promising in increasing the amounts of terpenoids emitted (Tholl 2006), which will consequently affect interactions with insect community.

Although plant metabolic engineer might be of great importance for crop plants, most of the studies refer to the model plant *Arabidopsis* (Aharoni *et al* 2003, Tholl *et al* 2005), which is easier to genetically manipulate (Meyerowitz 1987). Kappers *et al* (2005) generated a transgenic *Arabidopsis* to constitutively emit two terpenoids and attract predatory mites by overexpressing a linalool synthase gene from strawberry. In a similar approach, Schnee *et al* (2006) also transformed *Arabidopsis* by inserting a corn sesquiterpene synthase gene to emit attractive sesquiterpenes to experienced parasitoids.

Examples of enhanced attraction of transformed plants to natural enemies are not restricted to *Arabidopsis* plants though. Cheng *et al* (2007) generated transgenic rice plants that were more attractive to egg parasitoids than the wild type due to an increased expression of a TP gene (*OsTPS3*). Differently from the studies mentioned above, transgenic rice did not constitutively emit attractive volatiles to egg parasitoids, i.e., plants only emitted higher sesquiterpene amounts after treatment with MeJA, likely because *OsTPS3* activity requires expression of other genes mediating terpenoid precursors which were triggered by MeJA.

Degenhardt *et al* (2009) successfully restored the ability of American corn varieties in emitting (*E*)-β-caryophyllene, which was likely lost because of intensive breeding (Köllner *et al* 2008). The transformation of American corn with oregano (*E*)-β-caryophyllene sesquiterpenase resulted in constitutive emissions of the sesquiterpene by the roots, which represent important signals for host finding by entomopathogenic nematodes. As transgenic corn was continuously emitting volatiles signals into the soil, damage by western corn rootworm was much lower than in plants lacking the enzyme.

In contrast to the previous studies in which overexpression of TPs was exploited, Xiao *et al* (2012) showed that silenced rice plants impaired either in emissions of *S*-linalool or (*E*)-β-caryophyllene mediated distinct interactions with natural enemies and herbivores in the field. Based on the fact that *S*-linalool was attractive to egg parasitoids, but repellant to the brown plant hopper, and (*E*)-β-caryophyllene was attractive to both natural enemies and the plant hopper, a strategy using two transgenic lines at the same time to control plant hopper populations in the field was suggested: a linalool-impaired rice line emitting high amounts of (*E*)-β-caryophyllene on the edges to attract plant hopper and its natural enemies, and another transgenic line, which is the main crop, emitting high amounts of linalool, but no (*E*)-β-caryophyllene, in order to attract egg parasitoids and avoid plant hopper colonization.

Despite the well-succeeded cases described earlier, terpenoid metabolism manipulation is a complex task (Lücker *et al* 2007), and transformation can incur in detrimental effects to plant growth and development (Aharoni *et al* 2003) and attract pests and pathogens (Rodríguez *et al* 2011). It is important to point out that developing a transgenic variety that constitutively emits attractive volatiles to natural enemies irrespective of herbivory damage should be avoided. Continuous release of attractants to natural enemies may be disadvantageous because natural enemies would respond frequently without being rewarded with hosts or prey, provoking their emigration. Therefore, a better approach to enhance biological control would be to develop genotypes that emit superior or faster HIPV blends.

Final Considerations

Biological control has been gradually more accepted by growers as its potential in controlling pests in agriculture has been proved. We show here that HIPVs can be exploited in IPM strategies in order to enhance biological control efficacy in crops. There are four main strategies of using induced plant response to manipulate behavior of natural enemies with the aim to recruit, retain, and increase their foraging efficiency in plantations. As an ultimate result, we expect high parasitism and predation in a way that pest populations are suppressed and pesticide use reduced. All four strategies have successful cases in achieving this result; however, given that HIPVs can also be attractive to non-desirable organisms, such as herbivores and parasitic plants, use of these strategies can impose some non-target effects. Therefore, it is important to study each system and the particularities of the location where the strategy will be implemented. In addition, strategies that involve manipulation of plant physiology by means of elicitors and genetic engineering can negatively affect yield parameters, and therefore, plant response to these strategies needs to be carefully assessed.

Authors have emphasized that the best method is engineering crop plants in a way that they rapidly emit attractive volatiles and in higher amounts after damage, so parasitoids and predators will orient themselves to the right plants at the right time to find their host/prey (Degenhardt *et al* 2003, Turlings & Ton 2006). However, costs associated with transgenic plants and the technology, besides the low acceptability of organisms genetically modified by consumers, can be obstacles to use this method in combination with biological control. On the other hand, cultivating plant genotypes that have more efficient defenses and emit high amounts of HIPVs is a simple method that imply in low costs and can be easily implemented. Thus, it is desirable that biological control programs are integrated with plant breeding in order to develop a cultivar that has great plant defenses and yield (Fig 1).

In Brazil, biological control is challenging because of the large agricultural properties and the "pesticide culture" of growers (Parra 2011). There are a couple of successful examples of biological control using arthropods in Brazilian agriculture, such as the control of the sugarcane borer with *Cotesia flavipes* (Cameron) (Hymenoptera: Braconidae) in sugarcane. But applied studies that integrate biological control and plant volatiles are still missing for Brazilian crops. Therefore, the development of strategies using HIPVs adapted to our climatic conditions and considering our fauna and flora composition can empower biological control in Brazil and result in many more successful cases of biological control programs.

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