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Manipulation of Natural Enemies in Agroecosystems: Habitat and Semiochemicals for Sustainable Insect Pest Control

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1. Introduction

Plants are not capable of running away from their enemies, i.e., the herbivores that may eat them. However, under certain circumstances, plants can rely on the natural enemies of insect herbivores for protection. These natural enemies include other insects that are predators and parasitoids. To help protect plants from damage caused by insect herbivores, practical methods have been developed and evaluated to conserve and augment natural enemies of several agricultural pests. These strategies include improving the suitability of the crop landscape for natural enemies by manipulating the resources available for these insects, and the use of semiochemicals to attract predators and parasitoids. This chapter will review recent studies exploring the potential for manipulating the behavior of natural enemies through vegetational diversification of crop habitats and the use of semiochemicals to enhance biological control in agroecosystems, and we will discuss how these might be combined to improve crop protection.

2. Vegetational diversity

Increasing the diversity within crops is predicted to provide a greater number of opportunities for natural enemies to survive in agricultural systems (Fig. 1). Thus, pest outbreaks tend to be less common in polycultures than in monocultures (Root, 1973; Andow, 1991). Crop diversification tends to increase natural enemy abundance and diversity, providing a system more resilient to pest population increase. Overall farming diversity within the agroecosystem may also affect biological control by natural enemies, due in part to a wider range of flowering plants that provide nectar (carbohydrate) and pollen (protein) resources to insects during more times of the growing season. Vegetational diversity can also provide support for insect biological control at the local and landscape levels (Thies et al., 2003; Roschewitz et al., 2005; Bianchi et al., 2006; Gardiner et al., 2009). Farmers can make some simple changes to their crop systems to manipulate vegetational diversity, through addition of plants that provide specific functions (Landis et al., 2000; Gurr et al. 2003; Isaacs et al., 2009). Below, we provide an overview of those methods and describe situations where such changes have reduced pest infestation.
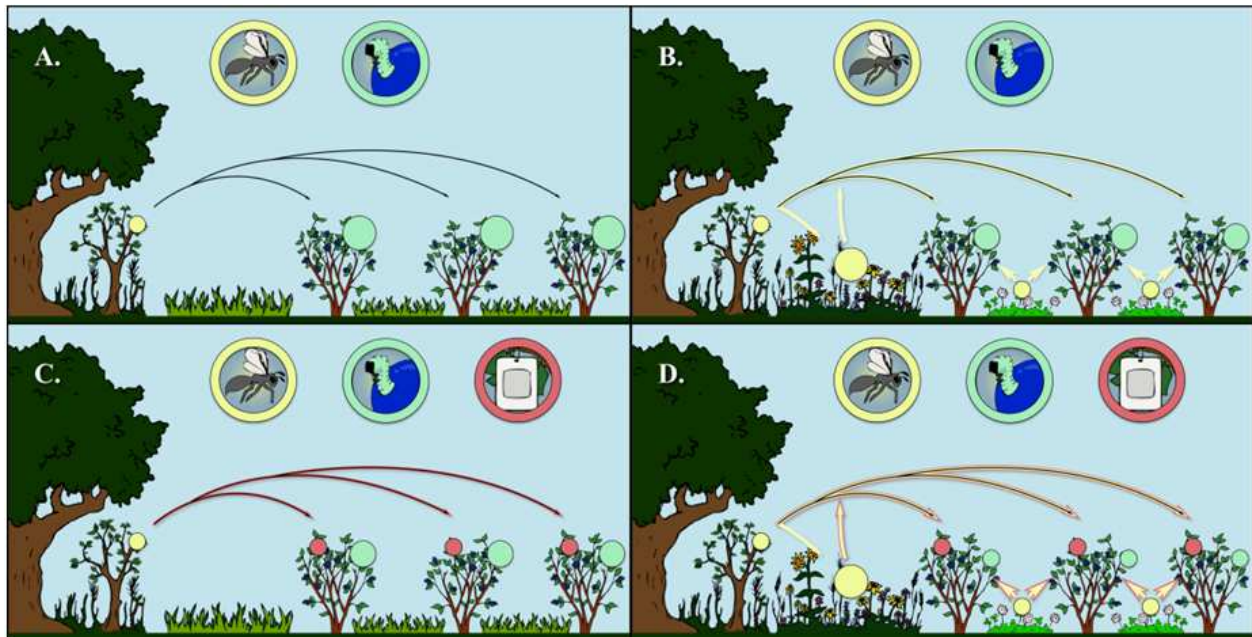
Fig. 1. Strategies for manipulating natural enemies in agroecosystems for enhanced insect pest control. A.) Conventional method with no manipulation of habitat leads to high pest numbers and few natural enemies entering the crop from the surrounding landscapes. Yellow circles represent natural enemy populations and green circles represent pest abundance. B.) The addition of inter-cropping, cover crops, or supplemental food sources to an agroecosystem may lead to an increase in natural enemy abundance and a potential decrease in insect pest abundance within field settings, but relies on the presence of insect pests to attract natural enemies into the crop. C.) The addition of semiochemical-based lures, such as herbivore-induced plant volatiles (HIPVs) may attract natural enemies into the crop to enhance biological control, but does not provide resources to directly enhance natural enemy abundance. HIPV lures are represented by pink circles. D.) Combining habitat manipulation and HIPV strategies in an agroecosystem may increase natural enemy abundance within field settings as well as directly attract natural enemies into the crop to enhance biological control.

2.1 Inter-cropping, monocultures, polycultures

The response of beneficial insect populations to habitat manipulation depends upon their ability to use or exploit one or more of the plant components of the agroecosystem (Altieri & Nicholls, 2004). Crop systems that are dominated by a single plant species only provide resources to those select organisms that can exploit that single plant species. Hence, monocultures are an example of agroecosystems with low diversity and may be more susceptible to pest or disease outbreaks (Theunissen, 1994; Altieri & Nicholls, 2004). Because of this increased susceptibility, management and external inputs are essential to support low diversity agroecosystems. On the other hand, reliance on diverse plantings, a range of natural enemies that are supported by these plants, and associated crop management strategies can in some cases help maintain pest populations below economic thresholds (Altieri & Nicholls, 2004).

Intercropping, which is the cultivation of two or more species within the same field, is a common method to increase beneficial insect diversity within agroecosystems (Fig. 1B) (Vandermeer, 1989; Theunissen, 1994). Intercropping crop plants with flowering species such as clovers can also provide a favorable habitat for a variety of beneficial insects that may not otherwise survive in a single crop environment, and hence intercropping may provide natural pest management by increasing the abundance and diversity of insect natural enemies in the agroecosystem (Theunissen, 1994). Diverse systems encourage complex food webs that involve more interactions among vegetation, pests, and natural enemies, providing resources for a diverse group of organisms and allowing for alternative resources and food sources. Thus, polycultures and natural ecosystems with higher diversity tend to be more stable and less subject to fluctuations in pest and disease populations (Altieri & Nicholls, 2004). As an example of this, Beizhou et al. (2011) recently reported that intercropping pear orchards with aromatic plants significantly reduced pest abundance and increased the ratio of natural enemies to pests when compared to orchards with only natural grass or clean tillage. They also found higher abundance of natural enemies and reduced numbers of major pests in intercropped orchards. Hence, intercropping the pear orchard with aromatic plants led to improved insect pest management by enhancing the activity of the insect natural enemy community.

2.1.1 Push-pull strategy

The 'push-pull' strategy uses a combination of stimuli to manipulate the behavior of insect pests and/or natural enemies and to alter their distribution and abundance in agroecosystems (Miller & Cowles, 1990; Khan et al., 1997). The push-pull approach works by repelling or deterring the pest insects (push) away from the main crop by using deterring chemical stimuli. Simultaneously, highly appealing stimuli are used to attract the pests (pull) from the main crop to other areas such as trap crops where the pests aggregate and are easier to control (Khan et al., 1997). While on their own each individual component (the push and the pull) of the approach may not be effective at reducing pest numbers below economic thresholds, combining the push and pull components increases the efficacy of such a strategy. Also, since the push and pull components are commonly non-toxic this strategy is compatible with supporting insect natural enemies and biological control (Khan & Pickett, 2004). A suitable push-pull strategy will be unique for each system it is used for, and hence the development of effective push-pull approaches requires an understanding of the targeted pest's biology and interactions with its hosts and natural enemies (Khan & Pickett, 2004).

Push-pull strategies are not a new idea, but one of the most successful examples was developed recently in Africa for controlling stem borers on cereal crops (Khan et al., 2001). Stem borers are moth larvae that feed on and destroy cereal crops. The adult stem borer moths are cryptic and nocturnal while the larvae feed within the crop stem making both adults and larvae difficult to see and to control. Chemical pesticides are a common method of control for stem borers, but this is not an economical or safe approach for many resource-poor, small-scale farms where these pests are common. Hence, a push-pull strategy was developed using technologies appropriate and economical for such farmers (Khan & Pickett, 2004). This strategy involves a combined use of intercropping and trap crops, and uses plants that are also locally-appropriate and that can be used in their agricultural system. While some push-pull

strategies use chemical deterrents and attractants to create the push-pull effect (see Section 3), this strategy does not use any chemical deterrents or toxins, but instead uses plant species that repel the pest away from the main crop while also attracting insect natural enemies to the fields. The repelled stem borers are attracted to nearby trap plants where the moths lay their eggs, but their larvae are unable to develop, thus reducing the number of trapped pest insects (Khan and Pickett, 2004). The farms that implemented the push-pull strategy in Africa have experienced lower pest abundance, and also an overall enhancement of beneficial insect abundance (Khan et al., 2001).

While the work of Khan et al. in Africa is primarily in cereal-based farming systems, the push-pull approach may be applicable to a much wider range of agricultural pest problems in a variety of crops, if the appropriate components can be developed and implemented.

2.2 Cover crops

A major means of conserving beneficial insects and stabilizing their populations is to meet the ecological requirements of these insects within or near the cropping environment (Landis et al., 2000). To be effective, many natural enemies and pollinators need access to alternate hosts, overwintering habitats, constant food supply, and appropriate microclimates. These requirements can be fulfilled through the inclusion of a diverse assemblage of flowering plants within agricultural landscapes.

Cover crops are planted in crop fields, either in rotation with annual crops or within perennial crops. These plants have been widely used to reduce soil erosion, add or retain soil nutrients, produce organic matter, reduce soil compaction, and also aid in pest control (Bugg, 1991; Bugg & Waddington, 1994). They are used in sustainable and organic agricultural systems to enhance soil health and crop nutrition.

Flowering species such as buckwheat (*Fagopyrum esculentum* Moench) or clovers (*Trifolium* spp.) have been promoted as cover crops to provide flowering resources for insects when the crop is not in bloom. Increasingly, the use of flowering cover crops is seen as one component of an overall 'farmscaping' approach that aims to make farmland suitable for a range of beneficial organisms throughout the growing season. Ideally, cover crops will provide shelter and resources for natural enemies, enhancing their populations and hence biological control of insect pests (Bugg & Waddington, 1994). Plants should be screened for their attractiveness to not only the target biological control agent, but also to other potential competitors for floral resources (Hogg et al., 2011) (see below).

The deployment of cover crops within the row middles of perennial crops may create a conflict with insecticide-based pest management activities that would kill the natural enemies active within the field. This will depend on the type of insecticide used (since many of the more recently-developed insecticides are quite selective), on the tolerance of the natural enemies to the insecticide, and on their ability to re-colonize fields from the perimeter. The potential for killing beneficial insects inside crop fields is one reason that strip plantings of flowering plants within field margins or perimeter plantings are considered. Placement of flowering resources adjacent to crop fields may minimize exposure to insecticides while also providing the resources for natural enemies that can then re-invade the crop fields. Indeed, flowering borders adjacent to blueberry fields have

enabled natural enemy populations inside the crop to rebound more rapidly after insecticide applications (Walton & Isaacs, 2011). An increase in natural enemies, particularly parasitoids, has been observed in apple orchards adjacent to flowering borders compared to orchards without flowering borders. This increase in parasitoid numbers also coincided with a doubling of parasitism of spotted tentiform leafminer (*Phyllonorycter blancardella* (Fabr.)) in apple trees adjacent to flowering borders, compared with orchards without flowering borders (Blaauw & Isaacs, unpublished data).

2.3 Selection of supplemental food sources

2.3.1 Flowering plants

Flowering field margins adjacent to crop fields can provide necessary resources for natural enemies of crop pests during periods when crop flowers are not present, thus maintaining high populations of insect predators and parasitoids, which are supported by a provision of nutrients throughout the season (Sotherton, 1984; Ahern & Brewer, 2002; Büchi, 2002; Sanchez et al., 2003; Wanner et al., 2006a, 2006b). Such natural areas were once common in most agricultural landscapes, particularly between plantings, along roadsides, or as part of woody hedgerows, but as the production of crops has increased and intensified, these non-cropped areas are becoming less common (Sotherton, 1998). Current crop production techniques shape the physical structure of agricultural landscapes (Robinson & Sutherland, 2002), and with increased reliance on mechanization and pesticides, vegetative diversity in farmlands has decreased causing negative impacts on natural enemies (Ryszkowski et al., 1993).

Flowering plant strips adjacent to fields help support beneficial insect biodiversity in agricultural landscapes (Baggen & Gurr, 1998; Dufour, 2000; Carreck & Williams, 2002; Fiedler & Landis, 2007a, 2007b; Tuell et al., 2008). Much of the testing of flowering plants has been done with non-native annual or biennial flowering species, although these often bloom in one growing season requiring annual sowing. This makes these resource plants costly to successfully maintain , whereas native perennial flowering plants are sown once, adapted to the local environment, less likely to become invasive, and may increase native beneficial insect diversity in agricultural landscapes (Stephens et al., 2006, Fiedler & Landis, 2007a, 2007b). A well-designed flowering border adjacent to a crop field will provide necessary resources and alternative food source for natural enemies during periods when crop pest and crop flower numbers are low, thus maintaining high populations of natural enemies supported by the provision of nutrients throughout the season (Landis et al., 2000; Isaacs et al., 2009; Hogg et al., 2011).

2.3.2 Nutritional requirements: Pollen and nectar resources

Sufficient flower abundance and appropriate vegetation structure are required to support diverse populations of insects (Zurbrügg & Frank, 2006), and therefore manipulation of structurally resource-poor habitats through the addition of flowering plants and grasses can increase beneficial insect populations in agricultural landscapes (Long et al., 1998; Kells et al., 2001; Rebek et al., 2005). Many beneficial insects, including natural enemies, require access to alternate hosts, overwintering habitats, a constant food supply, and appropriate microclimates in order to survive (Johnson & Triplehorn, 2005). The majority of predators and parasitoids are omnivores and require non-prey food, such as pollen and nectar, as part

of their diet. Natural enemies from a broad range of orders including Hymenoptera, Diptera, Coleoptera, Heteroptera, Neuroptera, Araneae, and Acari have been observed to require and/or benefit from access to flowering resources (Wäckers et al., 2005). Access to pollen and nectar sources can significantly increase the activity, longevity, and fecundity of these predators and parasitoids (Wäckers et al., 2008; Hogg et al., 2011), and thus, the availability of flowering resources can be essential to natural enemy efficacy in biological control of pest insects (van Rijn & Sabelis, 2005). These non-prey requirements can be fulfilled with a diverse assemblage of flowering plants, which will provide necessary resources that support populations of predators and parasitoids throughout the season.

Simple addition of flowering plants to farms may not be sufficient to gain the expected increase in biological control, however, and in some cases it may be counter-productive due to supplying resources for pest insects. In recent years there has been a much greater understanding of the need to tailor resource plants for the specific natural enemies that can provide pest suppression, but further investigation is needed to tailor this to specific crop systems (Jonsson et al., 2008). In one line of investigation, the nutritional quality of plant resources has been investigated in detail, revealing the range of suitability of different plants as food for parasitoids and predators (reviewed by Wäckers, 2005). Additionally, the need to select plants that are beneficial to the natural enemies without providing resources to pest insects has driven the careful evaluation of pest and natural enemy life history traits on candidate floral resources. Baggen et al. (2003) evaluated a range of potential resource plants and found that only lacy phacelia (*Phacelia tanacetifolia* Benth.) and Nasturtium (*Tropaeolum majus* L.) provided resources for natural enemies without also enhancing moth pest performance, as the other tested plants did. In field trials of this selective planting approach, Begum et al. (2006) found higher parasitism of light brown apple moth (*Epiphyas postvittana* (Walker)) eggs in vineyard plots where three types of flowering resource plants were sown under the vines. In more recent studies, this rewarding plant strategy has been combined with attraction of natural enemies (see Fig. 1) in an attract-and-reward approach. Initial reports from combining these two tactics indicate that while this approach has potential for synergy, further work is required to realize the full potential (Simpson et al., 2011a, 2011b).

2.3.3 Alternative prey

As mentioned above, most natural enemies benefit from having access to alternate hosts/prey. Taking advantage of this knowledge, banker plant systems (or open rearing systems) can be used to augment populations of natural enemies in greenhouse and field settings on ornamental and food crops (Van Driesche et al., 2008). Although many natural enemies can be purchased and released to augment biological control, they often leave or die once the targeted pest has been controlled. By combining aspects of augmentative and conservation biological control, banker plant systems attempt to alleviate these factors (Frank, 2010). Banker plant systems generally consist of a non-crop plant that is deliberately infested with a non-pest herbivore. The non-pest herbivores serve as alternative hosts/prey for a desired parasitoid or predator of the target crop pest. A banker plant system is typically based on the use of alternative host/prey in the form of non-pest herbivores, but it can also be based around the use of surrogate food, such as pollen for generalist natural enemies (Huang et al., 2011). As a form of conservation biological control, banker plant systems provide alternative food or hosts for natural enemies so they can survive and reproduce for long periods even when no pests are present in the crop (Frank, 2010). Banker

plants can also conserve released natural enemies to provide sustainable, long-term suppression of crop pests.

2.4 Shelters

Natural enemies of insect pests require shelter from environmental hazards, and a lack of shelter during periods of heat, cold, rain, or pesticide application may be highly detrimental to their survival. Availability of appropriate habitats may promote foraging, resting, overwintering, or nesting of natural enemies.

Physical environmental conditions profoundly affect natural enemy activity during the growing season. For example, excessive wind is thought to limit foraging by adult hoverflies (Beane & Bugg, 1998). Hedgerows, windbreaks, or shelter-belts can protect croplands in windy areas, and provide some protection to the windward as well as to the leeward side. Shelter can reduce soil erosion, and improve photosynthetic and water-use efficiency by crop plants, and can lead to locally elevated temperatures in the sheltered areas. Because hedgerows and windbreaks often contain flowering plants used by many natural enemies, the effects of shelter and of flowers may be difficult to separate (Beane & Bugg, 1998).

Overwintering and resting aggregations of various natural enemies are often observed in crop fields. Typical sites for such aggregations vary among species, and include herbaceous and woody plants as well as human-made structures (Beane & Bugg, 1998). Houses for lacewings have even been built and tested to provide shelter during harsh weather conditions (McEwen & Sengonca, 2001). These lacewing houses have been successfully used as a tool for augmenting biological control in crop fields by increasing the number of lacewings in the agroecosystem (McEwen & Sengonca, 2001).

At the small scale at which mite biological control operates, shelters are important for the survival of predatory species. Some plants have naturally-occurring shelters, called domatia, that predatory mites use as a protected location. They can then forage from these sites on leaves to reach pest mites, and leaves with greater domatia structures tend to have higher populations of predatory mites (Karban et al., 1995; Loughner et al., 2008). Leaves with domatia also protect predatory mites from other natural enemies (intraguild predation) (Norton et al., 2001), and lead to lower densities of leaf-feeding mites and foliar fungal pathogens (Norton et al., 2000; English-Loeb et al., 2005). These findings help explain why certain grape cultivars that possess domatia are less susceptible to mite and mildew outbreaks. Such information could be used in breeding programs to develop crop cultivars that are more likely to have lower pest mite populations, due to their harboring of predatory mites (English-Loeb et al., 2002).

2.5 Landscape influences on natural enemies

Research into landscape-level effects on biological control of insect pests has developed rapidly over the past 20 years, in concert with the expansion of the field of landscape ecology (Turner et al., 2001). New techniques and tools have become available for detailed analysis of aerial imagery or remotely sensed data of the landscapes surrounding crop fields, and combining this with measurements of pest-natural enemy interactions in crop fields has provided new insights, as reviewed by Bianchi et al. (2006). In general, increased

habitat fragmentation, isolation and decreased landscape structural complexity destabilize the biotic interactions that regulate pest populations (Robinson et al., 1992; Landis et al., 2000; Tscharntke et al., 2007). In practical terms, this means that farms in more intensively managed landscapes can rely less on naturally-occurring biological control than those that are in more diverse landscapes. In more diverse landscapes that contain multiple crop types, natural habitat, perennial wooded land, and a greater availability of flowering resources, natural enemies are more likely to have their ecological requirements met near to the crop field and are less likely to disperse. This then translates into a greater abundance and diversity of natural enemy insects available during periods of pest population growth to limit the trajectory of that growth and limit pest populations (Marino & Landis, 1996; Bommarco, 1998; Thies et al., 2003; Schmidt & Tscharntke, 2005, Tscharntke et al., 2005).

Having high landscape diversity, including flowering plants, near crop fields can also interact with the management approach taken on farms to affect the natural enemy population available to control pests in crop fields. Thus, Ostman et al. (2001) found that aphid population growth was slower in organic than conventional farms, and fields set in landscapes with greater proportion of perennial crops and with more field margins received more biological control. Spider populations are also sensitive to the landscape, with spider species richness increasing with the proportion of non-crop habitat in the landscape (Schmidt et al., 2005), irrespective of whether farms were managed using organic or conventional tactics. Density of spiders was 62% higher in organically managed fields, and within the conventional fields there was a positive correlation between the proportion of non-crop habitat in the surrounding landscape and the spider density. These trends indicate that field management as well as what landscape they are set in will influence the availability of natural enemies to provide biological control services to crop fields.

The economic implications of how crop management and landscape composition affect the services that natural enemies provide have only recently been addressed. Landis et al. (2008) examined the value of biological control being provided to limit populations of soybean aphid, *Glycines max* (L.), in the context of increasing corn production for ethanol. Their analyses found a $33/ha value of biological pest control for producers who employed integrated pest management, with this value provided largely from the surrounding landscapes. Increased planting of corn, and the associated reduction in landscape diversity led to a $58 million/yr cost to farmers caused by reduced biological control of this insect, and this translated into lower yields and higher pesticide costs. In a more recent study, Meehan et al. (2011) have analyzed broad-scale landscape, pest, and pesticide use data across the Midwestern United States. Landscape simplification was correlated with higher pest pressure and greater dependence on pesticides, with multi-million dollar costs to farmers that can be attributed in part to the changes in availability of natural pest regulation supplied by surrounding landscapes.

This section has highlighted the aspects of agricultural habitats that can be manipulated to provide resources for natural enemies. But, as we have just seen, not all landscapes have high abundance of natural enemies. It may therefore be important to focus populations of natural enemies at crop plants where their pest-controlling services are needed, by harnessing the chemical interactions among organisms. This is an active and exciting area of research that can exploit the power of chemical signaling to manipulate natural enemies for the benefit of agriculture.

3. Semiochemical-based manipulation

The term "semiochemical" (semeion = sign or signal in Greek) is used to describe a chemical or mixture of chemicals that can act as messengers in interactions among organisms (Nordlund & Lewis, 1976; Dicke & Sabelis, 1988; Vet & Dicke, 1992). It includes chemicals that mediate interactions among individuals within the same species, i.e., intraspecific communication (= *pheromones*), and those that mediate interactions among individuals belonging to different species, i.e., interspecific communication (= *allelochemicals*). Among allelochemicals, compounds can be classified as *allomones* if their production benefits the emitter, *kairomones* if their production benefits the receiver or *synomones* if their production benefits both the emitter and receiver (Dicke & Sabelis, 1988; Vet & Dicke, 1992).

An approach to using semiochemicals for pest control is to exploit ways to chemically augment, conserve, or enhance the efficacy of natural enemies in cropping systems. Here we provide a review of semiochemical-natural enemy interactions and describe ways in which these compounds, particularly those emitted by plants, can be employed to enhance natural enemy attraction and ultimately reduce pest populations.

3.1 Herbivore-induced plant volatiles (HIPVs)

Plant volatiles play a critical role as signals in tri-trophic level interactions. These are interactions involving three trophic levels; for example, plants (1st trophic level), herbivores (2nd trophic level), and the natural enemies of herbivores (predators and parasitoids) (3rd trophic level). Peter Price and collaborators (Price et al., 1980) were the first to specifically emphasize the importance of including the third trophic level when considering plant-herbivore interactions. Their seminal contribution was of particular importance because interactions among organisms from more than two trophic levels are known to be common in nature (Hunter & Price, 1992; Ohgushi, 2005).

Plants can influence the natural enemies of herbivores by emitting behavior-modifying volatile organic compounds. Specifically, plants damaged by herbivores often produce a blend of volatiles (Paré & Tumlinson, 1999), commonly referred to as herbivore-induced plant volatiles (HIPVs) (Mumm & Dicke, 2010). These HIPVs consist of a mixture of the so-called green-leaf volatiles (C_6 aldehydes, alcohols, and acetates), terpenes (monoterpenes, sesquiterpenes, homoterpenes), and aromatic compounds, among others (Pichersky et al., 2006). The release of HIPVs may signal the presence of potential prey or hosts and, therefore, can be exploited by natural enemies to locate the prey organism (Sabelis et al., 1999; Verkerk, 2004). In the last 10 years there has been an increased interest in using these compounds to manipulate natural enemy behaviors for insect pest control in agricultural crops.

3.1.1 Brief overview of HIPVs

Vinson (1976) described five steps parasitoids and other natural enemies need to follow during host searching and selection; these are: 1) host habitat location; 2) host location; 3) host acceptance; 4) host suitability; and 5) host regulation. It is clear now that plant chemical cues are particularly important in aiding parasitoids during the first step. In order to locate the host habitat, natural enemies use long-distance cues from plants. These cues (e.g. HIPVs)

originate mainly from plants damaged by the natural enemies' host or prey (e.g. pest insects). In most instances HIPVs provide natural enemies with a highly detectable and reliable signal. HIPVs are classified as synomones because they can benefit both the emitting plant as well as the responding natural enemy (Vet et al., 1991). Once the host habitat is located, natural enemies utilize compounds produced by the host or prey (kairomones), such as volatiles emitted from body scales, honeydew, or the herbivore's frass. Compared with HIPVs, kairomones are more reliable in providing information to natural enemies about the location of their host or prey; however, they are not as detectable (Vet & Dicke, 1992).

Dicke & Sabelis (1988) provided the first evidence that lima bean plants (*Phaseolus lunatus* L.) damaged by the two-spotted spider mite *Tetranychus urticae* Koch emit a blend of volatiles that attract the predatory mite *Phytoseiulus persimilis* Athias-Henriot. In these early studies, this phenomenon was referred to as a 'cry for help', because of the potential fitness benefits to the injured plants from attracting the natural enemies of herbivores (Dicke et al., 1990a; Dicke & Sabelis, 1992). A second tri-trophic system extensively studied in the early 1990s involved corn (*Zea mays* L.), the chewing herbivore *Spodoptera exigua* (Hübner), and its parasitoid *Cotesia marginiventris* (Cresson). Turlings et al. (1991, 1993) showed that *C. marginiventris* utilizes compounds emitted from corn seedlings damaged by the lepidopteran herbivore to locate its host. HIPVs can also mediate plants-aphids (sucking herbivores)-natural enemy interactions. For example, Du et al. (1998) showed that the parasitoid *Aphidius ervi* Haliday is attracted to beans, *Vicia faba* L., infested by the pea aphid *Acyrthosiphon pisum* (Harris). More recent evidence shows that egg deposition by herbivores can also induce a volatile response in plants and consequently attract egg parasitoids (Meiners & Hilker, 1997, 2000; Hilker & Meiners, 2002; Colazza et al., 2004). For example, Meiners & Hilker (1997) found that oviposition by the elm leaf beetle *Xanthogaleruca luteola* (Müller) induces volatile emissions from its host plant *Ulmus minor* Mill., that attract the egg parasitoid *Oomyzus gallerucae* (Fonscolombe).

This plant volatile response to herbivore damage often differs from artificial damage (Dicke et al., 1990a; Turlings et al., 1990; De Moraes et al., 1998), indicating that the caterpillar or other pest insect induces production of specific HIPVs in the plant. These can be induced locally, i.e. at the site of damage, as well as systemically, i.e. from distal undamaged parts of a damaged plant (Turlings & Tumlinson, 1992; Dicke et al., 1993; Röse et al., 1996).

3.1.2 Characteristics of HIPVs

The emission of HIPVs is common in plants (Dicke & Vet, 1999; Dicke & van Loon, 2000); however, the induced volatile blends are highly variable (Dicke, 2000; Turlings & Wäckers, 2004). The volatile blend often varies depending on plant cultivar (e.g. Loughrin et al., 1995; Gouinguené et al., 2001), plant age (Takabayashi et al., 1994; Turlings et al., 2002), plant part (Turlings et al., 1993), and abiotic factors (Gouinguené & Turlings, 2002). Emissions of HIPVs also vary depending on the species and age of the herbivore (Takabayashi et al., 1995; Gouinguené et al., 2003). For example, Takabayashi et al. (1995) found that corn plants emit greater quantities of volatiles when damaged by 1st and 2nd instar larvae of *Pseudaletia separata* Walker than when damaged by 5th instars. The parasitoid *Cotesia kariyai* (Watanabe) attacks young *P. separata* and is attracted to volatiles emitted by corn damaged by early

instar larvae (Takabayashi et al., 1995). To cope with this variability, natural enemies can learn to associate HIPVs with the presence of their prey or host (Lewis & Tumlinson, 1988; Vet & Dicke, 1992; Vet et al., 1995; Allison & Hare, 2009). This learning capacity is thought to be more critical for generalist natural enemies than specialists (Steidle & van Loon, 2003), because the latter should have an innate response to HIPVs.

Another important characteristic of HIPVs is their specificity (Turlings & Wäckers, 2004). The specificity of certain tri-trophic systems allows natural enemies to differentiate plant volatile blends associated with their prey from those of non-prey (Dicke, 1994; Du et al., 1996; Dicke, 1999). De Moraes et al. (1998) first demonstrated the specificity of the volatile response to herbivory in plants and the effects on natural enemies. The authors found that tobacco, maize, and cotton plants produce distinct volatile blends in response to damage by larvae of two related lepidopteran herbivores: *Heliothis virescens* (Fabricius) and *Helicoverpa zea* (Boddie). The parasitoid *Cardiochiles nigriceps* Viereck exploits these differences during host location by being attracted only to HIPVs released from its host *H. virescens* (De Moraes et al., 1998). This specificity has also been reported in the tri-trophic system involving pea plants, pea aphids (*A. pisum*), and the parasitoid *A. ervi* (Du et al., 1998; Powell et al., 1998). Other studies, however, have reported a lack of specificity. For example, McCall et al. (1993) found that the parasitoid *Microplitis croceipes* (Cresson) is equally attracted to volatiles induced by its host *H. zea* and its non-host *S. exigua*. Similarly, the tri-trophic system of cabbage-caterpillars-*Cotesia* sp. lacked specificity at the herbivore level, but not at the plant level where differences in attractiveness to parasitoids were found (Geervliet et al., 1996).

3.1.3 Belowground tri-trophic interactions

There is now an abundant literature showing that tri-trophic level interactions occur aboveground (as described above). However, relatively little is known about the way organisms from different trophic levels interact belowground. This is particularly true for the roles of HIPVs in attraction of soil-inhabiting natural enemies to root volatiles. For example, Boff et al. (2001) found that the entomopathogenic nematode *Heterorhabditis megidis* Poinar, Jackson & Klein is attracted to the roots of *Thuja occidentalis* L. damaged by the weevil *Otiorhynchus sulcatus* Germar. However, the volatile responsible for this attraction was not identified. Recently, Rasmann et al. (2005) found that larvae of the corn rootworm, *Diabrotica virgifera virgifera* LeConte, feeding on corn roots induce the emission of (E)-β-caryophyllene, which in turn attracts entomopathogenic nematodes. Similar to aboveground interactions, interactions belowground can be specific at both the plant and herbivore levels (Rasmann & Turlings, 2008).

3.1.4 Plant elicitors of HIPVs

Jasmonic acid (JA) and its volatile derivative methyl jasmonate (MeJA) are phytohormones involved in plant defenses against herbivores (Karban & Baldwin, 1997), that can also play a key role in the production and emission of HIPVs (Hilker et al., 2002; Kessler et al., 2004). Plants treated topically with JA or MeJA increase their volatile emissions (Hopke et al., 1994; Gols et al., 1999; Ament et al., 2004; Hare, 2007); however, the volatiles produced often differ from those induced by herbivore damage (Dicke et al., 1999; Rodriguez-Saona et al., 2001). Other phytohormones involved in the emission of HIPVs include salicylic acid (SA) and

ethylene (Schmelz et al., 2009). Salicylic acid is a phytohormone often associated with plant resistance against pathogens but also against sucking insects such as aphids and whiteflies (Walling, 2000). Exposure to exogenous (airborne) SA, or its volatile derivative methyl salicylate (MeSA), can induce a volatile response in plants (Ozawa et al., 2000). For example, activation of both the JA and SA pathways by *T. urticae* is required to attract predatory mites to damaged lima bean plants (Dicke et al., 1999). In fact, the predatory mite *P. persimilis* prefers lima beans releasing volatiles induced by *T. urticae* than those induced by JA (Dicke et al., 1999). This difference may be explained by the lack of MeSA from the blend induced by JA. In tomatoes, however, Ament et al. (2004) found that JA is necessary to induce the enzymatic conversion of SA into MeSA, and concluded that JA is essential for the emission of spider mite-induced volatiles. Despite the fact that MeSA can play an important role in predator attraction to plants (e.g. De Boer & Dicke, 2004a, 2004b; Rodriguez-Saona et al., 2011a), compared with the JA pathway, less is known on the importance of the SA pathway in the emission of HIPVs.

In addition, these phytohormones can interact synergistically or antagonistically (Walling 2000). For instance, SA can inhibit the plant's response to JA and *vice versa* (Koornneef & Pieterse, 2008). Horiuchi et al. (2001) demonstrated that the ethylene precursor, 1-aminocyclopropane-1-carboxylic acid, increases the induced volatile response to JA in lima bean and, as a result, increases the attraction of the predatory mite *P. persimilis*.

3.2 Manipulation of HIPVs to enhance biological control

This review will focus on three methods to manipulate HIPV emissions in agricultural fields: a) use of synthetic versions of HIPVs; b) increase of HIPV emissions through use of phytohormonal elicitors; and, c) increase of HIPV emissions via genetic engineering. Table 1 summarizes general physical, economical, and biological characteristics of these approaches.

3.2.1 Synthetic HIPV lures

The simplest way to manipulate natural enemy behaviors chemically in agricultural fields is to identify the natural HIPVs, produce them, and release synthetic versions of them (Fig. 1C). In this approach, natural enemies are exposed to a "supernormal" stimulus (i.e., a highly attractive HIPV), that is expected to outcompete the "normal" stimuli provided by the surrounding vegetation. Yet, compared with the large number of studies documenting the attraction of natural enemies to HIPVs under laboratory conditions, fewer studies have been conducted under field conditions (Hunter, 2002). In early studies, Flint et al. (1979) showed attraction of the common green lacewing *Chrysoperla carnea* (Stephens) to β-caryophyllene. Drukker et al. (1995) found an increased density of predatory anthocorids on pear trees near cages containing *Psylla*-infested trees compared with trees near cages containing non-infested trees. Similarly, Shimoda et al. (1997) found greater attraction of the predatory thrips *Scolothrips takahashii* Priesner to traps with *T. urticae*-infested lima bean plants compared with traps with uninfested plants. In a non-agricultural system, Kessler & Baldwin (2001) later showed that predation of *Manduca sexta* L. eggs by the generalist predator *Geocoris pallens* Stal. increases when plants of *Nicotiana attenuata* Torr. ex Wats are treated with the HIPVs (Z)-3-hexenol, linalool, and cis-α-bergamotene.

Attributes	Synthetic HIPV lures	Plant Elicitors	Genetic Engineering
I. Physical/Economics			
Longevity	Medium-long lasting. Slow-release devices (4 weeks or more)	Short-lasting - often quick activation of volatiles (likely less than a week)	Longest lasting approach. (throughout the plant's life)
Applicability/ Adoptability	Relatively easy to apply and adopt	Relatively easy to apply and adopt	May require long-time for development and adoption
Cost	Relatively cheap: will depend on cost of application, complexity of volatile blend, type of deployment device, number of point sources, etc	Can be expensive: will depend on acreage applied, cost of application and producing elicitor – e.g. JA is costly	The developmental phase can be costly
Commercial availability	Two lures commercially available to growers specifically for this purpose (see text for details)	No product commercially available for this purpose	No product commercially available
II. Biological			
Mode of action	Lures need to outcompete background volatiles May induce volatile emissions from exposed plants	A more "natural" attractant than synthetic lures; however, induced volatile blend often different from the herbivore-induced blend	The most "natural" volatile signal of the three approaches. Plants produce their own set of volatiles
Natural enemy efficacy	In the absence of host/prey, natural enemies can increase foraging time; thus, reduce their efficacy	In the absence of host/prey, natural enemies can increase foraging time	If plants are "primed" for increased induce volatile responses, it may increase natural enemy foraging efficacy
Specificity of signal	Generalized volatile signal: attract a wide range of natural enemies. Signal not specific neither at the plant nor herbivore levels	More specific blend; however, it affects natural enemies differently, some positive, negative, and neutral. Signal likely specific at the plant level but not the herbivore level	The most specific blend of the three approaches. Signal specific at both the herbivore and plant levels
Negative consequences	Natural enemy attraction likely to point source. High potential for association of HIPVs with lack of host/prey. Medium-high potential for natural enemy habituation to HIPVs	Natural enemy attraction likely to the treated habitat. Medium-high potential for association of HIPVs with lack of host/prey. High potential for habituation	Natural enemy attraction to the herbivore-damaged plant. Low potential for association of HIPVs with lack of host/prey. Low potential for habituation
Community-level effects	Medium-high potential for non-target effects, e.g. attraction of herbivores, pollinators	Highest potential for non-target effects, e.g. attraction of herbivores, negative effects on pollinators, cross-talk among defensive pathways, e.g. JA treatment can make plants more susceptible to pathogens	Reduced potential for non-target effects

Table 1. Comparative characteristics of different ways to manipulate natural enemies of herbivore by HIPVs in agriculture

The use of HIPVs to lure natural enemies to crop fields has been receiving increased attention in the last 10 years. James (2003a) evaluated the HIPVs MeSA, (Z)-3-hexenyl acetate, and (3E)-4,8-dimethyl-1,3,7-nonatriene to attract natural enemies in hop yards. The predatory mirid *Deraeocoris brevis* (Uhler), the anthocorid *Orius tristicolor* (White), and the coccinellid *Stethorus punctum picipes* (Casey) were attracted to sticky cards baited with (Z)-3-hexenyl acetate; while the geocorid *G. pallens*, hover flies, and *S. punctum picipes* were attracted to cards baited with MeSA. Synthetic MeSA also attracted green lacewing, *Chrysopa nigricornis* Burmeister (James, 2003b). In grape vineyards, sticky cards in MeSA-baited blocks captured greater number of *C. nigricornis*, *Hemerobius* sp., *D. brevis*, *S. punctum picipes*, and *O. tristicolor* (James and Price 2004). James (2005) tested 15 synthetic HIPVs and found attraction of *S. punctum picipes* to sticky traps baited with MeSA, cis-3-hexen-1-ol, and benzaldehyde. Other natural enemies were attracted to various degrees to different HIPVs (James, 2005). Similarly, Zhu & Park (2005) found attraction of the lady beetle *Coccinella septempunctata* L. to traps baited with MeSA, whereas 2-phenylethanol was more attractive to the lacewing *C. carnea* and syrphid flies. 2-Phenylethanol is also attractive to the multicolored Asian lady beetle, *Harmonia axyridis* (Pallas) (Sedlacek et al., 2009), and is currently being sold commercially by MSTRS Technologies (Ames, Iowa, USA) as the natural enemy attractant Benallure®. Phenylacetaldehyde is another plant attractant for the green lacewing *C. carnea* (Tóth et al., 2006, 2009).

To date, most studies have evaluated HIPVs individually; thus, the synergistic effects of HIPV mixtures on natural enemy attraction remain largely unknown. Yu et al. (2008) tested seven HIPVs and a mixture of nonanal and (Z)-3-hexen-1-ol in cotton fields. Interestingly, they found attraction of the syrphid fly *Paragus quadrifasciatus* Meigen to dimethyl octatriene, nonanal plus (Z)-3-hexen-1-ol, and octanal, whereas the syrphid fly *Epistrophe balteata* De Geer did not respond to any of the HIPVs tested (Yu et al., 2008), indicating differential responses of species of natural enemies to HIPVs within the same insect family. Also, most studies have used slow-release devices instead of spraying HIPVs directly onto crops. This latter approach was tested by Simpson et al. (2011c) who mixed different HIPVs (e.g. MeSA, MeJA, methyl anthranilate, benzaldehyde, (Z)-3-hexenyl acetate, and (Z)-hexen-1-ol) with the vegetable oil adjuvant Synertrol®, and sprayed them onto winegrape, broccoli, and sweet corn plants. They found greater abundance of several parasitic Hymenoptera and predatory insects near plants sprayed with the synthetic HIPVs (Simpson et al., 2011c).

3.2.1.1 MeSA – A natural enemy attractant

MeSA has received considerable attention lately for its potential to attract natural enemies in agricultural fields. This compound is a common component of the volatile blend emitted from several plant species (Pichersky & Gershenzon, 2002). MeSA is emitted from plants in response to feeding by cell-content feeders, e.g. *T. urticae* (Dicke et al., 1990b; Agrawal et al., 2002; van den Boom et al., 2004), phloem feeding, e.g. aphids (Staudt et al., 2010), and chewing herbivores, e.g. beetles (Bolter et al., 1997). In a recent meta-analysis, Rodriguez-Saona et al. (2011a) reviewed 14 publications that used MeSA to attract natural enemies in agricultural fields and found that natural enemies (i.e., coccinellids, syrphids, lacewings, predatory bugs, and parasitic Hymenoptera) are broadly attracted to MeSA. MeSA is now commercially available as PredaLure® (AgBio, Inc.; Westminster, Colorado, USA) to attract natural enemies of agricultural insect pests.

Commercial availability of PredaLure has allowed researchers a more standardized way to test natural enemy attraction to MeSA in agricultural fields, and three studies have recently done that. Lee (2010) found that PredaLures led to higher catches of lacewings and *O. tristicolor* on baited traps in strawberry fields, but the effect was found only at the point source and not at 5 or 10 m away from the lures. Ground-dwelling predators monitored using pitfall traps did not respond to the PredaLures (Lee, 2010). In soybean fields, Mallinger et al. (2011) captured greater numbers of syrphid flies and lacewings on sticky card traps adjacent to the PredaLures, but not on traps placed 1.5 m from the lures. In cranberry fields, PredaLure-baited sticky cards caught greater numbers of syrphid flies, lady beetles, and lacewings compared with unbaited traps (Rodriguez-Saona et al., 2011a). Syrphid abundance was greater on traps placed near PredaLures (0 m) than at 2.5, 5, and 10 m from the lures (Rodriguez-Saona et al., 2011a), so the spatial scale of influence over natural enemies seems to be restricted for this particular product.

3.2.1.2 Mechanism of attraction

The mechanism of natural enemy attraction to HIPVs remains unknown. Two possible mechanisms have been suggested (e.g. Khan et al., 2008): a) *Direct attraction*, where the natural enemies are attracted directly to the synthetic lure; b) *Indirect attraction*, where HIPV exposure triggers a volatile response from plants. These are not mutually exclusive mechanisms; in fact, it is likely that both mechanisms may act simultaneously. Additionally, arrestment of natural enemies near to sources of HIPVs requires further examination as a potential behavioral mechanism contributing to their location of the sources and higher abundance near to dispensers.

Direct attraction. Ample evidence exists in the literature from laboratory studies that natural enemies can respond to HIPVs (Mumm & Dicke, 2010). For example, *Anaphes iole* Girault, an egg parasitoid of *Lygus* spp., showed a strong antennal response (based on electroantennogram –EAG– analysis) to (Z)-3-hexenyl acetate and MeSA (Williams et al., 2008). Gas chromatographic-electroantennographic detection (GC-EAD) analysis showed that MeSA elicits a significant antennal response in *C. septempunctata* (Zhu & Park, 2005). Natural enemy attraction to HIPVs is often confirmed using behavioral assays (e.g. Y-tube olfactometers and wind tunnels). For example, four HIPVs: linalool, (E)-β-ocimene, (3E)-4,8-dimethyl-1,3,7-nonatriene, and MeSA attracted females of the predatory mite *P. persimilis* in Y-tube olfactometer assays (Dicke et al., 1990b; De Boer & Dicke, 2004a). In a wind tunnel, Williams et al. (2008) showed attraction of *A. iole* females to MeSA and α-farnesene. Thus, it is safe to infer that natural enemies are also being directly attracted to the synthetic lure in the field.

Indirect attraction. Less evidence exists to date on whether synthetic HIPVs can trigger a volatile response from plants under field conditions, or whether activation of this response in turn attracts the natural enemies of herbivores. In laboratory experiments, Dicke et al. (1990c) showed that undamaged lima bean plants exposed to HIPVs from *T. urticae*-damaged plants were more attractive to *P. persimilis* than unexposed plants. In the field, Simpson et al. (2011c) showed attraction of natural enemies for up to 6 days after treating plants with foliar sprays of synthetic HIPVs and, because of the extended period of activity, they concluded that plants might have been induced by exposure to the HIPVs to produce their own volatiles. Rodriguez-Saona et al. (2011a), in a greenhouse study, found that cranberry vines emit high amounts of MeSA when exposed to PredaLure dispensers,

whereas unexposed vines released undetectable quantities of MeSA. In maize fields, von Mérey et al. (2011) found that plants exposed to four synthetic green leaf volatiles ((Z)-3-hexenal, (Z)-3-hexenol, (E)-2-hexenal, and (Z)-3-hexenyl acetate) emit increased quantities of sesquiterpenes compared with non-exposed plants.

It is also unclear whether synthetic HIPVs can induce the release of volatiles from exposed plants or "prime" them for an increased volatile response once they are under attack by an herbivore (Ton et al., 2007; Frost et al., 2008). For example, Peng et al. (2011) showed that cabbage plants previously exposed to HIPVs and subsequently damaged by *Pieris brassicae* L. caterpillars attracted more *Cotesia glomerata* L. parasitoids than control plants. Similar studies need to be conducted under field conditions with a range of crop plants to determine whether HIPV lures can prime volatile emissions in exposed plants.

3.2.1.3 Impact of HIPVs on pest abundance

A key question is whether HIPV deployment can ultimately increase predation or parasitism of agricultural pests, and thereby reduce their populations. So far, however, only a few studies have addressed this question. An early study by Altieri et al. (1981) found that spraying a crude extract from corn or *Amaranthus* onto plants increases parasitism rates of *H. zea* eggs by *Trichogramma* wasps. However, this study did not test for specific HIPVs. Three studies have explicitly tested the effects of HIPVs on parasitism rates in the field. Titayavan & Altieri (1990) first showed higher levels of parasitism of the aphid *Brevicoryne brassicae* (L.) by its parasitoid *Diaretiella rapae* (M'Intosh) with applications of a allylisothiocyanate emulsion in broccoli. More recently, Williams et al. (2008) reported greater parasitism of *Lygus lineolaris* (Palisot de Beauvois) eggs by *A. iole* in cotton fields when dispensers containing (Z)-3-hexenyl acetate and α-farnesene were placed near the host eggs. In field cage studies in cotton, Yu et al. (2010) found higher parasitism of *Helicoverpa armigera* (Hübner) larvae by *Microplitis mediator* Haliday in cages treated with 3-7-dimethyl-1,3,6-octatriene. This compound was also active to *M. mediator* in EAG and olfactometer assays (Yu et al., 2010). Lee (2010) found no change in pest abundance in response to deployment of MeSA in strawberry.

Two studies so far have tested the effects of HIPVs on predation rates in the field. Ferry et al. (2009) tested dimethyl disulfide to attract predators (*Aleochara bilineata* Gyllenhal)) of the cabbage root fly, *Delia radicum* (L.), in broccoli. Although they found increased predator attraction, the number of *D. radicum* eggs predated were reduced in treated compared with untreated plots. Finally, Mallinger et al. (2011) showed lower abundance of soybean aphids, *Aphis glycines* Matsumura, in field plots baited with MeSA lures (PredaLures) compared with untreated plots.

3.2.2 Phytohormonal elicitors

Alternatively to the use of HIPV lures, plants can be treated with an exogenous elicitor in the field, such as jasmonates (e.g. JA, MeJA, or cis-jasmone), to induce production and emissions of their own blend of volatiles, and as a result attract natural enemies (Rohwer & Erwin, 2008). This is a more "natural" approach for attracting predators and parasitoids of pests into crops as compared with using synthetic lures because these phytohomones often induce an attractive blend of volatiles in quantities that are more comparable with those induced by herbivore feeding. However, besides inducing volatile emissions, jasmonates induce a wide array of responses in plants including increase of defenses that can negatively

affect the performance of natural enemies by reducing the quality and quantity of herbivores on plants (Thaler, 1999, 2002).

The effects of jasmonates on natural enemy attraction have been demonstrated under laboratory and field conditions. For example, in the laboratory, the predatory mite *P. persimilis* is attracted to an odor blend induced by JA from gerbera (Gols et al., 1999) and lima bean (Dicke et al., 1999) plants. Similarly, van Poecke & Dicke (2002) showed that treatment of *Arabidopsis thaliana* (L.) with JA increases attraction of *Cotesia rubecula* (Marshall) compared with untreated plants, whereas treatment with SA did not. Ozawa et al. (2004) also reported that treating maize plants with JA increases attraction for the parasitoid *Cotesia kariyai* Watanabe. However, natural enemies are sometimes less attracted to volatiles induced by JA than to those induced by herbivores (Dicke et al., 1999), indicating that there can be differences between the volatile blends induced by herbivores and JA treatment. In the field, Thaler (1999) showed that JA treatment of tomato plants increases parasitism of caterpillars near the treated plants. However, JA can affect natural enemies of herbivores differently. For instance, Thaler (2002) found that syrphid flies were negatively affected by JA treatment of tomato plants due to a decrease in herbivore abundance on JA-treated plants, but found no effects for a caterpillar parasitoid, an aphid parasitoid, or lady beetles. Also, Lou et al. (2005) demonstrated that egg parasitism of the rice brown planthopper, *Nilaparvata lugens* (Stål), by the parasitoid *Anagrus nilaparvatae* Pang et Wang on rice plants was two-fold higher when plants were surrounded by JA-treated plants than by control plants.

To our knowledge there is no commercial product currently available that uses plant elicitors (e.g. phytohormones) for the sole purpose of triggering HIPVs and attracting natural enemies in agricultural crops. This lack of commercial products may be due to the fact that phytohormones, such as JA, can activate multiple physiological responses in plants (including defenses against insects pests), but their effects on plant yield remains largely unknown. As a result, the risks of activating the JA pathway might outweigh its benefits if resistance to phytophagous insects reduces fitness of natural enemies on plants or increases plant susceptibility to pathogens (Table 1).

Practical application of HIPVs for insect pest control remains a goal that will require coordinated research by agricultural scientists and chemical ecologists. The involvement of commercial suppliers is a positive step towards development of cost-effective and efficaceous products for manipulation of natural enemies in crops.

3.2.3 Genetic engineering

Many of the risks associated with using lures or phytohormones to attract natural enemies may be avoided through genetic engineering because plants can be selected for enhanced HIPV emissions only when attacked by herbivores. 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. Two approaches can be taken: a) selective breeding, where the natural variation in the production of HIPVs among plants can be exploited in breeding programs to select for plants that enhance the foraging efficiency of natural enemies, or b) transgenic plants, where specific genes are incorporated to prime plants for an enhanced HIPV response.

3.2.3.1 Selective breeding

Plant breeding may produce crops with enhanced volatile emissions (Nordlund et al., 1981, 1988); however, to date, selective breeding for high HIPV production in plants has not been explored. Volatile emissions often differ within and among plant species (Elzen et al., 1985; Takabayashi et al., 1991), and selecting for plants that are more attractive to natural enemies may thus help biological control. For example, Elzen et al. (1985, 1986) found greater production of volatiles attractive to the parasitoid *Campoletis sonorensis* (Cameron) from glanded cotton (*Gossypium hirsutum* L.) than nonglanded cotton. However, use of highly attractive plants has the same disadvantage as synthetic lures because volatiles are not associated with the host/prey. A better approach is to select plants with greater induced volatile responses (HIPVs). For instance, HIPV emissions varied by 8-fold among maize cultivars (Gouinguené et al., 2001; Degen et al., 2004). Similarly, high variation in HIPV production among cultivars has been reported in apple (Takabayashi et al., 1991), cotton (Loughrin et al., 1995), and *Gerbera* (Krips et al., 2001). Among below-ground interactions, (E)-β-caryophyllene is a volatile induced from maize roots by herbivory that attracts entomopathogenic nematodes (Rasmann et al., 2005), and emissions of this attractant have apparently been lost in American maize varieties (Köllner et al., 2008). Thus, restoring this or other signals may enhance the effectiveness of biological control agents (e.g. Degenhardt et al., 2009). This would be particularly relevant in domesticated crops where breeding for high yielding crops might unintentionally reduce traits associated with insect resistance such as HIPV emissions (Rodriguez-Saona et al., 2011b).

3.2.3.2 Transgenic plants

There are a few literature reviews on the use of transgenic plants to augment HIPVs (Degenhardt et al., 2003; Aharoni et al., 2005, 2006; Turlings & Ton, 2006; Dudareva & Pichersky, 2008; Kos et al., 2009). Plant defense signaling pathways have been a target of genetic manipulation. For instance, mutant or genetically–modified plants with impaired JA production have been developed (Baldwin et al., 2001; Thaler et al., 2002; Ament et al., 2006), and are often less attractive to natural enemies (Thaler et al., 2002; Ament et al., 2004). Knock out of the JA pathways can also reduce direct defenses, thus making plants more susceptible to herbivory (Thaler et al., 2002; Kessler et al., 2004). Mutant plants also exist with impaired genes specifically involved in defense pathways (van Poecke & Dicke, 2002; van Poecke & Dicke, 2003; Shiojiri et al., 2006). These studies have improved our understanding on the ecological role of plant defensive pathways in tri-trophic level interactions; however, transgenic plants with modified production of HIPVs will be more useful for manipulation of natural enemy behaviors. Terpenoid biosynthesis has particularly been targeted for modification because of the dominance of terpenes in the HIPV blends of plants (Aharoni et al., 2005, 2006). For example, Kappers et al. (2005) modified the expression of a linalool/nerolidol synthase gene in *A. thaliana* to enhance constitutive emissions of the HIPV nerolidol and attraction of the predatory mite *P. persimilis* to plants. Schnee et al. (2006) transferred a sesquiterpene synthase gene that forms (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. Degenhardt et al. (2009) transformed a non-(E)-β-caryophyllene emitting maize line with a (E)-β-caryophyllene synthase gene from oregano, resulting in constitutive emissions of this sesquiterpene, less root damage and 60% fewer root herbivores than non-transformed, non-emitting lines.

An alternative to modifying plants to constitutively emit HIPVs, is to genetically "prime" plants for an enhanced HIPV response after herbivore attack (Turlings & Ton, 2006). These primed plants would thus invest less energy on potentially costly defenses such as HIPV emissions in the absence of herbivores. Although the molecular mechanisms remain largely unknown, once identified, genes involved in priming should provide a useful tool to manipulate HIPV emissions in plants.

3.3 Other sources for natural enemy attraction

The concept of using chemicals to manipulate natural enemy behavior in agricultural fields is not new (Dicke et al., 1990c). However, many of the tools currently used to isolate and identify HIPVs, such as sophisticated headspace volatile collection and gas chromatography apparatus, were not available when this research started in the 1970s-1980s. Thus, most of the early work focused on testing chemicals produced from the host/prey (kairomones), or those emitted from the natural enemies themselves (pheromones). Although researchers have so far found limited applicability for these chemicals because of their low volatility and high specificity, there is great potential for this approach and we expect significant advances in the coming years.

3.3.1 Chemicals from host/prey

Early studies to enhance the efficacy of natural enemies tested the use of kairomones under laboratory and field conditions. Lewis et al. (1975a, 1975b) showed increased egg parasitism rates of *H. zea* by *Trichogramma* spp. from 13% to 22% by spraying an extract from the host (moth) scales or synthetic kairomones onto soybean plants. The moth scales contain tricosane, which was found to be the main source of attraction (Jones et al., 1973). These field results were obtained, however, only at high host densities. At low to intermediate densities, parasitism rates were enhanced if moth scales or the synthetic kairomone (impregnated particles of diatomaceous earth) were applied around the host eggs (Lewis et al., 1979; Gross, 1981). Under these latter conditions, parasitoids apparently spent more time searching intensively in areas where the hosts were absent, resulting in lower parasitism. This problem can be overcome under unnaturally-high host densities (Lewis et al., 1975a, 1975b, 1979). This work first highlighted the potential of interfering with the natural enemies' foraging behavior by application of semiochemicals onto crops. Later studies revealed that volatiles from the ovipositor gland of female *H. zea*, which contains the moth sex pheromone, are also involved in *Trichogramma* spp. host search behaviors. Applications of the synthetic sex pheromone found in the gland increased egg parasitism in greenhouse and field experiments (Lewis et al., 1982).

Kairomones can also be used to "prime" natural enemies for enhanced searching behaviors before inundative releases. For example, Hare et al. (1997) demonstrated that laboratory-reared *Aphytis melinus* DeBach, a parasitoid of the California red scale (*Aonidiella aurantii* (Maskell)), more readily parasitized hosts when exposed to the kairomone O-caffeoyltyrosine prior to being released in the field.

3.3.2 Chemicals from natural enemies

Similar to other insects, natural enemies produce pheromones for intraspecific communication. Sex pheromones have been identified from various natural enemies since

the 1970s (e.g. Robacker & Hendry, 1977; Jones, 1989; Eller et al., 1984; Swedenborg & Jones, 1992); however, so far they have been tested only to assess natural enemy activity in the field, monitor their population densities, and to predict rates of host parasitism (Lewis et al. 1971; Morse & Kulman, 1985). Because these pheromones are often produced by the females to attract males, and attraction of females instead of males is desirable in biological control, use of sex pheromones from natural enemies to manipulate their behaviors in agricultural crops has been limited. In addition, unless a stable sex ratio is known to exist in the field, trapping males does not give a reliable prediction of female abundance (Powell, 1986).

Aggregation pheromones might be useful for mass trapping and inundative releases of natural enemies into crops because these compounds attract both sexes. For example, males of the generalist predator, the spined soldier bug (*Podisus maculiventris* (Say)), produce a long-range attractant pheromone that attracts both adult sexes and immatures (Aldrich et al., 1984; Sant'Ana et al., 1997). Both sexes of adult seven-spot ladybeetle *C. septempunctata* are attracted to 2-isopropyl-3-methoxypyrazine, a compound produced by conspecifics (Al Abassi et al., 1998). Pheromones can be combined with HIPVs to enhance natural enemy attraction in agroecosystems. In fact, Jones et al. (2011) recently tested the attraction of three lacewing species to HIPVs in apple orchards and found that the combination of MeSA and iridodial, a male-produced aggregation pheromone, was a stronger attractant than each compound alone.

4. Conclusion

The idea of manipulating natural enemy behaviors to improve biological control of crop pests is an appealing concept, but research on how to best achieve this in agroecosystems is still in its infancy despite the fact that scientists have made important advances in recent years. Several factors need to be considered before these strategies are widely adopted by growers; here we discuss three of them.

4.1 Efficacy

There are many questions that remain unanswered as to how to best deploy these strategies to enhance biological control of crop pests. Habitat for natural enemies needs to be tailored to the region, crop, and management system being used to ensure the greatest potential for benefits and to minimize undesirable effects on crop yield, insect pest populations, or weed pressure. Currently, there is little information on the link between provision of habitat for beneficial insects and the economic effect on crop production, but this is a key missing piece of the puzzle and is an active area of research. Table 1 includes some risks associated with the use of HIPVs. For example, when using HIPVs to attract natural enemies, we don't know where the insects are coming from. If a fixed number of natural enemies occur in the environment, it is likely that attraction of natural enemies to one area will deprive other areas of their services. Also, we have yet to determine the optimal density and concentration of attractants to effectively manipulate biological control agents in agroecosystems. Although MeSA has proven effective as a powerful natural enemy attractant, we have not fully tested other HIPVs in single blends or mixtures. It is likely that in nature different natural enemies use information from HIPV blends differently. Specificity to attract the most important natural enemy in a particular system can be added if HIPVs are combined with other semiochemicals such as volatiles produced from the natural enemies themselves (pheromones) or the herbivores (kairomones). Natural enemy behaviors are very plastic and

Manipulation of Natural Enemies in Agroecosystems:
Habitat and Semiochemicals for Sustainable Insect Pest Control
109

they can learn to associate synthetic HIPVs with the absence of prey/host. Inundating an area with HIPVs can also lead to habituation of the natural enemy's sensory system, potentially resulting in reduced foraging success. All these concerns need to be addressed before these strategies can be adopted by growers.

Not only can the plants be selected for enhanced HIPV emissions but the natural enemies themselves can also be artificially selected for a superior response to HIPVs. However, this concept has not been widely explored. In a belowground system, Hiltpold et al. (2010) selected the entomopathogenic nematode *Heterorhabditis bacteriophora* Poinar for an improved attractive response towards (E)-β-caryophyllene.

4.2 Costs

The costs of any strategy for manipulating natural enemy behaviors in agroecosystems have not been estimated. No matter how effective these strategies are, their adoption will depend on how comparable their costs are with currently available pest management practices. In fact, the benefits growers obtain from recruiting "free" natural enemies services to provide pest suppression should exceed the associated costs of deploying these strategies. For instance, habitat manipulation to create flower strips or planting alternative food-providing resources for natural enemies within a farm may use land that otherwise could be used in crop production. Even if land is used that is not appropriate for crop production, the expenses associated with preparing habitat for beneficial insects can be considerable. Cost-share programs are available in some countires for establishing beneficial insect habitat in agricultural landscapes. Despite the costs of habitat establishment or HIPV deployment, with the increasing costs of pesticides and consumer concerns about pesticide residues on fresh farm products, biological control is becoming a more attractive alternative. Although strategies to conserve and augment natural enemies described in this chapter are environmentally friendly, relying on the performance of natural enemies could, however, be risky for growers particularly when used to manage a pest in crops where the market has little to no tolerance for damage.

4.3 Combination of strategies

Individually, using strategies such as habitat diversification or the deployment of semiochemical lures to manipulating the behavior of natural enemies may enhance biological control in agroecosystems, but it is possible to further improve the efficacy of natural enemies by combining more than one strategy to manipulate their behaviors in field crops (Fig. 1D). For example, Simpson et al. (2011b) tested the concept of an "attract and reward" strategy that combines habitat manipulation with HIPVs. In their approach, several HIPVs (including methyl anthranilate, MeJA, and MeSA) were tested as attractants and buckwheat was used as a reward. They showed an increase in natural enemy abundance in fields treated with both the "attract" and "reward" strategies compared with those treated with a single strategy (Simpson et al., 2011b). This combined approach has also recently been tested in perennial crop systems, with increased predators and parasitoids (as well as herbivorous thrips) observed in response to HIPV application to vineyards, and parasitoids and thrips responding to provision of flowering plants (Simpson et al., 2011a). However, the combined treatments did not significantly affect natural enemy captures in treated plots. Although these first attempts to combine attract and reward are revealing additive rather

than synergistic effects of combining strategies, we expect that further investigations of operational parameters to optimize such systems will provide a more clear view of the situations in which attract and reward can support pest management. This approach is appealing because it overcomes the concern of bringing natural enemies into areas deprived of prey/host, which may lead to association of HIPVs with lack of food, by providing them with an alternative food source to enhance their residency time in treated areas. The approach is expected to work as long as the presence of a supplementary food source (e.g. nectar or pollen) does not interfere with the natural enemy's search behavior for prey or host, which may result in the unwanted outcome of greater herbivore abundance.

Integrated Pest Management (IPM) relies on multiple strategies to maintain pest populations below an economic threshold. Biological control can be combined with chemical control to develop an integrative pest management program. IPM programs based on reduced-risk, softer chemical control tactics, i.e., those with reduced harmful effects on natural enemies, are more desirable. Behavioral manipulation of natural enemies is compatible with these pesticides to conserve or augment natural enemies. For example, semiochemical-based attractants can be used as a tool to measure the impact of insecticides on natural enemy populations. They can also be used to conserve natural enemies within farms by minimizing their exposure to pesticides such that natural enemies are removed from fields before pesticide treatments by placing these attractants in adjacent non-treated fields. HIPVs and other semiochemicals can also be used in augmentative releases of natural enemies by mass trapping natural enemies and releasing them in areas of low population and high pest pressure.

5. Acknowledgment

6. References

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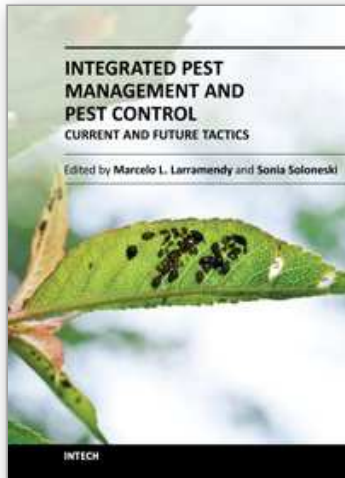
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Edited by Dr. Sonia Soloneski

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