International Journal of Botany Studies
ISSN: 2455-541X; Impact Factor: RJIF 5.12
Received: 01-11-2019; Accepted: 03-12-2019
www.botanyjournals.com
Volume 5; Issue 1; January 2020; Page No. 01-08

The role of herbivore-induced plant volatiles (HIPVs) as indirect plant defense mechanism in a diverse plant species: A review

Haftay Gebreyesus Gebreziher
Department of Horticulture, College of Agriculture and Environmental Science, Adigrat University Adigrat, Ethiopia

Abstract

In response to herbivore attack, plants release herbivore-induced plant volatiles (HIPVs) to the environment to communicate with higher trophic levels. The HIPVs are mainly important for attraction of natural enemies that attack the herbivore in which the interaction among the plant, herbivore and natural enemies is referred to as tritrophic interaction. Besides, HIPVs are important for plant-plant interaction and plant-herbivore interaction. The attractiveness of HIPVs to natural enemies in a tritrophic interaction varies depending on species diversity. Under natural and multiple cropping systems, tritrophic interaction is expected to be more complex than simple tritrophic interaction (one species per trophic level). In complex tritrophic interaction, diversity of different trophic levels affects attractiveness of HIPVs to natural enemies. From plant diversity point of view, HIPVs mixture emanating from herbivore-damaged multiple plant species are reported to affect behavioral responses and foraging behavior of natural enemies under laboratory and field conditions. This paper reviews findings on the role of HIPVs as indirect plant defense in tritrophic interaction systems consisting of diverse plants species.

Keywords: herbivore-induced plant volatiles (HIPVs), tritrophic interaction, natural enemies, plant species diversity

1. Introduction

In co-evolution, plants and insets have evolved a variety of deleterious and beneficial interactions (Maffei *et al*., 2007) [51]. In plant-insect herbivore interaction, plants are threatened by potentially hostile insect herbivores. On the other hand, plants are far from being passive victims of these attackers (Dicke *et al*., 2009; Das *et al*., 2013). They have evolved multitude of defense systems that protect them from being overeaten by the herbivores (Kessler and Baldwin, 2002; Heil and Karban, 2010) [47]. These could be either direct or indirect defense systems (War *et al*., 2015) [76].

When plants are attacked by herbivores, they release induced plant volatiles from leaves or other parts to the environment to communicate with higher trophic levels that attack the herbivores and such defenses are called indirect plant defenses (Pare and Tumlinson, 1999) [59]. When attacked by herbivores, plants release much greater quantities or produce *de nevo*, of low molecular weight volatiles which are called herbivore-induced plant volatiles (hereafter called HIPVs) that attract natural enemies of the herbivores (Drukker and Sabelis, 1990; Yu *et al*., 2010) [30]. Various arthropod natural enemies exploit HIPVs to locate and feed on their preys or parasitize their hosts (Dicke and Sabelis, 1988; Turlings and Wackers, 2004; Das *et al*., 2013; Dicke, 2015). To date, plethora of investigations have explored the attractiveness of HIPVs to natural enemies such as predators (such as Dicke and Sabelis, 1989; Tatemoto and Shimoda, 2008; Haftay and Nakamuta, 2016 a, b) [36] and parasitoids (Turlings *et al*., 1990; Van Poecke *et al*., 2001; Yu *et al*., 2010).

In addition to attracting natural enemies to the food source, HIPVs could arrest them to remain on the plants (Uefune *et al*., 2012). Uefune (2012) reported that the parasitic wasp *Cotesia vestalis* Haliday (Hymenoptera: Braconidae) had a longer residence time on plants treated with an attractive blend of four volatiles (*n*-heptanal, sabinene, α-pinene and (*Z*)-3-hexenyl acetate) which are induced from *Plutella xylostella* Linnaeus (Lepidoptera: Plutellidae) larvae-infested cabbage plants.

HIPVs may comprise compounds from different groups such as terpenoids, green leaf volatiles (GLV), phenylpropanoids/benzenoids, and aromatic compounds like indole and methyl salicylate (MeSA) (Dicke, 2009). These groups of HIPVs are synthesized through different biosynthetic pathway in different compartments of plant cells (Pare and Tumlinson, 1999; Das *et al*., 2013)[59] and are regulated by phytohormones such as jasmonic acid, salicylic acid, and ethylene (Ozawa *et al*., 2000; Menzel *et al*., 2014a)[58].

The attractiveness of HIPVs to natural enemies varies depending on species diversity of different trophic levels in a given environment. Under natural conditions, though different from place to place, the interaction among different trophic levels is expected to be more complex. For instance, in fields with diverse plant species, the plant volatiles released to the environment is expected to be with greater diversity both quantitatively and qualitatively. On the other hand, a plant species could be attacked by multiple herbivores which might result change in response of plants in releasing HIPVs compared to attack by single herbivore species. Recent studies show that in systems with diverse plant species, herbivore species or both affect release of HIPVs quantitatively and qualitatively, and in turn the response of natural enemies (Haddad *et al*., 2011; Moreira *et al*., 2012; Haftay and Nakamuta, 2016a, b) [36]. These findings are recent advances in the plants-herbivores-natural enemies' tritrophic interaction paradigm given that in natural and multiple cropping systems the interaction is more complicated and need further investigations by ecologists, evolutionists, naturalists etc. Therefore, the aim of this paper is to review the recent growing evidences on the role of HIPVs as indirect defense of plants in tritrophic interaction systems with diverse plants species.

2. Impacts of HIPVs on other organisms from the simple tritrophic interaction concept

Once HIPVs are released to the environment, they are not under the control of the plants. They might be exploited by various organisms from various trophic levels such as neighboring conspecific plants (Kost and Heil, 2006; Choh and Takabayashi, 2010) [7] or different plant species (Baldwin *et al*., 2006; Pearse *et al*., 2013) [60], conspecific herbivores (De Moraes *et al*., 2001; Carroll *et al*., 2008)[6] or different herbivore species (Bernasconi *et al*., 1998; Robert *et al*., 2012) [62], and natural enemies (Dicke and Sabelis, 1988; Yu *et al*., 2008; Yu *et al*., 2010; Zhang *et al*., 2012; Haftay and Nakamuta, 2016a,b) [36]. These attributes are thought to exert different selection pressures on the plant fitness (Hoballah and Turlings, 2001; Kost and Heil, 2006; Dicke and Baldwin, 2010). The impacts of HIPVs on other organisms in a simple tritrophic interaction are explained below.

2.1 Role of HIPVs in plant-plant interaction

One of the ecological roles of HIPVs is their involvement in plant-plant interaction. The release of HIPVs from herbivore-attacked plants might trigger responses, positive or negative effect, on the receiving plant of the same or different species. For instance, Kost and Heil (2006) [48] found that HIPVs emitted from herbivore-infested Lima bean plants as well as a synthetic HIPV mixture resembling the natural one induces another indirect defense that is a secretion of extrafloral nectar, an alternative food source for natural enemies, in a neighboring conspecific plant. This led to the attraction of a higher cumulative number of predatory and parasitoid insects and the plants get a fitness benefit such as an increased production of inflorescences and leaves (positive effect). Similarly, Choh and Takabayashi (2010) [7] found that uninfested Lima bean plants exposed to HIPVs attracted more predatory mites *Phytoseiulus persimilis* Athias-Henriot (Acarina: Phytoseiidae) and secreted larger amounts of extrafloral nectars than unexposed plants. They further reported that the predators survived longer when supplied with extrafloral nectar and stayed longer on uninfested plants that had been supplemented with additional extrafloral nectar. These findings imply that HIPVs play important role for plant-plant communications. It is expected that this might result in adjustment of mechanical and chemical defenses, and gene expression in the receiver plant.

2.2 Role of HIPVs in plant-herbivore interaction

HIPVs can also affect foraging behaviors of herbivores either conspecifics or heterospecifics. For example, De Moraes *et al*. (2001) reported that HIPVs emitted at night time from tobacco plants damaged by *Heliothis virescens* Fabricius (Lepidoptera: Noctuidae) larvae are highly repellent to and result in a lower ovipositing of eggs by conspecific adult moths. Additionally, HIPVs can repel heterospecific herbivore species. For example, Bernasconi *et al*. (1998) found that maize plants treated with regurgitant of the caterpillar *Spodoptera littoralis* Biosduval (Lepidoptera: Noctuidae) which induce emission of volatiles that attract natural enemies were repellant to corn leaf aphid *Rhopalosiphum maidis* Fitch (Homoptera: Aphididae). These findings are indicators for the possible use of HIPVs not only to attract natural enemies but also help the plant not to host other herbivores either conspecific or hetrospecifics. In addition to this, upon damage by herbivores, plants release toxic chemicals that is unpleasant for the herbivores. This helps the plant to avoid further damage by the herbivores. On the other hand, for some herbivore species, HIPVs could be attractive and might negatively affect the plant due to damage by the herbivore.

2.3 Role of HIPVs as indirect plant defense

Another well-established ecological role of HIPVs is their function as plant`s indirect defense by attracting arthropod natural enemies such as predators and parasitoids that attack the herbivores (Dicke *et al*., 1990a, b; Uefune *et al*., 2013; Haftay and Nakamuta, 2016a) [36]. The importance of the third trophic level for the plant indirect defense in a tritrophic plant-herbivore-arthropod natural enemy interaction was first suggested by Price and his colleagues (Price *et al*., 1980). This was followed by investigations on behavioral responses of natural enemies to plant volatiles emitted from herbivore-infested plants which led to the discovery of HIPVs that attract predators (Sabelis and Van de Baan, 1983; Dicke and Sabelis, 1988; Dicke *et al*., 1990a) and parasitoids (Turlings *et al*., 1990). Sabelis and Van de Baan (1983) revealed that volatiles (which they used the term “kairomones” for the volatiles) emitted from apple leaves infested by two-spotted spider mites *Tetranychus urticae* Koch (Acari: Tetranychidae) attracted the *P. persimilis* and *Metaseiulus occidentalis* Nesbit (Acarina: Phytoseiidae). Among other early works, Dicke *et al*. (1990a, b) revealed that, upon infestation by *T. urticae*, Lima bean plants emitted a blend of volatiles attracting the predatory mite *P persimilis* that effectively removed local populations of the spider mites. Similarly, corn plants damaged by caterpillars of *Spodoptera exigua* Hubner (Lepidoptera: Noctuidae) emitted volatiles that attracted the parasitoid *Cotesia marginiventris* Cresson (Hymenoptera: Braconidae) (Turlings *et al*., 1990). Since these discoveries, several behavioral and electrophysiological investigations had revealed the attractiveness of HIPVs to predators (such as Drukker *et al*., 1995; Zhang *et al*., 2009; Zhang *et al*., 2012) and parasitoids (e.g.: Turlings and Tumlinson, 1992; Yu *et al*., 2008; Yu *et al*., 2010). Some of the reports on the attractiveness of HIPVs from herbivore-infested plants to predators/parasitoids under laboratory and field conditions are summarized in Table 1 and Table 2 respectively.

As a result of attracting natural enemies, the plants are expected to get fitness benefit. There are reports which show plants get fitness benefits from the indirect defenses via HIPVs by attracting natural enemies. For instance, Hoballah and Turlings (2001) reported that maize plants (*Zea mays* L.) under attack by larvae of *S. littoralis* attracted *C. marginiventris* and *Campoletis sonorensis* Cameron (Hymenoptera: Ichneumonidae) which resulted higher parasitization and reduced feeding and weight gain of the host larvae. Consequently, at maturity, parasitized larvae-attacked plants produced 30% more seeds than plants attacked by unparasitized larvae did. Kost and Heil (2006) [48] reported that exposure of plants to HIPVs which result in higher extrafloral nectar attracting more predatory and parasitoid insects and the plants increased production of inflorescences and leaves as compared to unexposed plants.

Table 1: Attractiveness of volatiles emitted from herbivore-infested plants to predators or parasitoids in laboratory experiments

Infested plants (Source of HIPVs)	Herbivores	Attracted natural enemies	References
Lima bean (Phaseolus lunatus)	Tetranychus urticae	Phytoseiulus persimilis[1]	Dicke and Sabelis, 1988; Dicke *et al*., 1990a, b; Margolies *et al*., 1997
Corn (Zea mays)	Spodoptera exigua	Cotesia marginiventris[2]	Turlings *et al*., 1990; Turlings *et al*., 1991; Turlings and Tumlinson, 1992
Brussels sprouts (Brassica oleracea)	Pieris brassicae	Cotesia glomerata[2]	Mattiacci *et al*., 1994
Broad bean (Vicia faba)	Acyrthosiphon pisum	Aphidius ervi[2]	Guerrieri *et al*., 1999
Phaseolus vulgaris	T. urticae	Amblyseius womersleyi-Kyoto[1]	Maeda *et al*., 1999
Cucumber	T. urticae or Frankliniella occidentalis	Orius laevigatus[1]	Venzon *et al*., 1999
Pear	Cacopsylla pyricola	Anthocoris nemoralis[1]	Drukker *et al*., 2000a, b
Arabidopsis thaliana	Pieris rapae	Cotesia rubecula[2]	Van Poecke *et al*., 2001
Barley plant (Hordeum vulgare)	Rhopalosiphum padi	Coccinella septempunctata[1]	Ninkovic *et al*., 2001
Vicia faba or Phaseolus vulgaris	Feeding plus oviposiotion by Nezara viridula	Trissolcus basalis[2]	Colazza *et al*., 2004
Strawberry	T. urticae	Phytoseiulus macropilis[1]	Fadini *et al*., 2010
Cucumber	Thrips tabaci	Orius strigicollis[1] P. persimilis[1]	Tatemoto and Shimoda, 2008
Cotton	Helicoverpa armigera	Microplitis mediator[2]	Yu *et al*., 2010

[1]Predators, [2]parasitoids

Table 2: Attractiveness of HIPVs to natural enemies under field conditions

HIPVs or source of HIPVs	Attracted natural enemies	References
Volatiles emitted Psylla pyricola -infested pear	Anthocoris nemorum[1], Orius vicinus[1], Orius minutus[1]	Drukker *et al*., 1995
T. urticae- or F. occidentalis-infested cucumber	Orius laevigatus[1]	Vanzon *et al*., 1999
[(Z)-3-hexenyl acetate, MeSA, DMNT][a]	Multiple arthropod natural enemies[1,2]	James, 2003b
MeSA	Chrysopa nigricornis[1], Hemerobius sp. [1], Stethorus punctum picipes[1], Orius tristicolor[1]	James, 2003a; James and Price, 2004
13 HIPVs[a]	Multiple arthropod natural enemies[1,2]	James, 2005
[MeSA, MeJA, (Z)-3-hexenyl acetate][a]	Multiple arthropod natural enemies[1,2]	James and Grasswitz, 2005
MeSA	Coccinella septempunctata[1]	Zhu and Park, 2005
2-phenylethanol	Chrysoperla carnae[1]	Zhu and Park, 2005
Seven HIPVs[a]	Multiple arthropod natural enemies[1,2]	Yu *et al*., 2008
MeSA	Diadegma semiclausum[2], Anacharis zealandica[2]	Orre *et al*., 2010
3,7-dimethyl-1,3, 6-octatriene	Microplitis mediator[2]	Yu *et al*., 2010
[MeSA, (Z)-3-hexen-1-ol, (Z)-3-hexenyl acetate][b]	Stethorus punctum picipes[1]	Maeda *et al*., 2015
Allyl isothiocyanates	Diaretiella rapae[2]	Murchie *et al*., 1997; Titayavan and Altieri, 1990
Benzaldehyde	Chrysoperla plorabunda[1], O. tristicolor[1], Stethorus punctum picipes[1]	James, 2005
(Z)-3-hexen-1-ol	Anagrus daanei, O. tristicolor, S. punctum	James, 2005; Yu *et al*., 2008; Zhu *et al*., 1999, 2005
(Z)-3-hexenyl acetate	O. tristicolor[1], Orius similis[1], Coccinella septempunctata[1], Anagrus sp[1].	James, 2003a, b, 2005; James and Grasswitz, 2005; Yu *et al*., 2008; Jones *et al*., 2011
Limonene	Harmonia axyridis[1]	Alhmedi *et al*., 2010
MeSA, iridodial[b]	Chrysopa nigricornis[1], Ceropegia oculata[1]	Jones *et al*., 2011

[1]Predators, [2]parasitoids, [a]Applied singly, [b]applied as a mixture

3. Attractiveness of HIPVs to natural enemies in systems with multiple plant species

In a biological control system, it is crucial that the natural enemies are able to find prey-habitat location and the prey patches efficiently (Bouwmeester *et al*., 2003; Kaplan, 2012). Considering the higher detectability, HIPVs can be a reliable indicator of host or prey presence and their identities (Dicke *et al*., 1998; Cai *et al*., 2014) and thus predators and parasitoids utilize these volatiles for long-range prey-habitat location, and to locate host or prey in the habitat (Dicke *et al*., 1998). Thus, HIPVs play important roles in enhancing the efficiency of natural enemies as a biological control against insect pests in agricultural crops (Bouwmeester *et al*., 2003).

Most of the studies on electrophysiological and behavioral responses of natural enemies to HIPVs have focused on a single species of plant, herbivore and natural enemy tritrophic interaction. Beside to these factors, recently, evidences are accumulating beyond the simple tritrophic interaction paradigm that considers species diversity of different trophic levels (Dicke and Baldwin, 2010; Das *et al*., 2013). The emission of HIPVs constituents (quantitatively and qualitatively) is reported to be different based on the diversity plant species (Haftay and Nakamuta, 2016a, b) [36]. The high variability that characterizes the constituents of HIPVs as a result of plant species diversity influence success of natural enemies in locating their prey or host. The constituents of the HIPVs emitted from diverse plant species is different from a simple tritrophic interaction involving single species of each trophic level. Under natural conditions and multiple cropping agriculture systems, plants-herbivores-natural enemy interactions are thought to be more complex (Dicke *et al*., 2009). Under diverse plant species or multiple cropping system, natural enemies should detect herbivore-infested plants within the complex environment. Whether species diversity of a given trophic level contributes to a predator`s success in searching and locating of their prey in a given habitat consisting of multiple plant species will depend on the context in which the information is perceived by the predators or parasitoids. For instance, it has been reported that the abundances, behavioral and electrophysiological responses of predators to herbivore-damaged plants could be affected by diversity of plant species (Dicke and Van Loon, 2003; De Boer *et al*., 2008; Haddad *et al*., 2011; Dicke and Baldwin, 2010) [79].

From the plant species diversity perspective, the abundance and stability (i.e. lowered year-to-year variability) of arthropod natural enemies has been reported higher in systems with a diverse plant species or multiple cropping agriculture systems than a simplified or monoculture cropping systems (Haddad *et al*., 2011; Moreira *et al*., 2012; Haftay and Nakamuta, 2016a, b) [36]. Under such diverse plant species, natural enemies should locate their prey or host using different communication cues. The use of HIPVs is one of the communicating cues that mediate natural enemies to search a prey- or host-habitat location and to locate the prey or host within the habitat (Dicke *et al*., 1998).

From the plant species diversity perspective, plethora of studies had revealed that the constituents of HIPVs emitted from different plant species infested by the same herbivores are different (Fortuna *et al*., 2013; Haftay and Nakamuta, 2016a) [36]. Because of this, it is expected that the constituents of HIPVs released to the environment from herbivore-infested multiple plant species, such as in multiple cropping system or under natural vegetation, will be a complex mixture of volatile compounds. Haftay and Nakamuta (2016a) [36] found that multiple plant species involving tomato (*Solanum lycopersicum* L.), French bean (*Phaseolus vulgaris* L.) and sweet corn (*Zea mays* L.) infested by the polyphagous herbivore, African bollworm (*Helicoverpa armigera* Hubner, Lepidoptera: Noctuidae) released a complex mixture of HIPVs.

Recently, research findings are growing on the bottom-up influence of a mixture of HIPVs emanating from herbivore-damaged multiple host plant species on behavioral responses and foraging behavior of natural enemies under laboratory and field conditions. Under such complex mixtures of chemicals, the responses and foraging behavior of natural enemies is expected to be affected (Waschke *et al*., 2013, 2014; Haftay and Nakamuta, 2016a, b) [36]. Waschke *et al* (2013), in their review, suggested that natural enemies might use different foraging strategies under chemically complex environments which could involve avoiding, ignoring, preferring, or spatially responding to such environment depending on the benefits they gain.

For instance, Dicke *et al*. (2003) reported that behavior of the predatory mite, *P. persimilis* towards volatiles emitted from *T. urticae* -infested Lima bean plants was not affected by mixing with volatiles emitted from the caterpillar, *P. brassicae*-infested Brussels (*Brassica olerasceae* L.) plants both in a laboratory (except in one out of five experiments where the predator preferred volatiles from spider mite-infested Lima bean over mixed volatiles) and greenhouse experiment setup. The odor blends that were mixed have very different compositions and no overlap in compounds that are known to attract the predators. They suggested that the mixing of volatiles from caterpillar-infested Brussels plants that are not known in attracting the predator did not interfere with the attraction of volatiles emitted from spider mite-infested lima bean plants (or has been ignored by the predator) which consisted volatile compounds known to attract the predator. Because of this, the predators might have "ignored" the complex mixture which is one of the foraging strategies described by Waschke *et al*. (2013).

On the other hand, Haftay and Nakamuta (2016a, b) [36] reported that polyphagous herbivores feeding on multiple host plant species with a mixture of HIPVs from the different host plant species enhanced the behavioral response and foraging behavior of a generalist predator, *Orius strigicollis* (Heteroptera: Anthocoridea). According to their findings, *O. strigicollis* preferred mixture of volatiles emitted from *H. armigera*-damaged multiple plant species to volatiles emitted from *H. armigera*-damaged single plant species under laboratory (Haftay and Nakamuta, 2016a) [36] and field-cage conditions (Haftay and Nakamuta, 2016b) [36]. Besides, enhanced positive response of the predators to reconstituted HIPVs from multiple species than reconstituted HIPVs from single plant species was found in their laboratory and field-cage study. Moreover, the predator removes greater number of praise from multiple plant species than single plant species both under laboratory and field-cage condition. The enhanced attractiveness of mixture of HIPVs from multiple plant species to the predator shows a "preferring" type of foraging strategy as stated in Waschke *et al*. (2013). In this strategy, herbivore-damaged single plant species were attractive to the predator as compared to undamaged or mechanically damaged plants. When the plants are in mixture enhanced attractiveness to the predator was found. This might suggest that "synergistic or additive" effect in attractiveness of HIPVs is found when HIPVs from two or more than two attractive plant species are mixed and offered to the predator. Another possible mechanism for the enhanced attractiveness of HIPVs from multiple host plant species to *O. strigicollis* could be explained from the perspective of resource availability in which a diverse plant species system offers shelters or greater variety and amount of prey to the predators than a single plant species which also supports the 'prefer' foraging strategy.

However, if the chemicals emitted from either of plant species is repellent to natural enemies under multiple plant species system, the natural enemies are expected to prefer attractive chemicals emanating from single plant species to mixture of chemicals emanating from multiple plant species consisting of attractive and repellent plant species. In this scenario, the complex mixture of HIPVs will have an "antagonistic effect" on the foraging behavior of the natural enemies. For instance, Gohole *et al*. (2003) [33] reported that *Dentichasmias busseolae* Heinrich (Hymenoptera: Ichneumonidae), a pupal parasitoid of *Chilo partellus* Swinhoe (Lepidoptera: Crambidae), preferred volatiles from infested host plants, sorghum (*Sorghum bicolor* L.) or maize (*Zea mays* L.) to volatiles from a combination of the infested host plants and a non-host plant, molasses grass (*Melinis minutiflora* B.). They stated that the molasses grass in the combination was repellent, and thus, the parasitoid goes for the infested plants whose volatiles were attractive. This is an "avoiding" foraging strategy of natural enemies.

These different findings show that, the attractiveness of HIPVs from multiple plant species to natural enemies depends on the effect of the HIPVs from the single plant species on behavioral responses and foraging behavior of the natural enemy. In general, choosing and planting attractive plants in intercropping or multiple cropping systems is recommended to enhance the behavioral responses and foraging behaviors of natural enemies though other factors such as disease susceptibility, edaphic and environmental factors also determine the choice of plants to be used in intercropping or multiple cropping system.

4. Conclusions and recommendations

From the plant species diversity point of view, it might be possible to enhance or modify the olfactory responses and foraging behavior of natural enemies using a mixture of HIPVs from different host plant species to biologically control herbivorous insect pests. As majority of the study in this review depicted, natural enemies could be more frequently found on or attracted to multiple plant species (greater plant species diversity) such as natural vegetation or polyculture cropping systems than monoculture cropping systems. Therefore, use of mixture of synthetic or reconstituted HIPVs from multiple plant species could be as one of the important components of integrated pest management (IPM). However, most of the findings yet have been carried out in a laboratory, field-cage or small field conditions. Therefore, further investigations are needed on the attractiveness of mixture of synthetic or reconstituted HIPVs from multiple plant species to natural enemies in a larger and open field by designing a mono- versus mixed cropping systems experiment. Besides, the economic benefit that can be gained by using mixture of HIPVs need further investigation.

5. References

1. Alhmedi A, Haubruge E, Francis F. Identification of limonene as a potential kairomone of the harlequin ladybird *Harmonia axyridis* (Coleoptera: Coccinellidae). Eur. J Entomol, 2010; 107:541-548.
2. Baldwin IT, Halitsschke R, Paschold A, von Dahl CC, Preston CA. Valatiles signaling in plant-plant interaction: “Talking trees” in the genomics era. Science, 2006; 311:812-815.
3. Bernasconi ML, Turlings TCJ, Ambrosetti L, Bassetti P, Dorn S. Herbivore-induced emissions of maize volatiles repel the corn aphid, *Rhopalosiphum maidis*. Entomologia Experimentalis ET Applicata. 1998; 87(2):133-142.
4. Bouwmeester HJ, Verstappen FWA, Aharoni A, Lucker J, Jongsma MA. Exploring multi-trophic plant-herbivore interactions for new crop protection methods. Proc. BCPC Interl Congress Crop Sc. and Tech, 2003; 2:1123-1134.
5. Cai XM, Sun XL, Dong WX, Wang GC, Chen ZM. Herbivore species, infestation time, and herbivore density affect induced volatiles in tea plants. Chemoecol, 2014; 24:1-14.
6. Carroll MJ, Schmelz EA, Teal PE. The attraction of *Spodoptera frugiperda* Neonates to cowpea seedlings is mediated by volatiles induced by conspecific herbivory and the elicitor inceptin. J Chem Ecol, 2008; 34:291-300.
7. Choh Y, Takabayashi J. Herbivore-induced plant volatiles prime two indirect defenses in Lima bean. Trends in Acarology: Proc. Of the 12th international congress, 2010. DOI 10.1007/978-90-481-9837-5 41
8. Colazza S, Fucarino A, Peri E, Salerno G, Conti E, Bin F. *et al*. Insect oviposition induces volatile emission in herbaceous plants that attracts egg parasitoids. The Journal of Experimental Biology, 2004; 207:47-53.
9. Coll M, Guershon M. Omnivory in terrestrial arthropods: mixing plant and prey diets. Annual Review of Entomology, 2002; 47:267-297.
10. Cusumano A, Weldegergis BT, Colazza S, Dicke M, Fatouros NE. Attraction of egg-killing parasitoids toward induced plant volatiles in a multi-herbivore context. Oecologia, 2015. Doi. 10.1007/s00442-015-3325-3.
11. Das A, Lee S, Hyun TK, Kim S, Kim J. Plant volatiles as method of communication. Plant Biotechnol Rep, 2013; 7:9-26.
12. De Boer JG, Hordijk CA, Posthumus MA, Dicke M. Prey and non-prey arthropods sharing a host plant: effects on induced volatile emission and predator attraction. J Chem Ecol, 2008; 34:281-290.
13. De Moraes CM, Mescher MC, Tumlinson JH. Caterpillar-induced nocturnal plant volatiles repel conspecific females. Nature, 2001; 410:577-580.
14. De Vos M, Van Oosten VR, Van Poecke RMP, Van Pelt JA, Pozo MJ, Mueller MJ. *et al*. signature and transcriptome changes of *Arabidopsis* during pathogen and insect attack. MPMI. 2005; 18(9):923-937.
15. Dicke M. Behavioral and community ecology of plants that cry for help. Plant Cell Environ, 2009; 32:654-665
16. Dicke M. Herbivore-induced plant volatiles as a rich source of information for arthropod predators: fundamental and applied aspect. J of Indian Institute of Science. 2015; 95(1):35-42.
17. Dicke M. Isolation and identification of volatile kairomone that affects acarine predator-prey interactions. J Chem Ecol. 1990; 16(2):381-396.
18. Dicke M, Baldwin IT. The evolutionary context for herbivore-induced plant volatiles: beyond the ‘cry for help’. Trends in Plant Science, 2010; 15:167-175.
19. Dicke M, de Boer JG, Hofte M, Rocha-Granados MC. Mixed blends of herbivore-induced volatiles and foraging success of carnivorous arthropods. OIKOS, 2003; 101:38-48.
20. Dicke M, Sabelis MW. How plants obtain predatory mites as bodyguard. Netherlands J Zool, 1988; 38:148-165.
21. Dicke M, Sabelis MW. Does it play plants to advertise for bodyguards? Towards a cost-benefit analyses of induced synomone production. In: Lambers H, Cambridge ML, Konings H and Pons TL eds Causes and Consequences of Variation in Growth Rate and Productivity of Higher Plants. SPB Publishing, The Hague, Netherlands, 1989, 341-358.
22. Dicke M, Sabelis MW, De Jong M. Analysis of prey preference in phytoseiid mites by using olfactometer, predation models and electrophoresis. Experimental and Applied Acarology, 1988; 5:225-241.
23. Dicke M, Sabelis MW, Takabayashi J, Bruin J, Posthhumus J. Plant strategies of manipulating predator-prey interactions through allelochemicals: Prospects for application in pest control. J Chem Ecol, 1990; 16:3091-3118.
24. Dicke M, Takabayashi J, Posthumus MA, Schutter C, Krips OE. Plant-phytoseiid interaction mediated by herbivore-induced plant volatiles: variation in production of cues and in response of predatory mites. Experimental & Applied Acarology, 1998; 22:311-333.

25. Dicke M, van Loon JJA. Multitrophic effects of herbivore-induced plant volatiles in an evolutionary context. Entomologia Experimentalis et Applicata, 2003; 97:237-249.
26. Dicke M, Van Loon JJA, Soler R. Chemical Complexity of volatiles from plants induced by multiple attacks. Nature Chemical Biology, 2009; 5:317-324.
27. Drukker B, Bruin J, Jacobs G, Kroon A, Sabelis MW. How predatory mites learn to cope with variability in volatile plant signals in the environment of their herbivorous prey. Environmental and Applied Acarology, 2000; 24:881-895.
28. Drukker B, Bruin J, Sabelis MW. Anthocorid predators learn to associate herbivore-induced plant volatiles with presence or absence of prey. Physiol Entomol, 2000; 25:260-265.
29. Drukker B, Scutareanu P, Sabelis MW. Do anthocorid predators respond to synomones from *Psylla*-infested pear trees under field conditions? Entomologia Experimentalis et Applicata, 1995; 77:193-203.
30. Drukker B, Sabelis MW. Anthocorid bugs respond to odor emanating from *Psylla* infested pear trees. Netherlands Entomological Society, 1990; 1:88-89.
31. Fadini AM, Venzone M, Oliveira H, Pallini A, Vilela EF. Response of the predatory mite *Phytoseiulus macropilis* volatiles by strawberry plants in response to attack by Tetranychid mites (Acari: Phytoseiidae: Tetranychidae). Neotropical Entomol, 2010; 39:248-252.
32. Fortuna TM. A tritrophic approach to preference-performance hypothesis involving an exotic and native plant. Biol Invasions, 2013; 15:2387-2401.
33. Gohole LS, Overholt WA, Khan ZR, Vet LEM. Role of volatiles emitted by host and non-host plants in the foraging behavior of *Dentichasmias busseollae*, a pupal parasitoid of the spotted stemborer *Chilo partellus*. Entomologia Experimentalis et Applicata, 2003; 107:1-9.
34. Guerrieri E, Poppy GM, Powell W, Tremblay E, Pennacchio F. Induction and systemic release of herbivore-induced plant volatiles mediating in-flight orientation of *Aphidius ervi*. J Chem Ecol. 1999; 25(6):1247-1261.
35. Haddad NM, Crutsunger GM, Gross K, Haarstad J, Tilman D. Plant diversity and the stability of food webs. Ecol Lett, 2011; 14:42-46.
36. Haftay GG, Nakamuta K. Responses of a predatory bug to a mixture of herbivore-induced plant volatiles from multiple plant species. Arthropod-Plant Interactions, 2016; 10:429-444.
37. Haftay GG, Nakamuta K. A mixture of herbivore-induced plant volatiles from multiple host plant species enhances the attraction of a predatory bug under field-cage conditions. Arthropod-Plant Interactions, 2016; 10:507-515.
38. Heil M, Karban R. Explaining evolution of plant communication by airborne signals. Trends in Ecology and Evolution. 2010; 25(3):137-144.
39. Hoballah MEF, Turlings TCJ. Experimental evidence that plants under caterpillar attack may benefit from attracting parasitoids. Evol Ecol Res, 2001; 3:553-565.
40. James DG. Field evaluation of herbivore-induced plant volatiles as attractants for beneficial insects: methyl salicylate and the green lacewing, *Chrysopa nigricornis*. J Chem Ecol. 2003; 29(7):1601-1609.
41. James DG. Synthetic herbivore-induced plant volatiles as field attractants for beneficial insects. Environ. Entomol. 2003; 32(5):977-982.
42. James DG. Further field evaluation of synthetic herbivore-induced plan volatiles as attractants for beneficial insects. J Chem Ecol, 2005; 31:481-495. Doi: 10.1007/s10886-005-2020-y
43. James DG, Grasswitz TR. Synthetic herbivore-induced plant volatiles increase field captures of parasitic wasps. BioControl, 2005; 50:871-880. doi: 10.1007/s10526-005-3313-3.
44. James DG, Price TS. Field testing of Methyl Salicylate for recruitment and retention of beneficial insects in grapes and hops. J Chem Ecol. 2004; 30(8):1613-1628
45. Jones VP, Steffan SA, Wiman NG, Horton DR, Miliczky E, Zhang Q. *et al*. Evaluation of herbivore-induced plant volatiles for monitoring green lacewings in Washington apple orchards. Biological Control, 2011; 56:98-105.
46. Karban R, Baldwin IT, Baxter KJ, Laue G. Communication between plants: induced resistance in wild tobacco plants following clipping of neighboring sagebrush. Oecology, 2010; 125:66-71.
47. Kessler A, Baldwin IT. Plant responses to insect herbivory: the emerging molecular analysis. Annu. Rev. Plant Biol, 2002; 53:299-328.
48. Kost C, Heil M. Herbivore-induced plant volatiles induce an indirect defense in neighboring plants. J Chem Ecol, 2006; 94:619-628.
49. Maeda T, Kishimoto H, Wright LC, James DG. Mixture of synthetic herbivore-induced plant volatiles attracts more *Stethorus punctum picipes* (Casey) (Coleoptera: Coccinellidae) than a single volatile. J Insect Behav, 2015. Doi: 10.1007/s10905-015-9489-1
50. Maeda T, Takabayashi J, Yano S, Takafuji A. Response of the predatory mite, *Amblyseius womersleyi* (Acari: Phytoseiidae) toward herbivore-induced plant volatiles: variation in response to two local populations. Appl. Entomol. Zool. 9991; 34(4):449-454.
51. Maffei ME, Mithofer A, Boland W. Insect feeding on plants: Rapid signals and responses preceding the induction of phytochemical release. Phytochemistry, 2007; 68:2946-2959.
52. Mattiacci L, Dicke M, Posthumus A. Induction of parasitoid attracting synomone in Brussels sprouts plants by feeding of *Pieris brassicae* larvae: role of mechanical damaged and herbivore elicitor. J Chem Ecol. 1994; 20(9):2229-2247.
53. Menzel TR, Weldegergis BT, David A, Boland W, Gols R, Van Loon JJA. *et al*. Synergism in the effect of prior jasmonic acid application on herbivore-induced volatile emission by Lima bean plants: transcription of monoterpene synthase gene and volatile emission. J of Exp Bot, 2014. doi:10.1093/jxb/eru242
54. Moreira X, Mooney KA, Zas R, Samperdo L. Bottom-up effects of host-plant species diversity and top-down effects of ants interactively increase plant performance. Proc Royal Soc B, 2012. doi:10.1098/rspb.2012.0893
55. Murchie AK, Smart LE, Williams IH. Responses of *Dasineura brassicae* and its parasitoids *Platygaster subuliformis* and *Omphale clypealis* to field traps baited with organic isothiocyanates. J Chem Ecol. 1997;

23(4):917-926.

56. Ninkovic V, Al Abassi S, Pettersson J. The influence of aphid-induced plant volatiles on ladybird beetle searching behavior. Biological Control, 2001; 21:191-195.
57. Orre GUS, Wratten SD, Jonsson M, Hale RJ. Effects of an herbivore-induced plant volatile on arthropods from three trophic levels in brassicas. Biological Control, 2010; 53:62-67.
58. Ozawa R, Arimura G, Takabayashi J, Shimoda T, Nishioka T. Involvement of Jasmonate- and salicylate-related signaling pathways for the production of specific herbivore-induced volatiles in plants. Plant Cell Physiology. 2000; 41(4):391-398.
59. Pare PW, Tumlinson JH. Plant volatiles as a defense against insect herbivores. Plant Physiology, 1999; 121:325-331.
60. Pearse I, Hughes K, Shiojiri K, Ishizaki S, Karban R. Interplant volatile signaling in willows: revisiting the original talking trees. Oecologia, 2013; 172:869-875.
61. Price PW, Bouton CE, Gross P, McPheron BA, Thompson JN, Weis AE. Interactions among three trophic levels: Influence of plants on interactions between insect herbivores and natural enemies. Annu Rev Ecol Syst, 1980; 11:41-65.
62. Robert CA. Herbivore-induced plant volatiles mediate host selection by a root herbivore. New Phytologist, 2012; 194:1061-1069.
63. Sabelis MW, Van den Baan HE. Location of distant spider mite colonies by phytoseid predators: demonstration of specific kairomones emitted by *Tetranychus urticae* and *Panonychus ulmi*. Ent. Exp. and appl, 1983; 33:303-314.
64. Tatemoto S, Shimoda T. Olfactory response of predatory mites (*Neoseiulus cucumeris* and insects *(Orius strigicollis)* to two different plant species infested with onion thrips (*Thrips tabaci*). J Chem Ecol, 2008; 34:605-613.
65. Titayavan M, Altieri MA. Synomone-mediated interactions between the parasitoid *Diaeretiella rapae* and *Brevicoryne brassicae* under field conditions. Entomophaga. 35(4):499-507.
66. Turlings TCJ, Tumlinson JH. Systemic release of chemical signals by herbivore-injured corn. Proc. Natl. Acad. Sci, 1992; 89:8399-8402.
67. Turlings TCJ, Tumlinson JH, Heath RR, Proveaux AT, Doolittle RE. Isolation and identification of allelochemicals that attract the larval parasitoid, *Cotesia marginiventris* (Cresson), to the microhabitat of one of its host. J Chem Ecol. 1991; 17(11):2235-2250.
68. Turlings TCJ, Tumlinson JH, Lewis WJ. Exploitation of herbivore-induced plant odors by host-seeking parasitic wasps. Science. 1990; 250:1251-1253.
69. Turlings TCJ, Wackers F. Recruitment of predators and parasitoids by herbivore-injured plants. In: Advances in Insect Chemical Ecology, R T Carde and J G Millar. Cambridge University Press, 2004, 21-75.
70. Uefune M, Kugimiya S, Ozawa R, Takabayashi J. Parasitic was females are attracted to blends of host induced plant volatiles: do qualitative and quantitative differences in the blend matter? F1000Research, 2013; 2:57.
71. Uefune M, Kugimiya S, Takabayashi J. Herbivore-induced carnivore attractants enhance the residence time of carnivores on a host food plant. J ournal of Plant Interaction, 2012; 6(2-3).
72. Van Poecke RMP, Dicke M. Induced parasitoid attraction by *Arabidopsis thaliana:* involvement of the octadecanoid and salicylic acid pathway. J of Experimental Botany. 2002; 53(375):1793-1799.
73. Van Poecke RMP, Posthumus MA, Dicke M. Herbivore-induced volatile production by *Arabidopsis thaliana* leads to attraction of the parasitoid *Cotesia rubecula*: chemical, behavioral, and gene-expression analysis. J Chem Ecol. 2001; 27(10):1911-1928.
74. Venzon M, Janssen A, Sabelis MW. Attraction of a generalist predator towards herbivore-infested plants. Entomologia Experimentalis et Applicata, 1999; 93:305-314.
75. War AR. Mechanisms of plant defense against insect herbivores. Plant Signaling & Behavior. 2012; 7(10):1306-1320.
76. War AR, Paulraj MG, Ignacimuthu S, Sharma HC. Induced resistance to *Helicoverpa armigera* through exogenous application of jasmonic acid and salicylic acid in groundnut, *Arachis hypogaea*. Pest Manag Sci, 2015; 71:72-82.
77. Waschke N, Hardge K, Hancock C, Hilker M, Obermaier E. Habitats as complex odor environments: How does plant diversity affect herbivore and parasitoid orientation? PLoS ONE. 2014; 9(1):e85152.
78. Waschke N, Meiners T, Rostas M. Foraging strategies of parasitoids in complex chemical environments. In: Wajnberg E and Colazza S (eds) Chemical ecology of insect parasitoids, first edition. John Wiley and Sons, Ltd, Wiley-Blackwell, Chichester, 2013.
79. Wei J, Van Loon JJA, Gols R, Menzel TR, Li N, Kang Ld. *et al*. Reciprocal crosstalk between jasmonate and salicylate defense-signaling pathways modulates plant volatile emission and herbivore host-selection behavior. J of Experimental Botany, 2014. doi:10.1093/jxb/eru181
80. Yan Y, Yan Y, Wang C. Attractiveness of tobacco volatiles induced by *Helicoverpa armigera* and *Helicoverpa assulta* to *Compoletis chloridae*. Chinese Science Bulletin. 2005; 50(13):1334-1341.
81. Yu H, Zhang Y, Wu K, Gao XW, Guo YY. Field-testing of synthetic herbivore-induced plant volatiles as attractants for beneficial insects. Environ Entomol. 2008; 37(6):1410-1415.
82. Yu H, Zhang Y, Wychuys KAG, Wu K, Gao X, Guo Y. *et al*. Electrophysiological and behavioral response of *Microplitis mediator* (Hymenoptera: Braconidae) to caterpillar-induced volatiles from cotton. J of Environ Entomol, 2010; 39:606-609.
83. Zhang Y, Xie Y, Xue J, Peng G, Wang X. Effect of Volatile Emissions, especially α-pinene, From Persimmon Trees Infested by Japanese Wax Scales or Treated with Methyl Jasmonate on Recruitment of Ladybeetle Predators. Environ Entomol, 2009; 38:1439-1445.
84. Zhang Y, Xie Y, Xue J, Yang Z, Gong S. Response of predatory insect, *Chrysopa sinica*, toward the volatiles of persimmon trees infested with the herbivore Japanese Wax scalw. International J of Ecology, 2012. ID 653869. doi:10.1155/2012/653869
85. Zhu J, Cosse AA, Obry CKI, JJ Boo KS, Baker TC. Olfactory reactions of the twelve-spotted lady beetle,

Coleomegilla maculate and the green lacewing, *Chrysoperla carnea* to semiochemicals released from prey and host plant: Electroantenogram and behavioral responses. J Chem Ecol. 1999; 25(5):1163-1177.

86. Zhu J, Park K. Methyl salicylate, a soybean aphid-induced plant volatile attractive to the predator *Coccinella septempunctata*. J Chem Ecol. 2005; 31(8):1733-1746.