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

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Abstract

When plants are attacked by herbivores, they release plant volatiles called herbivore-induced plant volatiles (HIPVs) to the environment to communicate with higher trophic levels. HIPVs play different ecological roles such as plant-plant interaction, plant-herbivore interaction, tritrophic interaction and other related interactions. 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 single tritrophic interaction with 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. Similarly, from herbivore diversity point of view, in nature, plants are commonly attacked by more than one herbivore species. Constituents of HIPVs vary between plants infested by multiple and single herbivore species and this affects the behavioral responses and foraging behavior of natural enemies. This paper reviews recent findings on the role of HIPVs as indirect plant defense in systems with simple tritrophic interaction, and in diverse plants species and diverse herbivore species.

Introduction

In co-evolution, plants and insets have evolved a variety of deleterious and beneficial interactions (Maffei et al., 2007). 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). These could be either direct or indirect defense systems (War et al., 2015).

Direct plant defenses involve any plant traits such as spines, thorns, trichomes, primary and secondary chemical metabolites or proteinase inhibitors that affect the susceptibility to and/or the performance of attacking herbivores and thus increase plant fitness in environment with the herbivores (Kessler and Baldwin, 2002). Indirect plant defenses involve plant traits or adaptations such as provision of shelter or alternative food sources (e.g. extrafloral nectar) (Turlings and Wackers, 2004; Kost and Heil, 2006; Choh and Takabayashi 2010) or release induced plant volatiles upon herbivore infestation that result in the recruitment and sustenance of natural enemies such as predators and parasitoids that attack the herbivores (Dicke et al., 1988; Dick et al., 1990a; Turlings and Tumlinson, 1992; Yan et al., 2005; Tatemoto and Shimoda, 2008).

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). 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). They are released from the site of herbivore feeding and/or systematically from undamaged parts distal to the feeding site (Turlings and Tumlinson, 1992; Rose et al., 1998). Numerous arthropod natural enemies exploit the 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) 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) and are regulated by phytohormones such as jasmonic acid, salicylic acid, and ethylene (Ozawa et al., 2000; Menzel et al., 2014a). 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 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). 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 systems with simple tritrophic interaction, and in diverse plants species and diverse herbivore species.

Ecological role of HIPVs in a simple tritrophic interaction

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) or different plant species (Baldwin et al., 2006; Pearse et al., 2013), conspecific herbivores (De Moraes et al., 2001; Carroll et al., 2008) or different herbivore species (Bernasconi et al., 1998; Robert et al., 2012), and natural enemies (Dicke and Sabelis, 1988; Yu et al., 2008; Yu et al., 2010; Zhang et al., 2012; Haftay and Nakamuta, 2016a,b). 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 ecological roles of HIPVs in a simple tritrophic interaction might result in different effects in the environment. Some of the effects are explained below.

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) 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) 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.

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.

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). 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) 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.

Attractiveness of HIPVs to natural enemies in systems with multiple plant and herbivore 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 of herbivore species (Shiojiri et al., 2001; Delphia et al., 2007) and plant species (Haftay and Nakamuta, 2016a, b). The high variability that characterizes the constituents of HIPVs as a result of these factors influence success of natural enemies in locating their prey or host. The constituents of the HIPVs emitted from diverse plant and/or 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 such condition, natural enemies should detect herbivore-infested plants within the complex environment with a diverse species of different trophic levels such as diverse plant species or herbivore species. 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 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 and insect herbivore species (Dicke and Van Loon, 2003; De Boer et al., 2008; Haddad et al., 2011; Dicke and Baldwin, 2010).

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). 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).

Attractiveness of HIPVs to natural enemies in diverse plant species system

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). 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) 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 are expected to be affected (Waschke et al., 2013, 2014; Haftay and Nakamuta, 2016a, b). 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 experiment 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

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]	Venzon 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

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) 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) and field-cage conditions (Haftay and Nakamuta, 2016b). 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 prey 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) 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.

Attractiveness of HIPVs to natural enemies in diverse herbivore species system

From the herbivore species diversity perspective, in nature, plants are commonly attacked by more than one herbivore species (Dicke and Van Loon, 2003; Rasmann and Turlings, 2007; Holopainene and Gershenzon, 2010; Das et al., 2013) simultaneously or sequentially. In support of this perspective, recent studies had reported that volatiles emitted from plants simultaneously damaged by multiple herbivore species affected the behavioral responses of predators (Moayeri et al., 2007; De Boer et al., 2008; Dicke et al., 2009) or parasitoids (Shiojiri et al., 2001; Vos et al., 2001; Rasmann and Turlings, 2007; Cusumano et al., 2015). Studies had found that there are variations in the constituents of HIPVs between plants simultaneously infested by multi-species herbivores and plants infested by single herbivore species (Delphia et al., 2007; Rasmann and Turlings, 2007; De Boer et al., 2008). They suggested that these variations in constituent of HIPVs might have led to the modification of behavioral responses of the natural enemies.

For example, Moayeri et al. (2007) found that the predatory mirid bug, *Macrolophus caliginosus* (Heteroptera: Miridae) showed a stronger response to volatiles emitted from sweet pepper plants (*Capsicum annum* L.) simultaneously infested with the spider mite, *Tetranychus urticae* Koch (Acari: Tetranychidae) and the aphid, *Macrolophus caliginosus* Wagner (Heteroptera: Miridae) than to those emitted from plants infested by just one herbivore, irrespective of the species. In another study by Shiojiri et al (2001) found that *Cotesia glomerata* L. (Hymenoptera: Braconidae), parasitoid of larvae of *Pieris rapae* Linnaeus (Lepidoptera: Pieridae), preferred volatile blends emanating from cabbage (*Brassica oleracea* L.) simultaneously infested by diamond back moth, *Plutella xylostella* Linnaeus (Lepidoptera: *Yponomeutidae*) and cabbage white butterfly, *P. rapae* to those infested by only one herbivore species. Similarly, De Boer et al. (2008) reported that *P. persimilis* preferred volatiles induced by multi-species herbivory to volatiles induced by the larvae of beet armyworm, *Spodoptera exigua* Hubner (Lepidoptera: Noctuidae) alone or by *T. urticae* alone. They suggested that this was the predator`s reaction to the differences in the constituents of HIPVs between plants exposed to single and multiple herbivore species. This implies the variation in the constituents of HIPVs might have mediated the natural enemies to distinguish between volatiles emitted from plants exposed to a single and multiple herbivore species.

In support of these, some findings have detected differences in the constituents of HIPVs between plants infested by multiple and single herbivore species (Shiojiri et al., 2001; Rodriguez-Saona et al., 2003; Delphia et al., 2007; Moayeri et al., 2007; De Boer et al., 2008). For example, Delphia et al. (2007) reported that simultaneous feeding of tobacco plants (*Nicotiana tabacum* L.) by western flower thrips, *Frankliniella occidentalis* Pergande (Thysanoptera: Thripidae) and the chewing herbivore tobacco budworm, *Heliothis virescens* Fabricius (Lepidoptera: Noctuidae)

emitted greater amount of some volatiles such as α-humulene and caryophyllene oxide. Similarly, Shiojiri et al. (2001) found that cabbage plants simultaneously infested by larvae of *P. xylostella* and *P. rapae* emitted a different blend of volatiles compared to those infested by either of the two-herbivore species. The change in the constituents of HIPVs due to simultaneous multi-species herbivory consequently affects olfactory responses of arthropod natural enemies to HIPVs (Shiojiri et al., 2001; Moayeri et al., 2007; De Boer et al., 2008) mainly generalist natural enemies (Moayeri et al., 2007).

Other than simultaneous herbivory, plants are also frequently attacked by multiple herbivore species, which arrive at different time sequences (sequential herbivory). This might affect indirect defense of plants (Johnson et al., 2012; Menzel et al., 2014b; Wang et al., 2014) through HIPVs that attract natural enemies. Sequential herbivory by multiple herbivore species may influence indirect defense of plants in a positive, neutral or negative manner (Johnson et al., 2012; Menzel et al., 2014b). For example, Menzel et al. (2014b) reported that prior treatment of plants with oral secretions of the generalist caterpillar *Mamestra brassicae* L. (Lepidoptera: Noctuidae), as a mimic of caterpillar feeding, did not affect the attraction of *P. persimilis* to plants infested with its prey *T. urticae* (neutral effect). On the other hand, Johnson et al. (2012) reported that induced plant defense increases when above ground herbivores were feeding first followed by below ground herbivores (positive effect), whereas, the induced plant defense decreases when belowground herbivores were feeding first followed by aboveground herbivores (negative effect). In support of these findings, previous studies suggest that plants can form "memories" after sequential stressful events such as herbivory, which enable them to adjust their defense accordingly (priming), thus responding in an enhanced manner to a second stress (Johnson et al., 2012).

The difference in preference of natural enemies in diverse herbivore species might be related with the natural enemy`s prey or host preference and/or diet mixture. Single herbivore species-damaged plants might be less preferred by natural enemies compared to multiple herbivore species-damaged plants if both the herbivores are prey or host for the natural enemy. For the natural enemy, predators in particular, this can be explained by the higher profitability of finding a mixed diet (explanations about profitability of mixed diet can be found in Coll and Guershon 2002) or higher profitability in terms of accessing the most preferable herbivore species (Shiojiri et al., 2001; Moayeri et al., 2006; Xu et al., 2006; Harris et al., 2012; Ferrero et al., 2014). In case of sequential herbivory with varying arrival time, multiple factors such as priming of plant indirect defense for enhanced emission of HIPVs, predator`s prey preference and/or profitability of getting mixed diet might be playing their own roles for natural enemies to distinguish between volatiles emanating from different sequences of herbivory by the two herbivore species as well as between volatiles emanating from multi-species herbivory and single species herbivory. The various findings show that the difference in attractiveness of HIPVs emanating from multi-species herbivory can modify olfactory responses natural enemies to herbivore-damaged plants and this might be a result of different (perhaps interacting) factors such as priming of plant indirect defense, natural enemy`s prey or host preference and diet breadth.

The underlying mechanism for the variations in the constituents of HIPVs among plants exposed to single-, simultaneous and different sequences of multi-species herbivory might be phytohormone cross-talk. It has been reported that the phytohormone jasmonic acid (JA) and salicylic acid (SA) are involved in signaling and regulating HIPVs biosynthetic pathways (Ozawa et al., 2000; Menzel et al., 2014; Wei et al., 2014). JA or SA signaling pathways which modulate emission of HIPVs from plants have been reported different depending on the feeding mode of herbivores (Ozawa et al., 2000; van Poecke and Dicke, 2002; De Vos et al., 2005; Wei et al., 2014). Synergistic, additive or antagonistic effect from cross-talk between these phytohormones on emission of volatiles might occur after plants are attacked by multiple herbivore species (Arimura et al., 2011; Menzel et al., 2014; Wei et al., 2014) with different feeding habits and subsequently affect attraction to natural enemies. For example, Rodriguez-Saona et al. (2005) reported that, in tomato, simultaneous infestation of plants with caterpillars of *S. exigua* which induce the JA pathway and aphids *Macrosiphum euphorbiae* Thomas (Hemiptera: Aphididae) which induce SA pathway results in significant attraction of the parasitoid *Cotesia marginiventris* Cresson (Hymenoptera: Braconidae), a natural enemy of the caterpillars. Similarly, De Vos et al. (2005) reported that exposure of plants to simultaneous infestation by herbivores which induce different phytohormones biosynthesis pathway, results in a strong attraction of predators than volatiles from plants attacked by spider single herbivore species.

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 component 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.

From the herbivore species diversity point of view, attractiveness of HIPVs emanating from multi-species herbivory can modify olfactory responses and foraging behavior of natural enemies. In plant systems exposed to multiple herbivore species with the same or varying arrival time, multiple factors such as priming of plant indirect defense for enhanced emission of HIPVs, natural enemy`s prey or host preference and/or profitability of getting mixed diet might be playing their own roles for the predators to distinguish between volatiles emanating from the same or different sequences of herbivory by multiple herbivore

species as well as between volatiles emanating from multi-species herbivory and single species herbivory. For more elucidation, further study on the responses of the natural enemies to synthetic HIPVs with different constituents of volatiles that correspond with the most attractive sequences of multi-species herbivory is necessary to identify the most attractive blend of HIPVs so that it can be important component of IPM. In addition, investigating the effect of natural enemy`s prey or host preference and diet mixture or their interaction on the response of natural enemies to HIPVs emitted from simultaneous or sequential multi-species herbivory might further elaborate the possible mechanisms involved in the modifying of the olfactory response and foraging behavior of natural enemies. The underlying mechanism for the variations in the constituents of HIPVs among plants exposed to single-, simultaneous and different sequences of multi-species herbivory might be phytohormone cross-talk. Whether the variations in the constituents of HIPVs among plants exposed to same or different sequences of herbivory by multiple herbivore species with different feeding habits are modulated by pathway cross-talk between JA and SA signaling need to be investigated by determining the endogenous levels of JA and SA from different treatments.

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