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Herbivore-induced plant volatiles (HIPVs) in tritrophic interactions consisting of diverse 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 herbivore species 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 tritrophic interaction consisting of diverse herbivore species.

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

1. Introduction

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) [19, 6]. They have evolved direct or indirect defense systems that protect them from being overeaten by the herbivores (Kessler and Baldwin, 2002; Heil and Karban, 2010) [31, 26, 30].

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) [31]. 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) [48, 32] 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) [14, 16, 17, 45, 56, 44].

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) [37]. 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) [23, 58]. 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) [45, 41]. 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) [14, 16, 48, 6]. 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) [15, 44] and parasitoids (Turlings *et al*., 1990; Van Poecke *et al*., 2001; Yu *et al*., 2010) [47, 52, 58].

In addition to attracting natural enemies to the food source, HIPVs could arrest them to remain on the plants (Uefune *et al*., 2012) [50]. Uefune (2012) [50] 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.

These groups of HIPVs are synthesized through different biosynthetic pathway in different compartments of plant cells (Pare and Tumlinson, 1999; Das *et al*., 2013) [37, 6] and are regulated by phytohormones such as jasmonic acid, salicylic acid, and ethylene (Ozawa *et al*., 2000; Menzel *et al*., 2014a) [36].

The attractiveness of HIPVs to natural enemies varies depending on species diversity of different trophic levels in a given environment. Under natural conditions, the interaction among different trophic levels is expected to be complex. For instance, 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 herbivore species affect release of HIPVs quantitatively and qualitatively, and in turn the response of natural enemies (Haddad *et al*., 2011; Moreira *et al*., 2012). These findings are recent advances in the plants-herbivores-natural enemies tritrophic interaction paradigm given that in natural system 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 multiple herbivory.

2. 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 (Kost and Heil, 2006; Choh and Takabayashi, 2010) [32, 3]. The ecological roles of HIPVs in a simple tritrophic interaction might result in different effects in the environment such as in plant-plant interaction, plant herbivore-interaction, indirect plant defense by attracting natural enemies and related interactions. For instance, 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. In this case, Kost and Heil (2006) [32] 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 which led to the attraction of predatory and parasitoid insects. Similarly, Choh and Takabayashi (2010) [3] 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 which led to longer survival of predators. These findings imply that HIPVs play important role for plant-plant communications.

HIPVs also affect foraging behaviors of herbivores either conspecifics or heterospecifics. For example, De Moraes *et al*. (2001) [8] 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) [2] 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.

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) [17, 49]. 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) [38]. 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 [42]; Dicke and Sabelis, 1988; Dicke *et al*., 1990a) [14, 16, 17] and parasitoids (Turlings *et al*., 1990). Sabelis and Van de Baan (1983) [42] 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) [17] 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) [59] and parasitoids (e.g.: Turlings and Tumlinson, 1992; Yu *et al*., 2008; Yu *et al*., 2010) [45, 47, 57, 58].

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) [47] 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) [32] 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.

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

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) [30, 6]. 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) [43, 10]. 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) [19]. 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 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 insect herbivore species (Dicke and Van Loon, 2003; De Boer *et al*., 2008; Haddad *et al*., 2011; Dicke and Baldwin, 2010) [18, 7].

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) [18, 39, 28, 6] 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) [7, 19] or parasitoids (Shiojiri *et al*., 2001; Vos *et al*., 2001; Rasmann and Turlings, 2007; Cusumano *et al*., 2015) [43, 39, 9]. 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) [10, 39, 7]. 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) [43] 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) [7] 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) [10, 43, 7]. For example, Delphia *et al*. (2007) [10] 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) [43] 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) [7] mainly generalist natural enemies (Moayeri *et al*., 2007) [43].

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) [29] 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) [29]. 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) [29] 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) [29].

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) [4] or higher profitability in terms of accessing the most preferable herbivore species (Shiojiri *et al*., 2001; Moayeri *et al*., 2006a; Xu *et al*., 2006; Harris *et al*., 2012; Ferrero *et al*., 2014) [43, 34, 25, 24, 55]. 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*., 2014a; Wei *et al*., 2014) [36]. 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) [36, 51, 9, 1]. 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*., 2014a; Wei *et al*., 2014) [1] 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) [9] 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.

4. Conclusions and recommendations

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 phyto hormone 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.

5. References

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