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Advances in herbivore-induced plant volatiles (HIPVs) as plant defense and application potential for crop protection

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Abstract
Herbivore-induced plant volatiles (HIPVs), which are released when plants are attacked by herbivores, play important roles in plant defense through direct defense or change in behavior of lower and higher trophic level arthropods (indirect defense) mainly by recruiting arthropod natural enemies to herbivore-attacked plants. Plethora of investigations has explored the attractiveness of HIPVs to arthropod natural enemies. Natural enemies such as arthropod parasitoids and predators utilize HIPVs to locate and feed or parasitize their prey or host and by recruiting these mutualistic, the plant gets protection against antagonist herbivores. However, beyond the function in tritrophic interaction, utilization of HIPVs for crop protection is yet recently a focus of researchers from many disciplines. In this paper, we reviewed the function of HIPVs for plant defense and the possibilities of utilizing HIPVs for crop protection.

Keywords: Herbivore-induced plant volatiles (HIPVs), plant defense, tritrophic interaction, parasitoids, predators, crop protection

1. Introduction

Plant-arthropod interactions are important for understanding community dynamics and ecosystem function given that they are the critical link between primary production and food webs [1]. One of the plant-arthropod interaction channels is communication through chemicals, mainly volatiles organic chemicals. Volatile organic chemicals emitted from plant plays an important role in plant defense against attackers and behavioral choices of herbivores and natural enemies within the arthropods, which consequently influences the spatial distribution of the different trophic levels in food webs. In insects, communication by volatile organic chemical signals, also called olfaction, is the most important sensory system driving behavior; it influences, among others, food searching, mate finding, avoidance of enemies and competition [2, 3].

Among the volatile organic chemicals, plants release much greater quantities and qualities or produce *de nevo* of low molecular weight volatiles called herbivore-induced plant volatiles (here after referred as HIPVs), when attacked by herbivore arthropods [4, 5, 6, 7, 8]. The HIPVs can be released from the site of herbivore feeding and/or systematically from undamaged parts distal to the feeding site [9, 10]. and varies depending on plant and herbivore species, and environmental factors. The HIPVs plays important roles in plant defense and change in behavior of lower and higher trophic level arthropods (e.g. herbivores, predators, parasitoids, hyper parasitoids and extra guild predators) [4, 6, 11, 12, 13, 14, 15].

Plants release the HIPVs to the environment to communicate with higher trophic levels or with other plants (plant-plant interaction: conspecifics or hetro specifics). Of which, the response of plants to arthropods through emission of HIPVs that attract natural enemies of the herbivore arthropods, also called tritrophic interaction, have become field of interest for research since the first report in the area in late 1980s [3, 6, 11, 15, 16, 17, 18, 19, 20]. The plant defense mechanism through emission of HIPVs to attract natural enemies that attack herbivores is considered as indirect plant defense mechanism. The release of HIPVs by plants results in the recruitment and sustenance of natural enemies such as predators and parasitoids that attack the herbivores [9, 12, 17, 21, 22, 23, 24].

In the last four decades (since 1980s), plethora of investigations has explored the attractiveness of HIPVs to arthropod natural enemies. For instance several researchers revealed the attractiveness of HIPVs to predators [12, 13, 16, 20, 25, 26, 27, 23, 28, 29, 30], parasitoids [6, 18, 31, 32, 33, 34, 35, 36, 37, 38, 39, 40], both predators and parasitoids [41, 42]. and Hyper parasitoids [43]. These arthropod natural enemies, thus, utilize the HIPVs to locate their prey or parasitize their host which directly benefiting themselves and indirectly the plant as a “body guard”.

Beyond the function of HIPVs in the tritrophic interaction, recently researchers have been revealing the complex ecological function of HIPVs and their role in pest management. Therefore, this reviews the function of HIPVs for plant defense and the possibilities of utilizing HIPVs for crop protection.

2. Overview of the first evidence on three trophic level interactions (tritrophic interaction)

Since the late 1980s it has become clear that plants respond to arthropod her bivory with the induced production of volatiles that attract the enemies of the herbivores [11]. The first evidence on the concept of three trophic level interactions (tritrophic interaction) was by Price and his colleagues in 1980. The authors provided insightful review on three trophic level interactions introducing the concept of plant traits that have evolved to recruit natural enemies of herbivores [24]. They specifically suggested that plants might recruit the third trophic level (natural enemies) when under attack by herbivores, stressing the adaptive value of the interaction, which benefits the plant as well as its natural enemies. Following the finding by Price *et al* (1980), several pioneering studies during the last two decades of the 20th century [16, 17, 18, 44, 45, 46, 47] then paved the way for researchers in the field to explore more, leading to the initial chemical evidence for an active role of herbivore-damaged plants in recruiting arthropod natural enemies. Among the chemical evidences includes attraction of HIPVs to arthropod predators [16, 17, 49]. and parasitoids [19]. Since then, numerous studies have provided a wealth of evidence on the ecological relevance of HIPVs in plant-arthropods interactions.

Beyond to the effect of HIPVs on behavior of diverse members of predators and parasitoids, further studies revealed the effect of HIPVs on other herbivores of conspecifics [51, 52, 53]. or hetro specifics [54, 55, 56, 57], hyper parasitoids [58, 59], parasitic plants [60], neighboring plants [58, 59]. and in diverse herbivore species [61, 62, 63]. and diverse plant species [12, 13, 64, 65].

2. The HIPVs groups

Although the volatile profiles display an enormous range of diversity among plant species, different plant taxa exhibited a considerable overlap in production of HIPVs [7, 8, 66]. Most HIPVs could fall either into terpenoids, green leaf volatiles (GLV) or fatty acid derivatives, benzenoids/phenylpropanoids, C_5-branched compounds, and various nitrogen- and sulphur-containing compounds [7, 8]. Although there are multitudes of HIPVs, few examples from different categories/groups are listed in Table 1 as a reference.

Table 1: Examples of HIPVs from different groups

Categories	HIPVs
Terpenoids	(*E*)-ciemene
	(*E,E*)-Farnesene
	(*E*)-4,8-dimethyl-1,3,7-nonatriene (DMNT)
	(*E,E*)-4,8,12-trimethyl-1,3,7,11-triradecatetraene (TMTT)
	(*E*)-β-ocimene
	(*E*)-β-caryophyllene
	α-caryophyllene
	α-pinene
	Limonene
	β-myrcene
	β-Elemene
	α-Fanesene
	α-Selinene
	Germacrene D
	Linalool
Green leaf volatiles (Fatty acid derivatives)	(*z*)-3-Hexanal
	(*Z*)-3-hexen-l-ol
	(*Z*)-3-hexenyl acetate
	(*Z*)-3-hexen-1-ol
	(1)-hexanol
Benzenoids/ phenylpropanoids	Methyl salicylate (Me SA)
	cis-Jasmonate
	Methyl eugenol
	Iindole
Nitrogen- and sulphur-containing compounds	Isothiocyanates
	Nitriles

3. HIPVs for plant defense

In co-evolution, plants and insets have evolved a variety of deleterious and beneficial interactions [67]. In the plant-insect herbivore interactions, plants are threatened by potentially hostile insect herbivores. Plants have had to defend themselves against such hostility. Being rooted to the ground they are unable to flee from attacking herbivores. Thus, they have evolved multitude of defense systems that protect them from being overeaten by herbivores [19, 68, 69, 70, 71]. Although there are multitudes of direct and indirect defense mechanism of plants, the focus here will be limited to the role of HIPVs on plant defense. The HIPVs can serve as direct and indirect defense mechanism for plants.

3.1. HIPVS and indirect defense; as information for arthropod natural enemies

There are ample evidences on the role of HIPVs as indirect plant defense against arthropod herbivores. The HIPVs released from herbivore-damaged plants comprises many chemical components, singly or in blend, that attract arthropod natural enemies. The HIPVs comprise a complex mixture of tens up to more than 200 compounds, the composition of which may vary with herbivore species, herbivore developmental instar, plant tissue, and abiotic conditions [43, 72, 73]. Several electrophysiological and behavioral studies revealed that arthropod natural enemies utilize HIPVs for their own benefit so as to locate prey or host in a simple or complex vegetation and serving as a “bodyguard” for plants. The HIPVs serves as a ‘scream’ for help from herbivores’ natural enemies and alert neighboring plants of impeding attack [58, 66]. Parasitoid and predatory arthropods recognize these plant ‘screams’ as ‘dinner bells’ and move towards the plants to find the signaled food (herbivore). This is considered as indirect plant defense strategy to avoid attack by antagonist herbivores.

3.2. HIPVs and direct defense

Beyond the role as indirect plant defense mechanism, HIPVS could be involved in direct resistance by acting as feeding and/or oviposition deterrents or toxic to insect pests [51, 69] and provide protection against pathogens [8, 75]. For instance, for common HIPVs emitted from many plant upon herbivore attack, such as (*E*)-β-caryophyllene have been reported to kill pathogens [24, 75], and indole, which is toxic to caterpillars [76]. The direct negative impact of HIPVs on herbivores might indicate why volatiles emitted from plants upon herbivore damage have a repellent behavior for herbivores. But there are intriguing reports that HIPVs increase apparency of plant natural enemies and to certain specialized herbivores [77]. Given this dilemma, further investigation might need how plants balance the positive impact of HIPVs as direct defense or indirect defense through attraction of natural enemies and the negative impact of attracting more herbivores (antagonists).

In general, HIPVs mediating direct and indirect plant defenses can be considered as an integral part of plant resistance against antagonist herbivores. Considering this, HIPVs has to be considered as a potential mechanism for crop protection against insect pests.

4. Possibilities of HIPVs application for crop protection

It has been frequently proposed that the volatile signals that mediate tritrophic interactions can be exploited for application in agriculture, but it is only recently that serious efforts have been launched and some successes have been achieved [24, 78, 79]. Recent reports have shown that HIPVs can be utilized in agriculture in different ways/strategies [24]. Among the strategies that can be used singly or in combination (as the strategies are not mutually exclusive) involve: dispense volatile chemicals that affect arthropod foraging behavior; use companion plants that affect the attraction of pests and beneficial insects (such as apply in stimulo-deterrent diversionary (push-pull) strategy), apply inducing agents that alter the attractiveness of plants; breed for or otherwise create crops with enhanced volatile emissions through genetic engineering; and develop odor sensors to monitor for pests and diseases (Details of these strategies are reviewed in [8] and [24].

4.1 Use of HIPVs-inducing substances to recruit arthropod natural enemies

The use of synthetic HIPVS to attract arthropod natural enemies has been successfully tried in various studies (such as [13, 80, 81, 82, 83, 84, 85, 86, 87, 88]). Examples on the attractiveness of synthetic HIPVs to arthropod natural enemies under field condition have been presented in a review paper by [19].

However, direct application of synthetic HIPVs to a large field could be costly compared to the cost of the individual HIPVs. Thus, use of HIPVs-inducing substances could be a better strategy to attract natural enemies. For instance, dispensers with Methyl Salicylate (Me SA), which triggers defense responses in plant, and other attractants for beneficial insects are already commercially available [89]. However, Me SA has also repellency behavior for certain parasitoids (Snoer *et al* 2010) and also suppresses emission of certain HIPVs (that are triggered by other substances other than MeSA) that attract natural enemies. This, however, can be overcome by treating plants with other HIPVs-inducing substances or elicitors.

4.2 Breeding of plants for enhanced attractiveness to natural enemies

Breeding of new crop varieties or use of genetically modified plants (GMP) could be other mechanisms of enhancing plant attractiveness to natural enemies. Different crop varieties might differ in the quality and quantity of volatile emissions and subsequently their attractiveness to natural enemies and can show considerable differences in herbivore mortality in the field. Thus, breeding or otherwise creating crop varieties that are highly attractive to natural enemies may be a simple way to achieve better biological control of pests [90, 91, 92].

For instance, white cabbage varieties that were shown in the laboratory to be particularly attractive to parasitoids were also found to have higher parasitism rates in the field [93]. Maize lines differ dramatically in HIPVs [94] and this too is reflected in their attractiveness to parasitoids [95] and parasitism rates in the field [93]. Selecting appropriate varieties may therefore help to promote the effectiveness of biological control through enhanced emission of HIPVs to the environment. Recent advances in biotechnology enabled experts working on the genetics of plant defense to manipulate plant volatile emissions for their defensive functions [8]. There are promising reports on creating more attractive GMP to natural enemies. This was first shown with modified *A. thaliana* plants that express increased emissions of putative attractants. In laboratory and greenhouse assays, such plants indeed showed enhanced attractiveness to predators [96] and parasitoids [97]. Field evidence for the potential of such an approach comes from the successful genetic manipulation of maize to restore the Release of (*E*)-β-caryophyllene, a root-produced attractant for entomopathogenic nematodes [98]. In another study, the (*E*)-farnesene synthase gene cloned from *Mentha piperita* was successfully expressed in Arabidopsis thaliana to cause the emission of (*E*)-farnesene [99]. Similarly, transgenic maize plants with overexpression of the maize TPS10 gene produced (*E*)-farnesene, (*E*)-bergamotene and other volatile defense signals which attracted the natural enemies of maize herbivores, *Cotesia marginiventris* [100].

More recently, a hexaploid wheat, *Triticum aestivum* cv. Cadenza was genetically engineered to emit (*E*)-farnesene using a synthetic gene based on a sequence from peppermint with a plastid targeting amino acid sequence, with or without a gene for biosynthesis of the precursor farnesyl diphosphate [71]. The above few examples demonstrate the potential of manipulating HIPVs to provide better crop resistance against insect attack through attractiveness of the plant to natural enemies.

4.3 Use companion plants as source of volatiles to suppress pests and attract natural enemies

The utilization of HIPVs for pest management in crop production can also be related with the use of companion plants mainly in push-pull strategies which rely on plant odors to deter insect pests from crop fields. Pickett and Kahn [79] provided a comprehensive overview a push-pull technology in which companion plants that emit useful volatiles are used to fight agricultural pests and the strategy has become successful for tens of thousands of farmers in smallholder farmers in Africa.

The most prominent example of the successful deployment of this strategy involves the companion cropping of maize with the forage legume such as silver leaf desmodium (*Desmodium* spp) (push plant) (which also fixes nitrogen for crops and inhibit the notorious striga weed) and the forage grass such as Napier grass, *Pennisetum purpureum* Schumach (Poaceae) or Sudan grass (*Vulgare sudanaense*) (a pull plant) planted at the field margins [79, 102]. Volatiles produced by push plant repel (providing the “push,”) ovipositing insect pests such as stem borers and fall armyworm from the maize crop [103, 104] and attract natural enemies, while other volatiles produced by the pull plant planted on the margins attract the ovipositing females, thereby producing the “pull” away from the crop [79, 104] and is lethal to the offspring of the pest [103]. This strategy, and well researched variants, has been adopted by approximately 120,000 small holders in sub-Saharan East Africa [79].

The pest control by push-pull technology can be enhanced by using sentinel plants that are susceptible to a given pest (pathogen or herbivore) that respond strongly to such pest with the emission of volatiles that could induce protective defense responses in the neighboring main crop plants [79]. These sentinel plants could also be highly attractive to beneficial arthropods and be a breeding ground and source for effective biological control agents.

Thus, the push-pull (use of companion plants) along with use of sentinel plants can be considered as source of volatiles to suppress insect pests and attract natural enemies of the pests.

4.4 Development of odor sensors for pests

Beyond the above possibilities of utilizing HIPVs for pest

Management, developing odor sensors that sense the Presence of insect pests though use of specific herbivore-induced plant volatiles to detect herbivore infestations at an early stage would be a futuristic idea [24]. There are promising developments in this regard. Novel technologies are under development that allow for real-time detection of changes in volatile emissions. Sensors that are based on physiochemical technologies seem more suited for such purposes. The latest developments in proton transfer reaction–MS (PTR-MS) are particularly promising [105]. PTR-MS uses direct chemical ionization of headspace volatiles for real-time detection of volatile organic compounds [106], and the potential of this technique has been greatly improved with the introduction of PTR–time of flight–MS (PTR-TOF-MS) [107], which allows higher resolution and sensitivity [108]. For now, PTR-TOF-MS is too costly and bulky for field use, but further improvements such as development of sensors based on nano mechanical cantilevers (less bulky) may overcome these shortcomings [24].

Therefore, the discussions from 5.1 to 5.4 are among few examples how HIPVs can be utilized in crop protection against insect pests with most of the examples on findings presented are promising.

5. Conclusion

A wealthy of information (evidences) has been generated in the last four decades regarding the functions and ecological roles of HIPVs. The HIPVs are now become an interdisciplinary field of research interest mainly focusing on arthropod-plant interactions and pest management. Ample source of knowledge has been accumulated on the attractiveness of HIPVs to natural enemies either in a simple tritrophic interaction or complex interactions and its other ecological roles. This paves the way for proper understanding of and further investigation on biochemical, molecular and behavioral ecology of arthropod-plant interactions so as to utilize it to develop similar novel and sustainable pest management strategies. However, the application of the field of HIPVs studies in agriculture for crop protection is at infant stage and needs further investigation and innovation. There are promising findings that has shown the possibilities of utilizing HIPVs for crop protection against pests. This might be through the development of odor dispensers, odor sensors, push-pull technology, breeding of crops for higher attractiveness to beneficial arthropods, and genetic engineering to create GMP with enhanced HIPVs emission. Further investigation and innovation in the field of HIPVs is expected to pave a way for development of environment friendly, sustainable and cost-effective crop protection technologies.

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