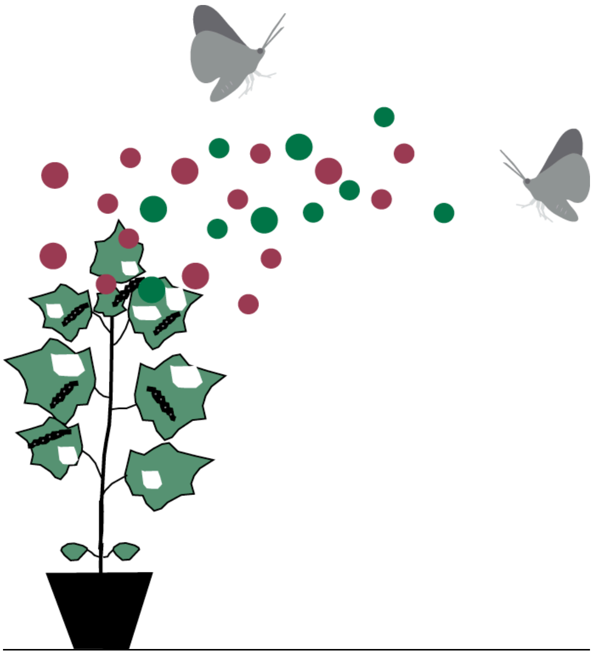
INDUCIBLE DEFENSES IN HERBIVORE-PLANT INTERACTIONS:

FUNCTIONS MECHANISMS AND MANIPULATIONS

Ali Zakir

Introductory Paper at the Faculty of Landscape Planning, Horticulture and Agricultural Science 2011:2
Swedish University of Agricultural Sciences
Alnarp, June 2011



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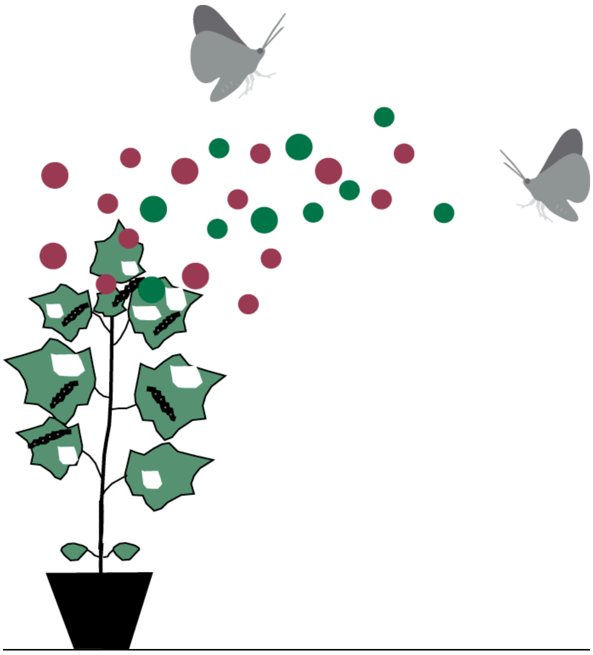


1. Summary

In the ecological context of insect-plant interactions, the interdependence of each other is important for their survival in complex ecosystem. Insect herbivores locate suitable host plants that can provide better resources for food and reproduction. In nocturnal herbivores, especially Lepidopterans, olfaction plays a major role during the selection of suitable host plants. Generally, Lepidopteran herbivores orient towards host plants using sensory cues such as volatile chemicals. Search for a host plant suitable for feeding, mating and oviposition is pertinent to the females while males are more conscious in mate and food findings. In addition, the chances of encountership between males and females increase in the presence of healthy host plants. Female moths prefer to lay eggs on healthy plants in order to provide better food resources for their offsprings. On the other hand, plants defend themselves from herbivore feeding by producing chemical volatiles as well as non-volatiles. The specific blend of volatile compounds in response to feeding damage by herbivores is commonly called as herbivore-induced plant volatiles (HIPVs). HIPVs are ecologically important because the plant species that release these compounds can improve their performance against attacking herbivores by several means e.g., by attracting the natural enemies of the herbivores or by repelling herbivores at a distance.

Here, I review induced defenses in plants based on their classification along with perception and signaling in response to herbivory. In addition, the ecological significance of HIPVs at different levels will be described. Furthermore, I will highlight the ease of screening HIPVs on olfactory basis, by using different approaches within the laboratory, for their future implications in plant protection program.

Contents

2. Introduction

Green plants are a food source for herbivores. The diversity of potential threats to plants in nature is wide and quite impressive. Important herbivores are mammals, reptiles, amphibians, birds, mollusks, worms, arthropods, viruses, bacteria, fungi, and other microorganisms. Representing a significant part of life on earth, insect herbivores are a considerable threat to the plants (Karban and Baldwin, 1997). Insects use various feeding strategies to obtain nutrients from all above (vegetative) and belowground (root) plant parts and inflict mechanical damage on plant tissues. The quantity and quality of injury varies greatly, depending on the feeding tactic. Approximately two thirds of all known herbivorous insect species are leaf-eating beetles (Coleoptera) or caterpillars (Lepidoptera) that cause damage with mouthparts designed for chewing, snipping, or tearing (Schoonhoven et al., 1998; Howe and Jender, 2008).

Plants are considered to be well defended if they have the abilities of either escaping from the herbivore preference during their attack or decreasing the performance of the herbivores or their population fitness after attack. The plants equipped with such traits are likely to be better represented in the future generations than those that failed to resist against their attackers. Plants have to evolve or select among such traits in order to combat the selection pressure of the attacking herbivores (Karban and Baldwin, 1997). Hence, the defensive traits of plants help them to develop resistance against herbivores and allow them to confront herbivores directly; by affecting either herbivore preference or their reproductive success on host plant, or indirectly; by attracting the natural enemies of the herbivores (Kessler and Baldwin, 2001; Dicke, 2009).

Expression of some defensive traits in plants is termed as constitutive because these traits develop under the continuous developmental program within the plant. Constitutive traits generally protect the plants against the direct effect of the biotic and abiotic factors, categorized into “direct defense”. Physical factors including morphological and structural features of the plants constitute direct defense e.g., reproductive tissues contain large amounts of defensive proteins and metabolites (Howe and Jender, 2008) (Fig.1). These plant’s inherited defensive traits cope with the situations such as *antixenosis* (when these morphological features have negative impact on the insect preference such as host plant selection, oviposition and feeding behaviour) and *antibiosis* (when these morphological traits have negative impact on the performance of insects such as growth rate, development and reproductive success).

Thus far, plant defenses were generally assumed to be constitutive i.e., always expressed in the plant and function independent of herbivore attack. Since after the initial report on proteinase inhibitor (PIs) by Green and Ryan (1972), numerous defensive traits have been identified in many plant species that are induced by herbivore-feeding or mechanical wounding. In their fascinating work, Green and Ryan showed that potato and tomato plants accumulate PIs throughout the plants′ tissues after damaging the leaves by adult *Colorado potato beetles* as compared to the control plants. They further suggested the role of PIs as a protection agent against further herbivore infestation. Karban & Baldwin (1997) referred these changes in plants after damage as "Induced Responses". Biochemical factors; such as anti-nutritive proteins & metabolites, and ecological factors; such as herbivore preference and performance & tritrophic interaction (involving other species), are the determinants of the induced responses (Karban and Baldwin, 1997; Kessler and Baldwin, 2001; Bruinsma and Dicke, 2008).

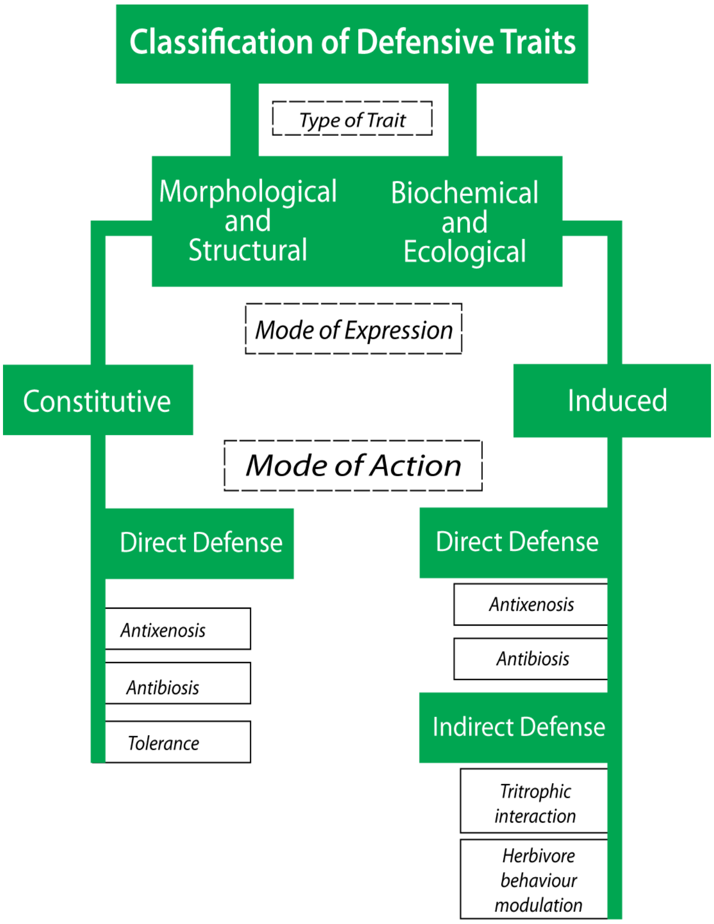


Figure 1. Classification of defensive traits in plants categorized under their mode of interactions with the insects. (Modified from Schaller, 2008)

3. Induced Responses in Plants

Nocturnal insects, esp. Lepidopterans, orient towards the host plants by exploiting the volatile chemical cues from the plants. Generally, the survival of offsprings in lepidopteran herbivores depends on the preference of the females during the selection of suitable host plants for oviposition. Once after hatching on the female selected plants, the Lepidopteran larvae are relatively immobile and have less choice to find alternative food plants (Renwick, 1989; Renwick and Chew, 1994). Soon after hatching, the Lepidopteran larvae start feeding on the green foliage of the selected host plant vigorously that can cause a significant loss of plant biomass. Some plant species efficiently produce secondary metabolites, both volatiles and non-volatile chemicals, in response to feeding damage by herbivorous arthropods. These secondary metabolites have been documented in several studies as a reliable source of increasing plant resistances against herbivores both at above-ground and below-ground levels (Paré and Tumlinson, 1996; Agrawal, 1998; Farmer, 2001; Heil, 2004; Kost and Heil, 2006; Rasmann and Turlings, 2007; Kost and Heil, 2008).

Induced response traits mainly depend on the environmental conditions prevailing around the host plants. Induced responses can be classified into; (1) induced resistance, and (2) induced defenses

3.1. Induced Resistance

The induced responses that reduce herbivore survival, reproductive out put, or preference for a plant are termed as “induced resistance”. Induced resistance has been discussed from the herbivore’s point of view, and it does not necessarily benefit the plant. For example, the investment in induced resistance may exceed the benefit from reduced herbivore damage, or induced resistance may render the plants more vulnerable to other potential danger (Karban and Baldwin, 1997; Agrawal and Karban, 1999)

3.2. Induced Defense

The induced responses that minimize the negative fitness consequences of the subsequent herbivore attacks on plants either by repelling them or by attracting the natural enemies (predators and parasitoids) of the herbivores are termed as “induced defenses”. Induced defense is viewed from plant’s point of view, and plant gain benefit from these responses in all circumstances (Karban and Baldwin, 1997; Agrawal and Karban, 1999).

4. Classification of Induced Defenses

Two types of induced defenses are commonly distinguished.

4.1. Induced Direct Defense

Defense is called direct if the induced responses affect the interaction between herbivore and its host plant directly. It relies on morphological features such as, thorns, spines, and trichomes, epicuticular wax film and wax crystals, tissue toughness, as well as secretory structures and latices and resins containing channels. They also include compounds for chemical defense, like secondary metabolites, digestibility-reducing proteins and anti nutritive enzymes (Howe and Schaller, 2008).

4.2. Induced Indirect Defense

Two systems are involved to understand the whole mechanism of induced indirect defense in plants under the attack of the herbivores:

4.2.1. Extrafloral Nectar Production
4.2.2. Herbivore Induced Plant Volatile Production

4.2.1. Extrafloral Nectar Production

Herbivore feeding induces plant defense by producing the extra-floral nectar (EFN) that is exploited as alternative food source by carnivorous arthropods. EFN-production has been described in *ca.* 1000 plant species belonging to at least 93 different families (Karban and Baldwin, 1997). Using an acquisitive approach towards indirect defense, many plants attract ants as well as other predators and parasitoids to their above ground parts by secreting nectar from extrafloral nectaries in order to increase their own reproductive fitness. In the context of EFN-production, vegetative plant parts such as stem and leaves as well as the flowers are actively involved (Wäckers et al., 2001; Röse et al., 2006; Wäckers et al., 2007; Heil et al., 2010).

Some of the well-documented examples from this system are as follows: The ant-acacia system is among the best-described system in EFN production by the plants for their defenses against the attacking herbivores. Due to the presence of eggs and damaged caused by the young larvae of the main herbivore *Ceratomia catalpae* (Sphingidae), the leaves of *Catalpa speciosa*

(Bignoniaceae) secrete more nectar compared to the unattacked leaves and reduce herbivory by enhancing more and frequent visitations of the ants as well as ladybird beetles and a parasitoid, *Apanteles congregatus*, of herbivores (Stephenson, 1982).

In repose to feeding damage by *Spodoptera littoralis* larvae, foliar EFN-production in caster *Ricinus communis* and cotton *Gossypium herbaceum* plants has been increased 2.5 and 12 folds respectively, as compared to the control plants or mechanically damaged plants (Wäckers et al., 2001). These plants efficiently adjust their nectar production in order to recruit the predators and parasitoids to the site of attack when exactly needed (Röse et al., 2006). Kost and Heil (2006) have shown that herbivore-induced EFN production in Lima bean *Phaseolus lunatus* plants results in increased numbers and duration of visits by carnivorous arthropods e.g. ants and wasps. Moreover, it has also been found previously that EFN production increases under the external application of jasmonic acid (a plant-hormone) on lima bean *P. lunatus* plants that help in reducing the amount of leaf damage indirectly via ants and wasps (Heil, 2004).

4.2.2. Herbivore-induced Plant Volatile Production

A second stretegy of induced indirect defense is the production of volatile organic compounds (VOCs) in response to various stimuli e.g., herbivore infestation, pathogen infection, mechanical damage etc. VOCs produced specifically in response to herbivore infestation are known as herbivore-induced plant volatiles (HIPVs). These HIPVs emanate from the exposed herbaceous parts (most probably from leaves and flowers) and provide airborn signals (chemical informations) either attract carnivorous arthropods (predators and parasitoids) or deter ovipositing females from their host plants (Dicke and Sabelis, 1988; De Moraes et al., 1998; Arimura et al., 2005; Turlings and Ton, 2006; Zakir et al., 2009; Dicke and Baldwin, 2010; Hare, 2011).

Thus, the plants use their induced direct defenses to alter the preference (oviposition site-selection) or performance (larval feeding) of the attacking herbivores. For example, cabbage *Brassica oleracea* plants reduce oviposition preference of adult female moths of *Pieris rapae* and larval performance after infestation (Fig. 2). Similarly, HIPVs help the attacked plants in reducing the further herbivore attack in two ways; i) through induced direct defense, by deterring the ovipositing females of cabbage butterfly *P. rapae,* as well as ii) through induced indirect defense, by attracting the larval parasitoid *Cotesia glomerata* (Fig. 2).

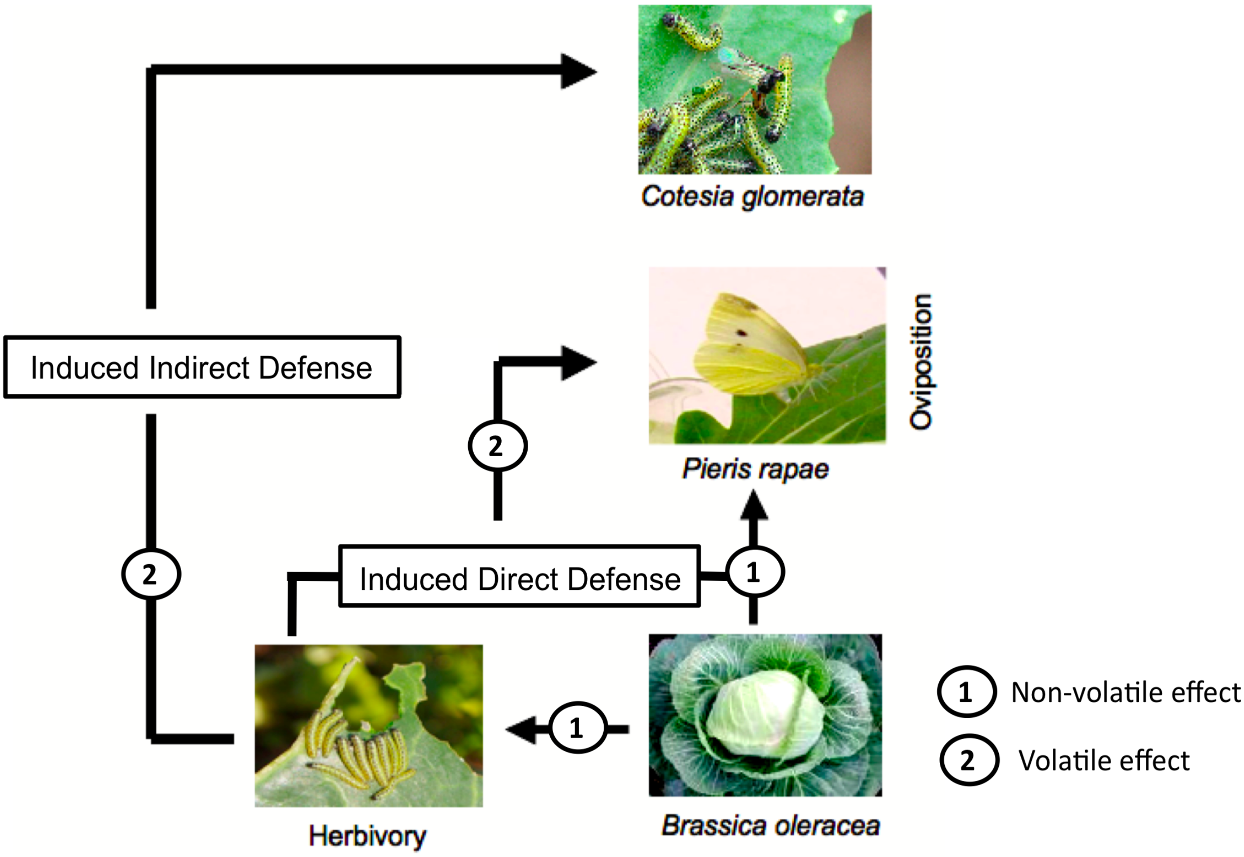


Figure 2. Illustration of induced direct and indirect defenses in response to herbivory in Brassica-Pieris system (Modified from Bruinsma and Dicke, 2008; Photos: Hans Smid / bugsinthepicture.com).

Further in our studies, we will try to highlight the investigations so far has been made in the field of induced direct and indirect defenses in plants in response to the herbivore attack as well as we will discuss the ecological significances of these induced defenses with respect to their possible role as future implications in the existing agricultural systems.

5. Investigations of Induced Defenses

Undamaged leaves of a plant release low levels of volatile chemicals, but when herbivorous insects damage a plant, the phenotype of the plant is entirely changed and many more volatiles are released. This type of phenotypic plasticity of plants in response to herbivory influences the community dynamics in the ecological systems both directly and indirectly e.g., through tritrophic interactions. The term "phenotypic plasticity" is defined as "independent of antagonists or mutualists, when individuals of two species interact in a community, one partner can adjust its phenotype in response to its respective partner" (Agrawal, 2001). As a result, the general appearance of the attacked plants become highly appealing towards natural enemies that enhance their foraging towards the damaged parts where the herbivores are feeding and that ultimately enhance the plant fitness by reducing herbivores (Turlings et al., 1995; De Moraes et al., 1998; Kessler and Baldwin, 2001).

Phenotypic plasticity in terms of “induced direct and indirect defenses” can influence many more interactions within the organisms belonging to different communities. The integrated knowledge of herbivore induction, mechanism of volatile production and their perception at different levels of organisms is important for understanding the ecological interactions and formulation of manipulative tools against attacking herbivores (Bruinsma and Dicke, 2008).

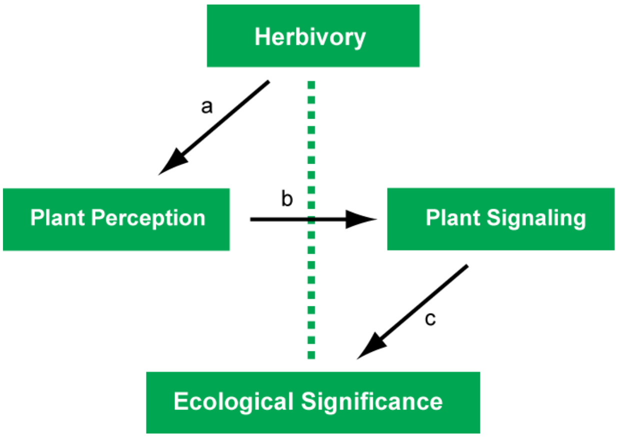


Figure 3. Herbivory and its related consequences in the ecosystem among insect-plant ineractions.

Herbivore-challenged plants survive in the complex ecosystem of insect-plant interaction under the following consequences:
(a) Perception of herbivore species: attacked plants introduce herbivore-associated molecular patterns (HAMP) in response to the specific herbivore-elicitors (Felton and Tumlinson, 2008; Mithofer and Boland, 2008).
(b) Further, these HAMP help plants in initiation of the signalling mechanism within the plant tissues according to the specific herbivore attack, (Kessler and Baldwin, 2002) and finally,
(c) Emissions of defensive compounds (volatiles and non-volatiles) occur from the attacked plants, both locally and systemically, in the surroundings for their protection against further herbivore attack (D' Alessandro et al., 2006; Kost and Heil, 2008) (Fig 3).

Now, it is important to investigate the above mentioned consequences in detail that how plants perceive and trail their signaling mechanisms in response to the herbivore attack and which defensive compounds are ecologically important for plants to synthesize and how these compounds are functional in nature.

5.1. Plant Perception of Herbivory

Recent work on plant perception of herbivory suggested that a component or components associated with feeding herbivores are helpful for the plants in distinguishing between general wounding and damage inflicted by chewing herbivores. Many plant species including cotton, tobacco, maize, potato, tomato and lima bean have been reported to release induced volatiles in response to the feeding damage of the their respective herbivores (Paré et al., 2005; Mithofer and Boland, 2008). For instance, cotton plants have been described as to modify their volatile profiles after their exposure to Lepidopteran larvae. Diurnal and nocturnal variation in the emission of the volatiles e.g., (E)-β-ocimene, linalool, (E)-β-farnesene, (E)-4,8-dimethyl-1,3,7-nonatriene (DMNT), (E,E)-4,8,12-trimethyl-1,3,7,11-tridecatetraene (TMTT) and indole, has also been described in among the herbivore damaged cotton plants (Mccall et al., 1994; Loughrin et al., 1995; Jönsson and Anderson, 1999) (Fig. 5).

Elicitation of these induced volatiles is due to high concentration of a signaling molecule jasmonic acid. An elicitor is a general term implied for any signaling compounds that can stimulate herbivore-induced plant responses. Basically, it is derived from plant-pathogen and plant-microbial interactions where they are classified as pathogen-associated molecular patterns (PAMPs) or microbe-associated molecular pattern (MAMPs). Similarly, HAMPs are herbivore-derived elicitor-like signaling molecules that interact with the particular host plants (Loughrin et al., 1994; Paré and Tumlinson, 1999; Felton and Tumlinson, 2008; Mithofer and Boland, 2008).

These HAMPs can be categorized into as chemical elicitors (produced by the herbivore oral secretions, saliva and oviposition fluids) and those that originate under herbivore specific wounding pattern. To date, five different herbivore-produced elicitors have been identified and documented with examples about their impressive role in the production of plant volatiles, which mediate complex, chemical interactions at plant-herbivore interface (Fig 4). Four of them are associated with herbivore feeding [three of these elicitors were isolated and identified from larvae of moths and butterflies and fourth from grasshoppers] while the fifth elicitor is derived from oviposition fluid deposited by weevils (Felton and Tumlinson, 2008; Jianqiang and Ian T, 2009).

β-Glucosidase is the first claimed elicitor separated from regurgitate of the white cabbage butterfly *P. brassicae* caterpillars. Mattiacci and her co-workers (1995) found that under the application of gut regurgitant of *P. brassicae* caterpillars on the healthy leaves of cabbage plant, a specific blend of volatiles (similar to that of herbivore-damaged plants) was being emitted that was highly attractive to parasitic wasps *C. glomerata*.

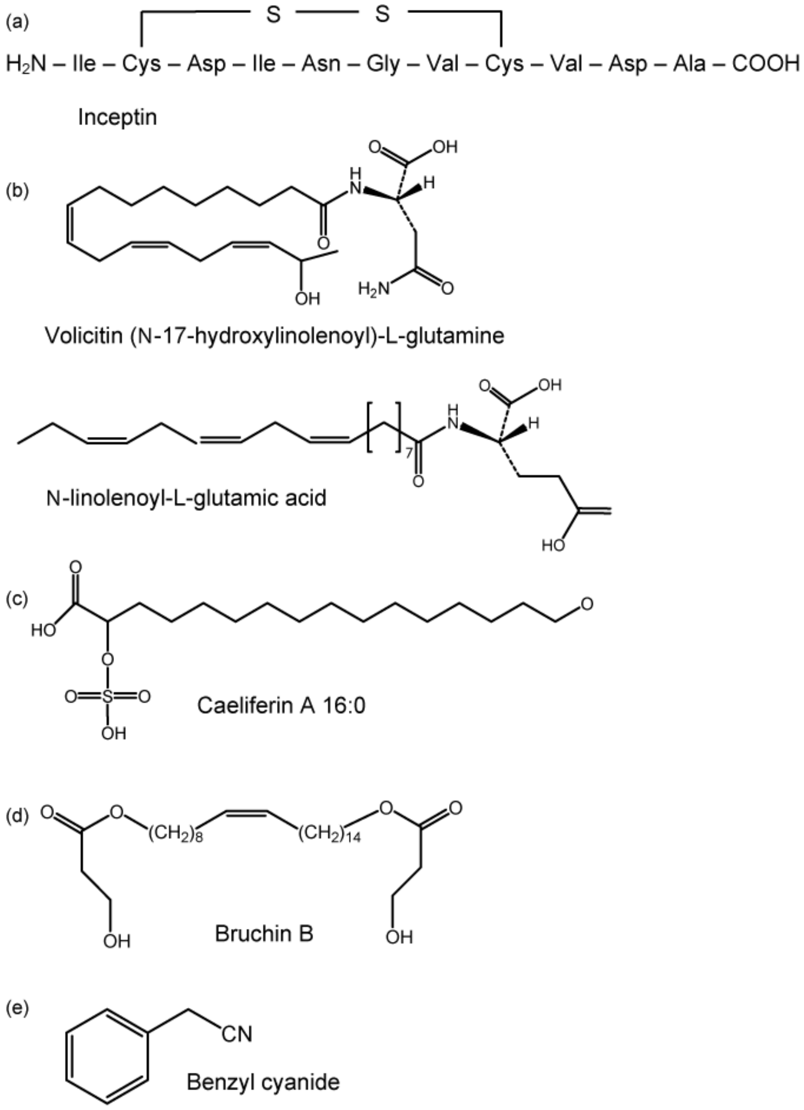


Figure 4. Herbivore-elicitors reported from oral secretions and oviposition fluids (Jianqiang and Baldwin, 2009).

Volicitin was isolated from oral secretion of beet armyworm *Spodoptera exigua* larvae (Fig. 4b). Female parasitic wasps, *C. marginiventris*, natural enemies of *S. exigua* larvae, were found highly attractive to the volatile blend emitted from the damaged maize *Zea mays* plants after applying volicitin as compared to the volatile blend emitted from only mechanically damaged plants (Alborn et al., 1997). In contrary, volicitin was unable to regulate the same mechanism of volatile induction in lima bean *Phaseolus lunatus* and cotton *Gossypium hirsutum* plants. Thus, volicitin should not be considered as a "general elicitor" of induced plant volatiles. Inceptin was isolated from the oral secretions of fall armyworm *S. frugiperda* caterpillars after feeding them on the cowpea leaves (Schmelz et al., 2006) (Fig. 4a). Another class of fatty acid elicitors of plant volatiles was isolated and identified from the oral secretions of the grasshopper *Schistocerca americana*. They were commonly occurring in the Orthoptera suborder Caelifera, and thus have been named as Caeliferins (Alborn et al., 2007) (Fig. 4c). The only known insect-produced elicitors involved in induced direct plant defenses are the Bruchins (Doss et al., 2000) (Fig. 4d). These compounds were deposited on pea *Pisum sativum* pods during oviposition by both pea weevils *Bruchus pisorum* and cowpea weevils *Callosobruchus maculates* and direct the plants to form callus tissue under the eggs to avoid the hatched larvae from burrowing directly into the pea pod. Recently, benzyl cyanide (BC) isolated from *P. brassicae* oviposition fluid has been identified as the second elicitor in oviposition fluid (Fig. 4e). The egg parasitoid, *Trichogramma brassicae*, was attracted to Brussels sprouts plants *B. oleracea* under the application of BC (1 ng) (Fatouros et al., 2008)

5.2. Plant Signaling in Response to Herbivore Damage

Depending on the type of the insect elicitors, plants adjust their innate response to insect feeding by activating several major signal-transduction pathways that leads to the induced production of a variety of secondary metabolites particularly terpenoids and green leaf volatiles (GLVs). All of these signal-transduction pathways are regulated by various plant hormones such as jasmonic acid (JA), salicylic acid and ethylene. These plant hormones are activated by insect feeding damage as well as by mechanical damage. In addition, synergistic and antagonistic relationship between these hormones suggests that plants and the interacting herbivores can profoundly effect the end results of the interactions i.e., by suppressing or overexpressing the induced volatiles (Arimura et al., 2005; Leitner et al., 2005; Mithofer et al., 2005; Mithofer and Boland, 2008; Arimura et al., 2009; Zhang et al., 2009).

The octadecanoid pathway, also known as lipoxygenase pathway, is a major signal-transduction pathway regulated by the plants in response to lepidopteran herbivores. Plants provide 18-carbon fatty acid (linolenic acid) to the lepidopteran larvae feeding on them as a precursor molecule to initiate the plant's innate defense mechanism via the octadecanoid pathway (Fig. 5). Though linolenic acid is a defensive element against lepidopteran herbivores, it is impossible for them to get rid of linolenic acid because it is an essential element for the growth and development of the young larvae. The breakdown of linolenic acid into various intermediate molecules such as 13-hydroperoxylinolenic acid, oxophytodienoic acid and others, leads to the production of JA (Paré and Tumlinson, 1999). Methyl jasmonate (MeJA) or *cis*-jasmone is a volatile derivative of JA. Both JA and MeJA are reported as defense inducing agents in plants against the attacking herbivores (Birkett et al., 2000; Bruinsma et al., 2009).

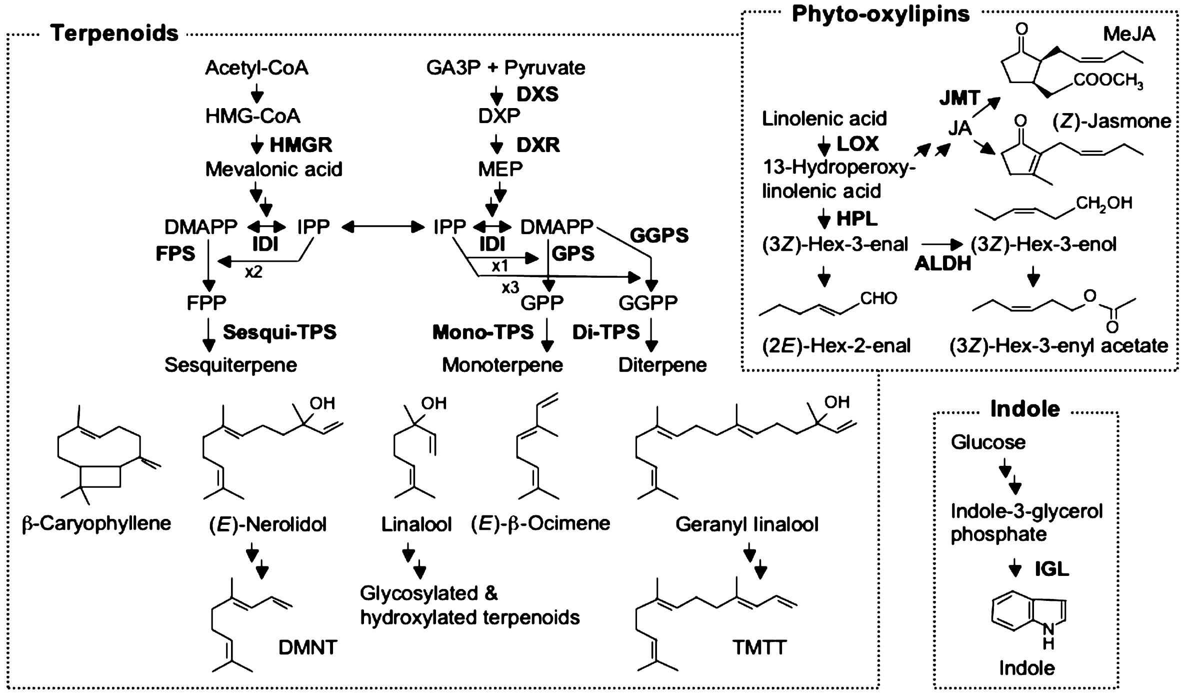


Figure 5. HIPVs signaling pathways demonstrating the production of terpenoids, jasmonic acid, green leaf volatiles (GLVs) and Indole by the feeding damage of the lepidopteran caterpillars on the plant (Arimura et al., 2005).

The importance of JA in the signal-transduction cascade has been confirmed by the fact that (i) the external application of JA helps in initiation of defense response sequences e.g., JA-treated plants of black mustard *B. nigra* were rejected by its specialist herbivore *P. rapae* and secondly JA application increased the plant performance by attracting a predator *C. glumerata* of the herbivores (Bruinsma et al., 2008). (ii) correlation exists between increased internal JA level after wounding and induced defense responses e.g., root application of MeJA increased the nicotine concentration in the above-ground parts of *Nicotiana attinuata* plants that significantly suppressed the herbivore attack of grasshopper *Trimerotropis pallidipennis* (Baldwin, 1998), and (iii) inhibition of JA producing pathway corresponds to the inhibition of defense responses e.g., phloem feeding insects (aphids, white fly) trigger salicylic acid mediated pathway and suppress the jasmonate signaling pathway that in turn suppress the production of terpenoids.

Similarly, jasmonate mutated tomato plants has shown less resistance against herbivores performance and less attraction to the predators after herbivore attack compared to wild-type tomato plants (Thaler et al., 2002; Leitner et al., 2005).

6. Ecological Significance of HIPVs: Specificity and Diversity

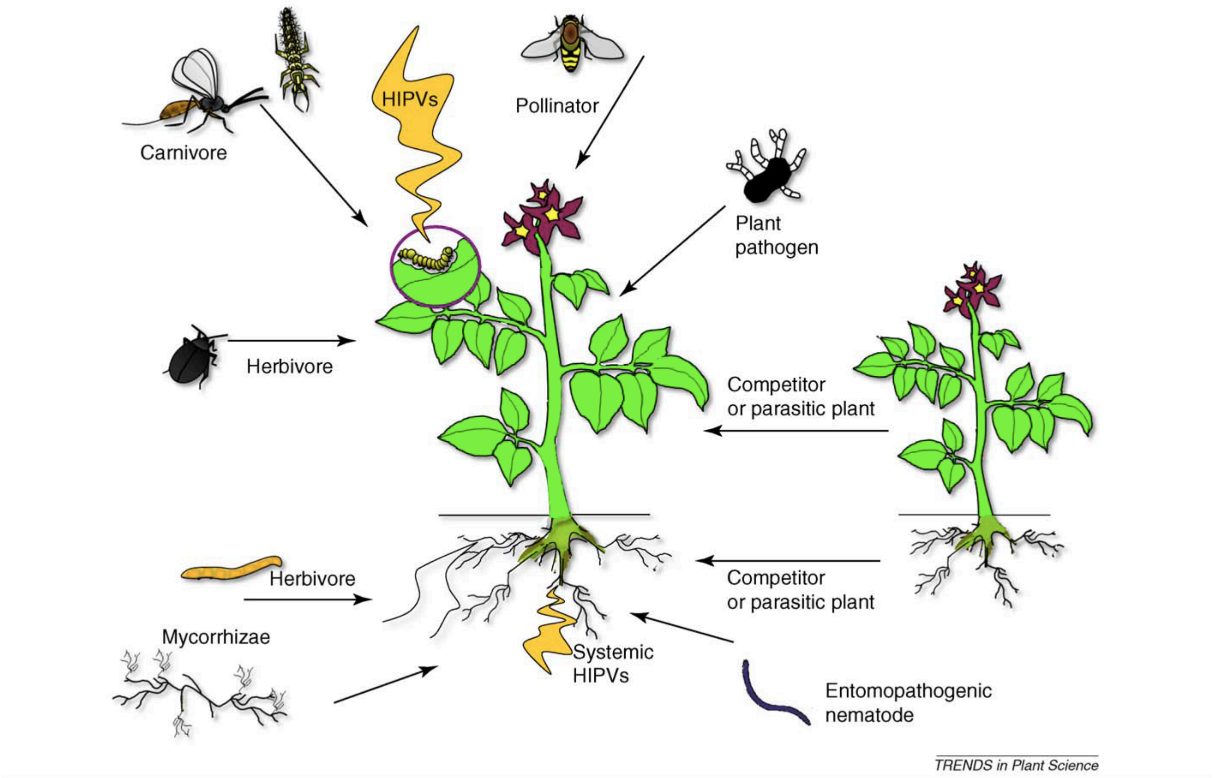
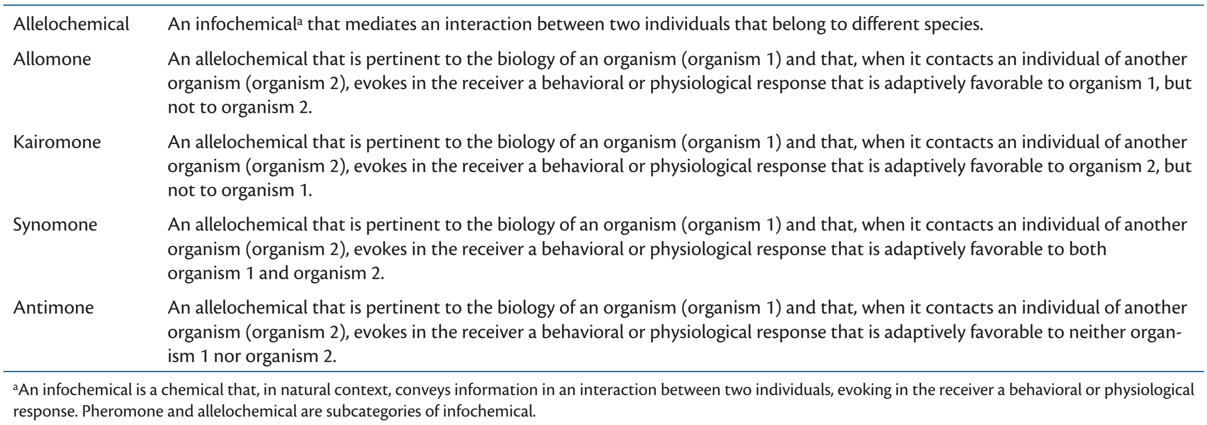


Figure 6. Herbivore-induced plant volatiles (HIPVs) associated interactions among different organisms (signal receivers) around a damaged plant (Dicke and Baldwin, 2010).

HIPVs emission from the plant and its perception in the surrounding organisms is quite fascinating because different species perceive these chemicals as information to survive in a complex environment (Fig. 6). In tritrophic system, HIPVs help the infested plants by attracting the natural enemies (predators and parasitoids) of the herbivores in order to reduce the further level of herbivore infestation. For example, HIPVs from maize *Z. mays* plants infested by Egyptian cotton leafworm *S. littoralis*, attract the parasitoids *C. marginiventris* and *Microplitis rufiventris* towards infested parts (D' Alessandro et al., 2006). Similarly, a lima bean plant *P. lunatus* release HIPVs after the infestation of the two-spotted spider mites *Tetranychus urticae* from the vegetative parts and attract predatory mites *Phytoseiulus persimilis* for protection against the increasing population of *T. urticae* (Dicke and Van Loon, 2000). A recent investigation has shown that tobacco *N. attenuata* releases (*E*)-isomers of green leaf volatiles (GLVs) instead of (*Z*)-isomers (produced on mechanical damage) after the infestation of *Munduca sexta*. This isomeric change in GLVs [(E)-isomers] ultimately influence the foraging efficiency of the generalist hemipteran predator *Geocoris spp.* towards the exact location of the neonates and eggs on the plants (Allmann and Baldwin, 2010). In addition, HIPVs provide protection to the below-ground plant parts against the attacking herbivores e.g., the roots of *Z. mays* plant infested by root-feeding beetles *Diabrotica virgifera virgifera*, release (E)-β-caryophyllene into the soil that can help in the foraging of entomopathogenic nematode *Heterorhabtitis megidis* towards the infested roots (Rasmann et al., 2005)). As HIPVs provide benefits to both the natural enemies and the infested plants, thus they can be categorized as synomones (Table 1).

Table 1. Types and functions of allelochemicals (Arimura et al., 2009)



Allelochemical	An infochemical[a] that mediates an interaction between two individuals that belong to different species.
Allomone	An allelochemical that is pertinent to the biology of an organism (organism 1) and that, when it contacts an individual of another organism (organism 2), evokes in the receiver a behavioral or physiological response that is adaptively favorable to organism 1, but not to organism 2.
Kairomone	An allelochemical that is pertinent to the biology of an organism (organism 1) and that, when it contacts an individual of another organism (organism 2), evokes in the receiver a behavioral or physiological response that is adaptively favorable to organism 2, but not to organism 1.
Synomone	An allelochemical that is pertinent to the biology of an organism (organism 1) and that, when it contacts an individual of another organism (organism 2), evokes in the receiver a behavioral or physiological response that is adaptively favorable to both organism 1 and organism 2.
Antimone	An allelochemical that is pertinent to the biology of an organism (organism 1) and that, when it contacts an individual of another organism (organism 2), evokes in the receiver a behavioral or physiological response that is adaptively favorable to neither organism 1 nor organism 2.

[a] An infochemical is a chemical that, in natural context, conveys information in an interaction between two individuals, evoking in the receiver a behavioral or physiological response. Pheromone and allelochemical are subcategories of infochemical.

Depending on the system and level of infestation, HIPVs exhibit both kairomonal and allomonal qualities during the selection (acceptance or rejection) of the suitable host plants at 2nd trophic level. Though the studies are limited but HIPVs has shown a great influence on the herbivore preference behavior during suitable-site selection for feeding, mating and oviposition (egglaying behavior in herbivores). Kessler and Baldwin (2001) showed kairomonal effect of HIPVs in a field study where ovipositing females of *M. sexta* avoid the healthy plants of tobacco *N. attenuata* attached with induced volatiles treated with lanolin paste compared to untreated plants. Nocturnal female moths of *Heliothis virescens* showed repellency to the induced volatiles of the tobacco *N. tabacum* plants produced by the feeding of their offsprings (De Moraes et al., 2001).

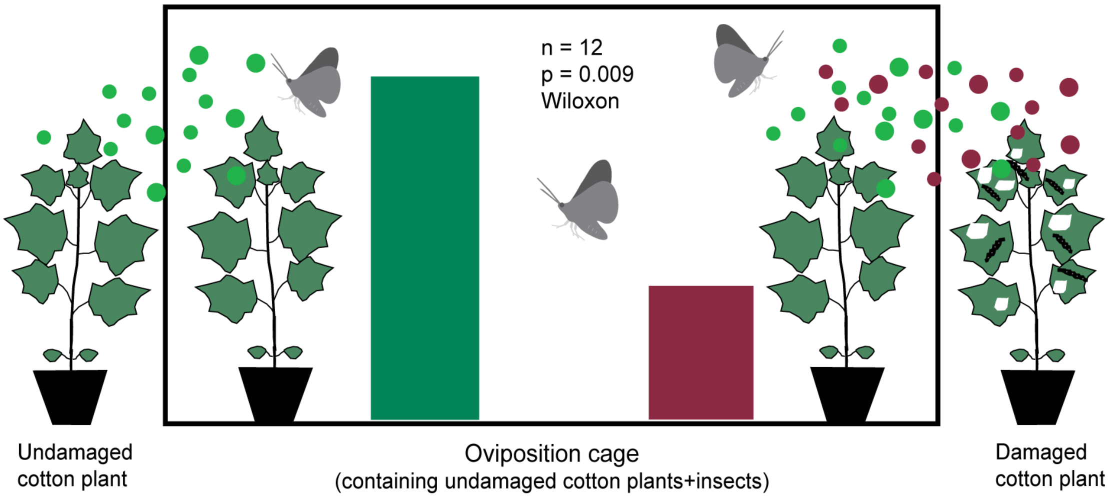


Figure 7. Influence of HIPVs on the oviposition behavior in *S.littoralis* (Zakir et al., 2009).

Cotton *G. hirsutum* plant has been reported to undergo stage-dependent induced changes after being attacked by the larvae of *S. littoralis* and these changes further suppress the preference for induced plants in the adult female moths of *S. littoralis* during the selection of the plants for oviposition (Anderson and Alborn, 1999). Furthermore, female moths of *S. littoralis* avoided healthy stands of cotton plants exposed to HIPVs produced by the neighboring cotton plants that are being infested by the larvae of *S. littoralis* (Zakir et al., 2009; 2010) (Fig. 7). Electrophysiological studies revealed that almost 18 compounds have been identified as antennal active on the antennae. At low infestation, a lima bean plant attracts more spider mites whereas it repels them at a high infestation level (Horiuchi et al., 2003).

In addition, the volatile produced by plants in response to herbivore infestation (HIPVs), pathogen infection and mechanical wounding, collectively called as volatile organic compounds (VOCs), can eavesdrop as well as prime the neighboring plants and it has been shown that these exposed plants can better protect themselves against the attacking herbivores (Farag and Pare, 2002; Farag et al., 2005; Heil and Kost, 2006; Kost and Heil, 2006; Frost et al., 2007; Heil and Silva Bueno, 2007; Barbosa et al., 2009). Various mechanisms of plant-plant communication has been shown to be activated by these VOCs (Fig. 8). Despite the fact that the interplant communication phenomenon via HIPVs is quite controversial, some plant species such as lima bean, cotton, poplar, black alder, sagebrush, sitka willow, tobacco, maize have shown intraspecific signaling while tobacco and tomato has been shown to induce defence responses when exposed to damaged sagebrush volatiles as interspecific signaling (Heil and Karban, 2010). Plants can get better resistance against attacking pathogens by the efficient use of the HIPVs (mechanism of pathogen attack detailed in plant perception of herbivory part). By producing GLVs [C6–aldehydes, –alcohols and –acetates], a prominent and specific part of HIPVs, plants can reduce pathogen attack. For instance, C6-aldehydes isolated from transgenic *Arabidopsis thaliana* overexpressed with 13HPL have been found active agents against a fungal pathogen *Botrytis cinerea*. Similarly (E)-2-hexen-1-ol enhance the resistance of citrus *Citrus jambhiri* against *Alternaria alternata*, while *in vitro* studies on cis-3-hexanol and (E)-2-hexenal has shown their anti-growth properties against *Pseudomonas* (Gomi et al., 2003; Prost et al., 2005; Felton and Tumlinson, 2008; Kishimoto et al., 2008).

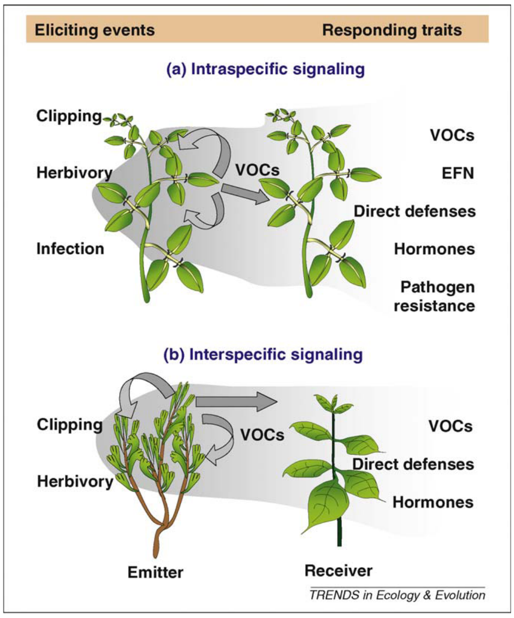


Figure 8. Mechanism of plant-plant communication via induced production of volatiles (VOCs) (Heil and Karban 2010)

7. Conclusion and Future Directions

Induction of a herbivore-plant interactions demonstrate that plants are efficient in synthesizing and releasing HIPVs in response to herbivore attack, from the perception of the attacking organism until the response reactions. In addition, such plant produced diverse blends of HIPVs depend on the species of the attacker (herbivore) as well as on the plant species itself (Arimura et al., 2009; Dicke and Baldwin, 2010). On the other hand, less effort has been made to find out the behavioral correlation between ecologically relevant HIPVs and their olfactory perception in the insects. At an organism level, it is important to sort out the compounds on olfactory basis in order to; i) find out specifically active compounds in the whole blend of HIPVs relevant to the insects perception, and ii) get rid of ones that have less/or no importance in the insect-plant communications (Bruyne and Baker 2008). Some electrophysiological studies i.e., gas chromatography coupled electroantennographic detections (GC-EADs), on the members of tritrophic interactions revealed that a key-volatile emanated from infested plants is important for the attraction of the predators towards the infested-sites. For instance, out of six EAG active compounds from the infested broad bean *Vicia faba* plant, 6-methyl-5-heptene-2-one was found as highly attractive for the aphid parasitoid *Aphidius ervi* (Du et al., 1998), similarly, (E)-β-caryophyllene induced by feeding of *Nezara viridula* on *V. faba* highly attracted an egg parasitoid *Trissolcus basalis* (Colazza et al., 2004). In other studies, a mixture of EAG active compounds elicited attraction in predators and parasitoids towards infested plants (Gouinguene et al., 2005; Sasso et al., 2009). Electrophysiological studies on herbivores showed that antennae of female moths of *S. littoralis* resoponded to several compounds present in the headspace samples of the infested cotton *G. hirsutum* plant, and interestingly the responses were highly selective and consistent to the specific compounds only (Anderson et al., 1995a; Anderson et al., 1995b; Jönsson and Anderson, 1999; Zakir et al., 2009). In addition, olfactory neurons (ORNs) present on the females antennae are highly sensitive to some of these compounds but not to all. In later studies, a blend of electrophysiologically active compounds elicited avoidance behaviour in *S. littoralis* during their oviposition-site selection that corresponded to the effect elicited by headspace collections from the infested cotton plants (Zakir et al., 2010).

In the light of the above discussion on induced plant defenses against herbivores we conclude that the risk of herbivory can largely be reduced if the host plants are efficient in producing the HIPVs in response to the herbivore attack. These HIPVs ultimately increase plant resistance by i) pushing the herbivores away as well as ii) by pulling the natural enemies of the herbivores towards the host plants. In order to cope with the herbivore attack, screening of pulling and pushing components from HIPVs blend is very important. From a practical perspective, it is important to screen the most relevant volatile compounds. Plant physiologists design different assays to highlight the functions of the volatile compounds at different organisms levels while insect physiologist are more interested in screening these compounds on temporal and spatial basis. Laboratory approaches such as GC-EADs and neurophysiological studies e.g., Ca++ imaging (Hansson, 1995) are used by insect physiologists for identification and understanding the relevance of different volatile compounds during host locations by the herbivores. After identifying the electrophysiologically active compounds, it can be much easier to design bioassays in the laboratory to find the best possible combinations of the most effective volatile compound(s) before using them in the field tests. Further, it is necessary to identify the temporal and spatial mechanism of neuronal interactions in the central nervous system (CNS) of the insects. No doubt, functional and mechanistic knowledge of HIPVs could help agricultural systems in monitoring and controlling the insect pests in a sustainable and environmentally safe manner. Thus, the best combination of these approaches can contribute to Integrated Pest Management (IPM) program.

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