

VOLATILES INVOLVED IN TRI-TROPHIC INTERACTIONS INDUCED BY INSECT HERBIVORY

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Introduction:

Plants are continuously under threat from a wide array of biotic and abiotic stresses, of which biotic stress due to herbivory by insects is an important constraint in crop production. However, plants have evolved several defense mechanisms against insect herbivory, which are quite dynamic. The effect of host plant resistance on the herbivores could be direct or indirect. Direct defenses against herbivory could be physical or chemical and include morphological barriers such as trichomes, cell wall lignification and silica deposition, and syntheses of toxic chemicals which act as repellents, deterrents, anti-nutrients, and anti-digestive compounds. Indirect defense is mediated through the release of volatile cues by the plants when attacked which is one of the important and immediate response of plants to herbivory. Herbivore-induced plant volatiles (HIPVs) are involved in plant communication with natural enemies of the insect herbivores, neighboring plants, and different parts of the damaged plant.

Herbivore-Induced Plant Volatiles (HIPVS):

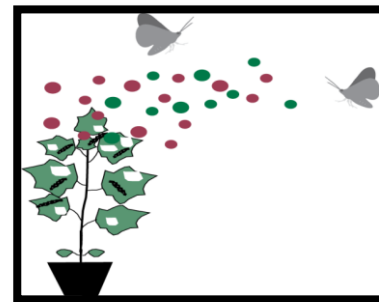
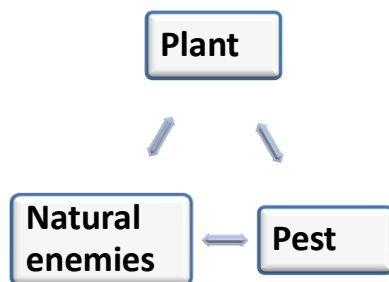
About 2,000 volatile compounds released in response to herbivore attack have been identified from 900 plant families. Herbivore-induced plant volatiles (HIPVs) not only communicate between the infested plant and natural enemies of the attacking insects, but also warn the neighboring undamaged plants of the forthcoming danger, besides communicating between different parts of the same plant (inter-plant and intra-plant signalling, respectively). The HIPVs also act as feeding or oviposition deterrents to insect pests. HIPVs are reliable cues for the natural enemies, since they are produced in large amounts by the plants when the plants are under herbivore attack. Moreover, the volatile blend released is specific for a particular insect-plant system, including the natural enemies, and the neighboring plants. It varies according to the plant and herbivore species, the developmental stage, and condition of the plants and the herbivores. Release of a wide variety of HIPVs in response to herbivore damage and their role in plant-plant, plant-carnivore and intraplant communications, represents a new facet of the complex interactions among different trophic levels (Schnee *et al.* 2006).

Jasmonic acid (JA) and its volatile derivative methyl jasmonate (MeJA), salicylic acid (SA) and ethylene are phytohormones involved in plant defenses against herbivores that can also play a key role in the production and emission of HIPVs (Kessler *et al.*, 2004). For example, the predatory mirid, *Deraeocoris brevis* (Uhler), the anthocorid, *Orius tristicolor* (White) and the coccinellid, *Stethorus punctum picipes* (Casey) were attracted to sticky cards

baited with (Z)-3-hexenyl acetate; while the geocorid, *Geocoris pallens*, hover flies and *S. punctum picipes* were attracted to cards baited with methyl salicylic acid (MeSA) (James, 2003).

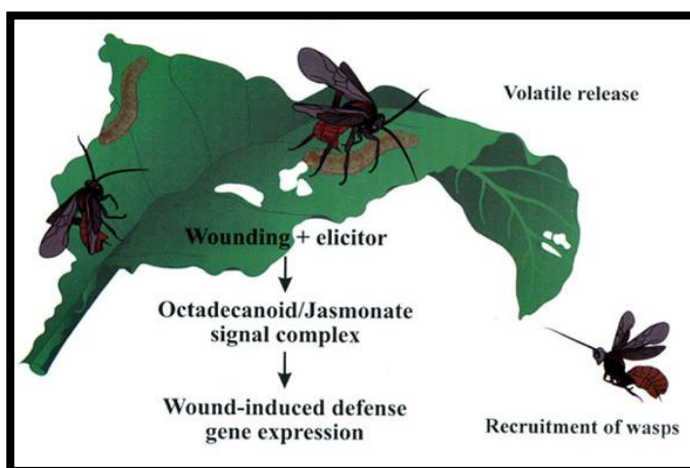
Similarly, Zhu & Park (2005) found attraction of the lady beetle *Coccinella septempunctata* L. to traps baited with MeSA, whereas 2-phenylethanol was more attractive to the lacewing *Chrysoperla carnea* and syrphid flies. 2-Phenylethanol is also attractive to the multicolored Asian lady beetle, *Harmonia axyridis* (Pallas) (Sedlacek *et al.*, 2009) and is currently being sold commercially by MSTRS Technologies (Ames, Iowa, USA) as the natural enemy attractant Benallure®.

Tritrophic Interactions:

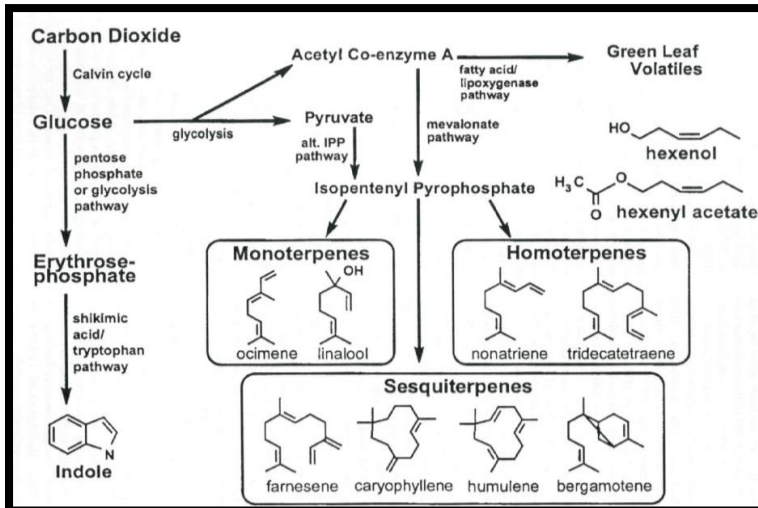


In nature, trophic relationships among organisms within a community rarely, if ever, consist only of simple food chains. More commonly, they comprise an extensive web of interactions extending across several trophic levels. The trophic relationships between plants, insect herbivores, and their parasitoids provide a good example of these complexities. Plant protection by natural enemies is well documented and has been manipulated in the development of biological control strategies in many crops. Plants are well placed to influence the efficiency of parasitism and predation and they mediate numerous interactions between entomophagous arthropods and herbivores.

De Moraes *et al.* (1998) demonstrated that plant emissions can transmit herbivore species-specific information that is detectable by parasitoids. It was shown that tobacco and cotton each produce distinct volatile blends in response to damage by two closely related herbivore species, *Heliothis virescens* (Fab.) and *Helicoverpa zea* (Boddie). The specialist parasitic wasp *Cardiochiles nigriceps* exploits these differences to distinguish infestations by its host, *H. virescens* from non-hosts. The production by these phylogenetically diverse plant species and exploitation by parasitoids of highly specific, information-rich chemical signals,



keyed to individual herbivore species, demonstrates the high degree of sophistication that can exist in plant parasitoid chemical interactions.



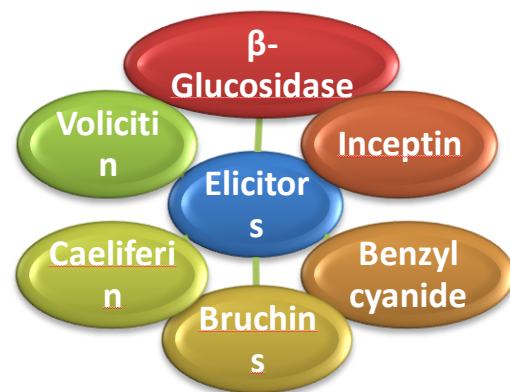
Biosynthesis of Induced Plant Volatiles:

The release of volatiles in response to herbivory is well documented. But little is yet known about how plants produce and regulate the blend of compounds released. So far four biosynthetic pathways have been identified which appear to be involved in the production of volatile signals. The isoprenoid precursor

isopentenyl pyrophosphate serves as a substrate for monoterpenes and sesquiterpenes, the fatty acid/lipoxygenase pathway generates green leaf volatiles and jasmone, and the shikimic acid/tryptophan pathway results in the nitrogen containing product indole.

Elicitors of Plant Volatiles:

An **elicitor** is a compound produced by an herbivore that induces a response, in the plant on which the herbivore feeds. Attraction of insect parasitoids by volatiles emitted from damaged plants has been well documented. Parasitoids use these volatiles as cues to search their prey and provide adaptive advantage to the emitting plants as long as volatile production persists. These interactions are specific to a particular insect-plant interaction. For example, *Zea mays* TPS10, is a herbivore-induced terpene synthase that forms (E)- β -farnesene, (E)- α -bergamotene, and other sesquiterpenes in *Arabidopsis thaliana*, which does not produce significant amounts of volatile terpenes, suggesting that a single herbivore-induced gene from *Z. mays* is sufficient to elicit this indirect defense. *Cotesia marginiventris*, a parasitoid of *Spodoptera litura* has been reported to be attracted to TPS10- producing *A. thaliana*. Damage by corn rootworm, *Diabrotica virgifera* larvae in maize roots induces the release of (E)- β -caryophyllene, which attracts the nematode, *Heterorhabditis megidis* that in turn feed on the larvae of *D. virgifera*.



Mattiacci *et al.* (1995) found that beta-glucosidase in *Pieris brassicae* (L.) caterpillars elicits the release of volatiles from cabbage leaves. The major active elicitor of the oral secretion of beet armyworm larvae was recently identified by Alborn *et al.* (1997) as (N-[17-hydroxylinolenoyl]-L-glutamine) and was named volicitin. Volicitin, in both its natural and synthesized forms, induces corn seedlings to release the same blend of volatiles induced by herbivore feeding. This blend has been shown to be exploited as a host location cue by the parasitic wasps that attack this herbivore.

Inceptin was isolated from the oral secretions of armyworm, *Spodoptera spp.* caterpillars after feeding them on the cowpea leaves (Schmelz *et al.* 2006). Volatiles were isolated and identified from the oral secretions of the grasshopper, *Schistocerca americana*. They were commonly occurring in the Orthopteran suborder Caelifera, and thus have been named as Caeliferins (Alborn *et al.* 2007). The only known insect-produced elicitors involved in induced direct plant defenses are the Bruchins (Doss *et al.* 2000). These compounds were deposited on pea *Pisum sativum* pods during oviposition by both pea weevils *Bruchus pisorum* and cowpea weevils *Callosobruchus maculatus* and direct the plants to form callus tissue under the eggs to avoid the hatched larvae from burrowing directly into the pea pod. Emission of blend of volatiles by plants in response to HIPVs exposure in the absence of herbivores could have ecological and physiological costs, since HIPVs might attract the natural enemies that may lead to their desensitization. Thus, plants need to have a more adaptive strategy to prime themselves for an increased volatile response after exposure to HIPVs.

Conclusion:

The HIPVs play an important role in host plant – herbivore – natural enemy interactions, and have the potential for enhancing the effectiveness of host plant resistance and biological control for integrated pest management. The use of HIPVs to lure natural enemies to crop fields has been receiving increased attention. Jasmonic acid (JA) and its volatile derivative methyl jasmonate (MeJA), salicylic acid (SA) and ethylene are the examples of herbivore- induced volatile compounds, that farmers can apply in field to attract the natural enemies.

Further studies need to be performed to identify the volatile compounds that govern the olfaction-directed behavior of insect pests and their natural enemies to formulate strategies for developing varieties with constitutive and induced resistance to insect pests and manipulation of such volatiles to attract the natural enemies of the crop pests for enhancing the effectiveness of bio-control agents for pest management.

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