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# TRITROPHIC INTERACTIONS: THE INTERCONNECTEDNESS OF LIFE, THE DELICATE BALANCE AND THE VIBRANT SYNERGY THAT SUSTAINS THE AGRICULTURAL ECOSYSTEM

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**ABSTRACT**
The natural defence of the plants may act directly or indirectly against pests. The direct defence by the plants is by affecting the preference of host plant or survival and reproductive success which is mediated by mechanical protection or by secondary metabolites. The indirect defence against insects is induced by the release of blends or combinations of volatiles that may attract natural enemies. Plants emit volatile and non-volatile compounds to defend themselves from herbivore attack. The volatiles released by the plants play a vital role as signals in tritrophic interactions. The three trophic levels involved are plants (1st trophic level), herbivores (2nd trophic level) and the natural enemies that include predators and parasitoids (3rd trophic level). The importance of third trophic level *i.e.,* natural enemies was initially emphasized by Price *et al.* (1980). The third trophic level is considered as part of a plant's battery of defences against herbivores. Multiple factors, including plant species, genotype, age, herbivore species, the severity of the attack, abiotic conditions, or any combination of these, may affect the release of HIPVs at the plant level. Initial observations of plant-to-plant communication were met with doubt, but it is now generally accepted that plants react to the stress signals of their neighbours. At the plant level, tritrophic interactions are shaped by the interplay between biotic and abiotic stressors. Ecosystem services rely on interactions among organisms, particularly in tritrophic interactions involving plants, herbivorous pests, and their natural enemies. These interactions are vital for sustainable agriculture and biocontrol services. Trophic cascades, which affect food webs by causing changes that impact multiple levels, can influence biological control in either positive or negative ways.

**KEYWORDS:** Tritrophic interaction, HIPVs, Semiochemicals, Induced defense, Elicitors

## INTRODUCTION

Plants are incessantly challenged by a wide range of abiotic and biotic stresses throughout their life cycle. Among these, biotic stress caused by herbivory is the most important constraint in crop production (Mithofer and Boland, 2012). Plant resistance in opposition to herbivory could be constitutive or induced. In case of constitutive resistance, plants respond irrespective of external stimuli, whereas induced resistance is activated following herbivore attack. Both constitutive and induced resistance play a major role in plant defence against insects. Though constitutive defence is the primary line of resistance against herbivores, induced resistance is effective and more reliable. Induced resistance alters the phenotypic plasticity of plants and enables them to tolerate herbivores by reducing the chances of insect attack (Hussain *et al*., 2014). In plants, induced defence is one of the significant components of pest management in agriculture (Howe and Jander, 2008). Trichomes are the best example of both constitutive and inducible defence mechanisms, and their secretions deter herbivores from feeding (Bhuva *et al.,* 2024). Many plant species interact with carnivores belonging to the third trophic level, to obtain protection from herbivores and pathogens which represent the second trophic level. Plants attract other organisms and provide them shelter to get rid of their enemies (pests), thereby reducing enemy pressure (Heil, 2008). Plants alter their volatile blends that they normally release when attacked by herbivores as well as their natural enemies (Mumm and Dicke, 2010). Investigating multitrophic interactions in more natural environments will facilitate the identification of mechanisms of evolutionary significance and highlight trends applicable to biological control practices. This review outlines the basic processes of tritrophic interaction, which can be beneficial for future scientific projects focused on eco-friendly pest management.

### Plant characters vs. searching behavior of natural enemies

Tritrophic interactions determine the population biology and evolutionary dynamics of species at all trophic levels and drive fundamental aspects of community structure and ecosystem dynamics. According to Price (1980), there are three types of interactions between these trophic levels: interactions mediated by physical factors, chemical interactions, and interactions mediated by semiochemicals. The structural characteristics of plants, including leaf toughness, trichome presence, and cuticle thickness, significantly influence the effectiveness of parasitoids in locating their hosts (Boethal and Eikenbary, 1986). The survival and fitness of parasitoids depend on strategic

decisions made by female parasitoids, such as the search duration and acceptance of host (Daniel Gingrass *et al.,* 2008). The Optimal Foraging Theory suggests that a forager should enhance its chances of coming across the most appropriate and rewarding hosts, and when there is a plentiful supply of hosts, it should avoid those of lesser quality (Stephens and Krebb, 1986). An important behavioural trait of female parasitoids is the allocation of time for searching and ovipositing on the host. High walking velocity results in a higher probability of encountering hosts or cues that may lead the female to the host (Suverkropp *et al.,* 2001). The majority of research on foraging theory and behaviour has concentrated on attributes of hosts, including their density and distribution; however, other factors such as habitat, plant type, and plant structure might also influence levels of parasitism (Romeis, 2005). Daniel Gingras *et al.* (2008) reported that the structure of the plant did not influence the time related to the locomotion behaviour of *Trichogramma turkestanica* (Hymenoptera: Trichogrammatidae). Nevertheless, it affected the area searched, which was significantly larger on simpler plant structures. Female parasitoids tend to be more efficient when searching on simple plant structures compared to complex ones. Eggs of host insects located on twigs are likely to be found more often than those laid on leaves. Several plant characters are known to affect the searching behaviour and parasitization efficiency of *Trichogramma* spp. (Hymenoptera: Trichogrammatidae) (Romeis *et al*., 1999). Plant features such as leaf toughness or hairiness, which in some cases defend plants against herbivores, may also affect natural enemies. Increased trichome density on leaves influences the walking speed of parasitoids and lowers their success in locating hosts (Van Driesche and Bellows, 1996).

Chemical cues play a significant role in mediating the behavioral steps leading to oviposition of both herbivores and parasitoids. Host plant selection for oviposition begins with the orientation of insects toward plants using chemical cues released by the host. Insects are attracted and land on plants when attractants or arrestants are present and repellents are absent (Anton and Cortesero 2022). After landing, the insect further evaluates the plant through contact chemoreception, detecting less volatile stimulants or deterrents on the plant surface (Amat *et al*., 2024). The final decision to accept or reject a plant for oviposition results from the combined effects of positive and negative chemical cues, along with the physical characteristics of the plant surface (Robert *et al.*, 1986). Additionally, factors such as the physiological condition of the gravid female, environmental conditions, previous experience, and the presence of other organisms can influence the selection of a suitable oviposition site (Lyu *et al*., 2023).

Despite considerable advancements, the knowledge of the chemical ecology of oviposition is still quite disparate across different taxa and systems with an overwhelming focus on economically significant agricultural pests and model insect species. The connection between the chemical makeup of an oviposition habitat, the sensory processing of those chemicals, the behaviors they generate, the ecological consequences, and other related aspects has yet to be systematically explored. Closing these gaps is crucial for both a more insightful basic understanding of insect behavior and for developing innovative ecological pest control methods.

**Semiochemical as plant defense**

Though plants protect themselves from herbivory through various defensive mechanisms, the immediate and important strategy used to protect the plants from herbivory is the induction of volatile emission. It exhibits complex interactions between different trophic level (Zhao *et al*., 2010; War *et al*, 2011). Semiochemicals from plants or insects act as an important tool, as they can be used for the manipulation of parasitoids, thus improving their impact on pest populations in agroecosystems (Godfray, 1994). The term “semiochemical” was described as the chemical stimuli that convey information between organism (Nordlund and Lewis, 1976). They played a major role in determining the insect life situations *viz.,* feeding, mating and egg laying and also acted as effective agents for selective control of insect pests (Norin, 2007). Thus, the naturally occurring semiochemicals were known to be eco-friendly and were used in Integrated Pest Management (IPM) strategies. The volatility of semiochemicals was high and also acted at long distances and dissipated rapidly. In addition to this advantage, due to the high sensitivity of olfactory system of insect only limited amount of semiochemicals were enough for pest control (Heuskin *et al.*, 2011).

From 900 plant families, about 2000 volatile compounds released due to herbivore damage have been recorded. Plants normally releasing certain volatiles but once attacked by insects the blend of volatiles have been changed. When the plants attacked by insects, large number of volatiles released into the atmosphere help natural enemies as a reliable cue to find their prey/host. A particular insect-plant system has a specific volatile blend. The blend of the volatiles varies depends on the herbivory, plant species, conditions and developmental stages of the herbivore and plant. Due to changes in the transcription of the defense related genes plant can perceive volatile signals. Herbivore-induced plant volatiles (HIPVs) play an important role in plant defence by either attracting the natural enemies of the herbivores or by acting as feeding and/or oviposition deterrent to the pest. The HIPVs include green leafy volatiles (GLVs), terpenes, methyl salicylate, ethylene and other volatile organic compounds (VOCs). Plant emits herbivore induced plant volatiles from their leaves, fruits and flowers into the atmosphere. HIPVs from roots diffused into the soil. HIPVs are involved in plant communication with natural enemies of the insect herbivores, neighbouring plants and different parts of the damaged plants (War *et al.*, 2012). The chemical signal from plant is exploited by both pest and natural enemies for foraging the food. The induced plant volatiles play a major role in alteration of plant interactions with environment. It also acts as oviposition and feeding deterrents. HIPVs perceived by undamaged plants also have altered defense related metabolite levels such as terpeniods, phenolic compounds and secondary inhibitors (War *et al*., 2011).

The current scenario of research on metabolomics, proteomics and genomics studies need information of plant volatiles. In recent decades, chemoecological approaches (tritrophic interaction) have received more attention as an alternative to synthetic pesticides due to its serious public and environmental concerns (Liu *et al.*, 2006). The HIPVs were not just the oozing out of volatiles from injured sites, they were the systemic release of volatiles, that occurred due to the feeding by herbivore that triggered the plant defense response. This resulted in the natural enemies' attraction of the herbivores (Turlings and Erb, 2018). Different groups of natural enemies such as predator and parasitoids can be attracted by HIPVs. Sensory perception of herbivore enemies to the plant volatiles is specific in nature. This specificity is used to find particular hosts and even the specific instars of the host, and whether hosts are parasitized or not. Generalist predators use single components of VOC blend which are generally released after diverse herbivore attack to locate their prey (Guo and Wang, 2019).

Some of the natural enemies were capable of distinguishing the volatile released by the host from the volatiles released from the non- host plants (Alborn *et al.*, 2007). HIPVs acted as the major cue to find the prey or host for the predators and parasitoids (Hare, 2011). The recognition of HIPVs by predators and parasitoids to the volatile mosaic region was due to the chemical breakdown of the compounds and mixing of the volatiles from different sources (Aartsma *et al.*, 2017). Rowen and Kaplan (2016) reported that chewing insects provoked more volatiles compared to phloem feeder/sap feeders. In many plants, VOC is released immediately after herbivore attack. In some plants, induced VOC may be stored in the glands present in the plants, volatile released when these glands damaged by herbivores (Alborn *et al*., 2007). Uninfested part of the infested plants also produces HIPV. It helps in detecting the signal more easily. Apart from this, it helps in communication between natural enemies and infested plants and also different parts of the same plant. HIPVs forewarn the neighbouring undamaged plants about the herbivore attack, a phenomenon called "priming" (Blassioli-Moraes *et al*., 2019). It also mediates communication between plants and microorganism (War *et al*., 2011). These volatiles differ depends on the plant, cultivars and genotype, age and species of the herbivore and time of the insect feeding (Abdella, 2010). The volatile blend released by the plants changed typically both in composition and quantity after the infestation by herbivore (Hagenbucher *et al.*, 2013). The released VOCs got transported by wind that resulted in the combination of volatile blends and simultaneously chemical breakdown happened. This heterogeneous mixing of compounds created a three-dimensional chemical environment namely volatile mosaic (Aartsma *et al.*, 2017).

HIPVs acted as the subset of VOCs released from the host plants (Hare, 2011). The amount and composition of the VOCs differed with the different species of plants and the genotype within the species, the cultivars, and herbivore species. The release of VOCs was also influenced by the environmental conditions in which the plants were grown (Hare, 2011). In addition to this, the number of herbivores that fed on the host plants also determines the release of VOCs. Seven-fold higher differences were noted between the undamaged and herbivore damaged host plants (Loughrin *et al.*, 1995; Alborn *et al.*, 1997; Gouinguene *et al.*, 2001).

The VOCs were composed of fatty acid derivatives, terpenoids and aromatic compounds. The composition of the VOCs varied with wounding, herbivore attack, egg deposition and other mechanical damages (Mondal *et al.*, 2019). Terpenoids and compounds derived from shikimic acid pathway are the main volatiles responsible for plant-insect and plant-plant communication. Maize, soybean, cotton, potato, tomato, wheat and rice has been reported to increase their volatile emission during herbivore damage (Blassioli-Moraes *et al*., 2013). Turlings and Wackers (2004) reviewed about the induction of volatiles for the attraction of parasitoids by herbivore damaged plants and reported that the undamaged plants released small amount of volatiles when compared to herbivore infested plants.

Due to higher volatile emission herbivore could attract their natural enemies towards herbivore damaged plants. By releasing herbivore induced plant volatiles, a plant could minimize more than 90 per cent of the herbivore population. War *et al.* (2011) observed that larval weight of the gypsy moth*, Lymantria dispar* (Linnaeus) reduced by 70 per cent when the caterpillars are observed on HIPV exposed leaves. Linalool and Farnesense present in HIPVs act as repellent for many caterpillars. In addition, HIPV influences host location behaviour of herbivores (Kessler and Baldwin, 2001). Turlings and Wackers (2004) reviewed about the induction of volatiles for the attraction of parasitoids by herbivore damaged plants and reported that the undamaged plants released small amount of volatiles when compared to herbivore infested plants.

Apart from aerial parts, roots also release HIPVs in response to the feeding activity of the below ground pests, Russian wheat aphid, *Diuraphis noxia* (Mordvilko), a subterranean pest triggers the emission of 1,8-cineole, which is repellent and toxic to insect pests. Roots of white cedar *Thuja occidentalis* (Linnaeus) upon black vine weevil*, Otiorhynchus sulcatus* (Fabricius) attack emit volatiles that are attractive to entomopathogenic nematode, *Heterorhabditis megidis*. Maize roots emit (E) -β-caryophyllene when attacked by the western corn root worm, *Diabrotica virgifera* LeConte which attract *H. megidis.* Herbivores use these HIPVs to decide either stay in a particular location and feed or move and search for the food (Abdella, 2010).

**Plant Semiochemical vs Herbivores vs Carnivores**

Natural enemies exploit the detailed information given by the plant volatile mixture to find out their host or prey. Diet breadth influences this behaviour of natural enemies (McCormick *et al*., 2012). While, quantity of HIPV increases carnivores select their host more easily which shows that carnivore attraction and amount of HIPV are in positive correlation. Predators will stay in the location until where they can detect prey related volatiles. Predators can also distinguish information about different prey species from the volatile semiochemicals. Predators successfully seek out their prey only if they can distinguish the chemical cues from the background

odours. HIPVs acts as an indicator for the presence of herbivore on predator attraction (Abdella, 2010). Kessler and Baldwin (2002) observed three compounds, such as Linalool, Cis-3-hexen-1-ol, and Cis-a-bergamotene, that improved egg predation by a generalist predator. Specialist parasitoids can differentiate between prey and non-host infested cotton, tobacco and corn plants by the distinct information from HIPVs. Maize roots emit volatiles that attract the parasitoids when their roots are damaged by corn root worm, *D. virgifera* (Rasmann *et al.,* 2005). Ortiz Carreon *et al.* (2019) observed the egg-larval parasitoid, *Chelonus insularis* (Cresson) was attracted to both healthy and *S. frugiperda* damaged maize plant volatiles, but shown a stronger attraction to damaged maize plant volatiles.

HIPVs that are detected by herbivores and their parasitic wasps can be utilized as biocontrol agents (Guo and Wang, 2019). These HIPVs can help manipulate natural enemies to enhance biological control, either by applying synthetic volatile compounds or through environmental modifications (Bernasconi *et al.,* 2001). Jones *et al*. (2016) identified that sticky traps with HIPVs were more efficient than sticky traps alone. The phenology and population densities of the natural enemies like Diptera and Hymenopteran parasitoids and predators such as Syrphidae and Chrysophidae were efficiently reported in walnut, apple and pear orchards. James (2003) evaluated three synthetic HIPVs such as (Z)-3-hexenyl acetate, methyl salicylate, (E)-4,8-dimethyl-1,3,7-nonatriene in the hop yard along with the sticky card for the attraction of natural enemies. Both (Z)-3-hexenyl acetate and methyl salicylate were attracted natural enemies like coccinellids (*Stethorus punctum picipes* (Casey)), geocorid (*Geocoris pallens* Stal.) and hover flies (syrphids) towards the herbivore. (E)-4,8-dimethyl-1,3,7-nonatriene did not attract any natural enemies. HIPVs have synergistic effect while they were used with pheromone traps. Six volatiles, (E)-4,8-dimethyl-1,3,7-nonatriene (DMNT), (R)-linalool, methyl salicylate, geranylacetone, β-caryophyllene and (3E,7E)-4,8,12-trimethyltrideca-1,3,7,11- tetraene (TMTT) were used in the same ratios in cotton plants with pheromone traps attracted both males and females of cotton boll weevil, *Anthonomus grandis* (Boheman) (Blassioli-Moraes *et al*., 2019).

Tao *et al.* (2002) identified that rice leaves infested with *Spodoptera litura* (Fabricius) produced large amounts of volatiles than healthy and mechanically damaged plants. The volatile blend consists of following volatiles, (CE)-2-hexenal, (E)-2-hexen-1-0l, (2)-3-hexen-1-01 and terpenoids. Rathika and Nalini, (2011) reported that moderately resistant and resistant varieties of leaf folder damaged plants emitted lower number of volatile compounds, whereas highly susceptible varieties released more volatile compounds. Mainly, Docosane was more in highly susceptible genotype TN 1 than the moderately resistant IR 72 and resistant Ptb 33 genotypes. This volatile could be the reason for the attraction of *Cotesia angustibasis* (Gahan) and *T. cnaphalocroci*s (Uchida). Lou *et al*. (2006) observed that the volatiles emanated from the rice brown planthopper damaged plants attracted the egg parasitoid, *A. nilaparvatae. Cotesia angustibasis* (Gahan) and *T. cnaphalocrocis* were more attracted to the leaves damaged by leaf folder than the healthy leaves. Parasitoids frequently visited the leaf folder damaged plants compared to the moderately resistant and resistant plants (Rathika and Nalini, 2011). Coccinellid predators depend mostly on volatiles to find the prey location (Pettersson *et al.,* 1994). Ninkovic and Pettersson (2003) were recorded *Coccinella septempunctata* (Linnaeus) (Coleoptera: Coccinellidae) attracted towards the plant previously attacked by aphid, *Rhopalosiphum padi* (Linnaeus) (Homoptera: Aphididae). Rapusas *et al*. (1996) reported that female mirid predator, *C. lividipennis* were attracted to the rice volatiles and the predator could distinguish prey-infested plants from uninfested plants and mostly preferred plants with eggs compared to plants with nymphs. Yuan *et al.* (2008) reported that out of the 28 volatile compounds terpenoids dominated the volatile composition of rice HIPVs when fed by fall armyworm, *S. frugiperda* caterpillars. These volatiles attracted the females of *Cotesia marginiventris* a parasitoid of Fall armyworm. Becker *et al.* (2015) reviewed about the various effects of abiotic factors on the volatiles released by host plants when fed by herbivore and the interaction among the host plants, herbivore and natural enemies. They quoted that the enhanced HIPVs resulted in increased attraction of parasitoids. The plant volatiles emitted from the rice plants when infested by *C. suppressalis* were in larger amount and a greater number of peaks was detected than the undamaged plants. No significant result was observed between Bt and non Bt damaged rice plants. Genetic engineering did not play any significant role and caused no disruption in the volatile profile of *C. suppressalis* infested rice plants. In general, the activity of parasitoids is lower in the genetically engineered *i.e.,* Bt field than in the non- Bt fields Qingsong *et al.* (2015).

**Elicitors vs Carnivores**

Elicitors are specific bioactive chemicals present at the wound site of the plant that may be derived from the plant, the insect or from the interactions between the organisms (Alborn and Schmelz, 2008). The elicitors present in the host plants and in the regurgitant of herbivore provoked the production of VOCs that were responsible for the attraction of the natural enemies (Schmelz *et al.*, 2006; Alborn *et al.*, 2007; Yoshinaga *et al.*, 2010; Bonaventure *et al.*, 2011; Aljbory and Chen, 2018). In general, the elicitors were produced in two ways. The first one being synthesized in the herbivore and then injected into the plant tissue through the oral secretion/ oviposition fluid of the herbivore. The second one was that the elicitors were synthesized in the host plants as a result of the damage caused by the herbivore (Erb *et al.*, 2012; Aljbory and Chen, 2018). The herbivore-associated elicitors included sulfur-containing fatty acids, peptides from plant proteins, fragments of cell wall (e.g., pectins and oligogalacturonides), esters, fatty acid conjugates, modified forms of lipids, and enzymes. Elicitors play major role in herbivore induced plant defenses (Howe and Jander, 2008). Volatiles were coming under chemical elicitors which stimulate defense responses in plants (Thakur and Sohal, 2013).

Voliticin present in the regurgitant of beet armyworm caterpillar (*Spodoptera exigua* (Hubner)) was found to be responsible for the activation of the release of VOCs when brought into contact with *Zea mays* L. leaves. A threefold increase in the binding of voliticin to the plasma membrane was observed when the plants were treated with methyl salicylate (Truitt *et al.*, 2004). Schmelz *et al.* (2006) isolated inceptin, a disulfide bridged peptide that were proteolytic fragments of chloroplastic ATP synthase from the oral secretions of *Spodoptera frugiperda* (J.E. Smith) (Fall armyworm) that induced the production of volatiles from the cowpea plants.

Yoshinaga *et al.* (2010) conducted fatty acid amino acid conjugates (FACs) screening in 29 lepidopteran species, out of which 19 species were found to contain FACs. They reported that all FACs containing species contained N- linolenyl – L- glutamine in common. These FACs were found in the oral secretion of noctuids and sphingid caterpillars that acted as elicitors of VOCs in corn plants. Caelifirins, a family of sulfooxy fatty acids that were isolated from the saliva of grasshopper acted as elicitors of plant immune response in corn and Arabidopsis which induced the attraction of natural enemies (O'Doherty *et al.*, 2011).

Volatile organic compounds (VOCs) could be used as insect repellent and plant defense elicitors to control pests in the field. VOCs prime plant defense either in the form of mixtures or as an individual compound. The use of HIPVs as elicitors, release primers or signallers of complete and correct blends of emissions that are attracting natural enemies, is striking possibility for manipulating parasitoid and predator populations in pest management (Khan *et al*., 2008). In tomato, application of methyl salicylate as the plant elicitor to the uninfested plant which immediately induced the plant defense thereby reduce the whitefly population and increase the plant yield upto 11% (Conboy *et al*., 2020). Herbivore induced volatile organic compounds elicit a defense response in uninfested plants (Ton *et al*., 2006; Heil and Bueno, 2007; Kim and Felton, 2013). A total of 25 HIPVs were found in the wild lima bean, which elicit a plant defense response (Heil and Bueno, 2007). Plants respond to VOCs by increasing the production of defense related phytohormones like JA, the emission of VOCs, production of proteinase inhibitors and/or phenolic compounds and changing transcription patterns of defence-related genes (Heil and Kost, 2006). Herbivory elicitors can either present in the herbivore or acquired from the plant while feeding. Herbivores can initiate a response which can be differentiated from mechanical damage in their host plants. These kinds of plant defenses have been triggered by a wide range of chemical elicitors that activate certain signaling pathways (Pare *et al*., 2005; Bonaventure *et al*., 2011). Different herbivores, based on the elicitors they release, may alter similar or distinctive form of gene expression. Herbivore induced transcriptional changes may differ among genotypes, plant species and growth conditions (Zhou *et al*., 2011). In plants, herbivore specific responses can be triggered by the elicitors present in the oral secretion (saliva and regurgitant), feaces and/or ovipositional fluids (Eichenseer *et al*., 2010; Acevedo *et al*., 2015). Oral secretion of cabbage butterfly, *Pieris brassicae* (Linnaeus) that triggers the emission of volatiles from cabbage plants when treated. The treated cabbage plants were more attractive to the parasitoid of *P. brassicae*, *Cotesia glomerata* (Linnaeus) (Mattiacci *et al*., 1995). Alborn *et al*. (1997), Turlings *et al*. (1993) and Spiteller (2001) reported the plant defense elicitor volicitin (N-[17-hydroxylinolenoyl]-L-glutamine) from oral secretions of beet armyworm, *S. exigua,* which was applied on the maize caused release of volatiles that attract natural enemies of the *S. exigua*. Halitschke *et al*. (2001) and Diezel *et al*. (2009) isolated elicitors of plant volatiles, N-linolenoyl-Glu from the regurgitant of tobacco hornworm, *Manduca sexta* (Linnaeus) present in the tobacco plants. N-linolenoyl-Glu has been applied on the tobacco plants which activates Jasmonic acid (JA), Salicylic acid (SA), Ethylene (ET), Mitogen-Activated Protein Kinase (MAPK), SA-Induced Protein Kinase (SIPK), Wound Induced Protein Kinase (WIPK). An elicitor, Inceptions were known to trigger the production of SA, JA and volatile compounds which were found in the oral secretion of the fall armyworm, *S. frugiperda* (J.E. Smith) feeding on the cowpea (VanDoorn *et al*., 2010). When the rice plants are infested by rice striped stem borer, *Chilo supressalis* (Walker) induces the accumulation of elicitor compounds Serotonin and Tryptamine (Ishihara *et al*., 2008). In maize plants, (Z)-3-hexanol triggers the emission of volatile blend similar to the caterpillar infestation (Ruther and Kleier, 2005). Caeliferins are non-lepidopteran elicitors isolated from American bird grasshopper, *Schistocera americana* (Drury) (Alborn *et al*., 2007). Feeding of cotton bollworm, *Helicoverpa zea* (Boddie) in cotton leaves results in a significant increase of SA (Ozawa *et al*., 2000). Plant induced response has been activated by contact with two main group of elicitors which is present in the insect oral secretion, that are fatty acid -amino acid conjugates and lytic enzymes. These elicitors initiate various signalling pathways by three main plant hormones JA, SA and ET (Penaflor and Bento, 2013). Exogenous application of these elicitors on undamaged plants enhances resistance by production of toxins and emission of HIPVs (Stout *et al*., 2002). Generally, chewing insects induces JA pathway where, sucking insects induce both SA and JA pathway (Penaflor and Bento, 2013). Both SA and ET signalling have been involved in synergistic crosstalk (Mur *et al*., 2006) or antagonistic crosstalk (Rayapuram and Baldwin, 2007) with JA signalling. In general, Salicylic acid was thought to supress Jasmonic acid related signalling events. But in the lower concentration, it increases signalling events which involves Jasmonic acid. Plants pre-treated with SA showed more than two-fold increase in the insect induced JA. Insect induced volatile organic compounds (VOCs) also significantly increased (Smith *et al*., 2009). Mur *et al.* (2006) reported that the interaction between the SA and JA pathways depends on the concentration of the hormones treated. Salicylate based and jasmonate based elicitors known to have suppressive effect on herbivores. Methyl salicylate and methyl jasmonate are the most intensively used elicitors to manipulate defense pathways in plants. Methyl salicylate modifies the production of phenolic compounds whereas, methyl jasmonate affects the production of terpenoids (Holopainen *et al*., 2009). Ethylene is a key regulator of plant defense which is elicited due to herbivore attack which plays a vital role in

induced resistance. Ethylene enhances the accumulation of defense proteins, volatile organic compounds and secondary metabolites like phenolics, terpenoids and alkaloids (Lu *et al*., 2014). The role of ethylene signaling pathway in the production of plant volatiles when fed by herbivores was highly emphasized by Yujie *et al.* (2006). Plants were treated with ethepron, a compound that broke down at cytoplasmic pH released ethylene. This induced the production of volatiles that were similar to that of those released by *Nilaparvata lugens* infested plants. The attraction of *Anagrus nilaparvatae* to both the ethepron treated plant volatiles and the herbivore fed plants were similar. Ethylene signaling plays a vital role in rice volatiles production by herbivore attack. Cheng *et al.* (2007) reported that the rice plants, after treatment with Methyl jasmonate overexpressed OsTPS3 that produced β-caryophyllene, thus attracting more parasitoids. The volatile terpenes played a prime role in indirect defense of rice plants. Upon herbivory damage plants induce signal transduction pathways, which make changes in the expression of defense related genes and lastly induce biosynthesis pathways (Thaler *et al*., 2012). By triggering phytohormones and kinase networks plants recruit defensive process when they identify elicitors from herbivores (Maffei *et al*., 2012).

Methyl salicylate and methyl jasmonate are the most important elicitors frequently exploited in the fields to attract the natural enemies (Bi *et al*., 2007). Petterson *et al.* (1994) stated slow-release methyl salicylate formulation deter many insects. In the maize field methyl salicylate reduced the number of aphid colonies in the crop. Applying synthetic volicitin to maize induced indirect defense by the production of volatiles which attracted the predators of insects. Apart from volicitin, maize could distinguish several other insect derived elicitors namely Caeliferin and Inceptin (Schmelz *et al*., 2009). Khan *et al*. (2008) examined elicitors treated grape field (Methyl salicylate (MeSA), Methyl jasmonate (MeJA) and Hexanyl acetate (HA)) with untreated grape field. Volatiles released from elicitor treated grape field attract higher number of encyrtid parasitoid (*Anagyrus* spp.). Farouk and Osman (2011) identified in common bean plants that the foliar spray of two defense elicitors *viz*., MeJA and SA reduced the infestation of two spotted spider mite population. SA at 100 mg/l shown the strongest control towards the two spotted spider mites. Von Merey *et al.* (2012) observed that the maize plants shown marginal parasitism on the herbivore *S. frugiperda* when the plants were treated with MeJA and benzo-(1,2,3) -thiadiazole-7-carbothioic acid S-methyl ester (BTH). Hussein *et al.,* (2015) examined effect of some elicitors *viz*., SA, benzothiadiazole (BTH) and L-ascorbic acid (L-AA) on tomato plants against leaf minor *Tuta absoluta* (Meyrick). L-AA and BTH significantly reduced the pest population in tomato plants. JA treatment increased parasitism and predation in the field, ultimately reduced the herbivory on crops. Higher parasitism in JA- treated plots resulted from extended larval development period because the herbivores were affected by the plant induced direct defenses or from variance in the attractiveness of JA-treated plants to natural enemies (Penaflor and Bento, 2013).

Salicylic acid (SA) and ethylene (ET) trigger plant defense against leaf folder in rice (War *et al*., 2018). Xiao *et al*. (2012) created two rice lines that impair the emission of (E)-β-caryophyllene and S-linalool. (E)-β-caryophyllene attracted parasitoids and also plant hoppers. Induced S-linalool attracted parasitoids, predators and chewing herbivores but deterred brown planthopper, *N. lugens.* Application of JA in the rice plant induce the production of phytoalexins, proteinase inhibitors, salt-induced proteins and pathogenesis-related genes and hence increase the volatile emission that enhance the attraction of parasitoid *A. nilaparvatae* and increase the egg parasitism of *N. lugens* (Lou *et al*. 2005). Huacai *et al*. (2002) studied that the volatiles released by the infestation of striped stem borer, *Chilo suppressalis* (Walker) attract *Cotesia chilonis* (Matsumura), a larval parasitoid of striped stem borer. Methyl salicylate (MeSA) and methyl benzoate (MeBA) were identified from fall armyworm damaged rice plants, which attract the female parasitic wasp, *Cotesia marginiventris* (Cresson) (Zhao *et al*., 2010). Methyl jasmonate (MeJA) application on rice field altered the survival and biology of leaf folder (Senthil-Nathan *et al*, 2009). Exogenous treatment of ethephon can trigger the production of volatiles and trypsin proteinase inhibitors (TrypPIs) (Lu *et al*., 2014). Hamm *et al*., (2010) evaluated the effect of JA applied rice plants and *S. frugiperda* infested rice plant against water weevil, *Lissorhoptrus oryzophilus* (Kuschel). Prior feeding by herbivore and JA treated plants resulted in increased resistance towards water weevil. Qi *et al*., (2016) reported JA, SA, gibberelins (GAs) and ET regulate the herbivore resistance in rice. Rice plant can recognize elicitor cues from the oral secretion of several herbivores such as rice skipper, *Parnara guttata* (Bremer et Grey), loreyi leafworm, *Mythimna loreyi* (Duponchel) and lawn armyworm *S. mauritia* (Boisduval). The SA pathway has been concerned in the defense of monocots against insects. In rice plants, induced SA levels, leading to increased ROS (Reactive Oxygen Species) and elevated resistance in plants (Stella da Freitas *et al*., 2019; Qi *et al*., 2018).

## CONCLUSION

Chemical ecology in pest management has been extensively researched over the past two decades. This approach is significant because it can be easily integrated with biological control methods and is environmentally friendly. Future research should focus on developing transgenic plants that release semiochemicals, which can be integrated with allelochemicals for effective pest management.

## DECLARATIONS


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There are no relevant financial or non-financial competing interests to report.

**Ethical approval**
Doesnot arise

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