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Volatile Mediated Plant-Insect Interactions: A Review

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Abstract: Semiochemicals are organic compounds (volatile and non-volatile) that allow organisms to communicate with one another. Plant volatile organic compounds (VOCs) are one such kind of semiochemical which helps insects to localize their vital resources and a potential mate. This review highlights the ecological importance of such VOCs in the widely diverse interactions between plants and insects. Additionally, this review provides an overview of the function that plant and insect associated microbial communities play in shaping such volatile mediated interactions. Understanding volatile semiochemical-mediated interactions between plants and insects, as well as the role of accompanying microorganisms in structuring such interactions, will be crucial for designing ecologically sustainable insect pest management solutions.

Keywords: Semiochemicals, Volatile organic compounds, Plants, Insects, Microbial communities, Endosymbionts

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Introduction

Herbivorous insects require plants as their food sources and as places of shelter. Plants also provide spaces for mating and egg-laying of insects. Herbivorous insects choose their host plants depending on a number of sensory cues that includes olfactory, gustatory, visual and tactile stimuli, as well as humidity and light intensity (Bernays and Chapman, 1994; Heard, 1999). Other behavioral elements that influence the insect herbivore host selection include the effects of experience-learning, memory and forgetting (Heard, 1999).

Nearly 2/3rd of all known insects are Phytophagous and they inflict major agricultural losses globally, both directly (via feeding) and indirectly (via spreading plant diseases) (Yactayo-Chang *et al*., 2020). Plants have to be capable of defending themselves against insect herbivores in order to survive and reproduce in the same area. Therefore, in response to insect attack, plants have adapted a number of strategies to deter or kill attackers. Plant defenses against herbivorous insects are often categorised as direct or indirect (Gols, 2014). Direct defenses are mediated by all plant aspects that determine herbivore biology, such as mechanical protection on the plant's surface (for example, hairs, trichomes, spines, thorns, and thicker leaves) or the generation of toxic chemicals including alkaloids, terpenoids, phenols, quinones and anthocyanins which either destroy or retard herbivore growth (Hanley *et al*., 2007; War *et al*., 2012). Whereas, indirect plant defense encompasses all features that although not having a major direct impact on the offensive herbivores, but can encourage natural predators of the insect herbivores, thereby minimizing crop looses (Aljbory and Chen, 2018).

Mutualistic, antagonistic and commensalistic interactions between plants and insects have long been recognized (Calatayud *et al*., 2018). Mutualistic interactions like plant-pollinator interactions are a good example. Plant-insect interactions that are antagonistic include phytophagy by insect pests such as whiteflies, plant hoppers and aphids. Monarch butterflies and milkweed, on the other hand are an example of commensalistic plant-insect interactions, with monarch butterfly caterpillars (*Danaus plexippus, Danaus chrysippus*) specialised to feed on milkweeds (*Asclepias* spp., Apocynaceae) and concentrate plant cardenolides into their hemocoel to store as a defensive measure against predators (Reichstein *et al.,* 1968; Petschenka *et al.,* 2018; Stenoien *et al*., 2019).

Concurrently, insects and plants have developed a variety of relationships with their microbial partners (endophytes and endosymbionts), which may influence the consequences of plant-insect interactions (Sugio *et al.,* 2015). A growing body of literature suggests that microbial diversity associated with plants and insect herbivores may modulate the plant defense mechanisms against the insects for the advantage of either insects or plants (Sugio *et al*., 2015). Similarly, microbes may alter insect biology, including behavior and metabolism, and have a profound influence on plant-insect relationships (Sugio *et al*., 2015). Bacterial symbionts, for example, play a vital role in the dietary ecology of host insects by assisting in food digestion or by providing nutrients that insects can not get enough from a phloem rich diet (Feldhaar, 2011; Su *et al.,* 2013). Endosymbionts also assist their hosts in resolving plant defense mechanisms by detoxifying plant secondary metabolites (Sharma *et al.,* 2021) or by transmitting plant viruses (Shi *et al*., 2021a). They may also have a profound influence on the chemical cues emitted from plants (as a result of herbivory) that parasitoids and predators use to detect their prey (Monticelli *et al*., 2019). Furthermore, some endosymbionts such as *Wolbachia pipientis*, may influence host reproductive activity by triggering parthenogenesis, cytoplasmic incompatibility, and feminization of genetic males (Koivisto and Braig, 2003). Plant associated microbes (endophytes), on the other hand, may directly support host plants via enhancing nutrient absorption, regulating growth and stress-associated plant hormones, as well as indirectly via improving plant health via combating pest insects and pathogenic microbes with hydraulic enzymes, antibiotics, nutrient deficiency and inducing plant defense responses (Afzal *et al*., 2019).

Thus, plants and insects have a multilayered relationship that has ecological and evolutionary consequences (Biere and Tack, 2013; Sharma *et al*., 2021). Understanding the complex relationship between plants, pest insects and their associated microorganisms will aid in the development of novel crop protection strategies such as designing crop plants for observing endogenous insect pest resistance, or treating crops with semiochemicals, endophytes etc. to make them less attractive. All these measures will benefit agriculture and forestry directly. Based on this, we have reviewed and synthesized the existing literature on the multilayered relationship between plant-insect interactions with a particular emphasis on plant volatile organic compounds (VOCs).

Emission of plant volatiles:

Wide ranges of secondary metabolites are produced by plants as defensive barriers against insect herbivores. Many herbivorous insects are well-adjusted to these phytochemicals and utilize such chemicals as basic host-seeking signals, defensive components, and even as sex attractant pheromones or their precursors by specifically detecting, integrating and sorting these phytochemicals (Nishida, 2014).

Plants produce and emit a wide spectrum of volatile organic compounds (VOCs) as secondary metabolites with varying chemical configurations. Biosynthesis of these organic compounds is primarily subjective to carbon, nitrogen and sulphur availability, and also the energy released during metabolism. Therefore, the availability of these building blocks in plants has a significant impact on the composition of any secondary metabolite, illustrating the close relationship between primary and secondary metabolism (Dudareva *et al*., 2013). According to Conchou *et al*. (2019), biosynthesis of a wide range of different VOCs branches off from four primary metabolic pathways: the mevalonic acid and methylerythritol phosphate pathways for terpenoid, the lipoxygenase pathway for fatty acid derivatives, the shikimic acid pathway for benzenoids and phenylpropanoids and the amino acid derivatives pathway (Baldwin, 2010) that generate numerous alkenes and oxygenated compounds of low molecular weight like ethylene, acetaldehyde, acetone, or methanol which may play an important role in insect-plant interactions (Bertrand *et al.,* 2021).

VOCs are naturally emitted by various plant parts such as roots, flowers, and leaves. The quantity of volatile emission often increases when plants are invaded by antagonists like insect pests or pathogens (Kigathi *et al*., 2019). However, the emission of VOCs from plants are species-specific and in some cases they are also adaptable to evolving environments, changing in response to biotic factors like herbivory and pathogen attack, and also abiotic variables such as temperature, soil nutrients and ultraviolet-B radiations (Effah *et al*., 2020).

Plant volatiles as host finding cues:

Insects have a well-developed olfactory system that helps them to sense and recognize plant volatiles in order to choose their nearest host plant and mate. By selectively detecting plant odours in the air (with the help of their olfactory system), insect herbivores are also capable of evading their predators, parasitoids and non-host plants (Carraher *et al*., 2015). Much research has been done on the olfactory system of drosophilas, and recently moths (de Fouchier *et al*., 2017), bark beetles and mosquitoes have been studied as well (Andersson *et al.,* 2015).

In case of insects, the sensilla of the maxillary palps and antennae are the primary olfactory organs, through which the insect can detect the plant volatiles or other semiochemicals to alter its host searching and oviposition activities (Liu *et al*., 2021). Each sensillum encompasses a set of olfactory sensory neurons, the dendrites of which extend into the sensillar lumen. The dendritic membrane detects odorant signals, converts them to electric signals and finally transmits those signals to the brain region (Haupt *et al*., 2009).

Interestingly, herbivorous insects rely mostly on unique proportion of ubiquitous plant volatile compounds to recognize and discriminate plant species (Bruce *et al*., 2005). As plant volatile content varies temporally and spatially due to biotic and abiotic pressures, therefore herbivores need behavioural plasticity to recognize these differences and distinguish host from non-host plants, as well as host phenology and physiology (Gouinguené and Turlings, 2002; Magalhães *et al*., 2018).

Behavioral plasticity and learning activity of herbivorous insects:

Experience, learning, forgetting, and memory are all important behavioural aspects for phytophagus insects when it comes to choosing a host. Learning is the process of changing one's behaviour as a result of earlier experience and it can happen quite fast (Heard, 1999). By drawing on previous experiences, insects can adjust to their local variation in resources (Anderson and Anton, 2014). A behavioral phenotypic plasticity driven by experience to plant volatiles at both the larval and adult stages could aid in host location (Anderson and Anton, 2014). Polyphagous insects (both herbivores and pollinators) respond to floral or vegetative plant odours primarily based on learning or previous experiences (Conchou *et al*., 2019). Pollinating insects (for example, honeybees) usually learn to correlate floral volatiles with reward status; therefore, they utilize floral volatile blends to locate their host plants (Knauer and Schiestl, 2015; Rering *et al*., 2020). Nectar guides and their modifications provide dependable signals to insect pollinators, enhancing reproductive success in both sexes (Zhang *et al*., 2017). Bees like *Apis mellifera* and *Bombus* spp. can learn to associate floral odours, colours, patterns, shapes, textures and locations with nectar rewards, and they can also learn to extract pollen (Jones and Agrawal, 2017). Similarly, social wasps' ability to establish associative learning of food odour may explain why they are such successful invaders of new environments, particularly those with abundant honeydew sources (El-Sayed *et al*., 2018; Elmquist and Landolt, 2018).

Learning also assists polyphagous insects in avoiding hazardous or nutritionally deficient food plants. For example, grasshoppers *Schistocerca americana* have learned to avoid nutritionally deficient foods like spinach, implying that food aversion learning is the mechanism causing the fall in food acceptability (Lee *et al*., 1988; Jones and Agrawal, 2017).

HIPV as cues to locate host plants by herbivore:

Herbivore-induced plant volatiles (HIPVs) are a class of volatile organic chemicals (VOCs) that are synthesized and released as a result of insect herbivory (Holopainen and Blande, 2013). Although several studies have shown that HIPVs are involved in direct plant defense by serving as insect pest feeding and oviposition deterrents, as well as indirectly by attracting herbivore natural enemies (War *et al*., 2011; Tamiru and Khan, 2017), however, HIPVs can also promote interactions between plants and their monophagous insect herbivores in order for the insects to forage for and discover appropriate plants for egg depositing (Silva and Furlong, 2012). Moreover, current research suggests that polyphagous herbivores can also employ HIPV in order to recognize their host plants (Sarkar *et al*., 2016; Karmakar *et al*., 2018; Silva and Clarke, 2020).

Several studies have recorded the role of HIPV in the aboveground mediated attraction of conspecifics (El-Sayed *et al*., 2016; Shivaramu *et al*., 2017). Interestingly, some recent studies have also demonstrated that volatiles produced by root feeding larvae/caterpillars can also attract aboveground conspecific adults. Sun *et al*. (2019) demonstrated that leaf volatiles produced by belowground *Bikasha collaris* larvae attracted conspecific aboveground adults while repelling heterospecific aboveground weevils (specialists), increasing folivory and thus benefiting belowground larvae via host plant improvement. Although these studies have recorded the role of HIPVs in the attraction of conspecifics, some other studies suggests that herbivorous insect caterpillars can suppress the emission of HIPVs from plants and this suppression is mainly due to the regurgitant's lower elicitation behaviour and variations in leaf damage patterns (De Lange *et al*., 2020). However, the attractiveness of a plant to a common insect parasite (parasitoid) was shown to be unaffected by HIPV inhibition, suggesting that parasitoid wasps can circumvent an insect's plant defense manipulation (De Lange *et al*., 2020). Recent research, on the other hand suggests that HIPV may undermine tritrophic relationships by decreasing caterpillar suitability and attractiveness to parasitoids. For example, indole induced by *Spodoptera littoralis* larvae boosts parasitoid wasp recruitment to maize plants, but it diminishes the wasp recruitment when the larvae themselves exist on the maize plants (Ye *et al.,* 2018a).

HIPV also performs an essential part in the behavioural connections between herbivorous insects of various guilds. A recent study, for example, found that the colorado potato beetle *Leptinotarsa decemlineata* prefers undamaged plants over those infested with the green peach aphid *Myzus persicae*. *Myzus persicae*, on the other hand, prefers plants infested with *Leptinotarsa decemlineata*. As a result, herbivore damage from one feeding guild can influence the host plant choice of an herbivore from a different feeding guild (Davidson- Lowe and Ali, 2021).

Role of salivary effectors in overcoming host defenses:

Herbivores have an abundance of salivary effectors that help them overcome host defenses. According to a recent study, NlEG1, a salivary endo-β-1, 4-glucanase of brown planthopper, is an effector that allows brown planthoppers to feed on rice by degrading plant cell wall celluloses while also avoiding jasmonic acid (JA), and jasmonoyl-isoleucine (JA-Ile) mediated defense reactions in rice (Ji *et al*., 2017). Another recent study reported that NISEF1 is most abundantly expressed in brown planthopper salivary glands and acts as an effector that can bind to Ca^{2+} and cause a decrease in cytosolic Ca^{2+} content in rice; which leads to decreased hydrogen peroxide (H_2O_2) levels and possible phloem plugging, thereby suppressing defensive mechanisms in rice plants (Ye *et al*., 2017).

Similarly, the salivary effector Bt56, which triggers the salicylic acid (SA) signaling pathway, is used by whiteflies to modulate plant defensive responses (Xu *et al*., 2019). BtFer1, a salivary ferritin protein released into tomato plants by whiteflies, reduces hydrogen peroxide, callose accumulation, and proteinase inhibitor (PI) development while suppressing JA-mediated defense responses and increasing whitefly efficiency (Su *et al*., 2019).

Herbivore salivary effectors can also specifically target JA signalling components in order to circumvent plant defenses. The whitefly salivary effector Bsp9, for example, associates with the JA-regulated transcription factor WRKY33 (an element of plant resistance), disrupts the association between WRKY33 and MPK6, and so reduces WRKY33-induced plant defensive responses against whitefly (Wang *et al*., 2019). Similarly, the cotton bollworm effector protein HARP1 has the ability to penetrate into host plant cells and interact with a variety of JASMONATE-ZIM-domain (JAZ) repressors. The connection between HARP1 and JAZ stabilises JAZ breakdown and prevents the transmission of JA signals (Chen *et al*., 2019).

Attraction preference of herbivore to VOCs:

It has been demonstrated that a herbivore's attraction preferences to VOCs may change over time (Binyameen *et al*., 2021). These preferences are often gendered. A recent study discovered that female cotton leafworm *Spodoptera littoralis* lost their affinity to floral odours after mating and instead switched to the green-leaf odour of the larval host cotton, *Gossypium hirsutum* (Saveer *et al*., 2012). Male *Spodoptera littoralis*, on the other hand, were greatly attracted to volatiles in lilac flowers regardless of mating status (Kromann *et al*., 2015).

So far, the gender-specific stimulation of VOCs produced by host plant and its implications for insect activity are poorly understood. A recent study found that males of *Nesidiocoris tenuis* were attracted to volatiles released from both eggplant and sesame plants stimulated by either females or males, whereas females were attracted to volatiles released from both eggplant and sesame plants stimulated only by females. This resulted in females concentrating on the same plant and synchronising with males drawn to the same plant too, suggesting that gender specific responses may influence male and female mating (Rim *et al*., 2018). Another study showed that VOC emission generated by conspecific leaf beetles *Phratora latticollis* of either gender could be important for both male and female *Phratora latticollis* to evaluate the appropriateness of the host for mating, but VOC emissions generated by both genders at the same time could warn the potential of overcrowding (Li *et al*., 2020).

Mate location by insect herbivores and the role of plant volatiles:

In insects, species-specific sex pheromones are often recognized as major signals leading to effective mating. However, accumulating evidence suggests that plant VOCs play an extra and crucial function in the mate finding process by synergizing the attractiveness of insects to their respective sex pheromones (Yang *et al*., 2004; Yu *et al*., 2015; Collignon *et al*., 2016; Barros-Parada *et al.,* 2018; Fang *et al*., 2018).

Few studies have reported that volatiles from host plants not only increase male attraction to sex pheromones, but they may also have an antagonistic effect in other organisms (Yang *et al*., 2004; Borrero-Echeverry *et al.,* 2018). Plant volatiles may also act as an agonist of a pheromone, attracting male insect species in the absence of pheromone. For instance, heptanal, a plant volatile can stimulate the pheromone-specific route in male *Agrotis ipsilon* and act as a partial agonist of a moth sex pheromone (Rouyar *et al*., 2015). Another recent study found that in the case of *Agrotis ipsilon*, heptanal exhibits partial pheromone agonism for Z7-dodecenyl acetate-Olfactory receptor neuron (Z7-ORNs) at high doses, but it is not an agonist for Z9- tetradecenyl acetate (Z9-ORNs)(even 0.1 per cent heptanal is a slight inhibitor)(Hoffmann *et al*., 2020).

Endosymbiont mediated plant-insect interaction:

Any microorganisms that create a symbiotic association with another organism, either obligately or facultatively are known as endosymbionts. Insects act as a haven for a varied range of microbial populations (for example- bacteria), influencing their interactions with other trophic levels and their surroundings (Acevedo *et al*., 2017). Some of the major services offered by insect-associated microorganisms include- food provisioning, modulating plant defense responses, plant metabolite detoxification, modulation of host plant volatile profile by virus transmission, regulation of insect-immune responses and host protection against predators and parasitoids.

Insect endosymbiont modulate plant defense responses:

Mechanical injury due to insect feeding, as well as constituents of oral secretions and saliva of insect herbivores, have been reported to alter jasmonic acid-mediated defensive mechanisms in plants (Acevedo *et al*., 2017). For example, bacteria from the fall armyworm (*Spodoptera frugiperda*) caterpillar's oral secretions altered JA-mediated defensive mechanisms of plants, influencing the insect's success on a specific host plant. Fall armyworm saliva has recently been discovered to be a complex fluid containing phytohormones and other compounds including enzymatic plant elicitors (GOX and PLC), which are also responsible for modulating plant defensive responses (Acevedo *et al*., 2019). Herbivores may also use symbiotic bacteria to bypass host defenses. Flagellin released by the colorado potato beetle's salivary endosymbiont *Pseudomonas decemlineata* inhibits JA-regulated defensive mechanisms against the host insects (Chung *et al*., 2013). Likewise, symbiotic bacteria such as Enterobacter BC-8 released by the Colorado potato beetle (Sorokan *et al*., 2020) and rickettsia secreted by whiteflies (Shi *et al*., 2021a) triggered SA-regulated defense while blocking the effective JA- mediated signaling pathway.

Endosymbionts may also influence the interaction between plants and insect herbivores via indirectly influencing the transcripts of herbivores salivary gland genes instead of being released into the plant directly. A recent study found that *Serratia symbiotica* upregulated histidine rich Ca^{2+} binding protein-like gene (ApHRC) in the salivary glands of pea aphids, enabling aphid colonization and evading plant defensive responses via decreasing Ca^{2+} elevation and reactive oxygen species (ROS) generation (Wang *et al*., 2020).

Role of endosymbionts in Plant Metabolite Detoxification:

To cope with plant secondary metabolites or toxins, herbivorous insects have evolved a variety of defensive mechanisms. Toxins are usually sequestered by different enzymes carried by the insect herbivores or their symbiotic microbial communities through a method known as "detoxifying symbiosis"(van den Bosch and Welte, 2017). *Candidatus Ishikawaella capsulata*, for example, is a stinkbug (*Megacopta punctatissima*) symbiont that contains a plasmid containing an oxalate decarboxylase gene that aids in the detoxification of plant oxalate (Nikoh *et al*., 2011). Similarly, endosymbiotic bacteria like *Serratia, Providencia, Pectobacterium* and *Acinetobacter* present in cabbage root fly maggots, detoxify isothiocyanates from cruciferous plants (Welte *et al*., 2016). *Pectobacterium* produces the enzyme SaxA, which degrades 2-phenylethyl isothiocyanate and exploits it as a source of nitrogen (Welte *et al*., 2016).

Caffeine, a defensive alkaloid contained in coffee, safeguards the plant against insect herbivores. A coffee berry borer, *Hypothenemus hampei*, defeats the toxin by detoxifying it with the help of a gut bacterium, *Pesudomonas fulva* (Ceja-Navarro *et al*., 2015). Similarly, two *Acinetobacter* species, *Acinetobacter calcoaceticus* and *Acinetobacter oleivorans* are involved in the breakdown of tea saponin in camellia plants (Zhang *et al*., 2020). Other examples of plant metabolite detoxification mediated by endosymbionts include: detoxification of oleuriopein by enterobacteriaceae of olive fruit fly larvae *Bactrocera oleae* (Ben-Yosef *et al*., 2015), detoxification of diterpene resin acids by gut bacterial community of pine weevil (Berasategui *et al*., 2017), pipine degradation by bacterial symbionts of *Dendroctonus valens* (Xu *et al*., 2016), detoxification of isothiocyanates by microbial symbionts of the cabbage stem flea beetle *Psylliodes chrysocephala*, specifically Pantoea (Shukla and Beran, 2020).

Modulation of the volatile profile of host plant by endosymbiont mediated viruses:

Plant viruses rely heavily on vectors to transmit and propagate. Recently it has been demonstrated that endosymbiont *Buchnera aphicola* of green peach aphid is associated with the transmission of cucumber mosaic virus (CMV) via modifying the host plant's volatile profile (Shi *et al*., 2021b).

Role of the endosymbiont in protecting their host (herbivore) from parasitoids:

Endosymbionts have the ability to influence the chemical cues generated by herbivore-fed plants, which wasps utilize to locate their hosts (Monticelli *et al*., 2019). The significance of facultative endosymbionts in protecting their hosts from wasp parasitoids has been widely explored in the common aphid endosymbiont *Hemiltonella defensa* (Zepeda-Paulo and Lavandero, 2021). *Hemiltonella defensa*, for example, protects aphids from parasitoid wasps, minimizes aphid mortality due to parasitoid attack, and changes the community composition of parasitoid wasps that feed on aphids (Rothacher *et al*., 2016). Parasitoid wasp *Aphidius ervi* has been shown to be less attracted to plants infested with aphids harboring the endosymbiont *Hemiltonella defensa* (Frago *et al*., 2017). However, the field and experimental findings of a recent study do not show any relationship between the aphid clone-endosymbiont associations and a proxy of total parasitism in the grain aphid *Sitobion avenae* (Zepeda-paulo *et al*., 2017).

Endosymbionts can influence parasitoid community composition and structure (Monticelli *et al*., 2019). Resistance to parasitoids mediated by symbionts may have an impact on the host-parasitoid food web structure, either by removing some trophic linkages entirely or, more likely, by weakening the strength of others (McLean *et al*., 2016).

Immune regulation of herbivore host by viral endosymbionts of parasitoid:

Although much research has been done on the impact of herbivorous insect symbionts on plant responses to herbivory (Su *et al*., 2015; Wang *et al.,* 2016; Schausberger, 2018), there has also been some recent research on carnivorous insect symbionts (Cusumano *et al*., 2018; Cusumano and Volkoff, 2021).

Viruses have established close relationships with parasitoids wasps (Beckage and Drezen, 2011), which emerge as parasites inside other insect hosts (Coffman and Burke, 2020), thereby disrupting host immune responses and enabling the parasitoid's offspring to survive (Zhu *et al*., 2018, Tang *et al*., 2021). Polydnaviruses (PDVs), which suppress the immunity of the parasitoid's host (typically a caterpillar), are the most well-known symbiont-mediated protection in parasitoid wasps (Dicke *et al*., 2020). Some PDV gene products suppress host immune responses, while others have an effect on host growth, metabolism and on the endocrine system (Ye *et al.,* 2018b). Both bracoviruses and ichnoviruses (two PDV genera) can influence herbivore growth and development. Polydnavirus of the *Microplitis croceipes* (McBv), for example, may inhibit the salivary elicitor glucose oxidase of the *Helicoverpa zea* caterpillar, undermining plant defense responses and enabling the caterpillar to grow, enhancing host suitability for the parasitoid (Tan *et al.,* 2018). Similarly, PDV can boost wasp fitness by decreasing chemical defenses, allowing *Pieris brassicae* caterpillars parasitized by *Cotesia glomerata* to consume more nutrient-dense plant resources, potentially leading to greater qualitative/quantitative resources for the larval parasitoid (Cusumano *et al*., 2018). PDV ichnovirus (IVs) genera, on the other hand, can impair larval development and growth in infected or parasitized larvae by altering expression of genes within the parasitized host, such as the down regulation of pattern recognition receptors (PRRs) (Darboux *et al*., 2019).

Other examples of viral symbionts mediated immune regulation of herbivore hosts, in addition to PDVs, include ascovirus, entomopoxvirus and reoviruses. Ascoviruses primarily infect noctuid larvae and are spread in the field by parasitoids. A solitary endoparasitoid wasp, *Microplitis similis* are capable of transmitting *Heliothis virescens ascovirus* 3h (HvAV-3h) among *Spodoptera exigua* larvae (Li *et al*., 2016). DpAV-4 is a symbiotic ascovirus of *Diadromus pulchellus* that induces immune-suppression in its lepidopteran host, *Acrolepiopsis assectella* (Renault *et al.,* 2002; Dicke *et al.,* 2020). DpAV-4 is a free virus capable of altering the defense mechanism of the parasitized host in order to promote the growth of the parasitoid wasp, *Diadromus pulchellus* (Renault *et al*., 2002). Similarly, *Diadromus pulchillus* reovirus 2 (DpRV-2), like the ascovirus DpAV-4 is capable of inhibiting the defense mechanism of *Acrolepiopsis assectella* pupae, thereby contributing to the parasitic success of *Diadromus pulchellus* wasps (Renault *et al*., 2003).

Another mutualistic virus found in the female parasitoid wasp *Diachasmimorpha longicaudata* is *Diachasmimorpha longicaudata* entomopoxvirus (D*l*EPV). D*l*EPV infects host (guava fruit fly, *Anastrepha suspensa* larvae) haemocytes, causing morphological changes that result in an encapsulation response (Lawrence, 2005; Jagdale and Joshi, 2019).

Endophyte mediated plant defense against herbivores:

Endophytes are microbial symbionts (bacteria, fungi) that live within plants for most of their lives without causing harm to the host plant (Kandel *et al*., 2017). Endophyte colonization is critical for providing numerous advantages to host plants. They can directly help their host plants via enhancing growth, nutrient absorption, and modifying plant volatile emission profiles, as well as by producing plant metabolites. In addition, they provide indirect benefit via drawing predators and parasitoids of insect herbivores.

Role of endophytes in plant metabolite production:

Endophytes are well known for their contribution to the generation of induced metabolites (Eberl *et al*., 2019). Following an insect attack, plants supplemented with root-associated microorganisms enhance the initiation of both primary and secondary metabolites (Kousar *et al*., 2020). Endophyte-mediated defense is primarily due to competition for survival with external microbial pathogens, which contributes substantially to secondary metabolite production (Prado *et al*., 2012; Kemp *et al*., 2020; Halecker *et al*., 2020). However, induction of endophyte-mediated plant defense is herbivore specific. The insect toxic alkaloid peramine, for example, has been shown to be induced in endophyte-infected grass by locust herbivores but not by aphid herbivores (Fuchs *et al*., 2017).

Endophytes have also been implicated in the development of plant resistance, with one study suggesting that ethylene overproduction triggered by an endophytic fungal isolate (*Fusarium solani* strain K) inoculation may be the key to tomato resistance to the zoophytophagous predator *Nesidiocoris tenuis* (Garantonakis *et al.,* 2018).

Endophyte mediated attraction of predators and parasitoids:

Plants emit specific volatile compounds when assaulted by insect herbivores, which can serve as a warning signal to predators. Recent studies indicated that interaction between endophytes and plants can alter plant volatiles and can attract predators of insect herbivores (Pappas *et al*., 2018; Fuches and Krauss, 2019; Bell *et al*., 2020). Similarly, the interaction between endophytes and plants has also the potential to attract parasitoid wasps (Pangesti *et al*., 2015). However, the effect of rhizobacteria on predator recruitment is species specific. For instance, a recent study showed that application of gram positive rhizobacteria *Bacillus* spp. suppressed the population of cabbage aphid, *Brevicoryne brassicae* by increasing the rate of parasitism by braconid endoparasitoid *Diaeretiella rapae*, but did not increase the population of other predators, such as ladybird beetle and syrphid fly (Gadhave *et al*., 2016; Friman *et al*., 2021).

Positive impact of endophytes on insect herbivore foraging and oviposition:

While the impacts of beneficial microorganisms on plant growth and development have been extensively studied, few researches have looked at how these effects affect insect herbivore foraging and oviposition. For instance, a recent study found that inoculating white cabbage roots with the entomopathogenic fungus, *Metarhizium brunneum*, can enhance the attraction and egg laying activities of female cabbage root flies *Delia radicum* (Cotes *et al*., 2020).

Conclusion

The present study reveals the role of volatile organic compounds of plants in aiding insects in selecting their vital resources and how diverse behavioral aspects influence such resource-finding behaviors. A brief overview of the roles played by endophytes and endosymbionts in mediating plant-insect herbivore-natural enemy interactions has also been provided. Since plants, herbivores, pollinators and natural enemies are all dependent on plant volatile compounds and scanty literature exists on the mechanisms underlying molecular interactions between plants, insects and microbes, the understanding of molecular relationships between them can become an intriguing environmental tool for mitigating various stresses in plants if properly explored. This knowledge may contribute to the improvement of pest management approaches and crop cultivation practices.

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