

UNDERSTANDING THE SEARCHING BEHAVIOUR OF PREDATOR AND PARASITOID INSECTS: A REVIEW

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ABSTRACT

The aim of this review is to understand whether the searching behaviour of natural enemies (parasitoids and predators) is affected by complex odour mixtures and if there are differences between specialist and generalist natural enemies. To accomplish this objective, a literature review of several research papers related to the topic was done. Natural enemies of herbivores mainly use herbivore induced plant volatiles (HIPVs) to find their prey or host. However, the chemical information conveyed through HIPVs toward natural enemies might be unreliable or sometimes undetectable for them (odour masking), thereby influencing their searching behaviour. Many factors influence the reliability and detectability of HIPVs such as: plant diversity, intensity of the herbivore attack, if one or more herbivore species attack the plant at the same time or sequentially, and environmental conditions like light intensity, fertilization levels, soil moisture, and high concentrations of ozone, hydroxyl, and nitrate radicals. Nevertheless, in order to overcome reliability and detectability problems of HIPVs, natural enemies have the ability to learn by association and use these HIPVs to find their prey or host. Further field experiments supported by laboratory assessments should be carried out to understand how the searching behaviour of natural enemies is affected in a multitrophic level context, where known biodiversity (above and below ground) and environmental conditions have the possibility to interact.

Keywords: Multitrophic level, plant diversity, herbivore attack, environment, plant volatiles

1. INTRODUCTION

Natural enemies (parasitoids and predators) make their foraging decisions based on chemical information produced by organisms interacting in a multitrophic context: the herbivore victim (second trophic level) and its plant food (first trophic level) (Rodriguez-Saona et al., 2020). The importance of this tritrophic interaction is reflected in the searching behaviour of herbivore's natural enemies (Vet and Dicke, 1992; Rashedi et al., 2019; Shao et al., 2021). According to Vet and Dicke (1992) a chemical that conveys information in an interaction between two individuals, evoking in the receiver a behavioural or physiological response, is called infochemical.

Natural enemies face detectability and reliability problems when sensing infochemicals produced by plants or herbivores. According to Vet and Dicke (1992), infochemicals produced by plants are more important than infochemicals generated by herbivores when regarding to detectability. Plants possess relatively more biomass than insects; therefore, they produce higher amounts of chemical information, which can be detected more easily by natural enemies at long distances. However, as explained below, kairomones can also be used by natural enemies to detect herbivores' presence at long distances (Ayelo et al., 2021). On the other hand, the chemical information generated by herbivores is more reliable than the chemical information provided by plants. The low detectability of the herbivore's chemical information is a consequence of its relatively small size and a continuous selection for low odour emission to avoid parasitisation and predation (Vet and Dicke, 1992 and Beyaert and Hilker 2014).

Natural enemies can exploit the pheromones used in herbivores' intraspecific communication as kairomones to find herbivore locations at long distances. Other herbivore products, different than pheromones, are used by parasitoids to find their host at short distances. Herbivore excrements can also emit volatiles that may reveal herbivores' presence to natural enemies (Weiss, 2006). However, herbivores can reduce this conspicuousness by having a concealed lifestyle, by selecting host plants or part of the host plants in which the production of volatiles is low or by moving frequently to other plant parts where volatiles are not emitted (Czarnobai De Jorge et al., 2022). This reduction of information conveyance by herbivores affects the searching behaviour of natural enemies by making them to resort to plant chemical information to a higher degree when looking for herbivores (Vet and Dicke, 1992).

As mentioned before, natural enemies can also use chemical information generated by plants. Damage caused by herbivores elicits the production of plant volatiles which can be non-specific or specific to the herbivore (Turlings & Erb, 2018). Plant volatiles produced strictly by mechanical cell damage are non-specific, while other plant volatiles are only produced when a specific herbivore causes the damage. If these specific volatiles attract natural enemies which activities favour to the plant, then they are called herbivore induced synomones (HIS) (Blassioli-

Moraes et al., 2016). Furthermore, HIS can also be plant-species specific and cultivar specific. This information could be used by a natural enemy to establish preferences based on plant-herbivore combination. A plant specific HIS could give an idea to the natural enemy about the specific traits of the plant that could affect its fitness directly (e.g. easy access to the prey or host) or indirectly (e.g. plant suitability for herbivore development) (Vet and Dicke, 1992).

Natural enemies can make use of HIS to detect herbivores in feeding stages. However, when the production of infochemicals by herbivores is limited (e.g. non feeding herbivore stages or concealed life style), natural enemies can remediate low detectability and reliability problems by infochemical detour (resorting to information from other herbivore developmental stages) (Wäschke et al., 2014) or associative learning, which takes place in a tritrophic context. On the other hand, dietary specialization at a particular trophic level (plant or herbivore level) determines the degree of specificity of the information needed for successful foraging, thereby influencing the way infochemicals are used by natural enemies. Specialists rely on specific chemical information, while generalists respond to non-specific cues. Specialists (parasitoids or predators) use kairomones to find the herbivore, while generalist do not use any host or prey derived chemical information (Morawo & Fadamiro, 2019). For example, the specialist parasitoid *Microplitis croceipes* uses kairomones produced by *Heliothis* species while generalist predators, such as formicine ants, do not use chemicals derived from their prey and eat all insect larvae found in their way. However, there are some predators with a limited prey range that also use kairomones. For example, coleopteran predators of bark beetles and phytoseiid mites feeding on herbivorous mites (Vet and Dicke, 1992). In addition, responses to herbivore derived product are more congenitally fixed and strong, while responses to plant volatiles are more variable and can be learned specially during adult foraging in which reliable host-derived stimuli are associated with unreliable but detectable synomones (Fratl et al., 2017).

According to Sheehan (1986) and Vet and Dicke (1992), research has been done mainly to understand how the presence of non-host plants affects the searching behaviour of herbivores. It has been found that herbivore searching behaviour, principally for specialist herbivores, is hampered by the presence of non-host plants (polyculture) (Morawo & Fadamiro, 2019). Such effect on the searching behaviour may be due to masking of attractant or arrestment cues, to the presence of repellent cues, or to a combination of these (Sheehan, 1986).

Furthermore, Sheehan (1986) and, Vet and Dicke (1992) stated that the masking odour effects on natural enemies has not been studied yet and expect that, as herbivores, natural enemies will also be confused in agricultural systems in which plants are grown in polyculture. However, Vet and Dicke (1992) consider that the searching behaviour of natural enemies is less affected as compared to the searching behaviour of herbivores, since they generally attack several species,

each with their own host-plant range. Besides, it is mentioned that the effect of polyculture on the searching behaviour of natural enemies may depend on their capacity to learn and adopt a new searching behaviour (Huang et al., 2020).

The aim of this paper is to understand whether the searching behaviour of natural enemies (parasitoids and predators) is affected by complex odour mixtures and if there are differences between specialist and generalist natural enemies, based on the following topics: plant biodiversity and its effects on host and prey location by natural enemies; 'cry for help': herbivores' attacks to plants stimulate the production of volatiles that attract herbivore's predators; host - plant experience (learning process); and environmental conditions.

2. PLANT BIODIVERSITY AND ITS EFFECTS ON HOST AND PREY LOCATION BY NATURAL ENEMIES.

Herbivores and their natural enemies must deal with detectability and reliability problems when searching for food (Vet and Dicke, 1992). Regarding to it, plant biodiversity is a factor that may influence the foraging behaviour of natural enemies (Beyaert and Hilker 2014; Wäschke et al., 2014; Blassioli-Moraes et al. (2016); Hauri et al., 2021). To understand how plant diversity may affect the searching behaviour of natural enemies, it is important to consider that multitrophic interactions take place in complex environments, formed primarily by host and non-host plants able to produce odour plumes (Beyaert and Hilker 2014 and Wäschke et al. 2014). It has been demonstrated that the production of volatiles differs quantitatively and qualitatively among crop species and even among cultivars (Huang et al., 2020; Cruz-Miralles et al., 2022). Additionally, the production of plant volatiles may be lower in herbivore infested plants than in uninfested ones as has been shown for some in maize cultivars (Hare 2011). In this way, in complex environments containing different plant odour plumes (qualitatively and quantitatively), it is very likely that these different plumes will intermingle, thereby masking the targeted plant odour plume, which might interfere with the attraction of natural enemies, or it may have a repellent effect, thereby affecting the searching behaviour of natural enemies (Beyaert & Hilker, 2014; Wäschke et al., 2014). Moreover, in an environment with high plant diversity, the existence of physical plant structures influences the turbulence and wind speed through the field, thereby affecting the odour plume arrays i.e. high wind speed produce turbulence, which reduce the odour concentrations (Beyaert and Hilker 2014).

Nevertheless, natural enemies can overcome these difficulties when detecting plant odour plumes. The capacity of natural enemies to find their food may rely on HIPVs, produced by the food plant associated with their prey or host (De Rijk et al. 2013). According to Vet and Dicke (1992), natural enemies are able to distinguish between qualitative and quantitative variations of plant odour plumes - even from plants of different cultivars. Wäschke et al., (2014), through

laboratory experiments, found that the parasitoid *Mesopolobus incultus* could differentiate between odours produced by the host complex (host plant *Plantago lanceolata* + host insect *Mecinus pascuoru*) in absence or presence of non-host plant volatiles (*Achillea millefolium* and *Agrimonia eupatoria*). The parasitoid gave preference to simple odour bouquets produced by the host complex. In agreement with this laboratory results, the same authors found that the abundance of parasitoids was not correlated with plant diversity but with the abundance of its host complex. According to Beyaert and Hilker (2014), a continued exposure to background volatiles in biodiverse plant habitats, as in the field experiments made by Wäschke et al., (2014), may change the responsiveness of natural enemies to those volatiles. It could be that the insect receptors become more sensitive, thereby increasing the response to host complex volatiles (Deletre et al., 2022); or it could be that the receptors get habituated to these background volatiles, thus reducing the physiological response. Both, sensitization and habituation may enhance the searching behaviour of natural enemies. Sensitisation may help to increase the capacity to recognize targeted odour plumes or background odour plumes leading to the food resource (cross-sensitization). On the other hand, habituation may help to suppress background odours acting as a filter to separate the targeted odour plume from the untargeted background odours.

3. 'CRY FOR HELP': HERBIVORES' ATTACKS TO PLANTS STIMULATE THE PRODUCTION OF VOLATILES THAT ATTRACT HERBIVORE'S PREDATORS.

According to Vet & Dicke (1992), and Turlings & Erb (2018), plants have the ability to produce herbivore induced plant volatiles (HIPVs) that can attract carnivore as a response to insect herbivory stimulus. Carnivores can be insect predators and parasitoids, entomophagous nematodes and possibly insectivorous birds. Besides, this response may be induced by oviposition or oral secretions of herbivorous insects. Additionally, this plant response is not restricted only to the damaged part of the plant, but it is also induced in undamaged parts of it, thereby producing a systemic defence. An attack to the plant could occur aboveground, producing a systemic defence belowground and vice versa (Bezemer and van Dam, 2005; Hare, 2011). This ability of plants to respond to insect herbivory has been named “crying for help” and has been demonstrated in over 13 plant families. An example of it is described in the experiments carried out by Venzon and Janssen (1999). In such experiments they found that bugs (*Orius laevigatus*) had more preference to odours released by cucumber plants infested with spider mites (*Tetranychus urticae*) than to odours released by clean plants. Furthermore, the herbivore induced plant volatiles that comprise several components including terpenoids, green leaf volatiles and aromatic compounds (Dicke, 2009) and their induction is mediated by jasmonic acid (JA), salicylic acid (SA), ethylene (ET) and abscisic acid (ABA) pathways (De Rijk et al. 2013).

The HIPV mixtures can be herbivore specific and are detectable and relatively reliable for carnivore arthropods (Vet and Dicke 1992). Carnivores can often discriminate between plant volatiles induced by different herbivore species. Doing this, plants offer to carnivore arthropods the chance to differentiate plants infested by herbivores with different value for them (Dicke, 2009). This information may reveal the development stage of the attacking herbivore, herbivore densities or duration since the last herbivore infestation (De Rijk et al. 2013). In addition, De Rijk et al. (2013) states that the foraging behaviour of parasitoids predicted in tritrophic systems should be nuanced for foraging behaviour of parasitoids in more complex habitats like agro ecosystems, in which it is possible to have diverse plant and herbivores species. In a high diversity context, there could be multi-herbivore communities involved in which non-host herbivores play an important role. According to Rodriguez and Chalmers (2005), and De Rijk et al. (2013), plant responses to one species of herbivore might be affected by the plant's response to other species of herbivores on the same plant. Generally, the feeding guild of herbivores determines the different plant defence signal transduction pathways. Root and leaf chewers generally activate the JA pathway, while phloem-sucking herbivores and pathogens mainly induce SA pathway (Bezemer and van Dam, 2005; Rodriguez and Chalmers, 2005; De Rijk et al. 2013). Nevertheless, this is not a rule and within feeding guilds, some herbivore species can induce more than one pathway simultaneously and herbivores from different feeding guilds can induce the same pathways (De Rijk et al. 2013). Moreover, through crosstalk, there is an interaction between the different signal transduction pathways induced by herbivore species that could influence emitted plant volatiles, therefore affecting the preference and performance of herbivores and their natural enemies. It has been found that JA pathway, induced by leaf chewers, is antagonistic to the SA pathway induced as a response to phloem-sucking herbivores (Rodriguez and Chalmers, 2005, and De Rijk et al. 2013), however, an additive effect of inducing both pathways simultaneously has been also observed for some species (De Rijk et al. 2013). With these antecedents, the herbivore's feeding habit alone is not sufficient to predict the effect of its feeding on the searching behaviour of parasitoids (Rodriguez and Chalmers, 2005).

According to De Rijk et al. (2013), the presence of non-host herbivores may affect the parasitoid foraging behaviour in two phases. First, in complex habitats, non-host herbivores induce plant volatiles can mask the HIPVs caused by host herbivores. Second, once the parasitoid is on the plant, the presence of non-host products may affect the foraging decisions like the time spent to search hosts (Ugine & Thaler, 2020). Both phases together predict parasitoid host-finding efficiency. In addition, the effect of non-host herbivores in these two phases could be determined by the feeding guild (Dicke et al. 2009), species, development stage and density of the non-host herbivore. Nevertheless, the host range specialization of parasitoids may determine the effect of non-host on parasitoid foraging decisions.

A multiherbivore attack to a same plant or neighbouring plants can affect the foraging behaviour of parasitoids (De Rijk et al. 2013). The neighbouring non-host infested vegetation may affect volatiles blends, thereby affecting the perception by foraging parasitoids. The same authors stated that the preference of some parasitoids can or cannot change when plants are attacked by two herbivore species (host and non-host) with the same feeding guild. In contrast, parasitoids are able to discriminate when different defence pathways are activated, i.e. when the plant is attacked by host and non-host herbivore of different feeding guild. Low attractiveness to HIPVs induced by non-host herbivores in neighbouring plants could reduce the attractiveness for parasitoids, thereby enhancing the foraging behaviour of parasitoids by influencing them to fly above host-herbivore infested plants. On the other hand, in complex environments, it could be possible to have a scenario where a plant is suffering a simultaneous or sequential infestation of host and non-host herbivores (dual infested plants). The same authors found that the preference for volatiles by parasitoids in this scenario was variable. Some cases showed that parasitoids preferred volatiles from host-infested plants than dual infested plants; other showed that parasitoids were not able to discriminate these volatiles, and in some other cases, parasitoids preferred dual infested plants than host-infested plants. The parasitoid response to situations in which plant volatiles are induced by non-host infestations depends on the specificity of plant responses to herbivores. Likewise, non-host effect may also depend on the density of host and non-host herbivores attacking the plant. For some species, the negative effect of non-host presence on the attractiveness of the plant is only observed when the non-host density surpasses a certain threshold. Besides, the developmental stage of the non-hosts herbivores could determine the attractiveness of dual infestation. An older stage can cause more damage in the plant, thereby increasing the production of HIPVs.

Besides, it has been shown that the permanence of parasitoids on host infested plants is longer than in non-host infested plants. Nevertheless, non-host herbivores may release similar host herbivore cues that could affect the behaviour of the parasitoids by making them to stay longer times in the plant. Not only HIPV's can influence the parasitoids' residence time on the plant but also the non-host herbivore cues (De Rijk et al. 2013).

In general, HIPV emission is a defence response that could benefit the plant by increasing the attraction of natural enemies of herbivores. However, since a plant can have variable responses against a multi-herbivore attack (host and non-host herbivores), the searching behaviour of parasitoids is difficult to predict as mentioned above. Although the effects on searching behaviour of predators have not been studied to the same extent when compared to parasitoids' behaviour, it may be that predators behave in a more predictable way than parasitoids; considering that parasitoids are more specialist than predators and depend more on HIPVs to enhance their searching behaviour (Vet and Dicke, 1992).

4. HOST - PLANT EXPERIENCE THROUGH LEARNING.

Learning experience created by associative learning can affect the searching behaviour of natural enemies (Vidal-Gomez et al., 2018). Natural enemies may be able to learn about many characteristics of their host's environment such as the odour of the host's food, forms and colours of the host's environment and even a particular part of the plant in which their host reside (Vet and Dicke, 1992).

According to Shimoda and Dicke (1998), odour blends produced by conspecific plants infested by different herbivores have same components but in different proportions. Moreover, plants of different species produce different odour blends (components and concentration). Nevertheless, in both cases, natural enemies can learn to discriminate between them and make use of these blends (Vet et al. 1998; Shimoda and Dicke, 2000). Vet and Dicke (1992) stated that an option for natural enemies to solve reliability and detectability problems of chemical signals is by learning to link easy to detect stimuli (HIPVs) with a reliable but hard to detect stimuli (kairomones). In this case, kairomones produce fixed responses in natural enemies, while responses to plant volatiles are more plastic, consequently convenient to learning for them. In addition, the responses to HIPVs and foraging decisions are linked to the plasticity of natural enemies which may be shaped by their experience (Vet and Dicke, 1992; Shimoda and Dicke, 2000; Hare, 2011; De Rijk et al. 2013; Beyaert and Hilker 2014).

Previous odour experience and its association with a rewarding resource location may affect the response to a stimulus (Vet and Dicke, 1992; Shimoda and Dicke, 2000; De Rijk et al 2013; Beyaert and Hilker 2014). However, a combination of rewarding and not rewarding experiences can help to distinguish between odours produced by very similar foraging sites (Shimoda and Dicke, 2002; Leonard et al., 2019). Linking previous experiences in good or bad quality patches with plant odours can alter future responses of parasitoids to HIPVs. This lets parasitoids judge the quality of a next patch (availability of resources and expected level of competition), thereby optimizing their foraging efficiency (Shimoda and Dicke, 2000 and De Rijk et al 2013).

In addition, learning process by parasitoids can be determined based on three criteria: learn responses can change many times according to gained experience, learned experience can be forgotten, and changing behaviour can also have a threshold (Vet and Dicke, 1992). Venzon and Janssen (1999) found that preference of the general predatory bug (*Orius laevigatus*), previously feed with eggs of *Ephestiakuehniella*, increased the preference for the plant-herbivore complex (cucumber plant + *Tetranychus urticae*) from 28.6% to 38.8% after a previous conditioning to this plant-herbivore complex. According to the authors, it may be that after the conditioning the predatory bugs increased their ability to search spider mites by learning to associate plant odours with the presence of spider mites, thereby increasing the chance to locate prey infested plants.

Furthermore, this conditioning also increased the predatory bug preference for cucumber plants infested by thrips. According to the authors, it is likely that the odour blends produced by both plant-herbivore complexes (cucumber plant + spider mites and cucumber plant + thrips) are highly similar, therefore inducing similar responses in predatory bugs.

On the other hand, associative learning process can also cause generalization, phenomena in which a highly similar stimulus could cause low discriminative responses in natural enemies, as found by Shimoda and Dicke, 2002. These authors exposed predatory mites (*Phytoseiulus persimilis*) reared on the plant-herbivore complex (Lima bean plant + spider mites) to odours emitted by the same herbivore-plant complex and to odours emitted by the plant-herbivore complex (Lima bean plant + beet armyworm caterpillars) previous an isolation period of 1 and 24 hours. After just one hour of isolation, the predatory mites could not discriminate between HIPVs emitted by plants of both plant-herbivore complexes, falling in a state of generalization. Additionally, the authors found that the learned experiences in predators can be forgotten as occurs in parasitoids. After 24 hours of isolation, the predatory mites lost their capacity to associate similar HIPVs emitted by Lima bean plants infested with the non-prey herbivore (*Spodoptera exigua*). Since predators have the trend stay relatively longer periods of time in the same patch in comparison to parasitoids, it may be that generalizations a functional behaviour of predators that help them to find a recently lost patch containing their prey. Furthermore, there are parasitoid species that are more able to learn than others. For example, *Cotesia glomerata* has more capacity to learn than *C. rubecula* when exposed to HIPVs induced by host and non-host herbivores in Brussels sprouts plants (Hare 2011).

Finally, when comparing predators with parasitoids it is possible to see a big difference in the way they develop experience. Relatively, parasitoids have more chance to effectuate foraging decisions due to a shorter handling time with their host. It allows them to develop more experience in relation to predators which require more time to handle with their prey (Vet and Dicke 1992; Shimoda and Dicke 2000).

5. ENVIRONMENTAL CONDITIONS

Environmental conditions can alter the production of HIPVs blends as well as the identity of HIPVs, thereby influencing the searching behaviour of natural enemies (Gish et al., 2015). First, it has been registered that the relative concentration of compounds in the HIPVs changes at different light intensity, fertilization, and soil moisture conditions (Loreto & Schnitzler 2010, Ingwell et al., 2018). Furthermore, an increasing temperature can induce the production of HIPVs without altering the relative concentration of individual components of HIPVs (Tingey et al. 1980, Hare 2011). At higher temperatures, the biosynthesis of terpene volatiles, such as monoterpenes, sesquiterpenes and isoprene, increases in several host plants (Loreto et al. 1996,

Sharkey & Yeh 2001, Duhl et al. 2008), because of the increases in vapor pressure of this compounds (Holopainen & Gershenzon 2010). As well as increasing temperature mainly affects emission of terpenes formed through enzymatic reactions (Loreto & Schnitzler 2010).

Secondly, high concentrations of ozone, hydroxyl and nitrate radicals can change specific ratios of the HIPVs components by degrading individual components such as terpenoids, thereby altering the identity of targeted odour plumes after they are released by the plant (Dicke, 2009 and Beyaert and Hilker 2014). In addition, high O_3 result in oxidative stress to host plants (Yuan et al. 2009) and could cause the emission of other HIPVs (Arimura et al. 2000, Vuorinen et al. 2004).

On the other hand, high CO_2 levels cause plant growth, but stomata density may be reduced, causing reduction on the emission of HIPVs (Woodward et al. 2002). Several studies indicated reduction on the emission of isoprene at higher concentrations of CO_2 (Rosenstiel et al. 2003, Centritto et al. 2004, Pegoraro et al. 2004, Wilkinson et al. 2009, Possell & Hewitt 2011).

Besides altering the production and concentration of components of HIPVs, environmental factors such as UV-B wavelengths can induce JA-mediated plant responses, which as mentioned above, influence the searching behaviour of natural enemies. Additionally, the presence of certain substances released by some plants in the environment, like isoprene, can restrict the attraction of parasitoids to HIPVs from host-damaged plants (Dicke 2009).

6. DISCUSSION

Many factors can lead to alterations in the targeted odour plumes of natural enemies, thereby affecting their searching behaviour. The production of HIPVs can be influenced by many factors. For instance, the production HIPVs differs among plant species, among cultivars from the same species, plant developmental stage and nutritional condition. Furthermore, the production of HIPVs fluctuate with environmental conditions such as light, temperature, soil moisture. Once HIPVs are emitted, pollutants in the air can influence the 'lifetime' of HIPVs. Additionally, HIPVs production depends on the intensity of the herbivores' attack, the feeding guild of the herbivores (indirect defence induced by different hormonal pathways), whether the plant is under multi attacks by herbivores of different feeding guilds and even on the presence plant symbionts and plant diseases.

On the other hand, all these plant responses to biotic and abiotic factors induce variable responses on the searching behaviour of natural enemies. For example, dual-infested plants by (host and non-host herbivores) produce a variable response in parasitoids which may depend on the specificity of the plant response to the herbivore attack, the density of the non-host herbivore and its developmental stage. Adding more complexity to the scenario, natural enemies can learn

to differentiate by association between different cues (targeted and non-targeted), which also influences their searching behaviour.

Understanding the searching behaviour of natural enemies is still complex because it could depend on different scenarios. There is still a lot of knowledge to be developed to understand how all these variables affect the searching behaviour of natural enemies. It could be that biological and environmental factors interact differently when they are considered in aggregate or separately. Hare (2011) and Wäschke et al. (2014) mention that the composition of HIPVs fluctuate when comparing field and laboratory experiments.

On the other hand, variations in the searching behaviour of natural enemies have also been observed when comparing tritrophic and multitrophic interactions in more complex environments (De Rijk et al. 2013). Generally, in laboratory experiments few plant species and few herbivores are used to evaluate the effect of biodiversity and a multi-herbivore attack on the searching behaviour of natural enemies respectively, and usually the environmental conditions such as temperature, light intensity, humidity, wind speed, among others are maintained constant. For instance, in laboratory experiments the use of olfactometers and small ventilated tunnels is very common to assess preference of odour plumes by natural enemies (Zjadic & Scholz, 2022). However, the effects of wind speed on the searching behaviour of natural enemies have not been researched yet, considering that the physical structure of the odour plumes can be altered by it (Beyaert and Hilker 2014).

Additionally, effects of volatiles produced by non-host plants on the searching behaviour of many natural enemies have been studied; however, there are still some questions that have not been answered yet, for example: Does plant density of non-host plants alter the preference of natural enemies? Are the targeted HIPVs masked by plume intermingling? Does the HIPV's loss identity with increasing non-host density due to adsorption of low volatility compounds of the HIPVs by physical structures of non-host plants? In the same context, as changes in temperature can affect the production of plant volatiles (Hare 2011), it can be that increases in temperature augments the production of volatiles in non-host plants than in host plants (depending on the plant species), increasing in that way the possibilities to have plume intermingling, thereby affecting the searching behaviour of natural enemies.

Moreover, in laboratory experiments the distances from the odour plumes to the insects are relatively short in comparison to nature, where long distances between the odour source and the natural enemies may occur (Sheehan, 1986). Distances may affect the searching behaviour of natural enemies because at longer distances the concentrations of the HIPVs blends are reduced (Beyaert and Hilker 2014), increasing the possibilities to that other odour sources mask the HIPVs. This may help to find differences between field and laboratory results. Going further, it

has been shown that root symbionts and plant diseases may also alter the production of HIPVs (Bezemer and van Dam, 2005). Nevertheless, relatively few is known about how plants react to such stimuli and how it affects the searching behaviour of natural enemies.

Additionally, it is known that insects can learn to differentiate odour plumes and their searching behaviour may depend on their previous experiences (Vet and Dicke 1992; Shimoda and Dicke 2000). Nevertheless, it is not known to what extent they are able to learn. In laboratory experiments the use of naive natural enemies, usually reared with different food sources than the one they are used to, does not allow scientists to appreciate their real potential to search for herbivores. It could be that in complex environments, natural enemies overcome cue reliability and detectability problems, caused by biotic and abiotic interactions, just by learning. With this background, further field experiments supported by laboratory experiments should be carried out to understand how the searching behaviour of natural enemies is affected in a multitrophic level context, where known biodiversity (above and below ground) and environmental conditions have the possibility to interact.

Finally, research studies about predator searching behaviour are relatively scarce in comparison to research studies about parasitoid searching behaviour. In that way, it is not possible to appreciate whether complex odour mixtures affect in the same way the searching behaviour of specialist and generalist natural enemies. However, considering that predators are more generalist than parasitoids (Vet and Dicke 1992), it is possible to have an idea about it. It may be that the searching behaviour of predators is less affected by complex odour mixtures in comparison to parasitoids which depend more on HIPVs to enhance their searching behaviour. Furthermore, when comparing predators with parasitoids it is possible to see a big difference in the way they develop experience. Relatively, parasitoids have more chance to effectuate foraging decisions due to a shorter handling time with their host. It allows them to develop more experience compared to predators which require more time to handle with their preys (Vet and Dicke 1992; Shimoda and Dicke 2000).

REFERENCES

- [1] Arimura, G., Ozama, R., Shimoda, T., Nishioka, T., Boland, W. & Takabayashi, J. (2000). Herbivory-induced volatiles elicit defence genes in lima bean leaves. *Nature* 406: 512-515
- [2] Ayelo, P. M., Pirk, C. W. W., Yusuf, A. A., Chailleux, A., Mohamed, S. A., & Deletre, E. (2021). Exploring the Kairomone-Based Foraging Behaviour of Natural Enemies to Enhance Biological Control: A Review. *FRONTIERS IN ECOLOGY AND EVOLUTION*, 9, Article 641974. <https://doi.org/10.3389/fevo.2021.641974>

- [3] Beyaert, I. and M. Hilker (2014). "Plant odour plumes as mediators of plant–insect interactions." *Biological Reviews* 89(1): 68-81.
- [4] Bezemer, T. M. and N. M. van Dam (2005). "Linking aboveground and belowground interactions via induced plant defenses." *Trends in Ecology & Evolution* 20(11): 617-624.
- [5] Blassioli-Moraes, M. C., Borges, M., Michereff, M. F. F., Magalhaes, D. M., & Laumann, R. A. (2016). Semiochemicals from plants and insects on the foraging behavior of Platygastriidae egg parasitoids. *Pesquisa Agropecuaria Brasileira*, 51(5), 454-464. <https://doi.org/10.1590/S0100-204X2016000500005>
- [6] Centritto, M., Nascetti, P., Petrilli, L., Raschi, A. & Loreto, F. (2004) Profiles of isoprene emission and photosynthetic parameters in hybrid poplars exposed to free-air CO₂ enrichment. *Plant, Cell Environment*. 27, 403–412
- [7] Cruz-Miralles, J., Cabedo-Lopez, M., Guzzo, M., Vacas, S., Navarro-Llopis, V., Ibanez-Gual, M. V., . . . Jaques, J. A. (2022). Host plant scent mediates patterns of attraction/repellence among predatory mites [Article]. *Entomologia Generalis*, 42(2), 217-229. <https://doi.org/10.1127/entomologia/2021/1237>
- [8] Czarnobai De Jorge, B., Hummel, H. E., & Gross, J. (2022). Repellent Activity of Clove Essential Oil Volatiles and Development of Nanofiber-Based Dispensers against Pear Psyllids (Hemiptera: Psyllidae). *Insects*, 13(8), 743.
- [9] de Rijk, M., M. Dicke and E. H. Poelman (2013). "Foraging behaviour by parasitoids in multiherbivore communities." *Animal Behaviour* 85(6): 1517-1528.
- [10] Deletre, E., Matu, F. K., Murungi, L. K., & Mohamed, S. (2022). Repellency Potential of Tomato Herbivore-Induced Volatiles Against the Greenhouse Whitefly (*Trialeurodes vaporariorum*) (Hemiptera: Aleyrodidae). *Journal of Economic Entomology*, 115(2), 565-572. <https://doi.org/10.1093/jee/toac015>
- [11] Dicke, M. (2009). "Behavioural and community ecology of plants that cry for help." *Plant, Cell & Environment* 32(6): 654-665.
- [12] Duhl, T.R., Helming, D., & Guenther, A. (2008). Sesquiterpene emissions from vegetation: a review. *Biogeosciences* 5, 761-777
- [13] Frati, F., Cusumano, A., Conti, E., Colazza, S., Peri, E., Guarino, S., . . . Salerno, G. (2017). Foraging behaviour of an egg parasitoid exploiting plant volatiles induced by pentatomids: the role of adaxial and abaxial leaf surfaces. *PEERJ*, 5, Article e3326. <https://doi.org/10.7717/peerj.3326>
- [14] Gish, M., De Moraes, C. M., & Mescher, M. C. (2015). Herbivore-induced plant volatiles in natural and agricultural ecosystems: open questions and future prospects. *Current Opinion in Insect Science*, 9, 1-6. <https://doi.org/https://doi.org/10.1016/j.cois.2015.04.001>

- [15] Hare, J. D. (2011). "Ecological Role of Volatiles Produced by Plants in Response to Damage by Herbivorous Insects." *Annual Review of Entomology* 56(1): 161-180.
- [16] Hauri, K. C., Glassmire, A. E., & Wetzal, W. C. (2021). Chemical diversity rather than cultivar diversity predicts natural enemy control of herbivore pests. *Ecological Applications*, 31(3), e02289. <https://doi.org/https://doi.org/10.1002/eap.2289>
- [17] Holopainen, J.K. & Blande J.D. (2013). Where do herbivore-induced plant volatiles go?. *Frontiers in Plant Science* 4(185): 1-13
- [18] Huang, D. D., Sun, M. X., Han, M. Z., Zhang, Z. H., Miao, Y. T., Zhang, J., & Yao, Y. C. (2020). Volatile organic compounds (VOCs) regulate the spatial distribution of Lepidoptera insects in an orchard ecosystem. *Biological Control*, 149, Article 104311. <https://doi.org/10.1016/j.biocontrol.2020.104311>
- [19] Ingwell, L. L., Avila-Ruiz, D. A., Foster, R., & Kaplan, I. (2018). Tailoring insect biocontrol for high tunnels. *Biological Control*, 123, 76-86. <https://doi.org/https://doi.org/10.1016/j.biocontrol.2018.04.012>
- [20] Leonard, R. J., Vergoz, V., Proschogo, N., McArthur, C., & Hochuli, D. F. (2019). Petrol exhaust pollution impairs honey bee learning and memory. *Oikos*, 128(2), 264-273. <https://doi.org/https://doi.org/10.1111/oik.05405>
- [21] Loreto F., Ciccioli, P., Cecinato, A., Brancaleoni, E., Frattoni, M. & Tricoli, D. (1996). Influence of environmental factors and air composition on the emission of alpha-pinene from *Quercus ilex* leaves. *Plant Physiology*. 110, 267–275
- [22] Loreto, F. & Schnitzler, J. (2010). Abiotic stresses and induced BVOCs. *Trends in Plant Science* 15(3): 154-166.
- [23] Morawo, T., & Fadamiro, H. (2019). The role of herbivore- and plant-related experiences in intraspecific host preference of a relatively specialized parasitoid. *Insect Science*, 26(2), 341-350. <https://doi.org/https://doi.org/10.1111/1744-7917.12537>
- [24] Pegoraro, E., Rey, A., Bobich, E., Barron-Gafford, G., Grieve, K., Malhi, Y. & Murthy R. (2004) Effect of elevated CO₂ concentration and vapour pressure deficit on isoprene emission from leaves of *Populus deltoides* during drought. *Functional Plant Biology* 31 (12): 1137–1147
- [25] Possell, M. & Hewitt, N. (2011). Isoprene emissions from plants are mediated by atmospheric CO₂ concentrations. *Global Change Biology* 17 (4): 1595-1610
- [26] Rashedi, A., Rajabpour, A., Rasekh, A., & Zandi-Sohani, N. (2019). Interactions between host plant, *Aphis fabae*, and its natural enemies, *Orius albidipennis* and *Lysiphlebus fabarum* in a tritrophic system. *Journal of Asia-Pacific Entomology*, 22(3), 847-852. <https://doi.org/https://doi.org/10.1016/j.aspen.2019.07.001>

- [27] Rodriguez-Saona, C., J. A. Chalmers, S. Raj and J. S. Thaler (2005). "Induced Plant Responses to Multiple Damagers: Differential Effects on an Herbivore and Its Parasitoid." *Oecologia* 143(4): 566-577.
- [28] Rodriguez-Saona, C., Urbaneja-Bernat, P., Salamanca, J., & Garzón-Tovar, V. (2020). Interactive Effects of an Herbivore-Induced Plant Volatile and Color on an Insect Community in Cranberry. *Insects*, 11(8), 524.
- [29] Rosenstiel, T.N., Potosnak, M.J., Griffin, K.L., Fall, R. & Monson, R.K. (2003) Increased CO₂ uncouples growth from isoprene emission in an agriforest ecosystem. *Nature* 421, 256–259
- [30] Shao, X., Cheng, K., Wang, Z., Zhang, Q., & Yang, X. (2021). Use of odor by host-finding insects: the role of real-time odor environment and odor mixing degree. *Chemoecology*, 31(3), 149-158. <https://doi.org/10.1007/s00049-021-00342-8>
- [31] Sharkey, T.D. & Yeh, S.S. (2001) Isoprene emission from plants. *Annual Review of Plant Physiology and Plant Molecular Biology*. 52, 407–436
- [32] Sheehan, W. (1986). Response by Specialist and Generalist Natural Enemies to Agroecosystem Diversification: A Selective Review.
- [33] Shimoda, T. and M. Dicke (2000). "Attraction of a predator to chemical information related to nonprey: when can it be adaptive?" *Behavioral Ecology* 11(6): 606-613.
- [34] Tingey, D.T., Manning, M., Grothaus, L.C. & Burns, W.F. (1980). Influence of Light and Temperature on Monoterpene Emission Rates from Slash Pine. *Plant Physiology* 65 (5). 797-801
- [35] Turlings, T. C. J., & Erb, M. (2018). Tritrophic Interactions Mediated by Herbivore-Induced Plant Volatiles: Mechanisms, Ecological Relevance, and Application Potential. In M. R. Berenbaum (Ed.), *Annual Review of Entomology*, VOL 63 (Vol. 63, pp. 433-452). <https://doi.org/10.1146/annurev-ento-020117-043507>
- [36] Ugine, T. A., & Thaler, J. S. (2020). Insect predator odors protect herbivore from fungal infection. *Biological Control*, 143, Article 104186. <https://doi.org/10.1016/j.biocontrol.2020.104186>
- [37] Venzon, M., A. Janssen and M. W. Sabelis (1999). "Attraction of a generalist predator towards herbivore-infested plants." *Entomologia Experimentalis et Applicata* 93(3): 303-312.
- [38] Vet, L. E. M. and M. Dicke (1992). "Ecology of Infochemical Use by Natural Enemies in a Tritrophic Context." *Annual Review of Entomology* 37(1): 141-172.
- [39] Vidal-Gomez, U., Rodriguez-Saona, C., & Kaplan, I. (2018). Constitutive exposure to the volatile methyl salicylate reduces per-capita foraging efficiency of a generalist predator to learned prey associations. *Entomologia Experimentalis Et Applicata*, 166(8), 661-672. <https://doi.org/10.1111/eea.12713>

- [40] Vuorinen, T., Nerg, A., Holopainen, J.K. (2004). Ozone exposure triggers the emission of herbivore-induced plant volatiles, but does not disturb tritrophic signalling. *Environment Pollution* 131 (2): 305-311.
- [41] Wäschke, N., K. Hardge, C. Hancock, M. Hilker, E. Obermaier and T. Meiners (2014). "Habitats as Complex Odour Environments: How Does Plant Diversity Affect Herbivore and Parasitoid Orientation?" *PLoS ONE*9(1): e85152.
- [42] Weiss, M. R. (2006). Defecation behavior and ecology of insects. *Annual Review of Entomology*, 51, 635-661. <https://doi.org/10.1146/annurev.ento.49.061802.123212>
- [43] Wilkinson, M.J., Monson, R.K., Trahan, N., Lee, S. & Brown, E. (2009) Leaf isoprene emission rate as a function of atmospheric CO₂ concentration. *Global Change Biology* 15, 1189–1200
- [44] Woodward F.I., Lake, J.A., Quick, W.P. (2002). Stomatal development and CO₂: ecological consequences. *New Phytologist* 153: 433-484
- [45] Yuan, J.S., Himanen, S.J., Holopainen, J.K., Chen, F., Neal Stewart, C. (2009). Smelling global climate change: mitigation of function for plant volatile organic compounds. *Trends in Ecology & Evolution* 24 (6): 323-331.
- [46] Zjadic, N., & Scholz, M. (2022). The role of food odor in invertebrate foraging. *GENES BRAIN AND BEHAVIOR*, 21(2), Article e12793. <https://doi.org/10.1111/gbb.12793>