



Plant Communication With Herbivores

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Abstract

Plants and herbivores both release volatile organic compounds that have important roles in mediating important biological functions related to defence and reproduction. Plants emit complex blends of chemicals that are involved in multitrophic interactions, coordination of systemic defence responses and pollination, whereas herbivorous insects release pheromones that play important roles in attracting mates, instigating defence responses and initiating aggregation. Interactions between plants and herbivores have been subject to a wealth of studies and knowledge on their biology, biochemistry, ecology and evolution is constantly expanding. In this chapter the idea of communication between plants and herbivores will be explored. Communication between organisms of consecutive trophic levels is somewhat controversial due to unidirectional reliance and competition precluding some of the requirements of a conventional communication process, but there are growing examples of where chemically mediated interactions between plants and herbivores can be viewed as eavesdropping by a signal recipient, or even as true communication where both chemical emitter and

receiver gain a benefit from communication. Examples of herbivores responding to plant-emitted cues and plants responding to herbivore-emitted cues are both explored, and suggestions for future directions in this field are provided.



1. INTRODUCTION

1.1 Plant Communication With Herbivores — Communication or Arms Race?

Plants and herbivores coexist in an evolutionary arms race, where plants evolve new ways to defend themselves from attack and herbivores evolve means to circumvent, tolerate or even utilize those defences (Ehrlich & Raven, 1964; Howe & Jander, 2008; Kant et al., 2015; Petschenka & Agrawal, 2016). Plants produce an enormously diverse range of secondary metabolites that mediate numerous ecological interactions and constitute a central focus of ecological and evolutionary studies into plant defence theory (Kessler, 2015). Some metabolites involved in plant defence also serve roles in plant communication. For example, plants constitutively emit volatile organic compounds into the atmosphere, but when they are damaged they alter the composition and quantity of the chemical blend; compounds within this induced blend may defend plants by intoxicating herbivores (Veyrat, Robert, Turlings, & Erb, 2016) or signal to a multitude of other organisms in the plant's community (e.g., Dicke, 2009; Dicke & Baldwin, 2010; Heil & Karban, 2010). As a consequence of this multifunctionality, the concept of plant communication with herbivores — the focus of this chapter — is difficult to disentangle from other functional hypotheses for the evolution of plant secondary metabolites and requires careful defining. Plant sensing, communication and the idea of plant intelligence have been the subjects of several recent books and definitions of plant behaviour, communication, cues and signals abound (Chamovitz, 2012; Karban, 2015; Mancuso & Viola, 2013; Trewavas, 2014).

In his book, *Plant Sensing and Communication*, Richard Karban (2015) provided a synthesis of the various definitions put forward by ecologists for the whole, or parts, of the communication process. Karban (2015) emphasized that there are no universally agreed-upon definitions of communication for either animals or plants, but that there are many advantages to viewing a signal to have evolved because of the effects it causes and that both the sender and the receiver of the signal should therefore experience a benefit of communicating. This definition will be utilized as

something of a holy grail, whereby interactions between plants and herbivores that satisfy these requirements can truly be considered to be a process of communication. However, there are simpler processes that can also come under the broader umbrella of signalling and communication. In this chapter the simplest process, signalling, whereby a receiving organism responds to an informative cue, an example of which would be a herbivore locating a host plant by using constitutively emitted volatiles to orientate, will be given some consideration. However, greater attention will be given to the process of eavesdropping, where emitters release an informative plastic cue that is received by a receiver organism without the emitter or receiver necessarily benefitting. A form of communication will also be considered to occur when receivers respond to a plastic cue that results in a benefit to the signal sender. Together, these ascendingly complex definitions of eavesdropping, communication and true communication will be used to satisfy, to different extents, the phenomenon of plant communication with herbivores.

Herbivores can utilize olfactory and visual cues to locate their host plants. While visual cues play essential roles in a plant's interactions with insects, including herbivores and pollinators (see Chapters 9 and 10 for an overview of plant communication with pollinators), this chapter will focus on communication based on secondary metabolites, and particularly volatile organic compounds. Communication between plants and herbivores based on herbivores responding to volatiles emitted by plants will constitute the first part of the chapter, we will then explore the phenomenon of plants detecting and responding to volatile pheromones and cues produced by herbivorous insects and then briefly consider the effects of herbivore-induced plant volatiles (HIPVs) on other organisms that impact on herbivore behaviour or survival. The chapter ends with a short summary and suggestions for future research directions.



2. HERBIVORES USE PLANT VOLATILE SIGNALS TO LOCATE THEIR HOSTS

Foraging by herbivorous insects can include oriented flight and selection of a host plant by winged herbivores that feed in the adult stage, oriented flight and selection of a host plant for oviposition by winged gravid female insects, and short distance on land searching for host plants by nonwinged insects. Plants constitutively emit a blend of volatile chemicals, which provides cues that herbivores can utilize to recognize their hosts at a distance (Bruce & Pickett, 2011; Bruce, Wadhams, & Woodcock, 2005).

The constitutive emissions of plants vary considerably throughout their life-cycle with changes reflecting the ontogenetic stage of the plant and its phenology (Hare, 2010). Effective processing of information encoded in the constitutive emissions of plants allows herbivores to colonize host plants when they are at the most suitable phenological stage for their exploitation (Brilli et al., 2009; Magalhães et al., 2016). For a wide range of herbivorous insects, there is substantial evidence demonstrating that peripheral receptors in the insect antennae are tuned to detect ubiquitous plant volatiles (Bruce et al., 2005 and references therein). Bruce et al. (2005) argued that if the majority of peripheral receptors of herbivorous insects are tuned to detect chemical compounds that are not unique to their host, the ratios of compounds in a blend emitted by their host plant becomes a vital component of the olfactory signal. Indeed, there are abundant examples of herbivores displaying behavioural responses to host plant volatile blends at levels that far exceed those of blend components tested individually (reviewed by Bruce & Pickett, 2011). These studies support an alternative to the token stimulus theory put forward in a seminal paper by Fraenkel (1959), which is based on host–plant recognition relying on volatiles that are highly specific to the host plant and absent from unrelated species. However, it should be noted that there are a few cases where herbivorous insects utilize taxonomically specific compounds as kairomones, chemicals that mediate interspecific interactions that benefit the receiver and harm the emitter. The most studied examples are the isothiocyanates, volatile catabolites of glucosinolates that are characteristic of the Brassicaceae and can be utilized by a range of insects among the Lepidoptera, Hemiptera, Diptera and Coleoptera (Bruce et al., 2005; Kostal, 1992).

There are numerous documented cases of herbivorous insects having a preference for a particular plant phenological stage, many of which relate to flowering or fruiting stages (Magalhães et al., 2016), that also involve the active recruitment of pollinating and seed dispersing animals by plants. Constitutive volatile cues from clover *Trifolium pratense* L. are attractive to the herbivorous root-boring beetle *Hylastinus obscurus*, but the beetle has particular preferences for plants of a certain age range, preferring plants aged 1.5–2.5 years over older and younger plants (Quiroz, Ortego, Ramirez, Wadhams, & Pinilla, 2005). These preferences are based on volatile cues, which reflect plants that are sufficiently advanced in their development to act as a host and yet young enough to be less likely recipients of earlier insect infestation (Quiroz et al., 2005). During the vegetative stages of a plant's development, it is unclear why it would advertize its presence

to insects, especially to herbivores that feed on the plant and may result in extensive damage and even death. Therefore volatile chemicals that make a plant more apparent to herbivores without serving a function that improves plant fitness would appear nonadaptive.

In addition to having roles in plant defence against biotic stress and communication with other organisms, plant volatiles also protect plants from some abiotic stress factors and the dynamics of plant emissions are strongly affected by abiotic conditions, such as temperature, humidity, light intensity, drought, ozone, CO₂ and nutrient availability (Blande, Holopainen, & Niinemets, 2014; Gouinguéné & Turlings, 2002; Pinto, Blande, Souza, Nerg, & Holopainen, 2010; Staudt & Lhoutellier, 2011). Plant volatiles — especially isoprene — have been linked to thermotolerance (Behnke et al., 2007; Sharkey & Singaas, 1995) and many compounds are emitted in larger quantities as temperatures increase, although floral volatile emissions do not always follow ambient temperature (Theis, Lerdau, & Raguso, 2007). De novo synthesized compounds, emissions of which are photosynthesis reliant, increase with temperature up to a threshold over which emissions can be decreased (Kleist et al., 2012). High temperatures that quantitatively increase volatile emissions may make plants more apparent to foraging herbivores, but this increased apparency would only be relevant if the high temperature also correlates with foraging activity of herbivores. Interestingly, isoprene has been shown to be avoided by foraging *Manduca sexta* larvae (Laothawornkitkul et al., 2008), which may reduce the attractiveness of some plants as hosts under high temperature conditions. However, the poplar leaf beetle *Chrysomela populi* is not affected by isoprene and electroantennography showed that although *C. populi* detects a range of monoterpenes and sesquiterpenes, it does not detect isoprene (Müller et al., 2015). According to the definitions outlined in the introduction, the process of herbivores locating undamaged host plants by volatile chemicals represents signalling, whereby a constitutively emitted signal is utilized in the process of host finding by a herbivore. It does not equate to a communication process in the common sense, but is a vital step in the ecology and evolution of plant–insect interactions.



3. INDUCTION OF VOLATILES BY HERBIVORES

Once a herbivore has located a host plant, accepts it as a suitable host, and starts to feed, it induces substantial changes in the volatiles emitted by the plant (Heil, 2014; Holopainen & Blande, 2013; Mithöfer & Boland, 2012).

This induction of plant volatiles has been the subject of a large body of work and a number of reviews have been published on the underlying induction mechanisms and the ecological significance of induced volatiles (e.g., Dicke & Hilker, 2003; Dicke & van Loon, 2000; Dicke, van Loon, & Soler, 2009; Kant, Bleeker, Van Wijk, Schuurink, Haring, 2009; Maffei, Mithöfer, & Boland, 2007; Paré et al., 2005). In addition to the feeding damage caused by herbivores, oviposition on or in a plant can also induce changes in plant defences and volatile emissions (Büchel et al., 2011; Fatouros et al., 2005; Hilker & Meiners, 2002; Meiners & Hilker, 2000; Mumm, Schrank, Wegener, Schulz, & Hilker, 2003; Pinto-Zevallos, Hellen, Hakola, van Nouhuys, & Holopainen, 2013; Wegener, Schulz, Meiners, Hadwich, & Hilker, 2001). The changes in plants induced by oviposition can have a significant effect on the plant responses to subsequent feeding by the larvae that emerge from the eggs (Pashalidou et al., 2015; and see Hilker & Fatouros, 2016). Even insects walking on a plant have been shown to stimulate early defence signalling events (Hall, MacGregor, Nijssen, & Bown, 2004). These changes are central to plant defence and communication between the plant and other organisms. Defence may be direct, through the repulsion of pests, and indirect, through the attraction of predatory and parasitic insects that prey on the herbivores. Communication based on HIPVs are known to exist between plants and a number of other community members including other herbivores, predatory and parasitic insects, other plants (see Chapter 1), and hyperparasitoids. The emission of volatiles by plants has great plasticity, with the emitted blends often specific to the herbivore feeding mode, and even to the herbivore species. The herbivore pressure may also affect the quantity of emitted volatiles (e.g., Blande, Korjus, & Holopainen, 2010); thus, herbivore-damaged plants emit volatiles that can convey information on the type of stress the plant is experiencing, and the extent of that stress. However, it should be noted that there can be substantial variation in both constitutive and induced plant emissions and it has been shown with tomato plants that the degree of uniformity of induced volatile emissions varies with herbivore species (Bautista-Lozada & Espinosa-Garcia, 2013). Herbivores can use volatile signals as indicators of host presence, competition and potential high density of natural enemies that can also utilize the same signals. These induced volatiles have been hypothesized to have first evolved as a means of direct defence serving a primary benefit and to have subsequently become a source of information to other organisms (Veyrat et al., 2016).

3.1 Herbivore Oral Secretions as Signal Providers or Plant Manipulators

It is well documented that different insect feeding modes affect the volatile emissions of plants, with substantial variation between herbivores with chewing mouthparts and those with stealthier feeding modes such as hemipterans that feed from the phloem via stylets. In addition to the extent and temporal dynamics of mechanical feeding damage, both of which affect the blends of volatiles (Mithöfer, Wanner, & Boland, 2005), other feeding-related cues derived from the saliva, regurgitant and faeces of herbivores, can trigger herbivore-specific responses in plants (Acevedo, Rivera-Vega, Chung, Ray, & Felton, 2015). There is an expanding body of work on the identification of the elicitors and effectors derived from herbivores, but our knowledge on plant receptors that perceive these herbivore-specific cues is still limited (Acevedo et al., 2015). It is essential to better understand how plants can perceive specific herbivores and activate responses that are tuned to a specific threat.

Factors in insect saliva are now recognized as having a critical role to play in herbivore-induced blends of volatiles. Elicitors in the oral secretions of Lepidoptera larvae were found to play a critical role in the differences observed between volatiles induced by a mechanical wound and volatiles induced by insect feeding. A β -glucosidase isolated from *Pieris brassicae* oral secretions (Mattiacci, Dicke, & Posthumus, 1995) and the compound N-(17-hydroxylinolenoyl)-L-glutamine, known as volicitin, isolated from the oral secretion of beet armyworm (*Spodoptera exigua*) are two well-documented elicitors (Alborn et al., 1997; Turlings, Alborn, Loughrin, & Tumlinson, 2000). However, factors in oral secretions can also suppress plant responses to damage, an example being glucose oxidase which was the first insect salivary enzyme shown to suppress wound-inducible plant defences (Musser et al., 2005, 2002). These examples of salivary constituents are among a number of factors derived from herbivores — often gathered under the term herbivore-associated molecular patterns — that fine-tune the information content of a volatile blend.



4. HERBIVORES EAVESDROPPING ON INFORMATIVE CHEMICAL CUES

HIPVs constitute a signal that can be utilized by herbivores in their foraging for and selection of host plants. Classifying this induced volatile-

mediated communication into a communication type is not as simple as for the constitutive emissions of plants, which are signals used by herbivores to find undamaged host plants. If the induced signal is viewed to have evolved either as a 'cry for help' to beneficial insects (predators and parasitoids that feed on the herbivores) (Dicke, 2009; Dicke, Sabelis, & Takabayashi, 1990), or a within plant signal to coordinate systemic defences within a damaged plant (Frost et al., 2007; Heil & Silva Bueno, 2007), utilization of those signals by herbivores could be classified as eavesdropping. That is the use of a plastic cue in an interaction that does not necessarily benefit the sender or the receiver. Transfer of information in the form of HIPVs has been shown to play a role in herbivore foraging in a range of empirical studies. HIPVs may make a plant more apparent to foraging herbivores and thus lead to increased colonization and feeding pressure on the plant. Conversely, herbivores may utilize HIPVs to determine that a potential host plant is already colonized by herbivores, thus indicating competition and a potentially poor host plant option (see Fig. 1).

Spodoptera frugiperda females have been shown to avoid plants infested with conspecifics as hosts for oviposition. Using the technique of gas chromatography coupled to electroantennography, which enables the

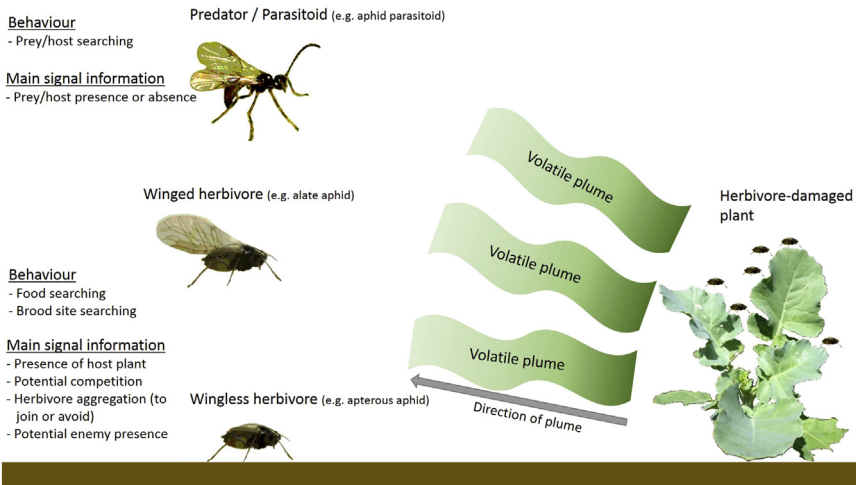


Figure 1 Summary of the information content in a plume of herbivore-induced plant volatiles (HIPVs). HIPVs convey information to predatory or parasitic insects foraging for prey or hosts, and winged or wingless herbivores searching for food or a host for offspring. The responses of the various HIPV recipients depend on interpretation of the information in the volatile plume and can result in attraction, repulsion or no behavioural response.

identification of compounds inducing an antennal response in insects, a range of the volatiles induced by conspecific larvae were shown to be detected by *S. frugiperda* adult females (Pinto-Zevallos, Strapasson, & Zarbin, 2016). *S. frugiperda* larvae are cannibalistic under field conditions, with cannibalism accounting for 40% of mortality in field experiments (Chapman et al., 2000). Greater larval density also correlates with a greater abundance of predatory and parasitic insects (Chapman et al., 2000). Therefore avoidance of plants infested with conspecific larvae has clear benefits for gravid *S. frugiperda* females.

Herbivores may also benefit from avoiding competition from heterospecific competitors. In behavioural tests in the laboratory, the whitefly *Bemisia tabaci* was shown to preferentially orientate towards undamaged plants over plants that had been previously infested with the aphid *Myzus persicae* (Saad, Roff, Hallett, & Idris, 2015). In this case, HIPVs may indicate competition, but may also indicate the presence of common natural enemies. Interestingly, in a study assessing the selection of host plants for oviposition by *Pieris rapae* butterflies, plants infested with *M. persicae* were selected as hosts at a level equal to noninfested plants (Layman & Lundgren, 2015). However, plants hosting a single predatory pink ladybird larva (*Coleomegilla maculata*) were selected significantly less often than noninfested plants and plants hosting aphids and a ladybird larva were selected even less often, which may have been due to a combination of HIPVs and aphid alarm pheromone released in response to predation by the ladybird larva (Layman & Lundgren, 2015).

The studies given as examples above have mostly focussed on choices made by adult insects foraging for host plants to feed on or host their young. Larval herbivore stages also make host choices based on perceived competition, which was demonstrated with *M. sexta* larvae, which preferentially select undamaged *Solanum carolinense* plants over plants that had been previously damaged by herbivores (Kariyat et al., 2014).

Relatively few studies have provided information on the chemical and sensory mechanisms underlying the avoidance of herbivore-infested plants, but a recent study has shed some new light on a mechanism underlying the phenomenon with cotton and the herbivore *Spodoptera littoralis*. As with the examples described earlier, herbivore-induced cotton volatiles suppressed the orientation of *S. littoralis* to host plants, but also orientation towards mates (Hatano et al., 2015). The homoterpene (*E*)-4,8-dimethyl-1,3,7-nonatriene (DMNT) was emitted in large amounts by herbivore-damaged plants and its role in suppressing the orientation of *S. littoralis* was tested by adding synthetically produced compound to attractive plant volatile

blends. Addition of DMNT to the blends strongly inhibited take off and up-wind flight orientation of female *S. littoralis*. Males are less attracted to plant volatiles than females and the addition of DMNT did not have a significant effect on male orientation to cotton, but it did have a significant effect on male orientation toward a main component of female pheromones, which suggests that DMNT significantly interferes with odour perception in both males and females (Hatano et al., 2015). Further studies are needed to determine whether DMNT interferes with the olfactory systems of other herbivores and if other volatiles emitted by different plants have similar effects.

Examples of herbivores avoiding plants damaged by either conspecific or heterospecific herbivores are abundant, but there are also examples of herbivore-induced volatiles being attractive to herbivores. The cotton boll weevil, *Anthonomus grandis*, is attracted by volatiles induced by conspecific herbivores over undamaged control plants, but not by volatiles induced by other herbivore species. The cotton boll weevils also showed a significant preference for reproductive plants over those at the vegetative stage (Magalhães et al., 2012). The responses of the insects to aggregation pheromone were also enhanced by the presence of conspecific HIPVs. It follows that herbivores that aggregate for either defence or reproductive reasons would utilize conspecific HIPVs as attractants, whereas herbivores that do not aggregate or have smaller aggregations would perceive similar cues as repellent.

In a recent study, a model was created that included a number of ecological parameters related to induced plant resistance with the aim of gaining information on how induced resistance affects aggregation patterns of herbivory (Rubin, Ellner, Kessler, & Morrell, 2015). Interestingly, the model showed that both increased aggregation and distribution evenness of herbivores can result from induced plant resistance based on volatile emissions and communication. The model supports the range of contrasting empirical observations for the responses of different herbivores.



5. TRUE COMMUNICATION BETWEEN PLANTS AND HERBIVORES

Instances of true communication between plants and herbivores are contingent on communication providing a benefit to both the plant and the herbivore. Due to the inherent necessity for herbivores to gain sustenance from their host plant, the benefit relayed by the herbivore will not

be without cost. However, there are conceivably circumstances where plants will gain a fitness benefit from the presence of certain herbivores, either through defence against other more damaging herbivores or services that are essential to a plant's lifecycle, such as pollination. If HIPVs are avoided by herbivores, ultimately preventing overcolonization of a plant and resulting in improved survival of both the plant and herbivores, there is an argument to say that the signal process is genuine communication between the organisms. Indeed, honest signalling of toxicity through induced repellent compounds is conceptually the simplest form of plant–herbivore communication. In this scenario a plant that is toxic could provide an honest signal of toxicity and thereby reduce damage caused by herbivores, and the herbivores could also benefit through reduced effort on lower quality plants. This form of communication would effectively prevent feeding on a plant by a herbivore, but there are several examples in the literature of true communication between plants and herbivorous insects that do feed on the plant.

One example of where a herbivorous insect may provide a fitness benefit to a plant is if that herbivore can deter or eliminate other herbivorous insects. Omnivores fit squarely into that category as they feed on plants in the absence of animal prey and may provide a beneficial role for plants as long as they do not themselves become pests and if their presence results in plants receiving less damage from herbivores and ultimately having improved reproductive success. One omnivorous predator, *Anthrenus nemorum*, responds to both constitutive and systemic HIPVs (Lehrman, Bodum, Stenberg, Orians, & Bjorkman, 2013). This insect is attracted to the volatiles of undamaged plants, but plants damaged by the herbivorous leaf beetle *Phratora vulgatissima* are more attractive. The effectiveness of this communication channel for the plant relies on the omnivore relieving the plant of more damage than it causes, while the omnivore can gain sustenance from the plant and locate a site for location of potential prey. Differential use of constitutive and induced volatiles by *A. nemorum* is consistent with animal prey being the preferred and more difficult to locate food source and the plant being an easier to locate resource of lower food quality.

In general, plant investment into defence and reproduction trade-off against each other. Plants under attack from herbivores tend to invest more resources into defence, whereas plants that are less under threat invest in reproductive success. In a recent study, the effects of *S. littoralis* feeding on *Silene latifolia* floral volatiles and pollination success were investigated (Cozzolino et al., 2015). The authors found that *S. littoralis*-infested plants emitted higher amounts of two floral volatiles, (*Z*)-3-hexenyl acetate

and β -ocimene, which appeared to attract more nocturnal pollinators and resulted in higher fruit production. These results suggest that the presence of a herbivore can potentially make a plant more attractive to pollinators and increase reproductive fitness. This is an intriguing observation as it implies that attraction of herbivores at a certain time in a plant's lifecycle can provide reproductive fitness benefits. The use of plant volatiles by such herbivores could thus fit the requirements of a true communication event between plants and herbivores in which the signal benefits both sender and receiver. Another interesting example of herbivory seemingly providing a fitness benefit to plants was found for field grown potato in the Colombian Andes. Herbivory by low numbers of potato moth larvae induced a 2.5-fold increase in potato yield over undamaged plants in a response that was consistent with a herbivore-elicited increase in primary productivity (Poveda, Gómez Jiménez, Halitschke, & Kessler, 2012; Poveda, Gómez Jiménez, & Kessler, 2010).

It is possible that some true herbivores could also be beneficial if they prevent more damaging herbivores from being present or if they effectively perform pollination tasks in their adult phases. Evaluating the beneficial versus negative effects of herbivore presence can be challenging, but to fully understand where communication channels exist in parallel to the plant–herbivore arms race, careful experiments need to be performed.

A prime example of where herbivores may be considered to have an indisputable beneficial role for plants is in brood site pollination mutualisms, where a plant provides a breeding ground and food resources for insects that perform pollination services (Borges, 2016; Hossaert-Mckey, Soler, Schatz, & Proffit, 2010). One of the best described brood site–pollination mutualisms is between figs and fig wasps, which are coevolved and mutually dependent upon each other for successful reproduction. Scent plays an essential role in mediating fig–fig wasp mutualism. During foraging fig wasps are required to make decisions that, if wrong, could result in reproductive failure (Borges, 2016). The fig is an enclosed globular inflorescence known as a syconium, which has a restricted opening that often damages the fig wasp wings and antennae during entrance making a decision to enter the syconium one of utmost importance. Adult fig wasps live for 24–48 h (Ghara & Borges, 2010), consequently, female fig wasps must find and select a syconium in the pollen-receptive stage within that time period. Coordination of the floral scent messages, the ability to receive those messages by the fig wasp, and the ability to gall fig flowers within the selected syconium are critical steps in successful reproduction of fig and fig wasp alike (Borges, 2016). While the

focus of this chapter is not to give exhaustive details on the mechanisms of these interactions, especially for interactions that are pollination based and will be covered elsewhere in this book (Chapters 9 and 10), it is important to consider that offering reward to other organisms can allow plants to accomplish functions that their sedentary lifestyle makes otherwise impossible.



6. PLANT EAVESDROPPING ON HERBIVORE-EMITTED CHEMICAL CUES

We earlier looked at the phenomenon of eavesdropping, whereby herbivores are able to utilize chemical cues that make their hosts more apparent or provide information on their physiological condition. In this section we will take a look at eavesdropping in the opposite direction, whereby plants are able to detect chemical cues emitted by insects, utilize them as a signal of a potential threat and modify their defences in response. Insects emit pheromones to communicate important information that is often necessary for their survival. Alarm pheromones and aggregation pheromones can play roles in processes related to defence and enemy avoidance. Sex pheromones are used to signal to potential mates and are essential for successful reproduction. From the perspective of the plant, detecting these pheromones may provide information about a potential threat and the form and immediacy of that threat. Alarm pheromones may indicate that herbivores on nearby plants are in an agitated state and could be about to disperse, this could indicate an immediate threat by either a small or large number of herbivores. Aggregation pheromones may indicate that large numbers of herbivores are present on neighbouring plants and could represent a future threat of large numbers of herbivores. Sex pheromones indicate that mating herbivores are in the vicinity and that plants may be subject to oviposition and future herbivory. If plants can utilize these cues to optimize their defences, they may gain a tangible fitness benefit (see Fig. 2).

The phenomenon of plants eavesdropping on insect-released chemicals is an emerging research area. Consequently, there is scant literature documenting these interactions. However, recent work with tall goldenrod, *Solidago altissima* L., and the specialist gall-inducing tephritid fruit fly, *Eurosta solidaginis*, has yielded evidence that exposure to a putative sex pheromone of the fly leads to tall goldenrod exhibiting increased defences and a reduced susceptibility to feeding damage by insects (Helms, De Moraes, Tooker, & Mescher, 2013). *S. altissima* and *E. solidaginis* are thought to be closely

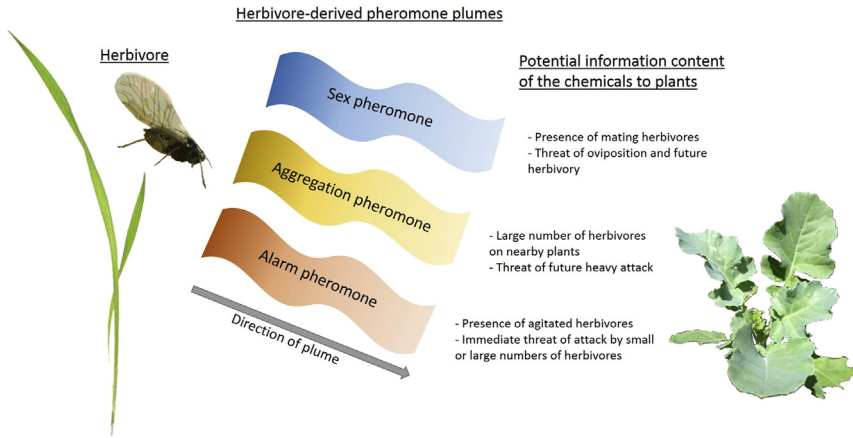


Figure 2 Summary of potential chemically encoded information that can be transmitted from insects to plants. Insect pheromones could function as kairomones to plants, providing information of benefit to the receiving plant and detriment to the fitness of the herbivore.

coevolved, with larvae of *E. solidaginis* inducing spherical galls in the stems of *S. altissima*, which substantially reduce plant growth and fitness (Helms et al., 2013 and references therein). Therefore preempting attack and optimizing defence allocation can potentially provide a substantial boost to plant fitness. The male *E. solidaginis* flies emerge before females and are found perching on leaves towards the top of tall goldenrod ramets. They release a volatile blend dominated by spiroacetal compounds, which were found to be attractive to female *E. solidaginis* flies in behavioural tests conducted in Y-tube olfactometers (Helms et al., 2013). The effect of exposure to male *E. solidaginis* volatiles on the susceptibility of *S. altissima* to oviposition and herbivore-feeding damage was tested in a field study (Helms et al., 2013). The tops of tall goldenrod ramets were enclosed in mesh nets and divided into four treatment groups. Three of the treatment groups contained an individual adult fly, either a male *E. solidaginis* fly, a female *E. solidaginis* fly or a single common housefly (*Musca domestica*), and a fourth group consisted of empty mesh nets as a control. The nets were removed after 3 days and the plants were observed weekly over a 4-week period to score for herbivore-damage and wounds caused by ovipuncture into the terminal buds. Plants exposed to *E. solidaginis* males had significantly lower incidence of ovipuncture and were subject to significantly lower levels of herbivore-feeding damage than each of the other treatments. Treated plants were also observed to

have a stronger induction of jasmonic acid, a defence-related phytohormone, than the control plants (Helms et al., 2013) and a stronger induction of HIPVs (Helms, De Moraes, Mescher, & Tooker, 2014). These observations provide evidence that the plant is responding to the insect-released chemicals, but the phenomenon appears to be rather specific to this particular plant–herbivore association. When similar tests were conducted with the same herbivore but with plants that have not coevolved, HIPV emissions were not altered and the plants did not have enhanced levels of defence against their herbivores (Helms et al., 2014).

Interestingly, a couple of recent studies have been conducted to assess the potential for the application of volatile 3-pentanol, a bacterial volatile derivative and a component of several insect pheromones, for the priming and induction of resistance to bacterial pathogens (Choi, Song, Yi, & Ryu, 2014; Song & Ryu, 2013) and aphids (Song & Ryu, 2013). These studies were conducted with the intention of elucidating the role of bacterial volatile organic compounds in defence against pathogenic infection. However, in a twist of fate, a field trial conducted by Song and Ryu (2013) involving the application of selected volatiles (3-pentanol and 2-butanone) to cucumber plants coincided with an unexpected outbreak of the peach–potato aphid, *M. persicae*. The authors took advantage of the situation to assess the effects of the volatile treatment on the susceptibility of plants to aphid infestation and found that 3-pentanol and 2-butanone treated plants had substantially reduced aphid infestation rates. This coincided with increased presence of ladybirds, a key natural enemy of aphids. In terms of herbivore to plant communication, these studies are rather preliminary and circumstantial, but they do provide evidence that a component of several insect pheromones has the potential to increase resistance of plants to herbivore attack.

The examples outlined above are based on volatile pheromone components, but herbivores also produce nonvolatile chemicals that come into contact with plants. A study of the snail, *Helix aspersa*, feeding on *Brassica nigra* found that seedlings regularly exposed to the mucus and faeces of the snail experienced reduced rates of attack (Orrock, 2013). The presence of mucus alone was not found to be a feeding deterrent, and kairomones were suspected of playing a key role in inducing the increased resistance of plants. However, the identity and source of those kairomones has not yet been determined. Interestingly, a screen for phytohormones in mucus from 13 different snail species showed that one species, *Deroceras reticulatum*, contained significant amounts of salicylic acid (Kästner et al., 2014). Application of

D. reticulatum mucus to leaves of *Arabidopsis thaliana* activated the promotor of the pathogenesis related 1 (*PR1*) gene, which demonstrated the potential for mucus to regulate plant defences. *H. aspersa* was not one of the snails screened by Kästner et al. (2014), which leaves the kairomonal mechanism observed by Orrock (2013) open for further experimentation.

Together, these studies highlight that a range of different chemical cues can be released by herbivores and received by plants. Although a relatively new research direction, it could be common for plants to eavesdrop on herbivore-derived chemical cues. This line of research could lead to enhanced understanding of coevolution between plants and herbivores and could also open up new strategies for manipulating plant defences in an applied agricultural context.



7. COMMUNICATION BETWEEN PLANTS AND HIGHER TROPHIC LEVELS

One of the most widely investigated volatile-mediated interactions is between herbivore-damaged plants and the predatory and parasitic natural enemies of the herbivores. The process of recruiting natural enemies of herbivores by releasing volatile attractants is referred to as indirect defence and has been observed in a range of different plant–insect combinations. As described above for plant–herbivore interactions, HIPV provide information that can be specific to the plant and the damaging agent, which provides information for predatory and parasitic insects to utilize in their pursuit of food prey or hosts (see Fig. 1). Blends of volatile organic compounds provide important foraging signals, but some specific individual compounds have also been shown to play important roles. For example, emission of 3-butenyl isothiocyanate, a product of glucosinolate degradation and characteristic of the Brassicaceae, was found to be induced by aphid feeding and attractive to the parasitoid *Diaeretiella rapae* (Blande, Pickett, & Poppy, 2007). A vast body of literature has been accumulated on tritrophic interactions involving plants, arthropod herbivores and arthropod natural enemies (see reviews by Dicke, 2009; Mumm & Dicke, 2010; Pierik, Ballaré, & Dicke, 2014; de Rijk, Dicke, & Poelman, 2013; Turlings & Benrey, 1998; Vet & Dicke, 1992). In recent times it has also been found that birds can also utilize HIPVs in their search for prey (Amo, Jansen, van Dam, Dicke, & Visser, 2013; Mäntylä et al., 2008). Evidence suggests that birds learn to utilize HIPVs and are not innately attracted to prey-infested trees by exposure to HIPVs alone (Amo, Dicke, & Visser, 2016), utilizing predominantly visual cues

in early foraging forays. Recent studies have also extended our knowledge beyond the responses of third trophic level organisms and elucidated the responses of hyperparasitoids — parasitoids that parasitize primary parasitoids — to HIPVs. Elegant experiments determined that plants respond to feeding by parasitized herbivores by releasing volatile blends that differ from those induced by nonparasitized individuals and that hyperparasitoids are able to exploit these differences in searching for hosts (Poelman et al., 2012). It was further shown that the hyperparasitoid *Lysibia nana* can utilize HIPV cues under field conditions and that they are equally attracted by *Brassica oleracea* plants damaged by two different herbivore species (*P. brassicae* and *P. rapae*) that are parasitized by the gregarious parasitoid *Cotesia glomerata* (Zhu et al., 2015). Parasitoid species affects the magnitude of the response of *B. oleracea* to herbivory by *Pieris* species, which can also be detected by gravid *Plutella xylostella* searching for a host for oviposition (Poelman et al., 2011). While signalling from plants to predators and parasitoids is a relatively clear cut example of interkingdom communication, it appears fantastical to view interactions with hyperparasitoids as anything more than eavesdropping on infochemicals. However, this eavesdropping has the potential to dramatically influence the interaction dynamics in complex ecological systems.



8. SUMMARY AND FUTURE DIRECTIONS

Plants communicate their physiological condition to a diverse range of organisms in their community through the emission of volatile organic compounds. Herbivores can utilize the chemical signals emitted by plants as foraging cues, and there are examples of plants gaining a benefit either through the repulsion of herbivores or the attraction of herbivores that can perform beneficial functions, such as roles in defence or pollination, either directly or indirectly. Recent research has shown that plants can also detect and process chemical information derived from herbivores (Helms et al., 2014, 2013). Pheromones emitted to coordinate essential parts of a herbivore's lifecycle can impart specific information to plants regarding a type of threat and its immediacy. Therefore detecting such information and utilizing it for the effective deployment of defences is potentially of great benefit to the plant. Where the arms race of plants evolving new defences and herbivores evolving ways to overcome them ends and communication begins is demarcated by an extremely blurry line. Even so, there are clear

examples of insects that feed on plants having positive (or even essential) effects on plants in interactions that are mediated by volatile organic compounds.

Future research on plant–herbivore communication should focus on discovering further examples of where herbivore presence can have a fitness benefit on plants. Determination of such a benefit opens doors to explore the functioning of plant herbivore interactions from the perspective of communication. Where the biology of herbivorous insects leads them to release large quantities of pheromone in the vicinity of plants, the effects of those pheromones on plant defences should be explored. If plant responses to insect pheromones are commonplace, the potential for utilizing pheromones not only in insect traps, but also as a mechanism to manipulate plant defences should be explored.

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