SYMPOSIUM

The Olfactory Neuroecology of Herbivory, Hostplant Selection and Plant–Pollinator Interactions

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Synopsis Plants experience often opposing energetic demands and selective pressures—for instance, where plants need to attract an insect that is both the pollinator and herbivore, or alternately, where plants attract prey (due to limited resources) and pollinators. Together, these selective pressures can modify the volatile signals available to the plant's mutualistic and antagonistic partners. Nevertheless, it remains an open question how changes in the information content of volatile signals modify behavioral responses in mutualists and antagonists, and what the underlying neural bases of these behaviors are. This review focuses on two systems to explore the impact of herbivory and resource availability on plant–pollinator interactions: hawkmoth-pollinated hostplants (where herbivory is common), and carnivorous bee-pollinated pitcher plants (where the plants differentially attract bee pollinators and other insect prey). We focus on (1) the volatile signals emitted from these plants because these volatiles operate as long-distance signals to attract, or deter, insect partners, (2) how this information is processed in the hawkmoth olfactory system, and (3) how volatile information changes spatiotemporally. In both the plants and their respective insect partner(s), volatile signaling, reception and behavior are dynamic and plastic, providing flexibility an ever-changing environment.

Introduction

Mutualists and antagonists play crucial roles in shaping trait evolution (Darwin 1859; Ehrlich and Raven 1964; Strauss and Irwin 2004; Thompson and Fernandez 2006; Sletvold et al. 2015), and insect–plant interactions are excellent examples of forces that shape evolution of traits. For instance, plant vegetative and floral phenotypes serve to mediate pollination services while mitigating the effects of insect herbivory (Bronstein et al. 2003; Bronstein 2011). Plant scent phenotypes in particular, are highly salient and can represent a balance of opposing interactions from mutualists and antagonists (Pichersky and Gershenzon 2002). For example, related to the apparency theory hypothesis (Feeny 1976; Euler and Baldwin 1996; Agrawal 2007), increasing volatile production can not only increase detectability by mutualists, but can also attract antagonists (Theis et al. 2007; Theis and Adler 2012; Schiestl 2015).

Plant-insect interactions also depend heavily on environmental context. Thus, although traditional insect sensory studies typically treat plant volatiles as static (e.g., Light et al. 1988, Li et al. 1992), volatile signals can be highly condition-dependent. For example, plants often alter their scent emissions following biotic and abiotic stressors, such as nutrient deficiencies and herbivory (Holopainen and Gershenzon 2010; Lucas-Barbosa et al. 2015). These modulated signals may be detected by insect associates and can fundamentally change whether the scent is attractive or aversive (e.g., McCormick et al. 2012; Castillo et al. 2013) (Fig. 1A). This context-dependency, both in terms of the plant, with the ability to constitutively change its defenses, and the pollinator and/or herbivore, with the ability to detect those differences and respond accordingly, may allow these interacting partners to coexist in a dynamic environment.
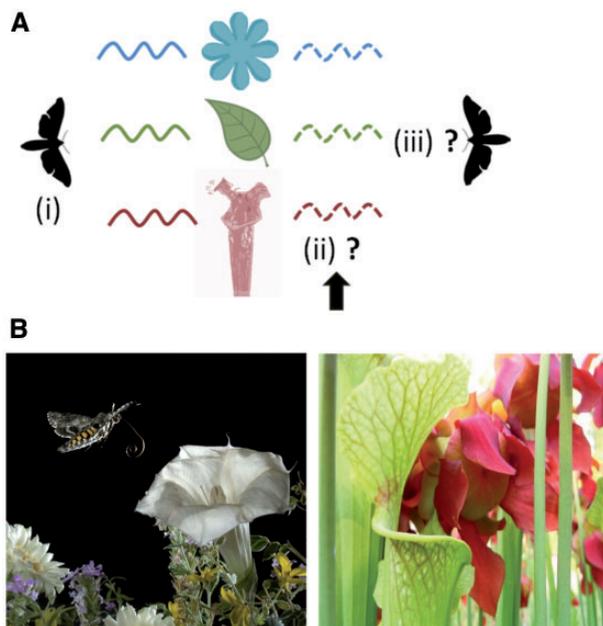
Fig. 1 Schematic and model systems for the interaction between herbivory, pollination, and environment in plant–insect interactions. (**A**) (i) Plant interactions with mutualists and antagonists are mediated by volatiles (depicted by solid, wavy lines) emitted from flowers, leaves, and in specialized taxa, trapping leaves. Here, we address how environmental variability in the form of (ii) herbivory and nutrient availability, interact to alter scent emissions across plant tissues (depicted by dashed wavy lines to denote dynamics of scent emission in both time and space), and (iii) how the insect olfactory system responds to these dynamic signals. (**B**) (*Left*) *Manduca sexta* feeding from its larval hostplant, *Datura wrightii*. Image courtesy of Charles Hedgcock. (*Right*) Mature flowers and the modified trapping leaf (veined) of *Sarracenia* spp. Both flowers and pitchers can contain nectar for pollinators and prey.

In this review, we describe recent studies examining how both herbivory and nutrient availability affect the volatile cues available to insect mutualists and antagonists, with an emphasis on how this information is dynamic both across time, and across plant organs. We begin with an overview contrasting pollination and herbivory, using the *Manduca sexta* moth as a model insect that operates not only as a hostplant specialist on the Solanaceae, but also is an important pollinator for many Solanaceae. We discuss how hostplant volatile signals are context-dependent, and how this information is processed by *M. sexta* to inform its decisions. Next, we use a carnivorous plant system to discuss how environmental resources can affect volatile production, and how volatile signals may operate on distinct channels to differentially attract pollinators and prey (Fig. 1B). Finally, we conclude with exciting possibilities for future research by examining how plasticity in insect

receivers and plant signalers allow for flexibility in a dynamic environment.

The interaction between herbivory and pollination—examples from hawkmoth-pollinated hostplants

Many plants have complex associations with their insect "partners," in which insects operate as both mutualists and antagonists. This "antagonistic mutualism", is common in many hawkmoth-pollinated taxa, where hawkmoths in the adult stage serve as important pollinators, but as larvae act as herbivores and consume plant vegetation. This herbivory comes at an energetic and fitness cost to the hostplant, but is balanced by increased fruit- and seed-set via hawkmoth pollination (Bronstein et al. 2009). These trade-offs are evident in many moth-pollinated hostplants, including *Datura wrightii* and *Nicotiana* spp., in which night-blooming flowers that emit fragrances attractive over long distances to adult moths, but which also emit volatile organic compounds (VOCs) from vegetation and flowers that are attractive to ovipositing females (Raguso et al. 2003; Riffell et al. 2008, 2013). VOC emissions from plant vegetation are dynamic in information content. For instance, plants respond to herbivory with changes in plant chemistry that include the emission of complex blends of VOCs that attract the natural enemies of the herbivores (De Moraes et al. 1998; Turlings et al. 1998; Baldwin and Preston 1999; Dicke and van Loop 2000; Schnee et al. 2006). These VOCs (which include a variety of potential signaling VOCs, such as monoterpenoids, sesquiterpenoids, aliphatic and aromatics) are produced systemically (De Moraes et al. 1998) and are qualitatively and quantitatively different from the the VOCs released by undamaged or mechanically damaged plants (Paré and Tumlinson 1999; Halitschke et al. 2000; De Moraes et al. 2001; Kessler and Baldwin 2001; reviewed by Reisenman et al. 2013). VOC emissions from damaged plants are induced by the oral secretions of feeding larvae; in particular, when *M. sexta* larvae are feeding their oral secretions contain an enzymatic component ($(3Z):(2E)$ isomerase) that alters the production of (Z)-3-hexenal and (E)-2-hexenal emitted from the damaged plant. These are potent volatilesthat attract parasitoid wasps which lay eggs in the moth larvae. Moreover, these volatiles also deter ovipositing female moths (Allmann et al. 2013).

Hawkmoths in this system operate as both pollinator and pest, which raises the question of how herbivory-evoked changes in plant VOCs subsequently impacts floral odor and the decision-making of adult pollinating moths. Vegetative

herbivory can modify the number and size of available flowers (Mothershead and Marquis 2000; Adler et al. 2001; Heil and Ton 2010), and lead to decreases in floral VOC emissions and lower pollinator visitation. Interestingly, leaf herbivory does not always change the floral emissions. For instance, although damage by *M. sexta* larvae significantly changes the floral scent of wild tomato plants (*Solanum peruvianum*) (Kessler and Halitschke 2009), floral scent was not modified in sweet tobacco (*Nicotiana suaveolens*) (Effmert et al. 2008), nor in *D. wrightii*, although the tropane alkaloid content in the nectar increased. Female moths find tropane alkaloids to be aversive, and over time the moths were able to learn the association between the floral scent and the alkaloid-rich nectar (Dacks et al. 2012), thus limiting their interactions with damaged plants although their behavioral attraction to the floral scent remained strong. Why these differences in induced changes in floral VOCs? One recent hypothesis is that damage-induced changes in vegetative VOC profiles are related to the reproductive strategy of the plant (Campbell and Kessler, 2013). However, this study showed that self-incompatible plants had more constitutive defenses compared to self-compatible plants which had more induced defenses. Thus, it remains an open question why some species exhibit damage-induced changes in their floral VOCs (*S. peruvianum*—self-incompatible), whereas others do not (e.g., *D. wrightii* and *N. suaveolens;* both self-compatible). From the perspective of the ovipositing and/or pollinating moth, how are plant volatile signals processed by the nervous system? Since ovipositing on an already-damaged plant would have strong consequences due to competition, one would hypothesize that female moths have sensory capabilities for distinguishing larva-damaged and undamaged plants. Indeed, the peripheral and central nervous systems of females have specialized olfactory receptors and neural circuits to process this information. Antennae are the main olfactory organs of moths, containing thousands of cuticular hairs, or sensilla, each of which contains one to four olfactory receptor neurons (ORNs) (Lee and Strausfeld 1990). ORN axons in each project centrally to one of the paired antennal lobes (ALs). Most types of ORNs express only one type of olfactory receptor protein (OR), and the axons of ORNs expressing the same OR converge on the same glomerulus, the functional modules of the AL and the first synaptic sites in the olfactory pathway (Boeckh and Tolbert 1993; Sun et al. 1997; Gao et al. 2000; Vosshall et al. 2000). The antennae of *M. sexta* have ORNs which respond to volatiles emitted by vegetative and floral

tissues, including aliphatic, aromatic, and terpenoid compounds (Shields and Hildebrand 2001; Späthe et al. 2013). In both males and females, the ORNs that respond to these compounds reside in cuticular hairs (sensilla), including basiconic and trichoid sensilla (Shields and Hildebrand 2001). The majority of glomeruli (approximately 60–70) that receive input from these ORNs in both males and females are sexually isomorphic and are involved in the processing of olfactory information about plant VOCs, especially VOCs associated with hawkmoth-pollinated flowers. Whereas male moths have an olfactory subsystem composed of three glomeruli devoted to processing female sex pheromone, females have a pair of large female-specific glomeruli (LFGs) which respond to particular host plant VOCs, including linalool enantiomers (Roche King et al. 2000; Reisenman et al. 2004) and are involved in mediating oviposition behavior. Given these differences between sexes, females are much more sensitive to plant-related VOCs than males, whose olfactory system is sensitive to sex pheromones emitted by females (Kaissling et al. 1989; Shields and Hildebrand 2001). However, a direct comparison between sexes in their sensitivities to floral VOCs has yet to be conducted.

How is floral and vegetative information processed by AL neurons? Two classes of AL neurons are involved in the processing of olfactory information in the AL of *M. sexta*: local interneurons (LN) and projection neurons (PNs); the former is restricted to the AL, receives input from the ORNs and makes dendritic connections to a few or many glomeruli, whereas the latter typically makes dendritic connections to one glomerulus and its axon projects to higher brain areas, such as the calyces of the mushroom bodies (MB). LNs play a major role in the processing of complex mixtures of VOCs through the release of neuromodulators, including GABA, thereby allowing for enhanced signal-to-noise ratio and contrast enhancement of PN output to the higher brain areas.

Female moths are able to discriminate between damaged and undamaged plants, and exhibit differences in attraction to hostplants when those plants are damaged, raising the question: how are those differences processed in the AL? Activation of multiple glomeruli in the AL plays a key role for allowing the discrimination of floral scents and larva-damaged and undamaged plants. *Datura wrightii* flowers emit both enantiomers of linalool at a ratio of approximately 55% (+)linalool:45% (−)linalool. Interestingly, herbivory does change the emission of *D. wrightii* leaf VOCs, but linalool is not one of the induced volatiles (Reisenman et al. 2010).

Despite the change in the VOC profile, female moths do not discriminate between larva-damaged and undamaged *D. wrightii* plants, but they do readily discriminate between larva-damaged and undamaged tomato (*Solanum lycopersicum*) plants. For *S. lycopersicum*, herbivory induces the emission of (−)linalool. The difference between *D. wrightii* and *S. lycopersicum* in terms of changes in VOC emission and oviposition preference by *M. sexta* may be related to that *D. wrightii* is a perennial, whereas *S. lycopersicum* is an annual, and that female *M. sexta* are able to smell changes in induced defenses, but further tests are needed to identify these mechanisms. Linalool is also an important constituent the floral scent that mediates attraction of male and female moths ([Riffell et al. 2009a](#), [2009b](#)), but the individual enantiomers of linalool influence female *M. sexta* oviposition behavior in a contrasting manner: (+)linalool is attractive and increases oviposition, whereas (−)linalool is repellent and deters oviposition. Both enantiomers of linalool are processed by sexually isomorphic glomeruli in a non-specific manner, but in females there are enantioselective glomeruli that perhaps mediate these differential responses in oviposition; the large female-specific glomeruli (LFGs).

In addition to those glomeruli processing linalool, the coordinated activity of PNs and LNs allows the moths to generalize, or similarly process, the scents from moth-pollinated flowers. Although *D.wrightii* flowers produce a bouquet of more than 60 volatiles ([Raguso et al. 2003](#)), a blend of just three constituents ((±)-linalool, benzaldehyde, and benzyl alcohol) was sufficient to recapitulate neural activity and behavioral responses to the entirety of the floral scent in *M. sexta* moths ([Riffell et al. 2009b](#)). In particular, the oxygenated aromatics (benzaldehyde and benzyl alchohol) elicited strong neural responses in the AL. These volatiles, or ones that are structurally similar, are also abundant in many diverse flowers visited by *M. sexta* moths. Stimulation of these different floral scents elicited the same network activity in AL neurons, as well as PN responses—specifically two PNs associated with glomeruli in the anterior region of the AL proximal to the glomerulus that receives input from ORNs on the labial palp. Disrupting LN-mediated inhibition in the AL by superfusing GABA-receptor antagonists modifies both the representation of the floral mixture as well as the ability of the PNs to follow the odor pulses ([Riffell et al. 2013](#), [2014](#)). This disruption in the neural processing is also reflected in behavior: moths that had the GABA-receptor antagonists injected into their ALs were not able to track the floral plume, while control moths with saline-injection were able to track and locate the source of the floral plume.

Neuromodulators like GABA play a key role in the processing of floral and leaf odors by AL neurons, but other neuromodulators, like dopamine, also play roles in moth decision making of appropriate flowers and plants. Foraging hawkmoths often encounter hostplants and floral resources that are spatially and temporally patchy. In addition, the environment in which the hostplants and moths inhabit can be harsh and semi-arid, necessitating that the moths locate these patches within a timeframe of minutes to hours in order to maintain energy for flight and prevent desiccation. Neuromodulation in the nervous system enables flexibility in behavioral activity levels so that the moths can adjust their responses in this variable environment. Learning-evoked neuromodulation is one example of these processes, where release of dopamine, serotonin, and octopamine in specific brain areas allows plasticity in neural processing and influences moth decision-making. For instance, as mentioned above, larva-damaged *D. wrightii* plants do not change their floral VOC emissions, but do change their leaf VOCs and tropane alkaloid content (e.g., scopolamine) in the floral nectar. Female moths learn the association between the toxic nectar and the floral and vegetative scent and lessen their visitation to these plants, although they still prefer the flowers ([Dacks et al. 2012](#); Riffell unpublished work). Aversive learning and signaling of an aversive stimulus has been shown to be mediated in part by the neuromodulator dopamine. Dopamine is thought to be released from large neurons that innervate the ALs and mushroom bodies (one site of learning and memory in the insect brain). When dopamine is superfused on to the AL, the neurons showed enhanced responses to the floral scent. Moreover, when dopamine receptor antagonists are injected into the AL, the moths are no longer able to learn the association between the floral scent and the aversive nectar. Dopaminergic modulation of olfactory circuits thus plays an important role in the decision-making by moths between floral scents in larva-damaged and undamaged plants.

The impacts of resources and nutrition, herbivory, and pollination: the unique system of the pitcher plants

The carnivorous plant system

As described above in the Solanaceae, changes in the biotic environment, such as presence of herbivores,

can alter the production of plant secondary chemistry and the information content of the emitted VOCs. These VOC emissions however, can be heavily influenced by resource availability, which can play a significant role in altering the secondary metabolism and volatile profiles of plants (Gershenzon 1984; Fajer et al. 1992). In certain plant taxa, insects serve not only as pollinators and herbivores, but are also captured and digested as prey. This fascinating interplay has been the subject of long-standing interest to ecologists and evolutionary biologists (Ellison and Gotelli 2001; Król 2012), and is thought to be adaptive in extreme environments with low nutrients, but abundant light and water (Givnish et al. 1984; Adamec 1997; Brewer et al. 2011). Prey insects are trapped by modified leaves as a source of heterotrophic nutrients (e.g., Chandler and Anderson 1976) which may be incorporated into secondary metabolites (Rischer et al. 2002). Nutrients derived from heterotrophy can alter photosynthetic efficiency (Moran and Clarke 2010; Pavlovič et al. 2014), and plant fitness (Zamora et al. 1998) suggesting that the nutrient influx from prey may be a direct mechanism by which adaptive plastic changes in volatile biochemistry occur. Of particular interest is the possibility that nutrient balance and resource quality is not necessarily a passive consequence of location, but that plants may play an active role in managing resources and nutrient balance in the form of prey attraction and capture. The carnivorous plants thus represent a unique and accessible system for teasing apart how VOC emissions and nutrient availability can balance important ecological exchanges between the plants and their insect pollinators and prey.

Pollinator–prey conflict

In carnivorous plants, insects serve as both pollinators and prey (Ellison and Gotelli 2001), but because insects which are consumed cannot then become pollinators, there is a trade-off between the benefit accrued from heterotrophic nutrients and the cost of removing potential pollinators (Juniper et al. 1989). Previous studies have also suggested that the traps of insectivorous plants may use volatiles to attract prey (Juniper et al. 1989), and volatile signals are hypothesized to provide one mechanism of alleviating this pollinator–prey conflict (PPC) (Jürgens 2012; El-Sayed et al. 2016), with pollinator and prey partitioning occurring if volatile signals are directed towards specific functional guilds.

Are volatile signals mediating plant–insect interactions in carnivorous plants?

Floral scent has long been noted in carnivorous taxa (Juniper et al. 1989; Schnell 2002), but only recently have studies taken a quantitative approach to identifying the composition and scent chemistry of carnivorous taxa, focusing primarily on the modified leaf which functions as an insect lure or trapping device. For example, Jürgens et al. (2009) quantified volatile production across trapping leaves in several carnivorous taxa. In the venus flytrap, *Dionaea muscipula*, leaves with a classic snaptrap morphology emitted a weak scent with few compounds, including the aromatics methyl salicylate and benzyl alcohol; the sundew *Drosera binata*, which has sticky leaves resembling flypaper, also emitted a weak scent that was dominated by monoterpenes. In contrast, traps from the new world pitcher plants traps tended to have higher volatile emission rates, producing mono- and sesquiterpenes, as well as nitrogenous compounds, aromatics, and fatty acid derivatives (Jürgens et al. 2009). The authors of this study suggest that olfactory signals may be more important for some pitcher plant species than others (Jürgens et al. 2009). In a subsequent study of *D. muscipula*, trapping leaves were found to produce terpene compounds p-cymene, limonene, and a-phellandrene and caryophyllene which were attractive to *Drosophila melanogaster* (Kreuzwieser et al. 2014).

Pitchers of the Asian pitcher plants *Nepenthes spp.* are also noticeably scented (*Moran* 1996; Di Giusto et al. 2008). In *Nepenthes rafflesiana*, upper traps, which tend to capture more flying insects, beetles and nectar-visiting mosquitoes, are more fragrant than lower pitchers. These upper traps produce a greater number of volatiles and higher percentages of the benzyl alcohol, benzaldehyde, and linalool, and were more attractive to *D. melanogaster* in olfactometer assays (Di Giusto et al. 2010). In *Nepenthes rajah*, which can catch small vertebrates, sweet-scented volatile compounds, that include hydrocarbons, alcohols, and esters are produced (Wells et al. 2011).

North American Sarraceniaceae

In the North American Sarraceniaceae, flowers are pollinated primarily by *Bombus* spp. queens (Juniper et al. 1986; Schnell 2002), but pollination by megachilid bees (Folkerts et al. 1999), solitary bees and sarcophagid flies have also been documented (Ne'eman et al. 2006; Meindl and Mesler 2011) are also documented. Pitchers capture a wide variety of prey items including hymenopterans,

dipterans, lepidopterans, coleopterans, and gastropods (Heard 1998; Folkerts et al. 1999; Horner et al. 2012), with some degree of species specialization observed in the proportions of insect orders consumed (e.g., Fish 1976). How do these different insect functional guilds respond to trap and flower volatile bouquets? And could scent phenotype be shaped by pollinator–prey conflict? The opportunity for PPC is greatest in outcrossing, pollen-limited species (Jürgens et al. 2012), and although Sarracenia and Darlingtonia are self-compatible, there is evidence for inbreeding depression, and fitness is limited by pollinator availability (Sheridan and Karowe 2000; Ne'eman et al. 2006; Meindl and Mesler 2011). Divergence in volatile production across traps and flowers may be one mechanism, in addition to spatial and temporal separation, to mitigate the risk of consuming pollinators (Zamora 1999; Anderson and Midgley 2001; Jürgens et al. 2012; Horner 2014). Although direct data on insect olfactory systems and behavior remain open questions in this system, we start here by comparing VOC profiles of traps and flowers in the NA Sarraceniaceae, and discuss implications for interactions with insect associates and resource availability.

Flowers and pitchers of the NA Sarraceniaceae both emit a wide variety of volatile terpenes, aromatics, and fatty acid derivatives. Many compounds are strongly correlated across floral and vegetative tissues, with caryophyllene and α-pinene, for example, produced in both flowers and traps in many species (unpublished data). Nonetheless, the scent profiles of flowers and traps separate into highly distinct areas of volatile space. Examining individual compounds produced in *Darlingtonia californica*, for example, shows that traps emit large amounts of sweet-scented linalool, and woodsy-scented (*E*)-ß-farnesene, whereas flowers produce a spicy, tea scented volatile bouquet that includes eucalyptol and *trans-α*-bergamotene (personal observation; unpublished data).

One of the immediate questions that arise is whether prey capture can modify the volatile blend, and modulate plant–insect relationships in an environment where resource availability can be highly variable. Such changes in volatile composition might occur through via changes in metabolic flux following the assimilation of nutrients, as discussed previously, or through the additive scent contributions of decaying matter in the pitchers. The presence of dimethyl disulfide (DMDS), associated with decomposition, has been noted in a pitcher with captured prey (Jürgens et al. 2009), and the presence of DMDS can be detected in artificially fed traps

(unpublished data). In the field, *Darlingtonia californica* traps with prey smell heavily of putrefaction, but only at very short-distances and when the pitcher is opened (personal observation). Nonetheless, if volatile production is costly, down-regulation of volatile emissions might occur if nutrient acquisition is no longer limiting. Consistent with this possibility, venus flytraps fed with powdered caterpillars showed decreases in terpenoid production, including caryophyllene, p-cymene, and limonene. Interestingly, this effect is specific to chemical class, and the emissions of aliphatic and aromatic compounds were not altered (Kreuzwieser et al. 2014).

The Sarraceniaceae provide a practical and accessible approach for understanding how scent plasticity mediates interactions with insect pollinators and prey, and how these relationships might change in a dynamic environment. We point out several questions that address gaps in our understanding of this multifaceted system. First, what role do insect sensory and olfactory systems play? Understanding how different insect functional guilds detect and respond to both floral and vegetative scents are critical to disentangling how volatiles negotiate multiple ecological interactions and services. Second, how do herbivores fit into these interactions? Although pollinators and prey are the most obvious players in carnivorous plant taxa, pitcher plants are often subject to strong herbivory from *Exyra* spp. moths, which are obligate associates of many *Sarracenia spp.* (Moon et al. 2008; Stephens and Folkerts 2012). Third, how does resource availability and nutrient limitation alter the dynamics of these interactions? The plasticity of volatile blends and blend constituents as a function of nutrient availability (selectively increasing VOC production) and herbivore damage (both increasing and decreasing individual VOC emission) suggests that changes in volatile profiles following prey capture should alter the relative attractiveness of pollinators, prey, and herbivores to both flowers and/or traps. Future studies on volatile plasticity and how insect sensory systems respond to shifts in the information content of VOC emissions will greatly enhance our understanding of the neuroecological context of complex ecological relationships.

Summary

Plant–insect associations are multifaceted and highly dynamic. The fluidity of these interactions result not only from flexibility in insect behavioral and perceptual responses, but also through plasticity in plant secondary metabolism and inducible defenses.

In the hawkmoth hostplant system, hawkmoths functioned as both mutualist (pollinator) and antagonist (herbivore), and specialized neural mechanisms allow insect receivers the flexibility to utilize or avoid hostplants based on volatile information content. In the carnivorous pitcher plant system, it is the plant which serves as both a mutualist (nectar for pollination) and antagonist (predator). Changes in volatile production induced via herbivory or nutrient availability may thus provide plants the behavioral flexibility to attract or deter insects from different functional guilds. The role of plasticity in both plants and insects, and how volatiles mediate interactions between pollination, herbivory, and prey capture remain poorly understood, but is an area ripe for future study.

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