

Signaling and Communication in Plants

James D. Blande
Robert Glinwood *Editors*



Deciphering Chemical Language of Plant Communication

 Springer

Signaling and Communication in Plants

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Preface

The concept that plants interact with other organisms by emitting volatile chemicals is well established. Through the emission of volatile chemicals, plants advertise their physiological condition, which can provide valuable information to organisms that detect the odorous bouquet. Take, for example, volatiles emitted by herbivore-damaged plants; they can be received by neighbouring plants that increase their defences, foraging herbivores that can opt to forage either in the same area or elsewhere depending on perceived competition, predatory insects for which the chemicals indicate the presence of their prey, and numerous other members of the community. Volatile chemicals, as well as being emitted by plants, can be detected by plants and elicit various responses. Therefore, plants are not only communicators delivering a volatile presentation to an audience, but are members of an audience receiving chemically encoded information from other sources.

In the last decades, efforts to understand and decipher the chemical language of plants have increased substantially. In this book, we traverse three parts that deliver cutting-edge knowledge on several critical components of volatile-mediated plant communication. Part I covers the production and emission of volatile chemicals and the complexity of chemical messages that plants deliver. Attention is given to the temporal dynamics of plant volatile emissions, the role of abiotic factors in regulating emissions and the impact of multiple stresses as interacting inducers of emissions. A picture begins to build about the complexity of the volatile bouquets emitted by plants and how they can be viewed as an informative chemical language. Throughout the book, there is a focus on chemical ecology, which comes to the fore in Part II. In Part II, a clear picture is developed of the myriad interactions mediated by plant volatiles, spanning interactions between plants and herbivores, predatory and parasitic insects, hyperparasitoids, vertebrates, other plants, pollinating insects, microorganisms and mutualists. Interactions occurring both above- and below-ground are featured. In Part III, there are two chapters on recent developments to understand the detection and processing of volatile signals by plants. Plant electrophysiology and volatile uptake and conversion are the key concepts explored, which complement and add to the ecology of plant–plant interactions covered in

Part II. Some chapters in the book, particularly Chaps. 4, 8 and 12, provide detailed information on current methodologies and offer perspectives on future applications to advance the field of chemical ecology and further elucidate the chemical language of plants. We finish with a synthesis of the key findings within the book and some further ideas for future research directions.

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Chapter 10

On the Air: Broadcasting and Reception of Volatile Messages in Brood-Site Pollination Mutualisms

Renee M. Borges

Abstract Brood-site pollination mutualisms are those in which plants offer sites to pollinators for the development of offspring or mimic the presence of these sites in exchange for pollination services. Floral scent is an important component of pollinator attraction in such mutualisms and is often composed of volatiles that are commonly emitted by plants in other contexts. Therefore, private channels that employ unusual scent compounds are not the norm. Pollinators must make sense of the volatile messages broadcast by plants against the ensuing background volatile noise using a combination of strategies at the peripheral olfactory system and at higher processing levels. Pollinator reproduction, parts of which occur on or within the host plant, imposes special restrictions on partner compatibility within brood-site pollination systems. A comprehensive understanding of constraints on volatile broadcasting and reception within ecological and evolutionary contexts in this cross-kingdom communication must inform and guide future research in this area.

I think the king is but a man, as I am: the violet smells to him as it doth to me: the element shows to him as it doth to me.

Shakespeare, *Henry V* (4.1.155-7)

It is a recognized fact that smell, ordinary smell, the smell that affects our nostrils, consists of molecules emanating from the scented body..... But what is materially emitted by the female *Bombyx* or Great Peacock? Nothing, according to our sense of smell. Should science one day, instructed by the insect, endow us with a radiograph of smells, this artificial nose will open out to us a world of marvels.

Jean-Henri Fabre, *The Life of the Caterpillar*, 1916

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10.1 Introduction

Shakespeare, the intelligent sixteenth century layman, was inspired to write of the similarity in olfactory perception within the human species. Four centuries later, the accomplished naturalist Jean-Henri Fabre hoped that science would solve the mystery of interspecies differences in scent perception. A century after Fabre, this chapter reviews what science has revealed about cross-kingdom communication using plant volatiles.

10.1.1 Scent Broadcasting by Plants for Pollination: Ecological Contexts

The immobility of plants places a special constraint on how they exchange gametes with each other. Excluding plants that use wind as a gamete motility agent, individual plants can move gametes within themselves or between other plants by engaging with the sensory systems of mobile animals and attracting them to visit reproductive structures either in an honest exchange of rewards or by deceiving them into visiting these structures even when no rewards exist. Plants may engage with the sensory modalities of vision, olfaction, gustation and thermal perception of their pollinators and offer rewards such as adult and larval food, mating sites, brood sites for offspring development, refuges from inclement weather and constituents of mating pheromones. While visual, thermal and gustatory signals are important and act at different scales, this chapter will focus only on olfactory signals. Furthermore, of all the possible rewards, this chapter will concentrate on brood sites as pollination benefits and on systems where plants may deceive pollinators about the presence of brood sites when none actually exist.

Brood-site or nursery pollination mutualisms are special cases of pollination mutualisms in which pollinators oviposit and their offspring develop within the plants that they pollinate (Sakai 2002). There are three major classes of these mutualisms: those where the brood are ovule or seed parasites, those where brood largely feed on pollen of fresh flowers and those whose brood feed on decaying tissues of flowers after pollination; the last category usually comprises the male parts of flowers in hermaphroditic species or staminate flowers in dioecious species (Sakai 2002; Dufaÿ and Anstett 2003). Another new class of brood site involves nesting space rewards to pollinators within domatia of ant-plants (Shenoy and Borges 2008).

A successful plant–pollinator relationship will exist when constraints are strategically overcome, and a net win–win outcome has been achieved. For a communication system between plants and pollinators that is based on olfaction, this will require that (1) volatiles associated with floral structures are emitted either at the time of pollen release or when stigmas are receptive to pollen, (2) these volatiles diffuse or are transported to locations where pollinators occur, (3) these volatiles

are intercepted by pollinator sensory systems, (4) the information content in the volatiles can be decoded by innate sensory networks or networks built on associative learning based on past experience of pollinators with plant rewards and (5) pollinators utilise this information to locate the source of the volatiles and thereby the expected location of floral rewards. A successful brood-site pollination system may also require that (1) the floral structures serve as sites for pollinator mating or that mated pollinator females are attracted to the floral structures and oviposit into them during or after pollination and (2) the floral structures, which could be single flowers or inflorescences, serve as viable brood sites that support the successful development of pollinator progeny. The latter requirement may place constraints on the size and reproductive strategy of the pollinators that could engage in this type of mutualism, since pollinator progeny must be able to acquire all resources from the brood site itself. Furthermore, the time taken for progeny ontogeny must match the trajectory of development, availability or senescence of the brood site which may be a fruit in ovule/seed parasites (e.g. fig wasps, yucca moths, leafhopper moths) or flowers in pollen parasites (thrips) or senescing and decomposing floral tissue (flies, cycad-pollinating beetles). It is therefore possible that a set of host plant and of pollinator traits may determine the degree of specificity between plants and pollinators in brood-site pollination mutualisms (Table 10.1).

Sakai (2002) noted that there was high specificity between pollinators and hosts in ovule/seed parasites; this may be necessitated by the requirement for synchronisation between the development times of fruit and pollinators. Such synchrony may not be necessary for pollen parasites or those developing on decaying flowers; therefore, there may be less specialisation of pollinators on such plant hosts, and individual pollinator species may use several host plant species as long as they provide brood sites and associated rewards. However, in both cases, there may be high specialisation of plants on certain groups of pollinators (Sakai 2002) that can successfully exploit these floral resources or are deceived into perceiving that such resources exist.

Pollinators in brood-site pollination mutualisms are often primarily attracted by floral scent over long distances (Hossaert-McKey et al. 2010). Floral scents encompass over 1700 compounds in several different chemical classes (Knudsen et al. 2006; Raguso 2008). The compounds that are attractive to pollinators may vary in concentration by orders of magnitude in different plant species (Schiestl 2015). Many active floral scent constituents may be preadaptations for other physiological purposes in the plant (Schiestl and Cozzolino 2008). Coupling the constraints of using an olfactory channel for communication with the constraints imposed by pollinator reproduction in a brood-site pollination system, certain predications can be made about the nature of the communication. Plants engaging in ovule-or seed-parasitic brood-site pollination systems must send out very specific volatile messages to attract particular pollinator species. Plants engaged in pollen-parasitic brood-site systems, or those in which decaying tissues are used as brood sites, may send out signals that attract certain groups of pollinators that may not be host-plant specific but more promiscuous in their affinities, e.g. cycad cone volatiles

Table 10.1 Biology of brood-site pollinators and floral scent characters

	Pollinator longevity	Adult feeding	Mating site	Sex engaged in pollination	Type of pollination	Flower filters	Larval development	Pupal development	Pollinator → plant host specificity	Plant → pollinator specificity	Other floral signals	Floral scent specificity
Fig wasps	1–2 days	No	For pollinator progeny	Only females	Active and passive	Yes (e.g. ostiole)	Yes (larvae immobile, confined to individual flower galls)	Yes	High	High	Fig surface chemistry	High
<i>Yucca</i> moths (<i>Tegeticula</i>)	Few days (3–5) ^a	No	Yes	Only females	Active	None?	Yes (larvae mobile, can feed on many seeds)	No	High	High	Flower colour?	High
Leaf-roller moths (<i>Epicpephala</i>)	Few days? ²	Yes?	?	Only females	Active	None?	Yes (larvae mobile, can feed on many seeds)	No	High	High	Flower colour?	High
<i>Greya</i> moths	Few days? ²	Yes	No	Both	Passive	None	Yes (only early instars)	No	Variable	Not specific	Flower colour?	?
<i>Hadena</i> moths	30 days ^b	Yes	No	Only females?	Passive?	None	Yes	No	Variable	Not specific	Flower colour?	?
<i>Chiasmodon</i> flies	?	Yes	Yes	Both	Passive	Yes, sepals	Yes	No	High	High	Yes, flower colour	Yes
Cycad thrips	?	Yes	Yes	Both	Passive	?	Yes	? Probably pupate in soil below plant	High?	High?	Yes, heat	Yes

Information to construct this table is available in the general references provided in the text with a few exceptions: ^a(Dodd and Linhart 1994), ^b(Lloyd 1920)

mediating pollination by thrips, weevils or both (Terry et al. 2004). In such cases, plants may achieve pollinator specificity and reproductive isolation by imposing morphological filters after a certain set of pollinator taxa have been attracted (Martos et al. 2015). However, *Cycadothrips chadwicki*, previously thought to pollinate up to ten *Macrozamia* cycad species in Australia within a brood-site system, is now believed to consist of a set of cryptic species each of which is more closely associated with fewer plant hosts (Brookes et al. 2015). Communication by volatiles in cycads is complicated by cone thermogenesis where heat influences the volatile emission/diffusion rate, constitutes a multimodal signal together with volatiles and functions as an independent reward (Suinyuy et al. 2013). The biology of the pollinator must also be taken into account when attempting to understand the specialisation of signals and the evolution of responses in brood-site pollination systems. For example, in bogus yucca moths, larval survivorship on host plants can affect the possibility of host shifts even though female moths may be attracted to the flowers of several yucca species (Althoff et al. 2014).

10.1.2 Scent Broadcasting in Brood-Site Pollination: Specific Examples

The volatiles produced in brood-site pollination systems have been extensively reviewed by Hossaert-McKey et al. (2010), and the intention of this chapter is to add new findings and more importantly to deal with the constraints that plants and pollinators have faced and the solutions they have come up with in evolutionary time to solve the problems of sending, receiving, interpreting and responding to these messages.

10.1.2.1 Brood-Site Scents in the Fig–Fig Wasp Mutualism

Of all brood-site pollination mutualisms, the fig–fig wasp mutualism has been most investigated from the perspective of volatile communication (van Noort et al. 1989; Grison-Pigé et al. 2002; Hossaert-McKey et al. 2010). The fig is an enclosed globular inflorescence (the syconium) with a single tight opening, the ostiole, which can serve as a mechanical filter to restrict fig wasp entry. Some fig species are protogynous and monoecious with male and female flowers in the same syconium, while others are dioecious in which male trees produce pollinators while female trees produce seeds (Cook and Rasplus 2003; Herre et al. 2008). In monoecious figs pollinator progeny develop within syconia where mating between winged female and wingless male offspring occurs. Winged females leave the natal syconium with pollen to find one in the female flower or pollen-receptive phase; pollinators locate such syconia using volatiles. Pollen-carrying wasps that enter

syconia pollinate and also oviposit into some of the uniovulate flowers, which develop into galls in which larvae feed on the endosperm. Flowers that receive only pollen develop seeds. Pollinator larvae are immobile and are confined to individual galls in which they complete their entire development until eclosion. In such a brood site, there is coordination between seed maturation and pollinator development and also clock gene-based regulation of pollinator eclosion such that males eclose first (Gu et al. 2014) to release females from their galls for mating. There are complex feedback loops between the myriad syconium inhabitants that may also comprise several parasitic fig wasp species (Borges 2015), and these feedbacks influence the tempo of brood-site development (Krishnan and Borges 2014).

The fig system is probably the only brood-site pollination system where the penalty for making mistakes can be as high as zero reproductive success for a wasp that enters the wrong host. This is because fig wasps often lose their wings and parts of their antennae during passage through the tightly fitting ostiolar opening of the syconium. Having entered the fig, the pollinator must be able to gall flowers to provide nutrition for its offspring. Therefore, there should be tight correspondence between the floral scent messages emitted by the syconia, those received by the pollinator and the ability to gall fig flowers within these syconia, since this ability is an important limiting factor for fig wasp reproduction (Ghana et al. 2015). Furthermore, pollinator lifespans range from 24 to 48 h (Ghara and Borges 2010), so host fig species with syconia in the pollen-receptive stage must be found within this short window of time. The close species specificity observed by Sakai (2002) in pollinating ovule/seed parasites and their host plants must derive in part from the high penalty for making mistakes as a result of the developmental constraints faced by pollinators in brood sites (Table 10.1). Also, since the offspring of pollinating fig wasps only mate within the syconium, the brood site is also the mating site for the next generation of pollinators; thus, there is an added selection pressure to enter the 'right' fig as mistakes could doom offspring to zero reproductive success. It is true, however, that since fig wasps have a haplodiploid breeding system, mated female fig wasps could lay either unfertilised haploid eggs resulting in male offspring or fertilised diploid eggs leading to females. Consequently, a single mated female wasp within the 'wrong' fig could at least ensure brother–sister matings. Should this breeding system encourage promiscuity in attraction to host fig species? In a set of six dioecious species, only 1.5 % of pollinators that entered the figs were the wrong species (Moe et al. 2011). Interestingly, while several fig species exhibit introgression of genes and hybridisation (Machado et al. 2005; Moe and Weiblen 2012; Wei et al. 2014), possibly resulting from pollinators entering unusual hosts, pollinators themselves constitute tighter genetic lineages and exhibit greater reproductive isolation (Machado et al. 2005). This may also result from the high amount of inbreeding that may occur in fig wasps (Askew 1968). Such mating restrictions can influence the repertoires of olfactory receptor (OR) genes and thereby the evolution of olfactory specialisation towards certain syconial scents. Therefore, the mating and developmental requirements of pollinators may be mostly responsible for keeping fig gene pools isolated. On the other hand, fig species that share pollinators

may prevent large-scale genetic introgression and hybridisation by ecological factors such as differences in flowering phenologies and geographical isolation (Wei et al. 2014). Whether the floral scents of this fig species complex that shares pollinators could facilitate the breakdown of scent-mediated prezygotic barriers to hybridisation is unknown.

In dioecious fig species, pollinators can only breed within male trees, and female trees produce only seeds (Cook and Rasplus 2003; Herre et al. 2008); this means that pollinators entering syconia on female trees doom their lineages to extinction since they are unable to breed within them. The cause of this fatal attraction is believed to be intersexual mimicry in volatile signals between the sexes such that pollinators leaving male trees are unable to distinguish between a pollen-receptive female tree and a male tree (Soler et al. 2012) and are thereby tricked into entering the unrewarding and fatally deceptive syconia on female trees (Grafen and Godfray 1991; Hossaert-McKey et al. 2016). Consequently, chemical mimicry between the sexes in dioecious species is tighter when both sexes flower at the same time (Hossaert-McKey et al. 2016). In dioecious species also, the constraints on host specificity imposed by the requirement for pollinator mating sites and successful development of pollinator progeny apply, and these constraints must exert considerable pressure on the evolution of the specificity of the interaction.

If there is a requirement for such compatibility between figs and pollinators based on constraints brought about by pollinator life histories, are pollen-receptive (floral) volatile signatures unique for each fig species? Most fig species do emit a species-specific scent (Hossaert-McKey et al. 2010; Borges et al. 2013). The scent glands are present on ostiolar bracts lining the opening of the syconium and in the epidermal and subepidermal tissues on the syconium surface (Souza et al. 2015). Therefore, the fig system appears to be one in which extrafloral structures in proximity to the exterior are involved in scent production and pollinator attraction. This is suitable for a system in which the flowers are enclosed within the syconium receptacle.

While the fig–fig wasp system is a remarkable instance of plant–pollinator co-diversification (Cruaud et al. 2012), there are several examples of breakdown in specificity. About 30 % of fig species are associated with more than one species of sympatric pollinator (Yang et al. 2014), and pollinator wasp species that utilise more than one fig species are known (Erasmus et al. 2007; Moe et al. 2011; Cornille et al. 2012; Liu et al. 2015). In one of these cases, the scents of the two fig species that are visited by the same pollinator are similar (Cornille et al. 2012); whether this applies for the other examples is not yet known. There are examples of the same individual fig tree hosting several species of pollinating fig wasps and even the same syconium hosting more than one species of pollinator at the same time (Compton et al. 2009; Conchou et al. 2014). The mechanisms behind such co-occurrences of pollinators are unknown, but Conchou et al. (2014) suggest that diel variation in fig syconium scent (Borges et al. 2013; Conchou et al. 2014) may be responsible for the arrival of two co-occurring pollinators at different times.

Two or more pollinators (co-pollinators) are as likely to occur in monoecious figs as in dioecious figs (Yang et al. 2014). By conducting experimental introductions of pollinators, Moe and Weiblen (2012) suggested that the fitness costs of

making mistakes and entering the wrong fig species are high in dioecious figs and attributed this to the inability of pollinators to develop in the wrong fig hosts. The fitness cost of entering the wrong fig has not been rigorously measured for monoecious figs (Yang et al. 2014) and merits investigation. Co-pollinators in monoecious figs were either sister species or unrelated species, while those in dioecious species were always sister species (Yang et al. 2014). From the host fig perspective, Proffitt and Johnson (2009) found that the scent profiles of two closely related species, *Ficus sur* and *Ficus sycomorus*, were quite different. Since sister species of pollinators are likely to have more closely related olfactory systems and closely related fig species may have greater similarity in syconial scents, the role of relatedness between host signals and between receivers in the co-diversification between figs and their pollinators may show patterns that can be predicted. However, the mechanisms involved in co-speciation or host switches are complex (Machado et al. 2005) and need careful examination.

The requirement for specificity between figs and their pollinators dictated by pollinator biology has led to the suggestion of private olfactory channels for communication between figs and pollinators, e.g. the use of 4-methylanisole that makes up almost 98% of the scent of receptive syconia in the dioecious *Ficus semicordata* (Chen et al. 2009; Soler et al. 2010). While 4-methylanisole has not been found in other fig species whose scents have been examined (Chen et al. 2009), it occurs in at least 17 angiosperm and two gymnosperm families (Schiestl 2010) and could therefore be available in the general background odours in a landscape where figs occur. Moreover, Wang et al. (2013) found that the pollinator of *F. semicordata* was also attracted by other volatiles produced by a sympatric fig variety usually pollinated by another fig wasp species and concluded that contact cues from the surface of the fig syconium are likely to be the deciding factor in reproductive isolation in this instance. While both wasp species could enter and oviposit in both fig varieties, fig syconia receiving hetero- or extra-varietal pollen were generally aborted and produced fewer seeds. Despite the viability of the hybrid seeds and their normal germination, reduced seed production can make it important for figs to ensure pollinator fidelity. Private channels may, however, not be generally employed in the fig system to ensure pollinator fidelity. Instead, figs appear to emit floral scents whose constituents are widely available in other plant species.

Another important feature of the biology of fig–pollinator mutualisms that may impact the specificity of syconial signals is that some species engage in active pollination (Cook and Rasplus 2003). Actively pollinating females have mesothoracic pockets into which they collect pollen that is deliberately unloaded onto the stigmas during pollination. Other fig species engage in passive pollination and produce massive amounts of pollen that adhere to pollinator bodies. Whether the specificity of fig scents and of pollinators are greater in actively pollinated systems compared to passive systems is unknown but should be investigated.

Fig wasp pollinators are wind dispersed and may carry pollen over distances up to 160 km (Zavadna et al. 2005; Ahmed et al. 2009). Indeed, monoecious fig wasps often exhibit weak population genetic structure over wide areas, reflecting such wide-ranging movement (Kobmoo et al. 2010). Dioecious fig species, on the other

hand, tend to have more structured genetic populations (Dev et al. 2011; Nazareno et al. 2013) probably due to denser fig populations and shorter movements of their pollinators. Yet, at a continental scale (India, China and Thailand), significant geographical variation in floral scent was observed in two widely distributed fig species, one monoecious and the other dioecious (Soler et al. 2011), suggesting that local factors influence syconial scent. This is difficult to reconcile for the monoecious fig species, especially since its pollinating wasp exhibits genetic homogeneity over much of South-east Asia, suggesting wide-ranging gene dispersion (Kobmoo et al. 2010). However, since the active ingredients relevant to pollinators within the syconial signature are unknown, it is possible that the statistically significant variation observed in syconial scent may be due to variation in components that are not necessary for the host species recognition signal.

10.1.2.2 Scents in Other Brood-Site Seed-Parasitic Pollination Mutualisms

There are several other classic cases of brood-site seed-parasitic pollination mutualisms that have begun to be investigated from the perspective of floral scent (Table 10.1). These include interactions between yuccas (*Yucca*) and yucca moths (*Tegeticula*); leafflowers (*Glochidion*) and leafflower moths (*Epicephala*); and the globeflower (*Trollius europaeus*) and anthomyiid flies (*Chiastocheta*). In these seed-parasitic mutualisms, the penalty for making mistakes is not as high as in the fig system. Does this mean that floral scent specificity is lower in such mutualisms compared to the fig system? As in some fig wasps, female yucca and leafflower moths also have specialised anatomical modifications to collect pollen (maxillary tentacles in yucca moths: Pellmyr 1997; Pellmyr and Krenn 2002; specialised proboscis hairs in leafflower moths: Kawakita and Kato 2006) and use these structures to engage in active pollination. The evolution of such innovative structures to facilitate active pollination should indicate high interaction specificity and may also suggest why active pollination is uncommon in insect pollinator lineages (Pellmyr 1997). In several mutualisms where pollinator moth larvae consume seeds [e.g. *Glochidion* (Okamoto et al. 2007) and *Breynia* pollinated by *Epicephala* moths (Svensson et al. 2010)], the floral scent attractive to females is composed of compounds that are part of the scent repertoire of several other plant species, suggesting a lack of private channels. However, there were statistically significant differences between the scents of different *Glochidion* species (Okamoto et al. 2007) suggesting specificity. In the interaction between *Yucca* and its mutualistic *Tegeticula* moths, floral scent across several allopatric *Yucca* species comprised commonly available floral scent compounds but was very similar between species, suggesting that scent composition is conserved in yuccas of section *Chaenocarpa* (Svensson et al. 2006, 2011). The geographical isolation of yucca species (Althoff et al. 2012) may contribute to this scent conservatism.

In another seed-parasitic system involving *Greya* moth species that pollinate several geographically isolated *Lithophragma* species, floral scent is an important

pollinator attractant (Friberg et al. 2014). Here, the different species of *Lithophragma* have divergent floral scents (Friberg et al. 2013), which may contribute to their reproductive isolation while in sympatry, even though they are serviced by the same moth species. However, in this system, multiple traits such as floral morphology and local variation in moth morphometrics and oviposition behaviour may also contribute to reproductive isolation between plant species and to the coevolution between plants and their pollinators (Thompson et al. 2013). In systems involving *Greya* and *Hadena* moths, host plants are also serviced by other pollinator taxa such as bees (Kephart et al. 2006) (Table 10.1); hence the specificity of the floral scents in attracting pollinators is questionable in these systems.

In the highly specific nursery pollination system involving the globeflower *Trollius europaeus* and *Chiastocheta* flies, six out of 16 compounds commonly found in the scents of freshly bloomed flowers are detected by the fly antenna (Ibanez et al. 2010). Furthermore, these active compounds showed less variation than other components of the floral scent, suggesting stronger selection on their emission through pollinator perception. In the *Trollius* system, as in figs, morphological filters, i.e. space between sepals, may serve to increase the specificity of floral visitors (Ibanez et al. 2009a). Flies use the closed *Trollius* flower as a mating site where males and females feed on nectar and both sexes engage in passive pollination (Després 2003). Several species of pollinating *Chiastocheta* flies arrive in sequence to oviposit early or late in the life of the single multicarpellate flower produced per plant. The earliest-arriving fly species is also the most mutualistic, and lays only a single egg in each flower, while later-arriving species deposit multiple eggs per flower (Després and Jaeger 1999). Since an individual flower receives pollen and pollinator eggs over several days, it is possible that the scent of the globeflower later in its life is mixed with herbivore-induced plant volatiles (HIPVs), resulting from feeding by early-arriving pollinator larvae, or with oviposition-induced plant volatiles (OIPVs) (Fatouros et al. 2012) resulting from a reaction to pollinator eggs. HIPVs and OIPVs may be part of the scent mixture that attracts later-arriving pollinator species. Globeflowers produce an induced chemical defence in response to egg deposition by pollinating flies, and this may help to control overexploitation of the carpellary brood sites by later-arriving pollinators (Ibanez et al. 2009b). It is not inconceivable that HIPVs and OIPVs contribute to a combined process of attraction and repulsion as suggested in figs (Borges et al. 2013; Borges 2015).

In another newly discovered seed-parasitic brood-site pollination mutualism, the fungus gnat *Bradysia* is attracted to 2-methyl butyric acid methyl ester produced by *Rheum nobile* flowers (Polygonaceae) (Song et al. 2014). Since this plant also sets seed by autonomous self-pollination and the specificity of this interaction is not yet known, further studies are awaited.

10.1.2.3 Brood-Site Mimicry Pollination Systems

In such systems, plants deceive pollinators by signalling the availability of brood sites when none actually exist. The scent production in these systems has been reviewed recently (Vereecken and McNeil 2010; Urru et al. 2011; Jürgens and Shuttleworth 2015) and will not be dealt with in detail in this chapter. There are three main pollination systems in which flowers mimic the scent and other features associated with oviposition sites: sapromyophily (involving dung and carrion flies), coprocanthrophily (attracting dung beetles) and mycetophily (utilising fungus gnats). In these systems, floral scent is extremely important in attracting pollinators, although visual and thermal signals may also be important. In such systems, pollinators do not usually oviposit into the flowers since additional short range cues that release egg-laying behaviour in real brood sites are missing (Vereecken and McNeil 2010; Urru et al. 2011). As in other mimicry systems, it is possible that frequency-dependent selection operates on the abundance of these flowers/plants such that these fraudulent structures have limited spatiotemporal representation in their habitats. However, since these pollination systems depend on the sensory exploitation of pathways that govern the innate attraction of pollinators to certain compounds, strict frequency-dependent constraints may be lifted on these mimics (Jürgens and Shuttleworth 2015).

10.2 Reception of Floral Volatiles by Pollinators

All pollinators in brood-site pollination mutualisms are insects, mostly Hymenoptera, Lepidoptera, Coleoptera, Diptera and Thysanoptera. Since there is very little knowledge of the olfactory systems of pollinators engaged in brood-site pollination mutualisms, the following sections will use principles of odour reception and detection that have been gleaned from studies on model organisms such as *Drosophila*, *Manduca sexta* and *Apis mellifera*. Since these are representatives of the Diptera, Lepidoptera and Hymenoptera that are so important in brood-site pollination, it is hoped that the general principles these models provide will apply to other pollinator representatives of these taxa. Also, since most insects associated with brood-site pollination mutualisms are relatively short-lived and specialised (Table 10.1), it is assumed that learning is not important in the host location process; consequently, the interaction between associative learning and olfaction-based host location has been ignored in this chapter.

10.2.1 *Signals, Cues and Pre-existing Biases*

Floral volatiles may have arisen as by-products of physiological processes in plants (Peñuelas and Llusà 2004); this is especially true for protective chemicals, which later acquired signal content (Steiger et al. 2010). This may explain the presence of many common volatiles in floral scents across plant families. Floral volatiles may have also evolved as a compromise between signalling to attract pollinators and third-party mutualists such as parasitoids and to repel unwanted visitors such as florivores or herbivores. Thus floral scent inevitably incorporates volatiles resulting from selection on the whole plant (Raguso 2008, 2009; Junker and Parachnowitsch 2015; Chap. 11). Floral scent could, therefore, inadvertently provide cues to unwanted visitors that are attracted and not repelled by its constituents. Abiotic features of the environment can also cause intraspecific variation in the quality and quantity of floral scent (Majetic et al. 2009). Yet, increasing the quantity of floral scent may not necessarily increase attraction as shown for *Manduca sexta*, which exhibited the same behavioural response to a 1000-fold variation in floral scent concentration (Riffell et al. 2009). Therefore, how much floral scent a plant should optimally produce is not well understood.

Floral scents may incorporate true evolutionary novelties and convergences onto scent components relevant to pollinators, such as prey alarm pheromones (Stöckl et al. 2011), green leaf volatiles that signal herbivorous prey to predatory wasps (Brodmann et al. 2008), mimics of pollinator sex pheromones (Peakall and Whitehead 2014), deceptive scents that signal availability of food to kleptoparasitic pollinators (Heiduk et al. 2015, Oelschlägel et al. 2015), the scent of brood sites involving mimicry of carrion odours attracting flies, dung/urine odours attracting beetles and flies and the fly-attracting odours of fermenting fruit (Urru et al. 2011; Moré et al. 2013). In floral scents that mimic vital features of insect biology such as food resources or mates, even imperfect mimicry is adequate to attract pollinators by capitalising on sensory exploitation (Schaefer and Ruxton 2009). Tapping into pre-existing olfactory circuits can effectively draw flies to pollinate flowers that mimic the odour of yeasts (Stöckl et al. 2010) or may be responsible for the convergence of moth-pollinated flowers towards certain scent combinations (Riffell 2011). Why moths have pre-existing circuits that are tuned to oxygenated aromatic compounds that dominate the scent of many moth-pollinated plants (Riffell et al. 2013) is not known; however, aromatic compounds are also emitted by many insect orders including Lepidoptera (Schiestl 2010). It is possible, therefore, that moth-pollinated plants emit volatiles that moths also employ in their own communication and hence exploit pre-existing biases in moth receivers to facilitate this cross-kingdom communication (Schiestl 2010).

10.2.2 Chemical Noise amid Floral Volatile Plumes

The airspace contains many volatiles of biogenic origin that also exhibit diel and seasonal changes (Laothawornkitkul et al. 2009; Jardine et al. 2015; Yáñez-Serrano et al. 2015). How pollinators deal with this background chemical noise considering that most floral scents are composed of a common set of compounds is one of the most challenging aspects of volatile reception and behavioural response (Schröder and Hilker 2008; Nehring et al. 2013; Wilson et al. 2015) and is the olfactory equivalent of the acoustic cocktail party effect (Krishnan et al. 2014) (Fig. 10.1). The insect pollinator olfactory detection and reaction system is hierarchical (Wicher 2015). The peripheral detection system consists of olfactory receptors (ORs) borne on olfactory receptor neurons (ORNs) housed in porous protuberances (sensilla) on the antenna. ORNs bearing similar ORs converge onto hubs or nodes (glomeruli) in the antennal lobe, and from here information is transferred to higher

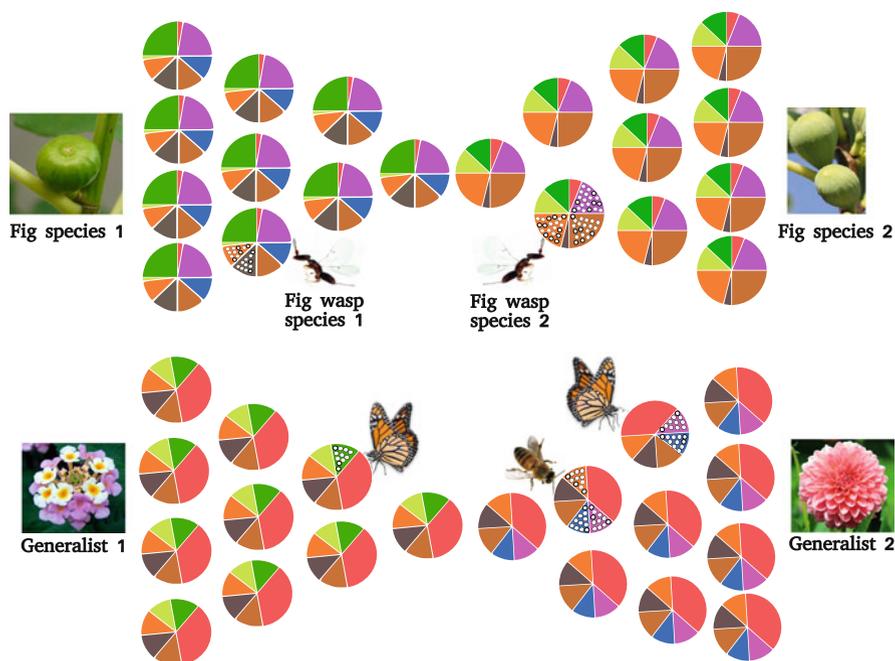


Fig. 10.1 Plants emit volatiles from flowers or associated structures to attract pollinators. Volatiles are emitted into the air and move as packets depicted here as pie charts, where each colour denotes a different volatile. *Dotted colours* indicate volatiles that are not detected by pollinator antennae. Though specialist plants such as fig species (1 and 2) emit many volatiles in common, they may do so in different ratios, and their specialist fig wasp pollinators (species 1 and 2) may not detect all compounds. This may confer specificity in the interaction between plants and pollinators. Generalist plants (1 and 2) may also share emitted volatiles and, if pollinated by the same species, may attract them using the same set of volatiles or a subset of these compounds based on what the antennae detect

processing centres such as the mushroom body or lateral protocerebrum where behavioural decisions are made (Szyszka and Galizia 2015) (Fig. 10.2).

Floral scents emitted from plants spread by the slow process of molecular diffusion and the faster process of advection via windy airflows which are often turbulent (Weissburg 2000). Scents move in filaments consisting of packets of high odour concentration interspersed with areas in which the odour is absent (Murlis et al. 1992). This means that a pollinator searching for a relevant floral odour could perform anemotaxis (using surging upwind flight). However, since the odour is intermittently available, many pollinators perform a casting or zigzagging behaviour when they first encounter an odour plume with some valence (i.e. behavioural relevance) in order to increase the probability of sustained encounter with the scent (Vickers 2000; Cardé and Willis 2008; Beyaert and Hilker 2013). Some insects use wing movements to actively draw air over the antennae (Sane and Jacobson 2006), which might effectively increase the encounter of antennal sensilla with floral scent compounds.

Wind speeds and the structures of odour plumes at the locations where pollinators encounter them will determine their responses and their ability to track floral resources. For example, the wind-dispersed pollinators of fig trees were captured throughout the diel cycle at heights ranging from 25 to 75 m above the ground in tropical forests in Asia where the canopy is about 35 m in height (Harrison and Rasplus 2006). Pollinators of dioecious figs may, however, be found at lower heights compared with those of monoecious figs (Harrison 2003); at these heights wind speeds are lower, and the scent plume structure and movement is likely quite different (Girling et al. 2013). Thrips that are important in brood-site pollination mutualisms are also wind dispersed (Appanah and Chan 1981). How fig wasps and thrips respond to odour plumes at the heights at which they travel is scarcely known. Since plumes are dynamic, the olfactory detection ability of pollinators must match this spatiotemporal variability. This is why the initial process of olfaction in insects is fast; olfactory transduction can occur within 2 ms and fluctuating odour stimuli can be resolved at frequencies of more than 100 Hz at the antenna (Szyszka et al. 2012, 2014).

10.2.3 Reception and Decoding of Volatile Messages

Although hundreds of volatiles may occur within a floral scent, the pollinator antenna can detect only a subset of these (Bruce et al. 2005) (Figs. 10.1 and 10.2). The detection can be influenced at a variety of levels.

10.2.3.1 Discrimination at the Olfactory Receptor Level

The first possible filter to ‘noise’ in the floral signal is the presence of odorant-binding proteins (OBPs) in the peri-sensillar space (Fig. 10.2); these OBPs are

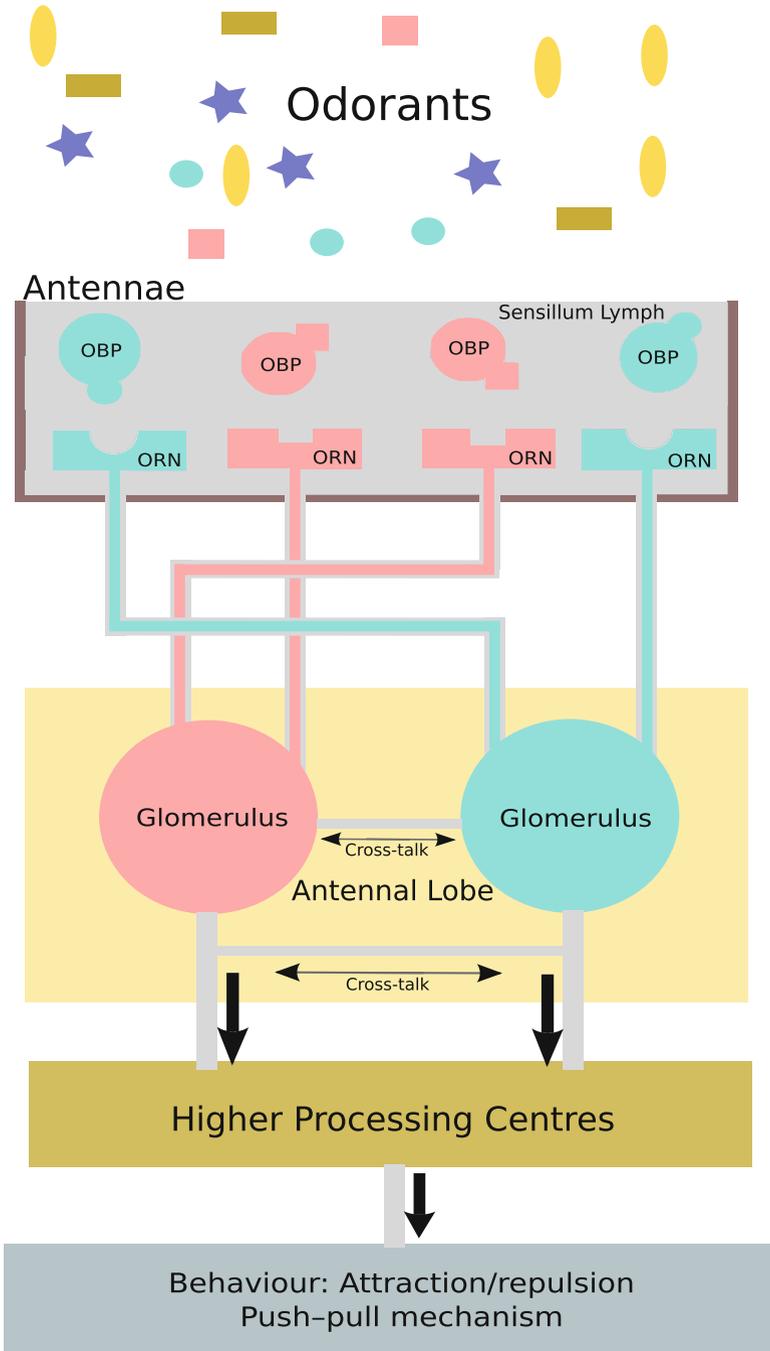


Fig. 10.2 Schematic depicting the flow of information from the peripheral olfactory detection system at the insect antenna to the higher processing centres culminating in attraction or repulsion behaviour in response to volatile reception and crosstalk (excitation or inhibition) between olfactory circuits at various levels. The figure is not drawn to scale and omits anatomical details.

highly diverse and may help in the transport of highly hydrophobic volatiles into the OR detection system (de Bruyne and Baker 2008). The fig wasp *Ceratosolen solmsi* that pollinates the dioecious *Ficus hispida* has only seven OBPs. This is one of the smallest insect OBP repertoires and may reflect its high host specificity (Wang et al. 2014). ORs show high rates of evolutionary change (McBride and Arguello 2007; Nei et al. 2008; Ramdya and Benton 2010; Cande et al. 2013). Compared to humans in which there are 800 OR genes and ~400 intact ORs (Mainland et al. 2014), insects have fewer OR genes, e.g. 163 in *Apis mellifera* (Robertson and Wanner 2006), 62 in *Drosophila melanogaster* (Robertson et al. 2003) and 79 in *Anopheles gambiae* (Hill et al. 2002). These numbers have been further reduced in the highly specialised fig wasp *C. solmsi* which has only 46 OR genes (Xiao et al. 2013) some of which are evolving rapidly (Lu et al. 2009). Similarly, specialist flies lose OR genes ten times faster than related generalist species (McBride 2007).

Despite the relatively small number of ORs, pollinators use volatiles to navigate and find their mates, resources and brood sites in a world of great volatile complexity. Much of the discrimination could occur at the peripheral olfactory system (Hansson and Stensmyr 2011; Bohbot and Pitts 2015). Most ORs are believed to harbour multiple sites where portions of odorants can bind; a combination of odorants binding at different receptors can trigger a seemingly endless set of coding combinations via a combinatorial code for odour detection (Malnic et al. 1999). While many receptors respond to a wide range of ligands (volatiles) at high concentrations (e.g. at the micromolar scale), they are actually narrowly tuned to only one ligand at lower concentrations (e.g. at the nanomolar scale) (Hughes et al. 2010; Liu et al. 2014; Bohbot and Pitts 2015); it is possible that such low concentrations have real ecological relevance in scent plumes (Andersson et al. 2015). Bohbot and Pitts (2015) plead for greater understanding of receptor binding and the search for ligands with ecological/behavioural valence at biologically relevant concentrations. This is why knowledge of ‘real’ concentrations of floral scent volatiles within ‘real’ plumes becomes so important in understanding host localisation by pollinators.

10.2.3.2 Discrimination at the Sensillum Level

Since pollinators encounter scent plumes with high intermittency of odour presentation owing to their dynamic nature in turbulent airflows, it is important that sensilla contain ORNs that are tuned to those components in the relevant mixture that are most likely to be found together (i.e. components of a host plant floral scent) compared within another odour plume in its vicinity. Binyameen et al. (2014)

Fig. 10.2 (continued) OBP odorant-binding protein in the peri-sensillar space; *ORN* olfactory receptor neuron. ORNs that bind to one type of odorant converge onto one type of glomerulus

showed that co-localisation of sensilla improved the spatiotemporal resolution of odours. Other workers have hypothesised that co-localisation of specific ORNs in sensilla may help detect ratios of ecologically relevant scents (Bruce et al. 2005). Often ORNs within the same sensillum may be tuned to volatiles within different biosynthetic pathways, and this may also give pollinators an additional level of discrimination about the source and valence of the volatiles (Bruce and Pickett 2011).

10.2.3.3 Discrimination at the Glomerulus Level and Higher

Within the antennal lobe, local neurons play an important role in inhibition, excitation and synergistic effects within and between glomeruli (Fig. 10.2). Output projection neurons convey this summated information to the mushroom bodies and to the lateral protocerebrum where higher-order processing of olfactory information occurs (Galizia 2014). Push–pull circuits must operate in the antennal lobe via exhibitory–inhibitory connections that exist between neurons and discrimination of scents may be fine-tuned by such interneuron activity (Cunningham 2012; Galizia 2014). However, in some insects, those glomeruli housing neurons that have narrowly tuned ORs tend to have fewer local interneurons (Chou et al. 2010) suggesting that they belong to dedicated circuits that do not require lateral inhibition (Galizia 2014). Only comparison between circuits in pollinator species that have different ecologies such as specialist versus generalist pollinators will suggest general design principles (see Burger et al. 2013 for such a comparison between an oligolectic bee and the generalist honeybee).

10.2.3.4 Co-ordinated Changes at Different Sensory Levels to Match Ecology and Physiology

The olfactory system can solve problems of reception and interpretation of volatile messages in various ways. In specialist insects, certain ORNs and corresponding glomeruli can be over-represented at the cost of others to improve detection and host localisation (Stensmyr et al. 2003; Dekker et al. 2006; Linz et al. 2013; Goldman-Huertas et al. 2015). If ORNs do not vary in number and type across insect lineages, they can vary in sensitivity and temporal firing pattern in response to preferred host volatiles (Olsson et al. 2006a, b) in order to solve the detection problem. Some volatiles in the scent blend may evoke a stronger positive response than volatiles tested alone, suggesting synergistic effects (Tasin et al. 2007). Some insects show the same behavioural response to the whole blend and to a subset of volatiles in the blend suggesting redundancy in volatile messages (Tasin et al. 2007). It is extremely important to investigate such information redundancy, especially in the context of atmospheric pollution that can degrade floral volatiles and interfere with the interpretation of floral messages by pollinators (Lusebrink et al. 2015).

Since (1) maintaining sensory tissue is expensive, selection for pruning unnecessary sensory circuits should occur (Niven and Laughlin 2008), (2) many species exhibit an over-representation of those ORs/ORNs/glomeruli pertinent to host ecology at the expense of irrelevant circuits indicating that such pruning does happen in the olfactory system, and (3) most insect species in brood-site pollination systems are small and have special life history constraints, it is tempting to speculate that such species may not be able to support generalised ‘jack-of-all-trades’ types of olfactory systems, and hence specialisation will be the norm.

Another way to increase the appropriateness of pollinator behavioural responses to volatile signals is to have the olfactory system modulated by physiological events such as mating. In male and female moths, responsiveness of antennal lobe glomeruli is modulated after mating, resulting in greater attraction towards volatiles of food resources or of oviposition substrates, respectively (Saveer et al. 2012; Kromann et al. 2014).

10.2.4 *Push–Pull Mechanisms in a Sea of Volatiles*

If pollinators encounter volatiles in different packets, and with differences in valence (some that signify food resources, while others signify toxins, predators or other ecological attributes), how might these differences guide their behaviour so that appropriate decisions are made? In the monoecious *Ficus curtipes*, pollinating fig wasps were most attracted by the scent of pollen-receptive female syconia and were actively repelled by the scent of male phase syconia from which wasps were dispersing (Gu et al. 2012). It is believed that this change in floral scents actively repels pollen-carrying pollinators that are leaving their natal figs from remaining in the same tree, thus avoiding geitonogamy (pollen delivery in the same tree), in case pollen-receptive figs are present at the same time on the natal tree (Gu et al. 2012). In *Macrozamia* cycads pollinated by specialist *Cycadothrips*, the thrips are attracted and then repelled by altered fractions of volatiles such that they move between male and female cones to effect pollination (Terry et al. 2007); however push–pull systems do not apply to all cycads (Suinyuy et al. 2013). In a highly specialised orchid system, male andrenid bees effect pollination by pseudocopulation with the sexually deceptive flowers; post-pollination production of farnesyl hexanoate by these flowers serves as a repellent to these bees since it serves as an antiaphrodisiac (Schiestl and Ayasse 2001). A pollinating moth in a brood-site pollination mutualism also avoids flowers infected by a pathogenic fungus as this would prevent successful development of seeds and of the seed-eating larvae (Biere and Honders 2006); however, whether fungal volatiles alone are responsible for this avoidance behaviour or whether the infected plants produced an altered volatile profile is not known.

Repellency plays an important role in push–pull systems. In this case, insects may also have receptors for volatiles produced by their non-host plants so that they can recognise and avoid them (Nottingham et al. 1991). Repellent odours affect

avoidance behaviour in several ways. Repellents may act at the peripheral olfactory system by serving as competitive or non-competitive antagonists of ORs or co-receptor subunits (Chen and Luetje 2013; Dickens and Bohbot 2013; DeGennaro 2015) and thus inhibit and mask the effect of a cognate ligand. Repellents may bind with the odorant and prevent its binding to the OR (Dickens and Bohbot 2013). They may act as molecular confusers by changing the response of several ORNs to the odorant and effectively scrambling odour coding by glomeruli (Pellegrino et al. 2011; DeGennaro 2015). Some repellents activate unique neural circuits dedicated to the avoidance response (Suh et al. 2004; Stensmyr et al. 2012). Repellents may carry messages about host unsuitability. For example, methyl jasmonate is an HIPV and is produced by stressed plants in which defence machinery has been activated (Schuman and Baldwin 2012). Herbivorous insects such as seed parasites in brood-site pollination mutualisms or mosquitoes in which nectar-feeding occurs (Zhou et al. 2014) should have innate avoidance behaviours to such stressed plants unless they use HIPVs to locate hosts as previously suggested. It is therefore interesting that the evolutionary origin and ecological significance of the action of the mosquito repellent *N,N*-diethyl-*meta*-toluamide (DEET) is believed to be due to its similarity in action and binding to the receptor for the plant volatile methyl jasmonate (Xu et al. 2014).

While individual volatiles may be repellent when presented singly, a blend containing the same volatiles may be attractive (Webster et al. 2010; Bruce and Pickett 2011) suggesting that the blend provides the appropriate behavioural context. Robust information coding systems that can distinguish host from non-host must also have the ability to cope with the prevalent intraspecific variation in host volatile profiles. Despite the importance of understanding odour repellency in host plant location, the phenomenon is not well understood.

10.3 An Evolutionary Perspective on Floral Scent in Brood-Site Pollination Mutualism: Putting It All Together

Some authors have suggested that an information theory approach could be useful in understanding volatile communication between plants and insects (Wilson et al. 2015). For such an approach, the detection of true patterns and the discovery of real processes are essential. It is clear that while common principles of volatile detection apply across systems, insects have solved the problem of locating their hosts in a variety of ways. Yet, it is important to remember that volatile communication using floral scents is a cross-kingdom communication. Since this communication signal has to work across kingdoms, from a signal fidelity point of view, i.e. being able to produce the same signal that evokes the same response in a receiver, it may be important for plants to co-opt reliable volatile production pathways that were already in existence for other basic functions; this may reduce

the efficiency cost of communication (Hackett et al. 2014). Could this explain why the same sets of common volatiles/volatile classes occur repeatedly in floral scents? The onus is then on the receiver to be able to extract the signal from the ‘noise’ and to even determine what the signal is; it is entirely possible that the same set of volatiles presented to two different receivers would be perceived as different signals (Kessler et al. 2013) (Fig. 10.1). This is why we need more studies such as Ayasse et al. (2000), Salzman et al. (2007) and Ibanez et al. (2010) who were able to show that the subset of floral scent compounds active at the pollinator’s antenna exhibited much less variation in the blend than those to which the antenna was insensitive. Blends at ecologically relevant concentrations need to be used in all tests and even in single sensillum recordings. We also need to measure volatile fluxes at the antenna in order to understand the concentrations at which this communication occurs (Andersson et al. 2012).

The type of behavioural assay used to determine valence of compounds and blends may also influence the results. For example, Wang et al. (2013) rightly point out that many fig wasps do not perform in conventional Y-tube olfactometers with dimensions that preclude wasps from performing normal flight, so interpreting results using such setups could be questionable. In *Drosophila*, for example, there is one pathway that can trigger aversion to CO₂ in walking flies but another that results in positive chemotaxis to CO₂ when flies are in flight (Mansourian and Stensmyr 2015). Clearly, functionally relevant assay systems must be employed.

Brood-site pollination mutualisms usually exhibit a high degree of specificity between plants and individual pollinator species or groups. Many of these insects also engage in active pollination, which should indicate tight specialisation between plants and pollinators. However, it may be useful to ask whether passive pollination necessarily means lower specificity in floral scents. This may be true in pollination by *Hadena* and *Greya* moths (Table 10.1) that also use other plant hosts, but may not be true of other brood-site pollination systems. It may also be useful to examine whether the occurrence of mating at the brood site increases the specificity of the interaction. In fig wasps, mating in the next generation (i.e. pollinator progeny) occurs within the brood sites, but in other species mating of pollinators occurs on or in the brood site (Table 10.1). Is it possible that some of the components of the mating pheromone or those that release the mating sequence may also be found in the floral scent of such systems?

In this chapter, the role of factors other than pollinator attraction in altering the compositions of floral scent has not been reviewed. These factors may include biotic stresses such as deterrence of florivores or pollen and nectar thieves (Kessler et al. 2013), as well as abiotic stresses, especially under the scenario of climate change and increases in tropospheric ozone and other atmospheric pollutants (McFrederick et al. 2008; Farré-Armengol et al. 2013; Blande et al. 2014). We need to address floral scents in the context of multimodal signals (Junker and Parachnowitsch 2015). For example, even classical studies, in which visual signals coupled with morphology were considered sufficient to explain differential pollinator visitation, now also invoke the role of floral scent in promoting reproductive

isolation (Byers et al. 2014a, b). It is insufficient to consider floral scents alone, even in highly specialised interactions (Rakosy et al. 2012).

We need perspectives from ecology, evolution, chemistry, atmospheric science, fluid dynamics, behaviour and neurobiology in order to make sense of the communication between plants and animals using volatiles. This is especially important in systems that are as complex as brood-site pollination mutualisms in which, besides the issues of attracting a pollinator and exchanging an ephemeral reward, there are a set of pollinator developmental and life history constraints that must be factored into our understanding. The need of the hour is collaboration between various disciplines that will provide better answers to Jean-Henri Fabre's query about a seemingly elusive communication using volatiles.

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