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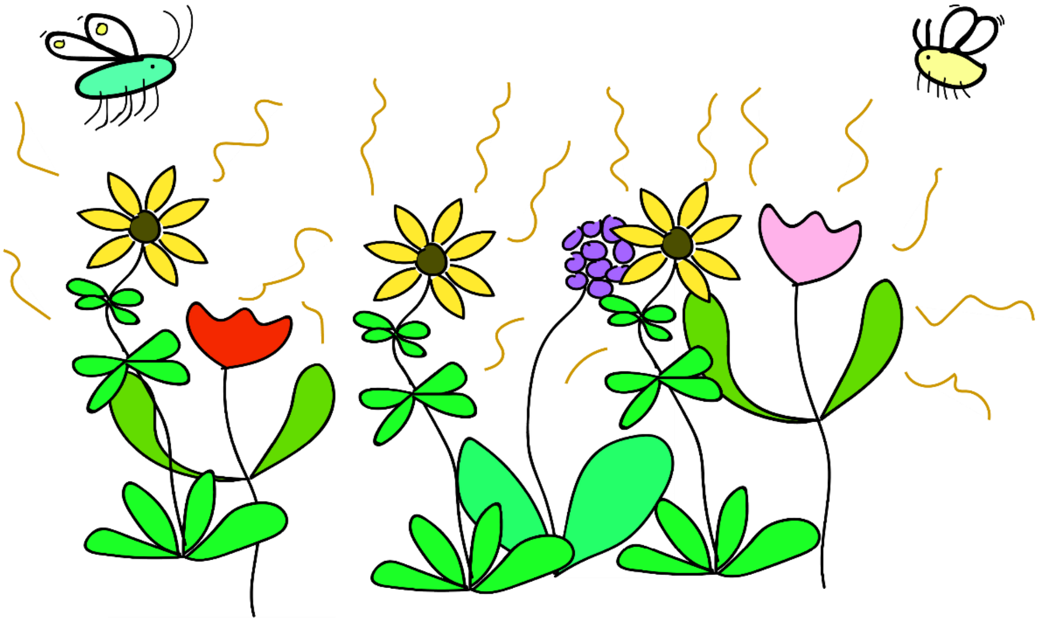
Department of Plant Protection Biology

Reliable Host Plant Recognition in Insects

Axel Rösvik



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Summary

Insects perceive their world to a large extent through olfaction. Volatile organic compounds released by the biota is therefore of utmost importance for host plant identification and selection in phytophagous insects. Plants release species-specific bouquets of volatile organic compounds which insects use as cues to guide behaviour in several life stages. For reliable localization of suitable host plants, insects need to be able to generalize and discriminate between these important cues. Several theories on the information of the odour bouquet that is used for reliable plant identification have been postulated during the last decades. Empirical studies have shown that plant identification in many species depend on ubiquitous volatile compounds, but that there are examples that insects use species-specific compounds or a combination of the two types of compounds. The response to plant cues can also show phenotypic plasticity and change depending on environmental conditions. For example, previous experience of particular host plants has been shown to affect the behaviour of insects through within-generation phenotypic plasticity. It is also possible that information from earlier experience could be transferred vertically from one generation to the other through transgenerational phenotypic plasticity.

This review gives an overview of host plant identification in insects. First, a brief overview of plant organic compounds and olfaction is made. Then the focus shifts to how volatile plant organic compounds are perceived by the olfactory system of insects and how they affect generalization and discrimination processes during host plant selection. Lastly, I discuss how plasticity, both within and across generations, can affect the behavioural outcome.

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1 Introduction

Host plant identification and selection is important for herbivorous insects, as plants, on which the herbivores feed, vary in suitability (Bernays and Chapman, 2007). In adult insects, the ability to identify a host plant is particularly important during oviposition where the fitness of the offspring often depends on the selection process of the mother. However, if an inferior host is chosen by the adult, the offspring can in some species make up for the mistake of the mother and themselves identify and select a suitable host plant to secure further development (Zalucki et al., 2002).

Many insects rely to a great extent on olfaction for decision-making and possess a sensitive olfactory system for detection and integration of various volatile cues (Bruce and Pickett, 2011). During host plant identification, olfactory cues perceived from a distance are together with visual cues the first step of identification (Schoonhoven et al., 2005). When emitted from a potential host plant, these cues trigger a searching behaviour and the insect starts to orient upwind towards the source of the stimuli. Odour cues released from host plants are thought to generate intermittent cone shaped plumes that supply an odour 'path' that can be followed by the receiver to reach the emitter (Beyaert and Hilker, 2014; Conchou et al., 2019). These odour paths are distributed from the emitter through diffusion and then transported further with the wind, creating a chemical trail much like that of a path in a physical landscape that can be seen as a part of an overall odourscape. These paths in the odourscape are steadily affected by various biotic and abiotic factors that change over a spatiotemporal scale creating a continuously changing odourscape (Figure 1). When a potential host plant has been approached by the insect, further evaluation is carried out through mechanosensation and gustation (Schoonhoven et al., 2005). During these selection processes, the sensory information can either lead to acceptance and thus next step in the selection process takes place, or avoidance if the plant is recognized as a non-host or of inferior quality (Bruce et al., 2005).

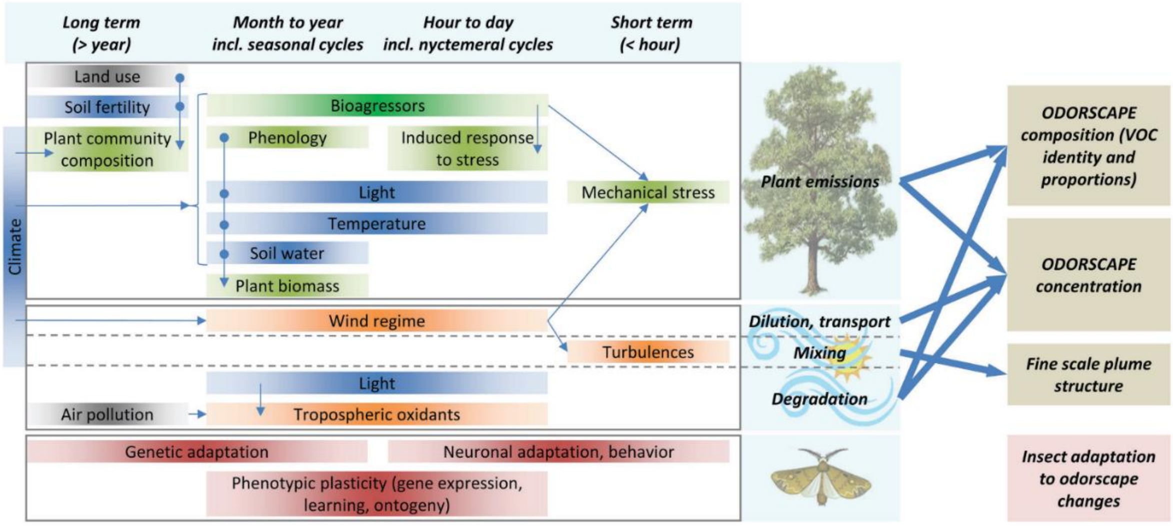

Figure 1. The left box indicate the various biotic and abiotic factors and the temporal scale on which they affect the emitter (top), receiver (bottom) and the odourscape (middle). Insect Odourscapes: From Plant Volatiles to Natural Olfactory Scenes from Frontiers in Physiology by Conchou et al. (2019), licensed under CC BY 4.0.

To be able to evaluate and discriminate between plants from a distance insects must be able to distinguish between the volatile headspace from host plants and non-host plants, but also plants of the same species with different odour emission indicating plant quality (Conchou et al., 2017). The volatile headspace of plants can consist of bouquets of up to hundreds of different volatile compounds in various combinations and concentrations (Bruce and Pickett, 2011). This creates a vast array of possible odour bouquets and a complex environment for these odour dependent organisms (Bernays and Chapman, 2007). In this environment, insects need to be able to process the olfactory information regarding the suitability of a potential host plant from the olfactory noise of the surrounding environment (Anderson and Anton, 2014).

The host plant range of insects is another factor of importance in how they respond to the volatile bouquets of plants (Bernays and Chapman, 2007). Insects show a variation in width of the host-plant range that they utilize, where specialist are dependent on one or a few plants, while generalists can use multiple plants for their survival. Specialist need to pay attention to the odour bouquet of the host plant on which they are specialized and distinguish it from non-host odours in the cocktail of volatile compounds present in the air (Bernays, 2001). Contrarily, generalists must be able to differentiate a wider array of odour bouquets since they utilize a larger range of host plants. This suggests that insects could be tuned differently to particular plant volatile bouquets depending on their host range (Bruce et al., 2005). The wide tuning in generalist herbivorous insects may also infer a neurologically more difficult task compared to fine-tuning towards a specific host and its odour profile found in specialists (Silva and Clarke, 2019). This can slow down decision making in generalists compared to specialists due to that the host selection process is more complex (Bernays, 1999; Bernays and Funk, 1999).

The underlying mechanisms of host-plant identification are not fully understood. Evidence of insects using species-specific volatile cues for host plant identification exist but they are scarce. Both the *Brassicaceae* specialists, *Ceuthorrynchus assimilis* and *Brevicoryne brassicae* show attraction to species-specific volatile cues, such as isothiocyanates, volatile compounds characteristic to plants of the *Brassicaceae* family (Nottingham et al., 1991; Blight et al., 1995). Generally, however, the majority of the peripheral receptors on the antennae of an insect are tuned to more ubiquitously occurring compounds (Bruce et al., 2005). This indicates that more generally occurring volatile compounds and the ratios of these are more important to the majority of insects when it comes to host-plant identification compared to single unique compounds. Conceptual models on host plant location are steadily evolving and additional theories such as the 'sequential cues hypothesis' favour that insect herbivores utilize a combination of both ubiquitous and species specific compounds on different spatial scales (Silva and Clarke, 2019).

2 Plant organic compounds

2.1 Primary and secondary metabolites

Living organism all produce primary metabolites that are involved in the growth and maintenance of the organism (Schoonhoven et al., 2005). The main groups are carbohydrates, proteins and lipids, which make up a potential food source for phytophagous organisms. In plants, these primary metabolites constitute the main part of the plant's total biomass (Abe and Higashi, 1991). In addition, plants also produce secondary metabolites (Schoonhoven et al., 2005). These originate from the primary metabolites and the distinction of the two is arbitrary. However, the main difference is that the secondary metabolites are not necessary for the direct maintenance of the organism (Crozier et al., 2006). Within the plant kingdom, over 100 000 secondary metabolites have been identified with a steady increase of new metabolites being identified on a daily basis (Schoonhoven et al., 2005). Although not necessary for the direct maintenance of the plant, these secondary metabolites have important ecological functions such as (i) protection against herbivores and microorganisms, (ii) attractants for pollinators and seed dispersers, (iii) growth inhibitors as allelopathic substances and (iv) signaling molecules towards mutualistic microorganisms (Crozier et al., 2006).

2.2 Volatile organic compounds

Volatile organic compounds (VOC) consist of metabolites with low enough molecular weight to volatilize (Schoonhoven et al., 2005). VOC's are continuously released by almost any kind of plant tissue and any type of plant through open stomates or through ruptured tissue of damaged plants. The vast majority of VOC's released by plants originates from four metabolic pathways, the mevalonic acid (MVA) and methylerythritol phosphate (MEP) pathways for terpenoids, the lipoxygenase (LOX) pathway for fatty acid derivatives, the shikimate acid pathway for benzenoids and phenylpropanoids, and the amino acid derivatives pathway (Figure 2). Additionally, other metabolic pathways exist for more species specific compounds (Dudareva et al., 2013). VOC's can be ubiquitous and released by a variety of plant species from different genera or more taxon-characteristic which means that they are less abundant in the plant kingdom (Schoonhoven et al., 2005). 'Green leaf volatiles' (GLV) are an example of more ubiquitously occurring VOC's (Scala et al., 2013). They consist of six-carbon saturated or monounsaturated alcohols, aldehydes and esters and are released through the damaged tissue of green plants although undamaged plant tissue also can release small amounts (Schoonhoven et al., 2005). Additionally, VOC's not considered GLV's can also show variation in the release rate due to biotic and abiotic conditions which can lead to fluctuations in the headspace composition of the plant (Conchou et al., 2019). Both abiotic and biotic stressors such as herbivores, pathogens and temperature can increase the production of GLV. An example of more taxon-specific VOC's are isothiocyanates, a group of sulfur-containing breakdown products from glucosinolates, characteristic for plants within the *Brassicaceae* family (Bernays and Chapman, 2007). Plant metabolites, including VOCs, can carry information perceivable by other individuals and species and are then considered as allelochemics. Depending on their function, they can forsee the receiver (kairomone), emitter (allomone) or both (synomone) with information (Nielsen et al., 2015).

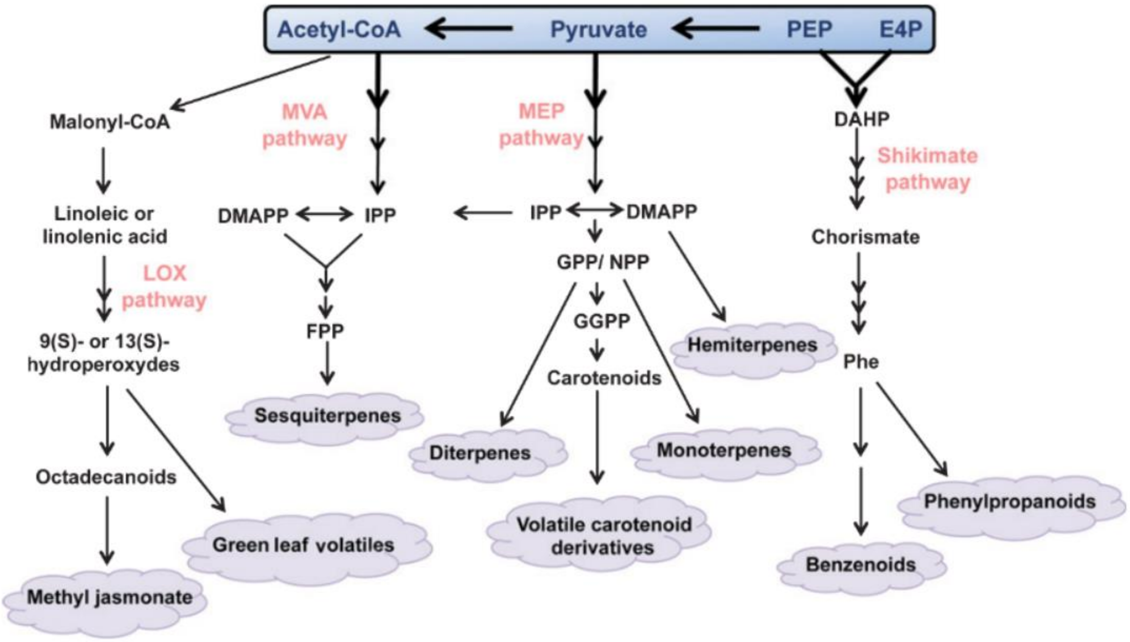

Figure 2. Overview of the four metabolic pathways originating from the precursors from the primary metabolism represented in the blue box. Lipoxygenase pathway (LOX) creating methyl jasmonate and green leaf volatiles, the melavonic acid pathway (MVA) creating sesquiterpenes, methylerythritol phosphate pathway (MEP) creating mono-, di-, and hemiterpenes and carotenoid derivatives, shikimate pathway creating benzenoids and phenylpropanoids. Single arrows indicate single enzymatic reactions while stacked arrows illustrate multiple enzymatic reactions. Abbreviations: DAHP, 3-deoxy-D-arabinoheptulosonate-7 phosphate; DMAPP, dimethylallyl pyrophosphate; E4P, erythrose 4-phosphate; FPP, farnesyl pyrophosphate; GGPP, geranylgeranyl pyrophosphate; GPP, geranyl pyrophosphate; IPP, isopentenyl pyrophosphate; NPP, neryl pyrophosphate; PEP, phosphoenolpyruvate; Phe, phenylalanine. Reprinted from New Phytologist, 198, Natalia Dudareva, Antje Klempien, Joëlle K. Muhlemann and Ian Kaplan. Biosynthesis, function and metabolic engineering of plant volatile organic compounds, 16-32, Copyright (2013), with permission from John Wiley and Sons.

Different plant species release various blends of VOC's (Dudareva et al., 2013). The vast number of VOC's creates a wide array of combinations that can be present in the headspace of a plant and thus no two plant species have the same headspace (Bernays and Chapman, 2007). Vegetative tissue usually releases less complex bouquets compared to flowers that can produce complex odour bouquets (Arimura, 2004; Knudsen et al., 2006). Insects are able to utilize these VOC's to localize host plants (Schoonhoven et al., 2005). When the VOC's travel downwind in odour pockets, they act as allelochemics and insects downwind can evaluate whether a potential host plant is located further upwind. In order for the insect to elicit a behavioural response, the VOC's must be presented in the right quality and quantity to create an 'odour image' perceivable by the insect (Hildebrand, 1995). This implies that the species-specific headspace of the plants is of utmost importance for phytophagous insects when it comes to finding a suitable host plant (Bruce et al., 2005).

3 Olfaction in insects

3.1 The peripheral olfactory system and the antennal lobe

The olfactory system of insects is less complex than that of mammals. However, this does not mean that insects are less sensitive to odour cues (Sachse and Krieger, 2011). Insects detect odour cues present in nature through their antenna which is their primary olfactory organ (Hansson, 1999). The insect antennae contain sensilla which are hair-like structures filled with sensillum lymph, which can be divided into different types depending on their morphological structure (Hansson and Stensmyr, 2011). The sensilla inhabit olfactory receptors (OR) and ionotropic receptors (IR) that are embedded in the cell membrane of the olfactory receptor neuron (Sachse and Krieger, 2011). The sensory receptors are activated by molecules that bind to the receptor and where some receptors responding to plant volatiles are broadly tuned while others can have a more narrower tuning (Andersson et al., 2015). The ORs are activated by binding ligands such as acetates, aldehydes and aromatics while the IRs are activated by ketones, acids and amines (Grabe and Sachse, 2018). ORs co-exist with the co-receptor Orco which is highly conserved between species (Butterwick et al., 2018). The co-existence of the two heteromeric cation channels is necessary for odour detection to be possible. Additionally, gustatory receptors that underpin the perception of taste can to some extent be used by the insect to detect olfactory information (Missbach et al., 2014).

A problem in host odour detection is to know the origin of the ubiquitous compounds in the surrounding air of an insect looking for a suitable host plant. The timing of the response to the different compounds has been found to be very important. According to the coincidence detection theory, the receptors in the sensilla must be able to pick out complex host cues traveling in distinct odour pockets released by the host plant in the heterogeneous cocktail of odours (Bruce et al., 2005; Baker, 2009). An important factor here is the co-location of ORNs present at the same sensillum of the antenna (Stensmyr, 2003), that allows the insect to detect very small time differences in the response to the different compounds and therefore be able to distinguish whether the compounds that hit the sensillum originates from the same source or not (Figure 3). Information from the same source are expected to travel within the same air pocket and thus activate the ORNs at the same time. The information received by the ORNs are then forwarded through the olfactory sensory neurons (OSN) to the central nervous system (CNS) of the insect where it enters the antennal lobe (AL) (Hildebrand, 1995; Hansson, 1999; Andersson et al., 2015).

The AL consists of round structures, glomeruli, where each glomeruli receives information from that particular type of receptor through the OSRs (Vosshall et al., 2000). The olfactory information is further transferred between glomeruli within the AL by local interneurons (Hansson and Anton, 2000). This is often considered the first step in the processing of olfactory information in insects. The number of glomeruli differ between insect species, ranging from 50 and 60 in fruit flies and moths, 160 in the honeybee and up to 1000 in some species within Orthoptera and Hymenoptera (Hansson and Anton, 2000; Sachse and Krieger, 2011). Males in some insect species, particularly moths, hold extra pheromone specific glomeruli that form the macroglomerular complex (Hansson, 1999).

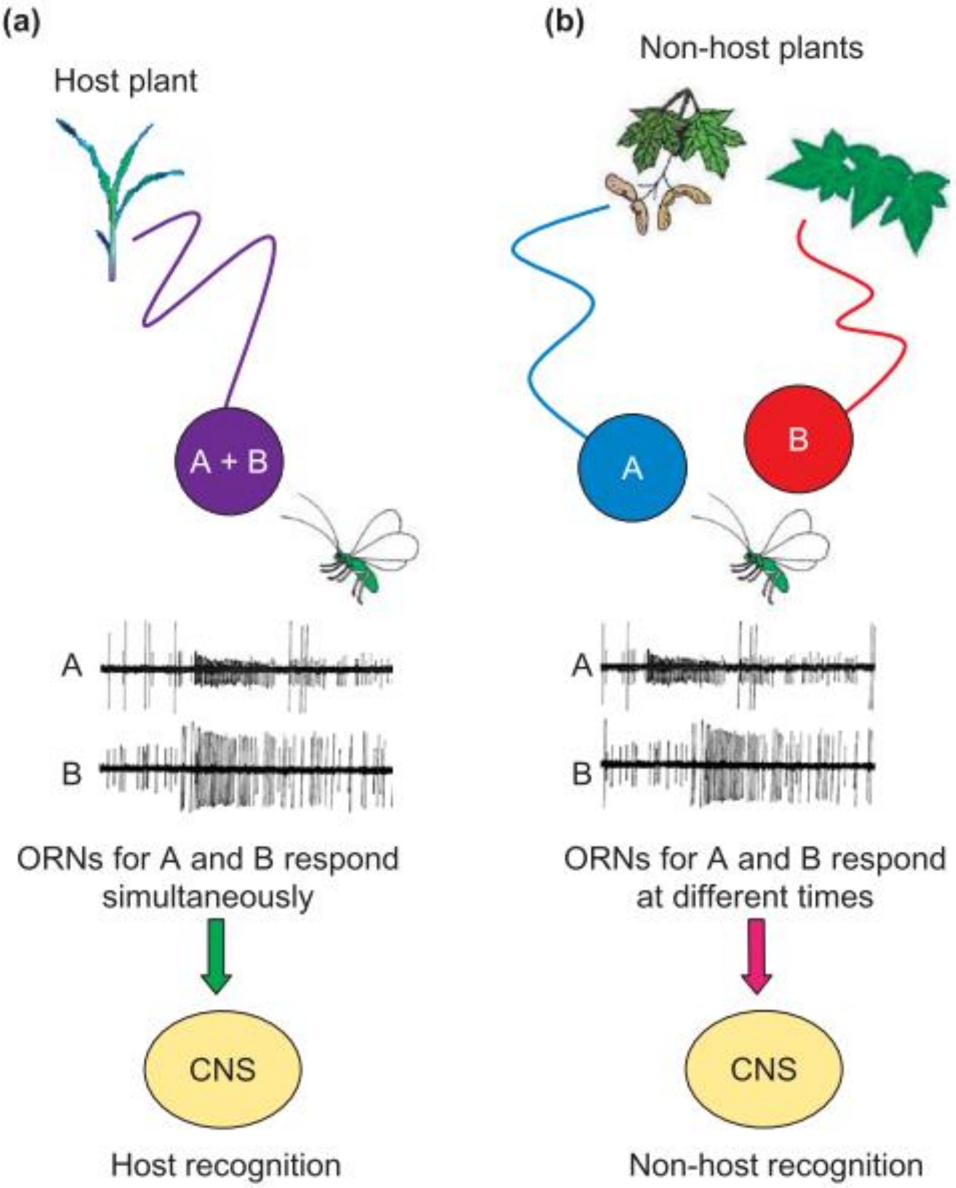

Figure 3. Coincidence detection theory. (a) ORNs for odour A and B fire simultaneously, indicating that the perceived odour cue is from a host. (b) ORN's for odour A and B fire at different times, indicating that the odour perceived emanated from two different non-hosts. Reprinted from Trends in Plant Science, 10, Toby J.A. Bruce, Lester J. Wadhams, Christine M. Woodcock, Insect host location: a volatile situation, 269-274, Copyright (2005), with permission from Elsevier.

3.2 The higher brain and the behavioural outcome

From the AL, the information is passed through projection neurons (PN) to the higher brain centers in the protocerebrum such as the mushroom bodies (MB) and the lateral horn (LH) which are the most prominent structures in the higher brain (Hansson, 1999). These structures are important in the interpretation of olfactory information and operates olfactory-related behaviour in insects (Hansson, 1999; Sachse and Krieger, 2011). Within the MB, the PN synapse into a large number of MB neurons, the Kenyon cells (KC), and it is believed that specific odours activate certain sets of KCs as a response to a particular odour (Heisenberg, 2003; Turner et al., 2008; Luo et al., 2010). The combinatorial activation of KCs are believed to be of importance during learning and memory formation in insects and have been well studied during the last decades.

In the LH, the PN from the AL reveals a more systematic zonal pattern compared to that of the MB (Grabe and Sachse, 2018). Each one of these zones are related to specific features of odours such as pheromones and food (Jefferis et al., 2007) e.g. attractive amines and aversive acids (Min et al., 2013). This suggests that the odour specificity is lost in the higher brain and instead categorized through the behavioural relevance of the odour (Grabe and Sachse, 2018). The output of the odour processing in the higher brain influences the premotor neural activity and triggers behavioural responses to the experienced odour stimuli (Hildebrand, 1995). An example of such behaviour is the upwind flight that is triggered when a phytophagous insect detect host plant VOC's (Schoonhoven et al., 2005).

4 Odour bouquets of plants – perception and meaning of plant odour cues to insects

The natural environment of insects is full of olfactory cues emitted from a wide array of plants. One single plant can release hundreds of VOC's that can be perceived by the insect (Bruce and Pickett, 2011). This implies that insects must be able to locate their host plants in complex olfactory environments, where a continuous cocktail of various compounds are released by the plant community. Fraenkel (1959) came up with two contrasting hypotheses on how this is done. The first hypothesis, called token stimulus theory, implies that insects use species-specific compounds for host recognition. Although there is sparse evidence for this, some insects rely on taxonomically specific compounds for host plant identification (Guerin et al., 1983; Nottingham et al., 1991; Bjostad and Hibbard, 1992; Blight et al., 1995; Baoyu et al., 2001).

Secondly, Fraenkel (1959) hypothesized that ratio-specific odour recognition might be the general way insects recognize host plants from non-host plants. This implies that insects instead of relying on a particular compound to identify their host plant rely on the blends and ratios of ubiquitously found compounds. This hypothesis is supported by behavioural and electrophysiological studies on a wide range of herbivorous insects (Bruce et al., 2005). In a study by Riffell et al. (2009), the moth *Manduca sexta* were not attracted by single compounds from its host plant flower and elicited random search flight trajectories when exposed to these compounds alone. However, when exposed to a synthetic nine-component blend of the host plant flower compounds, the moths responded to the synthetic blend to the same extent as to the host-plant flower itself. In total, 60 compounds were emitted from the headspace of the flower but only nine of them were of behavioural importance for *M. sexta*. In a similar study by Visser and Avé (1978), the same pattern was found. Potato odour was shown to be attractive to the Colorado beetle, *Leptinotarsa decemlineata*, but when the compounds in the potato blend were presented alone no attraction was shown for any of the compounds. Several other studies also support these findings and usually 3-10 compounds within the headspace of a plant that is considered key in host recognition (Table 1). In addition, a compound that is a part of an attractive blend could when presented alone in the same concentration be repellent (Webster et al., 2010).

Table 1. Examples where the behavioural outcome towards the volatile blend exceeds that of the individual compounds within the blend. Based on table from from Phytochemistry, 72, Toby J.A. Bruce,John A. Pickett, Perception of plant volatile blends by herbivorous insects – Finding the right mix, 1605-1611., Copyright (2011), with permission from Elsevier.

Insect	**Plant**	**VOC's**	**Ratio**
Lepidoptera			
Cabbage butterfly, *Pieris rapae*	Privet flowers, *Ligustrum japonicum*	Phenylacetaldehyde	
		2-phenylethanol	
		6 methylhept-5-en-2-one	
		Benzaldehyde	
		Methyl phenylacetate	
Cotton bollworm, *Helicoverpa armigera*	African marigold flowers, *Tagetes erecta*	Benzaldehyde	1
		(*S*)-limonene	1.6
		(*R*,*S*)-linalool	0.7
		(*E*)myroxide	1.4
		(*Z*)-b-ocimene	0.4
		Phenylacetaldehyde	4.4
		(R)-piperitone	2.7
Oriental fruit moth, *Cydia molesta*	Peach shoots, *Prunus persica*	(*Z*)-3-Hexen-1-yl acetate	4
		(Z)-3-hexen-1-ol	1
		Benzaldehyde	1
Codling moth, *Cydia pomonella*	Apple fruit, *Malus domestica*	(*E*,*E*)-a-Farnesene	10
		(*E*)-b-farnesene	0.1
		Ethyl (*E*,*Z*)-2,4-decadienoate	0.1
Grapevine moth, *Lobesia botrana*	Grapevine berries, *Vitis vinifera*	(*E*)-b-Caryophyllene	100
		(*E*)-b-farnesene	78
		(*E*)4,8-dimethyl-1,3,7-nonatriene	9
Hawkmoth, *Manduca sexta*	Sacred Datura flowers, *Datura wrightii*	Benzaldehyde	
		Benzyl alcohol	
		Linalool (unspecified enantiomer)	
		Nerol, b-myrcene	
		Methyl salicylate	
		Geraniol	

		(*E*)-caryophyllene and a-farnesene	
Diptera			
Mexican fruit fly, *Anastrepha ludens*	Fermenting yellow chapote fruit, *Sargentia greggii*	1,8-cineole	10
		Ethyl hexanoate	1
		Hexanal	1
		Ethyl octanoate	100
Vinegar fly, *Drosophila melanogaster*	Mango fruit, *Mangifera indica*	Ethanol	1
		Acetic acid	22
		2-phenylethanol	5
Orange wheat blossom midge, *Sitodiplosis mosellana*	Wheat panicles, *Triticum aestivum*	(*Z*)-3-Hexenyl acetate	3.4
		3-carene	7.4
		Acetophenone	1.3
		Octen-3-ol	1.7
		2-ethyl-1-hexanol	1.8
		2 tridecanone	607
Ethiopian fruit fly, *Dacus ciliates*	Galia melon fruit, *Cucumis melo*	Benzyl acetate	
		Hexanyl acetate	
		(*Z*)-3-hexenyl acetate	
		(*Z*)-3-octenyl acetate	
		Octanyl acetate	
		(*Z*)-3-decenyl acetate	
Coleoptera			
Garden chafer, *Phyllopertha horticola*	Not based on a particular plant species	(*Z*)-3-Hexen-1-ol	
		Geraniol	
		Eugenol	
		2 phenylethyl propionate	

Not only the components of the blends are important for host plant recognition, but also the ratios in which the compounds are presented in the blend (Bruce et al., 2005; Bruce and Pickett, 2011). Small alterations of the ratio between the VOCs in the blend can change the meaning of the olfactory stimuli to the insect. This is also true for cultivars of the same species where the only difference is the ratio of the VOCs in the odour bouquet (Wright et al., 2005). It has also been shown that different concentrations of behaviourally active blends are decoded by the insect in the same manner if the ratios in which they are presented are the same (Riffell et al., 2009). This implies that natural variations in the overall odour concentration should not affect the behavioural outcome but rather create a similar ‘odour image’. However, a non-natural concentration of a blend could change the perception of the blend and the behavioural outcome (Bruce et al., 2005).

Host plant range also plays an important role in insect host-plant recognition (Bruce et al., 2005). Specialists require host-specific cues to be able to tell whether their host is absent or present (Silva and Clarke, 2019). Contrarily, the ability by generalist herbivores to utilize ubiquitous compounds released by their host plants is thought to underlie the ability to identify a broad range of possible hosts that share VOCs. (Bruce et al., 2005). Therefore, having ORNs tuned to ubiquitous compounds implies that the insect can exhibit a plastic behaviour (Masson and Mustaparta, 1990). However, according to Silva and Clarke (2019), the use of ubiquitous compounds cannot entirely explain the ability of generalist insects to identify such a broad range of host plants. This creates a paradox since the use of ubiquitous occurring compounds is thought to be due to generalists insect having neural limitations to utilize both ubiquitous and species specific compounds to locate such a wide range of hosts (Silva and Clarke, 2019). To overcome this paradox, Silva and Clarke (2019) came up with the sequential cue hypothesis, which suggests that generalist herbivores use ubiquitous 'generalist' cues from afar and a combination of ubiquitous and species specific 'specialist' cues when close to the host plant (figure 4). According to this hypothesis, the ranking of hosts can be done by hosts having unique combinations of traits that make the insect able to discriminate between the hosts. Additionally, an additive mechanism where a smaller number of host cues can add up and the more of these cues that are present in a host the higher is the ranking of that host.

Apart from being able to distinguish host from non-host, the insect olfactory system is also able to distinguish between more and less suitable host plants of the same species (Bruce and Pickett, 2011). Host plants that have been previously damaged by insect pests change their odour headspace and volatiles referred to as herbivore-induced plant volatiles (HIPV) are produced in larger amounts (Dicke, 2009). An example of this is oat, *Avena sativa*, that increase its production of 6-methyl-5-hepten-2-one, (R)- and (S)-6-methyl-5-hepten-2-ol, and 2-tridecanone when infested by the bird cherry-oat aphid, *Rhopalosiphum padi* (Quiroz et al., 1997). An increase in these HIPVs acts repellent and tells *R. padi* that the particular host is unsuitable and already infested with conspecifics, which helps to prevent overcrowding.

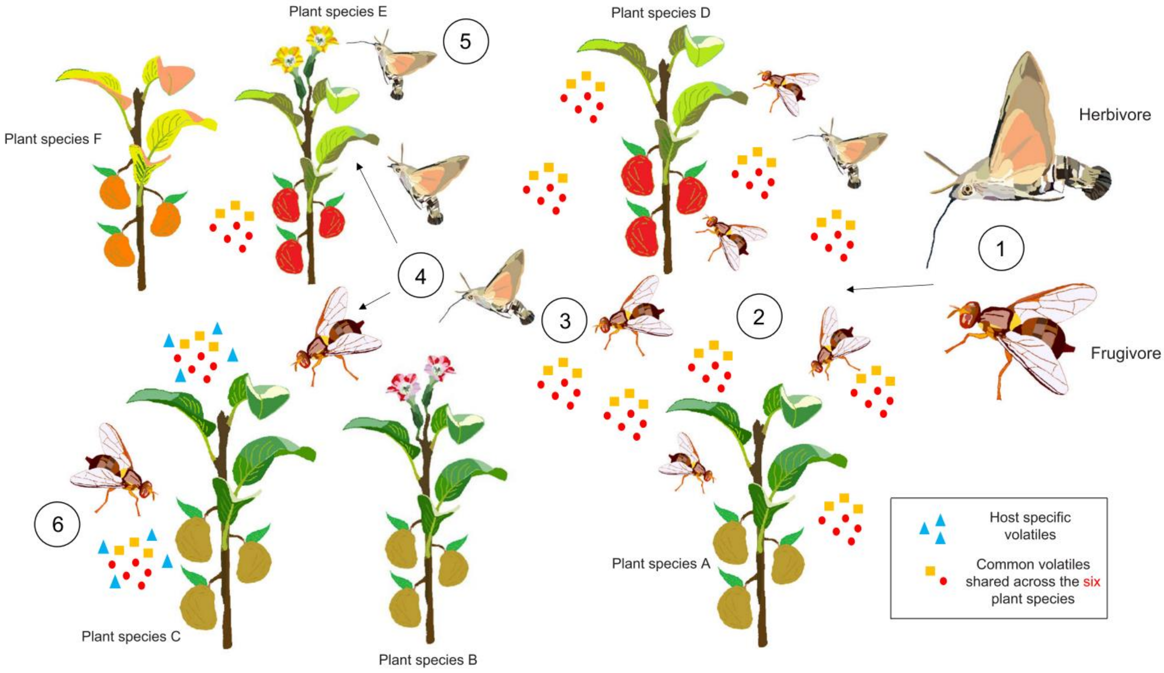

Figure 4. Illustration of host location in generalist insects according to the sequential cue hypothesis. Initially the generalist detect ubiquitous VOCs emitted from multiple plant species (step 1). These ubiquitous occurring compounds can be sufficient for reliable host plant recognition (step 2). Within the vicinity of the host, the insect can potentially use more refined cues (step 3-4) such as visual (part 5) and volatile cues (part 6). Reprinted from Insect Science, 0, Rehan Silva, Anthony R. Clarke, The "sequential cues hypothesis": a conceptual model to explain host location and ranking by polyphagous herbivore, Copyright (2019), with permission from John Wiley and Sons.

5 Discrimination and generalization

When an organism is about to make a decision, e.g. where to oviposit or which food source to utilize, it needs to be able to generalize and discriminate between the choices available. Generalization can be described as the ability to induce the same behavioural response to various resembling stimuli (Pearce, 1987). Discrimination is the ability to yield a behavioural change due to a change in stimulation (Ghirlanda and Enquist, 2003). Generalization has been viewed differently in the fields of psychology and ethology. While psychologists associate generalization directly with individual learning, ethologists tend to separate the two (Ghirlanda and Enquist, 2003). This separation was partly due to the belief that innate and learned behaviour are governed by different mechanisms. However, data on generalization processes show no difference between innate and learned behaviour and a separation between the two is therefore unsupported (Ghirlanda and Enquist, 1999). Although most studies carried out have been on higher organisms such as birds or mammals, insects and other invertebrates are able to generalize in the same way as vertebrates and this ability seems to be universal and independent of the phylum of the organism (Hogan, 1994; Ghirlanda and Enquist, 2003).

In order for an organism to generalize and discriminate, the sensory organs must be able to perceive the experienced stimuli (Ghirlanda and Enquist, 2003). If the properties of the stimuli are unable to be detected, there will be no perception and therefore no change in the behaviour of the organism. An example of this is ultraviolet light that elicits no behavioural response in humans, where this lack of a response is not necessarily due to the characteristics of the stimuli but simply because humans don’t have any photoreceptors that react to light of that particular wavelength (Ghirlanda, 2002). Secondly, the stimuli presented must be in an ecologically relevant context. If the OSNs of an insect are bombarded with an ecologically relevant compound but in an irrelevant concentration, the behavioural outcome within the organism wouldn’t reflect its natural behaviour because of the unnatural concentration of the stimuli (Bruce et al., 2005).

Various stimuli have different representation space and are therefore perceived differently by the organism (Ghirlanda, 2002). Light and sound are present on a ‘scale’ where a particular object space, such as the wavelength of a particular colour, is located at a specific position on the ‘scale’. However, in cases of chemical stimuli, there is no such ‘scale’ where a stimulus of a particular dimension is located at a specific position. Instead, the chemical stimuli activate a specific receptor cell and this type of representation space is therefore referred to as receptor space (Ghirlanda and Enquist, 1999). Due to their difference in stimuli perception, the two representation spaces face different problems when it comes to building explanatory models on how they affect generalization (Ghirlanda, 2002).

Generalization between two stimuli are more prone to occur if the stimuli are similar to each other and the more distant the two stimuli are the less generalization is observed (Sandoz et al., 2001). This is because stimuli that are similar to each other generate similar neural representation in the organism (Pearce, 1987; Shepard, 1987). Such similar stimuli could be common components such as chemical compounds that activate the same receptor space (Smith and Menzel, 1989; Ghirlanda, 2002) or stimuli such as light or sound that occupy similar object spaces (Ghirlanda and Enquist, 1999; Sandoz et al., 2001). However, discrimination training, where a given stimulus is reinforced with a reward while another stimulus is not, can induce changes in the following generalization within the conditioned organism though a 'peak shift' (Ghirlanda and Enquist, 2007). The response elicited by the conditioned organism is then displaced from the object space of the reinforced stimulus in the opposite direction of the unrewarded stimulus. In a study by (Lynn et al., 2005), such a peak shift was shown in bumblebees introduced to an artificial Batesian mimicry system after going through discrimination training. The change in the artificial flowering system led to the bumblebees visiting novel flower colours similar to previously conditioned ones. In a similar study by Gumbert (2000), bumblebees were shown to generalize between novel coloured flowers and previously experienced flowers if the novel colour was similar to the previously experienced colour. Interestingly, if the novel colour and experienced colour were too different, the bumblebees instead relied on its innate preferences. Generalization has been studied to a great extent in honey bees, a closely related species to bumblebees, due to their excellent ability of visual generalization (Stach et al., 2004; Mustard et al., 2008). Honey bees are able to use various features of a particular object such as size (Srinivasan et al., 1989; Ronacher, 1992), symmetry (Horridge and Zhang, 1995; Giurfa et al., 1996; Lehrer, 1999), concentric pattern organization (Horridge and Zhang, 1995), edge arrangement (Hateren et al., 1990; Horridge, 2006) and pattern disruption (Horridge, 1997) in order to identify novel objects similar to a previously experienced ones through generalization.

Apart from being able to generalize between resembling stimuli, organisms also need to be able to discriminate on small differences between stimuli. In a study by Mishra et al. (2010), larvae of *Drosophila melanogaster* showed no preference for the two similar compounds 1-octen-3-ol or 3-octanol after non-discriminative training of the odours. However, with discriminatory training of the odours together with a reward, larvae showed a conditioned preference for the rewarded odour. This indicates that the two odours induce similar peripheral activity in the organism and that larvae generalize between the two when exposed to non-discriminative training. However, when larvae are exposed to discriminative training, i.e. when one odour is coupled with a reward in presence of the other odour, the small difference in the peripheral processing between the compounds are highlighted and larvae are able to discriminate between the two. To verify the difference in the peripheral processing, Mishra et al. (2010) conducted a follow-up experiment with Orco mutants. These are flies that are genetically defect in the odourant co-receptor that underpins detection of odourants (Larsson et al., 2004). In the Orco mutants, the discriminative reinforcement behaviour previously shown in the wild type strain was lost (Mishra et al., 2010). This highlights the interaction of generalization and discrimination processes and the importance of the peripheral organs during these interactions (Ghirlanda and Enquist, 2003). Sandoz et al. (2001) mention that spatiotemporal activity patterns in the glomeruli of the insect can be modified by conditioning to various floral odours. Such activity patterns could be visualized through optical imaging and together with behavioural learning and generalization assays provide more information on the perception of olfactory stimuli (Galizia et al., 1997). Furthermore, in a study on taste behaviour in *D. melanogaster*, Masek and Scott (2010) showed that flies are able to distinguish between compounds based on the savoriness and the concentration of the compounds. When mutant flies with a blocked output from the MB were used for the bioassays, they did not show any signs of associative learning, indicating that the MB plays an important role in learning processes. The higher brain centers of the organism are therefore of great importance when it comes to the interpretation of neural information that underpins behaviour in the organism (Hansson, 1999; Sachse and Krieger, 2011; Grabe and Sachse, 2018). In summary, a general understanding of the studied organism, its individual experience and evolutionary history is of the utmost importance when studying generalization and discrimination.

6 Phenotypic plasticity affecting insect behaviour

Although many insects rely on innate behaviour to successfully decipher the world around them, they also to a great extent utilize information from surrounding environmental cues and are able to learn from these (Dukas, 2008). Situations where a single genotype is able to produce various phenotypes due to a difference in environmental conditions, are referred to as phenotypic plasticity (West-Eberhard, 1989). Phenotypic plasticity have been studied to a large extent in insects and evidence of behavioural plasticity have been found in several species, with an emphasis on holometabolous insects (Wright and Schiestl, 2009) in the orders Diptera (Busto et al., 2010), Lepidoptera (Anderson and Anton, 2014) and Hymenoptera (Turlings et al., 1993; Menzel and Müller, 1996). The ability of an insect to learn and be plastic in a phenotypic trait, such as behaviour, is of great advantage when experiencing novel or changing environments (Snell-Rood, 2013; Anderson and Anton, 2014). Phenotypic plasticity is thought to be particularly advantageous to generalist insects, compared to specialists, because of their wide host range (Cunningham and West, 2008). The ability to use previous experience could facilitate the daunting task of host plant selection (Anderson and Anton, 2014). However, the phenotype of an organism could not just be influenced by its genotype and the experienced environment, but also by the environment experienced by the parents (Mousseau and Fox, 1998). This is referred to as transgenerational phenotypic plasticity (TGP), a combination of mechanisms that can increase the fitness of the offspring by preparing it to a particular environment experienced by its parent (Mousseau and Fox, 1998; Agrawal et al., 1999). TGP involve various mechanisms, e.g. epigenetic modulations, nutrients received through the egg yolk and hormones. It has been referred to in several ways in the literature, e. g. maternal effects and parental effects (Mousseau and Fox, 1998; Bonduriansky et al., 2012). Mechanisms of TGP are considered favorable when (i) spatial and temporal fluctuations are experienced over generations, (ii) offspring environment is predictable by the parent and (iii) the cost of transferring information is low (Uller, 2008).

Extensive studies on the generalist moth *Spodoptera littoralis* have shown that phenotypic plasticity affect its behaviour in several ways (Anderson and Anton, 2014). Carlsson et al. (1999) showed that larvae of *S. littoralis* with previous experience to a particular odour showed a higher attraction to that odour compared to naïve larvae. Furthermore, larval experience to a particular host plant elevated that plant in the preference hierarchy of the adult moth in four out of five host plants tested (Thöming et al., 2013). This indicates that *S. littoralis* can retain information through metamorphosis and use this information for adult host plant selection decisions. This is a hypothesis first postulated by Hopkins (1917) and has then been called the Hopkins host selection principle. Examples of this principle has since then been demonstrated in orders such as Lepidoptera (Anderson et al., 2013), Coleoptera (Rietdorf and Steidle, 2002) and Diptera (Videla et al., 2010). Additionally, Jaenike (1983) came up with the neo-Hopkins host selection principle, stating that exposure of adult insects to odours early in life influence subsequent behaviour. This was shown in *Drosophila melanogaster* where larval experience did not seem to affect adult oviposition behaviour but early exposure during adulthood did. In the case of *S. littoralis*, adult host plant exposure alone does not affect subsequent behaviour, but a positive experience such as a successful mating together with host plant cues affects subsequent behaviour in both males and females towards those cues (Proffit et al., 2015). The studies on *S. littoralis* show the importance of behavioural phenotypic plasticity in both larval- and adult stage but also the transfer of information through metamorphosis.

Species within Lepidoptera that inhabits several mechanisms of WGP (Anderson and Anton, 2014) are suitable candidates for studies on TGP (Woestmann and Saastamoinen, 2016). Several studies on TGP in Lepidopterans have been published in the last decades with a focus on physiology and development but there is still a gap in studies focusing on TGP affecting host plant selection behaviour in insects. One of the few studies addressing this in the Lepidopteran *Bicyclus anynana* show that the diet of the parental generation affects the preference of their offspring, increasing the attraction to the odour experienced by the parent in the offspring (Gowri, 2019). The experimental setup allowed eggs to be present on green leaf material coated with the learned odour, inducing different responses in larvae from odour-coated leaves compared to uncoated control leaves. A possible explanation to this could be the ‘chemical legacy’ hypothesis, that hypothesized that chemical cues can be present on the egg and influence the behaviour of the hatching larvae (Corbet, 1985). However, larvae hatched on control leaves with difference in parental exposure to odour cues also showed difference in preference which favours the assumption that there could be other modes of transmission involved (Gowri, 2019). In a similar study on the arachnid *Neoseiulus californicus* the parental diet also affected the diet preference of the offspring and it was discussed whether chemical features could be learned during embryonic development . Other studies on chemosensory preference and threat sensitive learning support this assumption (Sneddon et al., 1998; Mathis et al., 2008; Ferrari and Chivers, 2010). Studies, such as the one on *Bicyclus anynana*, supports the idea of TGP influencing host plant selection behaviour in insects (Gowri, 2019). Thus, broadening our view on phenotypic plasticity, with an emphasis on host plant selection behaviour, in insects.

7 Concluding remarks and future perspectives

Phytophagous insects rely heavily on olfactory cues in order to generalize and discriminate between host and non-host plants. Several theories regarding such host plant identification have been postulated highlighting several important prerequisites for reliable host recognition ranging from the use of ubiquitous compounds, species-specific compounds and the combination of the two. At this point of time, the sequential cues hypothesis favouring the use of both ubiquitous and species-specific compounds can be considered the most plausible. Additionally, previous experience is known to affect phenotypic traits such as behaviour particularly in generalist insects. A well-studied example is the Egyptian cotton leaf worm, *S. littoralis*. Within this species, phenotypic plasticity has been shown to affect behaviour in several life stages. Due to its wide host range and its ability to use previous experience, *S. littoralis* can be considered a well-suited model organism for questions regarding discrimination and generalization and how these are affected through previous experience in both an intra- and a transgenerational context.

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