

REVIEW PAPER

# Interplay between insects and plants: dynamic and complex interactions that have coevolved over millions of years but act in milliseconds

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## Abstract

In an environment with changing availability and quality of host plants, phytophagous insects are under selection pressure to find quality hosts. They need to maximize their fitness by locating suitable plants and avoiding unsuitable ones. Thus, they have evolved a finely tuned sensory system, for detection of host cues, and a nervous system, capable of integrating inputs from sensory neurons with a high level of spatio-temporal resolution. Insect responses to cues are not fixed but depend on the context in which they are perceived, the physiological state of the insect, and prior learning experiences. However, there are examples of insects making ‘mistakes’ and being attracted to poor quality hosts. While insects have evolved ways of finding hosts, plants have been under selection pressure to do precisely the opposite and evade detection or defend themselves when attacked. Once on the plant, insect-associated molecules may trigger or suppress defence depending on whether the plant or the insect is ahead in evolutionary terms. Plant volatile emission is influenced by defence responses induced by insect feeding or oviposition which can attract natural enemies but repel herbivores. Conversely, plant reproductive fitness is increased by attraction of pollinators. Interactions can be altered by other organisms associated with the plant such as other insects, plant pathogens, or mycorrhizal fungi. Plant phenotype is plastic and can be changed by epigenetic factors in adaptation to periods of biotic stress. Space and time play crucial roles in influencing the outcome of interactions between insects and plants.

**Key words:** Chemical ecology, coevolution, herbivores, insect–plant interactions, pollinators, spatio-temporal dynamics.

## Introduction

The purpose of this review is to consider the important role played by time and space in insect–plant interactions. Great advances are being made in understanding the mechanistic basis by which insects interact with their host plants (reviewed by Hogenhout and Bos, 2011; Mithoefer and Boland 2012; Smith and Clement, 2012). The ecological and evolutionary context of these interactions requires consideration because they are dynamic and what occurs at one point in time may not occur at another. Insects are programmed to recognize and rapidly respond to patterns of host cues. Particularly specialist insect species have to find specific plant species on which they can feed and reproduce (host plants) among plant species that do not support feeding and/or reproduction of

the insects (non-host plants). Thus, in an environment with changing availability and quality of host plants, phytophagous insects are under selection pressure to find quality hosts (Bruce *et al.*, 2005). To maximize their fitness they need to locate suitable plants and avoid unsuitable hosts (Bruce and Pickett, 2011). Thus, they have evolved a finely tuned sensory system for detection of host cues and a nervous system capable of integrating inputs from sensory neurons with a high level of spatio-temporal resolution (Martin *et al.*, 2011). Time and space also influence plant responses to insects; for example, a history of pre-exposure can prime plant defence responses so that plants respond more quickly and strongly when they are attacked again (Ton *et al.*, 2007, Jinwon *et al.*, 2011).

The phytophagous insects that exist today and the plants they feed on are the product of a coevolutionary process that has been ongoing for 400 million years (Labandeira, 2013) (Fig. 1). However, insect responses to host plant cues from their external environment can be very quick because they have a sophisticated system for sensing their external environment and processing the sensory input (Martin *et al.*, 2011). In particular, decisions made during flight, such as which plant to land on, are exceedingly rapid and made in a timescale of tens to hundreds of milliseconds (Cardé and Willis, 2008; Baker, 2009; Bruce and Pickett, 2011). This is because odour plumes are patchy in structure and insects encounter pockets of host odour only for fractions of a second. Moreover, insect responses are sensitive to combinations of host cues because exposure to plant volatiles as a blend can elicit an entirely different response from individual compounds (Riffell *et al.*, 2009; Webster *et al.*, 2010). By being sensitive to combinations of cues, insects can maximize the information they gather from their environment. Consequently this means that the context of cues can be very important in influencing the behaviour elicited. Responses can also change with learning behaviour, such as if a particular cue or set of cues is associated with a reward (e.g. Hartleib *et al.*, 1999).

There is much interest in phytophagous insects due to their role as pests in agricultural ecosystems and the negative effect this has on food security for humanity (Bruce, 2010). However, other types of insect–plant interactions exist. Insects play very important roles as pollinators and the natural enemies of the herbivore insects are also beneficial. At the other extreme there are carnivorous plants that consume insects (Renner and Specht, 2013). For nature conservation in wild habitats, insect–plant interactions are very interesting because the coevolutionary forces can drive speciation and increase biodiversity.

## Coevolution

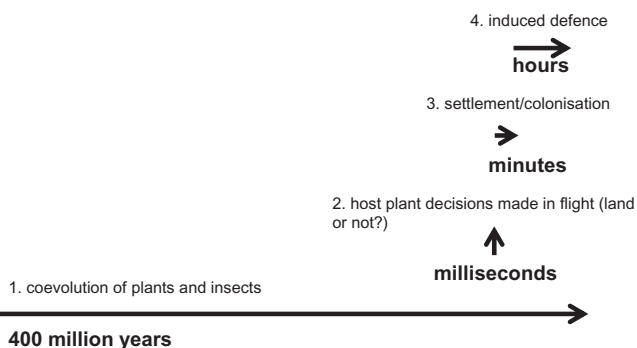
The huge number species of flowering plants on our planet (approximately 275 000) is thought to be the result of adaptive radiation driven by the coevolution between plants and

their beneficial animal pollinators (Yuan *et al.*, 2013). The fossil record shows that pollination originated 250 million years ago (Labandeira, 2013). Some plants have evolved with their pollinators and produce olfactory messages which make them unique for their specific pollinators (Grajales-Conesa *et al.*, 2011). For example, certain orchid flowers mimic aphid alarm pheromones to attract hoverflies for pollination (Stoekl *et al.*, 2011).

Furthermore, insect herbivores can drive real-time ecological and evolutionary change in plant populations. Recent studies provide evidence for rapid evolution of plant traits that confer resistance to herbivores when herbivores are present but for the evolution of traits that confer increased competitive ability when herbivores are absent (Agrawal *et al.*, 2012; Hare, 2012; Züst *et al.*, 2012). While phytophagous insects have been adapting to exploit their hosts, the plants have simultaneously been evolving defensive systems to counteract herbivore attack (Anderson and Mitchell-Olds, 2011; Johnson, 2011).

Studies of fossil plant–insect associations suggest that insects have been feeding on plants for 400 million years (Labandeira, 2013). Coevolution between insects and plants was drawn attention to in the classic review by Ehrlich and Raven (1964). Thus, the phenotypic traits and interactions we see today are the legacy of a long history of association between the organisms and reciprocal adaptations that provide fitness advantages (Gomez *et al.*, 2010). There is a trend for phytophagous insects to become more specialized in host plant use over time, although some important agricultural pest species are polyphagous. Ecological specialization involves subtle and complex interplay between species and is not limited to the plant and the herbivore but can also be influenced by multitrophic interactions (Forister *et al.*, 2012). There can also be bidirectionality in transitions between generalist and specialist lineages and Janz and Nylin (2008) have proposed an oscillation hypothesis in which periods of host range expansion are followed by periods of specialization, as seen in the leaf-mining fly genus *Phytomyza*.

Divergent selection exerted on ecological traits may result in adaptive population differentiation and reproductive isolation, and affect differentially the level of genetic divergence along the genome (Jaquiere *et al.*, 2012). The pea aphid (*Acyrtosiphon pisum*) genome has provided some insight into candidate genes that allow insect adaptation to host plants because it is a species complex of divergent host races. Differences between races were found in olfactory receptor genes and three genes encoding salivary proteins (Jaquiere *et al.*, 2012), although it is not known at which point in speciation these gene changes occurred or if they definitely played a causal role in the speciation process. *Drosophila sechellia*, which has evolved to specialize on *Morinda citrifolia* fruit, provides another interesting example: compared to *Drosophila melanogaster* it has higher expression levels of neurons ab3 and ab3B, sensitive to hexanoate esters and 2-heptanone, respectively, thus making it better able to recognize *Morinda* fruit odours (Ibba *et al.*, 2010).



**Fig. 1.** The different timescales associated with insect–plant interactions. The timescale over which mechanisms have evolved is very long whereas the actual mechanisms themselves operate over much shorter periods.

## Host/non-host odour recognition

The way in which insects use plant volatiles to recognize their host plants (Fig. 2), which usually involves blends of commonly occurring volatiles in specific combinations or ratios, has been reviewed previously (Bruce *et al.*, 2005; Bruce and Pickett, 2011) and will not be described at length here. The time dimension is of major significance because whether or not odours arrive simultaneously at the antenna can change the type of behavioural response elicited in the insect. Blend combinations play a crucial role as evidenced by a study with host odours of the black bean aphid, *Aphis fabae*, in which odours presented individually in an olfactometer were repellent but when put together as a blend became attractive (Webster *et al.*, 2010). This, although an extreme example, demonstrates that the behavioural response does not only depend on the molecular structure of the plant volatile but also on the context in which it is perceived.

In 2005, I suggested that insects use a ‘coincidence detection’ mechanism in which high spatio-temporal resolution of odours allows them to recognize host odour blends and distinguish them from combinations of non-host odours. A combination of olfactory and visual cues can further enhance attraction (e.g. Han *et al.*, 2012). There is also active avoidance of non-host odours (Bruce and Pickett, 2011). Early evidence for this came from the finding of olfactory receptor neurones (ORNs) tuned to specific non-host compounds, 3-butenyl isothiocyanate and 4-pentenyl isothiocyanate, in the black bean aphid (Nottingham *et al.*, 1991). When these isothiocyanates were tested in an olfactometer bioassay, they were found to be repellent.

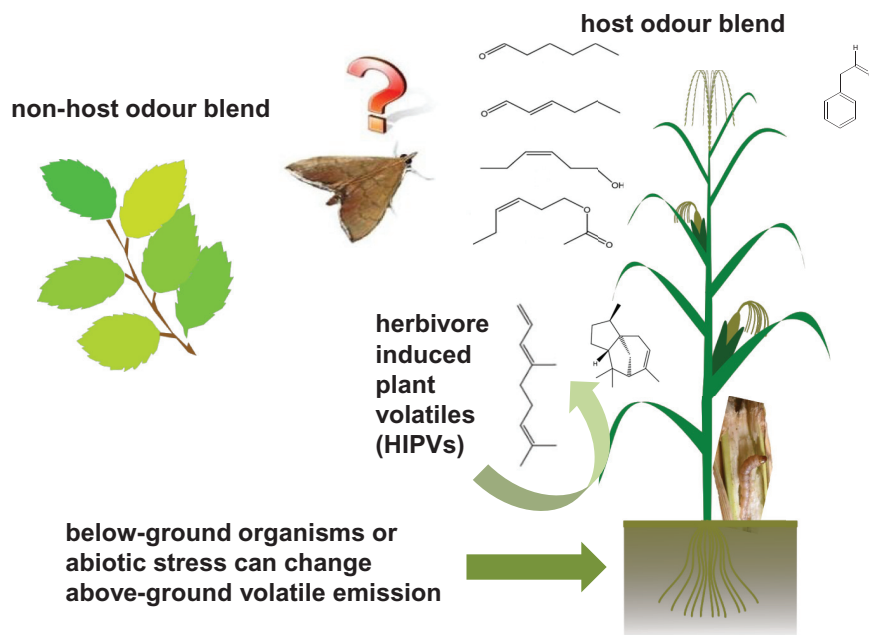
Ratios can also be important; for example, Cha *et al.* (2011) found that doubling the concentration of any one of

the components of a synthetic host volatile blend of grape odours (comprising (*E*)- and (*Z*)-linalool oxides, nonanal, decanal, (*E*)-caryophyllene, and germacrene-D), while keeping the concentration of the other compounds constant, significantly reduced female attraction in a wind-tunnel study with grape berry moth (*Paralobesia viteana*).

## How insect responses change over time

Insects have a nervous system and the capacity to learn which has consequences for their responses to plant volatiles (Cunningham *et al.*, 2004; Bruce and Pickett, 2011; Webster *et al.*, 2013). Learning behaviour, such as when an odour is associated with a reward, can affect the strength or even the type of response to plant stimuli. For example, hawkmoths (*Manduca sexta*) are innately attracted to blends of particular night-blooming flowers, but, when there are not enough of these hawkmoth-adapted flowers in the habitat, moths learn to associate the odours of bat-pollinated *Agave palm-eri* flowers which have a completely different smell (Riffell *et al.*, 2013). Thus, processing of stimuli through two olfactory channels, one involving an innate bias and the other a learned association, allows the moths to exist within a changing environment.

A more extreme example occurred in a laboratory study where *Spodoptera littoralis* moths were trained to extend their proboscis (a feeding response) in response to (*Z,E*)-9,11-tetradecadienyl acetate, which is a sex pheromone that usually elicits sexual behaviours (Hartlieb *et al.*, 1999). However, it has been shown that some odours are learnt better than others in particular insect–plant interactions; for example, honey bees learn linalool and 2-phenylethanol better than



**Fig. 2.** The challenge of host recognition: not only do herbivorous insects need to discriminate between host and non-host but they also have to select good quality hosts. Hosts already attacked by other insects may have defences induced and be lower quality. Other biotic and abiotic stresses that change plant quality can also change the profile of volatiles emitted thus providing further information to foraging insects. This figure is available in colour at JXB online.

other oilseed rape volatiles (Pham-Delegue *et al.*, 1993). This suggests that there is a hierarchy and an innate preference for certain odours (Bruce and Pickett, 2011). Natural enemies can also learn. It appears that generalist egg and larval parasitoids respond innately to herbivore-induced plant volatiles (HIPVs) whereas specialists rely more on associative learning (Peñaflor *et al.*, 2011a).

Innate responses allow insects to respond rapidly to reliable cues that occur in favourable situations, such as  $\gamma$ -octalactone, the Oriental fruit fly oviposition stimulant (Damodaram *et al.*, 2014) or, conversely, to avoid detrimental situations. An example of the latter is geosmin, a compound associated with harmful toxic microbes, that is repellent to *D. melanogaster* (Stensmyr *et al.*, 2012). They have a dedicated olfactory circuit with sensory neurons expressing the olfactory receptor Or56a that target the DA2 glomerulus and connect to projection neurons that respond exclusively to geosmin.

The physiological condition of an insect has long been known to influence insect–plant interactions (Dethier, 1982). When the insect is satiated it will be less motivated to respond to food odours; for example, the response of *D. melanogaster* to vinegar is modulated by hunger (Ruebenbauer *et al.*, 2008; Becher *et al.*, 2010). Similarly, when a female insect has already laid eggs she will be less attracted to oviposition cues. Female insects are influenced by mating which can induce profound physiological changes. After mating, *S. littoralis* switches its behavioural response to olfactory cues from food-associated ones to oviposition-associated ones (Saveer *et al.*, 2012). Unmated females are strongly attracted to lilac flowers but, after mating, attraction to floral odour is abolished and they fly instead to the green-leaf odour of the larval host plant cotton (*Gossypium hirsutum*).

## Plant defence

Plants have had to defend themselves against insect attack. Being rooted to the ground they are unable to flee from attacking herbivores. They have evolved a wide range of sophisticated defence systems to protect their tissues (De Moraes *et al.*, 2001; Kessler and Baldwin, 2001; Ballare, 2011). These include toxic or anti-feedant secondary metabolites that represent a major barrier to herbivory (Harborne, 1993; Mithoefer and Boland, 2012), and physical defences such as lignin (Franceschi *et al.*, 2005). These provide direct defence via toxic, anti-nutritive or repellent effects on herbivores.

Examples of defensive secondary metabolites include protease inhibitors in wild relatives of pigeonpea that are effective against the cotton bollworm, *Helicoverpa armigera* (Parde *et al.*, 2012), threonine deaminase in tomato that degrades threonine in the insect gut (Gonzales-Vigil *et al.*, 2011), 7-epizingiberene in the glandular trichomes of wild tomato (Bleeker *et al.*, 2012), and *O*-acyl sugars in the glandular trichomes of tomato and other plants in the Solanaceae (Schilmiller *et al.*, 2012). Some chemical defences are constitutive while others are induced after attack. The salicylic acid (SA) pathway is often, but not always, associated with

induced defence against pathogens and the jasmonic acid (JA) pathway with defence against herbivores (Ballare, 2011). However, numerous studies have shown a more complex picture, with varying involvement of both pathways in different pathogen and herbivore interactions depending on the species involved (Stout *et al.*, 2006; Bruce and Pickett 2007; Diezel *et al.*, 2009).

Plant secondary metabolism also provides indirect defence by attracting natural enemies of pests (Turlings *et al.*, 1990; De Moraes *et al.*, 1998; Dicke and van Loon, 2000; Heil, 2008). Studies with mutants have revealed that herbivore-induced plant volatile (HIPV) release requires the jasmonate-signalling pathway in *Arabidopsis* exposed to aphids (Girling *et al.*, 2008; de Vos and Jander, 2009) and in tomato exposed to hawkmoth larvae (Degenhardt *et al.*, 2010) but other systems could be different. The homoterpenes 4,8-dimethylnona-1,3,7-triene (DMNT) and 4,8,12-trimethyltrideca-1,3,7,11-tetraene (TMTT) are among the most widespread HIPVs produced by angiosperms and the metabolic pathway and biosynthetic pathway underpinning their production has been elucidated in *Arabidopsis* (Tholl *et al.*, 2011). Recently it has been shown that HIPVs can increase plant fitness; evidence for this was provided by a field study (Schuman *et al.*, 2012) in which HIPV-emitting *Nicotiana attenuata* plants produced twice as many buds and flowers as HIPV-silenced plants. Predators (*Geocoris* spp.) reduced herbivore loads by 50% on HIPV-emitters. There is variation in responsiveness to insects between different genetic lines of plants. This is particularly apparent in maize where some lines produce a clear HIPV signature following attack by larvae (Degen *et al.*, 2004; Degen *et al.*, 2012) or oviposition (Tamiru *et al.*, 2011) while others show little or no response. This suggests that some lines are better able to recognize insect elicitors (see How Plants Recognize Insects section below).

As well as influencing their natural enemies, HIPV emission can also affect the herbivores themselves by repelling further colonization (de Moraes *et al.*, 2001; Kessler and Baldwin, 2001; Bruce *et al.*, 2010). An elegant study by Signoretti *et al.* (2012) showed that female *Spodoptera frugiperda* moths respond strongly to maize HIPVs. Females preferred volatiles released by undamaged plants to those from herbivore-induced plants but the timing of events was important and the effect was not seen with freshly damaged maize odours (0–1 h) but only 5–6 h after attack. Preference for undamaged plants makes ecological and evolutionary sense because it provides an adaptive strategy to avoid competitors and natural enemies for offspring. Plants are also sensitive to HIPV emission from their damaged neighbours (Baldwin *et al.*, 2006). Responses to HIPVs and other stress-associated volatiles appear to occur over relatively short distances (Frost *et al.*, 2008). This may be an adaptive mechanism to avoid responding unless concentrations are high enough to indicate a real threat.

Not only do plants respond to insect feeding damage but they have also been shown to be responsive to insect egg laying, the very earliest stage of insect attack (Hilker and Meiners, 2006). This is of considerable adaptive value

because it allows the plant to prepare defences even before the damaging feeding stages of the insect life cycle have started. Thus, certain plants emit HIPVs following insect oviposition which attracts natural enemies (Tamiru *et al.*, 2011; Fatouros *et al.*, 2012) or increase direct defences so that insect growth rates are reduced on plants that are exposed to eggs (Beyaert *et al.*, 2012; JinWon *et al.*, 2012; Geiselhardt *et al.*, 2013). In some interaction systems oviposition actually leads to a suppression of plant volatile emission and a change in the ratio of compounds, something which natural enemies may (Bruce *et al.*, 2010) or may not (Peñaflor *et al.*, 2011b) be tuned into.

A highly interesting study by Gouhier-Darimont *et al.* (2013) showed that treatment of *Arabidopsis* with cabbage white butterfly (*Pieris brassicae*) egg extract caused a rapid induction of early PAMP-responsive genes. Expression of the defence gene *PR-1* required EDS1, SID2, and, partially, NPR1, thus implicating the SA pathway downstream of egg recognition. Then in a search for putative receptors of the egg-derived elicitors, a receptor-like kinase mutant, *lecRK-I.8*, was identified which displayed a much reduced induction of *PR-1* in response to egg extract treatment. This discovery of a putative plant receptor suggests that molecular recognition processes exist in plants that allow them to detect molecules associated with insects.

## How plant responses change over time

Plant defences are orchestrated both in time and space by highly complex regulatory networks that themselves are further modulated by interactions with other signalling pathways (Maffei *et al.*, 2007). Defences can be constitutive or induced. Time is of crucial importance where defences are induced or primed (Conrath *et al.*, 2006; Ton *et al.*, 2007; Bruce *et al.*, 2007). Primed plants respond more quickly and strongly when they are attacked again (Ton *et al.*, 2007; Jinwon *et al.*, 2011). Metabolites and energy can, thus, be more efficiently allocated to defensive activities when there is a mechanism for recognizing the herbivore challenge and triggering precise timing of the adaptive modulation of the plant's metabolism (Mithoefer and Boland, 2012).

Plants have evolved ways to adjust their phenotype in terms of defence gene expression levels according to the level of threat they face. Induced resistance represents a continuum of phenotypes that is determined by the plant's ability to integrate multiple signals of plant and herbivore origin (Jinwon *et al.*, 2011). Early events in induced defence such as accumulation of reactive oxygen species (ROS) and calcium signalling are very rapid and occur in the first few minutes of contact between the insect and the plant (Maffei *et al.*, 2007). Herbivores (and pathogens) induce  $\text{Ca}^{2+}$  influx by opening calcium channels and this triggers a series of cascade events, including ROS production. It is likely that these channels are associated with plant receptors tuned to insect elicitors. A rapid increase in ROS concentration can also occur after tissue damage caused by both biotic and abiotic injuries. Herbivore wounding is different from mechanical wounding;  $\text{Ca}^{2+}$  influx and depolarization is maintained after herbivore

wounding or application of herbivore oral secretions unlike mechanical wounding (Maffei *et al.* 2004). Recent evidence suggests that depolarization plays a role in the systemic spread of herbivore-induced defence through a plant (Mousavi *et al.*, 2013). Longer term changes can also occur after stress and increased resistance may even be observed in subsequent generations due to epigenetic imprinting (Bruce *et al.*, 2007; Luna *et al.*, 2012, Rasmann *et al.*, 2012).

The biological role of plant defence chemicals can change over time. Although many plant secondary metabolites have evolved as plant defence, insects may overcome the defences by coevolving adaptations such as cytochrome P450 monooxygenases (P450s) that metabolize plant toxins (Schuler and Berenbaum, 2013). For example, cotton bollworm (*Helicoverpa armigera*) uses a P450, CYP6AE14, to detoxify gossypol (Mao *et al.*, 2007); hawkmoth can feed on *O*-acyl-sugar-producing *N. attenuata* (Weinhold and Baldwin, 2011); and many Brassica specialists have evolved adaptations to thrive on glucosinolate-producing plants (Winde and Wittstock, 2011; Bruce, 2014). Specialist insects may even use the plant secondary metabolites to defend themselves against their own attackers at the third trophic level (Boppré, 1978). The molecular basis of resistance to toxic cardenolides has been well defined (Dobler *et al.*, 2012) and involves an amino acid change on the transmembrane sodium channel, which is the target site of the toxin. There has been convergent evolution with several insect species evolving the same amino acid change (Dobler *et al.*, 2012). Insights into the evolutionary process have been obtained from studies of the recent host shift to tobacco (*Nicotiana tabacum*) by the peach-potato aphid, *Myzus persicae*. Tobacco-adapted aphid races were found to overexpress a cytochrome P450 enzyme (CYP6CY3) that allows them to detoxify nicotine (Bass *et al.*, 2013).

## Insect effectors

Insect oral secretions contain specific proteins and chemicals that are likely to have evolved as effectors to inhibit plant defences but, with time, some plants have adapted to recognize some of these substances so that they may even trigger defence responses (Hogenhout and Bos, 2011). Salivary protein C002 was shown by Mutti *et al.* (2006) to play a crucial role in pea aphid survival and, when knocked down by RNAi, reduced time spent by aphids in contact with phloem sap when feeding on broad bean, *Vicia faba* (Mutti *et al.*, 2008). Candidate effectors were identified from the aphid *Myzus persicae* by Bos *et al.* (2010) and of these Mp10 and Mp42 reduced aphid fecundity whereas MpC002 enhanced aphid fecundity when overexpressed in *Nicotiana benthamiana*. Although there may be differences when these proteins are expressed by the aphid instead of being continuously expressed in the plant it appears that Mp10 and Mp42 benefit the plant rather than the aphid. It is possible that *N. benthamiana* has receptors that detect Mp10 and Mp42 and trigger defence metabolism. Phloem-feeding insects need to overcome plant physical defence mechanisms based on plugging the sieve tubes with callose or proteins (Will *et al.*, 2013) and

require effectors for this. With the increasing availability of aphid genome and transcriptome sequence data, aphid effector biology is an expanding area of research (Rodriguez and Bos, 2013).

Oral secretions are likely to be a major factor in limiting the host range of herbivorous insect species and biotypes, particularly aphids (Elzinga and Jander, 2013). Insect oral secretions include salivary enzymes such as glucose oxidase and  $\beta$ -glucosidase, peptides like inceptin, and fatty acid conjugates (FACs) like volicitin that can trigger plant defence responses (Wu and Baldwin, 2009) but also suppress defence (Eichenseer *et al.*, 2010; Consales *et al.*, 2012) depending on whether the plant or the insect is ahead in the evolutionary game. Aphid honeydew has also been shown to suppress induced plant defence (Schwartzberg and Tumlinson, 2013). Highly polyphagous species, like *Helicoverpa zea*, are more likely to possess relatively high levels of salivary glucose oxidase (GOX) for suppression of plant defences, compared to species with a more limited host range (Eichenseer *et al.*, 2010). However, plants can adapt; for example, recognition of *H. zea* GOX in tomato may represent a case for effector-triggered immunity (Tian *et al.*, 2012). Intricate adaptations have evolved with specialist herbivores; for example, velvet-bean caterpillar (*Anticarsia gemmatalis*) evades detection by cowpea by converting fragments of chloroplastic ATP synthase gamma-subunit proteins, termed inceptin-related peptides, that usually function as an elicitor of plant defence into an antagonist effector (Schmelz *et al.*, 2012).

## How plants recognize insects

All living organisms face the shared challenge of detecting and responding to chemical stimuli from their external environment. Detection of molecules associated with attacking organisms is crucial for eliciting behavioural, physiological, and biochemical responses to ensure survival. Being unable to flee from attack, plants have had to evolve sophisticated ways of detecting attackers and it is becoming increasingly clear that they can detect and respond to a wide range of molecules. Pattern recognition is a fundamental process in the immune responses of both plants and animals (Boller and Felix, 2009) and there is much biomedical literature relating to this subject (reviewed by Akira *et al.*, 2006). It is becoming increasingly clear that molecular recognition via ligand–receptor binding phenomena plays important roles in plants (Boller and Felix, 2009; Monaghan and Zipfel, 2012; Erb *et al.*, 2012) and that this plays a role in insect–plant interactions (Prince *et al.*, 2014; Chaudhary *et al.*, 2014). The identification of receptors and ligands is crucial to understand specificity in plant immunity to herbivores (Erb *et al.*, 2012). Plants possess surveillance systems that are able to detect highly specific herbivore-associated cues as well as general patterns of cellular damage, thus allowing them to mount defences. Molecular recognition mechanisms underpin this process with receptors tuned to herbivore-associated molecular patterns (HAMPs; Mithofer and Boland, 2008; Hogenhout and Bos, 2011; Bonaventure, 2012) or

damaged-self compounds produced after insect attack (Heil *et al.*, 2012). miRNAs have also been implicated in insect–plant interactions (Pandey and Baldwin, 2007; Kettles *et al.*, 2013). Sattar *et al.* (2012) found that *Aphis gossypii* miRNAs were differentially regulated during resistant and susceptible interactions with different melon lines, some possessing the *Vat* resistance gene and others not.

Recognizing the herbivore challenge to allow precise timing of appropriate plant metabolic responses is important so that metabolites and energy are efficiently allocated and correctly timed (Mithofer and Boland, 2012). However, for most insect–plant interactions, relatively little is currently known about the molecular basis of insect perception by plants, the signalling mechanisms directly associated with this perception, or how plants differentially discriminate between different species of attacking insects (Bonaventure, 2012). Plant–pathogen interactions have been better defined in this respect and effector-based models of insect–plant interactions are now being put forward (Hogenhout and Bos, 2011). The chemical ecology literature has many examples of plants responding to volatiles such as HIPVs and other chemicals that activate defence (reviewed by Baldwin *et al.*, 2006; Arimura *et al.*, 2009). Thus plants not only respond directly to molecules from attacking organisms but can also respond to volatiles released by other plants which are under attack (Arimura *et al.*, 2009).

Putative receptors are known but their ligands have not yet been identified. For example, three genes conferring resistance to insects have been identified in plants and are all members of the NB-LRR family: the *Mi-1* gene in tomato confers resistance to *Macrosiphum euphorbiae* (Rossi *et al.*, 1998), the *Bph14* gene in rice confers resistance to *Nilaparvata lugens* (Du *et al.*, 2009), and the *Vat* gene in melon provides resistance to *A. gossypii* (Boissot, 2010). The mechanism of resistance is thought to involve the putative receptors binding to as yet unidentified insect effectors. The pests involved are all in the insect order Hemiptera, which are stealthy herbivores with a sucking mode of feeding, and it seems likely that the HAMP is a small molecule or protein contained in the insect's saliva.

It is possible that the detergent-like properties of fatty acid conjugates could disrupt plasma membranes and cause influx of  $\text{Ca}^{2+}$  thus triggering responses. However, radiolabelled volicitin has been shown to bind rapidly, reversibly, and saturably to plasma membranes (Truitt *et al.*, 2004) suggesting that there is an interaction with a receptor. HAMPs have also been identified from insect egg ovipositional fluid (Hilker and Meiners, 2006; Tamiru *et al.*, 2011). The chemical structures of these have been identified as bruchins for the pea weevil, *Bruchus pisorum* (Doss *et al.*, 2000), and benzyl cyanide for *P. brassicae* (Fatouros *et al.*, 2008). Systemic changes in defence gene expression can also occur, such as when insect eggs are deposited on one leaf, other egg-free leaves also have induced volatile emission (Tamiru *et al.*, 2011).

A highly interesting study by Gouhier-Darimont *et al.* (2013) showed that treatment of *Arabidopsis* with *P. brassicae* egg extract caused a rapid induction of early PAMP-responsive genes. Expression of the defence gene *PR-1*

required EDS1, SID2, and, partially, NPR1, thus implicating the SA pathway downstream of egg recognition. Then in a search for putative receptors of the egg-derived elicitors, a receptor-like kinase mutant, *lecRK-1.8*, was identified which displayed a much reduced induction of *PR-1* in response to egg extract treatment. This discovery of a putative plant receptor suggests that molecular recognition processes exist in plants that allow them to detect molecules associated with insects.

## Interactions between insects and other organisms associated with plants

Although biologists often study individual interactions of one species of insect with one species of plant, the reality in nature is more complicated because plants are exposed to multiple attacking and beneficial organisms (Bruce and Pickett, 2007; Lucas-Barbosa *et al.*, 2011). Much less is known about the effect of multiple, co-occurring stress factors than individual biotic and abiotic stresses, despite the fact that multiple stresses are probably the rule under natural conditions (Holopainen and Gershenson, 2010).

Negative crosstalk between plant defence pathways means that time can have an impact on these multi-species interactions due to differences in the sequence in which plants are exposed to different organisms. Thus, the chronological order in which attackers arrive at a plant matters: later arrivals will perform better or worse according to the types of defence that have been induced or primed by the earlier arrivals. Soler *et al.* (2013) proposed that the outcome of intra-feeding guild interactions is generally negative due to induction of similar phytohormonal pathways, whereas between-guild interactions are often positive due to negative signal crosstalk. However, each interaction should be considered individually because it also depends whether the previous attacker managed to suppress plant defences against it or whether it activated them.

Interactions with the third trophic level can also change the outcome of insect–plant interactions. For example, Wilson and Leather (2012) found that cereal aphids preferred larvipositing on nutritionally superior wheat cultivars, but in the presence of the harlequin ladybird, *Harmonia axyridis*, they changed their preference to nutritionally inferior cultivars apparently because the risk of predation was lower on these. HIPVs are important in tritrophic interactions. Although this review has focussed mainly on plant–herbivore interactions, we should remember that any negative effects of HIPVs on pollinator visitation rates are likely also to exert selection pressure on HIPV emission (Lucas-Barbosa *et al.*, 2011). Another consideration is that attraction of natural enemies may be compromised if their hyperparasitoids are also attracted to the HIPVs (Poelman *et al.*, 2012).

Microbial mutualists may be more important ‘hidden players’ in insect–plant interactions than is currently realized (Frago *et al.*, 2012). A very interesting interaction between organisms is the use of symbiotic bacteria by Colorado potato beetle to evade antiherbivore defences of its host. These

beetles can secrete symbiotic bacteria into wounded plants that elicit SA-regulated defences (Chung *et al.*, 2013). Due to negative crosstalk with jasmonate-regulated defences this makes plants more suitable for the chewing herbivore. The traditional plant–herbivore concept needs to be updated to include the role of micro-organisms in insect–plant interactions; for example, yeast, not fruit volatiles, stimulate *D. melanogaster* attraction, oviposition, and development (Becher *et al.*, 2010). Sugio *et al.* (2011) showed that phytoplasma protein effector SAPI1 enhances insect vector reproduction by manipulating plant development and defence hormone biosynthesis.

By sharing the same host plant above-ground and below-ground insects can influence each other even though they are not in direct contact (Bruce and Pickett, 2007). For example, Robert *et al.* (2012) found that *Diabrotica virgifera* larvae showed stronger growth on roots previously attacked by conspecific larvae, but performed more poorly on roots of plants whose leaves had been attacked by larvae of the moth *S. littoralis*.

## Conclusions

Ecological interactions between insects and plants are complicated and dynamic. What occurs in one system at one snapshot in time may not occur again at another snapshot at a different time and each insect–plant system has its own unique features. Both the insect and the plant can change over time: the insect changes because of learning behaviour in the short term and by gene mutations in the longer term; the plant changes due to induced defence processes in the short term, epigenetic changes in the medium term, and gene mutations in the longer term. There is variation between different strains of both insects and plants. The genetic and temporal variability of biological material allows survival in an environment which is also dynamic and not entirely predictable. Interactions are complicated even further because the history of exposure to other associated insects can change the suitability of a plant to the insect being considered.

Agricultural environments are often simplified with less habitat diversity than natural ecosystems. Furthermore, many of the natural resistance traits that exist in wild plants may have inadvertently been lost while selecting for crop yield and quality in a pesticide-treated background. To reduce pesticide dependency, agriculturalists are faced with the challenge of bringing the resistance mechanisms found in wild plants back into the elite crop cultivars (Bruce, 2012) and improving biocontrol by natural enemies of pests. Reducing the losses to global harvests caused by pests, which remain high even with pesticide use, could provide a tangible way of producing more ‘crop per drop’ or unit area of land.

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