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Review
SPECIAL ISSUE: Using Non-Model Systems to Explore Plant-Pollinator and Plant-Herbivore Interactions

Plant defence against herbivory and insect adaptations

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Abstract. There is always a silent war between plants and herbivorous insects that we are rarely privy to. In this silent war, chemicals act as both weapons and messengers. Insect–plant co-evolution is going on for millions of years. Plants always look for new strategies to avoid insect pests and insects, in turn, are always ready to develop counter-adaptations. This intricate interaction has led to the development of a number of plant defensive traits and the counter-adaptive features in insects as well. Both plants and insects have developed morphological and biochemical defensive traits to dodge each other's strategies. However, biochemical interactions are considered more important and effective than morphological ones because of their dynamic nature. Some of the plant defensive traits evolved during this evolution include toxic furanocoumarins, toxic amino acids, trichomes, lignin and latex. Since there is an increasing focus on improving crop production through safe and sustainable means by reducing the reliance on pesticides, it is highly important to understand the plant defensive traits against insect herbivory. It is equally important to understand the adaptations by insect pests to these defensive traits in order to develop and deploy management strategies to outsmart the insect pests. Here we discuss the plant defence traits against insect herbivory, their induction by elicitors and/or insect damage, and the counter-adaptation by insect pests.

Keywords: Adaptations; induced resistance; insect pests; plant secondary metabolites; plant volatiles.

Introduction

Plants and insects have co-evolved continuously since the first appearance of phytophagous insects in the history of life. Insect herbivory forms a critical component in insect–plant co-evolution (Howe and Jander 2008; Zhao *et al.* 2009; Karban 2011). To avoid damage by insect pests, plants have developed an array of defensive strategies (Zhao *et al.* 2009; Karban 2011; War *et al.* 2012) by producing various morphological and biochemical defences that restrict the insect pests (Fig. 1; Howe and Jander 2008; War *et al.* 2012). The morphological defensive responses include increase in the trichomes, sclerophylly, latex deposition,

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etc. (Dalin and Björkman 2003; War *et al.* 2013a, b) and the biochemical traits include various toxic secondary metabolites produced in plants on account of insect herbivory (Karban 2011; Taggar *et al.* 2012; Holopainen and Blande 2013; War *et al.* 2013b; Kaur *et al.* 2015).

Plant defence may directly affect insect growth and development through toxic secondary metabolites or indirectly by recruiting the natural enemies of the insect pest through herbivore-induced plant volatiles (HIPVs) and extrafloral nectar (Arimura *et al.* 2009; Karban 2011; War *et al.* 2012). Induced resistance in response to herbivore attack makes host plants phenotypically plastic and plant tissues less nutritious, thus making them a less attractive food choice and practically unpalatable to insect pests (Karban 2011). Induced resistance is also sensed in the undamaged parts of the same plant and the neighbouring plants as well (Holopainen and Blande 2013). Further, induced resistance may also show a transgenerational effect, i.e. transferring from parents to their offspring as reported in wild radish, *Raphanus raphanistrum* infested by *Pieris rapae* (Agrawal 2002). The transgenerational effect of induced resistance makes plants more vigorous and reduces insect infestation in progeny (Agrawal 2002). However, insects precisely adapt to the plant defensive traits that allow them to feed successfully on the otherwise hostile and unpredictable host (Zhu-Salzman *et al.* 2003; Ahn *et al.* 2007; Després *et al.* 2007; War and Sharma 2014). This continuous race between the two entities to outsmart each other has led to the development of more defensive traits in plants and strong counter-adaptive strategies in insect pests (Zhu-Salzman *et al.* 2003; Sharma *et al.* 2009; War and Sharma 2014).

Co-evolution between plants and insects

Insect–plant co-evolution has been ongoing for 400 million years (Labandeira 2013). In response to insect

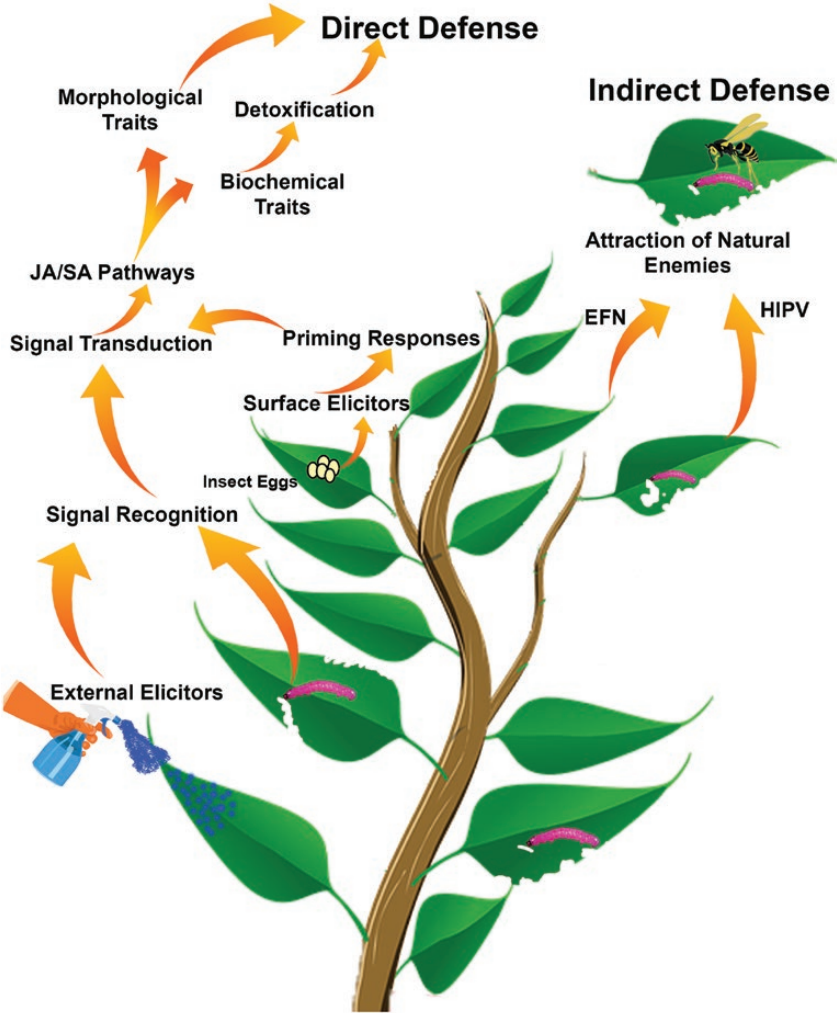

Figure 1. Plant defence against insect pests (EPF = extrafloral nectar; HIPV = herbivore induced plant volatiles; JA = jasmonic acid; SA = salicylic acid).

herbivory, natural selection has resulted in the evolution of morphological, behavioural and biochemical diversity among plants and insect pests. The plant defensive traits confer direct resistance against insect pests and also provide high competitive ability in the absence of insect pests (Agrawal *et al.* 2012; Hare 2012). The generalist and specialist insect herbivores show an evolution of some candidate genes responsible for their adaptation to host plants as reported in the pea aphid, *Acyrthosiphon pisum* (Jaquiery *et al.* 2012). Also, another specialist insect pest, *Drosophila sechellia*, evolved on *Morinda citrifolia* shows higher expression levels of neurons ab3 and ab3B. These neurons are sensitive to hexanoate esters and 2-heptanone, respectively, and enable the pest to recognize the odours from Morinda fruit (Ibba *et al.* 2010). Similarly, grubs of the bruchid beetle *Caryedes brasiliensis* feed on the seeds of *Dioclea megacarpa*, which contain a toxic non-protein amino acid L-canavanine. A modified tRNA synthetase in these grubs distinguishes between L-canavanine and arginine (Rosenthal *et al.* 1976). Eco-genomic tools have been implicated in studying the genetic basis of plant defensive traits in many plant systems (Schranz *et al.* 2009). They can further be used to study the constitutive and inducible defences by focusing on the polymorphic traits or follow the transgenic approaches to study the gene function and ecological consequences (Schranz *et al.* 2009).

Plant defence against insect herbivory

Host plant resistance is an important form of plant defence against insect herbivory and is widely implicated in crop protection against insect pests and diseases (Sharma *et al.* 2009; Maffei *et al.* 2012; Pieterse *et al.* 2012; War *et al.* 2012). The constitutive plant defence is present in plants irrespective of the external stimuli, while the induced defence is stimulated by insect feeding and/or the elicitor application (Sharma *et al.* 2009; War *et al.* 2012). Moreover, plants manage the resources between defence and growth by eliciting anti-herbivore defence only when necessary (Karban 2011).

A meta-analysis of genetic correlation between plant resistance to multiple enemies has shown positive correlations if both the compared species are generalist herbivores or both are specialist herbivores (Leimu and Koricheva 2006). Plant resistance to herbivores showed positive genetic correlation from herbivores with different feeding habits, such as gall inducers and leaf miners, miners and leaf folders, and leaf folders and gall inducers (Leimu and Koricheva 2006). Mechanism of resistance in the pairwise comparison between insects of different feeding guilds, such as phloem-feeding and leaf-chewing herbivores, showed the lowest genetic correlation (Leimu and Koricheva 2006).

Both morphological and biochemical defences in plants are important to withstand insect attack. Although morphological defence is primarily used by plants against insect pests, the biochemical-based defence is considered more effective as it directly affects insect growth and development (Kariyat *et al.* 2013). The HIPVs indirectly defend plants by recruiting the natural enemies of the insect pests, such as parasitoids and predators (Arimura *et al.* 2009; War *et al.* 2011). Induced resistance in plants against biotic stresses is attributed to the phenylpropanoid and octadecanoid pathways mediated by salicylic acid (SA) and jasmonic acid (JA), respectively (Zhao *et al.* 2009; Scott *et al.* 2010; He *et al.* 2011). These pathways produce a number of plant defensive secondary metabolites in intermediate steps, which affect insect growth and development and also release volatiles that attracts the insect's natural enemies (Howe and Jander 2008; He *et al.* 2011).

Plant defence elicitors

Plants recognize cues in the insect's oral secretion/saliva and in the ovipositional fluid (Schmelz *et al.* 2006; Alborn *et al.* 2007; Wu *et al.* 2007; Howe and Jander 2008). Insect oral secretions contain specific elicitors such as fatty acid conjugates (FACs), which stimulate plant defence. The first plant defence elicitor identified from the oral secretions of beet armyworm, *Spodoptera exigua*, was volicitin (*N*-(17-hydroxylinolenoyl)-L-glutamine), whose application on maize wounds resulted in the emission of a blend of volatiles that attracted natural enemies of the pest (Alborn *et al.* 1997). *N*-linolenoyl-glu, a potential elicitor of volatiles in tobacco plants isolated from tobacco hornworm, *Manduca sexta* regurgitate (Halitschke *et al.* 2001), when applied to the wounded leaves of tobacco activates mitogen-activated protein kinase (MAPK), wound-induced protein kinase (WIPK), SA-induced protein kinase (SIPK), JA, SA, ethylene (ET) and JA-isoleucine conjugate (JA-Ile) (Wu *et al.* 2007). The MAPK pathway is involved in plant growth and development and activates various signalling pathways in the host plant in response to biotic and abiotic stresses such as cold, drought, pathogens and insect attack (Wu *et al.* 2007). Further, 7-*epi*-JA induced by FACs elicits plant defensive genes against herbivory (Halitschke *et al.* 2001).

Inceptins and caeliferins in the oral secretions of many insects also activate plant defensive pathways against insect pests (Schmelz *et al.* 2006; Alborn *et al.* 2007). Plastidic ATP synthase, γ-subunit gives rise to inceptins, whereas the caeliferins are sulfated fatty acids (Schmelz *et al.* 2006; Alborn *et al.* 2007). The glucose oxidase (GOX) in the saliva of *Ostrinia nubilalis* and *Helicoverpa zea* mediates the defensive signalling pathways in tomato (Tian *et al.* 2012; Louis *et al.* 2013). Further, salivary components of *O. nubilalis* induce the expression of *Proteinase Inhibitor 2* (*PIN2*) and *maize protease inhibitor* genes in tomato and maize, respectively (Louis *et al.* 2013). Some reports show the suppression of plant defensive responses by insect oral secretions. For example, oral secretions of the African cotton leafworm, *Spodoptera littoralis* and cabbage butterfly, *Pieris brassicae* cause suppression of plant defence responses in *Arabidopsis* resulting in increased larval weights (Consales *et al.* 2012).

Mechanism of signal transduction pathways

Plants respond to herbivory by induction of signal transduction pathways, which lead to changes in the expression of defence-related genes and finally, the induction of biosynthesis pathways (Howe and Jander 2008; Maffei *et al.* 2012; Thaler *et al.* 2012). Plants recognize the plant defence elicitors from herbivores and initiate the defensive process by activating kinase networks and phytohormones (Maffei *et al.* 2012; Pieterse *et al.* 2012). The important plant signalling phytohormones are JA, SA and ET. Jasmonic acid and SA mediated signalling pathways against chewing insects (Howe and Jander 2008) and phloem-feeding insects (Pieterse *et al.* 2012), respectively. However, in rice plants, resistance to leaf folder *Cnaphalocrocis medinalis* is mediated by SA and ET signalling pathways (Wang *et al.* 2011). When plants are infested by sucking insect pests, activation of isochorismate pathway and the phenylalanine ammonium lyase pathways lead to the synthesis of SA (Dempsey *et al.* 2011). Accumulation of SA in plant tissues triggers translocation of the non-expressor protein of the pathogenesis-related genes 1 (*NPR1*) to the nucleus. The SA-responsive genes are regulated downstream of NPR1. The NPR1 targets the WRKY transcription factor genes, interacts with TGA-type transcription factors and leads to up-regulation of pathogenesis-related (PR) proteins (Durrant and Dong 2004). Salicylic acid signalling pathway has also been reported to be activated by insect eggs (Reymond 2013).

Jasmonoyl-isoleucine conjugate synthase 1 (JAR1) conjugates JA to the amino acid isoleucine (Ile) to form JA-Ile (Staswick and Tiryaki 2004). When JA-Ile binds to the F-box protein coronatine-insensitive 1 (COI1), the jasmonate ZIM domain (JAZ) repressor proteins are degraded, which bind to the transcriptional activators such as MYC2 and in turn repress the JA signalling (Thines *et al.* 2007). The removal of repression of JAZ proteins activates the JA-responsive genes such as the genes encoding JAZ proteins (Thines *et al.* 2007). The JA signalling pathway has two branches, MYC2 branch that regulates defence against insect herbivores and the ethylene response factor (ERF) branch that regulates plant defence against necrotrophic pathogens (Pieterse *et al.* 2012). The expression of wound-inducible vegetative storage protein 2 (*VSP2*) and lipoxygenase 2 (*LOX2*) genes is regulated by the MYC2 branch, while as ERF branch regulates the expression of ERF1 and octadecanoid-responsive *Arabidopsis* 59 (*ORA59*). These, in turn, regulate plant defensin genes such as plant defensin 1.2 (*PDF1.2*) (Dombrecht *et al.* 2007). Under multiple herbivore attacks, crosstalk occurs between signalling pathways to induce specific responses against insect herbivores (Pieterse *et al.* 2012). Jasmonic acid and SA crosstalk antagonistically and the process is mediated by the MAPKs, WRKY, NPR1 and ET (Pieterse *et al.* 2012; Thaler *et al.* 2012). Herbivores are sometimes benefited by the crosstalk between signalling pathways. For example, *M. sexta* feeding suppresses the nicotine but induces ET accumulation in nicotine plants (Kahl *et al.* 2000).

How do insects adapt to plant defence?

Insect pests can be generalist or specialist herbivores. The generalist herbivores feed on a number of host plants and have a complex defensive system since they encounter a wide variety of plant defensive chemicals, while specialist insect pests have a restricted host range and cannot adapt easily to the variety of toxic plant compounds. This makes induced resistance more successful against specialist herbivores than the generalists under field conditions (Karban and Agrawal 2002; Després *et al.* 2007). Insects have developed counter-adaptations to plant defensive traits through alteration in morphological, behavioural and biochemical traits (War and Sharma 2014; Fig. 2). Such adaptations enable the herbivores to withstand plant defence pressure and therefore, challenges the insect pest management programmes (Karban and Agrawal 2002; Després *et al.* 2007). For instance, mirid bug, *Pameridea roridulae*; cotton bollworm, *Helicoverpa armigera*; *H. zea* and *S. exigua* feed successfully on *Roridula gorgonais*, *Arabidopsis thaliana* and *Nicotiana tabacum*, respectively (Musser *et al.* 2002; Shroff *et al.* 2008).

One important factor for insects being successful organism is the strong olfactory system and its rapid evolution in short time spans (Hansson and Stensmyr 2011). Antennae, proboscis and/or maxillary palps are the important insect chemosensory organs through which

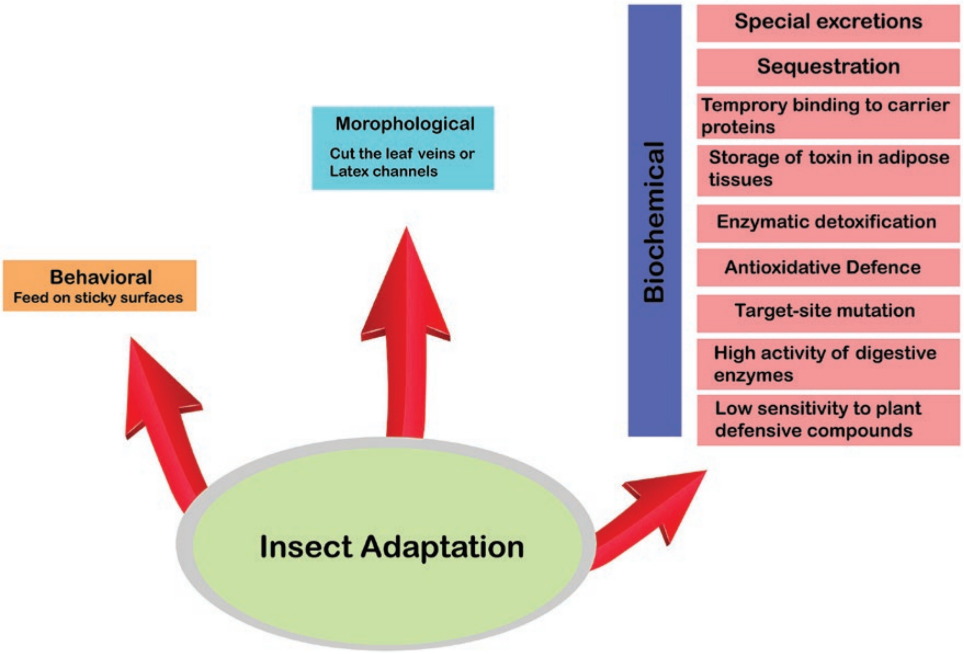

Figure 2. Counter-adaptations of insects to plant defensive systems (source: War and Sharma 2014).

the insects perceive plant compounds (by olfaction and taste) for selecting the suitable plants for oviposition and feeding (Bruce and Pickett 2011; Hansson and Stensmyr 2011). Recognition of the chemicals depends on the activation of specific proteins, including odorant-binding proteins (OBPs), olfactory receptors (ORs) and gustatory receptors (GRs). These chemosensory chemicals are solubilized and transported by the OBPs, which cause activation of chemosensory neurons (Leal 2013). For the insects with short contact and fast response time, ORs are highly important as they detect the diversity of chemicals and also perceive the airborne orders (Hansson and Stensmyr 2011; Getahun *et al.* 2012; Missbach *et al.* 2014). The evolution of OBPs and ORs/GRs has been attributed to the regulation of genes in insects in response to various stresses (Guo and Kim 2007; Vieira *et al.* 2007). In *D. sechellia* and *Drosophila erecta*, the evolution of OBP occurs rapidly (Vieira *et al.* 2007). *Drosophila sechellia* has developed physiological and behavioural adaptations to *M. citrifolia* due to the regulation of OBPs and related chemosensory genes (Matsuo *et al.* 2007; Kopp *et al.* 2008). Though differential expression of genes results in the loss of repellency to the acids in this pest, it perceives the key volatiles emitted by *M. citrifolia* (Matsuo *et al.* 2007). The GR gene family in *Bombyx mori* contains specific receptors that are involved in the sensing of plant secondary chemicals encountered during feeding (Wanner and Robertson 2008). The GRs in *Heliconius melpomene* are involved in plant-specific oviposition and show a high level of expression in the legs containing gustatory sensilla (Briscoe *et al.* 2013).

Insects respond to plant defensive traits by up- and/or down-regulation of a number of genes encoding various enzymes. *Callosobruchus maculatus* responds to soybean cystatin (a cysteine protease inhibitor, scN) by the up-regulation of genes encoding proteins and carbohydrates (Zhu-Salzman *et al.* 2003; Ahn *et al.* 2007). The turnip sawfly, *Athalia rosae* not only avoids plant defences, but also utilizes the plant tissues as a photosynthesis reservoir to draw the nutrients (Opitz *et al.* 2010; Abdalsamee and Müller 2012). It also reduces and/or modifies the toxic phenols in the gall and utilizes them for larval development (Nyman and Julkunen-Tiitto 2000). The larvae also sequester glucosinolates to avoid the formation of toxic isothiocyanates by converting them into desulfoGS sulfates (Opitz *et al.* 2010). *Manduca sexta* while feeding on tobacco plants accumulates the toxic nicotine in its body and uses it as a defence against parasitoids (Thorpe and Barbosa 1986; Harvey *et al.* 2007). In *O. nubilalis*, GOX in saliva induces or suppresses the plant defensive response by increasing the expression of *lipoxygenase* (LOX) and 12-*Oxo-phytodienoic acid* (OPR) genes (Musser *et al.* 2002; Tian *et al.* 2012; Louis *et al.* 2013). In tobacco plants, GOX in *H. zea* saliva suppresses the defence by inhibiting the signalling pathway for nicotine induction (Musser *et al.* 2002). Sap-sucking insects such as aphids pierce their stylet into the vascular bundles, draw the phloem sap and transmit a number of viral diseases besides injecting toxic chemicals into the plant (Giordanengo *et al.* 2010). Though plants do respond to the stylet piercing by sealing the puncture, aphids secrete saliva proteins that antagonize the sealing (Giordanengo *et al.* 2010). As compared to the black swallowtail, *Papilio polyxenes*, which feeds on various umbelliferous species (including wild parsnip), parsnip webworms metabolize xanthotoxin 10 times faster and metabolize them 300 times faster than the cabbage looper, *Trichoplusia ni* (Berenbaum 1991).

Role of protease inhibitors in plant defence and insect adaptation

Plant protease inhibitors (PIs) constitute one of the most important plant defensive traits against insect pests (Parde *et al.* 2012; Zhu-Salzman and Zeng 2015). They are highly effective against lepidopteran (Parde *et al.* 2012; Jadhav *et al.* 2016), hemipteran (Azzouz *et al.* 2005) and coleopteran insects (Zhu-Salzman *et al.* 2003; Ahn *et al.* 2007). Protease inhibitors inhibit the activity of a number of digestive enzymes such as serine, cysteine and aspartate proteinases and metallo-carboxypeptidases, thereby impairing insect digestion, which in turn affects insect growth and development (Dunse *et al.* 2010; Parde *et al.* 2012; War *et al.* 2012, 2017; Jadhav *et al.* 2016).

In counter defence, many insect pests have developed resistance/adaptation to the plant PIs (Zhu-Salzman and Zeng 2015), and therefore, have become a matter of concern in the development of transgenic crops with high levels of PIs. Insects adapt to PIs by the production of proteases that are insensitive to PIs (Bayes *et al.* 2006; Zhu-Salzman and Zeng 2015), hydroxylation and detoxification of PIs by alternative proteases and *de novo* synthesis, and up- and/or down-regulation of existing proteases (Zhu-Salzman *et al.* 2003). *Agrotis ipsilon*, *S. exigua*, *T. ni*, *H. zea*, *C. maculatus* and *Leptinotarsa decemlineata* produce proteases insensitive to the inhibitors (Volpicella *et al.* 2003; Zhu-Salzman *et al.* 2003; Gruden *et al.* 2004; Brioschi *et al.* 2007). The synthesis of new proteases, up- and/or down-regulation of existing proteases and degradation of PIs has been reported in fall armyworm, *Spodoptera frugiperda*, *H. armigera* and *Plutella xylostella* (Gatehouse *et al.* 1997; Brioschi *et al.* 2007; Yang *et al.* 2009). The larvae of cabbage flea beetle, *Psylliodes chrysocephala*, a pest of oilseed rape, showed increased protease activity when fed on the plants expressing cysteine proteinase inhibitor, oryzacystatin I (Girard *et al.* 1998). Further, *H. armigera* and *T. ni* when fed on a diet containing soybean Kunitz inhibitor and *S. exigua* feeding on transgenic tobacco plants overexpressing potato PI2 showed alteration of sensitive existing protease variants to insensitive proteases (Jongsma *et al.* 1995; Bown *et al.* 1997; Broadway 1997). The red flour beetle, *Tribolium castaneum*, shifts major cysteine proteases to minor serine proteases when fed on diets containing cysteine PI (Oppert *et al.* 2005). The proteolytic enzymes such as cathepsin L-like cysteine proteases (CmCPs) have been reported in *C. maculatus* against scN (Zhu-Salzman *et al.* 2003). Further, *C. maculatus* partly shifts cysteine proteases to aspartic proteases (Zhu-Salzman *et al.* 2003; Ahn *et al.* 2004, 2007). The JA treatment leads to the accumulation of cysteine and aspartic PIs in potato leaves, resulting in reduced gut proteolytic activity in Colorado potato beetles; however, the insect is able to avoid the toxicity of PIs by the synthesis of increased uninhibited proteases (Bolter and Jongsma 1995). The expression of a wide spectrum of digestive proteases and/or isoforms in insect midgut allows them to withstand dietary PIs. However, a majority of the gut proteinases are yet to be identified and characterized, and further studies are needed to unravel the sequences, their expression and regulation in insect systems.

Role of phenols in plant defence and insect adaptations

Phenols are plant secondary metabolites involved in plant defence against insect herbivory (Howe and Jander 2008; War *et al.* 2012) and are synthesized as monomeric and polymeric phenols and polyphenols from shikimate-phenylpropanoids-flavonoids pathways (Zhao *et al.* 2009; Scott *et al.* 2010; He *et al.* 2011). Though phenols are constitutively produced in plants, their concentration is induced in response to insect infestation as reported in coffee (Magalhães *et al.* 2008), wheat (Leszczynski 1995), castor (Rani and Ravibabu 2011), groundnut (War *et al.* 2015), cotton (Dixit *et al.* 2017), tomato (Bhonwong *et al.* 2009) and black gram (Taggar *et al.* 2014). Phenols are directly toxic to insects and/or act as feeding deterrents (Atteyat *et al.* 2012; War *et al.* 2013b; Dixit *et al.* 2017). Further, some phenols attract natural enemies of the insect pests (Heil 2008). Phenolic compounds, such as cucurbitacins that are bitter in taste and make plants hostile to a wide range of herbivores, including lepidopteran larvae, beetles, mites and vertebrate grazers (Tallamy *et al.* 1997; Agrawal *et al.* 1999; Balkema-Boomstra *et al.* 2003). They either directly affect insect growth and development (Agrawal *et al.* 1999; Balkema-Boomstra *et al.* 2003) or indirectly by acting as oviposition deterrents (Tallamy *et al.* 1997). Some reports suggest that cucurbitacins act as phagostimulants to insect pests. For example, *S. exigua* larvae showed higher performance on *Cucumis sativus* genotypes with higher levels of cucurbitacins than on the genotypes with reduced levels of cucurbitacins (Barrett and Agrawal 2004). Cucurbitacins B and D have been reported as major phagostimulants for leaf beetles, *Diabrotica speciose* and *Cerotoma arcuate* (Nishida *et al.* 1986; Nishida and Fukami 1990). Further, insect pests in genus *Aulacophora* are known to sequester the cucurbitacins (Nishida *et al.* 1992).

Role of tannins in plant defence and insect adaptation

Tannins constitute a diverse group of plant secondary metabolites involved in plant defence against insect pests. They possess an astringent (mouth puckering) and bitter taste that deters insect pests. They bind to the insect midgut proteins and digestive enzymes and precipitate them through hydrogen or covalent bonds, thereby limiting their availability to the insect pests and ultimately reducing the insect growth and development (Arnold and Schultz 2002; Peters and Constabel 2002; War *et al.* 2012). Further, tannins chelate the metal ions and produce midgut lesions in insect pests (Barbehenn and Constabel 2011). Deterrence for feeding by condensed tannins has been reported in a number of insects such as gypsy moth, *Lymantria dispar*; browntail, *Euproctis chrysorrhoea*; winter moth, *Operophtera brumata*; cowpea aphid, *Aphis craccivora*; and desert locust, *Schistocerca gregaria* (Feeny 1968; Grayer *et al.* 1992). Induction of tannins in plants in response to insect herbivory and their implication in insect pest management has been well documented (Arnold and Schultz 2002; Peters and Constabel 2002; Barbehenn and Constabel 2011; War *et al.* 2012). For example, *Pinus sylvestris* (Roitto *et al.* 2009), *Populus* sp. (Arnold and Schultz 2002; Peters and Constabel 2002; Stevens and Lindroth 2005), some *Quercus* spp. (Rossi *et al.* 2004) and groundnut (War *et al.* 2015) show induction of tannins upon insect infestation and/or application of plant defence elicitors.

Insect pests have not only adapted to the plant defensive tannins (War and Sharma 2014; Zhu-Salzman and Zeng 2015), they also utilize them for their growth and development. The tree locust, *Anacridium melanorhodon* showed an increase in growth by 15 % when fed with tannin-containing diet (Eswaran and Jindal 2013). Though the exact mechanism of insect adaptation to tannins is not known, higher gut pH and lower oxygen levels inhibit the autoxidation of tannins into toxic compounds (Appel 1993; Johnson and Barbehenn 2000). However, in some caterpillars, despite low oxygen levels in the gut, autoxidation of tannins leads to the formation of toxic compounds (Johnson and Barbehenn 2000). In some insects, tannins are absorbed through the peritrophic membrane, are polymerized and removed as polyphenols (Kopper *et al.* 2002). In addition, insect antioxidative compounds, such as glutathione, α-tocopherol and ascorbate reduce the tannin toxicity in grasshoppers (Krishnan and Sehnal 2006). Desert locust ultrafilters tannins in their theca (Bernays and Chamberlain 1980); however, in migratory grasshopper, *Melanoplus sanguinipes*, tannic acid does not bind to the peritrophic membrane (Barbehenn *et al.* 1996).

Role of cardenolides in plant defence and insect adaptation

Cardenolides are also involved in defence against insect herbivores (Rasmann *et al.* 2009; Green *et al.* 2011). Generally present in meager quantities in plants, they are induced upon insect infestation (Green *et al.* 2011; Agrawal *et al.* 2012). *Rhyssomatus lineaticollis*; monarch butterfly, *Danaus plexippus*; and red milkweed beetle, *Tetraopes tetrophthalmus* induced the levels of cardenolides in *Asclepias syriaca* (Akhtar and Isman 2003; Mooney *et al.* 2008; Rasmann *et al.* 2011; Vannette and Hunter 2011). JA pathways activated by insect herbivory mediates the production of cardenolides (Agrawal 2011). The Na^+ and K^+ gradients are highly important for the maintenance of the secondary transport and membrane potentials in insects (Jorgensen *et al.* 2003) and are the key targets of cardenolide toxicity. Cardenolides inhibit Na^+/K^+-ATPase pump required for the active transport of Na^+ out and K^+ into the cell. Any imbalance in ion levels is likely to have drastic effects on the insect growth and development. The larvae of *L. dispar* (a generalist) or *D. plexippus* (a specialist), when fed on cardenolide digitoxin, showed chronic toxicity (Karowe and Golston 2006; Rasmann *et al.* 2009). In addition, cardenolides such as digitoxin and cymarin deter cabbage looper, *T. ni* larvae (Akhtar and Isman 2003). Similarly, in treacle mustard, *Erysimum cheiranthoides*, *P. rapae* larvae were deterred by cardenolides (Sachdev-Gupta *et al.* 1993). The growth rate of *Aphis nerii* (a specialist sequestering insect) was found to be negatively correlated with cardenolides (Agrawal 2004). Further, a negative correlation has been reported between cardenolides and insect oviposition. For instance, the adult females of monarch butterfly do not prefer laying eggs on *Gomphocarpus fruticosus* and *Asclepias humistrata* plants with high cardenolides, fearing of the reduced larval growth and development due to cardenolides toxicity (Oyeyele and Zalucki 1990; Zalucki *et al.* 2001). Further, plants with low cardenolide content received about 70 % of eggs (Oyeyele and Zalucki 1990).

However, the mechanism of perceiving the cardenolides by monarch butterfly females and whether the cardenolides are present on the leaf surface of these plants needs to be investigated.

Development of counter-adaptations to toxic cardenolides by insects has posed a great threat to the use of these compounds in insect pest management (Agrawal *et al.* 2012; Dobler *et al.* 2012; Bramer *et al.* 2015; Groen *et al.* 2017). A number of factors have been suggested to reduce the efficacy of cardenolides in insect pests (Petschenka and Dobler 2009). Amino acid substitutions in Na/K-ATPase have been attributed to the counter-adaptation of insects to cardenolides. These substitutions block the cardenolides and reduce their binding to the Na/K pump (Bramer *et al.* 2015; Dobler *et al.* 2015) and increase the concentration of K^+ ions in insect haemolymph, resulting in cardenolide impermeability, sequestration and development of insensitivity towards cardenolides (Bramer *et al.* 2015). The formation of micelles by the cardenolides in peritrophic membranes of midguts of *S. gregaria* and *Periplaneta americana* renders them impermeable to cardenolide digitoxin (Scudder and Meredith 1982; Barbehenn 1999). Furthermore, organic ion transporters prevent Na^+/K^+-ATPase from Ouabain in *Drosophila melanogaster* Malpighian tubules (Torrie *et al.* 2004). However, the larvae of specialist herbivores such as *Empyreuma pugione*, *Daphnis nerii* and *Euploea core* do not contain any known substitutions in the Na/K-ATPase but still feed on plants with cardenolides by exhibiting insensitivity towards these compounds (Petschenka and Dobler 2009; Petschenka and Agrawal 2015). In addition to amino acid substitutions in Na/K-ATPase pump, metabolic detoxifications and efflux carriers could play a possible role in insect adaptation to cardenolides (Petschenka *et al.* 2013). Further, peritrophic membrane and the blood barrier membrane barriers (BBB) including septate junctions in insect gut form a potential barrier for hydrophilic cardenolides such as Ouabain (Petschenka and Agrawal 2015). The apolar cardenolides such as digoxin and digitoxin cross the peritrophic membrane of the insect gut but are restricted by the multidrug transporters (Mdrs) such as P-glycoproteins (P-gps) in the insect gut epithelial layer (Gozalpour *et al.* 2013; Petschenka *et al.* 2013). This prevents their contact with the target site Na^+/K^+-ATPase. In addition to the establishment of barriers for cardenolide diffusion, xenobiotic detoxification by cytochrome P450s and glutathione-S-transferases also plays an important role in cardenolide detoxification in insects (Chahine and O'Donnell 2009). Further, insect midguts contain Mdrs irrespective of the adaptation to cardenolides (Petschenka *et al.* 2013; Dobler *et al.* 2015) suggesting the co-evolutionary phenomenon between the two (Groen *et al.* 2017).

The sequestration of cardenolides has been reported in many insect pests. For example, *D. nerii* and *E. core* sequester cardenolides while feeding on cardenolide-rich oleander (Abe *et al.* 1996; Petschenka and Dobler 2009). *Danaus plexippus* and *Oncopeltus fasciatus* sequester and store cardenolides such as calotropin and its configurational isomer calactin from the tropical milkweed *Asclepias curassavica* or *Asclepias fruticosa* (Groeneveld *et al.* 1990), which is facilitated by the unidentified carriers (Frick and Wink 1995). Furthermore, cardenolide target site insensitivity has been reported in *D. plexippus*, *Chrysochus auratus*, *Chrysochus cobaltinus*, *Poekilocerus bufonius*, *Liriomyza asclepiadis* and *D. melanogaster* (Al-Robai 1993; Labeyrie and Dobler 2004; Dobler *et al.* 2012; Groen *et al.* 2017). The defensive spray of *P. bufonius* contains calotropin and calactin (von Euw *et al.* 1967). The specialist herbivores contain organic anion transporting polypeptides (Oatps) in the midgut, BBB and Malpighian tubules, which are also involved in metabolism and excretion of cardenolides (Hindle and Bainton 2014; Groen *et al.* 2017). Nevertheless, the role of Oatps in cardenolide-adaptation in insects has not been proven; however, Torrie *et al.* (2004) reported that Oatps subset in Malpighian tubules of *Drosophila* prevents Ouabain interference with Na/K-ATPase, suggesting that Oatps could have evolved in response to the cardenolide toxicity in insects. Further, the milkweed bugs show increased fitness on toxin sequestration along with other adaptations (Bramer *et al.* 2015).

Cardenolide production and their toxicity are also affected by physiochemical, physiological and environmental factors. The physiochemical factors include cardenolide polarity, the form in which the cardenolide is ingested (i.e. in leaf pieces, latex, phloem sap, etc.), matrix delivering the toxin (oil content of the food), physical form of the cardenolide (solution, emulsion) and K^+ in insect gut (Jorgensen *et al.* 2003; Dobler *et al.* 2015). The physiological factors such as absorption process of the cardenolides (carrier-mediated or not) affect the toxicity of cardenolide (Frick and Wink 1995; Agrawal *et al.* 2012). Abiotic factors such as CO_2, water stress and nitrogen fertilizers also affect cardenolide production in plants (Stuhlfauth *et al.* 1987; Hugentobler and Renwick 1995; Agrawal *et al.* 2012). Elevated levels of CO_2 from 350–700 ppm induced the expression of cardenolides in *Digitalis lanata* by 60–80 %, while as water stress reduced the levels of cardenolides (Stuhlfauth *et al.* 1987). However, Vannette and Hunter (2011) reported either decrease in cardenolides or no effect in response to elevated levels of CO_2 in *A. syriaca*. Further, reduction of cardenolides (erysimoside and erychroside) in response to nitrogen fertilization has been reported in wild mustard, *E. cheiranthoides* (Hugentobler and Renwick 1995). A 45 % reduction in cardenolides has been reported in *Asclepias* sp. in response to N:P:K fertilizers (Agrawal *et al.* 2012). The abiotic factors affecting cardenolides production demonstrate that environmental factors play an important role in the insect–plant interaction. Further, the implications of fertilizers on cardenolides production are a major challenge as plants need N:P:K for proper growth and development and any imbalance in either would have a major bearing on the plants. Thus, further investigation on insect adaptation to cardenolides and the role of fertilizers in cardenolide production is needed.

Role of iridoid glycosides in plant defence and insect adaptation

Iridoids constitute a class of cyclopentanoid monoterpene-derived compounds, which are bitter in taste but are a powerful line of defence against herbivores (Bowers and Puttick 1988; Puttick and Bowers 1988; Biere *et al.* 2004). Iridoid glycosides are either directly toxic to insect pests or reduce the nutritional quality of plant tissues, thereby rendering them less digestible to insects (Adler *et al.* 1995; Kim *et al.* 2000). Iridoid glycosides denature amino acids, proteins and nucleic acids by binding covalently to nucleophilic side chains via imine formation (Biere *et al.* 2004; Park *et al.* 2010). Iridoid glycosides also inhibit the activity of enzymes involved in the formation of prostaglandins and leukotrienes (Kim *et al.* 2000; Park *et al.* 2010). The larvae of *L. dispar* when fed on an artificial diet containing asperuloside showed reduced growth and development than those fed on the diet containing aucubin or catalpol (Bowers and Puttick 1988). However, in *Spodoptera eridania*, asperuloside did not have any adverse effect on the larval growth, while aucubin and catapol strongly reduced the larval growth and development of the insect (Puttick and Bowers 1988). Induction of iridoids by insect herbivory has been reported in *Plantago lanceolata* (Fuchs and Bowers 2004).

Insect pests have developed many strategies to withstand or avoid the toxicity of iridoid glycosides (Bowers 1984; L'Empereur and Stermitz 1990). Some specialist herbivores such as common buckeye, *Junonia coenia* females and other nymphalids use iridoid glycosides as oviposition and feeding stimulants (Bowers 1984; L'Empereur and Stermitz 1990; Nieminen *et al.* 2003). The larvae of *Ceratomia catalpae* and *J. coenia* feed on the host plants only if they contain iridoid glycosides (Bowers 1984; L'Empereur and Stermitz 1990). Nonetheless, the utilization of the consumed food is less in the larvae fed on the diets containing iridoid glycoside with lower survival than the plants with reduced iridoids (Adler *et al.* 1995). Sequestration of iridoid glycosides is another important strategy adopted by a number of lepidopteran insects (Lampert and Bowers 2010), beetles (Willinger and Dobler 2001), aphids (Nishida and Fukami 1989), orthopterans (Bowers 2009) and sawflies (Bowers *et al.* 1993; Opitz *et al.* 2010). Insect pests accumulate iridoid glycosides in the body and use them against natural enemies such as spiders (Theodoratus and Bowers 1999), ants (Opitz *et al.* 2010), stinkbugs and ladybird beetles (Nishida 2002) and birds (Bowers and Farley 1990). A ruby-red-coloured aphid, *Acyrthosiphon nipponicus* that feeds on *Paederia scandens* containing an iridoid glycoside paederoside, shows resistance to the predator *Harmonia axyridis* (Nishida and Fukami 1989). Further, aphids secrete paederoside and lipids into the predator's mouthparts; the latter then quickly flees from the aphid colony. In addition, insects fed on iridoid-containing plants experience less parasitism by parasitoids (Nieminen *et al.* 2003). The adaptations and the use of these compounds against natural enemies pose a major challenge for their implication in insect management.

Role of glucosinolate–myrosinase system in plant defence and insect adaptation

Glucosinolate–myrosinase system is a highly established and well-studied plant defence system against insect pests in brassicaceous plants (Halkier and Gershenzon 2006; Kim and Jander 2007; Hopkins *et al.* 2009; Müller *et al.* 2010). The damaged tissue of the *Brassica* plants releases glucosinolates, which are then hydrolyzed by myrosinases to toxic isothiocyanates (Halkier and Gershenzon 2006). A sudden release of these insecticidal compounds is termed as 'mustard oil bomb' (Hopkins *et al.* 2009; Müller *et al.* 2010). These compounds affect insect pests both by antibiosis (direct toxicity) and antixenosis (insects develop non-preference to the plants) (Hopkins *et al.* 2009). Glucosinolates are constitutively present in plants and are even induced in response to insect herbivory both in damaged and systemically in undamaged parts of the same plant (Travers-Martin and Müller 2007). The systemic increase in glucosinolates occurs due to its flow through the phloem or *de nova* synthesis in the target part of the plant (Chen *et al.* 2001). Studies on aphid infestation-induced indole glucosinolates in the detached leaves suggest that phloem transport of glucosinolates in undamaged parts is not so critical (Kim and Jander 2007). Some studies suggest that natural enemies utilize isothiocyanates to locate their insect hosts (Bradburne and Mithen 2000; Hopkins *et al.* 2009; Müller *et al.* 2010). However, their exact role in recruiting natural enemies of insect pests has not been studied in detail, since the blend contains many other compounds as well.

Glucosinolate–myrosinase system was considered at par with synthetic insecticides against insect pests such as *P. xylostella*; however, adaptation to toxic glucosinolates has been reported in many insect pests (Ratzka *et al.* 2002; Hopkins *et al.* 2009; Müller *et al.* 2010). Insects adapt to the glucosinolates either by enzymatic detoxification, excretion, sequestration or behavioural modifications (Hopkins *et al.* 2009). Diamond back moth larvae modify the glucosinolates by sulfatase gut enzyme and prevent their hydrolysis (Ratzka *et al.* 2002). The turnip sawfly, *A. rosae*, larvae of *Athalia liberta* and *B. brassicae* aphids sequester the glucosinolates by converting them to desulfo glucosinolate sulfates, thereby preventing the formation of toxic isothiocyanate (Müller and Brakefield 2003; Opitz *et al.* 2010; Kos *et al.* 2011). The glucosinolate sequestering in different species occurs by the uptake of certain glucosinolates through the gut membrane facilitated by selective transporters, because of the structural differences between the side chains of glucosinolates (Abdalsamee and Müller 2012). The adult flea beetles, *Phyllotreta striolata*, accumulate glucosinolates and hydrolyze them by using their own myrosinase (Beran *et al.* 2014). Some insects have adapted to glucosinolates to such an extent that they use them for their own defence against natural enemies. Glucosinolates in the haemolymph of green peach aphid, *Myzus persicae*; *A. rosae*; *B. brassicae*; mustard aphid, *Lipaphis erysimi*; and *P. rapae* are released when natural enemies attack these pests, and hence, deter them from the attack (Müller *et al.* 2002; Müller and Brakefield 2003; Vlieger *et al.* 2004; Opitz *et al.* 2010; Kos *et al.* 2011). Larvae of *A. rosae* sequester glucosinolates in haemolymph and release the same when attacked by the European wasp, *Vespula vulgaris* (Müller and Brakefield 2003) and common red ant, *Myrmica rubra* (Müller *et al.* 2002). The aposematic harlequin bug, *Murgantia histrionica*, uses the sequestered glucosinolates in body tissues and haemolymph to deter the predators (Aliabadi *et al.* 2002). However, in some cases, the sequestration of glucosinolates adversely affects insect growth and development (Abdalsamee and Müller 2012). Insect pests hydrolyze glucosinolates to nitriles instead of isothiocyanates (Wittstock *et al.* 2004). Nitrile specifier proteins in insect midgut reduce the toxicity of glucosinolates (Wittstock *et al.* 2004; Burow *et al.* 2006). The *S. littoralis* larvae feed more on plants with nitriles than the ones containing isothiocyanates (Burow *et al.* 2006). The *P. rapae* larvae modulate glucosinolate system into oviposition and feeding stimulants (Hopkins *et al.* 2009).

Plant secondary metabolites and insect detoxifying enzymes

Plant secondary metabolites constitute a major component of the plant defence arsenal against herbivory and adversely affect insect growth and development (Howe and Jander 2008; War *et al.* 2012). However, insects detoxify these toxic secondary metabolites using various detoxifying enzymes (Francis *et al.* 2005; Cai *et al.* 2009). The adaptations of insects to insecticides, plant allelochemicals and other toxic compounds depend on the diversity of the midgut detoxifying enzymes. Thee important detoxifying enzymes are cytochrome P450 monooxygenases (P450s), esterases (EST) and glutathione S-transferases (GSTs) (Francis *et al.* 2005; Scott *et al.* 2010; Saha *et al.* 2012; War *et al.* 2013b). These enzymes occur either constituently in insects and/or induced by the plant secondary metabolites (Scott *et al.* 2010; Saha *et al.* 2012; War *et al.* 2013b). These enzymes interact with phytochemicals such as gossypol, terpinen-4-ol, quercetin, tannic acid, rutin, nicotine and gramine in insect pests such as *H. armigera* (War *et al.* 2013b), *P. xylostella* (Luo and Zhang 2003), *Sitobion avenae*, *A. pisum* and *M. persicae* (Cai *et al.* 2009; Zhao *et al.* 2009; Ramsey *et al.* 2010). Further, the induction of these enzymes in insects in response plant secondary metabolites or insecticides has been reported in *H. armigera*, hoverfly, leaf beetles, leafhoppers, aphids, *T. ni* and bruchids (Zhu-Salzman *et al.* 2003; Francis *et al.* 2005; Scott *et al.* 2010; War *et al.* 2013b). Gossypol, deltamethrin and phenobarbital induce cytochrome P450 in *H. armigera* (Zhou *et al.* 2010; Tao *et al.* 2012). *Myzus persicae* larvae show increased activities of esterase and cytochrome P450 while feeding on tobacco plants (Cabrera-Brandt *et al.* 2010; Puinean *et al.* 2010). In *M. persicae*, GSTs are involved in the metabolism of isothiocyanates from Brassicaceous plants (Francis *et al.* 2005). *Spodoptera frugiperda* and *S. eridania* larvae show increased activities of GSTs and esterases, respectively, after feeding on plant secondary metabolites (Yu and Hsu 1993). Further, phenolic glycosides increase the GST activities in *L. dispar* larvae, forest tent caterpillar, *Malacosoma disstria* and tea mosquito bug, *Helopeltis theivora* larvae (Hemming and Lindroth 2000; Saha *et al.* 2012).

Role of volatiles in tritrophic interactions and the adaptation in herbivores

Since synthetic insecticides have many limitations such as toxicity to non-target organisms, residual effects, pesticide resistance, pest resurgence, etc., an important strategy to control insect pests could be to enhance the presence and efficacy of native biological control agents. To track down the herbivores, natural enemies utilize the chemical cues emitted by host plants (How and Jander 2008; Arimura *et al.* 2009; Sharma *et al.* 2009; Bruce and Pickett 2011; Karban 2011; War *et al.* 2012). The precision in locating an insect host depends on the amount of the volatiles released and their perception by the natural enemies (Arimura *et al.* 2009). Normally, low levels of volatiles are emitted by the plants, however, in response to herbivory; a blend of such chemical cues is released, which in turn, attract the natural enemies of the pest (Arimura *et al.* 2009; Bruce and Pickett 2011; War *et al.* 2011).

Plant volatile compounds also suffer adaptations by the insect pests. The dense egg masses deposited by *S. frugiperda* moths on maize suppress the emission of HIPVs (Peñaflor *et al.* 2011). However, when plants are influenced by a diverse community of chewing and sucking herbivores, a single HIPV compound could be an effective repellent to one herbivore but could act as an attractant to other herbivores and to insect predators/parasitoids (Xiao *et al.* 2012). Further, gregarious parasitoids sometimes stimulate the growth of the host insect pest, which may lead to increased plant damage (Harvey 2005). Thus, more research is needed to understand the mechanism of HIPV production, their perception by natural enemies and the possible adaptation by the insect pests.

Role of insect oviposition in plant defence and its counter-adaptations in insects

Insect oviposition is the first and foremost among the chain of events in insect–plant interactions. The suitability of the host plant for insect oviposition determines the plant resistance/and the success of the insect turnover (Hilker *et al.* 2002; Hilker and Meiners 2006). Surface chemicals, plant volatiles, trichomes and surface thickness of plant parts are important components that mediate host plant preference/non-preference for oviposition (Hilker *et al.* 2002; Taggar and Gill 2012; War *et al.* 2013a). Plants respond to insect oviposition through direct and indirect defences, which aim to get rid of the insect eggs and/or to kill them, thus avoiding the damage by larvae that would hatch from them (Hilker *et al.* 2002; Hilker and Meiners 2006). Induced secondary metabolites, anti-nutritive compounds and toxins in plants produced in response to insect infestation and/or elicitor application result in decreased oviposition and reduced larval growth and development (Seino *et al.* 1996; Petzold-Maxwell *et al.* 2011; War *et al.* 2013a). The neoplasm formation (excessive growth of hard tissue) (Doss *et al.* 2000; Petzold-Maxwell *et al.* 2011), hypersensitive response/necrosis (Balbyshev and Lorenzen 1997; Doss *et al.* 2000; Petzold-Maxwell *et al.* 2011; War *et al.* 2017), production of ovicides (Seino *et al.* 1996), release of volatiles to attract egg or larval parasitoids (Hilker *et al.* 2002; Hilker and Meiners 2006), egg crushing (Desurmont and Weston 2011) and egg extrusion (Videla and Valladares 2007) are some of the important plant defensive responses to insect oviposition.

In pea plants, eggs laid by pea weevil induce neoplasm formation, which dislodges the eggs by raising them above the surface (Doss *et al.* 2000). Oviposition of *P. brassicae* and the green-veined white, *P. napi* on *Brassica nigra* produces a hypersensitive response in plant tissues within 24 h of oviposition that kills eggs within 3 days (Balbyshev and Lorenzen 1997). The detachment of eggs through necrotic tissue formation has been reported in potato in response to *L. decemlineata* (Balbyshev and Lorenzen 1997). *Physalis pubescens* and *Physalis angulata* respond to *Heliothis subflexa* oviposition through necrosis, neoplasm and/or the combination of both (Petzold-Maxwell *et al.* 2011). In rice, oviposition by a white-backed planthopper, *Sogatella furcifera* induces the production of ovicidal compound benzyl benzoate (Seino *et al.* 1996; Yamasaki *et al.* 2003). The tissue wounding of European cranberry bush, *Viburnum* sp. in response to viburnum leaf beetle *Pyrrhalta viburni* oviposition is a strong defensive response that causes the destruction of eggs and/or their expulsion (Desurmont and Weston 2011). Jasmonates are considered as important elicitors of oviposition-induced resistance and have been reported in the eggs of various lepidopteran insects in higher concentration than in plant tissues or larval diet (Hilker and Meiners 2006; War *et al.* 2013a). Furthermore, JA-treated plants receive less number of eggs from *P. rapae*, *P. brassicae* and *H. armigera* as compared to the untreated control plants (Bruinsma *et al.* 2009; War *et al.* 2013a).

Oviposition by insect pests has been found to induce genes related to SA, which is a potent mediator of plant defence against pathogens and sap-sucking insects (Zhao *et al.* 2009). The SA and JA signalling pathways work antagonistically (Koornneef *et al.* 2008); thus, activation of SA pathway in plants by insect oviposition could lead to the suppression of JA signalling pathway (Koornneef *et al.* 2008), and the weakened defence against chewing insects.

Genetic variation and insect–plant interaction

Genetic variation, biotic and abiotic stresses affect the plant defensive traits against insect herbivores (Zhou *et al.* 2010; War *et al.* 2012; Gloss *et al.* 2013).

Substantial phenotypic and genetic variations occur in plants in both chemical and physical defences. These variations are exhibited in secondary metabolites, wax, lignin, trichomes, thorns, spines, C:N ratios and in plant phenology (Agrawal and Fishbein 2006; Schranz *et al.* 2009). It has been revealed through genome-wide scans that regions with loci have diverged in *A. pisum* host races depending upon the preference and/or non-preference to the host. This shows that the insect adaptations to plant defences maintain genetic differences between the host races (Jaquiery *et al.* 2012; Via *et al.* 2012). Further, in the large pine weevil, *Hylobius abietis* (a specialist insect pest), allele frequencies at a few loci differ based on the host plant (Manel *et al.* 2009). Significant genetic variation within and between populations has been reported in iridoid glycosides such as aucubin and catalpol and a phenylpropanoid glycoside verbascoside (Adler *et al.* 1995). Further, this variation differed depending on the age and chemistry of the leaf. The evolutionary theory of insect–plant interaction shows that the adaptation in plants to insect pests and the counter-adaptations in insects are essential to maintain the genetic variation within and among populations of plants and herbivores.

Conclusions and future perspectives

Plants have developed highly effective and dynamic defensive strategies against insect pests; however, these strategies are vulnerable to counter-adaptation. Therefore, an understanding of these interactions is important to develop robust pest management strategies. The counter defence by insects to plant defence is highly complex and has posed challenges in developing plant varieties with resistance to insect pests. Phytophagous insects try to cope with toxic plant secondary metabolites by the expression of sensory genes, insect proteins that are secreted into the plants and through insect detoxifying enzymes. Although the mechanisms of insect digestion and the role of insect digestive and defensive enzymes in adaptation to plant defence systems have been studied substantially, the studies on the regulation of gene expression in counter-adaptation are limited. From the highlighted studies, it is evident that insect pests have co-evolved to withstand the plant defence traits. Identifying the mechanism of insect counter-adaptations will help us to understand the pace at which the insects adapt to plant defence and would offer new targets for sustainable pest control programmes. Further, identification of genes coding the target counter-adaptive enzymes in insects can be exploited for use in RNAi technology for silencing them. Also, the information on insect and plant genome sequences could provide a valuable understanding of the highly dynamic and ever-evolving insect–plants interactions.

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Contributions by the Authors

A.R.W., H.C.S. and R.M.N. conceived the idea. A.R.W., G.K.T., B.H. and M.S.T. wrote the manuscript. All authors contributed to revisions on the manuscript.

Conflict of Interest

None declared.

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