

# Understanding plant defence responses against herbivore attacks: an essential first step towards the development of sustainable resistance against pests

M. Estrella Santamaria · Manuel Martínez ·  
Inés Cambra · Vojislava Grbic · Isabel Diaz

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**Abstract** Plant-herbivore relationships are complex interactions encompassing elaborate networks of molecules, signals and strategies used to overcome defences developed by each other. Herbivores use multiple feeding strategies to obtain nutrients from host plants. In turn, plants respond by triggering defence mechanisms to inhibit, block or modify the metabolism of the pest. As part of these defences, herbivore-challenged plants emit volatiles to attract natural enemies and warn neighbouring plants of the imminent threat. In response, herbivores develop a variety of strategies to suppress plant-induced protection. Our understanding of the plant-herbivore interphase is limited, although recent molecular approaches have revealed the participation of a battery of genes, proteins and volatile metabolites in attack-defence processes. This review describes the intricate and dynamic defence systems governing plant-herbivore interactions by examining the diverse strategies plants employ to deny phytophagous arthropods the ability to breach newly developed mechanisms of plant

resistance. A cornerstone of this understanding is the use of transgenic tools to unravel the complex networks that control these interactions.

**Keywords** Plant defence · Plant-herbivore interaction · Transgenic plants · Signalling pathway

## Introduction

Plants and arthropods coexist as friends or foes, sharing 400 million years of evolution. Currently, more than 50 % of a million of known insect species are phytophagous, although they are only represented in nine of the 29 insect orders (Ortego 2012). In addition, among the 5,000 species of acari identified, a significant number are plant-feeders (Helle and Sabelis 1985). The majority of herbivore arthropods are specialists, restricted to feeding on a single or a low number of plant species (mono- or oligo-phagous, respectively), while generalist herbivores (polyphagous) have preserved their association with a wide range of host plants over millions of years (Wheat et al. 2007). Throughout their co-evolution, phytophagous arthropods have developed morphological, physiological and behavioural adaptations, depending on their feeding habits and life styles, to overcome plant defences. They have developed a variety of strategies to avoid, excrete, sequester and degrade plant toxins. Although herbivores eat all plant organs,

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M. E. Santamaria · M. Martínez · I. Cambra ·  
I. Diaz (✉)  
Centro de Biotecnología y Genómica de Plantas  
UPM-INIA, Universidad Politécnica de Madrid, Campus  
Montegancedo, 28223 Pozuelo de Alarcón, Madrid, Spain  
e-mail: i.diaz@upm.es

M. E. Santamaria · V. Grbic  
Department of Biology, University of Western Ontario,  
1151 Richmond St, London, ON N6A 5B7, Canada

leaf tissues are the main target for potential feeders. Nearly two-thirds of phytophagous arthropods are leaf-feeding species, with sophisticated mouth structures for chewing, snipping or tearing. Alternatively, piercing-sucking herbivores use tube-like structures (thrips and spider mites) or specialised stylets (aphids and whiteflies) to suck nutrients from parenchymatic cells or vascular tissues. Leafminers feed between epidermal cell layers within leaf tissues, where they are protected from plant defences and predators (Howe and Jander 2008). In addition, plant feeders have adapted their digestive physiology (pH, redox potential, enzymes, protease inhibitors and detoxification systems) and have developed digestive strategies (endo- or exo-peritrophic compartments and time-sequenced enzymatic activities) to a particular feeding style, which correlates with their phylogenetic position (Ortego 2012).

Plants have evolved elaborated protection systems against herbivore attacks by combining constitutive basal defences with inducible defences in response to specific arthropods. Moreover, plants have developed an indirect defence mechanism using volatiles and nectars to attract natural enemies of herbivores. Many of the approximately 500,000 secondary metabolites produced by plants are powerful chemicals against pests (Wu and Baldwin 2010). Plant volatiles may also function as signals to prime defence responses of neighbouring plants not still infected by insects or mites (Alba et al. 2012). Even if this battery of protection systems is not fully successful, plants can implement emergency responses and induce localised senescence or cell death processes in the infested tissues to isolate the attacker (Liu et al. 2010; Kerchev et al. 2012).

The co-evolutionary dynamics of plant defences and herbivore adaptations triggers a complex network of molecular events from the plant that ends in a diversification of structures, metabolic pathways and biochemical compounds. Consequently, plants have developed the ability to avoid or minimise being eaten by herbivores (resistance) and to decrease the negative fitness effects of pest damage (tolerance). These two defence mechanisms against pests may complement each other (Carmona and Fornoni 2013). However, damage to crops from field pests is still a limiting factor agriculture, and, in some cases, pests such as aphid or mite species, cause secondary effects by acting as virus vectors. Moreover, stored organs (seeds, tubers) infested with beetles, borers, moths or

mites produce only a portion of their nutritive value and germination capacity, and subsequently lead to a decrease in grain sales and/or exportation.

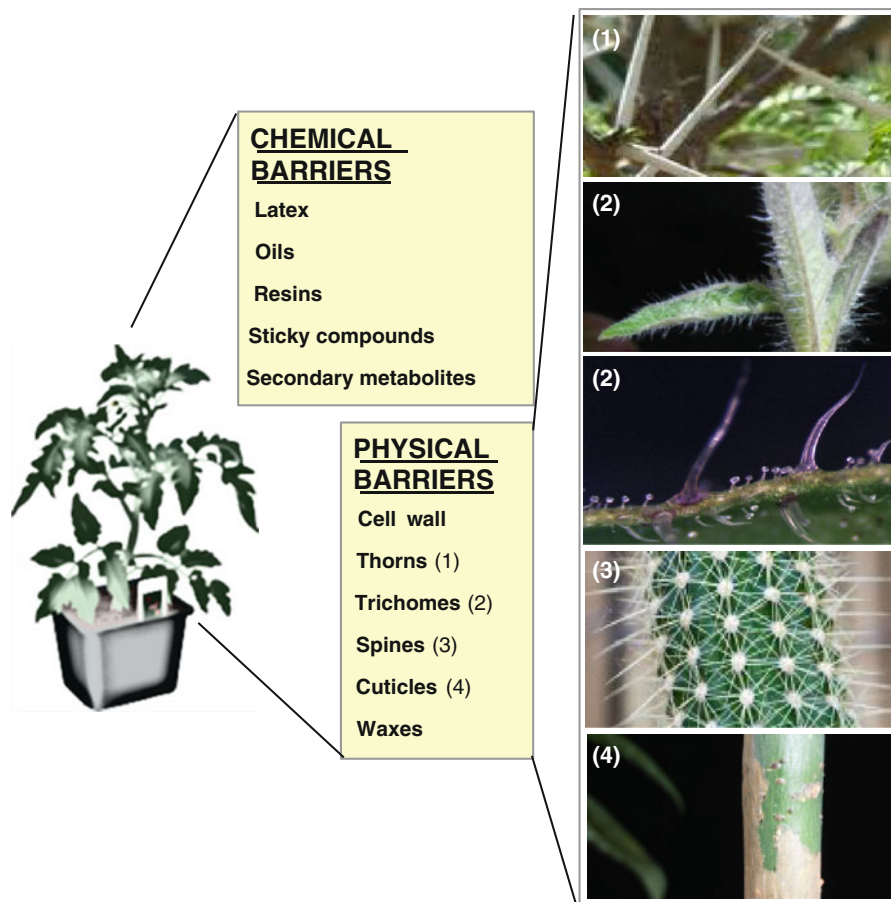
Genetic transformation has emerged as a significant tool in modern agriculture. For years, transgenic plant technologies have primarily been targeted at the enhancement of pest, disease and weed controls to increase crop yields. More recently, plant genetic transformation has focused on the improvement of resistance to abiotic stresses, the enhancement of nutritional quality and the production of modified or new biomolecules and biomaterials for industrial uses. Many recent reviews have reported the main advances in the genetic transformation of plant species (Chandler and Sanchez 2012; Christou 2013; Gambino and Gribaudo 2012; Holme et al. 2013). However, there are still only a few examples of commercial applications of transgenic plant even with the record 170.3 million hectares of biotech crops grown globally in 2012 (<http://www.isaaa.org/kc/cropbiotechupdate>). As a consequence of the increasing publication of plant and arthropod genomes (Martinez 2012), the functional analysis of genes has become highly relevant in basic research. Studies of functional genomics are becoming more and more important, being the majority of their results based on plant transgenic technologies. The overexpression or silencing of genes involved in the synthesis of specific plant molecules yields new insights and makes it possible to uncover regulatory mechanisms associated with specific metabolic processes. The current and future challenge of plant genetic engineering is to access the functional characterisations of gene networks involved in physiological pathways, with the purpose of exploiting intrinsic biological processes they have for use in breeding and IPM (Integrated Pest Management) programmes.

### Plant constitutive defences

Plants have developed an intricate basal defence system to decrease the chances of phytophagous arthropods using them as a source of nutrients. Constitutive defences are most likely essential for plant survival. They include physical barriers such as cuticular and cell wall modifications, surface waxes, trichomes, spines and thorns to hinder or deter herbivore accessibility, and the production of chemical defences, -mainly toxins and deterrents- to reduce

palatability and affect growth, development and digestion of herbivores (Fig. 1). Among the plethora of structural defences, the protective role of trichomes has been the most studied. Trichomes are hair-like epidermal structures mainly located on leaves and stems that interfere with herbivore movements or even entrap herbivores. They may also prevent insect/mite egg attachment to plant tissues after oviposition. Glandular trichomes produce, store and secrete different classes of toxic metabolites and repellents associated with resistance to herbivores (Glas et al. 2012). Trichome morphology, size and density influence host plant resistance to pests. Their defensive role has been demonstrated by the negative correlation between trichome density and rates of herbivore damage (Hanley et al. 2007). Moreover, trichome density can also be induced by herbivores and plant hormones (Tian et al. 2012).

Transgenic plant technologies, including manipulative and genetic methods, have been very useful in studying the protective function of trichomes. For example, flea beetle *Phyllotreta* spp. feeding decreased on transgenic canola (*Brassica napus*) seedlings with elevated trichome density. Beetles required twice as much time to reach satiation when feeding on leaves with enhanced pubescence than on control leaves (Soroka et al. 2011). This study suggests that dense pubescence developed in canola plants with a strong potential to deter feeding by crucifer flea beetles. Likewise, in a screen of activation-tagged *Populus tremula* x *Populus alba* trees, Plett et al. (2010) identified a *fuzzy* mutant line with increased foliar trichome density, which correlated with a significant resistance to feeding by larvae of the white-spotted tussock moth (*Orgyia leucostigma*). The *fuzzy* trichome phenotype was attributable to activation tagging and



**Fig. 1** Plant constitutive defences against phytophagous arthropods include physical and chemical barriers

increased expression of the gene encoding the PtaMYB186 transcription factor. Moreover, the transgenic overexpression of PtaMYB186 in poplar not only increased trichome density but also improved resistance against insects.

Plant transgenic approaches have also been used to analyse the impact of structural changes of the cell wall on pest behaviour. Sasidharan et al. (2011) recently reviewed how modifying the cell wall composition might result in a wall structure more resistant to physical penetration by invading attackers. In celery, aphid infestation induces a massive transcriptional reprogramming, including a group of genes encoding cell wall-modifying proteins as one of the major functional groups (Divol et al. 2007). Furthermore, silencing of *Manduca sexta*-induced pectin methyl esterases (PMEs), which catalyse the demethylesterification of pectins and therefore result in cell wall loosening or stiffening, increased herbivore feeding performance in PME knockdown *Nicotiana attenuata* plants (Korner et al. 2009). PME-silenced plants also had significantly lower levels of jasmonic and salicylic acid. Another experimental approach attempted to produce ferulic acid modifications, based on the potential of ferulic acid to form crosslinks between cell wall polysaccharides. Genetically engineered tall fescue (*Festuca arundinacea*) expressing a ferulic acid esterase gene showed reduced levels of ferulate cross-linking in cell walls, and an increased susceptibility to *Spodoptera frugiperda* feeding (Buanafina and Fescemyer 2012).

In addition to the structural adaptations developed by plants, some defensive chemicals are also continuously expressed irrespective of herbivore, although they are dependent on the plant species and their levels vary in plant tissues. These chemical products include peptides, proteins, protease inhibitors and other compounds with anti-nutritional or toxic properties. Approximately 10 % of angiosperms synthesise latex, oils, resins and other sticky substances that trap herbivores (Konno 2011). These substances are exuded from wounded points in plant tissues caused either mechanically or by plant feeders. In particular, latex is a complex mixture enriched in proteins (lectins, proteases and other enzymes) and secondary metabolites (terpenoids, alkaloids, cardenolides, furanocoumarins and phenolics) with important defensive roles (Konno 2011). Enzymatic adaptations to degrade latex ingredients have been described in

several herbivores (Hirayama et al. 2007). Secondary metabolites are also essential for reducing plant palatability, and have potential repellent, deterrent or even toxic effects against pests (Ibanez et al. 2012).

The defensive roles of many of these compounds have been revealed by silencing or blocking gene expression *in planta* through genetic engineering approaches. For example, *Nicotiana attenuata* transformed with consensus fragments of the putrescine *N*-methyl transferase gene in either the antisense or inverted-repeat orientation inhibited nicotine production, resulting in the destruction of 3-fold greater leaf area from a variety of herbivores compared to control plants (Steppuhn et al. 2004). Similarly, silencing of geranylgeranyl diphosphate synthase in *N. attenuata* blocked the synthesis of antifeedant diterpenoid glycosides and impaired resistance to the tobacco hornworm *Manduca sexta* (Jassabi et al. 2008). Notably, the wide variety of plant chemicals of glandular trichomes includes secondary metabolites, defence proteins and organic acids. The majority, constitutively expressed or induced by herbivores, produces drastic effects on arthropod performance and host-plant selection behaviour (Glas et al. 2012; Tian et al. 2012; War et al. 2012). The molecular engineering of glandular trichome chemistry has allowed a better understanding of plant structural defences to predict how plant morphological responses might influence plant-herbivore interactions. Wang et al. (2001, 2004) reported that the suppression of the cytochrome P450 hydroxylase in transformed tobacco plants, either by antisense inhibition or sense co-suppression, enhanced trichome exudate cembratrieneols and exhibited significant protection from aphid infestation in the field. More recently, Choi et al. (2012) have shown that tobacco plants overexpressing the *NLTP1* gene which plays a role in lipid secretion from trichome heads, resulted in a greater secretion of trichome exudates, including epicuticular wax, than control plants. These transgenic tobacco lines showed improved resistance to aphid infestation. In contrast, RNAi-treated tobacco in which lipid secretion from trichomes was strongly reduced but epicuticular wax secretion was not altered, showed increased aphid infestation levels.

### Plant inducible defences

Most plant defences against pests are induced by the feeder, primarily in the tissue where the infestation takes place, in which case it is termed the local

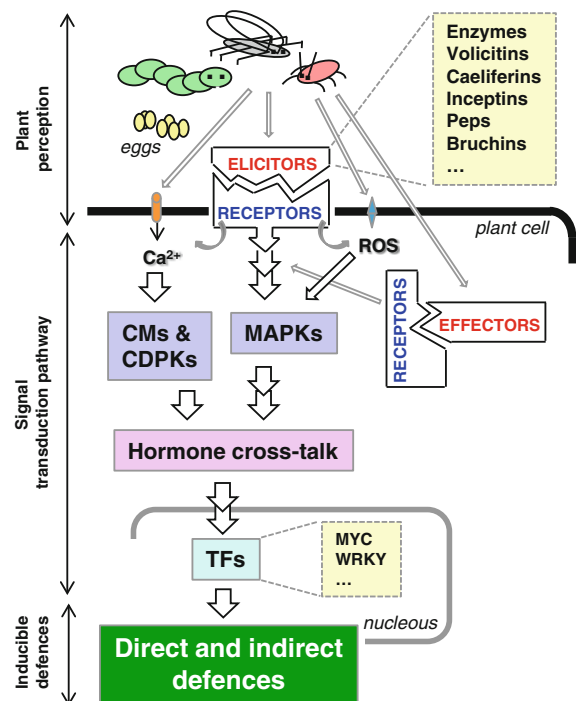
response, and then in distal undamaged tissues of the same plant, which is referred to as the systemic response. In both responses, the protection comprises structural and chemical modifications, some of which are similar to those previously described as constitutive defences. The induction of these plant reactions requires appropriated recognition systems (receptors) of the Herbivore-Associated Elicitors (HAEs), Herbivore Associated Molecular Patterns (HAMPs) or herbivore effectors. This recognition triggers signal transduction pathways that connect herbivore-specific elicitors to the expression of suitable defence genes (Fig. 2).

Plant perception

Mechanical wounding of plant tissues is the first consequence of plant-herbivore interactions although damaged tissue is not always an indicator of a pest attack. Plant perception begins with the herbivore contact. The physical pressures, cell disruption,

deposition of chemical compounds or arthropod oviposition are differentially recognised by plants as elicitors or effectors of the defence response (Balbyshv and Lorenzen 1997; Peiffer et al. 2009; Bonaventure 2012). Comparisons between host transcriptome profiles induced by mechanical injury or by arthropod feeding present an important overlap (Ralph et al. 2006; Lawrence et al. 2012). Nevertheless, it is clearly demonstrated that plants induce different responses by discriminating between herbivore feeding or application of insect oral secretions (OSs) to wounded sites from mechanical damages (Giri et al. 2006; Howe and Jander 2008; Lawrence et al. 2008, 2012). Moreover, current experimental approaches based on “omic”-technologies have shown that specific damage produced by chewing, phloem-feeding, mesophyll-sucking or leafminer herbivores are coupled to specific plant responses (Carolan et al. 2011; Lawrence et al. 2012; Zhang et al. 2012).

Among the molecules considered as HAEs or HAMPs, salivary enzymes of insect herbivores ( $\beta$ -glucosidases, glucose oxidases, oxireductases and proteases) and particularly FACs (Fatty acid-Amino acid Conjugates) have been widely studied (Bonaventure et al. 2011; Yoshinaga et al. 2007; Rodriguez and Bos 2013). FACs are fatty acids derived from plant membranes conjugated mainly with amino acids from herbivores, found in OSs. The first FAC characterised was the volicitin, *N*-(17-hydroxylinolenoyl)-L-glutamine, first identified in *Spodoptera exigua* (Alborn et al. 1997) and subsequently found in other lepidopteran and dipteran species (Yoshinaga et al. 2007). Other analogues of FACs are the caeliferins, sulphur-containing fatty acids isolated from regurgitants of several insects (Alborn et al. 2007). In addition, cryptic peptides derived from proteins can elicit plant defence. The best studied cryptic peptides are the inceptins, proteolytic products of the plant chloroplastic ATP synthase  $\gamma$ -subunit (cATPC) identified in cowpea plants after *Spodoptera frugiperda* feeding (Schmelz et al. 2006, 2007). Ingested cATPs are cleaved in insect midguts and subsequently form inceptins. Both volicitins and inceptins bind reversibly to plant cell membranes, most likely through specific receptors and trigger the release of volatile terpenes with a potential function as indirect defences (Truitt et al. 2004; Alborn et al. 2007). The application of volicitins and inceptins on mechanically damaged



**Fig. 2** Plant inducible defences against phytophagous arthropods require appropriated recognition systems to trigger signal transduction pathways that connect herbivore specific elicitors to the expression of suitable defence genes. *CMs* Calmodulins, *CDPKs*  $Ca^{2+}$  dependent protein kinases, *MAPKs* mitogen activated protein kinases, *TFs* transcriptional factors

leaves induces Mitogen Activated Protein kinase (MAPK), jasmonic acid (JA) and ethylene (ET) biosynthesis. Consequently, transcriptomic, proteomic and metabolomic responses are modified, and the amplification of direct and indirect plant defences is induced (Schmelz et al. 2007; Skibbe et al. 2008; Meldau et al. 2009; Wu and Baldwin 2010). In addition, families of elicitor peptides (Peps), which play an important role in plant resistance against pathogens, have also been implicated in defence against herbivores (Huffaker et al. 2013). Peps are plant C-terminal peptides derived from cytoplasmic PROPEP precursors, which are very well studied in *Arabidopsis* where their receptors have also been identified (Yamaguchi et al. 2010; Yamaguchi and Huffaker 2011). In addition, molecules identified in oviposition fluids also elicit specific defence responses in host plants. For example bruchins -long-chain  $\omega,\alpha$ -diols esterified at one or both oxygens with 3-hydroxypropanoic acid-, have been isolated from the oviposition fluid of pea weevils and benzyl cyanides have been detected in cabbage after *Pieris brassicae* oviposition (Doss et al. 2000; Fatouros et al. 2008).

Plant transgenic technologies have also been applied to study the functionality of genes encoding putative HAEs or HAMPs molecules. Bos et al. (2010) identified 48 effector candidates in the salivary glands of *Myzus persicae*, using transient plant overexpression assays to analyze elicitation of phenotype and effects on aphid performance. The same group of researchers demonstrated silencing of the aphid C002 effector by dsRNA feeding from plants (Pitino et al. 2011). Recently, Pitino and Hogenhout (2013) have found protein effectors that promote aphid feeding and colonisation in a plant-specific manner. *M. persicae* reproduction increased in transgenic *Arabidopsis* producing the C002, PintO1 and PINtO2 effectors, whereas its reproduction was not altered on *Arabidopsis* producing the *Acyrtosiphon pisum* orthologues of these proteins. Moreover, a plant-mediated RNAi approach has shown that *c002*- and *Pit02*-silenced *M. persicae* has reduced progeny compared with non-silenced aphids.

Notably, plant defence responses are induced not only by molecules derived from arthropods or by plants after arthropod feeding but also by endogenous host-plant elicitors as a consequence of wounding or herbivore attacks. Elicitors can be released by cell death, as small molecules or molecule fragments and

reactive oxygen species (ROS) are recognised as alarm signals. One example is the wound-signalling peptide systemin, a C-terminal peptide derived from prosystemin which promotes protease inhibitor (PI) and JA synthesis and systemic volatile emissions in tomatoes (McGurl et al. 1992; Degenhardt et al. 2010). There is direct evidence indicating that systemin activates a phospholipase A that releases linolenic acid from membrane lipids in wounded tomato leaves and consequently induces JA synthesis (Narvaez-Vasquez et al. 1999; Sun et al. 2011). When thrips and spider mites fed on prosystemin-overexpressing tomato, leaf damage was decreased and herbivore fecundity was reduced compared to results from control tomato (Li et al. 2002). Remarkably, 35S-prosystemin lines increased volatile terpenes emissions in tomatoes to attract insect enemies compared to wild type plants (McGurl et al. 1994; Li et al. 2002; Degenhardt et al. 2010). In contrast and as expected, transgenic plants expressing an antisense prosystemin cDNA were defective in the systemic expression of PIs, and this resulted in greater susceptibility to pest attacks (McGurl et al. 1992). These results provide strong evidence of an efficient defensive function of the systemin/JA signalling pathway and again highlight the value of transgenic techniques for plant defence research.

#### Plant receptors

Phytophagous arthropods are recognised when conserved HAE, HAMPs or effectors are detected by plant Pattern Recognition Receptors (PRRs) leading defensive reactions (Bos et al. 2010; Hogenhout and Bos 2011; Erb et al. 2012). This complex mechanism is similar to the PAMP or MAMP (pathogen/microbe-associated molecular patterns) and Effector Triggered Immunity (ETI) systems from microorganisms, widely described and responsible for activating plant immunity (Wu and Baldwin 2010).

A considerable number of trans-membrane receptor-like protein kinases (RLKs) have been associated with plant defence. RLKs often contain an extracellular receptor and a cytoplasmic catalytic kinase domain, identified as a Nucleotide Binding Site (NBS) and a Leucine Rich Repeat (LRR). These receptors transduce an extracellular recognition event into an intracellular signalling cascade to trigger host resistance to herbivores (Bonaventure 2012). In most

cases this step requires additional RLKs for full function (Yamaguchi and Huffaker 2011).

Until now, investigations to uncover the function of PRRs in herbivore resistance have not been well-established. However, the relation of genes encoding proteins of the NBS-LRR family to pest resistance has been determined by transgenic approaches. The tomato *Mi-1* gene was the first cloned NBS-LRR gene that confers resistance to aphids, psyllids and whiteflies when expressed in tomato plants (Rossi et al. 1998; Vos et al. 1998; Nombela et al. 2003; Casteel et al. 2006). *Mi-1*-mediated resistance to aphids requires the RLK, SISRK1, as confirmed by tomato virus-induced gene silencing experiments (Mantelin et al. 2011). In lettuce, silencing of several members of the RGC2 family encoding NBS-LRR proteins increases their susceptibility to root aphids (Wroblewski et al. 2007). In rice, overexpression of *Bph14*, a CC-NB-LRR encoding gene, activates the salicylic acid (SA) pathway and generates a higher resistance to the brown plant hopper (Du et al. 2009). Similarly, virus-induced gene silencing of the Lectin receptor kinase 1 (LecRK1) in *Nicotiana attenuata* prevents the full defence response against the lepidopteran *Manduca sexta*, because LecRK1 participates in the suppression of the insect-mediated inhibition of JA-induced defence responses (Gilardoni et al. 2011). Very recently, it has been described ML3, a putative MD2 lipopolysaccharide-recognition domain protein with a putative function as a regulator for HAMP recognition. *ML3* loss-of-function in *Arabidopsis* plants compromised the upregulation of herbivore-induced genes, and the larvae of *Spodoptera littoralis* that fed on *ml3* mutant plants gained more weight than those that fed on wild-type plants (Fridborg et al. 2013).

### Signal transduction pathway

Direct or indirect recognition of HAEs or HAMPs initiates a signal transduction pathway involving the rapid activation of numerous processes, including  $\text{Ca}^{2+}$ -signalling, production of ROS, phosphorylation cascades and transcriptional activation events that ultimately culminate in specific defence responses and the transmission of alerts to cells in other parts of the damaged plant (Maffei et al. 2007; Wu and Baldwin 2010; Bonaventure 2012; War et al. 2012).

Early events in plant-herbivore interactions start with ion imbalances, causing variations in membrane

potential and increases in the levels of cytosolic free calcium. Calmodulins (CMs) and  $\text{Ca}^{2+}$ -dependent protein-kinases (CDPKs) have been identified as  $\text{Ca}^{2+}$  sensors modulating the first step of a downstream cascade of defence effects. Calmodulin is activated in transgenic tobacco lines overexpressing a glutamate decarboxylase whose product, Gamma-aminobutyrate (GABA) is an inhibitory neurotransmitter. The activation of calmodulin correlates with GABA hyper accumulation, as those plants are more resistant to budworm larvae than control plants (MacGregor et al. 2003). Similarly, silencing of *Nicotiana attenuata*  $\text{Ca}^{2+}$ -dependent Protein Kinases CDPK4 and CDPK5 strongly up-regulates JA levels after wounding or *Manduca sexta* infestation with a parallel delay in the arva development rate (Yang et al. 2012).  $\text{Ca}^{2+}$  is also associated with NO synthesis and ROS production by modulating NADPH oxidase and polyphenol oxidase (PPO) activities (Wu et al. 2013). Although ROS function in signalling has not been extensively studied during herbivore attacks, it has been reported that insect/acari feeding increases plant ROS levels (Maffei et al. 2007; Santamaria et al. 2012). Transgenic tomato and poplar plants overexpressing PPO genes presented changes in redox levels and resulted in higher mortality of *Spodoptera litura* and *Malacosoma disstria*, respectively (Wang and Constabel 2004; Mahanil et al. 2008). In contrast, *rbdh D*-silenced plants, which lacked functional NADPH oxidases, were more vulnerable to insects (Miller et al. 2009; Wu et al. 2013).

In addition, strong evidence suggests that ROS signalling is closely related to hormone-signalling pathways in the plant-herbivore interactions. In particular, jasmonates have been proposed as the “master regulators” of plant defences. Herbivore elicits JA, and plant cells transduce JA signals into the activation of transcriptional regulation of defence-genes, with many dependent on the MAP kinase pathway (Kanchiswamy et al. 2010; Bonaventure et al. 2011). In a major branch of the JA pathway, JA conjugates with the amino acid isoleucine (JA-Ile) bind to the F-Box protein receptor COI1 (Yan et al. 2009) and causes ubiquitination and degradation of JAZ protein repressors (Chini et al. 2007; Thines et al. 2007). Consequently, their target transcription factors, such as the MYC class factors, are liberated (Pauwels et al. 2010). One of the MYC proteins, MYC2, is shown to activate several metabolic pathways involved in plant defence

against herbivores (Dombrecht et al. 2007). Moreover, Stotz et al. (2000) reported that *coi1-1* mutants were more susceptible to *Spodoptera littoralis* feeding than the wild type plants, and the triple mutant *myc2 myc3 myc4* was as impaired as *coi1-1* in the activation of defence against this pest (Fernández-Calvo et al. 2011). As part of this defence pathway, Schweighofer et al. (2007) showed that the PP2C-type phosphatase AP2C1 negatively regulated MPK4 and MPK6, modulated JA and ethylene levels in *Arabidopsis* and influenced the response to phytophagous mites and pathogens.

WRKY transcription factors are also important regulators of the JA response. The application of *Manduca sexta* FACs on *Nicotiana attenuata*-wounded leaves induces the activation of MAPKs, JA and ET biosynthesis and signalling, and WRKY factors, which ultimately produce the amplification and modification of wounding-induced transcriptomic, proteomic and metabolomic responses. This transduction pathway ends with the induction of direct and indirect plant defences (Wu et al. 2007; Skibbe et al. 2008). In contrast, silencing of *WRKY3*, *WRKY6* or both in *N. attenuata* rendered plants highly susceptible to *Manduca sexta* attack (Skibbe et al. 2008). Once more, transgenic approaches have been used to analyse gene functionality in vivo. Plants that over- or under-express several JA-regulated genes (*LOX*, *prosystemin*, or *pin2*) enhance or impair resistance to lepidopteran caterpillars (Royo et al. 1999; Ryan 2000; Kandoth et al. 2007).

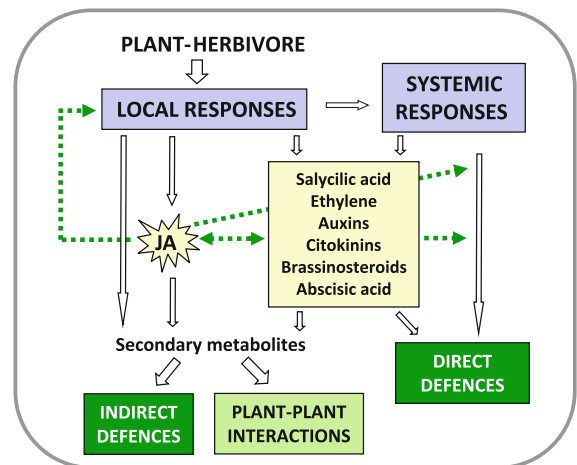
Many articles and reviews have covered particular aspects of the JA-induced responses against pests, including a complex cross-talk with other hormones (Ballare 2010; Robert-Seilaniantz et al. 2011). Two other hormones with a key role in orchestrating the expression of plant defences against herbivores are SA and ET. Generally, it is accepted that SA antagonises JA-induced resistance, but SA and ET may both have positive and/or negative effects. In this way, *Pieris brassicae* oviposition induced SA accumulation and reduced JA-responsive genes, leading to reduced *Arabidopsis* resistance against *S. littoralis* (Bruessow et al. 2010). Ethylene signalling reduces the resistance of *Arabidopsis* towards *Spodoptera littoralis* but not against *Plutella xylostella*. Moreover, the *hookless1* and *ein2* mutations, which affect components of ET signalling, conferred resistance to *S. littoralis* (Stotz et al. 2000). Auxins, abscisic acid, brassinosteroids,

cytokinins and gibberellins have received less attention as herbivore resistance modulators but the role of these hormones in mediating specificity in herbivore-induced defence responses has been recently reported (Robert-Seilaniantz et al. 2011; Erb et al. 2012). This hormonal cross-talk is summarised in Fig. 3. Furthermore, recent reports have revealed an integration of ROS and hormone signalling pathways in chloroplast in response to insects (Kerchev et al. 2012; Nabity et al. 2013). It can be concluded that phytohormones work in a very complex fashion, either in a cooperative or antagonistic role, and have become of increasing importance in plant defence research.

### Future challenges

As demonstrated throughout this review, there is a complex system of steps, signals and molecules induced in a plant after its interaction with phytophagous arthropods. The application of transgenic approaches has been essential for understanding the function of genes involved in the cascade of plant reactions to specifically develop either resistance or tolerance against each herbivore species.

An effective plant transgenic technology has been crucial for functional analysis of genes to understand



**Fig. 3** The expression of plant defences locally or systemically induced by feeders, are mainly regulated by jasmonic acid (JA) and a complex cross-talk with other hormones (salicylic acid, ethylene, brassinosteroids, abscisic acid, auxins and cytokinins). Consequently, direct and indirect defences against herbivores are produced and herbivore-challenged plants can emit volatiles to warn neighbour plants of the pest presence



their *in vivo* roles. However, this knowledge is still fragmentary, and increasing the understanding of what happens in the plant-herbivore interphase is critical for having more and new alternatives to enhance plant defences against pests. Hopefully, in the coming years a wider availability of plant genome sequences will broaden their usage and multiply the possible applications of transgenic approaches. In the near future, the induced plant responses to pests can be engineered genetically so that the defensive compounds can be constitutively produced in plants challenged by herbivores. Moreover, induced resistance can be manipulated by using chemical elicitors or secondary metabolites to confer resistance to herbivores. Elicitors of induced responses could be sprayed on crop plants to build up the natural defence system against specific damage caused by a specific herbivore. However, more advances should be made to improve transformation efficiencies, to reduce plant manipulation time-consumption, to overcome the transformation of recalcitrant species and finally, to increase the number of cultivars, variants and plant genome backgrounds to be transformed. It is our hope that continued advancements in basic plant research to translate will be applied to enhance the defence systems of agriculturally important crops.

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