Available online at www.sciencedirect.com
ScienceDirect
Phytochemistry 68 (2007) 2946–2959
PHYTOCHEMISTRY
www.elsevier.com/locate/phytochem

Review

Insects feeding on plants: Rapid signals and responses preceding the induction of phytochemical release

Massimo E. Maffei [a,*], Axel Mithöfer [b], Wilhelm Boland [b]

[a] Department of Plant Biology and Centre of Excellence CEBIOVEM, University of Turin, Viale P.A. Mattioli, 25, I-10125 Turin, Italy
[b] Max Planck Institute for Chemical Ecology, Department of Bioorganic Chemistry, Hans-Knöll-Str. 8, D-07745 Jena, Germany

Received 31 May 2007; received in revised form 2 July 2007
Available online 6 September 2007

Abstract

The ability of plants to withstand herbivores relies on direct and indirect chemical defense. By using toxic phytochemicals, plants can deter and/or poison herbivores, while by releasing volatile organic compounds (VOCs) into the atmosphere plants can attract predators of the herbivores. The activation of specific responses requires recognition and appropriate response towards the attacking enemy and most of the events which finally lead to gene activation (the signaling pathway) occur within a few minutes. Among the several signaling molecules involved, reactive oxygen species (ROS) and intracellular calcium signatures belong to early events, which are responsible for most of the ensuing cascades of chemical and molecular reactions. In this review, we will focus on rapid early events following insect feeding on plants that eventually lead to the production and release of phytochemicals. Furthermore, we compare and discuss the impact of mechanical and biotroph wounding.

Keywords: Plant–insect interaction; Direct and indirect defense; Calcium homeostasis; Reactive oxygen species; Volatile organic compounds

Contents

1. Introduction

By co-existing from at least 100 million years, plants and insects have evolved a variety of beneficial and deleterious interactions (Stotz et al., 1999). To avoid being overeaten, plants have evolved chemical defenses able to cause an effective and often drastic reduction in insect feeding (Harborne, 1993). These defenses have to be orchestrated both in time and space by highly complex regulatory networks that themselves are further modulated by interactions with other signaling pathways. The integrated responses ultimately lead to a characteristic gene expression pattern resulting, among many other activities, in the production

---

* Corresponding author. Tel.: +39 0116705967; fax: +39 0112365967.
E-mail address: massimo.maffei@unito.it (M.E. Maffei).

0031-9422/$ - see front matter © 2007 Elsevier Ltd. All rights reserved.
doi:10.1016/j.phytochem.2007.07.016

of phytochemicals that are directed against the invading or feeding organism. This was achieved throughout evolution of constitutive (e.g. primary and secondary metabolites, but also silica, thorns, trichomes etc.) and induced defenses [e.g. secondary metabolites, strengthening of cell walls, production of reactive oxygen species (ROS), etc.]. Whereas constitutive defense are mostly direct, induced defenses are either direct (e.g. phytoalexins, ROS) or indirect [e.g. volatile organic compounds (VOCs) such as terpenoids, aromatic compounds and green leaf volatiles, etc.]. Direct defenses are plant traits that by themselves affect insect performance and are generally categorized by their mode of action. Among secondary metabolites, many phytochemicals function as toxins by poisoning non-adapted herbivores and forcing adapted herbivores to invest limited resources in detoxification. In addition to direct defenses, plants express traits that facilitate 'top-down' control of herbivore populations by attracting predators and parasitoids to the feeding herbivore. Thus, indirect defense mediated by the herbivore-induced release of VOCs has received the most attention, but herbivore-induced nectar production by extrafloral nectaries functions similarly (Arimura et al., 2005; Baldwin et al., 2001).

Insects can locate their hosts even though the host plants are often hidden among an array of other plants, and plant volatiles play an important role in this host-location process (Bruce et al., 2005). Furthermore, these VOC-mediated interactions of plants with organisms of higher trophic levels suggest that they communicate similarly with each other (Dicke et al., 2003). VOC exposure alone, without actual herbivore attack, may directly increase the production of defenses. Alternatively, VOC exposure may allow nearby plants to ready their defenses for immediate use once the herbivores move from the neighboring plant to attack the "listening" receiver (Arimura et al., 2000; Baldwin et al., 2006; Heil and Bueno, 2007). Moreover, volatiles from primary host plants may also attract other insects, as is the case of male aphids (Powell et al., 2006; Powell and Hardie, 2001). Interestingly, parasitoids also use herbivore-induced responses to assess habitat profitability and adapt patch residence time (Tentelier and Fauvergue, 2007). Furthermore, herbivore-induced plant volatiles emissions are inducible by other biotrophs as well as abiotic agents (Holopainen, 2004). After release from leaves, flowers, and fruits to the atmosphere and from roots into the soil, plant phytochemicals defend plants against herbivores and pathogens or provide reproductive advantages by attracting pollinators (Dudareva et al., 2006). Moreover, certain volatiles may act as airborne signals that boost direct and indirect defenses in remote parts of the same plants (Heil and Bueno, 2007; Ton et al., 2007).

Besides the use of direct constitutive phytochemicals, several steps are involved from the detection of insect feeding to the production of indirect plant responses. These include disruption of leaf tissues, release of elicitors, signaling cascades and the activation of transcription factors eventually leading to the plant cell response. Current research in plant–insect interaction is focusing mainly on transcriptomics, genomics, proteomics and metabolomics, which are late events induced by biotic stress. In contrast, events within the first seconds to minutes, which are involved in recognition and signal transductions, are still poorly understood (Maffei et al., 2007).

Because many other reviews already covered the role of phytohormones (JA, SA, and ethylene) (Lorenzo and Solano, 2005; Murphy et al., 1999; van Loon et al., 2006) in plant–insect interactions, we will not repeat this. Instead we will focus on the role of calcium ions (Ca^{2+}) as a signal and on the double role of reactive oxygen species as both signals and defense compounds. Both types of signals preceed the generation of phytochemicals, which act in direct and indirect plant defense against herbivores. Finally, the impact of mechanical vs. herbivore wounding will be compared.

2. Calcium homeostasis and signaling

Each known system of signal transduction engages Ca^{2+} as an important second messenger and Ca^{2+} is also involved in the control of many processes such as growth and differentiation, photomorphogenesis and embryogenesis, perception of symbiotic signals, hypersensitive responses induced by biotrophs, assembling and disassembling of cytoskeleton elements, perception of red and blue light and regulation of stomata (all reviewed by Medvedev, 2005). Thus, regulation of intracellular calcium levels is important for the survival of the cell. The cytosolic Ca^{2+} concentration is balanced by the presence of a large number of Ca^{2+} stores which can release Ca^{2+}, the Ca^{2+} specific channels/pumps that regulate both Ca^{2+} influx and efflux in cells and subcellular compartments, and different (Ca^{2+}-binding) proteins that bind to Ca^{2+} either to sequestrate it or to perform some other complex tasks. All these components involved in regulation of Ca^{2+} concentrations in its equilibrium level constitute the complex network of Ca^{2+} homeostasis system (Pandey et al., 2000). In the resting state, Ca^{2+} levels are high in the apoplast, mitochondria, vacuole and ER (ca. 1 mM), and very low in the cytosol (ca. 0.0001 mM). In response to various stimuli, Ca^{2+} ions are released into the cytosol via channel proteins and pumped back into the organelles and apoplast via Ca^{2+} pumping ATPases (Lecourieux et al., 2006; Medvedev, 2005). In plant cells, Ca^{2+} plays a physiological key role as intracellular second messenger and is especially important for the maintenance of cellular homeostasis and signal transduction pathways (see below) (Anil and Rao, 2001; Reddy, 2001; Sanders et al., 2002).

The typical response patterns to different Ca^{2+} concentrations lie in the ability of cells to generate specific cytosolic Ca^{2+} concentration signatures. They may be unique, in terms of spatio-temporal characteristics and in response to an individual stimulus (Evans et al., 2001).

The specific biological role of Ca^{2+} in the wound response signaling cascade both from biotic and abiotic injury is still unclear. Increases in cytosolic Ca^{2+} levels have been shown in tomato to be triggered by the wound signaling peptide, systemin (an 18-amino acid polypeptide which functions in the cascades of a long-distance systemic signaling), resulting from an influx of extracellular Ca^{2+} through several types of Ca^{2+} permeable channels and mobilization of internal Ca^{2+} stores (Moyen et al., 2007). By altering intracellular levels of free Ca^{2+}, and then examining the effects of the altered Ca^{2+} levels on activation of the wound response cascade, Dombrowski and Bergey (2007) confirmed that in tomato Ca^{2+} channels play a role in mediating wound response activation and that inhibition of Ca^{2+}-ATPases affects the response to wounding and systemin in a similar way. Furthermore, a direct correlation was found between Ca^{2+} fluxes and wound gene activation, while elevated concentrations of Ca^{2+} in the apoplast significantly enhanced the biological activity of systemin.

Plants withstand various stress conditions by responses mediated via changes in cytoplasmic Ca^{2+} concentration (Pandey et al., 2000), but very likely also in other compartments such as the nucleoplasm (Lecourieux et al., 2006; Walter et al., 2007). In plant–pathogen interactions, a transient influx of Ca^{2+} occurs mainly into the cytosol and both omission of Ca^{2+} from the extracellular medium and application of inhibitors of Ca^{2+} channels abolished the plant defense response (Nürnberger et al., 1997). Cytosolic calcium ($[Ca^{2+}]_{cyt}$) variations have been observed by challenging plant cells with a series of pathogen-derived elicitors: cryptogein (a proteinaceous elicitor secreted by the oomycete *Phytophthora cryptogea*), oligosaccharide elicitors, oligogalacturonides, lipopolysaccharides, endopolygalacturonases, chitosan or yeast elicitors, proteins leading to necrosis (including harpin and elicitins) and non-necrotic protein elicitors (including flagellin) (all reviewed by Lecourieux et al., 2006).

Even after herbivore feeding there is a dramatic $[Ca^{2+}]_{cyt}$ influx limited to few cell layers lining the bite zone, visualized by using a Ca^{2+}-sensitive dye (Maffei et al., 2004). A Ca^{2+} spike was always observed and depended on Ca^{2+} channel activity, since the response could be reduced by the action of verapamil, a voltage-gated Ca^{2+} channel antagonist, EGTA (a calcium chelator) and ruthenium red (an inhibitor of calcium release from internal stores) (Maffei et al., 2004, 2006). From larval oral secretions, several classes of insect-derived elicitors have been isolated that may trigger defense responses in certain plants. For example, the fatty acid–amino acid conjugate group includes a series of saturated and unsaturated fatty acids that are 16 or 18 carbons in length and coupled to l-glutamate or l-glutamine through a peptide bond (Truitt et al., 2004). The ability of *N*-acyl-glutamines to initiate Ca^{2+} influx was independently confirmed with the test system of aequorin-transformed soybean cells (Maffei et al., 2004). Upon addition of the conjugates an immediate Ca^{2+} influx was observed without any obvious lag-phase suggesting a detergent-like effect rather than a receptor-mediated one. In contrast, Maischak et al. (2007) showed that still unknown compounds must be present in the oral secretion of *Spodoptera* spp. that are able to induce Ca^{2+}-transients in the same system, which much more resembles classical elicitor effects. These data indicate that other compounds than the *N*-acyl-amino acid conjugates are responsible for the insect feeding-induced Ca^{2+} burst. Interestingly, only the conjugate with l-glutamine has been shown to induce specific defense responses exclusively in maize (Alborn et al., 1997), demonstrating that additional specific interactions between *N*-acyl-glutamines and the plant are involved in the elicitation process of corn plants. The finding that in Lima bean the signaling pathway(s) mediating expression of defense genes in the receiver plants requires calcium influx into the cells has been confirmed by treatment with a chelator of extracellular Ca^{2+} ion, BAPTA [1,2-bis(2-aminophenoxy)ethane-N,N,N',N'-tetraacetic acid], or an inhibitor of serine/threonine protein kinases, staurosporine, which completely suppressed the expression of the five defence genes in Lima bean leaves that received spider mite (*Tetranychus urticae*) induced volatiles (Arimura et al., 2000). Finally, signals induced rapidly by herbivore attack have been found to spread over the leaf leading to a strong Ca^{2+}-dependent transmembrane potential (V_m) depolarization in the bite zone followed by a transient V_m hyperpolarization in the close vicinity and a constant depolarization in distances greater than 6–7 mm (Maffei et al., 2004).

As we discussed, regulation of Ca^{2+} homeostasis is important, particularly when calcium is involved as a signaling ion. Ca^{2+}-binding proteins serve also as regulators of internal free Ca^{2+} levels in plant cells. Ca^{2+}-binding proteins, such as calmodulin or calcium-dependent protein kinases, function to buffer intracellular Ca^{2+} levels or translate intracellular oscillations of free Ca^{2+} levels into signal-specific cellular responses (Yang and Poovaiah, 2003). In plant–aphid interactions, *Diuraphis noxia* feeding on wheat foliage and *Myzus persicae* feeding on *Arabidopsis* plants each induce increased expression of calmodulin binding proteins involved in plant defense signaling (Smith and Boyko, 2007). In corn, treatment with H_2O_2 leads to significant increases in $[Ca^{2+}]_{cyt}$ in the protoplasts of mesophyll cells and in the expression of the calmodulin 1 (CaM1) gene and the content of CaM in leaves of maize plants, and enhanced the expression of the antioxidant genes superoxide dismutase 4 (SOD4), cytosolic ascorbate peroxidase (cAPX), and glutathione reductase 1 (GR1) and the activities of the chloroplastic and cytosolic antioxidant enzymes. The up-regulation of the antioxidant enzymes was almost completely blocked by pretreatments with two CaM antagonists (Hu et al., 2007).

However, the main regulation of Ca^{2+} homeostasis depends on the activity of Ca^{2+}-ATPases located in various compartments of the cell, which constantly pump Ca^{2+} outside the cytsol (Allen et al., 1995).

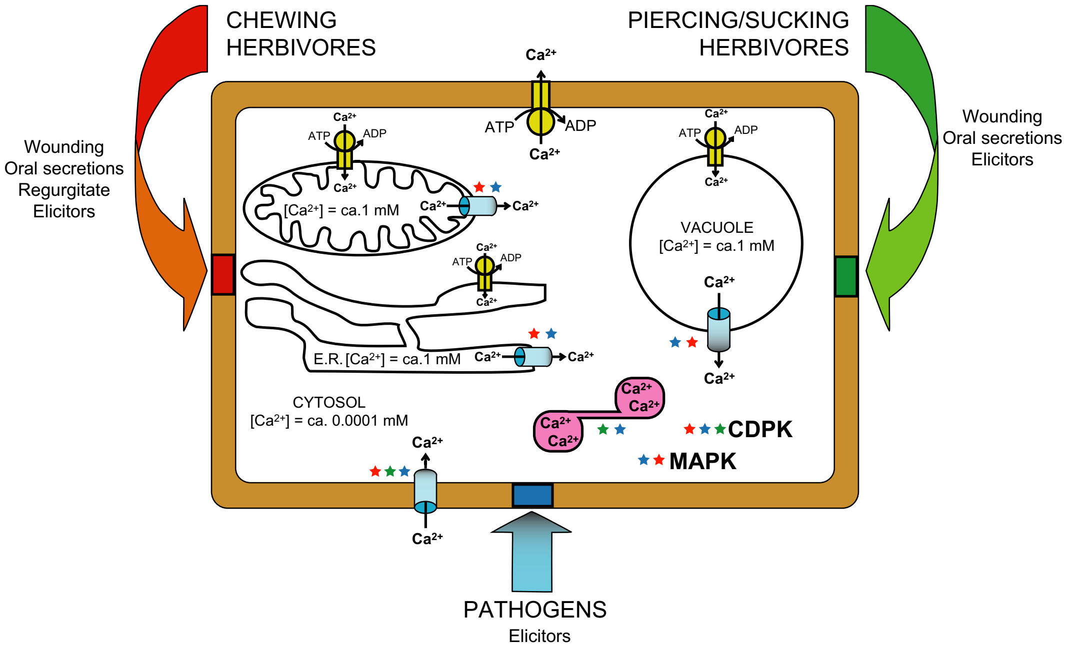

Fig. 1. Calcium homeostasis after biotic attack. Influx of Ca^{2+} into the cytosol is caused by a series of plasma membrane inward Ca^{2+} channels, which activity can be studied by the use of several inhibitors. Herbivores and pathogens have been demonstrated to induce Ca^{2+} influx that triggers a series of cascade events, including ROS production. Cytosolic Ca^{2+} concentration can be raised by opening of efflux Ca^{2+} channels located in the membranes surrounding plant cell internal stores such as mitochondria, endoplasmic reticulum (E.R.), and the vacuole. Both chewing herbivores and pathogens have been demonstrated to induce opening of these channels. In plant–pathogen interaction IP_3-gated Ca^{2+} channels have also been suggested. Cytosolic Ca^{2+} concentration can be lowered by the activity of Ca^{2+}-ATPase and by binding to proteins, such as calmodulin and CDPKs. Increase in calmodulin activity has been demonstrated in plant–pathogen and plant–aphid interactions, while CDPKs are activated by all trophic interactions as illustrated. Colored stars refer to the appropriate biotroph.

Since calcium-dependent protein kinases (CDPKs) are regularly involved in signal transduction of a variety of biotic and abiotic stresses, their involvement as active protein cascades in herbivore/wound responses cannot be excluded (Ludwig et al., 2004). Moreover, Wu et al. (2007) showed a local and systemic induction of mitogen-activated protein kinases (MAPK) in *Nicotiana attenuata* challenged with oral secretions of the herbivore *Manduca sexta*. In potato (*Solanum tuberosum*) plants JA has been reported to affect CDPK transcript level (Ulloa et al., 2002) and in tobacco a link between CDPKs (*Nt*CDPK2), MAP kinases, and JA and ethylene cross-talks has been suggested (Ludwig et al., 2005). It will be interesting to further address the question as to where the regulated kinases are positioned within the different signal transduction chains in plant cells and, more specifically, whether they represent components relaying insect-mediated changes in ion fluxes to specific transcription factors that are suspected to be involved in the activation of defense-related cellular responses. Fig. 1 summarizes calcium homeostasis after biotic attack.

3. Reactive oxygen species as signals and defense compounds

Oxidative stress, resulting from the generation of ROS, such as superoxide ($O_2^{\cdot -}$), hydrogen peroxide (H_2O_2) and hydroxyl radicals ($HO^{\cdot}$), is a common phenomenon in many plant responses to both abiotic and biotic stresses (Foyer and Noctor, 2005a). A close interaction exists between perception of ROS (particularly H_2O_2) and cytosolic calcium in response to biotic and abiotic stimuli in plant systems (Foreman et al., 2003; Hancock et al., 2002; Maffei et al., 2006; Pei et al., 2000; Sagi and Fluhr, 2001; Sanders et al., 2002; Yang and Poovaiah, 2002). Because many stress conditions cause cellular redox imbalances, it has been proposed that oxidative stress defense responses might be a central component mediating cross-tolerance. However, since ROS exert toxic effects, it has been difficult to distinguish the ROS signaling roles from the secondary effects caused by cytotoxicity (Bowler and Fluhr, 2000).

ROS are continuously produced by plants under different stress conditions and in different cellular compartments (Foyer and Noctor, 2003). Both the chemical identity of a given ROS and the intracellular site of its production seem to affect the specificity of its biological activity, further increasing the complexity of ROS signaling within plants (Laloi et al., 2004). Furthermore, different types of reactive oxygen species activate distinct signaling pathways (Laloi et al., 2007).

Plant cells very likely possess ROS sensors that process and translate this information into respective biological output programs. In several systems, various signaling pathways, particularly those involving (MAPKs, are modulated by ROS (Desikan et al., 2001, 2005; Neill et al., 2002, 2003; Pitzschke and Hirt, 2006). However, the prominent role of ROS has been revealed in the induction, signaling, and execution of plant cell death (Van Breusegem and Dat, 2006). Despite all the evidence, the main source of ROS production in plants in response to biotic attack is still a matter of debate (Bolwell, 1999).

In absence of stress and under physiological conditions, the level of ROS is maintained low by the activity of antioxidative systems, which include secondary plant metabolites and scavenging enzymes (see below) (Foyer and Noctor, 2005a,b; Pandhair and Sekhon, 2006). Both biotic and abiotic factors induce changes in the ROS equilibrium and trigger cascades of signals eventually leading to increased ROS production and/or decreased antioxidant and scavenging activities (Apel and Hirt, 2004; Asada, 2006; Davies et al., 2006; Foyer and Noctor, 2003; Hancock et al., 2002).

ROS are important regulators of plant development and there is a growing body of evidence that ROS play roles in cell growth, thus spatial regulation of ROS production is an important factor controlling plant anatomy and morphology (Gapper and Dolan, 2006).

The rapid increase in ROS concentration which is observed after both biotic and abiotic injuries is called "oxidative burst" (Bhattacharjee, 2005; Bolwell et al., 2002). In plant–pathogen interaction, the most widely studied system of plant–biotroph interaction, a consistent amount of data indicate the presence o two compartments in which ROS production takes place: the apoplast and the symplast. Quite often both compartments may be operative at the same time in the same plant or tissue. Subcellular localization of ROS after insect feeding also shows that both apoplastic and symplastic localization, with exocellular matrix, peroxisomes/mitochondria and plasma membrane being the main compartments, are involved (Maffei et al., 2006).

Apoplastic oxidative burst has been demonstrated in *in vivo* and *in vitro* experiments and appears to act in several plants as a first barrier against pathogen invasion both during pathogen and insect attack (Bolwell et al., 2002; Felton and Korth, 2000; Maffei et al., 2006; Orozco-Cárdenas et al., 2001; Powell et al., 2006). The activity of plasma membrane-localized NADPH oxidases (NOX) catalyzes the production of $O_2^{\cdot-}$, by the one-electron reduction of oxygen using NADPH as the electron donor. In plants, the human NOX homologs have been named respiratory burst oxidase homologs (Rboh) and are involved in ROS production in response to biotic attack (Sagi and Fluhr, 2006). Cellular fractionation of plant tissue indicates that Rboh proteins are stimulated directly by Ca^{2+}. Medium (or apoplast) alkalinization preceding their activation results from elicitor-induced depolarization of the V_m and subsequent K^+/H^+ exchange followed by Ca^{2+} influx/Cl^- efflux (Sagi and Fluhr, 2001, 2006). Superoxide, which is produced outside the plasma membrane, serves as a starting material for the production of a large variety of reactive oxidants, including oxidized halogens, free radicals, and singlet oxygen (Apel and Hirt, 2004). Superoxide dismutation yields hydrogen peroxide (H_2O_2), one of the most important ROS in plant–biotroph interaction. Recently, three studies from mammalian systems have provided evidence that H_2O_2, in addition to the well studied role in intracellular signaling, is also used as an intercellular signal molecule, implying a necessary step of transport of H_2O_2 or ROS across the plasma membranes of signal-producing and perceiving cells. Molecular genetic evidence for the diffusion of H_2O_2 through specific members of the aquaporin family has been demonstrated in *Saccharomyces cerevisiae* (Bienert et al., 2007 and references cited therein).

Besides NADPH oxidase, other possible sources of ROS are present in the plant apoplast. These include cell wall peroxidases and amine oxidases. Peroxidases have mainly been localized to apoplastic compartments although they are also vacuolar and can be purified from membranes. The role of cell wall peroxidases in the generation of ROS has been clearly shown in certain plant–pathogen interactions (Bindschedler et al., 2001; Blee et al., 2001; Bolwell and Wojtaszek, 1997). In plant cells, both polyamine oxidase and diamine oxidase are reported to be located in apoplast. Polyamine oxidase can convert spermine and spermidine, by oxidative cleavage, back to spermidine and putrescine, respectively, resulting in the formation of H_2O_2 (Laurenzi et al., 2001). Time-course analyses showed that within several hours after biotic elicitation, newly synthesized polyamines are efficiently degraded by polyamine oxidase in tobacco, releasing H_2O_2 in the apoplast (Yoda et al., 2003).

Symplastic oxidative burst includes the activity of plant cell organelles which may contribute to build up consistent levels of ROS. In plant cells, most of the symplastic ROS produced originate from peroxisomes, chloroplasts and mitochondria. Peroxisomes were considered to function mainly for the removal of toxic H_2O_2 by catalase (CAT, EC 1.11.1.6), one of the many ROS scavenging enzymes. However, it is now known that in addition to producing H_2O_2, peroxisomes can generate $O_2^{\cdot-}$ and NO, which are known cellular messengers with a variety of physiological roles in intra- and inter-cellular communication (del Rio et al., 2006). Nitric oxide and H_2O_2 can permeate the peroxisomal membrane and $O_2^{\cdot-}$ can be produced on the cytosolic side of the membrane (Corpas et al., 2001; del Rio et al., 2006). In the chloroplast thylakoids, the reaction centers of PSI and PSII are the major generation sites of ROS (Asada, 2006), but they do not appear to be involved in herbivore-elicited ROS production (Maffei et al., 2006). In non-green tissues, or in the dark, mitochondrial ROS production becomes predominant. The major site of ROS formation in mitochondria lies in the electron transfer chain, especially at the level of Complexs I and III, where superoxide, is produced (Navrot et al., 2007).

In plants, the links between ROS production and photosynthetic metabolism are particularly important, allowing the selection of antioxidative defense mechanisms, which place all aerobic cells in a state of pro-oxidant/

antioxidant balance that prevents cellular damage. Lepidopteran larval saliva contains an elicitor which originates predominantly in the labial glands, glucose oxidase (GOX), an enzyme that generates H_2O_2 through the oxidation of D-glucose (Bede et al., 2006; Merkx-Jacques and Bede, 2004). GOX, while inhibiting some plant defense responses, has also been suggested to be an elicitor of plant pathogen defenses (Musser et al., 2005). GOX has been suggested to increase the caterpillar's survival through the suppression of inducible anti-herbivore defenses in plants, while tobacco (*Nicotiana tabacum*) leaves fed on by caterpillars with ablated salivary glands had significantly higher levels of nicotine, an inducible anti-herbivore defense compound of tobacco, than leaves fed upon by caterpillars with intact labial salivary glands (Musser et al., 2006). On the other hand, the expression of an exogenous GOX resulted in enhanced resistance to biotic attack in transgenic potato (Felcher et al., 2003; Zhen et al., 2000). However, glucose is not the only sugar that can be oxidized to produce ROS. In the Asteraceae, an enzyme with a protein sequence displaying a high similarity with reticuline oxidase can utilize a range of reducing sugars, most notably hexoses that accumulate in plants upon biotic attack, resulting in the production of ROS (Custers et al., 2004).

Because ROS can potentially damage proteins, lipids, and nucleic acids, cells have a number of ROS scavenging systems that are able to remove these molecules and to maintain a relatively low and constant ROS concentration (Bienert et al., 2007).

Plants must find a balance between producing ROS for defense and producing ROS-detoxifying enzymes to help stabilize plant tissue damage due to oxidative degradation (Thompson and Goggins, 2005). On the other hand, since plant-generated ROS pose a serious challenge to herbivorous insect species during host interactions, insects have also evolved a complex antioxidant mechanism to overcome the toxic effects of ROS (Mittapalli et al., 2007).

In plants, the antioxidant defense is primarily constituted by the enzymatic actions of superoxide dismutase (SOD, EC 1.15.1.1), which catalyzes disproportionation of $O_2^{\cdot-}$ to H_2O_2 and O_2. SOD is considered to be one of the first line of defenses. CAT and ascorbate peroxidase (APX, EC 1.11.1.11) are responsible for the scavenging of H_2O_2. CAT converts H_2O_2 to H_2O and O_2 and APX catalyzes the reduction of H_2O_2 using ascorbate as an electron donor. Other peroxidases, including guaiacol peroxidase (POD, EC 1.11.1.7) are also involved in H_2O_2 elimination. POD catalyzes oxidation of many phenolic compounds at the expense of H_2O_2 and is considered to be a key enzyme in biosynthesis of lignin (Gaspar et al., 1991).

In plant–insect interactions, high enzyme activity and/or gene expression of ROS scavenging systems belong to the later responses following herbivore attack, but occur before production of volatile compounds (phytochemicals) as indirect defenses. The leaves of aphid-infested celery, sorghum, and wheat plants up-regulate a number of sequences participating in cell wall and cell membrane strengthening, as well as redox homeostasis and detoxification. Transcripts encoding proteins involved in protection against and detoxification of ROS and other toxins are up-regulated in celery and wheat, but are downregulated in *N. attenuata* (Smith and Boyko, 2007).

After insect feeding on Lima bean, SOD, one of the early enzymes involved in the reduction of the superoxide anion generated either by Mehler reaction and photorespiration or by the reduction of molecular oxygen in mitochondria and oxidase reaction (Apel and Hirt, 2004), is activated at the gene transcription and enzyme activity levels only after 6 h. On the other hand, the basal enzyme activity of SOD was found to be high early after treatment in both, HW and MD leaves, but dropped in MD leaves after 6 h (Maffei et al., 2006).

In plants, CAT scavenges H_2O_2 generated during mitochondrial electron transport, beta-oxidation of the fatty acids, and most importantly photorespiratory oxidation (Yang and Poovaiah, 2002). In Lima bean, gene activation of CAT reaches the highest activity 6 h after feeding. However, since SOD activity is about 7- and 37-folds higher than that of the CAT, the resulting effect of herbivore feeding on Lima bean is the net increase with time of H_2O_2 production (Maffei et al., 2006). Enzymes involved in ROS scavenging, such as peroxidases, are also prerequisites for plant cell wall building.

A low activity of APX is found after *Spodoptera littoralis* feeding on Lima bean and this is in agreement with the lack of ROS localization observed in chloroplasts and suggests a major role of non-photosynthetic H_2O_2 production after herbivore attack. GPX, which is involved in the detoxification of lipid peroxides rather than hydrogen peroxide *per se* (Apel and Hirt, 2004; Foyer and Noctor, 2005a) showed no increased activity and gene expression after insect feeding (Maffei et al., 2006). In aphid infested resistant wheat plants (Boyko et al., 2006) and in *M. persicae*-susceptible celery plants (Divol et al., 2006), genes involved in oxidative signal transduction through the control of cellular hydrogen peroxide concentrations, such as peroxidase, catalase, NADH-dependent glutamate synthase, and a mitochondrial adenosine triphosphate/adenosine diphosphate (ATP/ADP) carrier protein, are up-regulated.

H_2O_2 is a relatively stable partially-reduced form of oxygen and its ability to diffuse freely allows H_2O_2 to play a central role in the generation of the defense response in plants (Bóka et al., 2007), most studies focused on the analysis of this particular ROS species. In addition to the proposed direct antimicrobial effect, H_2O_2 acts *via* signal transduction pathways which lead to the expression of defense genes (Orozco-Cárdenas et al., 2001).

Generation of H_2O_2 occurs under a diverse range of conditions, and it appears likely that H_2O_2 accumulation in specific tissues, and in the appropriate quantities, is of benefit to plants and can mediate cross tolerance toward other stresses (Bolwell, 1999).

H_2O_2 is produced after herbivore feeding (Leitner et al., 2005; Maffei et al., 2006; Mithöfer et al., 2004; Powell et al., 2006; Walling, 2000), and oxidative changes in the plants have been demonstrated to correspond with oxidative damage in the midguts of insects feeding on previously wounded plants (Orozco-Cárdenas and Ryan, 1999). In response to herbivores, H_2O_2 levels are likely to be elevated as long as the attacks persist.

Maffei et al. (2006) found that in Lima bean leaves, the accumulation of H_2O_2 occurs at high levels in cell walls adjacent to intercellular spaces in the spongy mesophyll, after both mechanical and herbivore damage. However, after herbivore attack, Lima bean leaves show higher production of H_2O_2 with respect to mechanically damaged leaves. In tomato plants that constitutively express prosystemin, a precursor of systemin, the levels of H_2O_2 are constitutively elevated and might provide an early defense barrier (Orozco-Cárdenas and Ryan, 1999).

Unlike chewing insects that cause swift and extensive tissue damage, most phloem feeders cause minimal tissue damage as they use their stylet to access the vascular tissue or directly on plant cells to feed. This relationship is more analogous to a plant–biotrophic pathogen interaction, where the pathogen is sustained in a localized area and is dependent on living plant cells (Kempema et al., 2007; Walling, 2000). Although the majority of the aphid microarray studies reported to date have examined only a select group of genes and many of the published microarray studies have limited biological replications and/or do not measure significance using a statistical method, the current transcriptome analyses suggest that changes to aphids are drastically different than those observed by chewing insects and that aphids tend to induce gene sets more similar to fungal or bacterial pathogens (Kempema et al., 2007 and references therein).

Aphids also induce accumulation of H_2O_2 (Powell et al., 2006) and ROS are elicitors of defense signaling pathways with known involvement in the elicitation of plant response to aphid attack (Boyko et al., 2006). Barley, oat, and wheat plants produce elevated levels of H_2O_2 in response to feeding by *Schizaphis graminum*, *D. noxia*, and *Rhopalosiphum padi* (all reviewed by Smith and Boyko, 2007). The level of mRNAs for several genes, that enable scavenging of ROS and redox homeostasis, increased during silverleaf whitefly (*Bemisia tabaci*) feeding, suggesting that feeding may induce ROS in planta (Kempema et al., 2007). Infestation with *S. graminum* increased H_2O_2 content and total soluble peroxidase activity in barley, with a maximum level of H_2O_2 observed after 20 min of infestation and the maximum in soluble peroxidase activity after 30 min of infestation (Argandona et al., 2001). This suggests that the aphid–induced accumulation of soluble peroxidase activity is a consequence of the H_2O_2 burst and indicates that the accumulation of H_2O_2 could be the beginning of a cascade of events that triggers physiological and molecular plant responses to prevent or minimize insect attack, as already observed in plant–pathogen interactions (Blumwald et al., 1998; Kotchoni and Gachomo, 2006; Torres et al., 2005).

Even single mechanical damage induce ROS production (Maffei et al., 2006; Orozco-Cárdenas et al., 2001; Reymond et al., 2004) and, in addition, mechanically wounded Lima bean leaves react fast and dramatically to exogenous H_2O_2 by inducing a strong V_m depolarization. Changes in V_m or modulation of ion fluxes at the plasma membrane level are amongst the earliest cellular responses to biotic and abiotic stresses, and induction of ion fluxes and V_m depolarization have been demonstrated in response to insect feeding (Maffei et al., 2004, 2007; Maffei and Bossi, 2006).

According to Dangl et al. (1996), the presence of H_2O_2 in the plant in response to herbivory could be advantageous because timing of the induction of defense responses can be an important factor in the success or failure of plants to defend against subsequent pathogen invasion (Dangl et al., 1996; Dangl and Jones, 2001; Torres et al., 2006). Wound-generated H_2O_2 that occurs in the veins also could have a defensive role against bacteria, fungi, or viruses as they may invade leaves wounded by herbivores (Orozco-Cárdenas and Ryan, 1999). This is particularly true in *S. littoralis*-Lima bean interaction, since feeding insects introduce regurgitate from the foregut containing microorganisms into the freshly damaged leaf.

Fig. 2 summarizes events leading the production of ROS in the apoplast and the symplast as well as the main ROS scavenging enzymes.

4. Crosstalks between pathways and emission of volatile blends

Today more than 1700 volatile compounds have been isolated from more than 90 plant families. They constitute about 1% of plant secondary metabolites and are mainly represented by terpenoids, aromatic compounds, fatty acid derivatives, and amino acid-derived products (Dudareva et al., 2004, 2006). Although some of these compounds are constitutively emitted by undamaged healthy plants, considerably higher amounts are emitted after herbivore damage. Many of them are synthesized *de novo* in response to the attacking organism (Paré and Tumlinson, 1996; Piel et al., 1998). Characteristic for the induction process is a lag period of several hours (4–8) between the damage and the emission. Since the complex blends are fed by different biosynthetic pathways linked to a web of interacting signaling pathways, the volatiles can be considered as a "volatilome" that is particularly sensitive to different external triggers. The composition of the volatile blend seems to reflect an integrative "cross-talk" between Ca^{2+}-ions (Arimura et al., 2000, 2005), ROS (Mithöfer et al., 2005), jasmonic acid (Blechert et al., 1995; Boland et al., 1995; Schittko et al., 2000), 12-oxo-phytodienoic acid (Koch et al., 1999), salicylate (Bi et al., 1997; Engelberth et al., 2001), ethylene (Rojo et al., 2003), and other still unknown

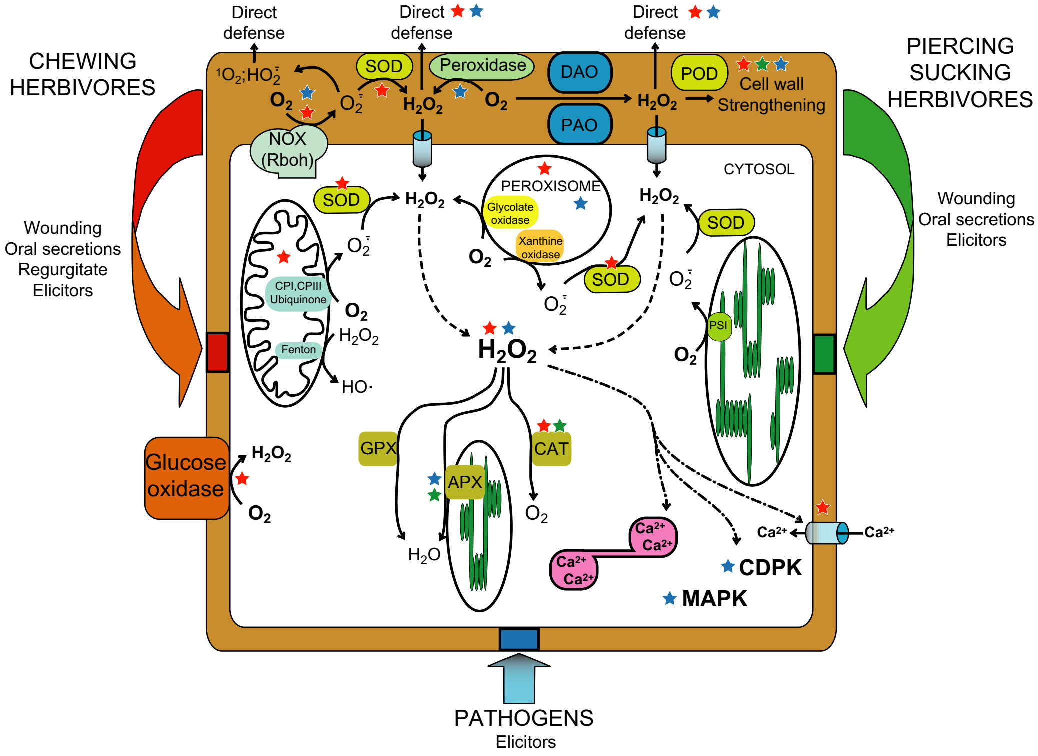

Fig. 2. Apoplastic and symplastic generation and scavenging of ROS upon biotic stress. One of the first barriers against plant cell invasion is the production of ROS at the first line of defense represented by the cell wall and the plasma membrane. Apoplastic ROS production depends on the activity of several cell wall enzymes, including Rboh, SOD, Peroxidases and amine oxidases. ROS produced in this environment may directly injure the attacking organisms or be used to strengthen the cell wall by increasing polymerization. Oral secretions of herbivores can generate H_2O_2 through the action of ROS as H_2O_2 can enter the cell through specific hydroperoxiporins that might increase the cytosolic H_2O_2 concentration. H_2O_2 and other ROS are also produced by plant cell organelles such as mitochondria, peroxisomes and chloroplasts. Scavenging enzymes like CAT, APX and GPX lower ROS toxicity and help to maintain H_2O_2 homeostasis. H_2O_2 also induces changes in Ca^{2+} homeostasis by interfering with Ca^{2+} channels and Ca^{2+} binding proteins. As in Fig. 1, colored stars refer to the effect of the biotroph on ROS production, scavenging and signaling.

members of the octadecanoid family. Methodological improvements of the last decade made the comprehensive assessment of volatilome possible and even allowed an almost real-time monitoring of the emitted compounds from living plants (Tholl et al., 2006). The volatiles may convey information on the plants' physiological status and the previously experienced stress. They may vary quantitatively, sometimes even qualitatively depending on growth conditions and the attacking organism. In particular, bioactive compounds from the oral secretions of herbivores or from invading microorganisms significantly influence their qualitative and quantitative composition. Therefore, the blend can be either more plant and/or more herbivore characteristic (De Moraes et al., 1998; Takabayashi et al., 1995). The composition of typical induced volatile blends has been reviewed for many plant systems (Dudareva et al., 2004, 2006) and their biological functions have been discussed (Arimura et al., 2005; Kessler and Baldwin, 2001; Van Poecke and Dicke, 2004; Vancanneyt et al., 2001). The composition of the blends also depends on the mode of damage such as single wounding, continuous wounding (Mithöfer et al., 2005), herbivore feeding (Paré and Tumlinson, 1996), and egg deposition (Hilker and Meiners, 2002). An herbivore-induced volatile blend may comprise more than 200 compounds (Dicke and van Loon, 2000), but often the same basic constituents are found as the major products. Besides addressing organisms from other trophic levels, induced volatiles also act on neighbored leaves from the same plant (Heil and Bueno, 2007), neighbored plants of the same species (Arimura et al., 2000; Engelberth et al., 2004; Kessler et al., 2006; Tscharntke et al., 2001) as well as neighbored plants of different species. Moreover, the volatile production generally shows a pronounced rhythmicity (see Fig. 3) by emitting the volatiles only during the light phase (Arimura et al., 2005; Kunert et al., 2002; Loughrin et al., 1994). However, to defend against night-active herbivores also nocturnal emissions are known (De Moraes et al., 2001; Kessler and Baldwin, 2001).

The composition of the herbivore-induced volatiles also strongly depends on abiotic factors, such as the availability of nitrogen and phosphorous (Schmelz et al., 2003a), soil and air humidity (Vallat et al., 2005), light intensity and temperature (Gouinguene and Turlings, 2002). The treatment of plantlets of the Lima bean with heavy metals (Hg^{2+}, Cu^{2+}, and Fe^{3+}) resulted in a characteristic blend of volatiles that was observed otherwise only after treatment of the plant with the channel forming peptide

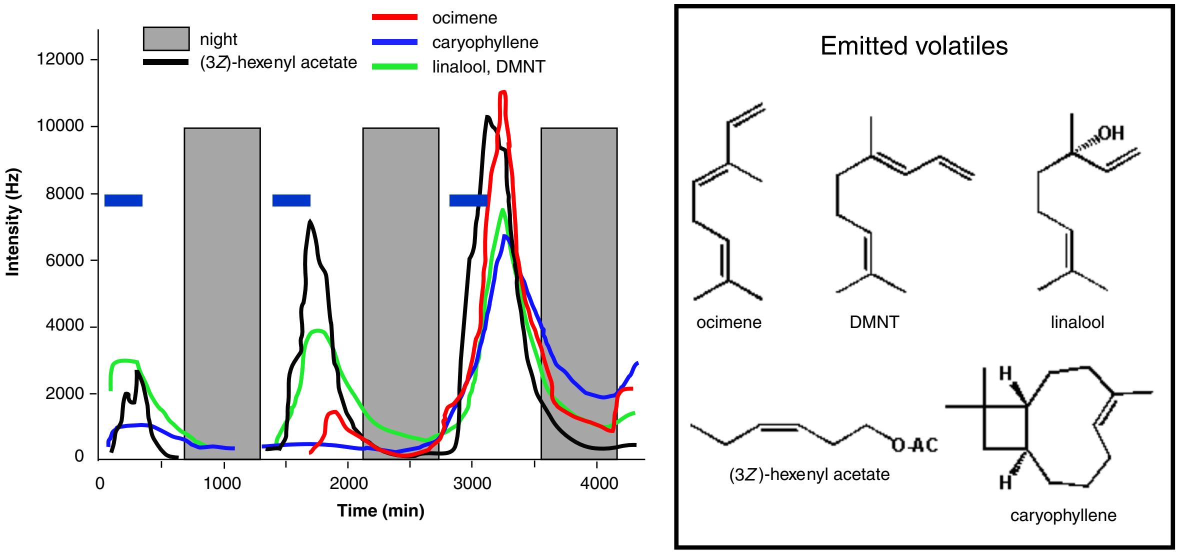

Fig. 3. Diurnal emission of volatiles from herbivore-damaged leaves of Lima bean (*Phaseolus lunatus*). The release of volatiles starts ca. 2 h after the onset of a continuous mechanical damage by the MecWorm system (Mithöfer et al., 2005). Comparable circadian profiles are observed after herbivore feeding (Kunert et al., 2002). Damage period: 6 h/day represented by a blue bar. Dark phase: grey area. Volatiles are only emitted during the light period. The amount of volatiles increases from day to day as long as the damage is continued. The emission ceases within 24–48 h after ending the continuous mechanical damage or removal of the herbivore. Interestingly, the composition of the blend changes dramatically in concentration from day to day, suggesting that attracted predators must be able to recognize these changes.

alamethicin (Engelberth et al., 2001). Common to both treatments is most likely the abundant generation of ROS which in Lima bean leaves generates an entirely different volatile blend than a feeding herbivore. A reason for this difference was found in the strong up-regulation of the salicylic acid biosynthesis which suppressed the production of jasmonic acid that is required for the general stimulation of volatile biosynthesis (Engelberth et al., 2004). This observation clearly stresses the outstanding importance of the "cross-talks" between the network of signaling pathways for an integrated and adjusted response that is ultimately reflected in the composition of the volatile blends or other phytochemicals.

In contrast to the delayed emission of induced volatiles, the so called "green leaf" volatiles are emitted almost instantaneously after damage. They are considered as wound signals and comprise degradation products of unsaturated fatty acids (Hatanaka, 1993). The typical green leave volatiles originate from linolenic acid and represent unsaturated six-carbon aldehydes, alcohols and esters (e.g. acetates, butyrates, benzoates). These compounds have recently gained particular interest since they seem to be involved in the "priming process" of undamaged leaves (Engelberth et al., 2004; Heil and Bueno, 2007; Heil and Kost, 2006; Kessler et al., 2006). A pronounced synergistic interplay of green leave volatiles and ethylene has been reported (Ruther and Kleier, 2005).

Mechanical wounding of plant tissues is an inevitable consequence of herbivory although the intensity and extent of damage is different and may vary with the mode of feeding, e.g. sucking or chewing. Therefore, in all studies analyzing the effects of insect feeding or insect elicitors on plant defense responses, control experiments with wounded plants have been performed using either a razor (blade) for scratching or cutting the leaf or a pattern wheel for puncturing leaf areas. This type of simulated herbivory resulted in induction of genes involved in defense strategies and also in up-regulation of activities addressing primary metabolism (Cheong et al., 2002; Major and Constabel, 2006; Reymond et al., 2004) but induction of defense-related VOC was not observed. Although it was apparent that wounding has an enormous impact on gene expression and physiological responses *in planta*, it remained questionable whether or not these treatments resembled insect feeding, since herbivorous insects consume leaves by continuous clipping off and ingesting small pieces of tissue. This process can be considered as a series of sequential mechanical wounds and it is conceivable that plants might recognize and discriminate a continuously sustained damage by feeding insects from a mechanical wounding that was set only once. The construction of a mechanical caterpillar allowed to simulate "herbivory" in a more realistic fashion (Mithöfer et al., 2005). Using continuous damage *via* the mechanical caterpillar (MecWorm) on Lima bean leaves, virtually the same blend of volatiles was detected as known from actual herbivore damage, although there were some quantitative differences. Strikingly, these experiments revealed that continuous mechanical wounding was sufficient to induce a local as well as a systemic emission of VOCs (Mithöfer et al., 2005). Both the duration and the area that has been mechanically damaged, contribute to the induction of the whole volatile response. By integrating those two parameters, time and intensity, which can replace each other to some extent, a damage level could be defined. That damage level exhibits a close linear relationship with the accumulation of fatty acid-derived volatiles and monoterpenes while other terpenoid volatiles and methyl salicylate respond in a non-linear manner. A detailed consideration of the impact of the two parameter involved, damage-time and damage-area, showed that the emission of representative compounds, hexenyl acetate, linalool, and methyl salicylate, based on different rules: the induction of the first compounds followed the product law stating that the product of damage time and area is the measure of stimulus strength; in contrast, the induction and accumulation of methyl salicylate followed the all-or-none law characterized by a certain threshold value. All these results demonstrate that the impact of continuous mechanical impact is clearly different from "single wounding events" and much more important than previously realized.

However, not all plants investigated so far responded to MecWorm treatment exactly as Lima bean or cotton did with an emission of identical volatile compounds of about 90%. For example, the levels of identical VOCs in tobacco were 78%, in maize 60%, and in potato 43%. Often the feeding process is accompanied by simultaneous introduction of saliva and foregut secretions from the insect. As stated above, oral secretions contain herbivore-specific compounds with elicitor capabilities, e.g. certain enzymes [glucose oxidase (Felton and Eichenseer, 1999); β-glucosidase (Mattiacci et al., 1995); alkaline phosphatase (Funk, 2001)] or fatty acid–amino acid conjugates such as volicitin (Alborn et al., 1997). Some of these compounds exhibited high VOCs inducing activities when added to certain single-wounded plants (Alborn et al., 1997; Halitschke et al., 2001; Landolt et al., 1999; Mattiacci et al., 1995; Schmelz et al., 2001, 2003b). However, insect-derived elicitors are not generally active as in Lima bean and cotton no induction of VOCs could be demonstrated (Spiteller et al., 2001), corresponding to the high level of solely mechanically induced VOCs in these particular species. Obviously, in different plant species the relative contribution of both the mechanical wounding and the chemistry of the insects' oral secretions in the process of VOCs induction can differ and is not unique.

5. Conclusions

Understanding insect–plant interactions is of interest not only from an ecological and evolutionary perspective but also for the development of novel crop protection strategies. Owing to the massive damage that herbivores cause to valuable crops, the deciphering of early signals from plants represent one of the most exciting fields of research in the first line defense. ROS and calcium signaling appear to be a common event in induced processes directed against hervivores (both chewing and piercing/sucking) and pathogens, but the way the plant discerns enemies lies in the speed and intensity of damage as well as in the nature of specific elicitors delivered to the attacked plant cell. VOCs production has been demonstrated after a wide range of biotrophic attacks and even in this case the plant respond with specific but variable blends, which can attract predators of the attacking enemies. Despite all evidence, the connection between early perception of the aggressor, the generation of ROS and second messengers, and the specific emission of VOC is still far from being clear and much work is still needed in order to better understand the important linkage between recognition of a particular biotic stress and the appropriate plant responses.

References

Alborn, H.T., Turlings, T.C.J., Jones, T.H., Stenhagen, G., Loughrin, J.H., Tumlinson, J.H., 1997. An elicitor of plant volatiles from beet armyworm oral secretion. Science 276, 873–879.

Allen, G.J., Morais, F., Muir, S., Jones, R.G.W., Leigh, R.A., 1995. Characterization of a Ca^{2+}-dependent ATP hydrolysis associated with the vacuolar membrane of wheat roots. Physiol. Plant. 94, 506–514.

Anil, V.S., Rao, K.S., 2001. Calcium-mediated signal transduction in plants: a perspective on the role of Ca^{2+} and CDPKs during early plant development. J. Plant Physiol. 158, 1237–1256.

Apel, K., Hirt, H., 2004. Reactive oxygen species: metabolism, oxidative stress, and signal transduction. Annu. Rev. Plant Biol. 55, 373–399.

Argandona, V.H., Chaman, M., Cardemil, L., Munoz, O., Zuniga, G.E., Corcuera, L.J., 2001. Ethylene production and peroxidase activity in aphid-infested barley. J. Chem. Ecol. 27, 53–68.

Arimura, G., Kost, C., Boland, W., 2005. Herbivore-induced, indirect plant defences. Biochim. Biophys. Acta-Mol. Cell Biol. Lipids 1734, 91–111.

Arimura, G., Ozawa, R., Shimoda, T., Nishioka, T., Boland, W., Takabyashi, J., 2000. Herbivory-induced volatiles elicit defence genes in Lima bean leaves. Nature 406, 512–515.

Asada, K., 2006. Production and scavenging of reactive oxygen species in chloroplasts and their functions. Plant Physiol. 141, 391–396.

Baldwin, I.T., Halitschke, R., Kessler, A., Schittko, U., 2001. Merging molecular and ecological approaches in plant–insect interactions. Curr. Opin. Plant Biol. 4, 351–358.

Baldwin, I.T., Halitschke, R., Paschold, A., von Dahl, C.C., Preston, C.A., 2006. Volatile signaling in plant–plant interactions: "Talking trees" in the genomics era. Science 311, 812–815.

Bede, J.C., Musser, R.O., Felton, G.W., Korth, K.L., 2006. Caterpillar herbivory and salivary enzymes decrease transcript levels of *Medicago truncatula* genes encoding early enzymes in terpenoid biosynthesis. Plant Mol. Biol. 60, 519–531.

Bhattacharjee, S., 2005. Reactive oxygen species and oxidative burst: roles in stress, senescence and signal transduction in plants. Curr. Sci. 89, 1113–1121.

Bi, J.L., Murphy, J.B., Felton, G.W., 1997. Does salicylic acid act as a signal in cotton for induced resistance to *Helicoverpa zea*? J. Chem. Ecol. 23, 1805–1818.

Bienert, G.P., Møller, A.L.B., Kristiansen, K.A., Schulz, A., Schjoerring, I.M.K., 2007. Specific aquaporins facilitate the diffusion of hydrogen peroxide across membranes. J. Biol. Chem. 282, 1183–1192.

Bindschedler, L.V., Minibayeva, F., Gardner, S.L., Gerrish, C., Davies, D.R., Bolwell, G.P., 2001. Early signalling events in the apoplastic oxidative burst in suspension cultured French bean cells involve cAMP and Ca^{2+}. New Phytol. 151, 185–194.

Blechert, S., Brodschelm, W., Holder, S., Kammerer, L., Kutchan, T.M., Mueller, M.J., Xia, Z.Q., Zenk, M.H., 1995. The octadecanoic pathway – signal molecules for the regulation of secondary pathways. Proc. Natl. Acad. Sci. USA 92, 4099–4105.

Blee, K.A., Jupe, S.C., Richard, G., Zimmerlin, A., Davies, D.R., Bolwell, G.P., 2001. Molecular identification and expression of the peroxidase responsible for the oxidative burst in French bean (*Phaseolus* *vulgaris* L.) and related members of the gene family. Plant Mol. Biol. 47, 607–620.

Blumwald, E., Aharon, G.S., Lam, B.C.H., 1998. Early signal transduction pathways in plant–pathogen interactions. Trends Plant Sci. 3, 342–346.

Bóka, K., Orbán, N., Kristóf, Z., 2007. Dynamics and localization of H_2O_2 production in elicited plant cells. Protoplasma 230, 89–97.

Boland, W., Hopke, J., Donath, J., Nuske, J., Bublitz, F., 1995. Jasmonic acid and coronatin induce odor production in plants. Angew. Chem. Int. Ed. 34, 1600–1602.

Bolwell, G.P., 1999. Role of active oxygen species and NO in plant defence responses. Curr. Opin. Plant Biol. 2, 287–294.

Bolwell, G.P., Bindschedler, L.V., Blee, K.A., Butt, V.S., Davies, D.R., Gardner, S.L., Gerrish, C., Minibayeva, F., 2002. The apoplastic oxidative burst in response to biotic stress in plants: a three-component system. J. Exp. Bot. 53, 1367–1376.

Bolwell, G.P., Wojtaszek, P., 1997. Mechanisms for the generation of reactive oxygen species in plant defence – a broad perspective. Physiol. Mol. Plant Pathol. 51, 347–366.

Bowler, C., Fluhr, R., 2000. The role of calcium and activated oxygens as signals for controlling cross-tolerance. Trends Plant Sci. 5, 241–246.

Boyko, E.V., Smith, C.M., Thara, V.K., Bruno, J.M., Deng, Y., Starkey, S.R., Klaahsen, D.L., 2006. The molecular basis of plant gene expression during aphid invasion: wheat Pto- and Pti-like sequences are involved in interactions between wheat and Russian wheat aphid (Homoptera: Aphididae). J. Econ. Entomol. 99, 1430–1445.

Bruce, T.J.A., Wadhams, L.J., Woodcock, C.M., 2005. Insect host location: a volatile situation. Trends Plant Sci. 10, 269–274.

Cheong, Y.H., Chang, H.S., Gupta, R., Wang, X., Zhu, T., Luan, S., 2002. Transcriptional profiling reveals novel interactions between wounding, pathogen, abiotic stress, and hormonal responses in Arabidopsis. Plant Physiol. 129, 661–677.

Corpas, F.J., Barroso, J.B., del Rio, L.A., 2001. Peroxisomes as a source of reactive oxygen species and nitric oxide signal molecules in plant cells. Trends Plant Sci. 6, 145–150.

Custers, J.H.H.V., Harrison, S.J., Sela-Buurlage, M.B., van Deventer, E., Lageweg, W., Howe, P.W., van der Meijs, P.J., Ponstein, A.S., Simons, B.H., Melchers, L.S., Stuiver, M.H., 2004. Isolation and characterisation of a class of carbohydrate oxidases from higher plants, with a role in active defence. Plant J. 39, 147–160.

Dangl, J.L., Dietrich, R.A., Richberg, M.H., 1996. Death don't have no mercy: cell death programs in plant–microbe interactions. Plant Cell 8, 1793–1807.

Dangl, J.L., Jones, J.D.G., 2001. Plant pathogens and integrated defence responses to infection. Nature 411, 826–833.

Davies, D.R., Bindschedler, L.V., Strickland, T.S., Bolwell, G.P., 2006. Production of reactive oxygen species in Arabidopsis thaliana cell suspension cultures in response to an elicitor from *Fusarium oxysporum*: implications for basal resistance. J. Exp. Bot. 57, 1817–1827.

De Moraes, C.M., Lewis, W.J., Pare, P.W., Alborn, H.T., Tumlinson, J.H., 1998. Herbivore-infested plants selectively attract parasitoids. Nature 393, 570–573.

De Moraes, C.M., Mescher, M.C., Tumlinson, J.H., 2001. Caterpillar-induced nocturnal plant volatiles repel conspecific females. Nature 410, 577–580.

del Rio, L.A., Sandalio, L.M., Corpas, F.J., Palma, J.M., Barroso, J.B., 2006. Reactive oxygen species and reactive nitrogen species in peroxisomes. Production, scavenging, and role in cell signaling. Plant Physiol. 141, 330–335.

Desikan, R., Hancock, J.T., Bright, J., Harrison, J., Weir, L., Hooley, R., Neill, S.J., 2005. A role for ETR1 in hydrogen peroxide signaling in stomatal guard cells. Plant Physiol. 137, 831–834.

Desikan, R., Mackerness, S.A.H., Hancock, J.T., Neill, S.J., 2001. Regulation of the Arabidopsis transcriptome by oxidative stress. Plant Physiol. 127, 159–172.

Dicke, M., Agrawal, A.A., Bruin, J., 2003. Plants talk, but are they deaf? Trends Plant Sci. 8, 403–405.

Dicke, M., van Loon, J.J.A., 2000. Multitrophic effects of herbivore-induced plant volatiles in an evolutionary context. Entomol. Exp. Appl. 97, 237–249.

Divol, F., Vilaine, F., Thibivilliers, S., Amselem, J., Palauqui, J.C., Kusiak, C., Dinant, S., 2006. Systemic response to aphid infestation by *Myzus persicae* in the phloem of *Apium graveolens*. Plant Mol. Biol. 57, 517–540.

Dombrowski, J.E., Bergey, D.R., 2007. Calcium ions enhance systemin activity and play an integral role in the wound response. Plant Sci. 172, 335–344.

Dudareva, N., Negre, F., Nagegowda, D.A., Orlova, I., 2006. Plant volatiles: recent advances and future perspectives. Crit. Rev. Plant Sci. 25, 417–440.

Dudareva, N., Pichersky, E., Gershenzon, J., 2004. Biochemistry of plant volatiles. Plant Physiol. 135, 1893–1902.

Engelberth, J., Alborn, H.T., Schmelz, E.A., Tumlinson, J.H., 2004. Airborne signals prime plants against insect herbivore attack. Proc. Natl. Acad. Sci. USA 101, 1781–1785.

Engelberth, J., Koch, T., Schuler, G., Bachmann, N., Rechtenbach, J., Boland, W., 2001. Ion channel-forming alamethicin is a potent elicitor of volatile biosynthesis and tendril coiling. Cross talk between jasmonate and salicylate signaling in Lima bean. Plant Physiol. 125, 369–377.

Evans, N.H., McAinsh, M.R., Hetherington, A.M., 2001. Calcium oscillations in higher plants. Curr. Opin. Plant Biol. 4, 415–420.

Felcher, K.J., Douches, D.S., Kirk, W.W., Hammerschmidt, R., Li, W., 2003. Expression of a fungal glucose oxidase gene in three potato cultivars with different susceptibility to late blight (*Phytophthora infestans* Mont. deBary). J. Am. Soc. Hort. Sci. 128, 238–245.

Felton, G.W., Eichenseer, H., 1999. Herbivore saliva and its effects on plant defense against herbivores and pathogens. In: Agrawal, A.A., Tuzun, S., Bent, E. (Eds.), Induced Plant Defenses against Pathogens and Herbivores: Ecology and Agriculture. American Phytopathology Society Press, St. Paul, pp. 19–36.

Felton, G.W., Korth, K.L., 2000. Trade-offs between pathogen and herbivore resistance. Curr. Opin. Plant Biol. 3, 309–314.

Foreman, J., Demidchik, V., Bothwell, J.H.F., Mylona, P., Miedema, H., Torres, M.A., Linstead, P., Costa, S., Brownlee, C., Jones, J.D.G., Davies, J.M., Dolan, L., 2003. Reactive oxygen species produced by NADPH oxidase regulate plant cell growth. Nature 422, 442–446.

Foyer, C.H., Noctor, G., 2003. Redox sensing and signalling associated with reactive oxygen in chloroplasts, peroxisomes and mitochondria. Physiol. Plant. 119, 355–364.

Foyer, C.H., Noctor, G., 2005a. Oxidant and antioxidant signalling in plants: a re-evaluation of the concept of oxidative stress in a physiological context. Plant Cell Environ. 28, 1056–1071.

Foyer, C.H., Noctor, G., 2005b. Redox homeostasis and antioxidant signaling: a metabolic interface between stress perception and physiological responses. Plant Cell 17, 1866–1875.

Funk, C.J., 2001. Alkaline phosphatase activity in whitefly salivary glands and saliva. Arch. Insect Biochem. Physiol. 46, 165–174.

Gapper, C., Dolan, L., 2006. Control of plant development by reactive oxygen species. Plant Physiol. 141, 341–345.

Gaspar, T., Penel, C., Hagege, D., Greppin, H., 1991. Peroxidases in plant growth, differentiation, and development processes. In: Lobarzewski, J., Greppin, H., Penel, C., Gaspar, T. (Eds.), Biochemical, Molecular and Physiological Aspects of Plant Peroxidases. University M. Curie-Sklodowska, Lublin, pp. 249–280.

Gouinguene, S.P., Turlings, T.C.J., 2002. The effects of abiotic factors on induced volatile emissions in corn plants. Plant Physiol. 129, 1296–1307.

Halitschke, R., Schittko, U., Pohnert, G., Boland, W., Baldwin, I.T., 2001. Molecular interactions between the specialist herbivore *Manduca sexta* (Lepidoptera, Sphingidae) and its natural host *Nicotiana attenuata*. III. Fatty acid–amino acid conjugates in herbivore oral secretions are necessary and sufficient for herbivore-specific plant responses. Plant Physiol. 125, 711–717.

Hancock, J.T., Desikan, R., Clarke, A., Hurst, R.D., Neill, S.J., 2002. Cell signalling following plant/pathogen interactions involves the generation of reactive oxygen and reactive nitrogen species. Plant Physiol. Biochem. 40, 611–617.

Harborne, J.B., 1993. Introduction to Ecological Biochemistry. Academic Press, London.

Hatanaka, A., 1993. The biogeneration of green odor by green leaves. Phytochemistry 34, 1201–1218.

Heil, M., Bueno, J.C.S., 2007. Within-plant signaling by volatiles leads to induction and priming of an indirect plant defense in nature. Proc. Natl. Acad. Sci. USA 104, 5467–5472.

Heil, M., Kost, C., 2006. Priming of indirect defences. Ecol. Lett. 9, 813–817.

Hilker, M., Meiners, T., 2002. Induction of plant responses to oviposition and feeding by herbivorous arthropods: a comparison. Entomol. Exp. Appl. 104, 181–192.

Holopainen, J.K., 2004. Multiple functions of inducible plant volatiles. Trends Plant Sci. 9, 529–533.

Hu, X., Jiang, M., Zhang, J., Zhang, A., Lin, F., Tan, M., 2007. Calcium–calmodulin is required for abscisic acid-induced antioxidant defense and functions both upstream and downstream of H_2O_2 production in leaves of maize (*Zea mays*) plants. New Phytol. 173, 27–38.

Kempema, L.A., Cui, X.P., Holzer, F.M., Walling, L.L., 2007. Arabidopsis transcriptome changes in response to phloem-feeding silverleaf whitefly nymphs. Similarities and distinctions in responses to aphids. Plant Physiol. 143, 849–865.

Kessler, A., Baldwin, I.T., 2001. Defensive function of herbivore-induced plant volatile emissions in nature. Science 291, 2141–2144.

Kessler, A., Halitschke, R., Diezel, C., Baldwin, I.T., 2006. Priming of plant defense responses in nature by airborne signaling between *Artemisia tridentata* and *Nicotiana attenuata*. Oecologia 148, 280–292.

Koch, T., Krumm, T., Jung, V., Engelberth, J., Boland, W., 1999. Differential induction of plant volatile biosynthesis in the Lima bean by early and late intermediates of the octadecanoid-signaling pathway. Plant Physiol. 121, 153–162.

Kotchoni, S.O., Gachomo, E.W., 2006. The reactive oxygen species network pathways: an essential prerequisite for perception of pathogen attack and the acquired disease resistance in plants. J. Biosci. 31, 389–404.

Kunert, M., Biedermann, A., Koch, T., Boland, W., 2002. Ultrafast sampling and analysis of plant volatiles by a hand-held miniaturised GC with pre-concentration unit: kinetic and quantitative aspects of plant volatile production. J. Sep. Sci. 25, 677–684.

Laloi, C., Apel, K., Danon, A., 2004. Reactive oxygen signalling: the latest news. Curr. Opin. Plant Biol. 7, 323–328.

Laloi, C., Stachowiak, M., Pers-Kamczyc, E., Warzych, E., Murgia, I., Apel, K., 2007. Cross-talk between singlet oxygen- and hydrogen peroxide-dependent signaling of stress responses in *Arabidopsis thaliana*. Proc. Natl. Acad. Sci. USA 104, 672–677.

Landolt, P.J., Tumlinson, J.H., Alborn, D.H., 1999. Attraction of Colorado potato beetle (Coleoptera: Chrysomelidae) to damaged and chemically induced potato plants. Environ. Entomol. 28, 973–978.

Laurenzi, M., Tipping, A.J., Marcus, S.E., Knox, J.P., Federico, R., Angelini, R., McPherson, M.J., 2001. Analysis of the distribution of copper amine oxidase in cell walls of legume seedlings. Planta 214, 37–45.

Lecourieux, D., Raneva, R., Pugin, A., 2006. Calcium in plant defence-signalling pathways. New Phytol. 171, 249–269.

Leitner, M., Boland, W., Mithöfer, A., 2005. Direct and indirect defences induced by piercing-sucking and chewing herbivores in *Medicago truncatula*. New Phytol. 167, 597–606.

Lorenzo, O., Solano, R., 2005. Molecular players regulating the jasmonate signalling network. Curr. Opin. Plant Biol. 8, 532–540.

Loughrin, J.H., Manukian, A., Heath, R.R., Turlings, T.C.J., Tumlinson, J.H., 1994. Diurnal cycle of emission of induced volatile terpenoids herbivore-injured cotton plants. Proc. Natl. Acad. Sci. USA 91, 11836–11840.

Ludwig, A.A., Romeis, T., Jones, J.D.G., 2004. CDPK-mediated signalling pathways: specificity and cross-talk. J. Exp. Bot. 55, 181–188.

Ludwig, A.A., Saitoh, H., Felix, G., Freymark, G., Miersch, O., Wasternack, C., Boller, T., Jones, J.D.G., Romeis, T., 2005. Ethylene-mediated cross-talk between calcium-dependent protein kinase and MAPK signaling controls stress responses in plants. Proc. Natl. Acad. Sci. USA 102, 10736–10741.

Maffei, M., Bossi, S., 2006. Electrophysiology and plant responses to biotic stress. In: Volkov, A. (Ed.), Plant Electrophysiology – Theory & Methods. Springer-Verlag, Berlin, pp. 461–481.

Maffei, M., Bossi, S., Spiteller, D., Mithöfer, A., Boland, W., 2004. Effects of feeding *Spodoptera littoralis* on Lima bean leaves. I. Membrane potentials, intracellular calcium variations, oral secretions, and regurgitate components. Plant Physiol. 134, 1752–1762.

Maffei, M., Mithöfer, A., Boland, W., 2007. Before gene expression: early events in plant-insect interaction. Trends Plant Sci. 12, 310–316.

Maffei, M.E., Mithöfer, A., Arimura, G.I., Uchtenhagen, H., Bossi, S., Bertea, C.M., Cucuzza, L.S., Novero, M., Volpe, V., Quadro, S., Boland, W., 2006. Effects of feeding *Spodoptera littoralis* on Lima bean leaves. III. Membrane depolarization and involvement of hydrogen peroxide. Plant Physiol. 140, 1022–1035.

Maischak, H., Grigoriev, P.A., Vogel, H., Boland, W., Mithöfer, A., 2007. Oral secretions from herbivorous lepidopteran larvae exhibit ion channel-forming activities. FEBS Lett. 581, 898–904.

Major, I.T., Constabel, C.P., 2006. Molecular analysis of poplar defense against herbivory: comparison of wound- and insect elicitor-induced gene expression. New Phytol. 172, 617–635.

Mattiacci, L., Dicke, M., Posthumus, M.A., 1995. Beta-glucosidase – an elicitor of herbivore-induced plant odor that attracts host-searching parasitic wasps. Proc. Natl. Acad. Sci. USA 92, 2036–2040.

Medvedev, S.S., 2005. Calcium signaling system in plants. Russ. J. Plant Physiol. 52, 249–270.

Merkx-Jacques, M., Bede, J.C., 2004. Caterpillar salivary enzymes: “eliciting” a response. Phytoprotection 85, 33–37.

Mithöfer, A., Schulze, B., Boland, W., 2004. Biotic and heavy metal stress response in plants: evidence for common signals. FEBS Lett. 566, 1–5.

Mithöfer, A., Wanner, G., Boland, W., 2005. Effects of feeding *Spodoptera littoralis* on lima bean leaves. II. Continuous mechanical wounding resembling insect feeding is sufficient to elicit herbivory-related volatile emission. Plant Physiol. 137, 1160–1168.

Mittapalli, O., Neal, J.J., Shukle, R.H., 2007. Antioxidant defense response in a galling insect. Proc. Natl. Acad. Sci. USA 104, 1889–1894.

Moyen, C., Hammond-Kosack, K.E., Jones, J., Knight, M.R., Johannes, E., 2007. Systemin triggers an increase in cytoplasmic calcium in tomato mesophyll cells: Ca^{2+} mobilization from intra- and extracellular compartments. Plant Cell Environ. 21, 1101–1111.

Murphy, A.M., Chivasa, S., Singh, D.P., Carr, J.P., 1999. Salicylic acid-induced resistance to viruses and other pathogens: a parting of the ways? Trends Plant Sci. 4, 155–160.

Musser, R.O., Cipollini, D.F., Hum-Musser, S.M., Williams, S.A., Brown, J.K., Felton, G.W., 2005. Evidence that the caterpillar salivary enzyme glucose oxidase provides herbivore offense in Solanaceous plants. Arch. Insect Biochem. Physiol. 58, 128–137.

Musser, R.O., Farmer, E., Peiffer, M., Williams, S.A., Felton, G.W., 2006. Ablation of caterpillar labial salivary glands: technique for determining the role of saliva in insect–plant interactions. J. Chem. Ecol. 32, 981–992.

Navrot, N., Rouhier, N., Gelhaye, E., Jacquot, J.P., 2007. Reactive oxygen species generation and antioxidant systems in plant mitochondria. Physiol. Plant. 129, 185–195.

Neill, S.J., Desikan, R., Clarke, A., Hurst, R.D., Hancock, J.T., 2002. Hydrogen peroxide and nitric oxide as signalling molecules in plants. J. Exp. Bot. 53, 1237–1247.

Neill, S.J., Desikan, R., Hancock, J.T., 2003. Nitric oxide signalling in plants. New Phytol. 159, 11–35.

Nürnberger, T., Wirtz, W., Nennstiel, D., Hahlbrock, K., Jabs, T., Zimmermann, S., Scheel, D., 1997. Signal perception and intracellular signal transduction in plant pathogen defense. J. Recept. Signal Transduct. Res. 17, 127–136.

Orozco-Cárdenas, M., Ryan, C.A., 1999. Hydrogen peroxide is generated systemically in plant leaves by wounding and systemin via the octadecanoid pathway. Proc. Natl. Acad. Sci. USA 96, 6553–6557.

Orozco-Cárdenas, M.L., Narvaez-Vasquez, J., Ryan, C.A., 2001. Hydrogen peroxide acts as a second messenger for the induction of defense genes in tomato plants in response to wounding, systemin, and methyl jasmonate. Plant Cell 13, 179–191.

Pandey, S., Tiwari, S.B., Upadhyaya, K.C., Sopory, S.K., 2000. Calcium signaling: linking environmental signals to cellular functions. Crit. Rev. Plant Sci. 19, 291–318.

Pandhair, V., Sekhon, B.S., 2006. Reactive oxygen species and antioxidants in plants: an overview. J. Plant Biochem. Biotechnol. 15, 71–78.

Paré, P.W., Tumlinson, J.H., 1996. Plant volatile signals in response to herbivore feeding. Florida Entomol. 79, 93–103.

Pei, Z.M., Murata, Y., Benning, G., Thomine, S., Klusener, B., Allen, G.J., Grill, E., Schroeder, J.I., 2000. Calcium channels activated by hydrogen peroxide mediate abscisic acid signalling in guard cells. Nature 406, 731–734.

Piel, J., Donath, J., Bandemer, K., Boland, W., 1998. Mevalonate-independent biosynthesis of terpenoid volatiles in plants: induced and constitutive emission of volatiles. Angew. Chem. Int. Ed. 110, 2622–2625.

Pitzschke, A., Hirt, H., 2006. Mitogen-activated protein kinases and reactive oxygen species signaling in plants. Plant Physiol. 141, 351–356.

Powell, G., Hardie, J., 2001. The chemical ecology of aphid host alternation: how do return migrants find the primary host plant? Appl. Entomol. Zool. 36, 259–267.

Powell, G., Tosh, C.R., Hardie, J., 2006. Host plant selection by aphids: behavioral, evolutionary, and applied perspectives. Annu. Rev. Entomol. 51, 309–330.

Reddy, A.S.N., 2001. Calcium: silver bullet in signaling. Plant Sci. 160, 381–404.

Reymond, P., Bodenhausen, N., Van Poecke, R.M.P., Krishnamurthy, V., Dicke, M., Farmer, E.E., 2004. A conserved transcript pattern in response to a specialist and a generalist herbivore. Plant Cell 16, 3132–3147.

Rojo, E., Solano, R., Sanchez-Serrano, J.J., 2003. Interactions between signaling compounds involved in plant defense. J. Plant Growth Regul. 22, 82–98.

Ruther, J., Kleier, S., 2005. Plant–plant signaling: ethylene synergizes volatile emission in *Zea mays* induced by exposure to (*Z*)-3-hexen-1-ol. J. Chem. Ecol. 31, 2217–2222.

Sagi, M., Fluhr, R., 2001. Superoxide production by plant homologues of the gp91(phox) NADPH oxidase: modulation of activity by calcium and by tobacco mosaic virus infection. Plant Physiol. 126, 1281–1290.

Sagi, M., Fluhr, R., 2006. Production of reactive oxygen species by plant NADPH oxidases. Plant Physiol. 141, 336–340.

Sanders, D., Pelloux, J., Brownlee, C., Harper, J.F., 2002. Calcium at the crossroads of signaling. Plant Cell 14, S401–S417.

Schittko, U., Preston, C.A., Baldwin, I.T., 2000. Eating the evidence? *Manduca sexta* larvae cannot disrupt specific jasmonate induction in *Nicotiana attenuata* by rapid consumption. Planta 210, 343–346.

Schmelz, E.A., Alborn, H.T., Tumlinson, J.H., 2001. The influence of intact-plant and excised-leaf bioassay designs on volicitin- and jasmonic acid-induced sesquiterpene volatile release in *Zea mays*. Planta 214, 171–179.

Schmelz, E.A., Alborn, H.T., Engelberth, J., Tumlinson, J.H., 2003a. Nitrogen deficiency increases volicitin-induced volatile emission, jasmonic acid accumulation, and ethylene sensitivity in maize. Plant Physiol. 133, 295–306.

Schmelz, E.A., Alborn, H.T., Tumlinson, J.H., 2003b. Synergistic interactions between volicitin, jasmonic acid and ethylene mediate insect-induced volatile emission in *Zea mays*. Physiol. Plant. 117, 403–412.

Smith, C.M., Boyko, E.V., 2007. The molecular bases of plant resistance and defense responses to aphid feeding: current status. Entomol. Exp. Appl. 122, 1–16.

Spiteller, D., Pohnert, G., Boland, W., 2001. Absolute configuration of volicitin, an elicitor of plant volatile biosynthesis from lepidopteran larvae. Tetrahedron Lett. 42, 1483–1485.

Stotz, H.U., Kroymann, J., Mitchell-Olds, T., 1999. Plant–insect interactions. Curr. Opin. Plant Biol. 2, 268–272.

Takabayashi, J., Takahashi, S., Dicke, M., Posthumus, M.A., 1995. Developmental stage of herbivore *Pseudaletia-separata* affects production of herbivore-induced synomone by corn plants. J. Chem. Ecol. 21, 273–287.

Tentelier, C., Fauvergue, X., 2007. Herbivore-induced plant volatiles as cues for habitat assessment by a foraging parasitoid. J. Anim. Ecol. 76, 1–8.

Tholl, D., Boland, W., Hansel, A., Loreto, F., Rose, U.S.R., Schnitzler, J.P., 2006. Practical approaches to plant volatile analysis. Plant J. 45, 540–560.

Thompson, G.A., Goggins, F.L., 2005. Transcriptomics and functional genomics of plant defence induction by phloem-feeding insects. J. Exp. Bot. 57, 755–766.

Ton, J., D'Alessandro, M., Jourdie, V., Jakab, G., Karlen, D., Held, M., Mauch-Mani, B., Turlings, T.C.J., 2007. Priming by airborne signals boosts direct and indirect resistance in maize. Plant J. 49, 16–26.

Torres, M.A., Jones, J.D.G., Dangl, J.L., 2005. Pathogen-induced, NADPH oxidase-derived reactive oxygen intermediates suppress spread of cell death in *Arabidopsis thaliana*. Nat. Genet. 37, 1130–1134.

Torres, M.A., Jones, J.D.G., Dangl, J.L., 2006. Reactive oxygen species signaling in response to pathogens. Plant Physiol. 141, 373–378.

Truitt, C.L., Wei, H.X., Pare, P.W., 2004. A plasma membrane protein from *Zea mays* binds with the herbivore elicitor volicitin. Plant Cell 16, 523–532.

Tscharntke, T., Thiessen, S., Dolch, R., Boland, W., 2001. Herbivory, induced resistance, and interplant signal transfer in *Alnus glutinosa*. Biochem. Syst. Ecol. 29, 1025–1047.

Ulloa, R.M., Raices, M., MacIntosh, G.C., Maldonado, S., Tellez-Inon, M.T., 2002. Jasmonic acid affects plant morphology and calcium-dependent protein kinase expression and activity in *Solanum tuberosum*. Physiol. Plant. 115, 417–427.

Vallat, A., Gu, H.N., Dorn, S., 2005. How rainfall, relative humidity and temperature influence volatile emissions from apple trees in situ. Phytochemistry 66, 1540–1550.

Van Breusegem, F., Dat, J.F., 2006. Reactive oxygen species in plant cell death. Plant Physiol. 141, 384–390.

van Loon, L.C., Geraats, B.P.J., Linthorst, H.J.M., 2006. Ethylene as a modulator of disease resistance in plants. Trends Plant Sci. 11, 184–191.

Van Poecke, R.M.P., Dicke, M., 2004. Indirect defence of plants against herbivores: using *Arabidopsis thaliana* as a model plant. Plant Biol. 6, 387–401.

Vancanneyt, G., Sanz, C., Farmaki, T., Paneque, M., Ortego, F., Castanera, P., Sanchez-Serrano, J.J., 2001. Hydroperoxide lyase depletion in transgenic potato plants leads to an increase in aphid performance. Proc. Natl. Acad. Sci. USA 98, 8139–8144.

Walling, L.L., 2000. The myriad plant responses to herbivores. J. Plant Growth Regul. 19, 195–216.

Walter, A., Mazars, C., Maitrejean, M., Hopke, J., Ranjeva, R., Boland, W., Mithöfer, A., 2007. Structural requirements of jasmonates and synthetic mimetics as inducers of Ca^{2+} signals in the nucleus and the cytosol of plant cells. Angew. Chem. Int. Ed. doi:10.1002/anie.200604989.

Wu, J., Hettenhausen, C., Meldau, S., Baldwin, I.T., 2007. Herbivory rapidly activates MAPK signaling in attacked and unattacked leaf regions but not between leaves of *Nicotiana attenuata*. Plant Cell 19, 1096–1122.

Yang, T., Poovaiah, B.W., 2002. Hydrogen peroxide homeostasis: activation of plant catalase by calcium/calmodulin. Proc. Natl. Acad. Sci. USA 99, 4097–4102.

Yang, T.B., Poovaiah, B.W., 2003. Calcium/calmodulin-mediated signal network in plants. Trends Plant Sci. 8, 505–512.

Yoda, H., Yamaguchi, Y., Sano, H., 2003. Induction of hypersensitive cell death by hydrogen peroxide produced through polyamine degradation in tobacco plants. Plant Physiol. 132, 1973–1981.

Zhen, W., Chen, X., Liang, H.B., Hu, Y.L., Gao, Y., Lin, Z.P., 2000. Enhanced late blight resistance of transgenic potato expressing glucose oxidase under the control of pathogen-inducible promoter. Chin. Sci. Bull. 45, 1982.

Massimo E. Maffei was born in Cambiano, Italy, in 1957. He was graduated in Plant Biology in the University of Turin, where he first became assistant professor, then associate professor and, since 2000, full professor of plant physiology, Faculty of Sciences, Department of Plant Biology. From 1987 to 1988, he moved to Washington State University and worked as a postdoctoral research associate under the direction of Rodney Croteau, studying monoterpene biochemistry in the genus *Mentha*. His current interest is the study of early signals in plant–biotrophs interaction which is accomplished by using confocal microscopy, electrophysiology and molecular biology techniques. He is the coordinator of the Ministerial Center of Excellence in Plant and Microbial Biosensing – CEBIOVEM – he is editor in chief of the Journal of Plant Interactions.

Axel Mithöfer was born in Osnabrück, Germany, in 1961. He studied Biology and did his Diploma in 1988. In 1992, he received his Ph.D. in Plant Physiology from the Ruhr-Universität Bochum. For his Habilitation at the Ludwig-Maximilians University Munich in 1999, he worked on physiological and molecular aspects in the *Phytophthora sojae* – soybean pathosystem together with Prof. J. Ebel. In 2000, he moved to the INRA in Toulouse, France. After returning to Munich for another 2 years he joined the Bioorganic Chemistry Department of the Max Planck Institute for Chemical Ecology in Jena in 2003 as the leader of the "Plant Defence Physiology" research group. He is associate professor at the Friedrich-Schiller University Jena. His main research interests lie in the field of plants' interactions with other organisms: signal perception and signal transduction processes.

Wilhelm Boland is director of the Department of Bioorganic Chemistry of the Max Planck Institute for Chemical Ecology in Jena (Germany).

He studied Chemistry at the Universities Münster and Cologne and received his Diploma and Ph.D. from the University of Cologne in 1975 and 1978, respectively. He became Research Associate at the Institute of Biochemistry (University of Cologne) until 1987 and, then, moved to the University of Karlsruhe as a professor for Organic Chemistry. In 1994, he became full professor for Bioorganic Chemistry at the University of Bonn. In 1997, he joined the Max Planck Society and became Director of the Department of Bioorganic Chemistry in the Max Planck Institute for Chemical Ecology in Jena. He was Managing Director of the newly founded Institute from 1997 to 2001. Since 1997, he is also associated with the Friedrich Schiller University in Jena as an Honorary Professor.

He was the first Simeone-Silverstein lecturer (1995) of the International Society of Chemical Ecology. He is a Fellow of the Royal Chemical Society of Great Britain, and member of the NRW Academy of Sciences since 2003. In 2005, he received the Hans-Herloff-Inhoffen Medal from the Technical University and the Society for Biological Research in Braunschweig.

Major fields of research cover plant–insect interactions with special emphasis on induced defenses in plants. Typical topics are: volatile biosynthesis, cross-talk between signaling pathways in plants, synthetic elicitors, and defensive chemistry in leaf beetles. He has published ca. 250 original papers and review articles.