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Signaling in plant-insect interactions: signal transduction in direct and indirect plant defence

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Abbreviations:

ABA	Abscisic acid
ACO	1-Aminocyclopropane-1-carboxylic acid oxidase
ACS	1-Aminocyclopropane-1-carboxylate synthase
CHS	Chalcon synthase
DMNT	4,8-Dimethyl-1,3(E),7-nonatriene
HMGR	3-Hydroxy-3-methylglutaryl coenzyme A reductase
HRPG	Hydroxyproline-rich glycoproteins
JA	Jasmonic acid
MeJA	Methyl jasmonate
MeSA	Methyl salicylate
DN-OPDA	dinor-oxo-phytodieoic acid
OPDA	12-oxo phytodienoic acid
PAL	Phenylalanine ammonia-lyase
PI	Proteinase inhibitor
Pin	Proteinase inhibitor gene
SA	Salicylic acid
TMTT	4,8,12-Trimethyl-1,3(E),7(E),11-tridecatetraene

1. Introduction

Insects make up the most speciose group of organisms that comprises more than 800,000 species (new species are still discovered at high frequency) and thus ca. 60% of all species on earth are insects (1). Also in numbers of individuals, insects are abundant and they occur in virtually all habitats on earth (1). About half of all insect species are herbivores and the majority of these are specialists that feed on one or a few related plant species (1). The main feeding modes of insects are chewing-biting, cell-sucking, and sap-feeding. Herbivorous insects may live on or inside the plant tissue. For instance, insects may feed externally on leaves or stem, they may live in the stem or in a leaf of the plant, or induce a gall to live in (1). There are ca. 300,000 vascular plant species (1) and it is unlikely for an individual plant to live without interactions with herbivorous arthropods. However, the intensity, frequency and diversity of these interactions may vary with plant species and environment.

In addition to interactions between plants and herbivorous insects, plants also have interactions with carnivorous insects that consume the herbivores. Many carnivorous insects inhabit plants (e.g., (2, 3)) and plant characteristics can influence carnivore behaviour and carnivore-herbivore interactions. In this chapter we will deal with signaling between plants and herbivorous as well as carnivorous arthropods in the context of plant defence. We will include reference to mites that, although not belonging to the class of insects, have very similar interactions with plants (4, 5).

2. Direct vs. indirect plant defence

Plants have evolved a wide range of defences to cope with the attack of herbivorous insects and mites (1, 6, 7). Traditionally, plant characteristics that directly affect herbivores have been studied (1, 7). This so-called ‘direct defence’ may involve physical defences (e.g., a thick cuticle, trichomes and thorns) and chemical defences (e.g., toxins, repellents and digestibility reducers). Defence chemicals can be found in all major classes of plant secondary metabolites: for instance, nitrogen-containing metabolites like alkaloids and glucosinolates, phenolics like phenylpropanoids and flavonoids, and terpenoids. Additionally, plants may use defence-related proteins. Physical and chemical factors are often combined; examples comprise toxic, deterrent and/or sticky compounds in glandular trichomes and deterrents in the epicuticular wax (1).

In addition to direct defences, plants can use other mechanisms to protect themselves. Herbivores have a variety of natural enemies such as predators or parasitic wasps (parasitoids) and plants may enhance the effectiveness of these enemies and employ them as ‘bodyguards’ (5, 8). This has been termed ‘indirect defence’. This type of defence may include the provision of shelter, alternative food and chemical information, either alone or in combinations (5, 8). For instance, many plants have so-called ‘domatia’ which are structures used as shelter by carnivores such as ants or predatory mites. These inhabitants provide protection to the plant by removing herbivores (9). Plants also provide floral or extrafloral nectar that carnivorous arthropods feed on and the production of these nutrient sources can be induced by herbivory (10, 11). Finally, plants may lure carnivorous arthropods with plant volatiles produced in response to herbivore attack (8, 12).

This chapter will focus on induced plant defence in response to insects and mites and the consequent interactions between plants and arthropods. The main interest will be a comparison of signal-transduction processes in direct and indirect defence.

3. Induction of direct defence

The inducibility of direct defence appears to be a general characteristic that has been demonstrated in more than 100 plant species in 34 families (7). Many types of direct defences can be induced in plants. This relates to both physical and chemical defences, but the induction of chemical defences has received most attention. Duration of the effect of induced defence ranges from a few hours to several years. The type and extent of defence varies with both the plant and herbivore species. Differences in induced defence can also be found within a plant: young plant parts often show a stronger induced defence than older parts.

An important aspect of herbivory is wounding of the plant and mechanical wounding can mimic the effect of herbivory in many induced direct defences. Therefore, mechanical damage has often been used to study the signal transduction pathway of defence induced by herbivory.

For many plant responses induced by insects the underlying mechanism is unknown (7). However, the mechanisms involved in several induced responses have been especially well-studied in the last decades, such as the wound-induced production of proteinase inhibitors (PIs) in solanaceous plants, especially tomato (13), and of nicotine in tobacco (14).

3.1 Proteinase inhibitors

Pioneering studies on induced direct defence were devoted to the induction of proteinase inhibitors in solanaceous plants. Herbivore feeding or mechanical wounding of potato and tomato plants result in the systemic expression of genes encoding PI proteins (15-18). PIs interfere with the digestive system of insects, retarding larval growth and development (19). This negative effect of PIs on larval growth and development has been shown for several plant-herbivore combinations (20). Elimination of PI induction can alleviate the effects on herbivores. For instance, mutant tomato plants, that are impaired in a specific step in the signal-transduction leading to PI-gene induction are more susceptible to feeding by *Manduca sexta* than wildtype plants (21).

PIs have been found in several plant families including the Brassicaceae, Cucurbitaceae, Fabaceae, Salicaceae and Solanaceae. It has been estimated that each plant genome contains one to two hundred different PI genes, grouped in several families and inhibiting each of the four classes of proteolytic enzymes (serine, cystein, aspartic, and metallo-proteinases) (7). This may be explained by the finding that herbivores can alter the set of digestive proteinases expressed, which may (temporarily?) overcome the inhibition of their digestive capabilities by the plant (22).

Apart from being involved in direct defence, PI’s may also affect indirect defence. The reduced growth rate that is caused by PI’s – even when occurring temporarily – may prolong the time window during which the herbivores are exposed to their natural enemies and thus may increase mortality incurred by carnivores (23).

3.2 Plant secondary metabolites

Herbivory or mechanical wounding can also result in the induced production of low molecular weight secondary metabolites that may originate from all major classes of secondary metabolites (e.g., (7, 24-26)). Genes encoding important enzymes in the production pathways of these metabolites can be induced by wounding or by treatment with plant hormones such as jasmonic acid. Examples are genes involved in the flavonoid biosynthesis like chalcone synthase (CHS) (25, 27) and phenylalanine ammonia-lyase (PAL) (28).

A well-studied system is induced nicotine production. Natural folivory or mechanical damage inflicted to tobacco induces the *de novo* biosynthesis of the alkaloid nicotine, resulting in a four- to tenfold increase in concentration in the leaves. These concentrations are high enough to be lethal for many herbivore species (14). The increased nicotine production takes place in the roots. The key regulatory enzyme in the nicotine synthesis, putrescine *N*-methyltransferase, is upregulated at mRNA level by wounding (29). Via the xylem, nicotine is then transported to the shoots (7, 30).

The consumption of nicotine by herbivores may have a negative effect on indirect defence. For instance, mortality among *M. sexta* caterpillars from parasitoids and pathogens is lower when the herbivores have fed on a high-nicotine food source (31, 32).

3.3 Signal transduction

The mechanisms of induction of direct defences have been well studied for several systems. A few major signal-transduction routes can be distinguished. These are centered around different plant hormones such as jasmonic acid and ethylene.

3.3.1 Jasmonic acid and other oxylipins

Jasmonic acid (JA) is a product of the lipoxygenase pathway, also called the octadecanoid pathway (33, 34). The lipoxygenase pathway starts with the substrate linolenic acid and results in products such as JA, traumatin and a variety of six carbon volatile compounds like hexanal, (*E*)-2-hexenal, and (*Z*)- and (*E*)-3-hexenol (33, 35). The pathway of JA biosynthesis is probably constitutively expressed (36)), but can additionally be induced by e.g. wounding (17, 27), feeding by insects (37, 38), or application of microbial cell wall components (37). Methyl jasmonate (MeJA) is a volatile derivative of JA, and may function as an airborne signal molecule (18, 39, 40). MeJA can probably be easily converted to JA in the plant (18). Therefore, MeJA is included in this section on jasmonic acid.

Jasmonic acid is a central molecule in induced direct defence against insects in many plant species (7). The importance of jasmonic acid in wound-induced defence responses has been demonstrated by the fact that (i) exogenous application of JA or MeJA induces these defence responses, (ii) the increase of endogenous JA after wounding correlates with the induced defence responses, and (iii) inhibition of the JA production pathway also inhibits the induction of the defence responses (30). In addition, transgenic plants and mutants have been important tools to elucidate the role of jasmonic acid in signal-transduction involved in direct plant defence (21, 41, 42).

Besides jasmonic acid, several other, related, oxylipins appear to function as signaling molecules as well. These comprise e.g., 12-oxo phytodienoic acid (OPDA) (37) and dinor-oxo-phytodieoic acid (DN-OPDA, (43)). For instance, OPDA and 10,11-dihydro-OPDA have been shown to induce the same production of secondary metabolites as JA in *Eschscholtzia californía* cell suspension cultures, without the conversion to JA being necessary (37). Combinations of oxylipins may result in specific plant responses and this has resulted in the designation of ‘oxylipin signatures’ being important in the induction of plant defences (43).

3.3.2 Systemin

An 18-amino acid polypeptide called systemin has been identified in tomato as a potent inducer of PIs. So far, systemin homologues have only been found in members from the Solanaceae plant family, namely tomato, potato, black nightshade and bell pepper (44). Most research has been done on tomato.

Wounding induces the systemic accumulation of systemin in tomato by an increased expression of the gene encoding the precursor of systemin, prosystemin (45). As prosystemin mRNA is systemically produced after wounding, it is not clear whether systemin is the systemic signal, inducing its own gene expression, or that another systemic signal is involved. It has been shown however, that systemin is transported from the wound site throughout the plant within 90 min. after wounding (46). Moreover, systemin induces prosystemin gene activity (47).

Application of systemin through the cut stems of tomato plants induced both the accumulation of PI proteins (48) and mRNA (47). In transgenic tomato plants with an antisense prosystemin gene, and thus a lowered systemin production, less PI protein accumulated after wounding. These transgenic tomato plants were more susceptible to feeding by *Manduca sexta* larvae (49). Besides the *Pin* (*P*rotein *in*hibitor) genes, several other tomato genes are induced by systemin. These include genes encoding for other defensive proteins like polyphenol oxidase (50), signal pathway-associated proteins like lipoxygenase, proteolytic enzymes and other proteins (47). These results show that systemin plays an important role in the signal transduction of wound-induced defences in tomato.

3.3.3 Ethylene

The plant hormone ethylene is produced in response to wounding (39), herbivory (51-53) and the application of systemin or JA in tomato cell suspensions (54, 55). In tomato, both genes encoding enzymes involved in ethylene production from S-adenosyl-methionine, 1-aminocyclopropane-1-carboxylate synthase (ACS) (56) and 1-aminocyclopropane-1-carboxylate oxidase (ACO) (57), are upregulated by wounding as well.

Like wounding, exogenous application of ethylene induces the production of enzymes, such as PAL, CHS, and hydroxyproline-rich glycoproteins (HRPG, involved in cell wall strengthening) mRNA (58). However, for HRPG it was shown that different isoforms are induced by wounding compared to ethylene application (58).

3.3.4 Abscisic acid

Abscisic acid is involved in several wound-induced responses, such as induced leucine aminopeptidase (59) or PI's (60), but see (59) and (61). In many other wound-induced responses ABA does not seem to play a role (e.g., (62)). In several induced defences the role of abscisic acid is not clear and its role in e.g. the induction of proteinase inhibitors is under debate (59) and

(61). How exactly ABA is involved in the signal transduction pathways is not clear. For example, water stress promotes an increase in endogenous ABA levels with a factor 8 to 10, but this does not lead to *Pin2* gene expression (60). The induction of water stress-responsive genes does not require *de novo* synthesis of proteins, whereas the induction of *Pin2* by JA does. Recent data suggest that ABA is not a primary signal for *Pin2* gene induction, but that it may modulate the responses to other signals (59, 61).

3.3.5 Electrical signals

Electrical signals may play a role in the systemic induction of PIs in tomato (63), but so far it remains unclear how these signals interact with chemical signals.

3.3.6 Insect damage versus mechanical damage: herbivore elicitors

As mentioned before, most research has been done on mechanical damage. Several publications report differences between herbivory- and wound-induced responses (e.g. (38, 64-67)). Of course, herbivory is more than mechanical wounding and plants may use for instance oral secretions from herbivores to differentiate between mechanical wounding and herbivory (38, 64, 67-69).

Differences between herbivory- and wound-induced responses have been found in *Pin2* gene expression in potato (69) and in nicotine accumulation in tobacco (38). Induction of the *Pin2* gene in potato appeared to occur faster by feeding of *Manduca sexta* larvae than induction by artificial wounding. Similar results were obtained with the 3-hydroxy-3-methylglutaryl-coenzymeA (HMGR) reductase gene family from potato. HMGR is the first enzyme in the mevalonic acid-derived terpenoid biosynthetic pathway. The early induction of both *Pin2* and HMGR mRNA could be mimicked by application of *Manduca sexta* larvae regurgitant on artificially wounded leaves and is probably caused by an insect-derived, heat-stable elicitor from the regurgitant. These results indicate that the signaling pathways of herbivory-induced and wound-induced plant defences may be at least partially different (69). In tobacco, herbivory by *Manduca sexta* larvae or application of their regurgitant decrease the induction of nicotine production compared to mechanical damage, even though JA induction was increased (38). A similar effect was recorded for the induction of trypsin inhibitor by *M. sexta* in tomato (70). It seems that *Manduca sexta* larvae are able to suppress induced defences by influencing the signal pathway (38).

A component of the saliva of *Helicoverpa zea* caterpillars, the enzyme glucose oxidase, has been found to induce the salicylate pathway in soybean, tobacco and cotton, resulting in systemic acquired resistance to *Pseudomonas syringae*. This effect was not found in response to mechanical damage (67, 71).

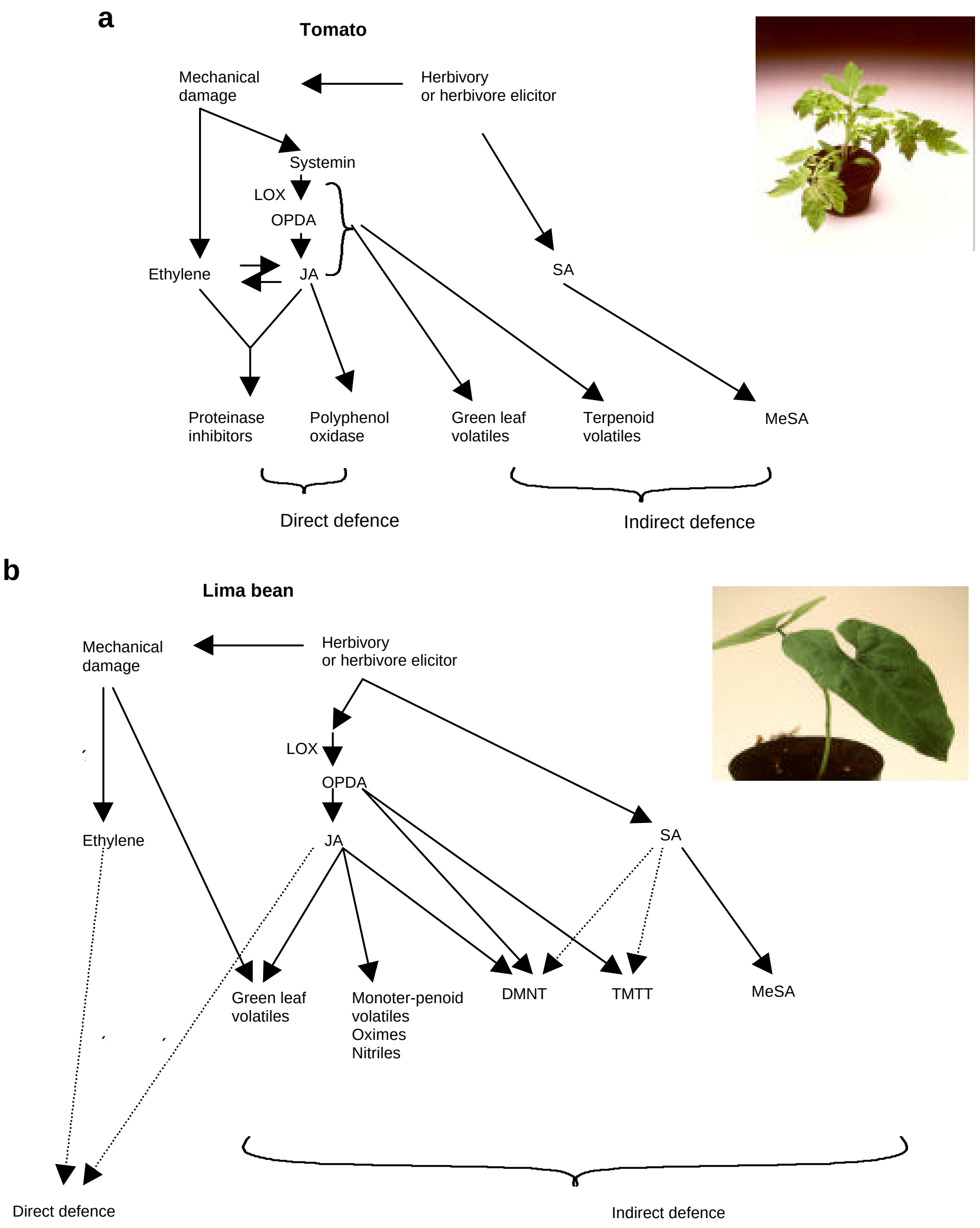

Figure 1: Signal transduction pathways involved in defences induced by herbivory versus mechanical damage. (a) in tomato, where herbivory and mechanical damage have many similar effects (based on refs.(4, 36, 54, 146)) and (b) in Lima bean where herbivory and mechanical damage have rather different effects (based on refs . (80, 111, 138, 146, 150)).

Although there are differences in plant responses to artificial wounding and herbivory, there are still enough indications that the signal pathways invoked by mechanical wounding or insect feeding share at least some components (Figure 1). Knowledge on the signal transduction pathway of wound-induced plant defences will help us unravel the signal transduction pathway of defences induced by herbivory.

3.3.7 Cross talk and interactions among signal-transduction pathways

The emerging picture of signal-transduction in direct defence is that different signal-transduction pathways interact. For instance, salicylic acid (SA), that can be induced by pathogen attack (see chapter 10), interferes with jasmonic acid-mediated responses involved in defence against herbivorous arthropods. SA blocks the biosynthesis of jasmonic acid and subsequent induction of gene expression (16, 17) and consequently affects the defence of plants against herbivores (72). For instance, treatment of plants with an SA mimic (benzothiodiazole-7-carbothioic acid *S*-methyl ester, BTH) alleviates the effect of JA-treatment of tomato plants on the induction of polyphenol oxidase activity and herbivory by caterpillars of *Spodoptera exigua* (72). Vice versa, JA can inhibit the effect of salicylic acid (73) or the synthetic mimic BTH (72). For instance, JA treatment of tomato plants eliminates the induction of the *PR-4* gene and reduces the protection of BTH-treated tomato plants against *Pseudomonas syringae* pv tomato (72). In other cases, cross-induction has been reported. For instance, the spider mite *Tetranychus urticae* and the fungus *Verticillium dahliae* induced resistance against spider mites and the fungus in cotton (74). How this is related to the induction of JA and/or SA remains unclear.

JA and ethylene act in concert in the induction of *Pin* gene expression in tomato (Figure 1A). These two plant hormones influence each other's level in wounded plants and are needed together for induction of PI's in tomato (54). Ethylene alone does not induce the *Pin* genes in tomato (75), but inhibition of ethylene action inhibits the induction of *Pin*2 in tomato by wounding, systemin, JA, and oligogalacturonide fragments. These results suggest that ethylene action is downstream from JA in the wound response pathway. However, when ethylene action is blocked, the induction of endogenous JA levels by wounding is reduced. It appears that ethylene and JA induce each others production (54).

Signal-transduction pathways can be specific for the plant species and the tissue within a plant. Tomato plants respond to cell-wall derived oligosaccharides or chitosan with *de novo* synthesis of JA which results in the accumulation of PI's (16, 54). In contrast, in *Arabidopsis* treatment with chitosan does not result in elevated JA levels, which is mediated by ethylene-dependent negative effects on JA effectiveness (76). This ethylene-dependent blocking of JA-mediated effects in *Arabidopsis* does not occur in systemic tissues. As a consequence, different responses are induced in local and systemic tissues (76). Also in nicotine induction in tobacco, ethylene and JA have opposite rather than synergistic effects (53). Thus, specifics of the interaction among different signal-transduction pathways seem to be dependent on the plant species. Obviously, more studies are needed to obtain a better understanding of general effects and exceptions.

4. Induction of indirect defence

Research on the induction of indirect defence has started in the mid 1980's (3, 77-82) and has mainly concentrated on the induction of carnivore-attracting plant volatiles. Herbivory by arthropods results in the emission of a blend of volatiles that attracts the enemies of herbivorous arthropods. This has been studied in depth for plant – spider mite – predatory mite interactions (e.g. (4)) and plant – caterpillar – parasitoid interactions (e.g. (82)).

The induction of plant volatiles has been recorded for more than 23 plant species from 13 families (83) and it seems that it is a common response of plants to herbivory. In all plant species investigated the ability has been found. Among the plant families investigated are e.g., the Fabaceae, Brassicaceae, Cucurbitaceae, Poaceae, Malvaceae, Solanaceae, Rosaceae, and the Asteraceae. Two types of plant response can be distinguished (83).

(1) In response to herbivory the plant produces a blend that is dominated by novel compounds that are not emitted by intact or mechanically damaged plants. This type of response can be found in e.g. Lima bean (Figure 1B), cucumber, maize, and gerbera (79, 80, 84, 85).

(2) In response to herbivory the plant produces a blend that is qualitatively similar to the blend emitted by intact or mechanically damaged plants. In the latter case, the emission rate from herbivore-damaged plants is much higher than from mechanically damaged or undamaged plants and it continues much longer after termination of the damage (e.g. (86)). This type of response has been recorded for e.g., cabbage, cotton, tomato (Figure 1A) and potato (4, 78, 86-88).

In both types of responses, de novo biosynthesis of volatiles has been reported (89, 90) and thus plants invest in the production of volatiles rather than passively emitting the contents of damaged cells. Moreover, herbivore-induced plant volatiles are emitted systemically (91-94) which further supports the conclusion that the emission of volatiles is an active response rather than a passive release of cell contents.

The herbivore species that have been shown to induce plant volatiles belong to 27 species in 13 families of insects and mites. These herbivores include folivores (chewing-biting and cell-sucking species), sap-feeding insects, and species that feed in the plant such as leaf miners and stem borers (83). Plants may even induce volatiles in response to oviposition by a herbivore (95).The emitted blend varies largely among plant species in a qualitative sense. In addition, the blend also varies among plants of the same species that are damaged by different herbivores. However, this variation is much more subtle and usually relates to quantitative variation in the blend composition, i.e. the blends are composed of the same constituents but the relative contribution of different constituents to the blend varies (see (96) for review). Sometimes, a qualitative difference between blends of plants emitted by different herbivores has been recorded, e.g. for faba beans infested with different aphid species (97). Furthermore, the blend may be affected by herbivore instar, as was recorded for maize plants damaged by caterpillars (98).

In addition, abiotic factors may affect the emission of plant volatiles in a quantitative and qualitative sense (e.g. (99, 100)), but little efforts have been made to investigate the effect of abiotic conditions on the emission of herbivore-induced plant volatiles.

In conclusion, herbivory results in a change in the emission of volatiles and the composition of the emitted blend varies with biotic and abiotic factors.

4.1 Identity of herbivore-induced plant volatiles

The major volatiles emitted by plants, either constitutively or induced, belong to several classes that are produced through distinct biosynthetic pathways: e.g. fatty acid-derivatives produced through the lipoxygenase pathway, terpenoids produced through the isoprenoid pathway and phenolics produced through the shikimic acid pathway.

The fatty acid-derived volatiles comprise C6-aldehydes, C6-alcohols and their esters such as (*Z*)-3-hexen-1-yl acetate. They are common plant volatiles (101) and are often referred to as green-leaf volatiles (102). They are emitted in response to artificial damage as well as herbivory (e.g., (78-80)). These compounds can be perceived by parasitoid chemoreceptors (103) and some parasitoid species are attracted by these green leaf odors (104).

Terpenoids comprise the largest and most diverse chemical group in plants. They can be produced through the mevalonic acid pathway (105) or through the 1-deoxy-D-xylulose-5-phosphate pathway (106) and many of them are well-known for their toxic effects on herbivores (105). Among the herbivore-induced terpenoids there are two compounds that are especially noteworthy, i.e. the homoterpenes 4,8-dimethyl-1,3(*E*),7-nonatriene and 4,8,12-trimethyl-1,3(*E*),7(*E*),11-tridecatetraene. These terpenoids have been recorded from many plant species after the infliction of herbivory or treatment with elicitors (79, 80, 107, 108). Herbivory leads to the induction of (3S)-(*E*)-nerolidol synthase in Lima bean, cucumber and corn and subsequently to the formation of 4,8-dimethyl-1,3(*E*),7-nonatriene (109, 110), which is a known attractant of the carnivorous mite *P. persimilis* (80).

Phenolics are produced through the shikimic acid pathway. Among the phenolics emitted in response to herbivory are indole and methyl salicylate. Indole is an intermediate product of tryptophan biosynthesis. It plays an important role in direct defence as a component of indole alkaloids and indole glucosinolates (e.g., (26)). It has also been recorded among herbivore-induced plant volatiles, e.g. from maize, cowpea, soybean, cotton, gerbera or Lima bean (79, 85, 88, 98, 111). Methyl salicylate is the volatile methyl ester of the plant hormone salicylic acid. It has been recorded in several plant species, such as Lima bean, apple, and pear (80, 112, 113).

Nitrogen-containing compounds such as nitriles and oximes are commonly reported from herbivore-damaged plants. In crucifers these compounds can be degradation products of glucosinolates (78, 114), whereas in other plant species such as cucumber, Lima bean or gerbera (80, 84, 85), they may be derived from amino acids (115).

4.2 Importance of herbivore-induced plant volatiles to carnivorous arthropods

For natural enemies, the most reliable information on the presence of their herbivorous victim of course originates from the herbivore itself. However, a herbivorous arthropod is only a small component of the environment with a small biomass. Moreover, herbivores have been under natural selection to avoid being detectable by their natural enemies (116). Behavioural studies show that herbivorous arthropods or their faeces are not very attractive to carnivorous enemies (e.g., (117-120)) and a chemical analysis showed that hardly any volatiles can be detected from *Spodoptera exigua* larvae and faeces (118). Plants represent a much larger biomass and detection of herbivores by their natural enemies can benefit plants (121). For example, arthropod carnivores such as predatory mites are well-known to exterminate local populations of their herbivorous prey (77).

It is well-established that herbivore-induced plant volatiles play an important role in the attraction of carnivores. For instance, the predatory mite *Phytoseiulus persimilis* (117), and the parasitoid wasps *Cotesia marginiventris* (118), *Cotesia glomerata* (119), *Cotesia rubecula* (120) and *Microplitis croceipes* (122) all prefer odours from the plant-host complex over those from faeces of their herbivorous host/prey. The blend of volatiles can be specific for the herbivore species that induced it. Many arthropod predators and parasitoids have been shown to discriminate between plants infested with different herbivore species and also chemical differences have been reported (see reference (96) for review). Thus, the induced plant volatiles are important cues for carnivores to locate their herbivorous victims. The discrimination among induced blends of plant odours may need to be learned or can be dependent on the physiological condition (e.g. starvation level) of the carnivore (96).

Because herbivore-induced carnivore-attractants are emitted at the site of damage as well as systemically from undamaged leaves (91-93), the odour source is much larger than the herbivore, which increases the detectability of the herbivore to its natural enemies.

4.3 Response by carnivorous arthropods and benefits to plants

Herbivore-induced plant volatiles are very important for carnivorous arthropods and the carnivores can use them during several foraging decisions. This has been shown for a large number of carnivorous arthropods, including e.g. parasitic wasps (79, 120), predatory bugs (112, 123), and predatory mites (4, 124). Parasitoids and predators can be attracted from a distance and this has been demonstrated in various setups, including olfactometers (124), windtunnels (119), semi-field setups (125, 126) and field tests (127). In addition, the volatiles can also mediate arrestment in a herbivore patch (128) or the suppression of long-range dispersal (129).

Plants can greatly benefit from the attraction of carnivorous arthropods. Carnivores such as predatory mites or predatory bugs eliminate the herbivores by predation. They can exterminate local prey populations and thus relieve the plant of their herbivores. However, in the case of parasitoids this benefit to the plant is not self-evident (121). After parasitization the herbivore is not killed but in most cases continues to feed from the plant, sometimes at a larger rate than when not being parasitized (130). The latter may be dependent on the number of parasitoid eggs deposited in the herbivore. In order to establish whether plants benefit from parasitoids, one should investigate the effect of parasitization on plant fitness e.g. in terms of seed production. This has recently been done for *Arabidopsis thaliana* plants infested with *Pieris rapae* caterpillars and the solitary parasitoid *Cotesia rubecula*. This study showed that parasitization of the caterpillars resulted in a large reduction in fitness loss compared to plants infested with unparasitized caterpillars (121). Whether this is a general phenomenon should become clear from the investigation of other plant-herbivore-parasitoid systems.

4.4 Herbivore-induced plant volatiles and responses by herbivores

After emission of the induced volatiles, the plant is no longer in control over who exploits the information. For example, herbivores that forage for food may exploit the information to find a host plant (Figure 2). To herbivores the volatiles may represent information on (a) the presence of a host plant, (b) the presence of competitors and (c) the presence of a potentially enemy-dense space and herbivores may exploit this information. However, these are conflicting types of information and one may predict that the responses of herbivores are dependent on external and internal conditions. For instance, the information may lead to a different response in a starved herbivore than in a satiated herbivore and the response may also depend on other information, e.g. on the presence of carnivorous enemies in the environment. Indeed, different responses have been recorded for herbivores (for reviews see references (5, 131, 132)). For instance, the spider mite *Tetranychus urticae* is attracted to volatiles from undamaged Lima bean plants and to volatiles from a combination of volatiles from undamaged leaves and from spider-mite infested leaves. In contrast, when only volatiles from spider-mite infested leaves are offered, the spider mites are repelled (133). Alternatively herbivores may be attracted to plants infested with heterospecific herbivores because the heterospecifics provide protection from natural enemies (134).

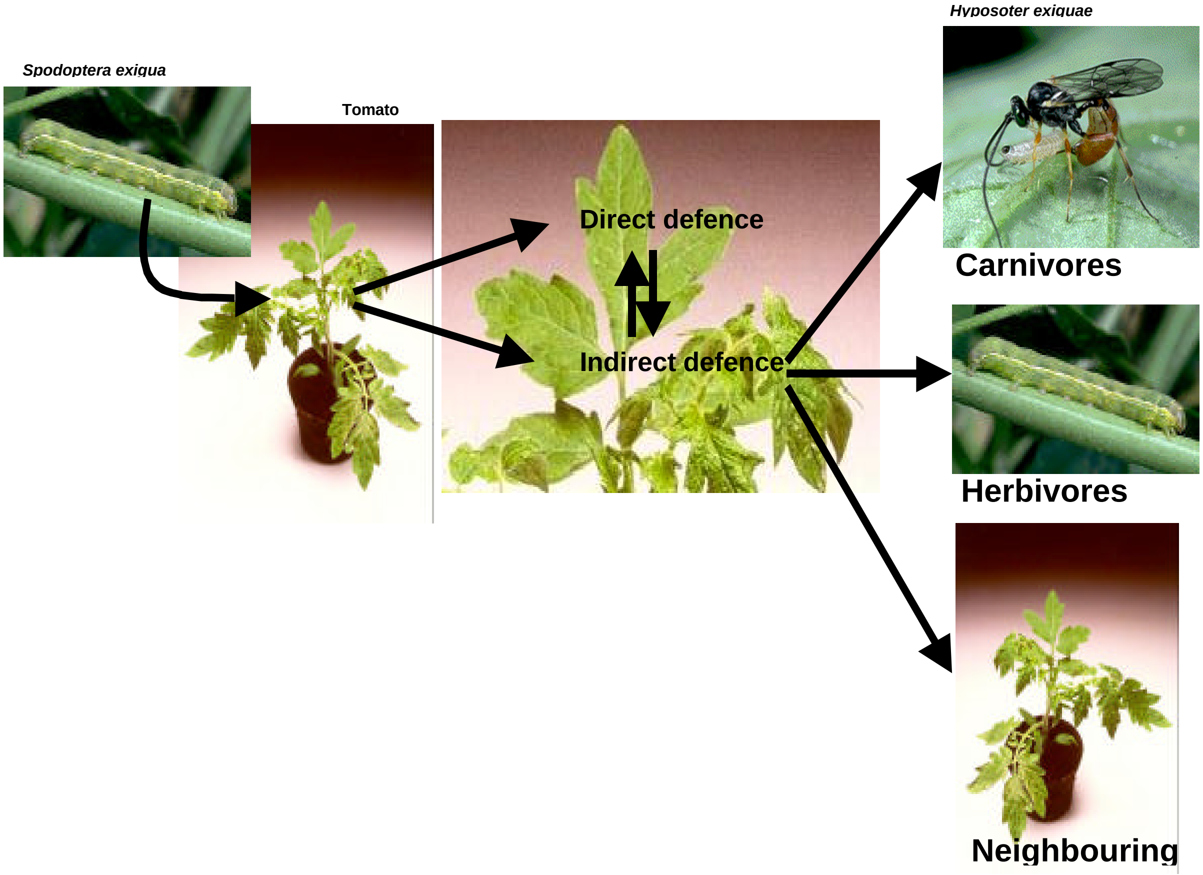

Figure 2: Herbivore-induced defences and effects on organisms at three different trophic levels, as exemplified for a tritrophic system consisting of tomato, *Spodoptera exigua* caterpillars, and the parasitoid *Hyposoter exiguae*. For specific information see text. Based on data from (4, 21, 36, 72, 136-138, 145). Photographs of caterpillar and parasitoid by Jack Kelly Clark, courtesy University of California Statewide IPM Project.

For herbivores that feed on the volatile-emitting plant, the volatiles may also have a direct negative effect. For instance, the green-leaf volatiles have a negative effect on the rate of population increase of aphids (135). This resembles the negative effect of these compounds on bacterial proliferation (35). Thus, these induced compounds may play a role in both direct and indirect defence. Most likely other induced volatiles such as terpenes can also interfere directly with herbivore performance and thus play a dual role.

4.5 Herbivore-induced plant volatiles and effects on neighbouring plants

The information emitted by infested plants may potentially also affect downwind uninfested neighbours (Figure 2). These neighbouring plants may exploit the information to initiate defences. After all, after the upwind neighbour has been overexploited by the herbivores they may reach the downwind neighbour on wind currents just as the information did. Information transfer between herbivore-infested and uninfested plants has been investigated since the mid 1980s (reviewed in references (7, 132, 136, 137). Evidence in favour of the exploitation of the information by downwind plants is increasing and recently some exciting new data have been published (40, 138).

4.6 Signal transduction

Carnivorous arthropods can discriminate between volatiles emitted by herbivore-damaged and mechanically-damaged plants (for reviews see e.g., (83, 116)). This is true both for plants that produce novel compounds in response to herbivory and for plants that produce the same compounds in response to herbivory and to mechanical damage. In the latter case the volatiles are emitted in larger amounts and especially during a longer period of time in response to herbivory than in response to wounding (e.g., (86)). This has stimulated the search for herbivore elicitors that enable the plant to discriminate between wounding and herbivory. In addition, the extensive knowledge on signal-transduction pathways in direct defence has been utilized to investigate their involvement in induced indirect defence.

4.6.1 Herbivore elicitors

As indicated above, mechanical damage can usually not effectively mimic herbivory in the induction of indirect defence. This can be explained by the role of herbivore elicitors. The application of oral secretions of herbivores onto mechanical damage can result in similar effects on volatile induction as herbivory itself (78, 79). The search for active components of the oral secretions has yielded two compounds: a β-glucosidase from *Pieris brassicae* caterpillars that induces volatiles in cabbage, maize and bean plants (139, 140) and the fatty acid-amino acid conjugate N-(17-hydroxylinolenoyl)-L-glutamine, called volicitin that induces volatiles in maize (141). In both cases, the application of the elicitor is a good mimic of herbivory, but it remains unknown what the exact effects of the elicitors are. Because glycosidically bound forms of the volatiles emitted have not been recorded, the glucosidase may release an internal elicitor. Volicitin, that has the fatty acid moiety 17-hydroxylinolenic acid, most likely activates the octadecanoid pathway (141). This pathway is known to be involved in the induction of carnivore-attracting volatiles (111, 139, 142, 143).

In some cases, mechanical damage can mimic herbivory in the induction of indirect defence. For example, caterpillar damage to cotton (*Gossypium herbaceum*) plants had the same effects on the induction of extrafloral nectar production as either mechanical damage in combination with caterpillar oral secretion or mechanical damaged plus water treatment (10). But in general, indirect defence induced by herbivores is different from the response to mechanical damage (e.g. (5, 81, 83)). An intriguing question is why herbivore elicitors appear to be more important in the induction of indirect defence than in the induction of direct defence. Is this difference an artifact, resulting from the use of different model plants? After all, the model plants of research on induced direct defence such as potato and tomato produce a similar odor blend in response to mechanical damage and herbivory, albeit that the effect of herbivory lasts longer (4, 86). Or is this the result of the interaction with carnivorous arthropods that base their foraging ‘decisions’ upon the information provided by the plant and therefore select for the emission of more specific signals in the plant?

4.6.2 Systemic elicitor

The induction of plant volatiles occurs systemically throughout the plant (91-93). An active compound has been extracted from spider mite-infested Lima bean plants, and when applied to an uninfested plant results in attraction of carnivorous mites (94). So far, the identity of the systemic elicitor(s) has not been elucidated.

4.6.3 Jasmonic acid and octadecanoid pathway

Treatment of Lima bean, maize, and gerbera plants with JA resulted in the emission of volatiles that are also induced by herbivory (111, 139, 142, 143). It is noteworthy that treatment with JA resulted in the induction of volatiles from different biosynthetic pathways in the same plant, such as the lipoxygenase pathway and the isoprenoid pathway. The volatile blend emitted by Lima bean after JA treatment is similar but not identical to the blend emitted by *T. urticae* infested plants. For instance, JA did not induce methyl salicylate or the homoterpene 4,8,12-trimethyl-1,3(E),7(E),11-tridecatetraene, while it induced two methyloximes in larger amounts than did spider mite damage. This difference in odour blend results in differential behaviour of the carnivorous arthropods (Figure 3). The carnivorous mite *P. persimilis* was attracted to JA-treated plants, but in a two choice situation preferred the volatiles from spider-mite damaged plants (111). In other plants (cucumber, tobacco, and *Arabidopsis thaliana*) MeJA induced the activity of two important enzymes in the green-leaf volatile production pathway, i.e. lipoxygenase (LOX) and hydroperoxide lyase (HPL), resulting in the increased emission of green leaf volatiles by plants (144). Treatment of plants with JA results in attraction of predators and parasitoids under laboratory and field conditions (111, 139, 142, 143, 145). For instance, in field-grown tomato plants JA-treatment resulted in a larger number of parasitoids (*Hyposoter exiguae*) and in a higher parasitisation percentage of *Spodoptera exigua* caterpillars (145). These results indicate an important role for JA as an endogenous signal molecule involved in induced production of volatiles. Indeed, both *Manducta sexta* herbivory and regurgitant treatment on mechanically damaged leaves resulted in an increase of endogenous JA levels in tobacco (38). Although JA is induced by herbivory, its methyl ester MeJA has never been recorded from herbivore-infested plants.

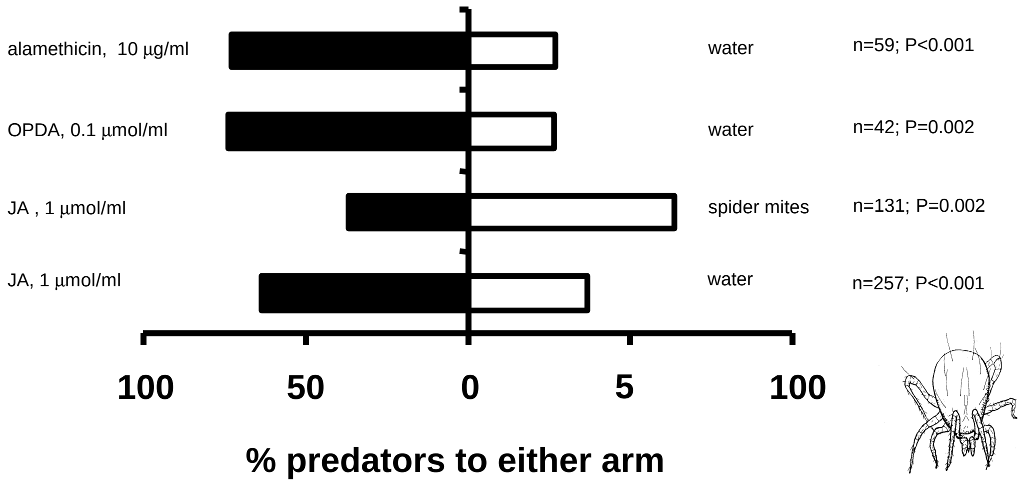

Figure 3: Attraction of predatory mite *Phytoseiulus persimilis* to Lima bean plants infested with herbivorous spider mites (*Tetranychus urticae)* or treated with jasmonic acid, OPDA or the peptaibol alamethicin. Experiments were carried out in a Y-tube olfactometer. For details of experimental setup see ref. (111). Data based on ref. (111) and M. Dicke & H. Dijkman (unpublished data).

Several intermediates from the octadecanoid pathway can induce plant volatiles. For instance, OPDA induces the two homoterpenes 4,8-dimethyl-1,3(E),7-nonatriene and 4,8,12-trimethyl-1,3(E),7(E),11-tridecatetraene in Lima bean (146) and OPDA treatment results in attraction of the predatory mite *P. persimilis* (Figure 3). Nonetheless, JA appears to be the most powerful member of the octadecanoids in terms of induction of Lima bean volatiles. A combination of octadecanoids may be responsible for the total induction pattern as recorded in response to spider mite damage. However, no herbivory-related elicitors have been found yet that induce methyl salicylate, a constituent of spider-mite induced Lima bean volatiles that attracts predatory mites (80).

Other compounds, such as conjugates of 1-oxo-indan-4-carboxylic acid, appear to have a strong inducing power as well. Coronatin (the coronamic acid conjugate of 1-oxo-indan-4-carboxylic acid) is the phytotoxin of certain *Pseudomonas syringae* pathovars and this compound induces a similar blend in Lima bean as JA, but in addition also induces the C16 homoterpene 4,8,12-trimethyl-1,3(E),7(E),11-tridecatetraene that is not induced by JA (142). A synthetic analogue such as 1-oxo-indanoyl-isoleucine (IN-Leu) induced a similar volatile blend in Lima bean as JA did (146). Most work on the effect of octadecanoids and their analogues has been done on Lima bean plants. To what extent these results apply to other plants remains unclear. The situation seems to be different in the monocotyledon maize. For this plant the differential effects of octadecanoids do not seem to apply (146).

Whether JA plays a role in other induced indirect defences as well, such as e.g. extrafloral nectar induction, has not been investigated.

4.6.4 Salicylic acid (SA)

A remarkable compound emitted by several plant species in response to herbivory is methyl salicylate. This compound is induced in e.g. spider-mite infested Lima bean and tomato plants (4, 80), in psyllid-infested pear plants (112) and in Colorado potato beetle-infested potato plants (86). It has also been recorded from tobacco mosaic virus-infested tobacco plants and was suggested to be a way of disposing of salicylic acid (SA) formed in infested plants (147). In cotton, herbivory by caterpillars of *Helicoverpa zea* leads to increased levels of SA, but no effect of SA induction has been found on the performance of the caterpillars (148). In an analysis of headspace volatiles of *H. zea*-infested cotton plants, an emission of methyl salicylate has not been reported (149). The application of gaseous MeSA to Lima bean plants was reported to induce the emission of the two homoterpenes 4,8-dimethyl-1,3(E),7-nonatriene and 4,8,12-trimethyl-1,3(E),7(E),11-tridecatetraene (150). It will be important to investigate the effect of SA production on indirect defence of plants, because SA is known to inhibit the effect of JA in direct defence. JA is important in the induction of plant volatiles and SA may inhibit this (151), but possibly the production of SA and the induction of plant volatiles by JA are spatially and/or temporally separated which would reduce the possiblity of interference (see below in section 4.6.7 ‘Cross talk’). If SA is induced by herbivory, its methylation and emission as MeSA is a way of avoiding the accumulation of SA in response to herbivory or possibly in response to microorganisms transmitted to the plant by the herbivore during feeding.

4.6.5 Ethylene

The induction of ethylene emission in response to herbivory or elicitors has been reported for several plants such as tobacco (53) and Lima bean (152). To our knowledge, there is no evidence that ethylene induces plant volatiles. However, the role of ethylene in induced indirect defence has received little attention to date. In tobacco, ethylene treatment did not induce the emission of (-)-*cis*-α-bergamotene or linalool (53), two compounds induced by *Manduca sexta* caterpillar feeding.

4.6.6. Other elicitors

Several other elicitors have been reported to induce plant volatiles. Among these are e.g. cellulysin and alamethicin, a mixture of the peptaibols, that are produced by the fungus *Trichoderma viride* (151). The peptaibols (oligopeptides) act as ion-channel forming compounds and are considered to mediate a very early step in the induction. In Lima bean they induce the production of a short peak of jasmonic acid and of salicylic acid. The latter phytohormone is produced at a high level for a long period of time. It is interesting to see that administration of the peptaibol alamethicin results both in a high level of SA in the plant and in the emission of MeSA. In addition to MeSA, the only other compounds emitted are the two homoterpenes 4,8-dimethyl-1,3(E),7-nonatriene and 4,8,12-trimethyl-1,3(E),7(E),11-tridecatetraene. This indicates that the SA inhibits the octadecanoid pathway beyond OPDA (151), as this octadecanoid intermediate induces the production of the two homoterpenes (146).

It appears that the blends of volatiles induced by these elicitors affect the behaviour of carnivorous arthropods: the predatory mite *P. persimilis* is attracted to peptaibol-treated Lima bean plants (Figure 3). This can be explained by the observation that two of the three volatiles emitted in response to alamethicin treatment, i.e. MeSA and the homoterpene 4,8-dimethyl-1,3(E),7-nonatriene, are known to attract this predatory mite (80). These volatiles are also induced by feeding damage of the spider mite *T. urticae*, on which this predatory mite preys.

4.6.7 Cross-talk

Research on signal transduction in induced indirect defence has a shorter history than that in induced direct defence. However, the few studies that have addressed it, indicate that this will be an essential subject for future investigations. The major pathway involved in indirect defence appears to be the octadecanoid pathway. From studies on direct defense it is well-known that the jasmonate and salicylate pathways interfere and methyl salicylate is induced in several plants by herbivory (see above). Different types of herbivores have different effects on volatile induction and the relative induction of the jasmonate and salicylate pathways may play a role. In Lima bean, spider mite feeding induces considerable emission of MeSA (80, 150), while caterpillar feeding damage does not (150). Application of JA and MeSA in different combinations also resulted in differences in volatile induction in Lima bean. Treatments that included both JA and MeSA applications induced compounds that are also induced by spider mite feeding, while application of JA exclusively resulted in the emission of volatiles that are also emitted in response to caterpillar feeding (150). The possible induction of SA by spider mite feeding is supported by gene expression studies that show that PR-4 gene expression is induced by spider mite feeding and MeSA treatement, but not by caterpillar feeding or JA treatment. If herbivores, like pathogens, produce ion-channel forming compounds that induce JA and SA in plants, then the relative timing and induced levels of these phytohormones may determine the volatile profile emitted (150, 151). This may be an important determinator of blend composition, that is known to vary with herbivore species or instar that feeds on the plant (96). In this context, it will be important to investigate the effects of pathogens on induced indirect defence against herbivores. So far, no studies are known to us that have investigated the effect of previous pathogen infestation (and thus likely induction of SA) on the ability of plants to induce volatiles that attract carnivores.

There is no evidence for an interaction of ethylene with JA-mediated volatile induction so far. In tobacco, ethylene treatment did not influence the MeJA-induced emission of (-)-*cis*-α-bergamotene. This contrasts to the interference of ethylene with MeJA induced production of nicotine (53).

5. Interaction between direct and indirect defence

Plants are attacked by a wide range herbivores and have evolved a variety of defences. The coordination of these defences seems to be a formidable task and may have several conflicts. The tailoring of defences seems to be a complex optimization problem, the outcome of which is dependent on the intensity and frequency of different types of attackers and their natural enemies.

For instance, plants are attacked by specialist and generalist herbivores. Specialist herbivores are usually well-adapted to the defences of their host plant. They may even exploit secondary compounds that provide protection against generalist herbivores as token stimuli to recognise their host plant. Oviposition in *Pieris* butterflies is stimulated by glucosinolates of their cruciferous host plants and for caterpillars these compounds act as feeding stimulants (153). Specialist herbivores can also exploit secondary metabolites of their host plant in their own defence. *Manduca sexta* caterpillars derive protection from pathogens and parasitoids by the intake of nicotine from tobacco leaves (31, 32). In addition, direct defences may interfere with natural enemies of herbivores without an involvement of the herbivore. Glandular trichomes on tomato stems are a defence against herbivores, but in addition they kill the majority of predatory mites that forage on the plant by entrapment. Therefore, this direct defence is incompatible with indirect defence through predatory mites. This shows that direct defences can interfere with the effectiveness of indirect defences and one may wonder whether there is a negative correlation between investments in direct and indirect defence. In this context it is interesting to note that tomato and cabbage, that have a strong direct defence, do not emit novel volatiles in response to herbivory compared to mechanical damage. As a consequence the information content is much lower than for plants like Lima bean or maize that emit novel compounds that dominate the blend in response to herbivory (132). At the individual plant level, an uncoupling of direct and indirect defence appears to be possible. In tobacco plants, damage by *M. sexta* caterpillars or treatment with their regurgitant results in an attenuation of induced direct defence (nicotine production) that is mediated by herbivore-induced ethylene. In contrast, there is no such effect on the induction of indirect defence (53).

6. Interaction between defences against pathogens and herbivores

Plants are also attacked by a wide range of pathogens. The defences induced against pathogens and herbivores may act synergistically (e.g.,(74)) or antagonistically (e.g., (72)). Yet, both in direct and indirect defences against herbivores and in defences against pathogens similar combinations of signal-transduction pathways may be induced. These pathways may act antagonistically, such as in the interference between SA- and JA-mediated defences. The current knowledge suggests that at certain points in the signal-transduction pathways, switchpoints are present that influence the final outcome of the collective signal transduction pathways. With an increasing knowledge of signal transduction in induced defences against pathogens as well as those against herbivores, it will be important to unravel where these switchpoints are, where crosstalk between pathways occurs and especially how crosstalk is regulated. This will be a major challenge for the forthcoming years. It will be important to investigate different plant species and populations, especially when different populations are under different relative pressures of herbivores and pathogens.

7. Comparative analysis of signal transduction in induction of direct and indirect defence: model systems

The signal transduction pathways involved in induction of direct defence have been well studied and there is a fertile area for the study of cross-talk. The research on signal-transduction in induced indirect defence is rapidly advancing and bridging the gap with the knowledge in direct defences. However, the two research fields have developed independently, mostly with different model systems. In induced direct defence the best studied model plants are the solanaceous plants tomato and tobacco, while in induced indirect defence these comprise e.g. Lima bean, maize, cotton and cabbage. There seems to be a difference in the way solanaceous and cruciferous plants employ indirect defence (few novel compounds induced) versus that of plants such as Lima bean and maize (major novel compounds induced by herbivory). To allow a better comparison of signal transduction in induced direct and indirect defence, common model systems are highly needed. Several model systems seem to be good candidates.

Tobacco has been well studied for induced direct defence against pathogens and insects and the signal transduction pathways involved (reviewed by (7, 14, 154)). Recently, these studies have also incorporated the induction of indirect defence (53). This will make tobacco a very interesting model system for a comparative analysis.

There is abundant knowledge on the induction of direct defences against pathogens and herbivores in tomato (13, 48, 72, 155, 156) and several mutants and transgenes are available (21, 49, 157). In addition, studies on the induction of indirect defence are emerging (4, 72, 145). Therefore, tomato will be an interesting model system too.

Arabidopsis thaliana has been well-studied for direct defence against pathogens (158). Studies on direct defence against insects are emerging as well (159, 160). In addition, there is abundant knowledge on direct defence in other crucifers (e.g., (26, 161-164)) against herbivores and pathogens. Recently, the first demonstration of induced indirect defence has been made in *Arabidopsis* (121, 165). Together with the presence of various mutants and transgenes that are affected in signal transduction pathways and the near completion of the genomic analysis, *Arabidopsis* will become an important model plant for comparative studies on signal transduction in direct and indirect defence.

When concentrating on such model plants, it remains important to consider other plant species as well. The above-mentioned three plant species all have in common that they have a well-developed direct defence. The blend of volatiles induced in tomato plants by spider mites is dominated by non-novel compounds (4) and thus contrasts to the situation in plants like Lima bean, cucumber and maize (79, 80, 111). Therefore, it remains important to include the latter three plant species as well to enable a comparison among plants with different types of induced indirect defence.

8. Major questions to be addressed

Developments in the research on signal transduction in induced defence against herbivorous insects have been numerous in the past decade. Induction of direct and indirect defence appear to share many signal transduction pathways. The octadecanoid signal-transduction pathway seems to be the major pathway involved in induced defences against insects. However, there are clear indications that other pathways play an essential role as well. Recent work demonstrates that the most important signalling molecule in addition to JA is SA. This is clear from e.g. the increasing number of reports on the emission of MeSA from herbivore-damaged plants. The formation of MeSA in response to herbivory as well as the influence on JA-mediated signalling deserves further investigation.

The induction of indirect defence against herbivorous insects seems to be more specific than the induction of direct defence. In many cases there is a clearly differential response to mechanical damage versus the response to herbivory or herbivore elicitors. The compositions of volatile blends can vary substantially with the species or instar of herbivore that damages the plant and this variation can have considerable consequences for carnivore attraction and thus for defence effectiveness. What signal transduction events mediate these subtly differential responses of plants will be a rewarding subject. Most likely the involvement of signal molecules from different signal transduction pathways will be found.

A signal molecule that has not received much attention to date, is ethylene. This molecule is involved in the induction of defences against pathogens or in responses to non-pathogenic microorganisms (166) and modulates the induction of nicotine in tobacco plants (53).

The rapid development in research on signal transduction in induced defence against insects enables the integration with research on induced defences against pathogens. This will be very important, because in nature plants are exposed to a gamut of attackers that include pathogens and herbivores. Investigating how plants integrate defences against all these attackers will be an important step.

In indirect defence, extensive knowledge is present on the attraction of carnivores to complete blends of volatiles emitted by herbivore-damaged or elicitor treated plants. However, knowledge on the bio-active compounds within the blend is limited to a few studies (131). The use of elicitors that selectively induce certain blend components as well as mutants or transgenes that are modified in signal-transduction pathways or in biosynthetic pathways (165) will provide excellent opportunities to elucidate which compounds are most important in attracting carnivores and how variation affects this.

With significant progress in the knowledge of mechanisms of induced plant defences, e.g., in molecular genetics, biochemistry, plant physiology, many tools will become available to investigate the function of these plant traits. Together with progress in the options of manipulating plant genotype, the ultimate step may be made, i.e. investigating the effects on plant phenotype in its interactions with biotic and abiotic components of the environment.

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