

# Behavioural and community ecology of plants that cry for help

MARCEL DICKE

Laboratory of Entomology, Wageningen University, 6700 EH Wageningen, the Netherlands

## ABSTRACT

**Plants respond to insect herbivory with the production of volatiles that attract carnivorous enemies of the herbivores, a phenomenon called indirect defence or ‘plants crying for help’. Plants are under selection to maximize Darwinian fitness, and this can be done by making the right ‘decisions’ (i.e. by responding to environmental stress in ways that maximize seed production). Plant decisions related to the response to herbivory in terms of the emission of herbivore-induced volatiles include ‘to respond or not to respond’, ‘how fast to respond’, ‘how to respond’ and ‘when to stop responding’. In this review, the state-of-the-art of the research field is presented in the context of these decisions that plants face. New questions and directions for future research are identified. To understand the consequences of plant responses in a community context, it is important to expand research from individual interactions to multispecies interactions in a community context. To achieve this, detailed information on underlying mechanisms is essential and first steps on this road have been made. This selective review addresses the ecology of herbivore-induced plant volatiles (HIPVs) by integrating information on mechanisms and ecological functions. New questions are identified as well as challenges for extending current information to community ecology.**

*Key-words:* headspace analysis; induced plant defence; infochemicals; insect behaviour; multidisciplinary approach; tritrophic interactions.

## INTRODUCTION

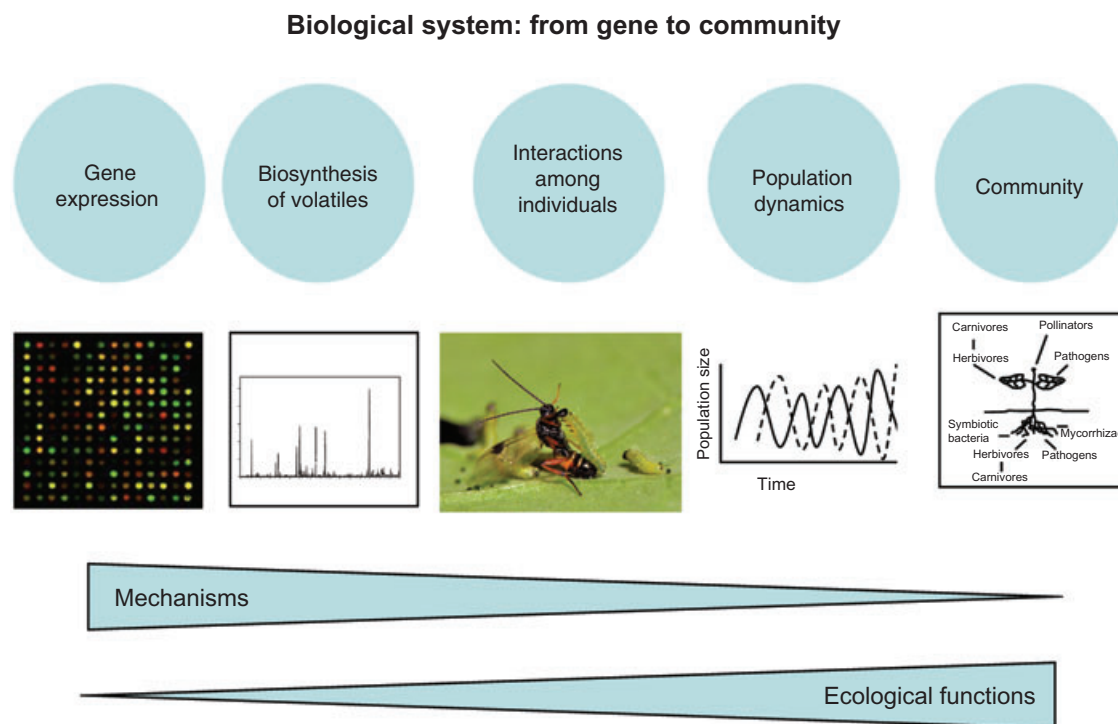
Plants are sessile organisms that are rooted in the soil. They are on the menu of a large number of mobile muggers ranging from microbes to mammals. The most diverse taxon of attackers consists of insects. At present, ca. 1 million insect species are known and the estimates of the total number of species are in the order of 2–6 million. Of the currently known insect species, approximately 50% are feeding on plants (Schoonhoven, van Loon & Dicke 2005). However, plants are far from passive victims of these attackers. They can activate a multitude of defence responses (Kessler & Baldwin 2002; Pieterse & Dicke 2007;

Heil 2008), and thus, they have a plastic phenotype. One of the defence strategies plants have to combat mobile attackers is to enlist mobile bodyguards such as insect predators and parasitoids (D’Alessandro & Turlings 2006; Bruinisma & Dicke 2008), or entomophagous nematodes (Rasmann *et al.* 2005) and possibly also insectivorous birds (Mantyla *et al.* 2008). This can be done by providing shelter, alternative food and/or the emission of herbivore-induced plant volatiles (HIPVs) (Dicke & Sabelis 1988; Arimura, Kost & Boland 2005; Heil 2008). Plants extensively communicate with organisms in the environment through volatiles, and these volatiles can be induced by herbivory (Pichersky & Gershenzon 2002). The induced emission of plant volatiles that attracts carnivorous organisms, a phenomenon also referred to as ‘crying for help’ (Dicke, Sabelis & Takabayashi 1990a), has been demonstrated for plants in at least 13 families and occurs in response to a wide variety of herbivorous insects and mites (Dicke 1999b). The induction of bodyguard-attracting plant volatiles was first demonstrated for foliage-feeding mites (Dicke & Sabelis 1988; Dicke *et al.* 1990b) and caterpillars (Turlings, Tumlinson & Lewis 1990). Later, it was also reported as a response to feeding by a range of other folivorous insects (Drukker, Scutareanu & Sabelis 1995; Du *et al.* 1998; Van Loon, De Vos & Dicke 2000a), stem borers (Potting, Vet & Dicke 1995), seed feeders (Steidle, Fischer & Gantert 2005) and root feeders (Van Tol *et al.* 2001; Rasmann *et al.* 2005). Furthermore, plants may even initiate the emission of induced volatiles in response to oviposition by herbivorous insects (Hilker & Meiners 2006) or in response to exposure to induced volatiles from herbivore-infested neighbouring plants (Dicke, Agrawal & Bruin 2003a; Baldwin *et al.* 2006).

Thus, in the past two decades, it has become clear that plants are very sensitive to the activities of organisms in their environment. Very soon after the first discoveries of the emission of herbivore-induced carnivore attractants (Dicke & Sabelis 1988; Turlings *et al.* 1990), this research field has expanded enormously and currently encompasses studies at various levels of biological integration, ranging from molecular genetics to community ecology (Kessler & Baldwin 2001; Kappers *et al.* 2005; Rasmann *et al.* 2005; Halitschke *et al.* 2008; Kollner *et al.* 2008; Poelman *et al.* 2008a; Zheng & Dicke 2008) (Fig. 1).

For a long time, HIPVs have been investigated for simple tritrophic systems with an emphasis on the induction process in the plant and the behavioural responses of

*Correspondence:* M. Dicke. Fax: +31 317 484821; e-mail: marcel.dicke@wur.nl



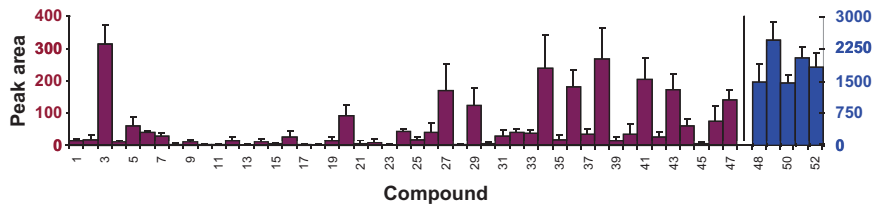
**Figure 1.** The emission of herbivore-induced plant volatiles (HIPVs) can be studied at different levels of biological integration that address ecological functions and the underlying mechanisms. The picture of the parasitic wasp *Cotesia glomerata* parasitizing a caterpillar of *Pieris brassicae* on *Brassica oleracea* is made by Hans Smid (Laboratory of Entomology, Wageningen University; <http://www.bugsinthepicture.com>).

carnivorous arthropods. Recent developments in this research field emphasize more complex systems and some take a community ecological approach investigating the effects of multiple infestation, responses by different community members and the effects on community composition. In this review, I will focus especially on these new developments. This review will take a plant-centred, functional ecological approach, and addresses the ‘decisions’ a plant needs to make before, during and after attack. Thus, my approach will be one that can be classified as behavioural ecology of plants (see also Karban 2008). We are mostly not used to consider decisions of plants and these decisions should, just like in behavioural ecology of animals (Krebs & Davies 1984), be seen in an evolutionary context and not as conscious decisions. Plants are exposed to natural selection, and those plants that perform better than their conspecific competitors will contribute more offspring to the next generation, and therefore, have a higher Darwinian fitness. By taking a behavioural ecological approach and addressing the decisions that plants are expected to make so as to maximize Darwinian fitness, new research questions can be identified. This goes beyond describing plant behaviour and includes considering what decisions would be adaptive to plants (Karbon 2008). What decisions plants actually make should then be investigated. This approach is well respected in animal behavioural ecology (Krebs & Davies 1984). It has also been rewarding in the research on herbivore-induced emission of plant volatiles,

although here it has usually not been presented in a plant behavioural ecological context.

### Plants cry for help: the mechanism

The attack of an herbivore results in a large-scale transcriptional rearrangement in the attacked plant (De Vos *et al.* 2005; Ralph *et al.* 2006; Broekgaarden *et al.* 2007; Kempema *et al.* 2007). This includes the induction of genes involved in phytohormone biosynthesis and the biosynthesis of secondary metabolites (Van Poecke, Posthumus & Dicke 2001; Kessler, Halitschke & Baldwin 2004). HIPV blends can comprise tens up to hundreds of components (Turlings *et al.* 1990; Krips *et al.* 2001). Thus, a herbivore-infested plant emits a complex blend of volatile compounds (Fig. 2). These include, for example, terpenoids, green leaf volatiles and aromatic compounds such as indole and methyl salicylate (Fig. 3); however, only a subset of this complex mix of components mediates the attraction of carnivorous arthropods (Dicke *et al.* 1990b; Turlings *et al.* 1991; De Boer, Posthumus & Dicke 2004; Van den Boom *et al.* 2004; Kappers *et al.* 2005; D’Alessandro *et al.* 2006; Schnee *et al.* 2006; Shiojiri *et al.* 2006a; Gershenzon & Dudareva 2007; Halitschke *et al.* 2008). Identifying which compounds are involved in the attraction can be done by offering individual compounds, or by interference with their induction or biosynthesis in the plant (Kessler & Baldwin 2001; Snoeren, De Jong & Dicke 2007; Halitschke *et al.* 2008; Mumm, Posthumus & Dicke

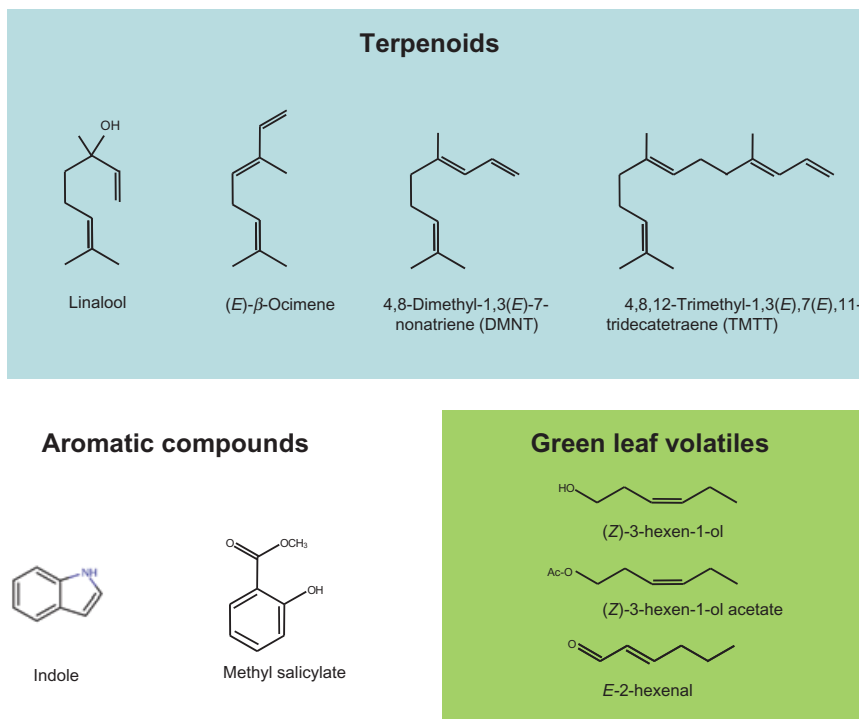


**Figure 2.** Composition of the headspace of five lima bean plants infested with two-spotted spider mites (*Tetranychus urticae*). The average and standard deviation are given for five independent replicates; one peak area unit is ca  $0.17 \pm 0.05$  ng. Numbers represent different compounds: 1: 2-methyl-propanal-*O*-methyl oxime; 2: 2-methyl-2-propenal; 3: 2-butanone; 4: 3-butene-2-one; 5: 2-methyl-butanal-*O*-methyl oxime; 6: 3-pentanone; 7: 3-methyl-butanal-*O*-methyl oxime; 8: 3-methyl-3-buten-2-one; 9: 2-methyl-propane nitrile; 10: 2-butanol; 11: 2-methyl-3-buten-2-ol; 12: hexanal; 13: 2-methyl-butane nitrile; 14: 3-methyl-butane nitrile; 15: myrcene; 16: 3-heptanone; 17: 1-penten-3-ol; 18: pentyl acetate; 19: unknown; 20: (*Z*)-beta-ocimene; 21: (*E*)-2-hexenal; 22: 1-pentanol; 23: 3-octanone; 24: (*Z*)-4,8, dimethyl-1,3,7-nonatriene; 25: hexyl acetate; 26: octanal; 27: (*Z*)-3-hexen-1-ol; 28: (*Z*)-3-hexen-1-ol butanoate; 29: nonanal; 30: rose furan; 31: 1-octen-3-ol; 32: (*Z*)-3-hexen-1-ol 2-methylbutanoate; 33: alpha copaene; 34: decanal; 35: unknown; 36: linalool; 37: unknown; 38: beta caryophyllene; 39: 1-nonanol; 40: unknown; 41: unknown; 42: unknown; 43: unknown; 44: 4,8,12-trimethyl-1,3,7,11-tridecatetraene isomer; 45: unknown; 46: benzyl cyanide; 47: indole; 48: (*E*)-beta-ocimene; 49: (*E*)-4,8, dimethyl-1,3,7-nonatriene; 50: (*Z*)-3-hexen-1-ol acetate; 51: methyl salicylate; 52: (*E, E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene isomer. After data in Dicke *et al.* (1999).

2008; van Wijk, De Bruijn & Sabelis 2008). For example, transgenic tobacco plants that are compromised in the emission of certain plant volatiles (terpenoids and green leaf volatiles) are less attractive to a predatory bug (Halitschke *et al.* 2008); mutant *Arabidopsis* plants that are compromised in green leaf volatile emission are less attractive to the parasitoid *Cotesia glomerata* (Shiojiri *et al.* 2006b), and spider mite infested lima bean plants in which a specific step in terpenoid biosynthesis has been blocked are compromised in their attraction of predatory mites upon spider mite infestation (Mumm *et al.* 2008).

Elicitors of HIPV induction are present in herbivore oral secretions (Turlings *et al.* 1990; Mattiacci, Dicke &

Posthumus 1995; Halitschke *et al.* 2003; Schmelz *et al.* 2006; Carroll, Schmelz & Teal 2008). Application of oral secretion, or the elicitors that are present in it, can mimic the effect of herbivory (Turlings *et al.* 1990) and induces the activation of signal transduction pathways (Kahl *et al.* 2000). The induction of HIPV is mediated by phytohormones such as jasmonic acid (JA), ethylene and salicylic acid (SA) (Boland *et al.* 1995; Dicke *et al.* 1999; Ozawa *et al.* 2000, 2004; Horiuchi *et al.* 2001; Van Poecke *et al.* 2001; Ament *et al.* 2004). For instance, the application of JA to lima bean plants induces a volatile blend that is similar, but not identical, to the blend induced by spider mite feeding, and carnivorous mites that feed on the spider mites can



**Figure 3.** Representative compounds of the three major classes of compounds that can be found in the headspace of various plant species after insect herbivory.

discriminate between JA-induced and spider mite-induced plant volatiles (Dicke *et al.* 1999). An important compound lacking in the JA-induced blend is methyl salicylate, the methyl ester of the phytohormone SA, and the lack of this compound in the JA-induced blend is a major determinant of the differential attraction of predatory mites to spider mite-infested and JA-induced lima bean plants (De Boer & Dicke 2004). Moreover, exposure of lima bean plants to the ethylene precursor 1-aminocyclopropane-1-carboxylic acid (ACC) enhances the volatile induction by JA as well as the attraction of the predatory mite *Phytoseiulus persimilis* (Horiuchi *et al.* 2001). JA seems to be the most important phytohormone mediating HIPV emission. Recent studies have identified a family of proteins (JAZ proteins) that act to repress transcription of jasmonate-responsive genes; upon JA treatment, these proteins degrade which results in the transcription of the previously blocked genes (Thines *et al.* 2007).

The emission of HIPV occurs locally at the site of infestation, but also systemically from uninfested leaves (Turlings & Tumlinson 1992). Stem borers such as the maize stem borer *Chilo partellus* induce the emission of HIPV from the foliage of plants whose stem they infest, and consequently the foliage attracts parasitoids that after landing move downwards to locate the opening in the stem to localize the stem borer larva (Potting *et al.* 1995). Thus, the odour plume that is related to herbivore feeding is much larger than when the odour plume would originate only from the herbivore itself or from the tissue that is damaged by the herbivore.

### Plants cry for help: the carnivore perspective

Carnivorous arthropods that search for their herbivorous victim face a problem because their victim is under natural selection to minimize the emission of cues that can guide the carnivores to them. However, HIPV emitted by the plants from which the herbivores feed can solve this problem: they are emitted in relatively large amounts and the composition of the mixture can be herbivore specific. Thus, HIPV are both detectable and relatively reliable cues that can be exploited by carnivorous arthropods (Vet & Dicke 1992). A wealth of carnivorous species has been demonstrated to be attracted by HIPV, such as parasitoids, predatory mites, bugs and beetles (Dicke 1999b; D'Alessandro & Turlings 2006). These mites and insects are usually more sensitive to the volatiles than the analytical equipment. Carnivores can often discriminate between plant volatiles induced by different herbivore species (Du *et al.* 1998; Dicke 1999a; Rasmann & Turlings 2008), and HIPV composition indeed can be herbivore species specific (Takabayashi, Dicke & Posthumus 1991; Turlings *et al.* 1993; Rasmann & Turlings 2008). Many carnivore species can effectively learn to respond to or discriminate between HIPV (Vet, Lewis & Cardé 1995; Drukker *et al.* 2000; De Boer & Dicke 2006; Schnee *et al.* 2006; Smid & Vet 2006; Smid *et al.* 2007; Schroder *et al.* 2008), and thus can temporarily specialize to respond to certain volatile blends (Vet

*et al.* 1998). The carnivore perspective has been extensively reviewed (e.g. Vet & Dicke 1992; D'Alessandro & Turlings 2006; Takabayashi *et al.* 2006).

### Plant 'decisions'

The phenomenon of HIPV emission has often been considered from an animal point of view, focusing on how insects exploit the information. Often, the role of the plant has been considered a passive one in an evolutionary sense, and the adaptiveness of crying for help has been challenged (e.g. Van der Meijden & Klinkhamer 2000). Yet, the evidence that plants benefit in terms of Darwinian fitness increases (Dicke & Sabelis 1989; Van Loon, De Boer & Dicke 2000b; Fritzsche-Hoballah & Turlings 2001), and the evolutionary ecological aspects of plants crying for help receive ample interest (e.g. Sabelis & de Jong 1988; Dicke & Vet 1999; Kobayashi & Yamamura 2007; Halitschke *et al.* 2008)

Behavioural ecologists that investigate animals standardly address questions related to animal 'decisions' in the context of the environment and alternative decisions, and the cues that are used by animals to base their decisions on (Krebs & Davies 1984). Such an approach can analogously be taken to investigate the responses of plants to their environment, although this has much less been identified as a behavioural ecological approach. Yet, plant biologists can learn from the extensive experience of animal behavioural ecologists (Karban 2008). It is obvious by now that plants are not the passive organisms that many assume them to be and, therefore, considering plant responses to herbivore attack in terms of 'decisions', just as is done by animal behavioural ecologists is likely to yield new questions on plant responses (e.g. Ballaré 2009). In the following paragraphs, I will address some of these plant 'decisions' in a non-exhaustive manner and will identify several questions to be addressed in future studies.

### To respond or not to respond

When an herbivore attacks a plant, cells will be damaged and, consequently, compounds will unavoidably leak out of the plant, including volatiles. This is similar to what happens when mechanical damage occurs because of, for example, sand being blown over the plant or an animal moving through the vegetation. However, for a plant, these types of damage can have dramatically different consequences. Mechanical damage is likely to be a discrete event, while a feeding herbivore may continue to feed, to reproduce and thus inflict damage over a longer period of time, possibly resulting in defoliation of the plant. Thus, it may pay plants to be able to discriminate between different types of damage and respond differentially. Recent work has shown that WRKY transcription factors may mediate the discrimination between mechanical damage and herbivory by influencing the dynamics of JA titer in the plant; these transcription factors mediate responses in terms of resistance to herbivores and the emission of HIPV with subsequent effects on herbivory intensity (Skibbe *et al.* 2008). In



response to mechanical damage, the plant's first interest may be to close the wound, while herbivory requires more extensive action. The volatiles emitted after a single bout of mechanical damage can attract carnivorous arthropods, but usually this is a short-lasting event (Steinberg, Dicke & Vet 1993). However, when mechanical damage continues in a pattern resembling herbivore feeding, the volatile bouquet includes many compounds that are also induced by herbivory (Mithofer, Wanner & Boland 2005); it will be interesting to investigate the behavioural responses of carnivorous arthropods to the volatiles emitted in response to such repeated mechanical damage in comparison to their responses to herbivory-induced volatiles.

Sometimes, it may not pay the plant to emit HIPV. Parasitoids that attack caterpillars usually attack young caterpillars because old caterpillars are much better at defending themselves. The parasitoid *Cotesia kariyai* attacks caterpillars of the lepidopteran herbivore *Mythimna* (= *Pseudaletia*) *separata* in the first few instars. Older instars cannot be parasitized as these large caterpillars have an effective physical defence that may even kill the parasitoid. This parasitoid is not attracted to maize plants infested with fifth or sixth instar larvae, but is attracted to plants infested with first through fourth larval instar caterpillars. The effect can be mimicked by applying regurgitant from third versus sixth instar larvae, indicating that elicitors in regurgitant of the caterpillars are age dependent (Takabayashi *et al.* 1995). Yet, plants that shut down the volatile emission may lack the help from other bodyguards such as birds (Mantyla *et al.* 2008).

A relevant question is whether plants should respond to herbivory with the emission of HIPV when their neighbours already do so. If the emission of volatiles has costs and the neighbours have already started to pay these costs, plants may benefit from exploiting the carnivores that are attracted by the neighbours without paying the costs themselves. Modelling studies show that there are conditions where such a strategy may evolve (Sabelis & de Jong 1988). Indeed, evidence for plant–plant communication has been recorded for a range of plant species including, for example, cotton, tobacco, alder, tomato and lima bean (Dicke *et al.* 2003a; Baldwin *et al.* 2006). Recent evidence shows that 'priming' (Frost *et al.* 2008) may be an important mechanism mediating plant–plant communication (Engelberth *et al.* 2004; Heil & Kost 2006; Kessler *et al.* 2006). The exposure to volatiles from herbivore-infested plants may affect the response of downwind neighbouring plants to subsequent herbivory. The exposure itself does not induce a response in terms of volatile emission, but potentiates the response to herbivory and results in enhanced volatile emission and stronger attraction of carnivorous arthropods in response to herbivory (Choh *et al.* 2004; Ton *et al.* 2007). Such priming of HIPV emission may also be elicited by previous herbivory (Mattiacci *et al.* 2001) or by exposure to phytohormones such as JA (Gols *et al.* 2003). Volatiles do not only mediate communication between plants but may also influence within-plant communication through priming (Frost *et al.* 2007; Heil & Bueno 2007; Heil & Ton 2008).

Thus, through within-plant signalling, HIPV may influence, for example, the emission of volatiles (Frost *et al.* 2007) or the production of extrafloral nectar in undamaged leaves of the same plant (Heil & Bueno 2007).

The 'decision' to respond can have important consequences. As soon as the volatiles are emitted, they may influence the behaviour of any member of the community, not only carnivores. For instance, herbivores may exploit the information during host plant selection. Some herbivores avoid the induced plant volatiles (Dicke 1986; De Moraes, Mescher & Tumlinson 2001), while others may be attracted (Bolter *et al.* 1997; Kalberer, Turlings & Rahier 2001; Shiojiri *et al.* 2002; Halitschke *et al.* 2008). Parasitic plants may also exploit a plant's volatiles to find a suitable host plant (Runyon, Mescher & De Moraes 2006). The investigation of the effect on pollinator attraction has only just begun (Kessler & Halitschke 2007; Bruinsma *et al.* 2008). The emerging view on the ecological effects of the emission of HIPVs is that they can result in important changes in interactions with community members (Kessler & Baldwin 2001; Poelman, van Loon & Dicke 2008b). The emission of HIPVs is especially beneficial to plants in a bodyguard-dense environment. It would be interesting to investigate whether the composition of the surrounding community affects the intensity of the plant response. So far, laboratory studies where plants have been grown under insect-free conditions have shown the induction of HIPVs for plants of many laboratory-reared species, which suggests that the presence of carnivorous arthropods is not a prerequisite for this plant response. However, the response may be potentiated by information about the presence of bodyguards, which may be available in the form of, for example, nectar loss in extrafloral nectaries (Heil *et al.* 2000). Whether the removal of extrafloral nectar is used by plants in making decisions on the production of HIPV remains to be investigated.

### How fast to respond

A major constraint in inducible defences is the time lag between damage and the induction of a defence response. Inducible defences of plants involve herbivore perception, transcriptional responses, protein formation and biosynthetic responses. The very first responses to damage can be observed within seconds to minutes, and involve changes in the plasma membrane potential (Maffei, Mithofer & Boland 2007). Subsequent steps involve phytohormonal signalling and transcriptional responses (Kessler & Baldwin 2002). Damage also results in the emission of volatiles, some of which are not induced but constitutively present, for example, in glands on the leaf surface. Their emission, therefore, is not under the control of the plant, but a mere consequence of the rupture of cells. Green leaf volatiles such as C6 alcohols, aldehydes and esters that are produced through the lipoxygenase pathway are usually among the first volatiles to be recorded. Terpenoids come later (Turlings *et al.* 1998). Metabolic changes in plants are usually expressed within hours to days after damage, and these

include the emission of HIPVs (Kunert *et al.* 2002). Moreover, attraction of carnivorous arthropods to HIPVs is also initiated within hours (Scascighini *et al.* 2005). These data show that the lag phase between the onset of herbivory and the attraction of bodyguards is in the order of hours. It should be realized, however, that these studies all used an artificial set-up in that the lag phase was assessed as the period since an introduced herbivore started feeding. In nature, many herbivore feeding events are preceded by oviposition. The deposition of eggs can induce volatiles and other changes in plant metabolites (Hilker & Meiners 2006; Fatouros *et al.* 2008). Prior induction can modify later plant responses to other herbivores (Kessler & Baldwin 2004), and it remains to be investigated whether such an interaction also occurs between oviposition and subsequent herbivory by the eclosing larvae. That the lag time between herbivory and the emission of HIPV can be important is demonstrated in a modelling study for the tritrophic system *Brassica oleracea*–*Pieris rapae*–*Cotesia rubecula* (Puente *et al.* 2008a). The study shows that a lag phase of more than 1 d eliminates the benefit for the parasitoids to respond to HIPV. For *B. oleracea*–*Pieris brassicae*–*Cotesia glomerata* interactions, empirical data show that the attraction of the parasitoids is already apparent after 30–60 min (Scascighini *et al.* 2005), and so it seems that the plant response is fast enough to result in selection on parasitoids to use the HIPV.

Although the time lag between herbivory and the expression of the induced defence is a constraint, plants are likely under selection to optimize rather than maximize the response rate. After all, the induction of a certain defence may boomerang on the ability to induce other defences. For instance, cross talk between the SA pathway and the JA pathway may prevent the induction of JA-inducible defences after an SA-dependent response has been induced (Zarate, Kempema & Walling 2007). Therefore, any plant individual that initiates the JA pathway too soon may be compromised in inducing SA-dependent defences and vice versa. Herbivores may exploit this cross talk and may induce a signalling pathway that does not induce an effective defence and interferes with the induction of an effective defence (Musser *et al.* 2002). This represents the informational arms race that plants and herbivorous insects are engaged in.

### How to respond

A plant that is attacked has a wide array of potential responses, including various direct and indirect defences. Mounting direct defences, such as toxic secondary metabolites, may be an appropriate first action to stop generalist herbivores. However, many specialist herbivores tolerate or detoxify secondary metabolites of their host plant (Van der Meijden 1996; Wheat *et al.* 2007; Gols *et al.* 2008). Moreover, specialists may sequester secondary plant metabolites and exploit them in their own defence against carnivores, which is clearly counterproductive to the plant's investments. Mounting direct defences may, therefore, not be the most appropriate response to combat specialists. In

*Nicotiana attenuata*, when compared to the response to mechanical damage, herbivory by the specialist herbivore *Manduca sexta* results in an attenuated nicotine response and an induced emission of terpenoids that may be part of the plant's indirect defence (Kahl *et al.* 2000).

There are ample examples showing that plants can respond differentially to different herbivores, for example, in terms of gene expression (Voelckel & Baldwin 2004; De Vos *et al.* 2005) and composition of the volatile blend (Takahayashi *et al.* 1991; De Moraes *et al.* 1998; Du *et al.* 1998). The differences in volatile bouquets can be discriminated by carnivores (De Moraes *et al.* 1998; Du *et al.* 1998).

By emitting different odour blends in response to infestation with different herbivore species, a plant provides carnivorous arthropods with a possibility to discriminate between plants infested with herbivores with a different value to the carnivore. However, one may wonder whether the emission of different volatile blends in response to different herbivores represents an evolved trait in plants. After all, why would the plant invest in such differentiation? As long as an effective carnivore is attracted, the plant's problem is solved. However, different carnivore species may not only be valuable in removing herbivores from the plant; they may also exhibit intraguild predation, thereby possibly removing other, more effective, carnivores (Gnanvossou, Hanna & Dicke 2003). Thus, not all carnivore species have the same bodyguard value to a plant.

### Plant responses within a community context

HIPV have long been investigated for simple linear tritrophic food chains. However, the emitted HIPVs are available to all community members, and each of them may exploit the volatiles to its own benefit. Thus, herbivores (Bolter *et al.* 1997; Kalberer *et al.* 2001) or parasitic plants (Runyon *et al.* 2006) may exploit them to locate a suitable host plant. Furthermore, they may influence pollinator behaviour, but this has received little attention to date (Kessler & Halitschke 2007; Bruinsma *et al.* 2008).

HIPVs are usually studied in simple laboratory set-ups such as olfactometers and wind tunnels (Gols *et al.* 2003). Such studies provide information on the potential role of HIPV in plant–carnivore interactions under natural conditions. Several studies have extended these bioassays to semi-field and field set-ups, and compared the results with those from olfactometers and wind tunnels (Janssen 1999; Kappers *et al.* 2005; Halitschke *et al.* 2008). The limited number of studies that addressed carnivore responses under more natural conditions generally confirm the data from laboratory bioassays. Yet, the conditions under more realistic settings can be more challenging to carnivores. For instance, the diamondback moth parasitoid *Diadegma semiclausum* is attracted to volatiles from *B. oleracea* plants infested with diamondback moth (*Plutella xylostella*) larvae in a Y-tube olfactometer (Bukovinszky *et al.* 2005). Moreover, uninfested white mustard (*Sinapis alba*) plants also attract this parasitoid (Bukovinszky *et al.* 2005). When the parasitoid is exposed to host-infested *B. oleracea* plants in a

glasshouse, the parasitoids enter the set-up faster but take more time to find the host-infested plants when white mustard plants are also present than in the absence of white mustard plants (Gols *et al.* 2005). In contrast, the attraction of the predatory mite *P. persimilis* to prey-infested bean plants was not affected by the simultaneous presence of volatiles from non-prey-infested cabbage or cucumber plants, neither in an olfactometer nor in a glasshouse set-up (Dicke *et al.* 2003b).

Moreover, under natural circumstances, abiotic conditions may affect the production of HIPV and the responses by insects. For instance, UV-B is known to induce JA-mediated plant responses, and UV-B exposure of plants affects the interactions with herbivorous insects as well as their parasitoids (Caputo, Rutitzky & Ballare 2006; Foggo *et al.* 2007). Atmospheric ozone degrades HIPV components such as terpenoids and can reduce the attraction of parasitoids to infested plants (Pinto *et al.* 2007). Also, plant-produced compounds emitted by other plants in the environment may affect HIPV-mediated interactions. For instance, the presence of isoprene in the environment, emitted by trees such as oaks, willows and poplars, can negatively influence the attraction of parasitoids to HIPV from host-damaged plants (Loivamäki *et al.* 2008).

Plants are members of complex communities, and the infestation of a plant by a single attacker is the exception rather than the rule. There is ample evidence that herbivores may compete through plant-mediated mechanisms such as induced resistance (Kaplan & Denno 2007). Moreover, multiple infestation of a plant may also influence the emission of HIPV. This has been shown for, for example, plant–insect interactions (Rodriguez-Saona *et al.* 2005; Delphia, Mescher & De Moraes 2007; Soler *et al.* 2007; De Boer *et al.* 2008) and plant–microbe–insect interactions (Guerrieri *et al.* 2004; Cardoza & Tumlinson 2006; Rostas & Turlings 2008). The two attackers may attack different plant tissues, such as roots and shoots (Guerrieri *et al.* 2004; Soler *et al.* 2007) or may be separated in time (Kessler & Baldwin 2004). This shows the importance of temporal as well as spatial aspects of herbivory and HIPV, and adds another level of complexity to the investigation of the role of HIPV in natural systems. Different herbivore species may elicit different signal transduction pathways (De Vos *et al.* 2005) that may exert cross talk (Koornneef & Pieterse 2008). Most information on cross talk is available for a negative interaction between the JA and SA signal transduction pathways (Koornneef & Pieterse 2008). A herbivore like the silverleaf whitefly *Bemisia tabaci* that induces SA-dependent defences, represses JA-dependent defences (Zarate *et al.* 2007). Thus, herbivores may manipulate plant defences as a decoy strategy, evidence for which is also available for other systems (Musser *et al.* 2002).

Plant responses to early-season herbivores may drastically alter the phenotype as a result of extensive transcriptional changes, and this can have important consequences for interactions with subsequent attackers (Kessler & Baldwin 2004; Poelman *et al.* 2008a). Herbivory-induced plant responses can change the associated insect

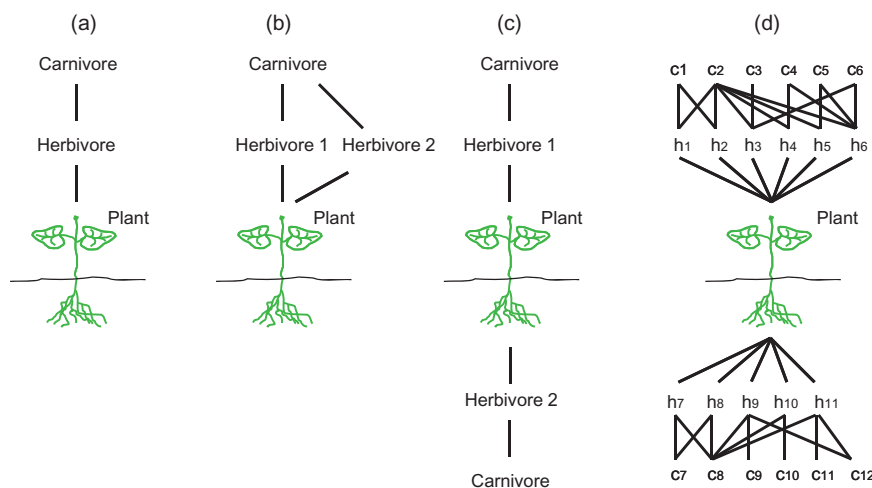
community into one that is more dominated by specialists than by generalists, and induced plant volatiles are likely to play a role in this (Van Zandt & Agrawal 2004; Poelman *et al.* 2008b). The consequences of herbivory-induced plant volatiles for community composition have been mostly neglected to date. It will be important to address these so as to expand our knowledge on HIPV from simple tritrophic systems to complex communities.

### When to stop responding

Most research efforts on the dynamics of HIPV emission have concentrated on the onset of the emission. However, given that the emission of HIPV has costs, plants are expected to terminate the emission as soon as carnivores have eliminated the herbivores or have reduced their activity. The application of caterpillar regurgitant to a plant results in the emission of HIPV during several days, so it is likely that after elimination of the herbivore, the emission of HIPV continues, albeit at a diminishing rate (Loughrin *et al.* 1994). Carnivores can also discriminate between HIPV induced by unparasitized and parasitized herbivores (Fatouros *et al.* 2005). Parasitization of caterpillars results in large-scale physiological changes. One of these is apparent in their regurgitant. When cabbage plants are induced with the regurgitant of parasitized or unparasitized *Pieris* caterpillars, *Cotesia* parasitoids prefer the volatiles from plants treated with regurgitant from unparasitized caterpillars (Fatouros *et al.* 2005). The lack of data on the termination of HIPV emission is partially compensated by two interesting modelling studies that address the effects of HIPV dynamics on parasitoid foraging success (Puente *et al.* 2008a; Puente, Kennedy & Gould 2008b). These studies show that parasitoids do not benefit from using HIPV when their emission continues for several days after pupation or elimination by predators (Puente *et al.* 2008b). From the parasitoid point of view, it is important whether the plant produces the same odour bouquet in response to all herbivore instars or not. This is especially true for parasitoids that can only parasitize a limited subset of the developmental stages of their host. The data of these modelling papers (Puente *et al.* 2008a,b) show the relevance of collecting data on the temporal as well as the spatial dynamics of HIPV emission.

### Future directions

In the first two decades of research on HIPV, many exciting aspects have been investigated in-depth for individual interactions between one plant, one herbivore and one carnivore (Fig. 4a). In more recent years, this has expanded to investigating more complex systems such as those including two herbivore species, either both above-ground (Delphia *et al.* 2007) or one above and one below-ground (Soler *et al.* 2007) (Fig. 4b,c). Moreover, the consequences of HIPV for community composition and community dynamics (Fig. 4d) are an exciting field that has only just started to be explored (Kessler *et al.* 2004; Kessler & Halitschke 2007; Snoeren *et al.* 2007; Poelman *et al.* 2008b). The complexity of plant–



**Figure 4.** The cry for help of plants has initially been investigated for simple tritrophic systems (a), and subsequently for systems with two herbivores feeding on above-ground plant tissues (b), two herbivores feeding on above- and below-ground tissues (c) and more recently a community ecological approach has been initiated (d).

insect communities provides a challenge to incorporate in studying the ecology of HIPV. Detailed information on the mechanisms that underlie the induction process in plants (Kessler & Baldwin 2002) as well as the responses of carnivorous insects (Smid *et al.* 2007) provides exciting tools for manipulative studies addressing the role of HIPV in the complex communities that plants and insects constitute (Bruinsma & Dicke 2008) (Fig. 1). This can be done by specifically silencing individual genes in plants and exposing them to the natural community (Kessler *et al.* 2004), or by inducing plants with specific treatments such as feeding damage by an early-season herbivore (Poelman *et al.* 2008a). In doing so, we will gain important progress in understanding how HIPV mediate not only interactions between individuals, but also the dynamics of communities and the resulting biodiversity (Poelman *et al.* 2008b). This is an exciting prospect as it is a major step forward to understanding the ecological consequences of a plant's cry for help in response to insect herbivory in a community context.

As a result of a better understanding of community dynamics in the context of induced plant defences, we will also be able to identify those community members whose responses to HIPV deserve to be investigated. At present, most knowledge is available on the responses of parasitoids and predators of herbivorous insects, and studies on pollinators have been initiated. Non-volatile secondary metabolites of plants are known to affect higher trophic levels (Harvey *et al.* 2007). It will be interesting to investigate the effects of HIPV on insects at the fourth and higher trophic levels as these insects can be quite abundant in communities (Bukovinszky *et al.* 2008).

The effects of abiotic factors on HIPV-mediated biotic interactions have received only limited attention to date. Yet, there is ample information on plant volatiles and abiotic stresses (Loreto, Kesselmeier & Schnitzler 2008). Given that abiotic conditions change rapidly, increasing our knowledge on effects of the abiotic environment on HIPV-mediated interactions will be important to appreciate the changes in ecological communities in the context of HIPV.

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