

Research review

Herbivore-induced plant volatiles: targets, perception and unanswered questions

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Summary

Plants respond to mechanical wounding, herbivore feeding or infection by pathogens with the release of volatiles. Small C₆ molecules termed green-leaf volatiles form a general element in most of these blends; however, the overall composition is usually sufficiently specific that other organisms are able to determine the nature of the attacker. Receivers of herbivore-induced volatile organic compounds (HI-VOCs) comprise distant parts of the same plant ('within-plant signalling'), neighbouring plants ('plant–plant signalling'), herbivores, and multiple carnivores that respond to the 'plant's cry for help', such as parasitoids and hyperparasitoids, entomopathogenic nematodes, and predatory mites, beetles, bugs and birds. In spite of intensive research efforts, many central questions still remain. How do plants perceive volatiles? What is the relative impact of each of the interactions with different receivers of HI-VOCs on the fitness of the emitting plant and that of the interacting organisms? How long can these compounds remain stable in the atmosphere? Why are VOC-mediated effects on herbivores and beneficial organisms not used as a common tool in sustainable agriculture? Here, I briefly summarize the ecological effects of HI-VOC perception and discuss the most pertinent questions raised by participants at the 32nd *New Phytologist* Symposium in Buenos Aires.

Introduction

In the 1980s, first studies reported the ecological effects of herbivore-induced volatile organic compounds (HI-VOCs) that are released from damaged plants and target external organisms in a resistance-related context. In 1983, David Rhoades reported enhanced resistance in willow (*Salix sitchensis*) growing close to herbivore-infested conspecifics and speculated that an airborne signal had warned the as yet uninfested neighbours of the upcoming danger (Rhoades, 1983). His hypothesis was confirmed soon after by Ian T. Baldwin and Jack C. Schultz in a study on poplar (*Populus × euroamericana*) (Baldwin & Schultz, 1983). In the late 1980, researchers in two labs discovered that HI-VOCs can also be perceived by carnivores. Marcel Dicke and Maurice W. Sabelis reported that blind predatory mites use HI-VOCs emitted from infested lima bean (*Phaseolus lunatus*) to locate their prey (Dicke & Sabelis, 1988), and Ted C. J. Turlings and colleagues found that parasitoid hymenopterans use HI-VOCs to localize

their host caterpillars (Turlings *et al.*, 1990). These studies opened up a new and fruitful research area (Fig. 1): the terms 'talking trees' or 'plant–plant communication' were coined to describe VOC-mediated interactions of plants with their neighbours, whereas the attraction of carnivores to prey on herbivores was termed 'indirect defence'.

In spite of thousands of follow-up studies, important questions remain unanswered. What is the evolutionary origin of HI-VOCs and how does their emission affect the fitness of emitters and receivers in nature? Are HI-VOCs co-evolved signals or simply cues that other organisms use to determine the defensive status of a plant? Are HI-VOCs just the physiologically unavoidable consequence of internal, resistance-related processes (Peñuelas & Llusía, 2004)? Does the emitter benefit from warning its neighbours? Which VOC-mediated effects represent the evolutionary drivers of VOC synthesis and release? How do plants release and perceive VOCs? Scientists working on these topics met at the 32nd *New Phytologist* Symposium in Buenos Aires in November 2013. In this

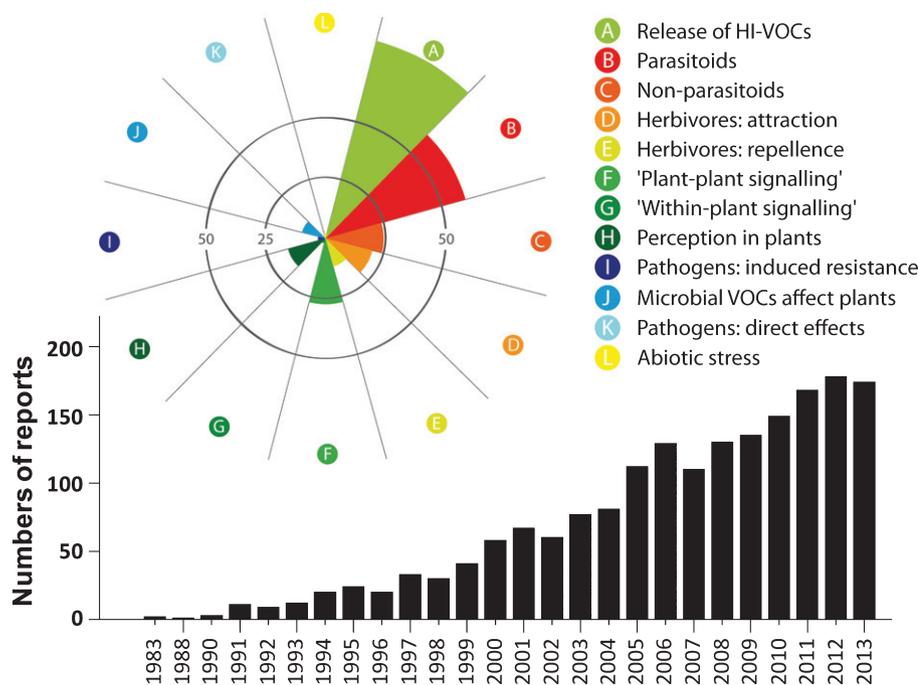


Fig. 1 Literature survey of reports on herbivore-induced volatile organic compounds (HI-VOCs) published between 1983 and 2013. The bars depict the number of reports found in a non-filtered search for 'plant volatil* AND induced NOT oil' conducted on 26 March 2014 in the ISI Web of Science. The inset indicates the number of reports that were found in a more detailed search (by reading titles and occasionally abstracts) on the various research topics that are related to HI-VOCs: A, biotic, abiotic and molecular factors affecting the production or release of HI-VOCs; B, effects of HI-VOCs on parasitoids; C, effects of HI-VOCs on non-parasitoids; D, direct effect on herbivores (attraction); E, direct effect on herbivores (repellence); F, effect on neighbouring plants; G, effects on the same plant; H, genetic/physiological changes in the receiver; I, effects on pathogens (induced resistance); J, effects of microbial VOCs on plant resistance; K, direct effect on pathogens (inhibited growth); L, role of HI-VOCs in abiotic stress.

review, I discuss some of the recent advances in our understanding of HI-VOC targets and perception and the most pertinent open questions identified by participants during discussions at the symposium and in correspondence after the symposium.

Effects of HI-VOCs on other organisms

It goes beyond the scope of this review to report in detail on all the ecological effects of HI-VOCs. Here, I give only a short overview on how the different biological classes of HI-VOC receivers have been reported in the literature (Fig. 2).

Plant–plant communication by airborne signals

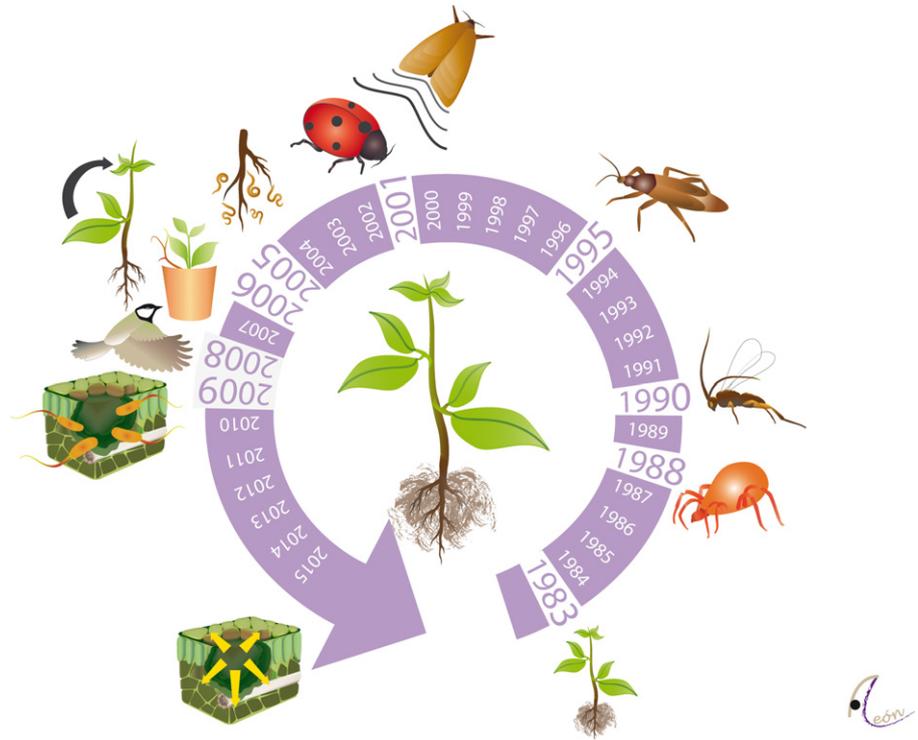
The first reports on 'talking trees' (Baldwin & Schultz, 1983; Rhoades, 1983) proved to be highly controversial. Many plant scientists considered the concept of 'plant–plant communication' to be esoteric and could not imagine how a trait enabling an infested plant to help its neighbours prepare for future danger could remain evolutionarily stable (Heil & Karban, 2010). Studies under controlled conditions (Shulaev *et al.*, 1997; Bate & Rothstein, 1998), by contrast, were criticised for using unnaturally high concentrations of the active VOCs. However, further studies confirmed the occurrence of this phenomenon in nature using, among others, alder (*Alnus glutinosa*) (Dolch & Tscharnke, 2000), sagebrush (*Artemisia tridentata*) and wild tobacco (*Nicotiana attenuata*) (Karbon *et al.*, 2000; Karban & Shiojiri, 2009), barley (*Hordeum vulgare*) (Glinwood *et al.*, 2004) and lima bean (Kost & Heil, 2006). VOC-mediated 'plant–plant communication' is now considered to be a well-established phenomenon (Karbon *et al.*, 2014), although there is still ongoing debate as to whether the phenomenon is correctly termed 'communication'. As Rick Karban (University of California at Davis, USA) says, 'the

most pressing questions are whether this communication has important consequences for plant fitness under natural conditions, who communicates, and how this communication is accomplished'.

Effects on animals at higher trophic levels

The idea of odour-mediated tritrophic interactions has been less controversial than the concept of 'talking trees': multiple parasitoids and predators use plant-derived VOCs (which usually, but not always, are more strongly emitted after herbivory) to locate their herbivore prey (Kaplan, 2012a; Halloran *et al.*, 2013; Penaflo & Bento, 2013; Vieira *et al.*, 2013) or are attracted to HI-VOCs such as methyl salicylate (MeSA), linalool, or β -caryophyllene (James, 2003; Mallinger *et al.*, 2011; Xiao *et al.*, 2012). These effects can enhance the rates of predation and parasitism of herbivores (Khan *et al.*, 1997; Thaler, 1999; Mallinger *et al.*, 2011; Kaplan, 2012a; Uefune *et al.*, 2012) and thereby reduce the numbers of herbivores on a plant (Kessler & Baldwin, 2001; Mallinger *et al.*, 2011). Following reports on predatory mites (Dicke & Sabelis, 1988) and parasitoids (Turlings *et al.*, 1995; de Moraes *et al.*, 1998), this effect was also reported for predatory bugs (Drukker *et al.*, 1995; Kessler & Baldwin, 2001), ladybird beetles (Ninkovic *et al.*, 2001) and birds (Mäntylä *et al.*, 2008; Amo *et al.*, 2013). Even hyperparasitoids use HI-VOCs to locate their parasitoid hosts (Poelman *et al.*, 2012). 'This study really lays an extra layer onto the more traditionally studied tritrophic interactions', says James Blande (University of Eastern Finland, Finland), and he adds 'and the results were compelling'. In summary, HI-VOCs aid in the host-location behaviour of diverse animals and the enhanced presence of carnivores can benefit the emitting plants. However, pertinent questions 'still lie in the ecological significance of the laboratory observations that we make and possibly even for

Fig. 2 Order of discovery of the herbivore-induced volatile organic compound (HI-VOC) receivers. This image depicts the years in which milestone articles on the most prominent receivers of HI-VOCs were published: other plants (Baldwin & Schultz, 1983; Rhoades, 1983), predatory mites (Dicke & Sabelis, 1988), parasitoid wasps (Turlings *et al.*, 1990), predatory bugs (Drukker *et al.*, 1995), predatory lady beetles (Ninkovic *et al.*, 2001), herbivorous moths, which are repelled (de Moraes *et al.*, 2001), parasitic plants (Runyon *et al.*, 2006), nematodes (Rasmann *et al.*, 2005), systemic parts of the same plant (Karban *et al.*, 2006), predatory birds (Mäntylä *et al.*, 2008) and resistance to pathogens (Yi *et al.*, 2009). Considering the depolarization events and Ca^{2+} influxes in membranes exposed to HI-VOCs (Zebelo *et al.*, 2012) it is tempting to speculate that the next discovery will concern their perception by local cells that are surrounding the injured tissues, where HI-VOCs elicit local and – perhaps – systemic wound responses.



some of the more homogeneously arranged field studies', adds Blande.

Effects on herbivores: repellence, attraction and associational resistance

HI-VOCs indicate the presence of a plant that is being damaged by herbivores and, therefore, can also be used by the herbivores themselves to locate suitable hosts or to avoid resistance-expressing plants. For example, female moths (*Heliothis virescens*) avoided HI-VOCs emitted from tobacco (*Nicotiana tabacum*) plants that were infested by conspecific caterpillars (de Moraes *et al.*, 2001). Similarly, the odour of resistance-expressing plants was repellent to Egyptian cotton leafworm (*Spodoptera littoralis*) (Zakir *et al.*, 2013b) and to female adults of *Gynandrobrotica guerrieroensis* (Chrysomelidae) and *Cerotoma ruficornis* (Chrysomelidae), which avoided jasmonic acid (JA)-treated lima bean plants in a dosage-dependent manner (Ballhorn *et al.*, 2013). Such repellent effects can make the air around resistance-expressing plants sufficiently unattractive to herbivores that neighbouring plants are also protected in a passive way (Zakir *et al.*, 2013b). HI-VOCs can even be absorbed to the cuticle of an exposed plant and then re-released (Himanen *et al.*, 2010). Both phenomena lead to an 'associational resistance' in which a plant passively benefits from VOCs released by its neighbours. Surprisingly, even the volatiles that are emitted from leaf galls can lead to an 'associational resistance' that protects the host tree from herbivorous mammals (Rostas *et al.*, 2013).

However, many herbivores prefer plants that emit HI-VOCs, at least up to certain concentrations (for recent reports, see Mérey *et al.*, 2011; Ballhorn *et al.*, 2013; Smart *et al.*, 2013; Zakir *et al.*,

2013a; Bedoya-Perez *et al.*, 2014; for a recent review on host choice behaviour by herbivorous insects see Knolhoff & Heckel, 2014). It is tempting to speculate that specialist herbivores in particular use HI-VOCs or constitutively emitted VOCs as cues for host location.

Effects on pathogens

To date, there has been limited investigation of VOC-mediated effects on microorganisms; however, these are likely to be at least as important as the effects on arthropods. Several classical HI-VOCs can contribute significantly to plant resistance to pathogens. For example, methyl jasmonate (MeJA) inhibits the growth of several plant pathogens (Goodrich-Tanrikulu *et al.*, 1995; Zhang *et al.*, 2006) and limonene inhibits the growth of *Fusarium verticillioides* (Dambolena *et al.*, 2008).

Exposure to airborne MeSA was shown to induce resistance in tobacco to pathogens (Shulaev *et al.*, 1997) and exposure to GLVs induced resistance-related genes in Arabidopsis (Bate & Rothstein, 1998). Similarly, nonanal has been shown to trigger resistance expression in lima bean to the bacterial pathogen *Pseudomonas syringae* (Yi *et al.*, 2009) and MeJA induced resistance in maritime pine (*Pinus pinaster*) to a pathogenic *Fusarium* species and in field elm (*Ulmus minor*) to *Ophiostoma novo-ulmi* (Vivas *et al.*, 2012). Therefore, plant VOCs can play a dual role as direct anti-microbial agents and as resistance inducers (Scala *et al.*, 2013). However, microorganisms such as rhizobacteria and fungal endophytes can also induce multiple plant resistance traits and strongly interfere with the emission of HI-VOCs (Yue *et al.*, 2001; Pineda *et al.*, 2013; D'Alessandro *et al.*, 2014). It goes beyond the scope of this review to discuss all the effects that microbial VOCs or colonization by microorganisms can have on plant resistance (for recent reviews

see, for example, Pineda *et al.*, 2010; Yuan *et al.*, 2010; Van Dam & Heil, 2011). In the view of Ted C. J. Turlings (University of Neuchâtel, Switzerland), 'We are finally accepting that microorganisms are essential contributors to all possible interactions and it will become increasingly clear that this is also the case for volatile mediated interactions'. It appears likely that this aspect is a severely understudied area with high potential for application in agriculture and for increasing our understanding of the ecological effects and evolutionary origins of HI-VOCs production.

Volatile within-plant signals

Competition is strong among plants and a signal is unlikely to be evolutionarily stable when it helps only organisms other than the emitter to survive. Furthermore, although plant–plant signalling can be more efficient among genetically identical plants (Karban *et al.*, 2013), the effect crosses the species boundary, as clipped sagebrush triggers resistance in wild tobacco (Karban *et al.*, 2000; Kessler *et al.*, 2006). The phenomenon of 'cross-species signalling' suggests that group selection or benefits via a generalized resistance to shared enemies is unlikely to represent a major evolutionary driver of plant–plant signalling. However, what about effects that serve the emitter more directly? Studies in four plant species – sagebrush, lima bean, poplar and blueberry (*Vaccinium corymbosum*) – found that HI-VOCs mediate systemic resistance expression within the same plant in response to local damage (Karban *et al.*, 2006; Frost *et al.*, 2007; Heil & Silva Bueno, 2007; Rodríguez-Saona *et al.*, 2009). Volatile resistance-related signals enable particularly large and anatomically complex plants to overcome long distances and vascular constraints, to quickly reach those organs that most urgently need to be warned about the presence of an enemy: the parts that are spatially, but not necessarily anatomically, close to the wound site.

Resistance induction by HI-VOCs

Enhanced resistance to pathogens or herbivores in VOC-exposed plants is a commonly reported phenomenon. However, how plants perceive volatiles still needs to be determined. In the following paragraphs I briefly summarize what we know about the physiological and genetic changes in plants that are triggered by their exposure to HI-VOCs.

Transcriptomic responses and priming

The first report on transcriptomic shifts after exposure to HI-VOCs concerned lima bean plants that were exposed to the air around spider mite-infested conspecifics (Arimura *et al.*, 2000). Many transcriptomic studies followed and it is beyond the scope of this review to go into detail. However, traditional gene expression studies do not suffice to detect all relevant responses to HI-VOCs. Volatiles commonly prime rather than induce plants: after VOC exposure, there is no detectable change in gene expression, but it remains ready to mount a faster and stronger response once the plant is being attacked. This phenomenon was first reported for maize (*Zea mays*) seedlings that were exposed to HI-VOCs from

neighbouring conspecific plants (Engelberth *et al.*, 2004). Priming by plant VOCs has also been found in other species and affects the indirect resistance of lima bean and maize to attack by herbivores (Heil & Kost, 2006; Ton *et al.*, 2007), the direct resistance of wild tobacco to attack by herbivores (Kessler *et al.*, 2006; Rasmann *et al.*, 2012) and the direct resistance of bean to infection by pathogens (Yi *et al.*, 2009). Priming by volatiles can even remain over more than one generation (Rasmann *et al.*, 2012), which indicates the involvement of an epigenetic component. Indeed, reduced methylation rates in the promoter region of a JA-responsive resistance gene was found in maize plants after exposure to HI-VOCs (Ali *et al.*, 2013); however, the phenomenon is far from being fully understood at the molecular level.

Electrophysiological effects

Priming and transcriptomic effects are highly relevant but they act downstream of the perception step. How are HI-VOCs perceived by plants? Membrane depolarisation and influx of Ca^{2+} are crucial early events in the perception of ongoing herbivory (Maffei & Bossi, 2006; Maffei *et al.*, 2007; Wu & Baldwin, 2010) and also characterize odour perception in animals. Therefore, it was perhaps not too surprising to find the same events in tomato (*Lycopersicon esculentum*) plants that were exposed to HI-VOCs (Zebelo *et al.*, 2012). Green-leaf volatiles that are well known for their resistance-enhancing effects, such as (Z)-3-hexenal, (E)-2-hexenal and (Z)-3-hexenyl acetate, caused rapid and strong membrane depolarization in plants exposed to them and this response was dosage-dependent. Similarly, exposure to α -pinene and β -caryophyllene caused detectable depolarization at 50 ppm and stronger effects at 100 and 300 ppm, although no difference was detected between the latter two concentrations (Zebelo *et al.*, 2012). These studies have received some criticism for the high concentrations used, which might be a valid consideration when we think about HI-VOCs in the context of signalling from one plant to another. However, the targets of HI-VOCs might be located much closer to the wound site than is generally assumed. Green leaf volatiles in particular might serve mainly as local 'damaged-self signals' (see the sections 'Pertinent questions' and 'Conclusions' below). First we need to identify the evolutionarily relevant targets of HI-VOCs before we can decide which concentrations to use in physiological experiments aimed at finding biologically relevant early responses in plants.

Physicochemical properties of VOCs and the specificity of the effects

The HI-VOCs for which resistance-enhancing effects in plants are most commonly being reported comprise (Z)-3-hexenal, (E)-2-hexenal, (Z)-3-hexen-1-ol and (Z)-3-hexenyl acetate (Bate & Rothstein, 1998; Engelberth *et al.*, 2004; Kishimoto *et al.*, 2005; Kost & Heil, 2006; Scala *et al.*, 2013), allo-ocimene (Kishimoto *et al.*, 2005), nonanal (Yi *et al.*, 2009), *cis*-jasnone (Birkett *et al.*, 2000; Blassioli Moraes *et al.*, 2007; Bruce *et al.*, 2008), MeJA and MeSA. The two latter compounds can be converted into the active hormones JA and salicylic acid (SA), which provides an obvious

mechanism for their resistance-enhancing effects in as yet uninfected plants (Shulaev *et al.*, 1997; Park *et al.*, 2007; Wasternack, 2007). However, what do the other compounds have in common? The activity of both (Z)-3-hexenal and (E)-2-hexenal indicates that stereochemistry is not important in this context, and a 'search for the active motif' in VOCs that induce EFN secretion in lima bean revealed no significant differences among (Z)-3-hexenyl acetate, (E)-3-hexenyl acetate, (E)-2-hexenyl acetate, 5-hexenyl acetate, (Z)-3-hexenyl isovalerate and (Z)-3-hexenyl butyrate (Heil *et al.*, 2008). Thus, VOC perception in plants is not as specific as their perception in the olfactory systems of animals and the lack of stereo-specificity excludes odorant-binding proteins as candidates for the as yet unknown VOC receptors in plants. In this context, based on the observation that more lipophilic components had stronger effects (Maffei *et al.*, 2001), it is tempting to speculate that lipophilic compounds might dissolve in the membrane and enhance its permeability to ions such as Ca^{2+} and K^+ , which then could initiate changes in the membrane potentials. This hypothesis is in line with observations that indicate the involvement of an accumulation step in the perception of VOCs: plants that are exposed over longer periods of time, or repeatedly, to low concentrations of VOCs, can exhibit detectable responses that are not observed after shorter (6 h instead of 24 h) or single exposure events (Girón-Calva *et al.*, 2012; Shiojiri *et al.*, 2012). However, a simple physicochemical process does not explain the specificity that ensures differential resistance to herbivores or pathogens, in plants exposed to the respective VOC blends.

In summary, we still lack convincing evidence for the early molecular mechanisms used by plants to perceive VOCs and translate them into specific responses. However, considering the chemical diversity of compounds, it seems likely that more than one general piece of 'VOC-perception machinery' exists: chemically diverse volatile components are likely to interact with plant metabolism via an array of mechanisms (that are perhaps equally diverse).

Stability of HI-VOCs in the atmosphere

Plant–plant signalling has been shown to enhance the resistance of the receivers in the field at distances ranging from 60 cm to 1 m for sagebrush, lima bean and alder (Dolch & Tschardt, 2000; Karban *et al.*, 2006; Heil & Adame-Álvarez, 2010), although one study has reported stable recruitment of braconid wasps to phenylethyl alcohol from up to 8 m in experimental fields of soybean (*Glycine max*) (Braasch & Kaplan, 2012). In this context, the question arises: how long do VOCs remain stable in the atmosphere? Ozone at elevated concentrations can impair plant–plant signalling, likely due to the oxidation of the active compounds (Blande *et al.*, 2010). Even exposure to natural ozone levels and UV radiation is likely to reduce the half-life of HI-VOCs in the atmosphere. 'Where do herbivore-induced plant volatiles go?' (Holopainen & Blande, 2013). We are still a long way from being able to answer this question. Indeed, the reduced stability of HI-VOCs in natural versus laboratory setups might be a crucial issue when we want to estimate their true relevance in natural ecosystems or use HI-VOCs as reliable cues for beneficial arthropods in biocontrol programs.

HI-VOCs as promising tools in biocontrol?

HI-VOCs appear to be a promising tool for biocontrol (Kaplan, 2012a) and several authors have attempted to transform plants to enhance their potential to emit HI-VOCs (Brillada *et al.*, 2013). However, the only system in which plant odours are consciously and successfully being used for biocontrol in agriculture appears to be the push–pull system (Khan *et al.*, 1997; Hassanali *et al.*, 2008). Of course, we cannot exclude the possibility that many other successful intercropping schemes make use of this or similar effects. However, to date, the numerous studies on the orientation of parasitoids towards HI-VOCs (inset in Fig. 1) have apparently not been converted into a successful application of this effect in agriculture.

A major limiting factor might be that top–down control has not been favoured by plant breeding, which frequently might have impaired the beneficial interactions of crops with the third trophic level. For example, commercial cultivars of cotton (*Gossypium hirsutum*) release seven times lower overall quantities HI-VOCs than a naturalized line (Loughrin *et al.*, 1995) and North American cultivars of maize do not emit the nematode attractant (E)- β -caryophyllene from their roots (Rasmann *et al.*, 2005). It is unlikely that HI-VOCs have been consciously counterselected in plant breeding and, indeed, the quantities of emitted VOCs have not been reduced in certain *Brassica* and *Phaseolus* cultivars (Benrey *et al.*, 1998) or in the aboveground-parts of several maize lines (Gouinguéné *et al.*, 2001). However, it appears likely that many crops suffer from reduced capacities to attract and maintain beneficial arthropods.

Most importantly, however, the topic remains severely understudied. 'I would strongly argue that an incredibly few number of field studies have attempted using volatiles in biocontrol', says Ian Kaplan from Purdue University (Lafayette, IN, USA). Agronomic ecosystems are more complex than laboratory setups (Kaplan, 2012a) and to protect crops successfully from pests more needs to be done than just attracting beneficial insects in an olfactometer. Which ones are the problems that were encountered most frequently when people aimed at applying HI-VOCs in an agronomic context? First, an enhanced attraction of parasitoids to HI-VOCs did not enhance parasitism rates of herbivores in the field (von Mery *et al.*, 2012; Vieira *et al.*, 2013). Second, parasitized herbivores occasionally grow larger and consume more than unparasitized ones (Alleyne & Beckage, 1997; Harvey *et al.*, 2010). Third, HI-VOCs represent information that is 'publicly available' and can also be used by herbivores and hyperparasitoids (see the section 'Effects of HI-VOCs on other organisms' above). Maize plants that were treated with green-leaf volatiles for resistance induction appeared more heavily infested by *Diabrotica* beetles and *Spodoptera frugiperda* larvae and, consequently, were more damaged than the nonexposed control plants (Mérey *et al.*, 2011). Indeed, a quick literature survey of studies that have been published since 2009 revealed more reports on the attraction of herbivores to HI-VOCs than on their repellence (inset in Fig. 1). Likewise, the attraction of hyperparasitoids might strongly reduce the putative protective effects of HI-VOC emission (Kaplan, 2012b). Fourth, HI-VOCs represent mere information but no resource *per se*, and

parasitoids and predators will quickly learn or adapt to avoid plants that emit HI-VOCs without carrying herbivores. Fifth, agronomic ecosystems simply might not sustain the populations of beneficial arthropods that would be required for the stable biocontrol of pests. Finally, strategies using the top-down control of pests will suffer from severe problems of acceptance as long as breeders and agronomic companies aim at 100% avoidance of infestation: these more natural strategies usually do not completely eliminate the enemies from the system.

In order to develop an effective biocontrol strategy we should widen our perspective and include reward-based defensive traits such as EFN and leaf domatia, which can significantly contribute to indirect defence via tritrophic interactions (Simpson *et al.*, 2011; Orre-Gordon *et al.*, 2013). We should also think more about the direct effects of HI-VOCs on pests and pathogens, rather than focusing completely on indirect effects. Indeed, repellence has been an important component in cases where HI-VOCs have been successfully used in agricultural setups (Hassanali *et al.*, 2008; Braasch & Kaplan, 2012; Xiao *et al.*, 2012) and the anti-microbial properties of HI-VOCs certainly require more attention. Wild plants do not rely on one isolated defence strategy and biocontrol should follow their example. Planting field margins with EFN-bearing species might be a promising avenue (Olson & Wäckers, 2007; Géneau *et al.*, 2012). Similarly, the active release of beneficial arthropods in combination with planting EFN-producing species could create interesting possibilities. In this scenario, EFN would keep the biocontrol agents at stable population levels within the agricultural field even during pest-free periods, and HI-VOCs would guide them to the plants that currently are under attack.

Research imbalances: reasons and problems

The number of reports relating to the different receivers of HI-VOCs (see inset in Fig. 1) shows that the dominance of a phenomenon in the literature does not necessarily indicate its relevance for the affected organisms, let alone for natural communities. Science is a social effort and group dynamics are strong. The number of studies on different topics related to HI-VOCs, therefore, can be explained to a large part by historical effects (follow-up studies tend to use the same models and/or questions as found in the first reports), the productivity of certain groups of researchers, and the general group-sociological effect in science that considers topics and models to be important when many people are already working on them. In our specific case, for example, only one report exists on the reduced presence of herbivores on wild plants in nature due the attraction of a predator (Kessler & Baldwin, 2001) and, to the best of my knowledge, no study has demonstrated that the attraction of parasitoids has had a fitness-enhancing effect on plants in any natural ecosystem. As far as I am aware, there is also no study on the relevance of the capacity to respond to HI-VOCs for the fitness of a parasitoid in nature. Nevertheless, reports on the effects of HI-VOCs on parasitoids dominate the literature and the few studies that deal with predators focus on mites and nematodes. By contrast, studies on predatory beetles are scarce, even though beetles are the

most diverse group of insects, and very few reports exist on the response of birds to HI-VOCs (Mäntylä *et al.*, 2008, 2014; Amo *et al.*, 2013). Birds can enhance the growth of trees in nature due to their insectivorous activity (Mooney & Linhart, 2006) and, thus, are likely to exert a strong predation pressure on herbivores. A more neutral and, perhaps, scientifically more relevant way would be to evaluate the quantitative importance of the different effects in the environment of interest (the wild for ecologists and the agronomic field for applied scientists) and then to focus research efforts on those phenomena that are most relevant for the survival and fitness of the interacting organisms.

Pertinent questions

The evolutionary origin of HI-VOCs and the ecological relevance of plant–plant signalling for the emitter were the most controversial topics discussed at the 32nd *New Phytologist* Symposium. Did HI-VOCs originally evolve as ‘cry for help’ in the tritrophic context or, rather, as external ‘within-plant signals’? ‘Perhaps, the plant can simply not avoid producing them’, says Marcel Dicke from Wageningen University (the Netherlands), and in this respect agrees with earlier scepticism concerning a ‘primarily ecological’ function of plant volatiles (Peñuelas & Llusiá, 2004). If the production of HI-VOCs in damaged tissues was really unavoidable, they could function as ‘damaged-self signals’ (Heil, 2009): molecules that inevitably are produced in disrupted tissues and that serve as reliable indicators of the wounding. In this scenario, all receivers, including the emitting plant itself, would have evolved secondarily to make their own use of this information. For the locally damaged organ, HI-VOCs would indicate the necessity to seal a wound and to locally induce resistance to infection. For the distant parts of the same plant and for neighbouring plants, the same cues would indicate the presence of a potentially harmful agent. For herbivores, HI-VOCs would enable host plants to be located and enable the herbivore to make a judgement regarding the defensive status of the plants, whereas carnivores would interpret HI-VOCs as indicators of the presence of prey.

Some people working in this research field (including myself) feel that the primary role of HI-VOCs must lie in the emitting plant itself (perhaps as danger signals), whereas others argue that the beneficial effects on the defensive status of the neighbours can feed back to the emitter when local populations of herbivores or pathogens decrease, owing to the joint resistance efforts of multiple plants. However, the functioning of this effect depends on the degree to which these enemies are shared among the communicating plants. Although the observation that signalling is strongest among genetically related – or identical – plants (Karban *et al.*, 2013) supports this idea, the reports on enhanced lethality of seedlings close to mother plants (Hersh *et al.*, 2012; Liu *et al.*, 2012; for an overview see García-Guzmán & Heil, 2014) show that signalling among kin is not strong enough to avoid ‘Janzen–Connell’ effects. Turlings remarked that ‘The notion that plants communicate with their neighbours gains in popularity, but eventually most of us will realize that the emitters are releasing the compounds for other reasons (e.g. within-plant signalling or

interactions with micro-organisms), and that the receivers are eavesdropping on these interactions’.

Although these topics were controversial, there was a broad agreement on the most pertinent open questions.

(1) We are far from having reliable quantitative information on the selective relevance of the multiple volatile-mediated interactions for each of the affected species. ‘The most pertinent open questions lie in the ecological significance of the laboratory observations that we make’, commented Blande, and Karban asks ‘whether this (plant–plant) communication has important consequences for plant fitness under natural conditions’. Indeed, this question applies to all interacting organisms: local and systemic tissues of the emitter, plant neighbours, parasitoids, predators and herbivores.

(2) We are still searching for the ‘nose’ of plants. Membrane depolarization and epigenetic effects are likely to form important parts of the signalling cascade. Unfortunately, it has not been possible to connect membrane depolarization directly to downstream genetic or epigenetic mechanisms so far. ‘Although we could successfully open the first door for the underlying mechanisms, there are still many questions left over’, remarked Gen-Ishiro Arimura (Kyoto University, Japan). Concordantly, Turlings identified ‘the chemical and molecular mechanisms by which plant volatiles are produced, released and perceived’ as one of the ‘four hot topics at the Buenos Aires workshop’, and Junji Takabayashi (Kyoto University, Japan) agrees that ‘odour receiving mechanisms is a big question for me’.

(3) The concentrations of HI-VOCs remain unknown. Surprisingly, this statement applies to all layers: from the concentrations in the VOC-producing plant tissues to those that are reached in the headspace at different distances to the plants. Without knowing these concentrations, no biologically meaningful experiments will be possible. Of course, this problem is further complicated by the as-yet unknown stability of VOCs under different environmental conditions.

(4) Finally, many people feel that HI-VOCs and other indirect defence mechanisms have an as yet unexplored potential in sustainable agriculture. The lack of application is rather due to a lack of knowledge than to the general lack of suitability of these mechanisms. According to Blande, ‘one part of the future strategy surely has to lie in developing many more novel applications related to clean and sustainable crop production’. Similarly, Turlings and Takabayashi agreed that an application of HI-VOCs must be a central goal in the future research efforts. ‘Scepticism about the potential of using volatiles in crop protection prevails, but the African push–pull example wonderfully shows that it can work’ adds Turlings.

Conclusions

Perhaps, the circle (Fig. 2) is about to be closed. The first receivers of HI-VOCs discovered historically were plants, and, personally, I feel that we are about to discover that the main – and perhaps evolutionarily dominating – target of HI-VOCs is the emitting plant itself. Small volatile plant molecules play multiple roles as direct resistance agents in and around the wound site, and they serve

as signals to prepare distant parts of the same plant for upcoming damage. Further studies should investigate whether the main targets of HI-VOCs are other leaves, or branches, as has been speculated earlier, or rather tissues around the wound site. In this scenario, the concentrations of the VOCs applied by Massimo Maffei’s group (Zebelo *et al.*, 2012) would perhaps be too low, rather than too high, and HI-VOCs would first have evolved as ‘damaged-self signals’. In this scenario, plants would necessarily have the molecular machinery to perceive the chemically highly diverse group of molecules that we term ‘HI-VOCs’ and, thus, would inevitably be able to make use of relevant VOCs that come from their neighbour. Animals would have evolved secondarily to make use of these cues for their own benefits, with positive, neutral or negative effects on the emitting plant. This scenario does not mean that other and more indirect effects do not play highly important roles in the biology of all interacting organisms. We still need to find out the relative quantitative contribution of each volatile-mediated process to the fitness of each of the interacting organisms, as well as search for the VOC-perception machinery. Finally, we should try to find out what went wrong in those few agronomic ecosystems where HI-VOCs have been tested and did not appear to work as expected. Have we overestimated the role of HI-VOCs in the natural ecosystems, do agro-ecosystems lack an element that is essential for the function of volatile-mediated resistance, or have we simply not yet found the best way to make use of HI-VOCs? The low abundance and biodiversity of beneficial arthropods represents an obvious explanation in this context, but we should also think about the possibility that breeding might have deprived our crops of traits that are required for functioning tritrophic defence strategies.

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