

# The Role of Herbivore-induced Plant Volatiles in Trophic Interactions: The Swiss Connection

Ted C. J. Turlings\* and Thomas Degen

**Abstract:** It is increasingly evident that plants actively respond to the threats and challenges that they come to face while growing. This is particularly manifested in the dynamic responses to insect herbivory, especially in terms of the volatile compounds that the attacked plants emit. Indeed, many plants respond to insect-inflicted damage with the synthesis and release of volatile organic compounds. These emissions, commonly referred to as herbivore-induced plant volatiles (HIPVs), play important roles in the interactions between the emitting plants and their biotic environment. The odorous signal can be picked up and exploited by various organisms: neighbouring plants, herbivores and their natural enemies, such as predators and parasitoid wasps. Coincidence or not, scientists currently working in Switzerland have made numerous key contributions to the work in this field. By highlighting their work, we attempt to give a somewhat historic overview of this field of research.

**Keywords:** Plant defence · Plant–insect interactions · Plant signalling · Plant volatiles



**Ted Turlings** is originally from The Netherlands where he studied at Leiden University. He did his PhD at the University of Florida under the direction of the late James Tumlinson, and it was during this time that he discovered the ecological importance of herbivore-induced plant volatiles. After a brief post-doctoral period in Florida, he moved to Switzerland in 1993. He first spent three years at the ETHZ and in 1996 he

obtained a START-fellowship, which he took to the University of Neuchâtel to start his own research group. Eventually the university appointed him full professor. He is directing the laboratory of Fundamental and Applied Research in Chemical Ecology (FARCE).



**Thomas Degen** graduated in biology at the University of Basel. After his PhD thesis carried out at the Swiss Federal Agricultural Research Station Wädenswil (now Agroscope), he joined Ted Turlings' team at UniNE as a postdoctoral researcher to study the variability of herbivore-induced volatile emissions in maize. Ever since, he has been a scientific collaborator in the FARCE lab.

## 1. Introduction – A Key Discovery

Plants rely on a range of physical and chemical means to protect themselves against herbivores and pathogens, whereby secondary metabolites play a particularly important role. A vast arsenal of non-volatile and volatile compounds can interfere with the physiology and the behaviour of the attackers in a way that is detrimental to their proliferation. While the non-volatile metabolites act only upon contact, the odorous signals can be perceived at a distance by many other organisms belonging to different trophic levels, which may exploit them to their benefits, *e.g.* by using them as cues for host location. Healthy plants may release some volatiles in a constitutive way, but in response to being infested by herbivores they can change emissions dramatically both in terms of

quality and quantity. These herbivore-induced volatiles (HIPVs) serve as signals in a wide range of ecological interactions among organisms belonging to different trophic levels, an overview of which is given in Fig. 2. Each section of this review will deal with a specific type of interaction, highlighting the contributions of researchers active at Swiss institutions. A list of abbreviations for these research institutions is given at the end of this article.

Key to all of the subsequent work was the discovery of the role of methyl jasmonate in plant-mediated interactions (Fig. 1).<sup>[1]</sup> This revelation came from a study by Edward (Ted) Farmer (now at UNIL) during his post-doc with the late Clarence 'Bud' Ryan, a pioneer in the field of plant signalling, at Washington State University. They were the first to demonstrate that jasmonates control the induction of wound-response defence proteins. In the case of tomato plants this leads to the expression of genes for proteinase inhibitors that deter insect feeding.<sup>[2]</sup> One of the first

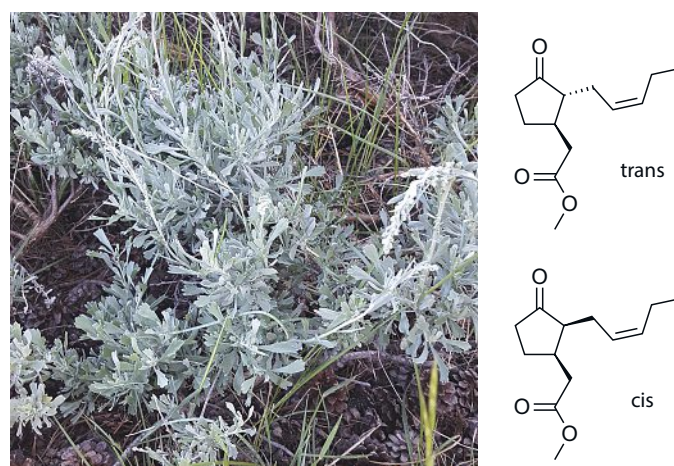


Fig. 1. Sagebrush *Artemisia tridentata*, a shrub growing in arid regions of Western North America, constitutively releases two epimers of methyl jasmonate, but emissions increase when the plant is damaged by herbivores. Perception of methyl jasmonate triggers a cascade of defence responses in many plants (Photo credit: Patrick Grof-Tisza).

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steps towards this discovery was a series of experiments conducted by Farmer to test the hypothesis that methyl jasmonate, a lipid-derived volatile molecule, might serve as an airborne signal. Indeed, spraying tomato plants with a solution containing methyl jasmonate strongly induced proteinase inhibitor synthesis and accumulation.<sup>[1]</sup> To substantiate this key finding, he incubated sagebrush branches (depicted in Fig. 1), which produce exceptionally large amounts of methyl jasmonate, with a tomato plant and indeed observed a substantial increase in levels of defensive proteinase inhibitors in the tomato plants.

This incredibly important discovery set the stage of much of the research on plant–plant interactions involving volatile signaling. For instance, numerous ecological as well as molecular studies involve the spraying of plants with methyl jasmonate in order to induce plant defence responses,<sup>[3]</sup> including studies by Swiss teams.<sup>[4]</sup> In 1992, Farmer moved to the University of Lausanne where he continued to unravel and teach the intricacies of inducible plant defences. Recent highlights are his book entitled *Leaf Defence*,<sup>[5]</sup> and the discovery that electrical signals play a role in systemic plant defence responses.<sup>[6]</sup>

## 2. Tritrophic Interactions

A next key discovery was the role of inducible plant volatiles in tritrophic interactions.<sup>[7]</sup> While the plant's own direct defences are important to regulate herbivore populations, often referred to as from the 'bottom up', organisms belonging to the third trophic level such as predators and parasitoids contribute to control herbivores in a 'top down' manner. Price *et al.*<sup>[8]</sup> had hypothesized that plants may interfere with the interactions between insect herbivores and natural enemies to their own evolutionary benefit, *e.g.* by facilitating prey/host location.

### 2.1 Herbivory

In the late eighties, two Dutch PhD students independently and almost at the same time found convincing evidence in support of the Price *et al.*<sup>[8]</sup> hypothesis with two different tritrophic systems. Marcel Dicke at the University of Wageningen, the Netherlands, demonstrated that spider mites feeding on bean leaves induce the release of plant volatiles that are attractive to predatory mites.<sup>[7a]</sup> Working in the group of Jim Tumlinson at Florida State University in Gainesville, USA, Ted Turlings (now at UniNE) observed that maize plants infested by beet armyworm *Spodoptera exigua* emit HIPVs that are exploited by the parasitoid wasp *Cotesia marginiventris* for host location.<sup>[7b]</sup> These discoveries inspired a lot of research that reported similar findings with various tritrophic systems, suggesting that the phenomenon is widespread in nature.

HIPV emissions are variable both temporally and spatially depending on the type of compounds involved. Some plant volatiles are released immediately as a direct consequence of the mechanical damage locally inflicted to the plant by the herbivores. In most cases this involves the so-called green leaf volatiles (GLV), aldehydes, alcohols and esters of 6-carbon compounds derived from the oxylipin pathway and ubiquitously occurring among green plants (Fig. 2). In contrast, other compounds are systemically released throughout the plant with a delay, for example indole and terpenoids (Fig. 2), which are *de novo* synthesized and liberated by maize plants a few hours after they have been exposed to leaf-eating caterpillars.<sup>[9]</sup> It was found that mere mechanical damage is not sufficient to trigger the intense odour emission, but that it requires the perception of an elicitor in the oral secretion of the caterpillars.<sup>[7b]</sup>

### 2.2 Elicitors

Since the first indication of their involvement in the induction of HIPVs,<sup>[7b,10]</sup> various insect-derived elicitors have been identified. One of the first was isolated from the oral secretions of beet armyworm caterpillars and was identified as

*N*-(17-hydroxylinolenoyl)-L-glutamine and named volicitin (Fig. 2).<sup>[11]</sup> The search for other such elicitors revealed that they can be specific of plant and insect species. Tobacco plants too respond to volicitin and similar fatty acid-amino acid conjugates.<sup>[12]</sup> The oral secretions of grasshoppers have been found to contain disulfoxy fatty acids, named caeliferins, that also trigger HIPVs in maize plants.<sup>[13]</sup> Yet, bean plants, for instance, respond to an entirely different caterpillar-derived elicitor, a peptide resulting from proteolysis of the chloroplastic ATP synthase of the plant on which the caterpillars feed.<sup>[14]</sup> For this latter elicitor a receptor was recently identified in cowpea plants<sup>[15]</sup> with a modest but important contribution by the NPAC under the guidance of Gaetan Glauser (UniNE). Elicitors of plant defence responses do not only derive from the feeding stages of herbivores, as we will see next.

### 2.3 Insect Eggs

Plants not only react to being fed upon by herbivores, but can also perceive signals that are way more subtle: specific chemicals associated with eggs deposited by herbivorous insects can also induce or otherwise affect defence responses, including the release of HIPVs.<sup>[16]</sup> This is a topic that has been extensively studied by the group of Philippe Reymond (UNIL).<sup>[17]</sup> In most of the studied cases, scientists report that eggs prime or induce defence responses in plants.<sup>[16b]</sup> Interestingly, Reymond and co-workers found that eggs of the specialist butterfly *Pieris brassicae* may suppress defences in brassicaceous plants targeted against insect herbivores. Instead the eggs trigger changes that are similar to those caused by fungal and bacterial pathogens, thereby possibly benefitting caterpillar development.<sup>[18]</sup> They observed that in response to *Pieris* eggs, *Arabidopsis thaliana* upregulates the salicylic acid pathway and that this triggers systemic acquired resistance (SAR) against pathogens.<sup>[18]</sup> Yet, egg-associated compounds also cause localized cell death, resulting in necrotic leaf tissue, causing eggs to die because of detachment and/or desiccation.<sup>[19]</sup> A multi-team effort that also involved the group of Jean-Luc Wolfender (UNIGE) resulted in the identification of phosphatidylcholines as the key egg-associated elicitors that induce the observed responses in *Arabidopsis*.<sup>[20]</sup> Recently, the Reymond group showed that egg-induced belowground signals can be transmitted to neighbouring plants, even causing SAR in the neighbours,<sup>[21]</sup> another amazing example of plant-plant signalling.

## 3. The Various Functions of HIPVs

### 3.1 Indirect Defence

The discovery that HIPVs are exploited by parasitoids and predators of herbivores to locate their victims (Fig. 3)<sup>[7]</sup> prompted the suggestion that plants purposely emit these volatiles as a 'call for help'.<sup>[22]</sup> This topic, among others, has been addressed extensively by Consuelo De Moraes and Mark Mescher (ETHZ), two major contributors to the field of plant volatiles and their ecological importance. They joined the Swiss scene in 2014 when they created the Biocommunication group at the ETHZ. Before coming to Switzerland, they already made several ground-breaking discoveries with their studies at the USDA labs in Tifton (Georgia, USA) and Gainesville (Florida, USA), as well during their professorships at Penn State University. In high-profile publications, also under guidance of the late Jim Tumlinson, they first showed that HIPVs can be specific depending on the attacking herbivore and that a specialized parasitoid can recognize the HIPV bouquet induced by its specific host.<sup>[23]</sup> The De Moraes and Mescher team further made the unique discovery that parasitic plants may also exploit plant volatiles. They found that the growing sprouts of *Cuscuta pentagona* orient themselves in the direction of typical plant-released terpenes in their 'search' for suitable host plants.<sup>[24]</sup> In the same study they also showed that *Cuscuta* sprouts were repelled by (Z)-3-hexenyl acetate, a typical HIPV, suggesting that

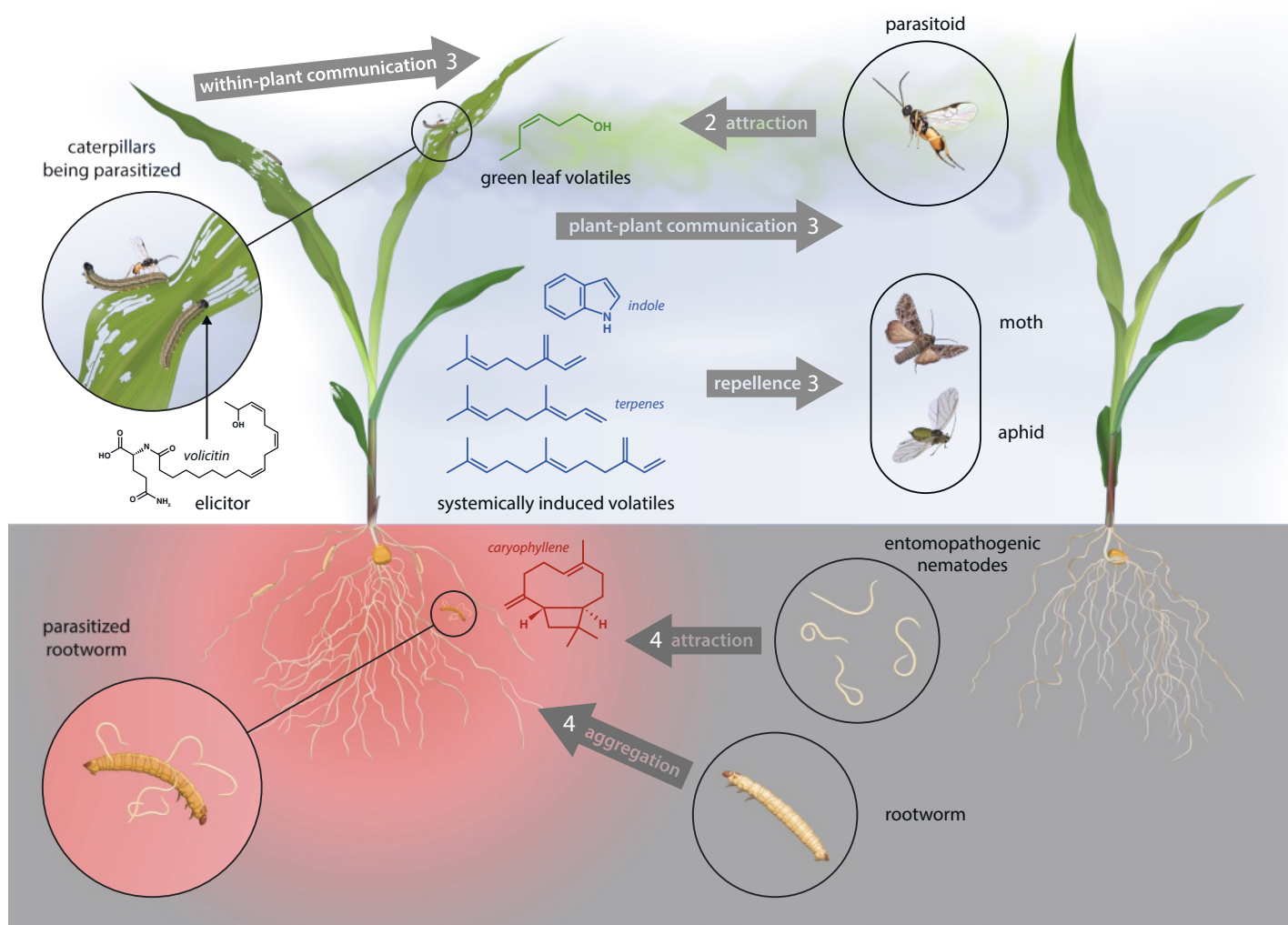


Fig. 2. Overview of the interactions among organisms from different trophic levels mediated by herbivore-induced plant volatiles. This example highlights the tritrophic interactions involving maize, associated herbivores and natural enemies from the third trophic level. The number in the arrows indicates the section in the text that deals with the respective topic.

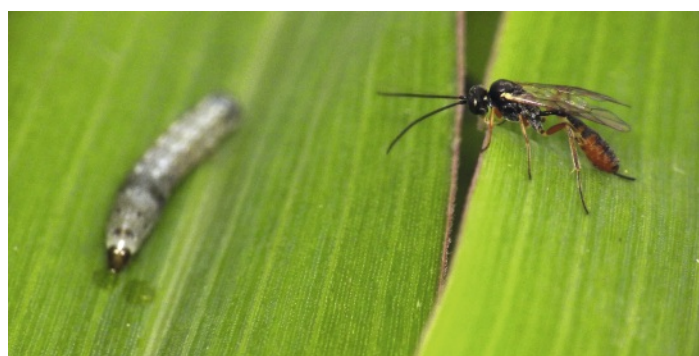


Fig. 3. A female parasitoid wasp *Campoletis sonorensis* eyeing its prospective victim, a *Spodoptera littoralis* caterpillar about to be parasitized. The wasps use HIPVs to locate plants infested with potential hosts (Photo credit: Matthias Held).

the parasite avoids insect-infested host plants. At the ETHZ the team continues to make major discoveries on the sophisticated strategies that insects and plants employ in their continuous arms race.<sup>[25]</sup>

A relative newcomer to the Swiss scene is Meredith Schuman (UZH), who comes from the renowned Ian Baldwin team in Jena. She is also interested in the defensive role of plant volatiles and has studied the specific mechanisms and ecological consequences of inducible volatile emissions in wild tobacco plants, and in

general has contributed to a better understanding of plant responses to herbivores.<sup>[i.e.26]</sup> Of particular interest is her demonstration that two different enantiomers of a common HIPV, linalool, released by wild tobacco plants may have opposite effects on oviposition preferences of a specialist moth.<sup>[27]</sup> Most notable, in a two-year field study in Utah, using knock-down versus wildtype plants, she demonstrated that the attraction to HIPVs of tiny predatory bugs can enhance plant fitness.<sup>[28]</sup> This key finding is one of very few, or possibly the only, true demonstration(s) of a fitness enhancing indirect defence function of HIPVs. Other ‘Swiss’ evidence comes from a cage study in which teosinte, the wild ancestor of maize, survived caterpillar attacks much better in the presence of parasitic wasps than in their absence.<sup>[29]</sup> An additional collaborative Swiss-Dutch-Chinese study on the defensive function of HIPVs provides evidence that HIPVs are indeed favoured by natural selection when natural enemies of herbivores contribute to the selection pressures and can diminish the negative impact of key herbivores on plants. This evidence comes from the evolutionary history of an invasive plant, common ragwort. This toxic weed was found to release considerably less HIPVs in its invasive range (North America, New Zealand and Australia), where it has no major pressures of insect herbivores, than in its native range (Europe) where a specialist caterpillar induces HIPVs emissions that attract its parasitoids.<sup>[30]</sup> Interestingly, the opposite was found for constitutively emitted volatiles, which were released in larger quantities by the invasive plants, possibly because they do not attract specialist herbivores and can repel non-specialist herbivores.



### 3.2 Plant–Plant Signalling

In the context of the above-mentioned phenomenon of volatile-mediated plant–plant signalling that was first revealed by Farmer (UNIL),<sup>[1]</sup> various advances were made in Switzerland using maize as a model. This research was prompted by the first demonstration of defence priming in maize plants after exposure to HIPVs.<sup>[31]</sup> As opposed to true defence induction, whereby plants immediately express enhanced defence traits, primed plants only show enhanced defences by responding faster and stronger when they are attacked themselves. Jurriaan Ton (at the time at UniNE) conducted experiments that demonstrated the biological significance of priming of maize. He confirmed that after exposure to caterpillar-induced maize plant volatiles, conspecific plants would launch a faster and stronger defence response when they themselves were attacked by caterpillars. This enhanced responsiveness was both in terms of direct defence (proteinase inhibitor production) and indirect defence (HIPV emissions). He could show that this resulted in poorer development of caterpillars and increased attractiveness to parasitoids.<sup>[32]</sup> Detailed studies led by Matthias Erb (first at UniNE, now at UniBE) have revealed that indole plays a key role in within and between plant signalling in maize<sup>[33]</sup> and rice.<sup>[34]</sup> It was also found that indole can have direct negative effects on herbivores. Below we highlight the effects of indole to demonstrate that HIPVs may indeed also function as a direct defence.

### 3.3 Direct Defence

The repellent effect of HIPVs on herbivores may already be considered a direct effect that benefits plants. For example, it was demonstrated that HIPV emitted by maize plants are repellent to female moths seeking plants on which to deposit their eggs<sup>[35]</sup> and to aphids.<sup>[36]</sup> Various of the specific volatiles in the HIPV blends are also known to have toxic effects, including GLVs and terpenes and derived products.<sup>[5,37]</sup> A particularly common and highly bioactive HIPV is indole, an aromatic heterocyclic volatile compound (Fig. 2).<sup>[38]</sup> The work by Matthias Erb (UniBE) not only revealed that indole is an important plant–plant signal,<sup>[33]</sup> but also revealed that it has detrimental effects on exposed caterpillars.<sup>[39]</sup> Surprisingly, exposure to indole makes caterpillars eat less but grow bigger, yet survive poorly.<sup>[39a]</sup> One apparent mechanism is the effect of indole on the microflora of the caterpillars, which makes the caterpillars become more vulnerable to entomopathogens.<sup>[39c]</sup> Intriguingly, exposure to indole also makes the caterpillars smell differently and thereby less appealing to parasitoids, which makes sense because the parasitoids perform better if they develop in unexposed caterpillars.<sup>[39b]</sup> The outcomes of these detailed studies illustrate how complex the multiple physiological and ecological effects of HIPVs can be and suggest that many such effects remain to be discovered. This will not only be the case for interactions aboveground, as HIPVs can also mediate interactions in the rhizosphere.

### 4. Belowground Signalling

At the University of Neuchâtel, Sergio Rasmann (UniNE), as a PhD student, and Ivan Hiltbold (Agroscope), as a master's student, working together, made the discovery that roots, similar to leaves, also respond to herbivore attack by synthesizing and releasing volatiles that can attract natural enemies. They found that maize roots when damaged by rootworms emit relatively large quantities of (*E*)- $\beta$ -caryophyllene into the soil, and that this common sesquiterpene is attractive to entomopathogenic nematodes (EPN).<sup>[40]</sup> These tiny insect-killing roundworms (Fig. 4) have great potential as biological control agents against root pests,<sup>[41]</sup> and in the case of maize plants, as recently shown, can also readily be applied to leaf pests.<sup>[42]</sup>

Interestingly, most American maize varieties have lost the ability to release (*E*)- $\beta$ -caryophyllene,<sup>[40]</sup> also from their leaves when attacked by caterpillars.<sup>[43]</sup> This greatly reduces the

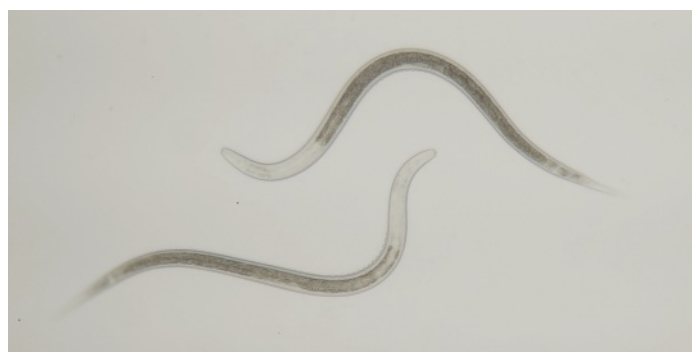


Fig. 4. Two entomopathogenic nematodes (EPN). These tiny insect-killing worms find their victims in the soil with the help of HIPVs emitted by roots (Photo credit: Neil Vilard).

attractiveness of their roots to EPN. For his PhD project, Ivan Hiltbold (Agroscope), in collaboration with the Max Planck Institute for Chemical Ecology in Jena, Germany, used a transgenic approach to restore the release of (*E*)- $\beta$ -caryophyllene in an American variety.<sup>[44]</sup> This resulted in enhanced attraction of EPN, which provided better protection against rootworm damage. This proof-of-concept study showed, for the first time, the potential of manipulating plant volatile signals to improve biological pest control.

Our hope that rootworm control could be improved by enhancing (*E*)- $\beta$ -caryophyllene release was soon negated by a detailed study on the foraging behaviour of rootworm larvae by Christelle Robert as part of her PhD project at UniNE. She showed that the western corn rootworm uses plant-produced (*E*)- $\beta$ -caryophyllene to aggregate on maize root systems, on which they perform better when feeding together, up to a limit.<sup>[45]</sup> Christelle is continuing her exciting work on belowground interactions as a professor at UniBE in the context of climate change.<sup>[46]</sup>

### 5. Interference, Manipulation and Cooperation

As with any form of communication, signalling through HIPVs can be disrupted and lead to communication breakdown. This can be expected when new herbivores enter a particular ecosystem and trigger novel, locally unknown signals, something that should occur more and more frequently with climate change as postulated in a synthesis paper.<sup>[47]</sup> The potential of such disruptive effects on HIPVs and parasitoid attraction were demonstrated in a series of laboratory assays.<sup>[48]</sup>

The attractive effects of HIPVs can also be affected when plants in addition release volatiles that serve another purpose, such as the attraction of pollinators. In a collaboration of the FARCE lab (UniNE) with Florian Schiestl (UZH), a prominent researcher in the field of pollination ecology, it was found that flower volatiles may interfere with the attractiveness of HIPVs to parasitoids, and shown how plant phenology and the simultaneous release of flower volatiles in addition to HIPVs affects the responses of parasitoids.<sup>[49]</sup>

That herbivores themselves can exploit the miscommunication and interference effects of HIPVs was demonstrated by Chinese research teams collaborating with UniNE. One such study involved whiteflies, which are tiny insects that are much more related to aphids than flies. They are masters at circumventing<sup>[50]</sup> and manipulating plant defence responses,<sup>[51]</sup> including HIPVs. These exceedingly important crop pests have been shown to trigger defence responses in plants that mainly target pathogens, not insects.<sup>[52]</sup> Because of that, whitefly-infested plants become resistant to pathogens, but more susceptible to insects, including whiteflies. The ‘mistaken’ plant response is also observed at the level of HIPV emissions, which are also similar to pathogen-induced emissions, but this does not fool specialized whitefly-

attacking parasitoids, which were found to use the unusual HIPV blend for host location.<sup>[52b]</sup> In contrast, plants appear to be deceived by the whiteflies-induced volatiles: when healthy tomato plants are exposed to the volatiles emitted by whitefly-infested tomato plants, this primes their pathogen-specific defences at the cost of insect-specific defences. As a result, the exposed plants become more vulnerable to the next generation of whiteflies.<sup>[53]</sup> This phenomenon maybe an important reason why whiteflies are such successful global pests.

Another particularly intriguing recent example of how HIPVs can be exploited by herbivores comes from studies from another collaborating Chinese research team. They studied two of the most important pests of rice, the brown planthopper and the rice striped stem borer, and showed that they benefit from each other when they infest rice plants simultaneously.<sup>[54]</sup> These benefits are the result of opposing plant defence responses triggered by each herbivore, which also results in unusual HIPV blends that are no longer attractive to the respective parasitoids of the herbivores.<sup>[54]</sup> The adult hoppers and borers have a strong preference to oviposit on rice plants that are already infested by the other herbivore, indicating that their interaction has evolved into a true collaboration.<sup>[54b]</sup>

Understanding the intricacies of the interactions between plants and pests may be of help in the development of novel strategies for sustainable crop protection.<sup>[55]</sup> This is one of several lines of research on HIPVs that can be expected to be focussed on in the near future, as we will discuss next.

## 6. What's next?

Much is now known about the molecular and biochemical steps that lead to the production and release of HIPVs. It is also clear that they play key roles in plant–plant interactions and the foraging behaviour of arthropods at different trophic levels. Yet, evidence that they are of significant ecological importance under realistic natural conditions is still scarce<sup>[55a]</sup> and future research may want to explore this more, especially if there is a wish to exploit HIPVs for crop protection. For belowground signals, specifically the maize-produced sesquiterpene (*E*)- $\beta$ -caryophyllene, it has been shown that its release can be manipulated to enhance the attraction of insect-killing nematodes. For the aboveground attraction of parasitoids, despite various claims to the contrary, it remains largely unknown what volatile compounds are of key importance<sup>[55a,56]</sup> and therefore it remains unclear what compounds would be good candidates for enhanced production. As it is more and more recognized that biological control is a viable and sustainable alternative to the use of pesticides, renewed focus on identifying key attractants for parasitoids and other biological control agents can be of great value.

Another applied use of HIPVs is as signals that can be used to assess the status of plants. This would be particularly useful if the volatiles can be monitored real-time as indicators of pest infestations or pathogen infections. Indeed, HIPV emissions may be specific enough that they can be distinguished among attackers. They are released in significant amounts very early, at the onset of an insect attack,<sup>[9]</sup> and if detected by sensors can alert a farmer long before significant harm has been done by a pest. This will allow a farmer to take specific action and limit the application of pesticides or costly biological control agents only to when and where they are needed. This may be far more sustainable and cost-effective than frequent and blanket application of pest control sprays.

A final aspect of HIPV research that we believe will get a lot of attention still and may have great promise for application concerns the role of elicitors and effectors. Various elicitors have been identified, with volicitin<sup>[11a]</sup> and inceptin<sup>[14]</sup> having received the bulk of the attention. Considering that different plant species may respond to different elicitors and only a few plants have so far been studied, it is likely that numerous other elicitors still need

to be discovered. Their identification will shed further light on the mechanisms of induction and make it easier to manipulate emissions in crops. With the identification of a receptor in bean plants that is involved in the specific perception of inceptin,<sup>[15]</sup> the stage is set to not only identify receptors of elicitors in other plants, but possibly transgenically move such receptors from one plant genotype to another genotype and thereby possibly boosting the defence response and direct and indirect pest resistance in a receiving crop. Swiss research groups have all the competences, resources and incentives to contribute to these new challenges.

## Acknowledgements

We dedicate this review to the renowned chemical ecologist James (Jim) Tumlinson who passed away this year. Much of the work presented here started under his guidance. We like to specifically thank the former FARCE members who have carried the torch and now continue to make exciting contributions to the field of plant-insect interactions, as are the other colleagues in Switzerland with whom we have interacted in an exceptionally pleasant manner over the years. We wrote this paper as part of our project AGRISCENTS, which focuses on HIPVs and their possible exploitation for crop protection. This project is supported by advanced grant 788949 from the European Research Council.

## Abbreviations of the research institutions

ETHZ – Swiss Federal Institute of Technology Zurich  
 NPAC – Neuchâtel Platform of Analytical Chemistry  
 UniBE – University of Bern  
 UNIGE – University of Geneva  
 UNIL – University of Lausanne  
 UniNE – University of Neuchâtel  
 UZH – University of Zurich

Received: September 5, 2022

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