

# Exploiting scents of distress: the prospect of manipulating herbivore-induced plant odours to enhance the control of agricultural pests

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In response to feeding by arthropods, plants actively and systemically emit various volatile substances. It has been proposed that these herbivore-induced volatiles (HIPVs) can be exploited in agricultural pest control because they might repel herbivores and because they serve as attractants for the enemies of the herbivores. Indeed, recent studies with transgenic plants confirm that odour emissions can be manipulated in order to enhance the plants' attractiveness to beneficial arthropods. An additional advantage of manipulating HIPV emissions could be their effects on neighbouring plants, as a rapidly increasing number of studies show that exposure to HIPVs primes plants for augmented defence expression. Targeting the right volatiles for enhanced emission should lead to ecologically and economically sound ways of combating important pests.

## Addresses

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## Introduction

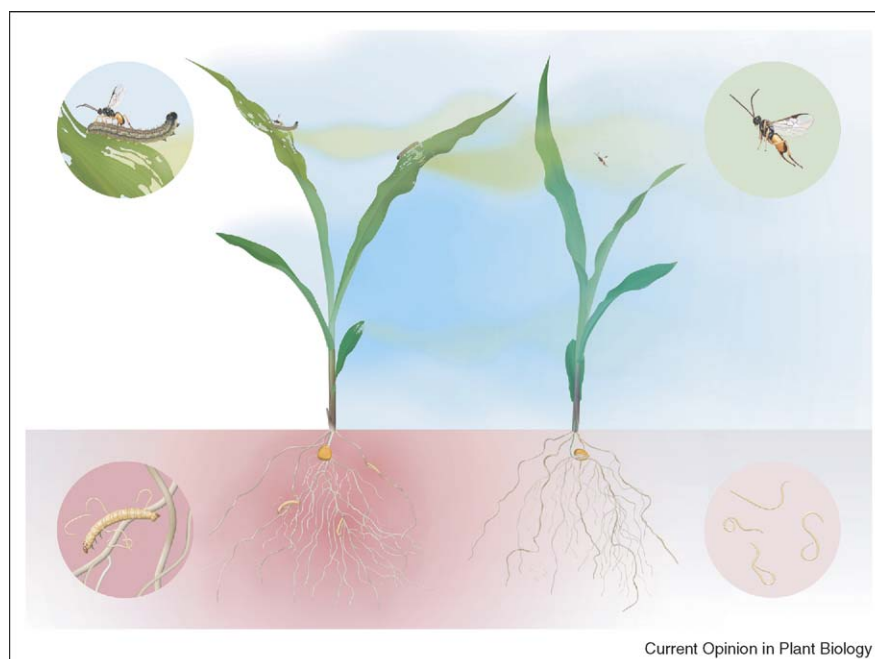
Plant defences against herbivores are not limited to physical and chemical barriers that directly aim to harm their attackers, it is becoming increasingly evident that plants also employ strategies of indirect defence. One form of indirect defence in plants is to attract predators and parasitoids by signalling the presence of potential prey or hosts. This attraction of the third trophic level is one of the presumed functions of herbivore-induced plant volatiles (HIPVs), which are released more or less specifically in response to herbivore attack. The first evidence for tritrophic signalling [1,2] has generated a remarkable interest in this phenomenon from scientists from a broad range of disciplines. This interest has resulted in what can

be considered the most interdisciplinary approach to any aspect of plant–arthropod interactions. A rapidly increasing number of behavioural, chemical and evolutionary ecologists, plant physiologists and crop scientists devote their research efforts to the understanding of the mechanisms, selective pressures and ecological consequences of the interactions. Moreover, there is increased interest in understanding the implications of induced plant signalling in the light of agricultural pest control, as has been outlined in previous reviews [3–5]. Here we focus, after a brief historical account, on the latest developments in this area. In addition, we address the recent studies that point to a priming effect in plants that are exposed to certain HIPVs, conferring an enhanced defensive capacity against future insect attack [6,7–11]. We conclude, with some reservations, that there is not only reason for optimism that manipulation of HIPVs emissions can indeed lead to enhanced repulsion of pests and attraction of their natural enemies but, moreover, that enhanced volatile information transfer between plants might, if exploited appropriately, improve the efficiency of the plant's direct and indirect defence strategies through priming [4,12]. Figures 1 and 2 summarize the various interactions in which HIPVs are implicated as we have studied them for maize plants.

## The role of HIPVs in indirect plant defences

Price and colleagues [13] were the first to specifically address the possibility of an active recruitment of the third trophic level by plants that are under herbivore threat. The first combined chemical and behavioural evidence for the role of HIPVs in such recruitment came from studies on mites, whereby feeding by spider mites was shown to induce the plants to emit volatiles that were attractive to predatory mites [1,14]. Soon afterwards, it was reported that caterpillar-damaged plants release considerable amounts of volatiles that are highly attractive to parasitic wasps [2]. Follow-up work has revealed a remarkable sophistication to the interactions, which were found to involve elicitors in the oral secretions of the herbivores [15–18] that trigger the systemic emission [19] of variable blends of *de novo* synthesized [20] volatiles. The induction of volatile emissions occurs not only in response to herbivore feeding on leaves but can also result from the deposition of insect eggs on plant parts [21] and from feeding by insect larvae on roots [22,23•], again resulting in the attraction of the respective enemies that use the eggs or root feeders as food. In each case, there

Figure 1



Young maize plants, when damaged by caterpillars immediately release several typical octadecanoid-derived 'green leaf volatiles' from the damaged sites (indicated in green). In addition, elicitors in the caterpillar's oral secretions cause the induction of a systemic release of volatiles that mainly comprise terpenoids but also include some phenolics, such as indole and methyl salicylate (indicated in blue). This blend of HIPVs is highly attractive to various parasitic wasps that lay their eggs in the caterpillars [2]. It is still unclear which compounds are the most important for this attraction [49]. Belowground beetle larvae might cause the emission of similar signals by damaged roots [22,23\*\*] (indicated in red). Maize roots release one dominating compound, (E)- $\beta$ -caryophyllene, in response to root feeding. This sesquiterpene was found to be attractive to entomopathogenic nematodes and to increase the effectiveness of these nematodes in finding and killing herbivore larvae [23\*\*]. In addition, the HIPVs might repel other herbivores and can induce or prime defence responses in neighbouring plants. All of these effects might be exploitable for the control of agricultural pests. Drawing by Thomas Degen.

appears to be a clear potential to improve the effectiveness of such natural enemies by enhancing the plants' emission of attractants.

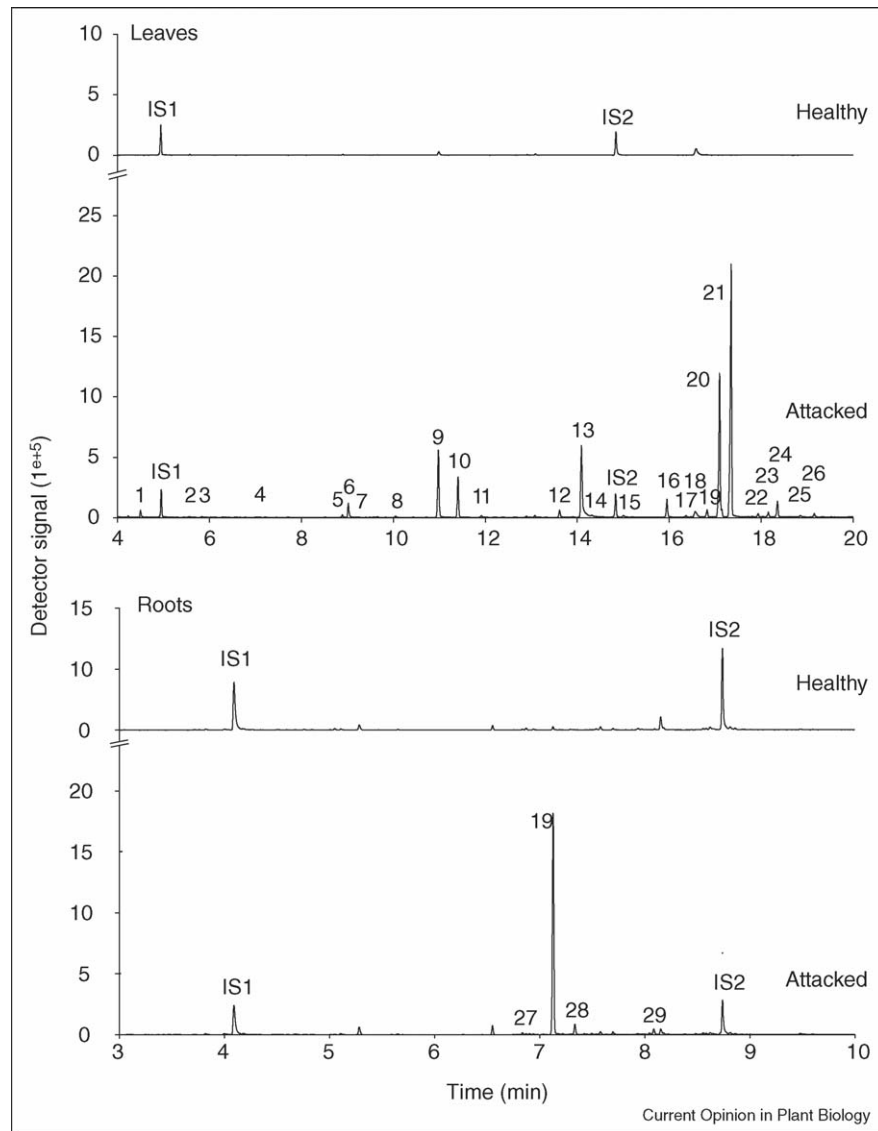
### Priming for enhanced plant defence as an additional benefit

After many years of scepticism, it has finally been fully accepted that plants can perceive and respond to volatiles that are emitted by their neighbours [24\*]. It is clear that, at sufficiently high doses, several substances can immediately mobilize direct and indirect defences in perceiving plants [7,10,25–27]. However, it is likely that, at lower more realistic dosages, the defences are not induced directly but instead the plants are induced to prepare themselves molecularly for future attack. This so-called priming for defence has proven to be an important mechanism behind induced resistance against pathogens [28], and has now also been reported as a likely mechanism behind volatile-induced resistance [6\*,24\*]. Priming through volatiles might also be important in enhancing indirect defences [6\*,7,29].

Priming for defence against pathogens has been shown to involve considerably fewer costs than the induction of

direct defence, and the benefits derived from this priming outweigh the costs under conditions of disease pressure [12]. The phenomenon of volatile-induced priming against insects also fits in this ecological context of costs and benefits. Plants that are merely primed for enhanced defence after the reception of distress signals from nearby plants are better protected in an environment of herbivore pressure, without suffering from costly energy investments in defence mechanisms. Therefore, an additional agronomical benefit can be expected if the emissions of the appropriate volatiles were to be enhanced in crop plants. However, the identity of the volatile(s) that trigger priming is not always clear, and might differ amongst different plant species. In maize, Engelberth *et al.* [6\*] have shown that volatile-induced priming for enhanced jasmonic acid (JA) biosynthesis can be mimicked by exogenous application of the 'green leaf volatiles' (Z)-3-hexanal, (Z)-3-hexen-1-ol, or (Z)-3-hexenyl acetate. Other typical HIPVs from maize do not appear to trigger priming in maize [6\*]. In contrast, Paschold *et al.* [8] found that the volatile blend emitted by *Nicotiana attenuata* plants that are infested with *Manduca sexta* caterpillars fails to prime neighbouring *N. attenuata* plants, even though this blend contains compounds that induce

Figure 2

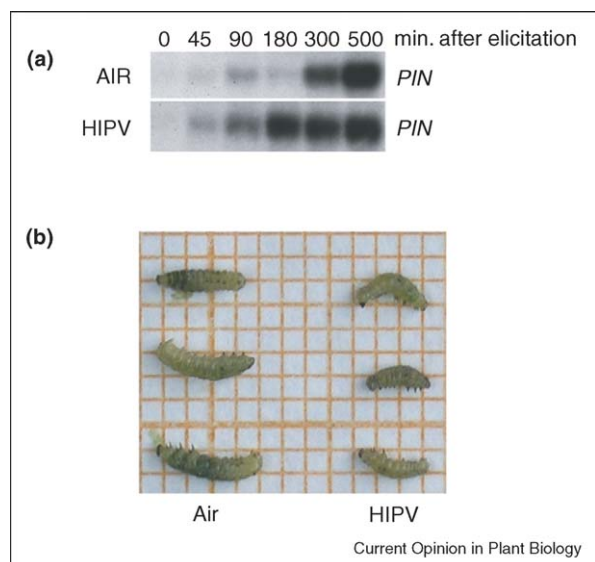


Typical chromatograms of volatiles collected from healthy and herbivore-damaged maize plants. The second chromatogram is from volatiles emitted by maize leaves that have been attacked by caterpillars and the fourth chromatogram is from roots attacked by beetle larvae. The labelled compounds are: 1) (*Z*)-3-hexenal, 2) (*E*)-2-hexenal, 3) (*Z*)-3-hexenol, 4) (*Z*)-2-penten-1-ol acetate<sup>N</sup>, 5)  $\beta$ -myrcene, 6) (*Z*)-3-hexenyl-acetate, 7) (*E*)-2-hexenyl acetate, 8) (*Z*)- $\beta$ -ocimene, 9) linalool, 10) (3*E*)-4,8-dimethyl-1,3,7-nonatriene, 11) benzyl acetate, 12) phenethyl acetate, 13) indole, 14) unknown, 15) methyl anthranilate, 16) geranyl acetate, 17) unknown, 18) unknown, 19) (*E*)- $\beta$ -caryophyllene, 20) (*E*)- $\alpha$ -bergamotene, 21) (*E*)- $\beta$ -farnesene, 22) unknown sesquiterpenoid, 23) unknown sesquiterpenoid, 24)  $\beta$ -sesquiphellandrene<sup>N</sup>, 25) (*E*)-nerolidol, 26) (3*E*, 7*E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene, 27) (-)- $\alpha$ -copaene<sup>N</sup>, 28)  $\alpha$ -humulene<sup>N</sup>, 29) caryophyllene-oxide<sup>N</sup>. IS1 and IS2, internal standards (*n*-octane and nonyl-acetate). <sup>N</sup>Tentative identification.

priming or resistance in other plant species [6•,7]. Yet, exposure to the volatiles from clipped sagebrush (*Artemisia tridentata*) primes *N. attenuata* for augmented proteinase activity [30•]. Apparently, volatile-induced priming is a common defence strategy in plants [24•], but the volatile(s) that trigger priming might differ amongst different plant species. This is an important consideration for future strategies that aim to manipulate HIPVs in crops.

The physiological and molecular mechanisms behind volatile-induced priming remain largely unknown. Nevertheless, it seems evident that volatile-induced priming targets defence responses that are controlled by JA [6•,30•]. Our work on maize suggests, however, that JA is not the only signal that controls volatile-induced priming. Volatiles from *Spodoptera littoralis*-infested maize prime for enhanced expression of only a sub-set of JA-inducible defence genes (J Ton *et al.*, unpublished;

Figure 3



HIPV-induced priming and resistance. (a) Typical HIPV-induced priming pattern of defence-related gene expression. Exposure to the HIPV from neighbouring plants alone does not induce a JA-inducible *Proteinase Inhibitor (PIN)* gene in maize. However, subsequent defence elicitation by wounding the leaves and application of regurgitant from *Spodoptera littoralis* caterpillars results in a faster and initially stronger expression of the gene in the HIPV-exposed plants. (b) HIPV-induced resistance against feeding by *S. littoralis* caterpillars. Exposure to HIPV from neighbouring plants reduces subsequent growth and damage by *S. littoralis* caterpillars on exposed plants. This is reflected in the difference in the size of caterpillars that were recovered from exposed and control plants.

Figure 3). Hence, not all JA-inducible genes are priming-responsive, suggesting the existence of additional layers of regulation that involve as-yet-unidentified signalling compounds. Interestingly, a similar form of priming has been reported in response to root colonization by certain non-pathogenic rhizobacteria. In *Arabidopsis*, root colonization by *Pseudomonas fluorescens* WCS417r triggers an induced systemic resistance (ISR) against pathogens that are sensitive to JA-inducible defence mechanisms [31,32]. Large-scale transcription profiling experiments of ISR-expressing *Arabidopsis* have revealed that a distinct sub-set of JA-inducible genes show augmented activation in ISR-expressing plants upon elicitation of defence [33,34]. Interestingly, the promoter regions of these priming-responsive genes were enriched in binding sites for specific transcription factors (CMJ Pieterse, pers. comm.). This points to a sophisticated regulatory mechanism in which specific transcription factors specify the set of JA-inducible, priming-responsive defence genes.

### Field evidence that exploitation of priming could actually work

Differences in attractiveness between plant genotypes can lead to dramatic differences in rates of parasitism.

For example, when the parasitoid *Cotesia plutella* was given a choice between larvae of the diamond back moth on Chinese cabbage or on common cabbage, parasitism of larvae was up to 15 times higher on the attractive Chinese cabbage than on the less attractive common cabbage [35]. Moreover, several field studies give reason to be optimistic that biological control can indeed be enhanced by manipulating volatile plant signals. For instance, Thaler [36] treated tomato plants with JA to induce typical emissions of HIPVs and observed that parasitism of lepidopteran larvae was significantly higher on treated plants than on untreated plants. A study with wild tobacco plants in a natural setting showed that spiking the plants with synthetic versions of several typical HIPVs increased consumption of lepidopteran eggs that were placed on these plants and consequently reduced damage by herbivores considerably [37]. Below ground, the emission of the sesquiterpene (E)- $\beta$ -caryophyllene in maize roots is necessary to attract entomopathogenic nematodes to roots damaged by the ferocious maize pest *Diabrotica virgifera virgifera*. Maize varieties that lack this signal have been shown to be far more vulnerable to the pest [23<sup>••</sup>].

We and others [3] have argued that a constitutive release of volatiles should be avoided and that emissions should occur when a plant is actually under attack by herbivores. A constitutive release might not only be costly for the plant, and thereby lead to reduced yield, but might also defy the purpose of the release [3], which is to attract parasitoids and predators to the plants that are actually under attack by herbivores. There are now several studies, however, which suggest that these concerns might not be entirely warranted. The release of volatiles is not necessarily very costly [5] and various plants constitutively release some of the compounds of interest. The nicest demonstration that constitutive emissions might benefit pest control comes from the successful so-called 'push-pull' studies by Kahn and colleagues [38]. These researchers planted the odorous grass *Melinis minutiflora* in African maize fields. The grass constitutively emits a compound that is typically released by maize in response to caterpillar damage. This resulted in largely reduced damage by a lepidopteran stemborer, evidently because the pest was repelled by the odour of the grass but also because one of its main parasitoids was attracted to the mixed fields, leading to high parasitism rates. The grass' odour attracted the parasitoid, and apparently did not confuse them nor prevent them from using other cues to locate their hosts on infested plants. That a general attraction of natural enemies into a field can result in significant reduction of herbivore numbers is also evident from studies in which synthetic attractants that were released from dispensers in crop fields increased the numbers of natural enemies and reduced pest numbers [39]. Methyl salicylate is one of the compounds that seems to be of particular importance in mediating attraction of several natural enemies [4,39–41], some other

likely candidates for manipulation are discussed below. Continuous releases might also be the most effective means of repelling herbivores and to prime for plant defences.

### The first successes in manipulating volatile emissions

Terpenoids usually dominate the HIPV blends and have therefore been the logical first targets for manipulation. There are ample possibilities to engineer plants for enhanced terpenoid production, but targeting early steps in general terpene synthesis has rarely lead to desired results [3,5]. It is evident that enhancing the attractiveness of crop plants for natural enemies of pests will require specific compounds to be targeted. In this respect, important progress has been made in the three years since the publication of an insightful review in which the necessary steps towards this goal were outlined [3]. In two recent publications, it was shown that it is indeed possible to manipulate the production of attractants through transformation. In the first study [42<sup>••</sup>], a linalool/nerolidol synthase gene from strawberry (*FaNES1*) was introduced into *Arabidopsis thaliana*, causing the transformed plants to constitutively release (3*S*)-(E)-nerolidol (and in some transformants (3*E*)-4,8-dimethyl-1,3,7-nonatriene), which rendered them attractive to predatory mites. In the other study [43<sup>••</sup>], *Arabidopsis* was transformed with a maize terpene synthase gene (*TPS10*) that is responsible for emissions of the blend of sesquiterpenes that is typically released in response to caterpillar feeding. The transformed plant was attractive to parasitoid females that use induced maize volatiles to find their caterpillar hosts, but only after the wasps had learned to associate the sesquiterpene blend with the presence of hosts. These latter results suggest that the manipulation of other typically induced volatiles might be more effective at attracting this parasitoid. A third *Arabidopsis* transformant, which expresses a (E)- $\beta$ -farnesene synthase gene, has been announced [4]. Enhancing the emissions of this sesquiterpene offers possibilities in aphid control because it is a common aphid alarm pheromone that might repel aphids and attract their natural enemies. For most systems, it remains to be determined which compounds would be most effective in pest control.

### Which signals to target?

The demonstration that the attractiveness of plants to beneficial arthropods can be altered [42<sup>••</sup>,43<sup>••</sup>] is an important first step toward the application of manipulated volatile emissions for pest control, but several essential additional steps are needed. First, the appropriate changes need to be made in crop plants and not just in the model plant *Arabidopsis*. Moreover, if we wish to exploit HIPVs in crop protection, the signals that are specifically implicated in the attraction of beneficial arthropods would be the logical targets. There are good indications that plants' responses to herbivory can be

highly specific: some plants emit different odours in response to different herbivores and the natural enemies of these herbivores are able to pick up on this. Probably the best behavioural example comes from a study on the specialist parasitoid *Cardiochiles nigriceps*, which can only develop in larvae of the moth *Heliothis virescens*. Females of this wasp show an amazingly keen ability to distinguish between the odours from plants that have been attacked by those specific hosts and plants that are attacked by closely related non-hosts [44]. This distinction was made even when the damaged leaves had been removed from the respective plants, clearly implying that the plant's signal allowed the wasps to make the distinction [44], but it remains to be determined which compound(s) are implicated. It is known that *Aphidius ervi*, a parasitoid of aphids, specifically uses 6-methyl-5-hepten-2-one as a cue to recognize plants that have been infested by potential hosts [45]. This volatile molecule is therefore an obvious candidate for augmented emissions, which is currently being investigated in cereals [4]. Although specificity in other systems can be much more ambiguous [46], there are various compounds that are strong candidates as attractants for predators and parasitoids. In our studies of below-ground interactions, we have been extremely fortunate in finding that the roots of various maize varieties emit only one compound, (E)- $\beta$ -caryophyllene, in significant amounts in response to root herbivory [23<sup>••</sup>]. This potent attractant for entomopathogenic nematodes is another logical target compound for enhanced production, especially in American maize varieties, which appear to have lost the ability to produce this signal [23<sup>••</sup>,47].

For priming, other compounds might be more appropriate. As discussed, plants species differ in their sensitivity to different compounds. Green leaf volatiles have proven to be particularly active [6<sup>•</sup>,7,9,27] although their manipulation is not practical, but one candidate compound for improved priming for defence is *cis*-jasmonone [4]. This compound has been shown to induce both direct defence against aphids and the production of the aphid repellent 6-methyl-5-hepten-2-one, the key attractant for an important aphid parasitoid. Methyl salicylate is another compound that can be expected to play an important role in plant-plant communication, and in repelling herbivores and attracting beneficial arthropods [4,40,41,48]. But overall, there is still a major need to improve our knowledge of what compounds are of key importance [43<sup>••</sup>,49,50].

### Conclusions

Progress in research on the molecular mechanisms that are involved in herbivore-induced volatile emissions has provided reason for optimism that we will soon be able to produce crop varieties that have improved abilities to repel herbivores and to attract natural enemies of herbivores. The increased emissions of volatiles might have the additional advantage that they could also prime defences in neighbouring plants. It remains to be



determined if it is more desirable to have constitutive emissions of key compounds or if the emissions should be inducible, so that they only take place upon attack by arthropods. The latter might be preferred to avoid excessive energy and resource investment by the plant and to avoid confusing natural enemies in their efforts to locate the herbivores [3]. However, field studies seem to suggest that the latter concern might not be entirely warranted. A few compounds have been identified as likely candidates for enhancement [23<sup>••</sup>,26,39,40], whereas other compounds might not be as powerful as previously assumed [49]. For most natural enemies, the key attractants remain to be identified. In some cases, this could prove exceedingly difficult, but progress in volatile trapping, analytical methods and data processing, as well as interdisciplinary collaborations are likely to yield the desired results soon [50].

We should stress that the multiple interactions in which HIPVs play a role make it difficult to fully predict the consequences of their manipulation. Therefore, field applications will continue to be a matter of trial and error, although some potential failures can be prevented. Obviously, increased emissions of volatiles that are known to attract herbivores should be avoided [3], and it can be expected that herbivores will rapidly adapt their responses to repellents if they are no longer indicative of poor or unsafe resources. Moreover, the natural enemies that have evolved to exploit the signals will also adapt and reduce their responses to the signals if they no longer lead them to profitable resources. This could, in fact, already occur within the lifetime of an individual; various natural enemies have been shown to be good learners and negative associations could soon render the signals ineffective in attracting them [51]. Finally, it should be stressed that the exploitation of plant signals by natural enemies can be highly variable among species and that the emissions should be fine-tuned for each of them. In this respect, it is good to focus on determining the principle attractants for those natural enemies that have the greatest potential to control a certain pest. In all cases, the effects of the enhanced emissions on neighbouring plants should also be taken into consideration.

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