Journal of the Indian Institute of Science
A Multidisciplinary Reviews Journal
ISSN: 0970-4140 Coden-JIISAD

REVIEWS

Herbivore-Induced Plant Volatiles as a Rich Source of Information for Arthropod Predators: Fundamental and Applied Aspects

Marcel Dicke

Abstract | Plants respond to arthropod herbivory with the induction of volatiles that attract predatory arthropods that attack the herbivores. These so-called herbivore-induced plant volatiles (HIPVs) appear to be important sources of information that mediate many interactions within a plant–arthropod community. Predators can use HIPVs to find a food source in a complex environment. Moreover, predator responses are modulated by starvation and specific dietary deficiencies. In addition, HIPVs can influence the behaviour and distribution of other community members such as parasitic plants, herbivores, and hyperparasitoids. The collective outcome of these interactions determines the effect of the HIPVs on plant fitness and this has fuelled a debate on whether HIPVs can be beneficial to plants. Interestingly, the origin of the research on HIPVs has been an investigation of how predatory mites exterminate populations of their prey, the herbivorous spider mites. The value of HIPVs for durable pest control is discussed.

Keywords: *predator, herbivore, herbivore-induced plant volatiles, crop protection*

1 Introduction

Since the late 1980s it has become clear that plants respond to arthropod herbivory with the induced production of volatiles that attract the enemies of the herbivores.[1–3] Because earlier studies in the 1980s had indicated that plant volatiles could mediate interactions between damaged and undamaged plants,[4–6] the research on plant volatiles in plant–carnivore interactions has especially focussed on the adaptiveness of herbivore-induced plant volatiles (HIPVs) to the plant, to establish whether it pays plants to advertise for 'bodyguards'.[7] This has resulted in a continued discussion[8–10] that is fed by ample studies on the effects of HIPVs on various members of the community that interacts with the emitting plant,[11–16] to investigate whether the emission of HIPVs is adaptive to plants.[16] It appears that HIPVs affect the behaviour of diverse members of the community including not only predators and parasitoids but also herbivores,[17,18] hyperparasitoids,[13] parasitic plants,[19] and neighbouring plants.[20] While the issue of the adaptiveness of HIPVs is an exciting topic, in this discussion the use of HIPVs by carnivores has often been reduced to their exploitation of the cues and the fact that carnivores can learn to respond to them. However, HIPVs provide important information to carnivores that can be used to make foraging decisions not only related to finding a food source but to additional aspects of food quality and solving the dietary needs that predators may face.

2 Microscopic and Macroscopic Carnivores

HIPVs are used by a wide range of enemies of herbivorous arthropods. In a recent review of the literature,[21] 68 species of carnivorous arthropods were recorded to use HIPVs to locate their herbivorous victims. This relates to 41 parasitoid species and 26 predator species. In addition, some entomopathogenic nematodes[22,23]

Herbivore-induced plant volatiles (HIPVs): plant volatiles that are actively produced by the plant in response to herbivory.

Community: an assemblage of populations of different species, interacting with one another.

Hyperparasitoid: parasitoid that attacks another parasitoid.

Parasitoid: organism that lives on or in another organism during the juvenile stages and kills its host.

Laboratory of Entomology, Wageningen University, Radix Building, Droevendaalsesteeg 1, 6708PB Wageningen, The Netherlands.
marcel.dicke@wur.nl

and insectivorous birds[24,25] use HIPVs to locate their herbivorous host or prey. Most information exists, however, for arthropod carnivores. In the discussion on the relative value of predators and parasitoids for the plant in terms of the elimination of herbivores, predators have been indicated as being of most value because they immediately kill and remove herbivores from the plant.[8] Predators are generally more generalistic carnivores than parasitoids, although some highly specific predators occur as well.[26] This paper will focus especially on arthropod predators and the information value of HIPVs to these predators.

3 Taxonomic Diversity

The predatory lifestyle is widely distributed among arthropods. Predators occur in the Arachnida and in 15 insect orders, some of which consist predominantly or exclusively of predators, such as the Odonata and Neuroptera.[27] Yet, the 26 species of predators for which experimental data are available,[21] represent only a limited taxonomic diversity: Hemiptera (7 species), Neuroptera (2 species), Coleoptera (3 species), Thysanoptera (1 species) and the family Phytoseiidae within the Acari (13 species). This diversity is most likely to represent the taxonomic interest of the research groups addressing HIPVs rather than an indication that the use of HIPVs is limited to only a few taxonomic groups. I am not aware of any study of predators and their response to HIPVs that did not record a response. Some species, such as social insects like ants and paper wasps, may be excellent candidates to be expected among the predators that use HIPVs. Social insects are well known to use infochemicals. Indeed, some ant species have been found to exploit plant volatiles,[28–30] but no example of their use of HIPVs is known to me. Recent studies recorded the appearance of social wasps, *Polistes dominula, Vespula germanica, and V. vulgaris* in experimental plots of *Brassica nigra* plants with *Pieris brassicae* caterpillars once the caterpillars reached the fourth instar and not in neighbouring plots with plants without caterpillars.[31] This may have been the result of the predators responding to caterpillar-induced plant volatiles but proof for this remains to be collected.[31]

4 HIPVs to Locate Prey

Imagine that you are a tiny predator, only a millimeter in size, and searching for prey that is of roughly the same size and located somewhere in a three dimensional maze with dimensions far beyond your own size. This is the situation that predatory arthropods face when searching for their herbivorous prey in complex vegetation. Moreover, the prey is under natural selection not to give away its presence to its predators. In this situation, any type of information that can guide the predator to its prey will reduce its searching time and enhance the odds of finding food and thus contributing to the next generation. This has resulted in the formulation of the reliability–detectability problem[32] for which HIPVs provide one of the solutions. HIPVs are plant volatiles that are produced in response to herbivory. They comprise a complex mixture of tens up to more than 200 compounds, the composition of which may vary with herbivore species, herbivore developmental instar, plant tissue, and abiotic conditions.[15,33,34] Moreover, the emission rate of HIPVs is much higher than the volatile emission rate by herbivores themselves. Thus, HIPVs combine high detectability with considerable reliability[32] and constitute a valuable source of information to predators.

Apart from finding prey, the identity of the prey may influence a predator's fitness. Prey quality may influence a predator's reproduction rate and prey quality can be decisively influenced by the host plant on which the prey feeds.[35] Thus, HIPVs as a source of information originating from plants can also inform a predator about the food source of its prey.[32]

5 HIPVs to Resolve Specific Dietary Needs

Prey quality to a predator may be determined by various factors, e.g. nutritional quality, physical properties, or the prey's diet.[36–39] Predators can use HIPVs to select the best prey. For instance, the predatory mites *Phytoseiulus persimilis* and *Metaseiulus occidentalis* are attracted to volatiles related to feeding by its prey, the two-spotted spider mite *Tetranychus urticae,* but not to volatiles related to feeding by the European red spider mite *Panonychus ulmi*. The reverse was found for the predatory mites *Amblyseius potentillae* and *Amblyseius finlandicus*.[26] These behavioural responses reflected the value of the spider mites as prey for the predators. The ladybird beetle *Aiolocaria hexaspilota* uses HIPVs from *Salix eriocarpa* to select the most suitable stage of its prey, the leaf beetle *Plagiodera versicolora*.[40] The predatory mites *A. potentillae*, *A. finlandicus* and *Typhlodromus pyri* used HIPVs from apple leaves to select the prey species that yields the highest reproductive success.[41] It is interesting to see that the predator's preference for HIPVs matches with their prey preference as assessed under laboratory conditions or as assessed from their gut contents in the field.[41] The behavioural responses of the predators are dependent on their degree of starvation in terms of gut content.[26] Moreover, it is interesting that a deficiency in specific nutrients can affect predator responses to HIPVs. The predatory mite *A. potentillae* requires β-carotene or vitamin A for assessing day length and entering diapause. This predator has a clear preference for HIPVs associated with its main prey, the spider mite *P. ulmi*. When this predator lacks β-carotene or vitamin A, it is attracted to plant volatiles associated with several inferior prey species that they are not attracted to when their vitamin A-deficient diet is supplemented with vitamin A.[42,43] These inferior prey species can provide the predators with vitamin A and, therefore, are a prey that can relieve their dietary deficiency. Thus, the predators respond to a wider spectrum of HIPVs when vitamin A-deficient to resolve their dietary deficiency. Yet, carotenoid-deficient predators are not attracted to HIPVs associated with herbivores that cannot serve as prey and thus cannot relieve their carotenoid deficiency.[42]

6 Prey Sabotaging HIPV Emission and Thus Interfering with Predator Attraction

A recurring question is whether herbivores can interfere with the HIPV production by the plant, e.g. by stealthy feeding. Some herbivores, such as phloem-feeding aphids, are known to reduce the degree of physical damage while feeding. These herbivores move their stylets in the plant intercellular space and make only limited punctures in parenchymal cells on their way to the phloem.[44] Yet, these herbivores also induce plant responses including the production of HIPVs.[45] The induction of HIPVs involves elicitors in oral secretions.[46] These oral secretions are often applied to the plant during feeding[47,48] and are likely involved in the start of digestion of food. The induction of defence in general by plants and of carnivore attractants in particular is likely to be under selection for herbivores to make themselves undetectable by the plant. This is likely an arms race where plants recognize herbivore elicitors and mount a defence. Subsequently, the herbivore evolves effectors that suppress the induction by the plant, followed by plant responses that now exploit the effectors as cues to initiate induced defence. This is then followed by the evolution of new effectors suppressing the plant's response and so on. This is the so-called zigzag model representing the current view of plant immune systems[49] and has been especially developed for plant–pathogen interactions in which knowledge of effectors is rapidly increasing. For plant–arthropod interactions, knowledge on the suppression of induced defences has only just started.[50–60] Herbivores may suppress induced defences by hijacking phytohormonal signal transduction in the plant.[55,57] For instance, one population of the spider mite *T. urticae* is known that does not induce jasmonic acid-mediated defences, including the induction of jasmonic acid-dependent HIPVs.[57] The suppression of plant defence induction may not only benefit the herbivore that suppresses the defence[54,55] but also other herbivores that feed on the same plant.[54,61] By suppressing the induction of defences, the herbivore may suppress the emission of HIPVs;[54,57,61,62] a functional phytohormonal signaling in the plant is needed for this as well.[62] As a result of the suppression of HIPV emission, predator attraction is reduced; for example, the attraction of the predatory mite *P. persimilis* to plants infested with its herbivorous prey *T. urticae* is attenuated when the whitefly *Bemisia tabaci* co-infests the plant. The magnitude of this attenuation is dependent on whitefly density.[61]

Phytohormone: plant hormone; the production of several plant hormones is induced by herbivory and mediates further induction processes.

7 Plants Enhancing the Emission of HIPVs

While herbivores may suppress the induction of HIPVs, plants may be under selection to enhance their response to herbivores. After all, indirect defence through HIPVs has a temporal delay between not only recognizing the herbivore and synthesizing the volatiles but additionally there is the delay of the response of carnivores, provided they are nearby. Therefore, any way of accelerating or intensifying the response may promote the effectiveness of induced indirect defence. One way of enhancing HIPV emission is by priming.[63] Plants may be primed by exposure to HIPVs from neighbouring plants.[64] For example, lima bean plants that have been exposed to HIPVs from neighbouring plants respond with a more intense response to spider mite infestation in terms of HIPV emission and consequently are more attractive to predatory mites than unexposed plants infested with spider mites.[65] In addition to being primed by volatiles from neighbouring plants, plant responses may also be primed by HIPVs emitted from other leaves from the same plant.[66,67] For example, undamaged lima bean leaves from a beetle-damaged plant that were exposed to HIPVs from the beetle-damaged leaves responded with the production of extrafloral nectar, a component of indirect plant defence.[66]

Interestingly, plant responses to herbivory may also be affected by interactions of the plant with other community members, such as soil

Priming: a phenomenon where herbivory does not induce a change in the plant but alters the plant so that a second attack results in a faster or more intense plant response than in a plant without previous attack.

Elicitor: a compound produced by an herbivore that induces a response in the plant on which the herbivore feeds.

Effector: a compound produced by an herbivore that suppresses a defence response of the plant on which the herbivore feeds.

microbes.[68] For instance, the interaction of bean plant roots with the mycorrhizal fungus *Glomus mosseae* influenced the composition of HIPVs produced in response to infestation of the spider mite *T. urticae* and this affected the attraction of the predatory mite *P. persimilis*.[69]

Thus, plants within a community that each have their own history in terms of an interaction network may differ in the intensity with which they respond to herbivory with HIPV emission and, consequently, herbivores are likely to have differential mortality on plants within a community. It will be interesting to investigate whether herbivores can assess this differential value of plants with regard to their fitness and whether this affects their host plant choices. Some preliminary information for this is available: *T. urticae* spider mites prefer to feed on leaves of lima bean plants infested with the whitefly *Bemisia tabaci*. On these plants the spider mites have a better performance in terms of plant quality as assessed in terms of egg production and in addition the whiteflies interfere with the emission of one of the HIPVs resulting in a reduced attraction of the spider-mite predator *P. persimilis*.[61]

8 Application of HIPVs in Agriculture

HIPVs mediate interactions between plants, herbivores and their enemies. The origin of the research on HIPVs lies in agricultural studies that aimed to understand how the predatory mite *P. persimilis* exterminates populations of its prey, the spider mite *T. urticae,* in cucumber.[70,71] Modelling of the predator–prey population dynamics only matched with experimental observations on prey extermination when the model included a behaviour in which predators returned to a prey patch upon leaving it, owing to the steep odour gradient of a putative odour, thus being arrested within the prey patch;[71] this behaviour was later found to be mediated by volatiles emitted from infested plants.[72] The source of these volatiles appeared to be the plant that produced the volatiles in response to spider-mite feeding.[1,2] Thus, the plant's response to herbivory in terms of HIPV emission was identified as being the essential component of prey eradication by predators, and thereby successful biological control of spider mites. This has stimulated research on improving crop quality in terms of HIPV emission so as to breed for crops with enhanced capacity for interaction with biological control agents;[73–80] these efforts include short-term trials in agricultural settings.[77,79] For instance, in a glasshouse setting, cucumber cultivars that differed in predator attraction upon spider-mite infestation under laboratory conditions, also differed in predator arrival in a distant prey patch.[77] This shows that laboratory studies on attraction may be extrapolated to field conditions as was also observed in other studies.[81,82] However, to date no commercial breeding programme is known to have been initiated to develop a commercial cultivar to be marketed for its enhanced attraction of biological control agents. It would be interesting to have such a cultivar available and to investigate the effects on pest control in an agricultural setting in a comparative way. Another option is to supplement an agricultural field with HIPVs to attract natural enemies from the surroundings. Several interesting examples of this have been reported,[83–86] although it remains to be investigated what the consequences are for neighbouring fields.[87] Yet, given the fact that there is no report of a plant–herbivore–carnivore interaction where HIPVs do not mediate the attraction of carnivores to HIPVs, and the finding that, at least in successful biological control of spider mites by their predators, HIPVs play a crucial role, it is likely that HIPVs already mediate biological control on a large scale. Improving on this to enhance the successes of sustainable pest management in a systems approach such as Integrated Pest Management is an important route ahead. A very interesting case in this context is the push–pull system developed to control stem borers in maize in Africa. Here a cropping system has been developed that combines different plants so as to repel stem borer moths and make them oviposit on trap plants, while attracting parasitoids of the stem borers with plants that emit one of the HIPV components that attract the parasitoids.[88,89] This cropping system has been widely adopted by farmers in central Africa and makes an important contribution to local food security.[90] Making progress in such applied research is more important than ever in times when still ca 20–40% of crop losses occur due to insect pests, while we need to increase production to feed the rapidly growing human population.

Received 23 September 2014,
Revision accepted 9 October 2014.

References

1. Dicke, M. & Sabelis, M.W. How plants obtain predatory mites as bodyguards. *Netherlands Journal of Zoology* **38**, 148–165 (1988).
2. Dicke, M., Van Beek, T.A., Posthumus, M.A., Ben Dom, N., Van Bokhoven, H. & De Groot, A.E. Isolation and identification of volatile kairomone that affects acarine predator-prey interactions. Involvement of host plant in its production. *Journal of Chemical Ecology* **16**, 381–396 (1990).

3. Turlings, T.C.J., Tumlinson, J.H. & Lewis, W.J. Exploitation of herbivore-induced plant odors by host-seeking parasitic wasps. *Science* **250**, 1251–1253 (1990).
4. Baldwin, I.T. & Schultz, J.C. Rapid changes in tree leaf chemistry induced by damage: evidence for communication between plants. *Science* **221**, 277–279 (1983).
5. Rhoades, D.F. Responses of alder and willow to attack by tent caterpillars and webworms: Evidence for pheromonal sensitivity of willows. In *Plant resistance to insects. American Chemical Society Symposium Series 208* (ed. P.A. Hedin), pp. 55–68. Washington D.C. (1983).
6. Rhoades, D.F. Pheromonal communication between plants. In *Chemically mediated interactions between plants and other organisms. Recent Advances in Phytochemistry* (eds. G.A. Cooper-Driver, T. Swain & E.C. Conn), pp. 195–218. Plenum Press, New York (1985).
7. Dicke, M. & Sabelis, M.W. Does it pay plants to advertize for bodyguards? Towards a cost-benefit analysis of induced synomone production. In *Causes and consequences of variation in growth rate and productivity of higher plants* (eds. H. Lambers, M.L. Cambridge, H. Konings & T.L. Pons), pp. 341–358. The Hague, SPB Publishing (1989).
8. Dicke, M. & Baldwin, I.T. The evolutionary context for herbivore-induced plant volatiles: beyond the 'cry for help'. *Trends in Plant Science* **15**, 167–175 (2010).
9. Hare, J.D. Ecological role of volatiles produced by plants in response to damage by herbivorous insects. *Annual Review of Entomology* **56**, 161–180 (2011).
10. Kessler, A. & Heil, M. The multiple faces of indirect defences and their agents of natural selection. *Functional Ecology* **25**, 348–357 (2011).
11. Arimura, G., Kost, C. & Boland, W. Herbivore-induced, indirect plant defences. *Biochimica et Biophysica Acta* **1734**, 91–111 (2005).
12. Heil, M. Indirect defence via tritrophic interactions. *New Phytologist* **178**, 41–61 (2008).
13. Poelman, E.H., Bruinsma, M., Zhu, F., Weldegergis, B.T., Boursault, A.E., Jongema, Y., van Loon, J.J.A., Vet, L.E.M., Harvey, J.A. & Dicke, M. Hyperparasitoids use herbivore-induced plant volatiles to locate their parasitoid host. *PLOS Biology* **10**, e1001435 (2012).
14. Loreto, F., Dicke, M., Schnitzler, J.P. & Turlings, T.C.J. Plant volatiles and the environment. *Plant, Cell & Environment* **37**, 1905–1908 (2014).
15. McCormick, A.C., Unsicker, S.B. & Gershenzon, J. The specificity of herbivore-induced plant volatiles in attracting herbivore enemies. *Trends in Plant Science* **17**, 303–310 (2012).
16. Schuman, M.C., Barthel & Baldwin, I.T. Herbivory-induced volatiles function as defenses increasing fitness of the native plant *Nicotiana attenuata* in nature. *eLife* **1**, e00007 (2012).
17. De Moraes, C.M., Mescher, M.C. & Tumlinson, J.H. Caterpillar-induced nocturnal plant volatiles repel nonspecific females. *Nature* **410**, 577–580 (2001).
18. Pinto-Zevallos, D.M., Hellen, H., Hakola, H., van Nouhuys, S. & Holopainen, J.K. Induced defenses of *Veronica spicata*: Variability in herbivore-induced volatile organic compounds. *Phytochemistry Letters* **6**, 653–656 (2013).
19. Runyon, J.B., Mescher, M.C. & De Moraes, C.M. Volatile chemical cues guide host location and host selection by parasitic plants. *Science* **313**, 1964–1967 (2006).
20. Karban, R., Yang, L.H. & Edwards, K.F. Volatile communication between plants that affects herbivory: a meta-analysis. *Ecology Letters* **17**, 44–52 (2014).
21. Mumm, R. & Dicke, M. Variation in natural plant products and the attraction of bodyguards involved in indirect plant defense. *Canadian Journal of Zoology* **88**, 628–667 (2010).
22. Rasmann, S. & Turlings, T.C.J. First insights into specificity of belowground tritrophic interactions. *Oikos* **117**, 362–369 (2008).
23. Rasmann, S., Kollner, T.G., Degenhardt, J., Hiltpold, I., Toepfer, S., Kuhlmann, U., Gershenzon, J. & Turlings, T.C.J. Recruitment of entomopathogenic nematodes by insect-damaged maize roots. *Nature* **434**, 732–737 (2005).
24. Amo, L., Jansen, J.J., van Dam, N.M., Dicke, M. & Visser, M.E. Birds exploit herbivore-induced plant volatiles to locate herbivorous prey. *Ecology Letters* **16**, 1348–1355 (2013).
25. Mantyla, E., Klemola, T. & Haukioja, E. Attraction of willow warblers to sawfly-damaged mountain birches: novel function of inducible plant defences? *Ecology Letters* **7**, 915–918 (2004).
26. Sabelis, M.W. & Van de Baan, H.E. Location of distant spider mite colonies by phytoseiid predators: demonstration of specific kairomones emitted by *Tetranychus urticae* and *Panonychus ulmi*. *Entomologia Experimentalis et Applicata* **33**, 303–314 (1983).
27. Gullan, P.J. & Cranston, P.S. *The Insects: An outline of entomology.* 4th edition. USA, Blackwell Publishing. pp. 584 (2010).
28. Dattilo, W., Izzo, T.J., Inouye, B.D., Vasconcelos, H.L. & Bruna, E.M. Recognition of host plant volatiles by *Pheidole minutula* Mayr (Myrmicinae), an Amazonian ant-plant specialist. *Biotropica* **41**, 642–646 (2009).
29. Ranganathan, Y. & Borges, R.M. Predatory and trophobiont-tending ants respond differently to fig and fig wasp volatiles. *Animal Behaviour* **77**, 1539–1545 (2009).
30. Brouat, C., McKey, D., Bessière, J-M., Pascal, L. & Hossaert-McKey, M. Leaf volatile compounds and the distribution of ant patrolling in an ant-plant protection mutualism: Preliminary results on *Leonardoxa* (Fabaceae: Caesalpinioideae) and *Petalomyrmex* (Formicidae: Formicinae). *Acta Oecologica* **21**, 349–357 (2000).
31. Lucas-Barbosa, D., Poelman, E.H., Aartsma, Y., Snoeren, T.A.L., van Loon, J.J.A. & Dicke, M. Caught between parasitoids and predators—Survival of a specialist herbivore on leaves and flowers of mustard plants. *Journal of Chemical Ecology* **40**, 621–631 (2014).

32. Vet, L.E.M. & Dicke, M. Ecology of infochemical use by natural enemies in a tritrophic context. *Annual Review of Entomology* **37**, 141–172 (1992).
33. Takabayashi, J., Dicke, M. & Posthumus, M.A. Volatile herbivore-induced terpenoids in plant-mite interactions: Variation caused by biotic and abiotic factors. *Journal of Chemical Ecology* **20**, 1329–1354 (1994).
34. Gouinguene, S.P. & Turlings, T.C.J. The effects of abiotic factors on induced volatile emissions in corn plants. *Plant Physiology* **129**, 1296–1307 (2002).
35. DeMoraes, G.J. & McMurtry, J.A. Physiological effect of the host plant on the suitability of *Tetranychus urticae* as prey for *Phytoseiulus persimilis* (Acari: Tetranychidae, Phytoseiidae). *Entomophaga* **32**, 35–38 (1987).
36. Gnanvossou, D., Yaninek, J.S., Hanna, R. & Dicke, M. Effects of prey mite species on life history of the phytoseiid predators *Typhlodromalus manihoti* and *Typhlodromalus aripo*. *Experimental and Applied Acarology* **30**, 265–278 (2003).
37. Furuichi, H., Yano, S., Takafuji, A. & Osakabe, M. Prey preference of the predatory mite *Neoseiulus womersleyi* Schicha is determined by spider mite webs. *Journal of Applied Entomology* **129**, 336–339 (2005).
38. Ferry, N., Mulligan, E.A., Stewart, C.N., Tabashnik, B.E., Port, G.R. & Gatehouse, A.M.R. Prey-mediated effects of transgenic canola on a beneficial, non-target, carabid beetle. *Transgenic Research* **15**, 501–514 (2006).
39. Venzon, M., Janssen, A. & Sabelis, M.W. Prey preference and reproductive success of the generalist predator *Orius laevigatus*. *Oikos* **97**, 116–124 (2002).
40. Yoneya, K., Kugimiya, S. & Takabayashi, J. Can herbivore-induced plant volatiles inform predatory insect about the most suitable stage of its prey? *Physiological Entomology* **34**, 379–386 (2009).
41. Dicke, M., Sabelis, M.W. & de Jong, M. Analysis of prey preference of phytoseiid mites as determined with an olfactometer, predation models and electrophoresis. *Experimental and Applied Acarology* **5**, 225–241 (1988).
42. Dicke, M. & Groeneveld, A. Hierarchical structure in kairomone preference of the predatory mite *Amblyseius potentillae*: dietary component indispensable for diapause induction affects prey location behaviour. *Ecological Entomology* **11**, 131–138 (1986).
43. Dicke, M., Sabelis, M.W. & Groeneveld, A. Vitamin A deficiency modifies response of predatory mite *Amblyseius potentillae* to volatile kairomone of two-spotted spider mite, *Tetranychus urticae*. *Journal of Chemical Ecology* **12**, 1389–1396 (1986).
44. Tjallingii, W.F. & Hogen Esch, T. Fine structure of aphid stylet routes in plant tissues in correlation with EPG signals. *Physiological Entomology* **18**, 317–328 (1993).
45. Pickett, J.A., Wadhams, L.J., Woodcock, C.M. & Hardie, J. The chemical ecology of aphids. *Annual Review of Entomology* **37**, 67–90 (1992).
46. Bonaventure, G., VanDoorn, A. & Baldwin, I.T. Herbivore-associated elicitors: FAC signaling and metabolism. *Trends in Plant Science* **16**, 294–299 (2011).
47. Peiffer, M. & Felton, G.W. Do caterpillars secrete "oral secretions"? *Journal of Chemical Ecology* **35**, 326–335 (2009).
48. Storms, J.J.H. Some physiological effects of spider mite infestation on bean plants. *Netherlands Journal of Plant Pathology* **77**, 154–167 (1971).
49. Jones, J.D.G. & Dangl, J.L. The plant immune system. *Nature* **444**, 323–329 (2006).
50. Maffei, M.E., Arimura, G.I. & Mithofer, A. Natural elicitors, effectors and modulators of plant responses. *Natural Product Reports* **29**, 1288–1303 (2012).
51. Hogenhout, S.A. & Bos, J.I.B. Effector proteins that modulate plant-insect interactions. *Current Opinion in Plant Biology* **14**, 422–428 (2011).
52. Carolan, J.C., Caragea, D., Reardon, K.T., Mutti, N.S., Dittmer, N., Pappan, K., Cui, F., Castaneto, M., Poulain, J., Dossat, C., *et al.* Predicted effector molecules in the salivary secretome of the pea aphid (*Acyrthosiphon pisum*): A dual transcriptomic/proteomic approach. *Journal of Proteome Research* **10**, 1505–1518 (2011).
53. Eichenseer, H., Mathews, M.C., Powell, J.S. & Felton, G.W. Survey of a salivary effector in caterpillars: Glucose oxidase variation and correlation with host range. *Journal of Chemical Ecology* **36**, 885–897 (2010).
54. Sarmento, R.A., Lemos, F., Bleeker, P.M., Schuurink, R.C., Pallini, A., Oliveira, M.G.A., Lima, E.R., Kant, M., Sabelis, M.W. & Janssen, A. A herbivore that manipulates plant defence. *Ecology Letters* **14**, 229–236 (2011).
55. Zarate, S.I., Kempema, L.A. & Walling, L.L. Silverleaf whitefly induces salicylic acid defenses and suppresses effectual jasmonic acid defenses. *Plant Physiology* **143**, 866–875 (2007).
56. Kahl, J., Siemens, D.H., Aerts, R.J., Gäbler, R., Kühnemann, F., Preston, C.A. & Baldwin, I.T. Herbivore-induced ethylene suppresses a direct defense but not a putative indirect defense against an adapted herbivore. *Planta* **210**, 336–342 (2000).
57. Kant, M.R., Sabelis, M.W., Haring, M.A. & Schuurink, R.C. Intraspecific variation in a generalist herbivore accounts for differential induction and impact of host plant defences. *Proceeding of the Royal Society Series B: Biological Sciences* **275**, 443–452 (2008).
58. Schwartzberg, E.G. & Tumlinson, J.H. Aphid honeydew alters plant defence responses. *Functional Ecology* **28**, 386–394 (2014).
59. Chung, S.H., Rosa, C., Scully, E.D., Peiffer, M., Tooker, J.F., Hoover, K., Luthe, D.S. & Felton, G.W. Herbivore exploits orally secreted bacteria to suppress plant defenses. *Proceedings of the National Academy of Sciences USA* **110**, 15728–15733 (2013).
60. Barr, K.L., Hearne, L.B., Briesacher, S., Clark, T.L. & Davis, G.E. Microbial symbionts in insects influence down-regulation of defense genes in maize. *PLOS ONE* **5**, e11339 (2010).
61. Zhang, P.J., Zheng, S.J., van Loon, J.J.A., Boland, W., David, A., Mumm, R. & Dicke, M. Whiteflies interfere with indirect plant defense against spider mites in Lima

bean. *Proceedings of the National Academy of Sciences USA* **106**, 21202–21207 (2009).

62. Zhang, P.J., Broekgaarden, C., Zheng, S.J., Snoeren, T.A.L., van Loon, J.J.A., Gols, R. & Dicke, M. Jasmonate and ethylene signaling mediate whitefly-induced interference with indirect plant defense in *Arabidopsis thaliana*. *New Phytologist* **197**, 1291–1299 (2013).
63. Conrath, U., Beckers, G.J.M., Flors, V., Garcia-Agustin, P., Jakab, G., Mauch, F., Newman, M.A., Pieterse, C.M.J., Poinssot, B., Pozo, M.J. *et al.* Priming: Getting ready for battle. *Molecular Plant-Microbe Interactions* **19**, 1062–1071 (2006).
64. Engelberth, J., Alborn, H.T., Schmelz, E.A. & Tumlinson, J.H. Airborne signals prime plants against insect herbivore attack. *Proceedings of the National Academy of Sciences USA* **101**, 1781–1785 (2004).
65. Choh, Y., Shimoda, T., Ozawa, R., Dicke, M. & Takabayashi, J. Exposure of lima bean leaves to volatiles from herbivore-induced conspecific plants results in emission of carnivore attractants: Active or passive process? *Journal of Chemical Ecology* **30**, 1305–1317 (2004).
66. Heil, M. & Bueno, J.C.S. Within-plant signaling by volatiles leads to induction and priming of an indirect plant defense in nature. *Proceedings of the National Academy of Sciences USA* **104**, 5467–5472 (2007).
67. Heil, M. & Ton, J. Long-distance signalling in plant defence. *Trends in Plant Science* **13**, 264–272 (2008).
68. Pineda, A., Zheng, S.J., van Loon, J.J.A., Pieterse, C.M.J. & Dicke, M. Helping plants to deal with insects: the role of beneficial soil-borne microbes. *Trends in Plant Science* **15**, 507–514 (2010).
69. Schausberger, P., Peneder, S., Jurschik, S. & Hoffmann, D. Mycorrhiza changes plant volatiles to attract spider mite enemies. *Functional Ecology* **26**, 441–449 (2012).
70. Sabelis, M.W., van Alebeek, F., Bal, A., van Bilsen, J., van Heijningen, T., Kaizer, P., Kramer, G., Snellen, H., Veenenbos, R. & Vogelezang, J. Experimental validation of a simulation model of the interaction between *Phytoseiulus persimilis* and *Tetranychus urticae* on cucumber. *IOBC/WPRS Bulletin* **6**, 207–229 (1983).
71. Sabelis, M.W. & Van der Meer, J. Local dynamics of the interaction between predatory mites and two-spotted spider mites. In *Dynamics of physiologically structured populations. Springer lecture notes in biomathematics 68* (eds. J.A.J. Metz & O. Diekman), pp. 322–343 Berlin, Springer (1986).
72. Sabelis, M.W., Vermaat, J.E. & Groeneveld, A. Arrestment responses of the predatory mite, *Phytoseiulus persimilis*, to steep odour gradients of a kairomone. *Physiological Entomology* **9**, 437–446 (1984).
73. Dicke, M., Sabelis, M.W., Takabayashi, J., Bruin, J. & Posthumus, M.A. Plant strategies of manipulating predator-prey interactions through allelochemicals: prospects for application in pest control. *Journal of Chemical Ecology* **16**, 3091–3118 (1990).
74. Krips, O.E., Willems, P.E.L., Gols, R., Posthumus, M.A., Gort, G. & Dicke, M. Comparison of cultivars of ornamental crop *Gerbera jamesonii* on production of spider mite-induced volatiles, and their attractiveness to the predator *Phytoseiulus persimilis*. *Journal of Chemical Ecology* **27**, 1355–1372 (2001).
75. Gouinguene, S., Degen, T. & Turlings, T.C.J. Variability in herbivore-induced odour emissions among maize cultivars and their wild ancestors (teosinte). *Chemoecology* **11**, 9–16 (2001).
76. Degenhardt, J., Gershenzon, J., Baldwin, I.T. & Kessler, A. Attracting friends to feast on foes: engineering terpene emission to make crop plants more attractive to herbivore enemies. *Current Opinion in Biotechnology* **14**, 169–176 (2003).
77. Kappers, I.F., Hoogerbrugge, H., Bouwmeester, H.J. & Dicke, M. Variation in herbivory-induced volatiles among cucumber (*Cucumis sativus* L.) varieties has consequences for the attraction of carnivorous natural enemies. *Journal of Chemical Ecology* **37**, 150–160 (2011).
78. Kappers, I.F., Aharoni, A., van Herpen, T.W.J.M., Luckerhoff, L.L.P., Dicke, M. & Bouwmeester, H.J. Genetic engineering of terpenoid metabolism attracts, bodyguards to *Arabidopsis*. *Science* **309**, 2070–2072 (2005).
79. Degenhardt, J., Hiltpold, I., Kollner, T.G., Frey, M., Gierl, A., Gershenzon, J., Hibbard, B.E., Ellersieck, M.R. & Turlings, T.C.J. Restoring a maize root signal that attracts insect-killing nematodes to control a major pest. *Proceedings of the National Academy of Sciences USA* **106**, 13213–13218 (2009).
80. Brillada, C., Nishihara, M., Shimoda, T., Garms, S., Boland, W., Maffei, M.E. & Arimura, G. Metabolic engineering of the C-16 homoterpene TMTT in *Lotus japonicus* through overexpression of (*E,E*)-geranyllinalool synthase attracts generalist and specialist predators in different manners. *New Phytologist* **200**, 1200–1211 (2013).
81. Janssen, A. Plants with spider-mite prey attract more predatory mites than clean plants under greenhouse conditions. *Entomologia Experimentalis et Applicata* **90**, 191–198 (1999).
82. Poelman, E.H., Oduor, A.M.O., Broekgaarden, C., Hordijk, C.A., Jansen, J.J., Van Loon, J.J.A., Van Dam, N.M., Vet, L.E.M. & Dicke, M. Field parasitism rates of caterpillars on *Brassica oleracea* plants are reliably predicted by differential attraction of *Cotesia* parasitoids. *Functional Ecology* **23**, 951–962 (2009).
83. James, D.G. Synthetic herbivore-induced plant volatiles as field attractants for beneficial insects. *Environmental Entomology* **32**, 977–982 (2003).
84. James, D.G. Further field evaluation of synthetic herbivore-induced plant volatiles as attractants for beneficial insects. *Journal of Chemical Ecology* **31**, 481–495 (2005).
85. James, D.G. & Price, T.S. Field-testing of methyl salicylate for recruitment and retention of beneficial insects in grapes and hops. *Journal of Chemical Ecology* **30**, 1613–1628 (2004).

86. Kelly, J.L., Hagler, J.R. & Kaplan, I. Semiochemical lures reduce emigration and enhance pest control services in open-field predator augmentation. *Biological Control* **71**, 70–77 (2014).

87. Kaplan, I. Attracting carnivorous arthropods with plant volatiles: The future of biocontrol or playing with fire? *Biological Control* **60**, 77–89 (2012).

88. Cook, S.M., Khan, Z.R. & Pickett, J.A. The use of push-pull strategies in integrated pest management. *Annual Review of Entomology* **52**, 375–400 (2007).

89. Khan, Z.R., Ampong-Nyarko, K., Chiliswa, P., Hassanali, A., Kimani, S., Lwande, W., Overholt, W.A., Pickett, J.A., Smart, L.E., Wadhams, L.J. *et al.* Intercropping increases parasitism of pests. *Nature* **388**, 631–632 (1997).

90. Khan, Z.R., Midega, C.A.O., Pittchar, J.O., Murage, A.W., Birkett, M.A., Bruce, T.J.A. & Pickett, J.A. Achieving food security for one million sub-Saharan African poor through push-pull innovation by 2020. *Philosophical Transactions of the Royal Society Series B: Biological Sciences* **369**, 20120284 (2014).

Marcel Dicke is professor of Entomology and head of the Laboratory of Entomology of Wageningen University. He received his Ph.D. from Wageningen University and specializes on the molecular and chemical ecology of multitrophic interactions. He is the author of the 2nd edition of the textbook "Insect–Plant Biology".