Advances and challenges in the identification of volatiles that mediate interactions among plants and arthropods

Marco D'Alessandro and Ted C. J. Turlings*

The relatively new research field of Chemical Ecology has, over the last two decades, revealed an important role of plant-produced volatile organic compounds (VOCs) in mediating interactions between plants and other organisms. Of particular interest are the volatile blends that plants actively emit in response to herbivore damage. Various efforts are underway to pinpoint the bioactive compounds in these complex blends, but this has proven to be exceedingly difficult. Here we give a short overview on the role of herbivore-induced plant volatiles in interactions between plants and other organisms and we review methods that are currently employed to collect and identify key volatile compounds mediating these interactions. Our perspective on future directions of this fascinating research field places special emphasis on the need for an interdisciplinary approach. Joint efforts by chemists and biologists should not only facilitate the elucidation of crucial compounds, but can also be expected to lead to an exploitation of this knowledge, whereby ecological interactions may be chemically manipulated in order to protect crops and the environment.

Introduction

Until recently, it was not common knowledge that plants have a way to express themselves. They mainly do so by emitting odours and the chemical composition and intensity of these odours can carry information on the plants' physiological status and on the stresses that they are being subjected to. In fact, plants emit an enormous spectrum of volatile organic compounds (VOCs). At present, more than 1000 of these low molecular weight organic compounds are known, ranging from terpenoids, fatty acid derivatives, benzenoids and phenylpropanoids, C5-branched compounds and various nitrogen and sulfur containing compounds.[1] Some of these VOCs are constitutively emitted by undamaged, healthy

University of Neuchâtel, Institute of Zoology, Laboratory of Evolutionary Entomology, Case Postale 2, CH-2007 Neuchâtel, Switzerland. E-mail: ted.turlings@unine.ch; Fax: +41 32 718 30 01; Tel: +41 32 718 31 85

plants, but herbivore damage commonly induces plants to emit much larger amounts and may even cause several VOCs to be synthesised *de novo*[2–4] (Fig. 1). These herbivore-induced plant volatiles (HIPVs) are known to be emitted by various parts of the plant, including leaves[4–7] and flower buds[8] as well as roots.[9] Not only feeding by a herbivorous insect induces the release of HIPVs; even deposition of eggs by herbivorous insects has been shown to induce the plant to emit HIPVs.[10–12] In addition, HIPV emission is not limited to the site of damage but occurs systemically throughout the plant, also from undamaged leaves.[13–17] Many insects are well aware of this fragrant lingo of plants and have evolved ways to exploit it (Fig. 2). Recently, researchers have also become aware of this and now HIPV emissions have been the subject of an increasing number of investigations that have revealed an important role of HIPVs in communication and self-protection. Although molecular and genetic approaches are now frequently applied to reveal the intricacies of

Marco D'Alessandro is currently finishing his PhD thesis in Chemical Ecology at the University of Neuchâtel under the supervision of his co-author Ted Turlings. During his research Marco has developed and employed different methods to identify key volatile organic compounds that attract parasitic wasps. He previously studied at the University of Zurich and at the Swiss Federal Institute of Technology Zurich, and worked as a research assistant at the USDA research station, Tifton, Georgia, USA and at the Swiss federal research station in Reckenholz (FAL), where he studied physiological and ecological aspects of the interactions between plants and insects. Currently he is also working on belowground interactions between plants and microbes and on the effects of these interactions on other organisms aboveground.
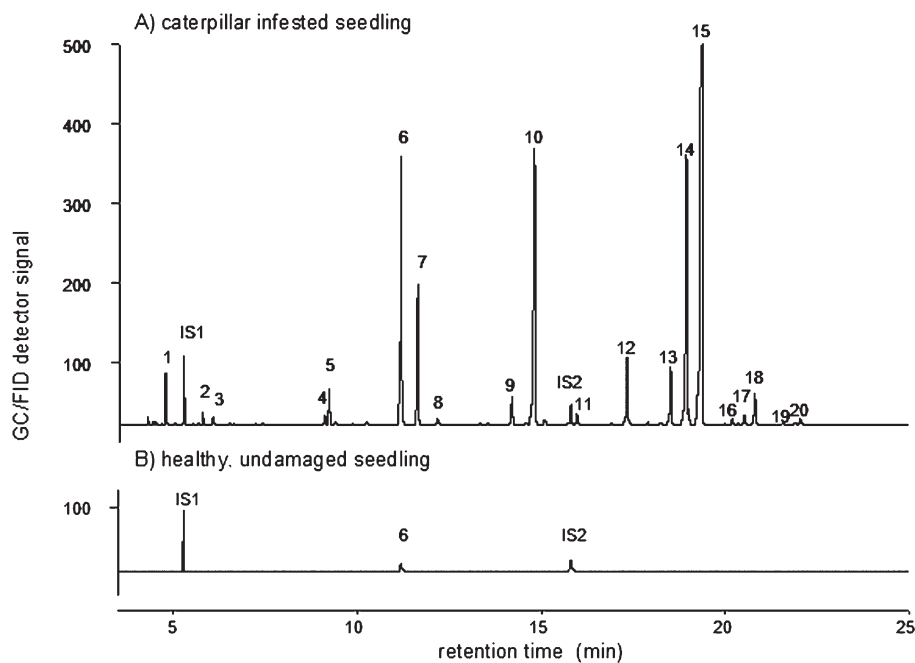
Fig. 1 Example of GC-FID chromatograms obtained with the collected volatiles of 10-day old maize seedlings, (A) seedlings infested with *Spodoptera littoralis* larvae (B) undamaged seedlings. Further details on material and methods are given by D'Alessandro and Turlings.[103] Compounds are: 1 = (Z)-3-hexenal, 2 = (E)-2-hexenal, 3 = (E)-3-hexen-1-ol, 4 = β-myrcene, 5 = (Z)-3-hexen-1-ol acetate, 6 = linalool, 7 = (3E)-4,8-dimethyl-1,3,7-nonatriene, 8 = benzyl acetate, 9 = phenethyl acetate, 10 = indole, 11 = methyl anthranilate, 12 = geranyl acetate, 13 = (E)-β-caryophyllene, 14 = (E)-α-bergamotene, 15 = (E)-β-farnesene, 16 = unknown sesquiterpenoid, 17 = unknown sesquiterpenoid, 18 = β-sesquiphellandrene, 19 = (E)-nerolidol, 20 = (3E,7E)-4,8,12-trimethyl-1,3,7,11-tridecatetraene. IS1 and IS2 = internal standards.

plant-mediated interactions, the chemical analyses of HIPVs remain an integral part of virtually all studies.

Below we provide a short overview of what is known about the physiological and ecological role of HIPVs in interactions between plants and other organisms (for recent reviews see ref. 18–21), we further review methods commonly used by biologists to collect and analyse HIPVs and highlight the challenges that remain to be tackled in this area of research. The focus is on techniques used to study the importance of

Fig. 2 A female of the parasitic wasp *Cotesia marginiventris* lays an egg in a caterpillar. The wasp found its victim with the use of volatiles emitted by the plant in response to being damaged by the caterpillar. Picture by Matthias Held.

such HIPVs for the attraction of arthropods aboveground, and we propose some methods that could be useful in future studies, including the analysis of HIPVs belowground. Further details on these techniques and on techniques used to analyse plant VOCs in general have been described and reviewed elsewhere (*e.g.* ref. 22–26). Finally, we discuss and stress the importance of testing the biological relevance of HIPVs with appropriate behavioural bioassays and we propose that the remarkable sensitivity of insect chemoreceptors to VOCs make them exploitable as tools for future research on plant odours.
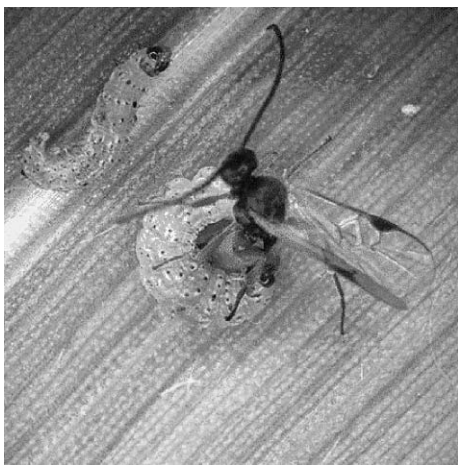
Physiology, ecology and application of biologically relevant HIPVs

HIPV-blends are complex and consist of a variety of divergent VOCs, including alkanes, alkenes, aldehydes, alcohols, ketones, ethers, esters and carboxylic acids. It is unlikely that every VOC emitted by plants serves an ecological or physiological role[27] and there is still disagreement about the evolutionary history and function of plant VOCs.[20,27–33]

Undoubtedly, HIPVs play a central role in mediating interactions between plants and herbivores, between herbivores and their natural enemies, between plants and microorganisms, but also between plants themselves.[21,34,35] For example, laboratory studies have shown that HIPVs deter oviposition by arthropod herbivores,[36,37] attract natural enemies of these herbivores[4,5,9] and even induce defence genes and VOC emission in neighbouring plants[38–40] or prime these plants to respond faster to future herbivore attack.[41] In field studies, HIPVs have been shown to have the potential to

reduce the damage by pests of various plants including crop plants.[9,42–45] This opens the possibility of exploiting HIPVs for the development of novel strategies in crop protection. Indeed, an experiment whereby a hop yard was baited with methyl salicylate (MeSA) resulted in a significant increase in the numbers of beneficial predatory insects and in a dramatic reduction in spider mite numbers, the major arthropod pest of hops.[46] Recent advances in the biochemistry and molecular genetics of terpene biosynthesis in various plant families[47–59] should enable breeders to engineer plants to emit odours that more effectively attract the enemies of herbivores and thus reduce herbivory.[60,61] That this is a realistic possibility was demonstrated with *Arabidopsis thaliana* plants that were transformed with sesquiterpenoid synthase genes, making them release two additional terpenoid compounds that were attractive to the predatory mites, *Phytoseiulus persimili*.[62] Further field studies with synthetic HIPVs and genetically modified plants releasing such HIPVs will provide additional indications as to whether such manipulations could be included in agricultural practices to protect crops and the environment.

Various studies have provided detailed knowledge on the physiological and molecular basis of plant volatile synthesis and indirect defence responses in plants (reviewed by ref. 1,18,19). Still, our understanding of how the biosynthetic pathways are induced and interact with each other is rudimentary, probably because the induction and emission of HIPVs depends on the interaction between biotic factors, such as plant hormones,[19,63–68] herbivore-derived elicitors,[69–74] associated microorganisms[75,76] and abiotic factors, such as wounding,[77–80] O_3 and CO_2 concentration,[81–84] temperature and light,[85–87] UV-radiation[88] and many other factors.[89,90] Applying several stresses simultaneously to get a better understanding of how different pathways interact, will be one of the challenges in future studies on the physiology of plant volatiles.

There is a current boom in interest among ecologists to include the belowground interactions in studies on plants and associated organisms,[91–94] and VOCs have been found also to be involved in tritrophic signalling belowground.[16,95–97] Chen *et al.*[98] characterized a root-specific *Arabidopsis* terpene synthase responsible for the formation of the volatile mono-terpene 1,8-cineole, which is possibly involved in belowground interactions. Recently, Rasmann *et al.*[9] identified a sesquiterpene, (E)-β-caryophyllene, as a belowground herbivore-induced volatile signal that attracts entomopathogenic nematodes, which infect and kill larvae of the corn rootworm, *Diabrotica virgifera virgifera*, a voracious pest of maize. Another challenge in future studies will be to determine how such belowground interactions might influence aboveground volatile emissions and *vice versa*.

Collection and analysis of HIPVs

Sampling aboveground

The literature on HIPVs released by vegetative plant parts is vast and is continuously growing. In most cases it is unknown which compounds have biological activity and therefore biologists mostly try to sample and analyse the full range of HIPVs. This is usually achieved by collecting VOCs in the headspace of herbivore-induced plants that are enclosed in collection chambers using an adsorbing material with a relatively broad spectrum of adsorption (*e.g.* ref. 4,99). Subsequently the collected volatiles can be analysed by gas-chromatography (GC) and mass-spectrometry (MS) or a combination of both (GC/MS).

Fig. 3 shows the frequency with which the most commonly used sampling methods have been applied in the research of HIPVs during the last 10 years. Although this literature survey probably includes only part of all studies on herbivore-induced volatiles, it is clear that collection on adsorbents followed by desorption with solvents has been the most commonly used method. One advantage associated with solvent desorption is that it results in liquid samples that can be stored, which then can be used several times. This can be very useful for repeated analyses in GC, GC/MS and GC-EAD (gas-chromatography and electroantennogram-detection),[100] for further fractionation,[101] for peak enhancement coinjections[102] and for bioassays.[103–105] Adsorbents and solvents used in these studies vary, but the porous polymer Super Q[106] (80–100 mesh, Alltech, Deerfield, Illinois, USA) and the solvent dichloromethane are widely used by many groups. Although this adsorbent–solvent combination has proven highly effective in HIPV adsorption and desorption, Harper[107] argues that more than one adsorbent might be required to cover different classes of compounds, such as amines, aldehydes and aromatic hydrocarbons. There exist a wide range of adsorbent materials that can be used for this purpose, including activated charcoal, Anasorb 747, carboxens, silica gel, carbon molecular sieves and porous polymers such as Tenax, Chromosorb.[107,108] Choosing a combination of appropriate adsorbents may increase the number of compounds found in HIPV-blends. Still, only a small volume of the desorbed compounds can be injected into the GC, leaving minor compounds undetected, and the solvent peak can mask some highly volatile compounds. These problems can be avoided by using a desorption method without solvent, like thermal desorption, or solid-phase microextraction (SPME).[22,24,108–113]

The SPME technique employs a small fibre coated with an adsorbing material and has found widespread application in many fields, mostly for qualitative and semi-quantitative analyses in environmental and food analyses, but also
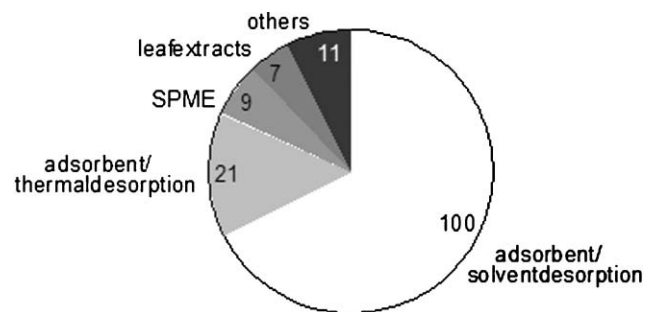

Fig. 3 The most commonly used HIPV collection methods during the last ten years. The numbers represent the number of studies found with a search on the ''Web of Science'' by entering the terms: ''induc* and volatil* and plant*'' from 1995–2004.
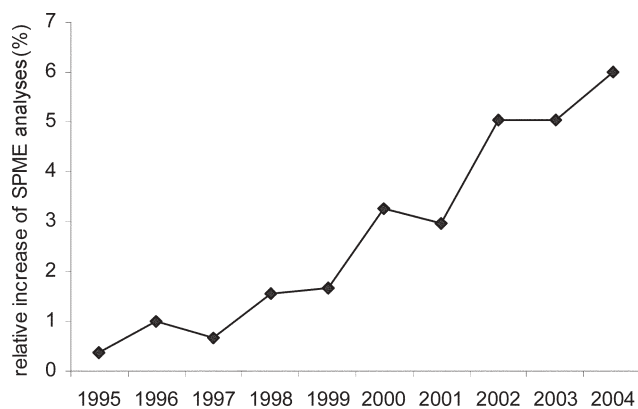
Fig. 4 Relative increase of the use of SPME to collect plant volatiles. The graph depicts the percentage of all surveyed plant volatile collection studies that employed the SPME technique. This information was obtained with a search on the "Web of Science" using the terms: "SPME and plant* and volatil*" and "volatil* and plant*".

quantitatively in analytical chemistry.[22] SPME has also gained increasing popularity in analyses of living biological samples, including plant VOCs[111] (Fig. 4). It has a number of advantages, like simplifying sample preparation, increasing reliability, selectivity and sensitivity and reducing analysis time. Various coating materials for the SPME fibres are available,[22,24,111] and choosing the appropriate fibre and sampling conditions are crucial for this technique to be effective. Still, the biggest limitation of SPME in studies on HIPVs is that the sample is lost after analysis and cannot be used for further analyses, GC-EAD, bioassays or fractionation.

Higher selectivity and sensitivity could also be obtained by using techniques specifically adapted for compounds with known functional groups. For example, damaged *Allium* plants produce and release sulfur containing VOCs, presumably to prevent insect herbivory.[114] To analyse true onion volatiles, Arnault *et al.*[115] used a combination of SPME-GC/MS and solvent extraction followed by GC/MS analyses specifically developed for these compounds. Other compounds might be trapped by using microchemical techniques such as derivatization and degradation methods.[116,117] Such techniques have played crucial roles in the determination of the structure of insect pheromones[118,119] and are widely used in ambient air analyses.[110,120–122] In pheromone studies, micro-reactions have three main uses; derivatization to aid chromatographic properties, functional group modification to help with MS structure determination, and assignment of absolute configuration to chiral centres.[118] In analyses of HIPVs these techniques are rarely used, despite the fact that such techniques seem ideal for sampling trace amounts or highly reactive VOCs, which are difficult to sample with any other technique. For example, aldehydes can be sampled using a 2,4-dinitrophenylhydrazine (DNPH)-coated filter, and amines with a filter coated with 1-naphthyl isothiocyanate.[122] Pre-treated filters are available from various companies (*e.g.* Supelco, SKC) and can easily be adapted to selectively adsorb HIPVs with a specific functional group. In our research, we used DNPH-coated silica (Supelco) to selectively adsorb 3-(Z)-hexenal and 2-(E)-hexenal, the two

major aldehydes emitted by maize plants under caterpillar attack (see below and Fig. 5).

An additional problem faced in analyses of HIPVs is that the release of some volatiles is highly dynamic, depending on the time after the plant is damaged,[3,123] but also on the time of day[36,124] and even season.[89,125,126] Insects can perceive minor changes in odour quantity and quality. Therefore, a good understanding of the kinetics of formation and release of HIPV is highly desired. Specifically designed and automated headspace collection systems and GC-analyses allow time dependent collection of volatile plant compounds,[3,99,127] and novel techniques even allow real time analyses of the emission of VOCs. For example, proton-transfer-reaction mass spectrometry (PTR-MS)[128–130] and portable artificial noses[131] permit fast sampling and real time (one measurement per second) analyses of plant volatiles and thus provide new insights into the kinetics of plant volatile releases. These techniques have the limitation that they do not distinguish between different VOCs with the same mass. Yet, Penuelas, Filella and co-workers[132] nicely show that the PTR-MS technique can be used to monitor small volatiles, like methanol released by *Succisa pratensis* leaves infested with caterpillars of *Euphydryas aurinia*. Such highly volatile compounds are likely to break through from sorbent tubes or are masked by the solvent peak in liquid sample GC-analyses and are seldom reported in HIPV studies using sorbent trapping.

To fully understand how HIPVs are produced and released, more comprehensive metabolomic approaches are needed. Schmelz *et al.*[66,133] have introduced an elegant technique based on vapour phase extraction and analysis by chemical ionization-GC/MS that simultaneously analyses phytohormones, phytotoxins, and VOCs in plants. Derivatization techniques are widely employed in metabolic profiling (reviewed in ref. 134) and combining metabolic and transcript
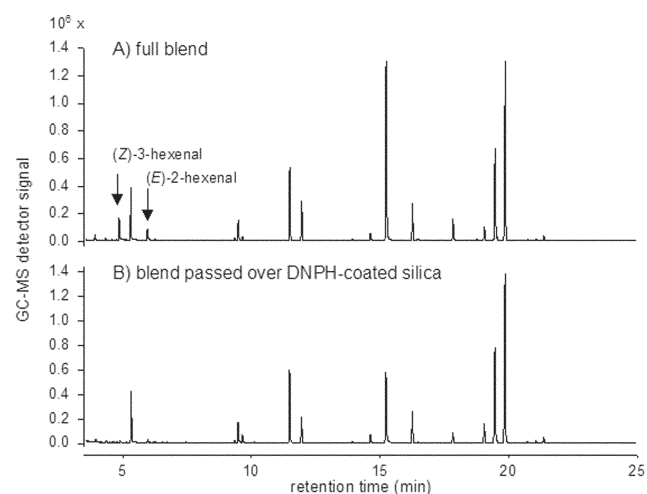

Fig. 5 GC-MS chromatograms obtained with the collected volatiles of caterpillar-infested maize seedlings. (A) Complete caterpillar-induced maize blend adsorbed on Super-Q filters and desorbed with dichloromethane. (B) Volatiles from the same blend after it was passed over a DNPH-coated silica filter, which selectively adsorbs carbonyl compounds. This breakthrough blend of HIPVs was collected and analysed as in (A). Further details on material and methods are given by D'Alessandro and Turlings.[103]

analyses might provide new insights into which genes are involved in the production of HIPVs.[135]

Deciding on which technique to use remains difficult, as several comparisons of different sampling techniques can result in quantitative and qualitative differences.[136–138] We suggest that the most reliable results in HIPV-analyses can be expected from the use of a combination of different approaches, including techniques specifically developed and calibrated for quantification of compounds with known functional groups. Knowing the exact relative quantities can be essential because often ratios among different compounds can be important in determining the attractiveness of odour blends to insects.[139–141]

Sampling belowground

Studies on belowground interactions bring new challenges to develop collection and analytical methods. So far, research on belowground allelochemicals mainly used extracts of root exudates,[142–144] but other methods to analyse VOCs from soil samples are also available.[130,145–150] As in aerial VOC analyses, comparing various sampling methods can lead to different quantities of VOCs.[148] It is therefore pertinent to include more than one method in the belowground collections. The soil is much more heterogeneous than the air and large differences in soil properties and VOC concentrations can occur over extremely short distances, which must be taken into account during sampling.[151] Biotic and abiotic factors that are known to affect the quantity and quality of HIPV-blends aboveground are likely to significantly affect belowground volatiles as well. Therefore, a major challenge for the analyses of belowground HIPVs will not only be to choose appropriate sampling and analysis tools, but also to obtain detailed knowledge on their kinetics, concentrations and distribution in the soil. Probably a good way to start is to analyse HIPVs in relatively well-defined, homogeneous soil types and then to repeat the measurements in more complex soils as well as in field experiments. For example, to determine the role of insect-induced (E)-β-caryophyllene from maize roots as an attractant for nematodes, an initial comparison was made between insect-damaged and undamaged maize roots, using pulverized roots. In subsequent tests, it was confirmed that (E)-β-caryophyllene rapidly diffuses through sand and attracts the nematodes, and finally the attractiveness of this sesquiterpene was tested in field experiments under natural conditions.[9]

Bioassays and bioassay-linked HIPV analyses

Using HIPVs as novel tools in crop protection implies not only a need for detailed knowledge about the biosynthesis and release of plant VOCs, but also about the perception and exploitation of these chemical signals by the animals. The identification of the specific, behaviourally active compounds within a complex blend has proven to be difficult. Commonly, such compounds are identified with a combination of behavioural studies and chemical analyses of the tested odour blends.[36,103,105,152–156] Another frequently practised method is gas chromatography combined with electroantennogram detection (GC-EAD) or with single cell recordings

(GC-SCR),[157] whereby the end of the GC column is split and one part of the effluent passes into the normal flame ionization detector (FID) and the other part is passed over an antenna or a single olfactory sensillum of the study insect. With the use of electrodes and amplifiers the responses of the antennal receptors can be measured and registered. Correlating these responses with the chromatogram obtained with FID detection reveals which compounds are perceived by the antennae.[100,158–162] Advances in this methodology that allow recordings to be made inside the central nervous system in combination with the novel technique of *in vivo* calcium-imaging have helped neurobiologists to start to understand how plant VOCs are detected and processed by insects.[163–165]

While methods such as GC-EAD or GC-SCR might give information on whether a compound is perceived by the olfactory system of an animal,[157] only behavioural tests will show if the animals are indeed attracted or repelled by a particular compound. So far, methods for testing the attractiveness of odour blends to arthropods consisted mainly of dynamic air bioassays using olfactometers,[166,167] wind tunnels,[4,168,169] or static air bioassays.[170,171] In these experiments arthropods are released at a defined distance from an odour source and their behaviour and attraction is recorded. In most cases chemical information on the odour sources had to be obtained in separate analytical studies. However, natural HIPV-blends exhibit not only high interspecific and intraspecific variability,[172–174] but quantity and quality of the compounds depends also on the degree and time after infestation.[3,175] To account for such variation, newer approaches attempt to standardize odour blends and to closely link chemical profiles with the insect behaviour.[175,176] For example, we have developed an olfactometer in which six odour sources can be tested simultaneously for their relative attractiveness, and during the assays part of each odour blend can be trapped for further analyses.[175] This device not only provides a direct link between the chemical profiles and the insect behaviour, but it also allows direct comparison of the attractiveness of a multitude of odour sources with multi-variate statistical approaches, including principal component analysis (PCA) and redundancy analysis (RDA). Multivariate statistical analyses are widely applied in analyses of food volatiles[177–179] and might also provide additional information in the analyses of HIPVs[172,180] and reveal key compounds that attract arthropods.

Another way of studying the importance of individual VOCs within a complex blend is to compare the attractiveness of volatile blends differing in only a few known compounds. These blends can be obtained by using different chemical elicitors and inhibitors[181–183] or by silencing genes involved in indirect defences.[184,185] Adding back missing VOCs to incomplete blends is a sound way to study the importance of individual compounds. For example the predatory mite *Phytoseiulus persimilis* prefers a methyl salicylate (MeSA)-containing volatile blend, induced by the spider mite *Tetranychus urticae* to a similar but MeSA-free blend, induced by jasmonic acid.[152] Adding synthetic MeSA to the MeSA-free blend significantly increased attraction to this odour, suggesting an important role for MeSA as a foraging cue for this predatory arthropod.[152,186]

We used an additional approach to obtain blends differing in only a few known compounds,[103] for which we modified the six-arm olfactometer described by Turlings *et al.*[175] in order to install adsorbing filter tubes between the odour source vessels and the arms of the olfactometers. By passing the induced volatile blend over these filter tubes, some compounds can be retained by the adsorbent material, while others break through and can be tested for attraction (Fig. 5). Furthermore, synthetic compounds can readily be added to the HIPV-blend and thus we are able to evaluate the importance of individual or groups of specific compounds. This novel technique has revealed an unexpected importance of minor compounds for the attraction of parasitic wasps to the complex HIPV-blends, whereas several of the dominating compounds appear to be only important after the wasps learn to associate them with the presence of hosts.[103] These experiments once more showed that responses towards HIPVs are not fixed. Indeed, it is well known that responses of insects to VOCs are highly plastic, depending on the physiological state of the animals and on previous experiences with odour sources.[187–189] Different forms of learning may modify the perception of chemical compounds and the response of insects towards odour sources.[190–193] This flexibility in the insects' responses, as well as the great variability in the odours produced[172,174,194–196] duly complicates the elucidation of key attractants, and learning experiments should be included in behavioural assays.

Conclusions and prospects

HIPVs play crucial roles in the interactions among various organisms. A good understanding of the key compounds involved in these interactions will not only provide important fundamental ecological knowledge, but should also allow us to manipulate certain of these interactions to our advantage, especially in agriculture. The complexity and variability of volatile blends emitted by herbivore-infested plants have proven to greatly complicate the identification of the principal compounds mediating interactions between the emitting plants and associated organisms. Renewed efforts should be made to integrate and adapt the latest techniques in analytical chemistry for this purpose. Choosing appropriate methods for sampling and analysing HIPVs is crucial. It might be possible to directly exploit insects' olfaction and behaviour to develop new selective and sensitive biosensors.[197–201] Insect chemoreception is known to be more sensitive and specific than any chemical detection system available today.[189] For example, in the moth *Spodoptera littoralis*, a change in heartbeat frequency can be triggered when fewer than six molecules of a key pheromone component hit the antennae of the insect.[202] Thus, the insects themselves might be most capable of informing us on which are the key substances that they use in their behaviour. Including well-designed electro-physiological and behavioural bioassays can provide essential additional information about bioactive compounds that cannot or can barely be detected in chemical analyses. In future studies biosensing techniques including electronic noses[203–206] might add to classical chemical analyses of HIPVs. If biologists, chemists and engineers join forces in this effort they will undoubtedly be able to fully unravel the fascinating world of chemically-mediated interactions between plants and their biotic environment. Such insight will then open the way to manipulate the interactions for our own benefit.

Acknowledgements

References

1 N. Dudareva, E. Pichersky and J. Gershenzon, *Plant Physiol.*, 2004, **135**, 1893–1902.
2 P. W. Paré and J. H. Tumlinson, *Plant Physiol.*, 1997, **114**, 1161–1167.
3 T. C. J. Turlings, U. B. Lengwiler, M. L. Bernasconi and D. Wechsler, *Planta*, 1998, **207**, 146–152.
4 T. C. J. Turlings, J. H. Tumlinson and W. J. Lewis, *Science*, 1990, **250**, 1251–1253.
5 M. Dicke and M. W. Sabelis, *Neth. J. Zool.*, 1988, **38**, 148–165.
6 R. M. P. Van Poecke, M. A. Posthumus and M. Dicke, *J. Chem. Ecol.*, 2001, **27**, 1911–1928.
7 T. Maeda and J. Takabayashi, *Appl. Entomol. Zool.*, 2001, **36**, 47–52.
8 U. S. R. Röse and J. H. Tumlinson, *Planta*, 2004, **218**, 824–832.
9 S. Rasmann, T. G. Köllner, J. Degenhardt, I. Hiltpold, S. Töpfer, U. Kuhlmann, J. Gershenzon and T. C. J. Turlings, *Nature*, 2005, **434**, 732–737.
10 T. Meiners and M. Hilker, *Oecologia*, 1997, **112**, 87–93.
11 R. Schröder, M. Forstreuter and M. Hilker, *Plant Physiol.*, 2005, **138**, 470–477.
12 R. Mumm, K. Schrank, R. Wegener, S. Schulz and M. Hilker, *J. Chem. Ecol.*, 2003, **29**, 1235–1252.
13 T. C. J. Turlings and J. H. Tumlinson, *Proc. Natl. Acad. Sci. USA*, 1992, **89**, 8399–8402.
14 U. S. R. Röse, W. J. Lewis and J. H. Tumlinson, *J. Chem. Ecol.*, 1998, **24**, 303–319.
15 L. Mattiacci, B. A. Rocca, N. Scascighini, M. D'Alessandro, A. Hern and S. Dorn, *J. Chem. Ecol.*, 2001, **27**, 2233–2252.
16 N. Neveu, J. Grandgirard, J. P. Nenon and A. M. Cortesero, *J. Chem. Ecol.*, 2002, **28**, 1717–1732.
17 E. Guerrieri, G. M. Poppy, W. Powell, E. Tremblay and F. Pennacchio, *J. Chem. Ecol.*, 1999, **25**, 1247–1261.
18 G. Arimura, C. Kost and W. Boland, *Biochim. Biophys. Acta, Mol. Cell Biol. Lipids*, 2005, **1734**, 91–111.
19 R. M. P. van Poecke and M. Dicke, *Plant Biol.*, 2004, **6**, 387–401.
20 J. K. Holopainen, *Trends Plant Sci.*, 2004, **9**, 529–533.
21 T. C. J. Turlings and F. Wäckers, in *Advances in Insect Chemical Ecology*, ed. R. T. Cardé and J. G. Millar, Cambridge University Press, Cambridge, UK, 2004.
22 G. Vas and K. Vekey, *J. Mass Spectrom.*, 2004, **39**, 233–254.
23 R. M. Smith, *J. Chromatogr., A*, 2003, **1000**, 3–27.
24 E. Baltussen, C. A. Cramers and P. J. F. Sandra, *Anal. Bioanal. Chem.*, 2002, **373**, 3–22.
25 P. Ciccioli, E. Brancaleoni, M. Frattoni and C. Maris, in *Environmental Monitoring Handbook*, ed. F. R. Burden, I. McKelvie, U. Forstner and A. Guenther, McGrawHill, New York, 2002, ch. 21.
26 J. G. Millar and K. F. Haynes, *Methods in Chemical Ecology*, Chapman & Hall, New York, 1998.
27 J. Penuelas and J. Llusia, *Trends Ecol. Evol.*, 2004, **19**, 402–404.
28 D. R. Gang, *Annu. Rev. Plant Biol.*, 2005, **56**, 301–325.
29 S. M. Owen and J. Penuelas, *Trends Plant Sci.*, 2005, **10**, 420–426.

30 U. Niinemets, F. Loreto and M. Reichstein, *Trends Plant Sci.*, 2004, **9**, 180–186.

31 T. N. Rosenstiel, A. L. Ebbets, W. C. Khatri, R. Fall and R. K. Monson, *Plant Biol.*, 2004, **6**, 12–21.

32 A. Janssen, M. W. Sabelis and J. Bruin, *Oikos*, 2002, **97**, 134–138.

33 M. Dicke, in *The Ecology and Evolution of Inducible Defenses*, ed. R. Tollrian and C. D. Harvell, Princeton University Press, Princeton, 1999, pp. 62–88.

34 M. Dicke, R. M. P. van Poecke and J. G. de Boer, *Basic Appl. Ecol.*, 2003, **4**, 27–42.

35 I. T. Baldwin, A. Kessler and R. Halitschke, *Curr. Opin. Plant Biol.*, 2002, **5**, 351–354.

36 C. M. De Moraes, M. C. Mescher and J. H. Tumlinson, *Nature*, 2001, **410**, 577–580.

37 P. J. Landolt, *Entomol. Exp. Appl.*, 1993, **67**, 79–85.

38 J. Ruther and S. Kleier, *J. Chem. Ecol.*, 2005, **31**, 2217–2222.

39 M. A. Farag, M. Fokar, H. A. Zhang, R. D. Allen and P. W. Paré, *Planta*, 2005, **220**, 900–909.

40 G. Arimura, R. Ozawa, T. Shimoda, T. Nishioka, W. Boland and J. Takabyashi, *Nature*, 2000, **406**, 512–515.

41 J. Engelberth, H. T. Alborn, E. A. Schmelz and J. H. Tumlinson, *Proc. Natl. Acad. Sci. USA*, 2004, **101**, 1781–1785.

42 A. Kessler and I. T. Baldwin, *Science*, 2001, **291**, 2141–2144.

43 J. S. Thaler, *Nature*, 1999, **399**, 686–688.

44 M. L. Bernasconi, T. C. J. Turlings, L. Ambrosetti, P. Bassetti and S. Dorn, *Entomol. Exp. Appl.*, 1998, **87**, 133–142.

45 D. G. James, *J. Chem. Ecol.*, 2003, **29**, 1601–1609.

46 D. G. James and T. S. Price, *J. Chem. Ecol.*, 2004, **30**, 1613–1628.

47 S. Aubourg, A. Lecharny and J. Bohlmann, *Mol. Genet. Genomics*, 2002, **267**, 730–745.

48 S. C. Trapp and R. B. Croteau, *Genetics*, 2001, **158**, 811–832.

49 E. Fridman and E. Pichersky, *Curr. Opin. Plant Biol.*, 2005, **8**, 242–248.

50 D. Tholl, F. Chen, J. Petri, J. Gershenzon and E. Pichersky, *Plant J.*, 2005, **42**, 757–771.

51 Y. Jia, D. R. Xia and E. S. Louzada, *J. Am. Soc. Hortic. Sci.*, 2005, **130**, 454–458.

52 D. M. Martin, J. Faldt and J. Bohlmann, *Plant Physiol.*, 2004, **135**, 1908–1927.

53 A. Aharoni, A. P. Giri, S. Deuerlein, F. Griepink, W. J. de Kogel, F. W. A. Verstappen, H. A. Verhoeven, M. A. Jongsma, W. Schwab and H. J. Bouwmeester, *Plant Cell*, 2003, **15**, 2866–2884.

54 J. Faldt, G. Arimura, J. Gershenzon, J. Takabayashi and J. Bohlmann, *Planta*, 2003, **216**, 745–751.

55 F. Chen, D. Tholl, J. C. D'Auria, A. Farooq, E. Pichersky and J. Gershenzon, *Plant Cell*, 2003, **15**, 481–494.

56 J. Degenhardt and J. Gershenzon, *Planta*, 2000, **210**, 815–822.

57 C. Schnee, T. G. Köllner, J. Gershenzon and J. Degenhardt, *Plant Physiol.*, 2002, **130**, 2049–2060.

58 T. G. Köllner, C. Schnee, J. Gershenzon and J. Degenhardt, *Plant Cell*, 2004, **16**, 1115–1131.

59 T. G. Köllner, C. Schnee, J. Gershenzon and J. Degenhardt, *Phytochemistry*, 2004, **65**, 1895–1902.

60 J. Degenhardt, J. Gershenzon, I. T. Baldwin and A. Kessler, *Curr. Opin. Biotechnol.*, 2003, **14**, 169–176.

61 N. Dudareva and F. Negre, *Curr. Opin. Plant Biol.*, 2005, **8**, 113–118.

62 I. F. Kappers, A. Aharoni, T. van Herpen, L. L. P. Luckerhoff, M. Dicke and H. J. Bouwmeester, *Science*, 2005, **309**, 2070–2072.

63 G. L. de Bruxelles and M. R. Roberts, *Crit. Rev. Plant Sci.*, 2001, **20**, 487–521.

64 E. Rojo, R. Solano and J. J. Sanchez-Serrano, *J. Plant Growth Regul.*, 2003, **22**, 82–98.

65 J. S. Thaler, R. Karban, D. E. Ullman, K. Boege and R. M. Bostock, *Oecologia*, 2002, **131**, 227–235.

66 E. A. Schmelz, J. Engelberth, H. T. Alborn, P. O'Donnell, M. Sammons, H. Toshima and J. H. Tumlinson, *Proc. Natl. Acad. Sci. USA*, 2003, **100**, 10552–10557.

67 K. Ament, M. R. Kant, M. W. Sabelis, M. A. Haring and R. C. Schuurink, *Plant Physiol.*, 2004, **135**, 2025–2037.

68 E. E. Farmer, E. Almeras and V. Krishnamurthy, *Curr. Opin. Plant Biol.*, 2003, **6**, 372–378.

69 J. H. Tumlinson and C. G. Lait, *Arch. Insect Biochem. Physiol.*, 2005, **58**, 54–68.

70 D. Spiteller and W. Boland, *J. Org. Chem.*, 2003, **68**, 8743–8749.

71 R. Halitschke, U. Schittko, G. Pohnert, W. Boland and I. T. Baldwin, *Plant Physiol.*, 2001, **125**, 711–717.

72 L. Mattiacci, M. Dicke and M. A. Posthumus, *Proc. Natl. Acad. Sci. USA*, 1995, **92**, 2036–2040.

73 T. Alborn, T. C. J. Turlings, T. H. Jones, G. Stenhagen, J. H. Loughrin and J. H. Tumlinson, *Science*, 1997, **276**, 945–949.

74 M. Merkx-Jacques and J. C. Bede, *Phytoprotection*, 2004, **85**, 33–37.

75 J. Huang, Y. J. Cardoza, E. A. Schmelz, R. Raina, J. Engelberth and J. H. Tumlinson, *Planta*, 2003, **217**, 767–775.

76 Y. J. Cardoza, H. T. Alborn and J. H. Tumlinson, *J. Chem. Ecol.*, 2002, **28**, 161–174.

77 R. Fall, T. Karl, A. Hansel, A. Jordan and W. Lindinger, *J. Geophys. Res., [Atmos.]*, 1999, **104**, 15963–15974.

78 G. A. Howe, *J. Plant Growth Regul.*, 2004, **23**, 223–237.

79 E. A. Schmelz, H. T. Alborn and J. H. Tumlinson, *Planta*, 2001, **214**, 171–179.

80 A. Mithöfer, G. Wanner and W. Boland, *Plant Physiol.*, 2005, **137**, 1160–1168.

81 J. Beauchamp, A. Wisthaler, A. Hansel, E. Kleist, M. Miebach, U. Niinemets, U. Schurr and J. Wildt, *Plant, Cell Environ.*, 2005, **28**, 1334–1343.

82 T. Vuorinen, A. M. Nerg and J. K. Holopainen, *Environ. Pollut.*, 2004, **131**, 305–311.

83 T. Vuorinen, A. M. Nerg, M. A. Ibrahim, G. V. P. Reddy and J. K. Holopainen, *Plant Physiol.*, 2004, **135**, 1984–1992.

84 R. Jasoni, C. Kane, C. Green, E. Peffley, D. Tissue, L. Thompson, P. Payton and P. W. Paré, *Environ. Exp. Bot.*, 2004, **51**, 273–280.

85 A. B. Guenther, P. R. Zimmerman, P. C. Harley, R. K. Monson and R. Fall, *J. Geophys. Res., [Atmos.]*, 1993, **98**, 12609–12617.

86 J. Takabayashi, M. Dicke and M. A. Posthumus, *J. Chem. Ecol.*, 1994, **20**, 6, 1329–1354.

87 S. P. Gouinguené and T. C. J. Turlings, *Plant Physiol.*, 2002, **129**, 1296–1307.

88 C. B. Johnson, J. Kirby, G. Naxakis and S. Pearson, *Phytochemistry*, 1999, **51**, 507–510.

89 J. Penuelas and J. Llusia, *Biol. Plant.*, 2001, **44**, 481–487.

90 J. Kesselmeier and M. Staudt, *J. Atmos. Chem.*, 1999, **33**, 23–88.

91 D. A. Wardle, R. D. Bardgett, J. N. Klironomos, H. Setala, W. H. van der Putten and D. H. Wall, *Science*, 2004, **304**, 1629–1633.

92 T. M. Bezemer, R. Wagenaar, N. M. Van Dam and F. L. Wäckers, *Oikos*, 2003, **101**, 555–562.

93 N. M. van Dam, J. A. Harvey, F. L. Wäckers, T. M. Bezemer, W. H. van der Putten and L. E. M. Vet, *Basic Appl. Ecol.*, 2003, **4**, 63–77.

94 W. H. Van der Putten, L. E. M. Vet, J. A. Harvey and F. L. Wäckers, *Trends Ecol. Evol.*, 2001, **16**, 547–554.

95 N. S. Aratchige, I. Lesna and M. W. Sabelis, *Exp. Appl. Acarol.*, 2004, **33**, 21–30.

96 R. van Tol, A. T. C. van der Sommen, M. I. C. Boff, J. van Bezooijen, M. W. Sabelis and P. H. Smits, *Ecol. Lett.*, 2001, **4**, 292–294.

97 M. I. C. Boff, F. C. Zoon and P. H. Smits, *Entomol. Exp. Appl.*, 2001, **98**, 329–337.

98 F. Chen, D. K. Ro, J. Petri, J. Gershenzon, J. Bohlmann, E. Pichersky and D. Tholl, *Plant Physiol.*, 2004, **135**, 1956–1966.

99 N. G. Agelopoulos, A. M. Hooper, S. P. Maniar, J. A. Pickett and L. J. Wadhams, *J. Chem. Ecol.*, 1999, **25**, 1411–1425.

100 S. Gouinguené, J. A. Pickett, L. J. Wadhams, M. A. Birkett and T. C. J. Turlings, *J. Chem. Ecol.*, 2005, **31**, 1023–1038.

101 T. C. J. Turlings and M. E. Fritzsche, in *Insect-Plant Interactions and Induced Plant Defence*, N. f. S. 223, ed. D.J. Chadwick and J. A. Goode, Wiley, Chichester, UK, 1999, pp. 21–38.

102 J. A. Pickett, in *Chromatography and Isolation of Insect Hormones and Pheromones*, ed. A. R. McCaffery and I. D. Wilson, Plenum Press, New York, 1990, pp. 299–309.

103 M. D'Alessandro and T. C. J. Turlings, *Chem. Senses*, 2005, **30**, 739–753.

104 S. Udayagiri and R. L. Jones, *J. Chem. Ecol.*, 1992, **18**, 1841–1855.

105 T. C. J. Turlings, J. H. Tumlinson, R. R. Heath, A. T. Proveaux and R. E. Doolittle, *J. Chem. Ecol.*, 1991, **17**, 2235–2251.

106 R. R. Heath and A. Manukian, *J. Chem. Ecol.*, 1992, **18**, 1209–1226.
107 M. Harper, *J. Chromatogr., A*, 2000, **885**, 129–151.
108 K. Dettmer and W. Engewald, *Anal. Bioanal. Chem.*, 2002, **373**, 490–500.
109 T. Gorecki and J. Namiesnik, *TrAC, Trends Anal. Chem.*, 2002, **21**, 276–291.
110 J. A. Koziel and I. Novak, *TrAC, Trends Anal. Chem.*, 2002, **21**, 840–850.
111 F. Augusto and A. L. P. Valente, *TrAC, Trends Anal. Chem.*, 2002, **21**, 428–438.
112 G. A. Mills and V. Walker, *J. Chromatogr., A*, 2000, **902**, 267–287.
113 L. Pillonel, J. O. Bossett and R. Tabacchi, *Lebensm.-Wiss. Technol.*, 2002, **35**, 1–14.
114 S. Dugravot, E. Thibout, A. Abo-Ghalia and J. Huignard, *Entomol. Exp. Appl.*, 2004, **113**, 173–179.
115 I. Arnault, N. Mondy, F. Cadoux and J. Auger, *J. Chromatogr., A*, 2000, **896**, 117–124.
116 A. B. Attygalle, in *Methods in Chemical Ecology*, ed. J. G. Millar and K. F. Haynes, Chapman & Hall, New York, 1998, vol. 1.
117 E. E. Stashenko and J. R. Martinez, *TrAC, Trends Anal. Chem.*, 2004, **23**, 553–561.
118 G. R. Jones and N. J. Oldham, *J. Chromatogr., A*, 1999, **843**, 199–236.
119 A. B. Attygalle and E. D. Morgan, *Angew. Chem., Int. Ed. Engl.*, 1988, **27**, 460–478.
120 S. Uchiyama and S. Hasegawa, *Atmos. Environ.*, 1999, **33**, 1999–2005.
121 P. von Zweigbergk, R. Lindahl, A. Ostin, J. Ekman and J. O. Levin, *J. Environ. Monit.*, 2002, **4**, 663–666.
122 J. O. Levin and R. Lindahl, *Analyst*, 1994, **119**, 79–83.
123 M. E. Hoballah and T. C. J. Turlings, *J. Chem. Ecol.*, 2005, **31**, 2003–2018.
124 J. H. Loughrin, A. Manukian, R. R. Heath, T. C. J. Turlings and J. H. Tumlinson, *Proc. Natl. Acad. Sci. USA*, 1994, **91**, 11836–11840.
125 A. Blaakmeer, J. B. F. Geervliet, J. J. A. Vanloon, M. A. Posthumus, T. A. Vanbeek and A. Degroot, *Entomol. Exp. Appl.*, 1994, **73**, 175–182.
126 A. Hern and S. Dorn, *Phytochem. Anal.*, 2003, **14**, 232–240.
127 R. R. Heath and A. Manukian, *J. Chem. Ecol.*, 1994, **20**, 593–608.
128 J. A. De Gouw, C. J. Howard, T. G. Custer, B. M. Baker and R. Fall, *Environ. Sci. Technol.*, 2000, **34**, 2640–2648.
129 S. Hayward, A. Tani, S. M. Owen and C. N. Hewitt, *Tree Physiol.*, 2004, **24**, 721–728.
130 M. Steeghs, H. P. Bais, J. de Gouw, P. Goldan, W. Kuster, M. Northway, R. Fall and J. M. Vivanco, *Plant Physiol.*, 2004, **135**, 47–58.
131 M. Kunert, A. Biedermann, T. Koch and W. Boland, *J. Sep. Sci.*, 2002, **25**, 677–684.
132 J. Penuelas, I. Filella, C. Stefanescu and J. Llusia, *New Phytol.*, 2005, **167**, 851–857.
133 E. A. Schmelz, J. Engelberth, J. H. Tumlinson, A. Block and H. T. Alborn, *Plant J.*, 2004, **39**, 790–808.
134 J. M. Halket, D. Waterman, A. M. Przyborowska, R. K. P. Patel, P. D. Fraser and P. M. Bramley, *J. Exp. Bot.*, 2005, **56**, 219–243.
135 P. Mercke, I. F. Kappers, F. W. A. Verstappen, O. Vorst, M. Dicke and H. J. Bouwmeester, *Plant Physiol.*, 2004, **135**, 2012–2024.
136 J. Faldt, M. Eriksson, I. Valterova and A. K. Borg-Karlson, *Z. Naturforsch., C: Biosci.*, 2000, **55**, 180–188.
137 N. G. Agelopoulos and J. A. Pickett, *J. Chem. Ecol.*, 1998, **24**, 1161–1172.
138 H. Rothweiler, P. A. Wager and C. Schlatter, *Atmos. Environ., Part B*, 1991, **25**, 231–235.
139 C. M. De Moraes, W. J. Lewis, P. W. Paré, H. T. Alborn and J. H. Tumlinson, *Nature*, 1998, **393**, 570–573.
140 J. F. Tooker, W. A. Koenig and L. M. Hanks, *Proc. Natl. Acad. Sci. USA*, 2002, **99**, 15486–15491.
141 T. J. A. Bruce, L. J. Wadhams and C. M. Woodcock, *Trends Plant Sci.*, 2005, **10**, 269–274.
142 C. Nguyen, *Agronomie*, 2003, **23**, 375–396.
143 C. Bertin, X. H. Yang and L. A. Weston, *Plant Soil*, 2003, **256**, 67–83.
144 Inderjit and S. O. Duke, *Planta*, 2003, **217**, 529–539.
145 J. S. Alvarado and C. Rose, *Talanta*, 2004, **62**, 17–23.
146 T. E. Lewis, A. B. Crockett and R. L. Siegrist, *Environ. Monit. Assess.*, 1994, **30**, 213–246.
147 M. B. Wise, C. V. Thompson, R. Merriweather and M. R. Guerin, *Field Anal. Chem. Technol.*, 1997, **1**, 251–276.
148 M. W. Couch, C. J. Schmidt and S. C. Wasdo, *Adv. Environ. Res.*, 2000, **4**, 97–102.
149 M. Ojala, I. Mattila, V. Tarkiainen, T. Sarme, R. A. Ketola, A. Maattanen, R. Kostiainen and T. Kotiaho, *Anal. Chem.*, 2001, **73**, 3624–3631.
150 M. D. G. Meniconi, R. Parris and C. L. P. Thomas, *Analyst*, 2003, **128**, 1232–1237.
151 B. A. Schumacher and M. M. Minnich, *Environ. Sci. Technol.*, 2000, **34**, 3611–3616.
152 J. G. De Boer and M. Dicke, *J. Chem. Ecol.*, 2004, **30**, 255–271.
153 M. Dicke, T. A. van Beek, M. A. Posthumus, N. B. Dom, H. van Bokhoven and A. de Groot, *J. Chem. Ecol.*, 1990, **16**, 2, 381–396.
154 M. E. F. Hoballah, C. Tamó and T. C. J. Turlings, *J. Chem. Ecol.*, 2002, **28**, 951–968.
155 M. A. Birkett, C. A. M. Campbell, K. Chamberlain, E. Guerrieri, A. J. Hick, J. L. Martin, M. Matthes, A. Napier, J. Pettersson, J. A. Pickett, G. M. Poppy, E. M. Pow, L. J. Pye, L. E. Smart, G. H. Wadhams, L. J. Wadhams and C. M. Woodcock, *Proc. Natl. Acad. Sci. USA*, 2000, **97**, 9329–9334.
156 P. Scutareanu, B. Drukker, J. Bruin, M. A. Posthumus and M. W. Sabelis, *J. Chem. Ecol.*, 1997, **23**, 2241–2260.
157 A. Wibe, *J. Insect Physiol.*, 2004, **50**, 497–503.
158 H. A. Smid, J. J. A. van Loon, M. A. Posthumus and L. E. M. Vet, *Chemoecology*, 2002, **12**, 169–176.
159 T. Rostelien, A. K. Borg-Karlson and H. Mustaparta, *J. Comp. Physiol. A: Sens. Neural Behav. Physiol.*, 2000, **186**, 833–847.
160 B. Weissbecker, J. J. A. Van Loon, M. A. Posthumus, H. J. Bouwmeester and M. Dicke, *J. Chem. Ecol.*, 2000, **26**, 1433–1445.
161 Y. J. Du, G. M. Poppy, W. Powell, J. A. Pickett, L. J. Wadhams and C. M. Woodcock, *J. Chem. Ecol.*, 1998, **24**, 1355–1368.
162 E. N. Barata, H. Mustaparta, J. A. Pickett, L. J. Wadhams and J. Araujo, *J. Comp. Physiol. A: Neuroethol. Sens. Neural Behav. Physiol.*, 2002, **188**, 121–133.
163 H. T. Skiri, C. G. Galizia and H. Mustaparta, *Chem. Senses*, 2004, **29**, 253–267.
164 C. G. Galizia, S. Sachse and H. Mustaparta, *J. Comp. Physiol. A: Sens. Neural Behav. Physiol.*, 2000, **186**, 1049–1063.
165 H. Mustaparta, *Entomol. Exp. Appl.*, 2002, **104**, 1–13.
166 S. Steinberg, M. Dicke, L. E. M. Vet and R. Wanningen, *Entomol. Exp. Appl.*, 1992, **63**, 163–175.
167 L. E. M. Vet, J. C. van Lenteren, M. Heymans and E. Meelis, *Physiol. Entomol.*, 1983, **8**, 97–106.
168 T. C. Baker and R. T. Cardé, in *Techniques in Pheromone Research*, ed. H. E. Hummel and T. A. Miller, Springer-Verlag, New York, 1984, pp. 45–73.
169 J. H. Visser, *Entomol. Exp. Appl.*, 1976, **20**, 275–288.
170 J. Ruther and J. L. M. Steidle, *J. Chem. Ecol.*, 2000, **26**, 1205–1217.
171 O. T. Jones and T. H. Coaker, *Physiol. Entomol.*, 1977, **2**, 189–197.
172 T. Degen, C. Dillmann, F. Marion-Poll and T. C. J. Turlings, *Plant Physiol.*, 2004, **135**, 1928–1938.
173 S. Gouinguené, T. Degen and T. C. J. Turlings, *Chemoecology*, 2001, **11**, 9–16.
174 C. E. M. Van Den Boom, T. A. Van Beek, M. A. Posthumus, A. De Groot and M. Dicke, *J. Chem. Ecol.*, 2004, **30**, 69–89.
175 T. C. J. Turlings, A. C. Davison and C. Tamó, *Physiol. Entomol.*, 2004, **29**, 45–55.
176 N. Scascighini, L. Mattiacci, M. D'Alessandro, A. Hern, A. S. Rott and S. Dorn, *Chemoecology*, 2005, **15**, 97–104.
177 A. C. Noble and S. E. Ebeler, *Food Rev. Int.*, 2002, **18**, 1–21.
178 C. G. Zambonin, L. Balest, G. E. De Benedetto and F. Palmisano, *Talanta*, 2005, **66**, 261–265.
179 S. Mildner-Szkudlarz, H. H. Jelen, R. Zawirska-Wojtasiak and E. Wasowicz, *Food Chem.*, 2003, **83**, 515–522.
180 R. Mumm, T. Tiemann, S. Schulz and M. Hilker, *Phytochemistry*, 2004, **65**, 3221–3230.

181 M. Dicke, R. Gols, D. Ludeking and M. A. Posthumus, *J. Chem. Ecol.*, 1999, **25**, 1907–1922.

182 T. Koch, T. Krumm, V. Jung, J. Engelberth and W. Boland, *Plant Physiol.*, 1999, **121**, 153–162.

183 T. C. J. Turlings, H. T. Alborn, J. H. Loughrin and J. H. Tumlinson, *J. Chem. Ecol.*, 2000, **26**, 189–202.

184 A. Kessler, R. Halitschke and I. T. Baldwin, *Science*, 2004, **305**, 665–668.

185 R. M. P. van Poecke and M. Dicke, *Plant, Cell Environ.*, 2003, **26**, 1541–1548.

186 J. G. de Boer and M. Dicke, *Entomol. Exp. Appl.*, 2004, **110**, 181–189.

187 K. Ueno and T. Ueno, *J. Ethol.*, 2005, **23**, 43–49.

188 L. E. M. Vet and M. Dicke, *Annu. Rev. Entomol.*, 1992, **37**, 141–172.

189 M. Dicke, *Entomol. Exp. Appl.*, 1999, **91**, 131–142.

190 R. L. Davis, *Neuron*, 2004, **44**, 31–48.

191 T. C. J. Turlings, F. L. Wäckers, L. E. M. Vet, W. J. Lewis and J. H. Tumlinson, in *Insect Learning. Ecological and Evolutionary Perspectives.*, ed. D. R. Papaj and A. C. Lewis, Chapman & Hall, New York, 1993, pp. 51–78.

192 L. E. M. Vet, W. J. Lewis and R. T. Cardé, in *Chemical Ecology of Insects*, ed. R. T. Cardé and W. J. Bell, Chapman & Hall., New York, 1995, pp. 65–101.

193 D. R. Papaj and A. C. Lewis, *Insect Learning*, Chapman and Hall, New York, London, 1993.

194 O. E. Krips, P. E. L. Willems, R. Gols, M. A. Posthumus, G. Gort and M. Dicke, *J. Chem. Ecol.*, 2001, **27**, 1355–1372.

195 J. Takabayashi, M. Dicke and M. A. Posthumus, *Chemoecology*, 1991, **2**, 1–6.

196 J. H. Loughrin, A. Manukian, R. R. Heath and J. H. Tumlinson, *J. Chem. Ecol.*, 1995, **21**, 1217–1227.

197 K. C. Park and T. C. Baker, *J. Insect Physiol.*, 2002, **48**, 1139–1145.

198 S. Schutz, B. Weissbecker, U. T. Koch and H. E. Hummel, *Biosens. Bioelectron.*, 1999, **14**, 221–228.

199 Y. Kuwana, S. Nagasawa, I. Shimoyama and R. Kanzaki, *Biosens. Bioelectron.*, 1999, **14**, 195–202.

200 G. C. Rains, J. K. Tomberlin, M. D'Alessandro and W. J. Lewis, *Trans. ASAE*, 2004, **47**, 2145–2152.

201 M. Tertuliano, D. M. Olson, G. C. Rains and W. J. Lewis, *Entomol. Exp. Appl.*, 2004, **110**, 165–172.

202 A. M. Angioy, A. Desogus, I. T. Barbarossa, P. Anderson and B. S. Hansson, *Chem. Senses*, 2003, **28**, 279–284.

203 D. James, S. M. Scott, Z. Ali and W. T. O'Hare, *Microchim. Acta*, 2005, **149**, 1–17.

204 M. Trojanowicz and M. Szewczynska, *TrAC, Trends Anal. Chem.*, 2005, **24**, 92–106.

205 D. L. Garcia-Gonzalez and R. Aparicio, *Grasas Aceites*, 2002, **53**, 96–114.

206 C. G. Pinto, M. E. F. Laespada, J. L. P. Pavon and B. M. Cordero, *Quim. Anal.*, 2001, **20**, 3–11.