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Can plants betray the presence of multiple herbivore species to predators and parasitoids? The role of learning in phytochemical information networks

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Special Feature**Relationships between biodiversity and ecosystem functioning across different scales**

Can plants betray the presence of multiple herbivore species to predators and parasitoids? The role of learning in phytochemical information networks

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Abstract In response to feeding by phytophagous arthropods, plants emit volatile chemicals. This is shown to be an active physiological response of the plant and the released chemicals are therefore called herbivore-induced plant volatiles (HIPV). One of the supposed functions of HIPV for the plant is to attract carnivorous natural enemies of herbivores. Depending on which plant and herbivore species interact, blends of HIPV show qualitative and quantitative variation. Hence, one may ask whether this allows the natural enemies to discriminate between volatiles from plants infested by herbivore species that are either suitable or unsuitable as a food source for the natural enemy. Another question is whether natural enemies can also recognise HIPV when two or more herbivore species that differ in suitability as a food source simultaneously attack the same plant species. By reviewing the literature we show that arthropod predators and parasitoids can tell different HIPV blends apart in several cases of single plant–single herbivore systems and even in single plant–multiple herbivore systems. Yet, there are also cases where predators do not

discriminate or discriminate only after having learned the association between HIPV and herbivores that are either suitable or non-suitable as a source of food. In this case, suitable herbivores may profit from colonising plants that are already infested by another non-suitable herbivore. The resulting temporal or partial refuge may have important population dynamical consequences, as such refuges have been shown to stabilise otherwise unstable predator–prey models of the Lotka-Volterra or Nicholson-Bailey type.

Keywords Herbivore-induced plant volatiles · Predator · Prey · Phytochemicals

Introduction

One of the interesting features of chemical communication is that the emitter cannot control who will be the receiver once the chemical information is released. This creates the opportunity for other organisms of the same or a different species to use the information to their own benefit. Conflicts of interest may then arise when receivers of the information act against the interests of the sender. Such conflicts may then become a driving force for natural-selection moulding traits of senders and receivers. The result is a complex network of information exchange, where the behaviour of one organism cannot be understood without considering the responses of others.

Here, we review the phytochemical information network that plays a role in the interaction between plants and the herbivorous and predatory arthropods that live on plants. Herbivory is shown to induce the plant to release specific volatile chemicals that arrest and/or attract natural enemies of the herbivores (e.g. Dicke and Sabelis 1988; Dicke et al. 1990a, b; Turlings et al. 1990, 1995; Takabayashi and Dicke 1996). These chemicals are called herbivore-induced plant volatiles (HIPV). Several lines of evidence support an active role of the plant in releasing them: (1) whereas many natural enemies are attracted to plants that harbour herbivores suitable as prey, the herbivores themselves and some of the products they deposit on the plant (e.g. faeces, silk) can be eliminated as the source of volatiles found in blends of HIPV (e.g. Sabelis et al. 1984); (2) the compounds identified in blends of HIPV have been reported to occur in plants (e.g. Dicke et al. 1990a; Turlings et al. 1990; Scutareanu et al. 1997; Du et al. 1998); (3) pathways for biosynthesis of compounds in blends of HIPV exist in the plants and are shown to be inducible by herbivory (e.g. Paré et al. 1999; Bouwmeester et al. 1999); (4) blends of HIPV not only emanate from the leaf under attack by the herbivore, but are also systemically induced in the plant (Turlings and Tumlinson 1992; Dicke 1994; Guerrieri et al. 1999); (5) application of jasmonic acid (JA), a phytohormone, to

wild-type plants or defence-signalling mutants leads to production of volatiles similar to HIPV (Hopke et al. 1994; Ozawa et al. 2000; Gols et al. 2003; Thaler et al. 2002; Van Poecke and Dicke 2003; Ament et al. 2004); (6) herbivore-induced gene expression patterns in plants are similar to those mediated by jasmonates (e.g. Kant et al. 2004; Ament et al. 2004; Mercke et al. 2004; Reymond et al. 2004); (7) elicitors of HIPV synthesis in the plant have been found in the regurgitate/saliva of herbivores [N-(17-hydroxylinolenoyl)-L-glutamine or volicitin: Alborn et al. 1997, 2000; β -glucosidase: Hopke et al. 1994; Mattiacci et al. 1995]s.

Although the active role of the plant is strongly supported by experimental evidence, it is less clear who are the receivers and—more importantly—which receivers use the phytochemical information to their own benefit, thereby possibly acting in line with or against the interests of the plant (Sabelis et al. 1999a, b, c, 2002, 2005a, b; Dicke 1999). In theory, the plant may produce a chemically simple, general alarm when attacked by any herbivore, but this would allow natural enemies of the herbivores only to discriminate between damaged and undamaged plants and this would leave them the considerable task of finding plants with herbivores that are suitable prey. If by making the chemical alarm more specific, the plant gains by receiving assistance more quickly from the herbivore's enemies, then natural selection will favour plants that produce an alarm signal specific to the type or even species of attacker. But, how far will plants evolve in diversifying their call for help? Will they be able to send out different signals when simultaneously attacked by different herbivore species? Will the herbivores' enemies be able to tell plant signals associated with prey and non-prey apart? And if they can, is this ability innate or can it be learned? These questions are of obvious importance to understand how plants can effectively employ the herbivore's enemies as an indirect defence against herbivory. For example, if plants cannot provide a sufficiently diversified alarm in case they are attacked by several herbivores, then some herbivores may use plants that are already attacked by other herbivores as enemy-free or enemy-sparse space.

In this article, we review the literature to assess specificity in eliciting a response from the enemies of herbivores that is either innate or that is learned from an experience with certain combinations of HIPV and herbivore species. We distinguish between HIPV from plants attacked by a single herbivore species and HIPV from plants attacked by multiple herbivore species, and we focus on the behavioural response of the herbivore's enemies to HIPV, not on the chemical details of HIPV.

How specific are blends of HIPV from singly infested plants?

One of the striking features of HIPV as a means to attract natural enemies is that there are usually several compounds involved and that these mixtures of volatiles contain a great deal of specific information. In an olfactometer study by Sabelis and van der Baan (1983), predatory mites (*Phytoseiulus persimilis* and *Metaseiulus occidentalis*) known to control spider mites (*Tetranychusurticae* and *Tetranychusviennensis*) were shown to prefer volatiles from lima bean leaves and apple leaves infested by these *Tetranychus* mites when clean leaves were the alternative, but they did not respond to apple leaves infested by non-prey, such as fruit-tree red spider mites (*Panonychus ulmi*) and apple rust mites (*Aculus schlechtendahl*i). Similarly, predatory mites (*Amblyseius andersoni* and *Neoseiulus finlandicus*) known to control fruit-tree red spider mites and apple rust mites were shown to respond to apple leaves with these herbivorous mites, but not to lima bean leaves or apple leaves infested with *Tetranychus* mites. This differential response makes sense because *Tetranychus* mites use silken webs as an effective defence against *A. andersoni* and *N. finlandicus*, but this web is much less effective against *P. persimilis* and *M. occidentalis* (Sabelis and van der Baan 1983; Sabelis and Bakker 1992). Although a role of prey-produced odours in this attraction cannot be fully excluded, evidence so far points at odour components that are of plant origin (Dicke et al. 1990a, b; Takabayashi et al. 1991; Dicke 1994; Thaler et al. 2002; Gols et al. 2003). This implies that the plant provides predators with information that is sufficiently specific to allow discrimination by olfaction. This hypothesis was confirmed by De Moraes et al. (1998) in a study on olfactory responses of the parasitoid *Cardiochiles nigriceps* to three species of host plants (tobacco, maize and cotton) that were attacked by two closely related herbivore species, the tobacco budworm (*Heliothis virescens*) and the corn earworm (*Helicoverpa zea*). These authors found that tobacco, cotton and maize plants each released distinct volatile blends in response to damage by the two herbivore species, and that the parasitoid exploits these differences in odour blends to distinguish infestation by its host, *H. virescens*, from that by the non-host *H. zea*. Most convincingly, these preferences persisted when the leaves with the herbivores had been removed and, thus, only systemically produced odours were offered.

Another comprehensive study showing herbivore specificity of HIPV was done by assessing the choice of a braconid parasitoid (*Aphidius ervi*) for broad bean plants (*Vicia faba*) infested by either of two aphid species, one suitable host (the pea aphid, *Acyrtosiphum pisum*) and one non-host (the black bean aphid, *Aphis fabae*) (Du et al. 1998; Guerrieri et al. 1999). Air entrainment extracts of volatiles collected from a broad bean plant infested by the non-host aphid or from an

uninfested broad bean plant elicited few oriented flights and landing responses by female parasitoids. These extracts were significantly less attractive than extracts collected from a broad bean plant infested by the host aphid, indicating the specificity of HIPV from the same plant species attacked by different aphid species. A similar example exists for whiteflies (*Trialeurodes vaporariorum*). They induce de novo synthesis and release of four volatiles in beans, and three of those elicit oriented flight and landing of the parasitoid, *Encarsia formosa*, when offered in pure form, whereas a mixture of two volatiles [(Z)-3-hexen-1-ol and 3-octanone] was most effective (Birkett et al. 2003).

Learning to cope with variability in HIPV from singly and multiply infested plants

Because the same species of herbivore can induce different plant species to produce different odours, and different species of herbivores can induce the same plant species to produce different odours, predators that use their olfactory senses to find their preferred prey face a difficult task. The number of chemicals in blends of HIPV is large, but limited. Thus, blends of HIPV may differ qualitatively, but they often share components and hence differ quantitatively. There is evidence for a genetic component of olfactory responses in predatory mites (Margolies et al. 1997; Maeda et al. 1999, 2001; Jia et al. 2002) and parasitoids (Gu and Dorn 2000; Wang and Dorn 2003; Wang et al. 2004), but it is hard to see how fixed responses suffice in a world full of variation in odours. The ability to associate odours with rewards is well established for parasitoids (Papaj and Lewis 1993; Roitberg et al. 1993; Turlings et al. 1993; Vet et al. 1995), and this is now also shown for HIPV as a cue associated with the occurrence of hosts for the parasitoids (Vet and Dicke 1992; Geervliet et al. 1998a, b; Storeck et al. 2000).

Predatory arthropods were much less intensively investigated for their ability to learn, but it was known that their olfactory responses may depend on conditions during rearing (Takabayashi and Dicke 1992; Krips et al. 1999; see also De Boer and Dicke 2004). That predatory arthropods can also learn to associate HIPV with herbivores as profitable prey is a new finding (Drukker et al. 2000a, b). This has led to the following hypothesis on the role of fixed and plastic responses to HIPV (Sabelis et al. 1999a, Drukker et al. 2000a, b). Predatory arthropods often grow up on a plant with herbivores as prey. On this host plant, they experience HIPV in the presence of abundant prey, resulting in a positive association. However, predation causes prey densities to decline to levels where they are not sufficiently abundant to the predator. The herbivore-infested plants,

however, continue to produce HIPV, even when herbivores have declined in numbers. Hence, predators will experience HIPV in presence of low prey density. This causes the predators to build up a negative association with HIPV, triggering dispersal away from the herbivore-poor plant. Although not yet proven for predators (but see Papaj et al. 1994 for evidence in parasitic wasps), it is likely that this negative association will quickly fade away with time spent in dispersal. Then, the predators will switch to rely on the initial positive association (e.g. Papaj et al. 1994) or perhaps an innate odour preference. Upon arrival on a new plant with prey, the starved, predatory arthropods start to feed on this prey. While experiencing this reward they learn that contextual cues such as HIPV are associated with the presence of their newly found prey. To stay in those areas of the plant where the prey density is highest, the arthropods may sample the prey densities on the plant and upon depleting a patch they may search locally to find other prey-patches on the same plant. Predatory arthropods switch from local searching behaviour to dispersal behaviour (e.g. aerial) when their prey decline to levels where they are not sufficiently abundant to the predator. To find their next meal, the predators rely on both their memory and their innate preferences. It is conceivable that—during this phase—the predators are attracted to the HIPV of non-prey-infested plants, and it is expected that the predators, after a local exploration, disperse again until they find yet another plant with herbivores as prey. Some predators may also be able to learn from the encounters with non-prey and use this experience to avoid future mistakes and enhance their ability to differentiate between HIPV associated with non-prey and HIPV associated with prey.

A number of cases have been reported where predatory arthropods and parasitoids respond to HIPV from plants with non-prey or non-host herbivores (Agrawal and Colfer 2000; Shimoda and Dicke 2000; Thaler et al. 2002; Dicke et al. 2003; Van Poecke and Dicke 2003; A. Janssen and M. Van Wijk 2005, unpublished data). Shimoda and Dicke (2000) collected females of the predatory mite *P. persimilis* from a culture that was fed spider mites (*T. urticae*) on bean and starved them for 1 h or 1 day. Predators that were starved for 1 h responded positively to HIPV from bean leaves infested by a non-prey herbivore (the beet armyworm, *Spodoptera exigua*), but females that were starved for 1 day did not. The authors argue that 1-h starvation corresponds to a real-life situation where the predator recently lost track of prey-associated cues, and thus must be close to its prey (and thus there is little risk of visiting leaves with non-prey). For that case, the authors hypothesize that the predator responds to a subset of volatile chemicals from the full HIPV blend, in particular those shared between blends from bean infested with prey (spider mites) and bean infested with non-prey (*S. exigua*). One day of starvation would then represent a situation in which the original site where the predators were fed with prey is too distant. For that case, the authors hypothesize

that the predators avoid the risk of visiting a plant with non-prey. Thus, the predators may only initially (1 h) generalise between the learned blend associated with prey (spider mites) on bean and the blend associated with non-prey (beet armyworm) on bean. After 24 h, all predators equally prefer a blend associated with their prey (spider mites). Strikingly, 1-h starved predators appear not to generalise between blends when they were collected from a culture with prey (spider mites) on cucumber and offered the blend associated with non-prey (beet armyworm) on bean.

In another series of experiments with the same arthropods, De Boer et al. (2004) showed that *P. persimilis* predators fed with spider mites on bean plants respond positively to HIPV from bean plants infested by a sufficiently high number of spider mites, when HIPV from other plants infested by beet armyworm larvae were the alternative. Chemical analysis of the different odour blends from plants infested by either one or the other herbivore species showed mainly quantitative differences in composition, suggesting that the predatory mites discriminate between ratios of volatile chemicals in the HIPV blends (De Boer et al. 2004). Thus, the predatory mite *P. persimilis* can locate plants with prey in a mixture of HIPV from plants infested by prey herbivores and plants with non-prey herbivores. De Boer et al. (2005) also found that non-rewarding experiences (e.g. starvation in the presence of HIPV from *S. exigua*-infested bean plants) have much less effect on olfactory choice between HIPV from *S. exigua*-infested and *T. urticae*-infested bean plants than rewarding experiences (feeding on *T. urticae* in the presence of HIPV from *T. urticae*-infested bean plants), whereas providing these rewarding and non-rewarding experiences shortly after each other had the strongest effect.

A. Janssen and M. Van Wijk (2005, unpublished data) investigated innate and acquired responses of three species of predatory mites (*P. persimilis*, *Iphiseius degenerans*, *Neoseiulus cucumeris*) to HIPV produced by cucumber plants with prey (the spider mite *T. urticae* for *P. persimilis* and the western flower thrips *Frankliniella occidentalis* for the other two predator species) and non-prey (thrips for *P. persimilis* and spider mites for the other two predator species). Although all three species discriminated between plants with prey and plants with non-prey, this resulted from quite different processes. One species (*N. cucumeris*) showed innate attraction to volatiles from plants with prey, but not to volatiles from plants with non-prey. A second species (*I. degenerans*) showed an innate aversion to volatiles from plants with non-prey and was not attracted to plants with prey. A third species (*P. persimilis*) was attracted to plants with prey and non-prey, but preferred volatiles from plants with prey when offered a choice. When this last species was given an experience of 1 day with non-prey in presence of HIPV induced by non-prey, it was still attracted to these volatiles, but an experience of 2 days resulted in loss of such attraction. Thus, predatory arthropods

are equipped with a remarkable set of innate responses. To cope with the variability in HIPV, they are able to associate HIPV with the presence of prey. It is far less clear how long these memories persist and what factors may contribute to loss or retention. Negative experiences such as starvation or the presence of non-prey in combination with HIPV can further fine-tune the response of the predatory arthropods to HIPV. A key question for the future remains how predators quickly assess that an initially attractive plant is actually infested with non-prey and how, and at what time scale, predators decide to leave.

Although learning is a relatively fast process compared to the rate of population dynamical change, it does take time and—more importantly—it does require a certain frequency of similar experiences, which takes even more time. This may give a head-start advantage to herbivores that colonise a host plant already occupied by a herbivore that does not have the same natural enemies. Plants that are simultaneously infested by two species of herbivores are unlikely to produce blends similar to those infested by one of the two herbivore species. Hence, the natural enemies of the herbivores have to learn the association between their victim and the HIPV released from plants with prey and non-prey herbivores. This learning process has not yet been studied in depth, but a possible advantage to the herbivore of joining other herbivore species on a plant has been demonstrated. Shiojiri et al. (2001, 2002) studied how infestation of a host plant (cabbage) by two herbivore species (the diamondback moth, *Plutella xylostella*, and the small cabbage white butterfly, *Pieris rapae*) affected mortality by specialist parasitoids (*Cotesia plutellae* and *Cotesia glomerata*). They found that diamondback moth larvae suffered much lower parasitisation risk on plants that were also infested by cabbage white larvae. Moreover, they found that female diamondback moths preferred to oviposit on plants infested by cabbage white larvae, rather than on uninfested or diamondback moth-infested plants that were offered as the alternative (Shiojiri et al. 2002).

The ecological importance of phytochemical networks

Evidence is accumulating that several plants—when attacked by a single herbivore species—release chemical information that is specific enough for predators and parasitoids to tell prey and non-prey apart. There is some evidence that this also holds within vegetation with prey and non-prey on different plants and even when part of the plants harbour both prey and non-prey. However, there are also cases of multiple herbivore attacks where the plant releases signals that make one or another herbivore go unrecognised by its specific natural enemy. This lack of recognition may be a temporary phenomenon when natural enemies happen to visit plants infested by multiple herbivore species and learn new associations between HIPV from this plant and the presence of a herbivore

species that is suitable as prey. We do not know how general and how fast is the process of associative learning in vegetation consisting of several plant species with a variable number of prey and non-prey herbivore species. It seems likely that this will take at least some time, however, and this will create a temporary refuge for the prey. If such temporary refuges last long enough, herbivores may evolve a preference for the enemy-scarce space on a plant already infested by another herbivore species. This may have been the case for diamondback moths, as they prefer to oviposit on plants infested by cabbage white larvae (Shiojiri et al. 2002). Such temporary or partial refuges may have an important impact on population dynamics, as they are shown to increase prey density, yet promote the persistence of otherwise unstable one predator–one prey systems of the Lotka-Volterra or Nicholson-Bailey type (Hassell 1978; Sabelis et al. 1991, 2005a, b), as well as more complex and diverse systems (e.g. Vos et al. 2001). This shows that phytochemical information networks can affect the structure and persistence of arthropod communities on plants (Sabelis et al. 2005a, b).

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References

- Agrawal AA, Colfer RG (2000) Consequences of thrips-infested plants for attraction of conspecifics and parasitoids. *Ecol Entomol* 25:493–496
- Alborn T, Turlings TCJ, Jones TH, Stenhagen G, Loughrin JH, Tumlinson JH (1997) An elicitor of plant volatiles from beet armyworm oral secretion. *Science* 276:945–949
- Alborn HT, Jones TH, Stenhagen GS, Tumlinson JH (2000) Identification and synthesis of volicitin and related components from beet armyworm oral secretions. *J Chem Ecol* 26:203–220
- Ament K, Kant MR, Sabelis MW, Haring MA, Schuurink RC (2004) Jasmonic acid is a key regulator of spider mite-induced volatile terpenoid and methyl salicylate emission in tomato. *Plant Physiol* 135:1–13
- Birkett MA, Chamberlain K, Guerrieri E, Pickett JA, Wadhams LJ, Yasuda T (2003) Volatiles from whitefly-infested plants elicit a host-locating response in the parasitoid, *Encarsia formosa*. *J Chem Ecol* 29:1589–1600
- Bouwmeester HJ, Verstappen FWA, Posthumus MA, Dicke M (1999) Spider mite-induced (3S)-(E)-nerolidol synthase activity in cucumber and lima bean. The first dedicated step in acyclic C11-homoterpene biosynthesis. *Plant Physiol* 121:173–180
- De Boer JG, Dicke M (2004) Experience with methyl salicylate affects behavioural responses of a predatory mite to blends of herbivore-induced plant volatiles. *Entomol Exp App* 110:181–189
- De Boer JG, Posthumus MA, Dicke M (2004) Identification of volatiles that are used in discrimination between plants infested with prey or nonprey herbivores by a predatory mite. *J Chem Ecol* 30:2215–2230
- De Boer JG, Snoeren TAL, Dicke M (2005) Predatory mites learn to discriminate between plant volatiles induced by prey and nonprey herbivores. *Anim Behav* 69:869–879
- De Moraes CM, Lewis WJ, Paré PW, Alborn HT, Tumlinson JH (1998) Herbivore-infested plants selectively attract parasitoids. *Nature* 393:570–573

- Dicke M (1994) Local and systemic production of volatile herbivore-induced terpenoids—their role in plant-carnivore mutualism. *J Plant Physiol* 143:465–472
- Dicke M (1999) Are herbivore-induced plant volatiles reliable indicators of herbivore identity to foraging carnivorous arthropods? *Entomol Exp Appl* 91:131–142
- Dicke M, Sabelis MW (1988) How plants obtain predatory mites as bodyguards. *Neth J Zool* 38:148–165
- Dicke M, van Beek TA, Posthumus MA, Ben Dom N, van Bokhoven H, de Groot AE (1990a) Isolation and identification of volatile kairomone that affects acarine predator–prey interactions: involvement of host plant in its production. *J Chem Ecol* 381–396
- Dicke M, Sabelis MW, Takabayashi J, Bruin J, Posthumus MA (1990b) Plant strategies of manipulating predator–prey interactions through allelochemicals: prospects for application in pest control. *J Chem Ecol* 16:3091–3118
- Dicke M, de Boer JG, Hofte M, Rocha-Granados MC (2003) Mixed blends of herbivore-induced plant volatiles and foraging success of carnivorous arthropods. *Oikos* 101:38–48
- Drukker B, Bruin J, Jacobs G, Kroon A, Sabelis MW (2000a) How predatory mites learn to cope with variability in volatile plant signals in the environment of their herbivorous prey. *Exp Appl Acarol* 24:881–895
- Drukker B, Bruin J, Sabelis MW (2000b) Anthocorid predators learn to associate herbivore-induced plant volatiles with presence or absence of prey. *Physiol Entomol* 25:260–265
- Du YJ, Poppy GM, Powell W, Pickett JA, Wadhams LJ, Woodcock CM (1998) Identification of semiochemicals released during aphid feeding that attract parasitoid *Aphidius ervi*. *J Chem Ecol* 24:1355–1368
- Geervliet JBF, Ariens S, Dicke M, Vet LEM (1998a) Long-distance assessment of patch profitability through volatile infochemicals by the parasitoids *Cotesia glomerata* and *C. rubecula* (Hymenoptera: Braconidae). *Biol Control* 11:113–121
- Geervliet JBF, Vreugdenhil AI, Dicke M, Vet LEM (1998b) Learning to discriminate between infochemicals from different plant-host complexes by the parasitoids *Cotesia glomerata* and *C. rubecula*. *Entomol Exp Appl* 86:241–252
- Gols R, Roosjen M, Dijkman H, Dicke M (2003) Induction of direct and indirect plant responses by jasmonic acid, low spider mite densities, or a combination of jasmonic acid treatment and spider mite infestation. *J Chem Ecol* 29:2651–2666
- Gu H, Dorn S (2000) Genetic variation in behavioral response to herbivore-infested plants in the parasitic wasp *Cotesia glomerata* (L.) (Hymenoptera: Braconidae). *J Insect Behav* 13:141–156
- Guerrieri E, Poppy GM, Powell W, Tremblay E, Pennacchio F (1999) Induction and systemic release of herbivore-induced plant volatiles mediating in-flight orientation of *Aphidius ervi*. *J Chem Ecol* 25:1247–1261
- Hassell MP (1978) The dynamics of arthropod predator-prey systems. Monographs in population biology 13. Princeton University Press, Princeton, 237 pp
- Hopke J, Donath J, Blechert S, Boland W (1994) Herbivore-induced volatiles—the emission of acyclic homoterpenes from leaves of *Phaseolus lunatus* and *Zea mays* can be triggered by a beta-glucosidase and jasmonic acid. *FEBS Lett* 352:146–150
- Jia F, Margolies DC, Boyer JE, Charlton RE (2002) Genetic variation in foraging traits among inbred lines of a predatory mite. *Heredity* 89:371–379
- Kant MR, Ament K, Sabelis MW, Haring M, Schuurink R (2004) Differential timing of spider mite-induced direct and indirect-defenses in tomato plants. *Plant Physiol* 135:483–495
- Krips OE, Willems PEL, Gols R, Posthumus MA, Dicke M (1999) The response of *Phytoseiulus persimilis* to spider mite-induced volatiles from *Gerbera*: influence of starvation and experience. *J Chem Ecol* 25:2623–2641
- Maeda T, Takabayashi J, Yano S, Takafuji A (1999) Response of the predatory mite, *Amblyseius womersleyi* (Acari: Phytoseiidae), toward herbivore-induced plant volatiles: variation in response between two local populations. *Appl Entomol Zool (Jpn)* 34:449–454
- Maeda T, Takabayashi J, Yano S, Takafuji A (2001) Variation in the olfactory response of predatory mite, *Amblyseius womersleyi* (Acari: Phytoseiidae), of 13 populations to herbivore-induced plant volatiles. *Exp Appl Acarol* 25:55–64

- Margolies DC, Sabelis MW, Boyer JE (1997) Response of a phytoseiid predator to herbivore-induced plant volatiles: selection on attraction and effect of prey exploitation. *J Insect Behav* 10:695–709
- Mattiacci L, Dicke M, Posthumus MA (1995) β -Glucosidase: an elicitor of herbivore-induced plant odor that attracts hostsearching parasitic wasps. *Proc Natl Acad Sci USA* 92:2036–2040
- Mercke P, Kappers IF, Verstappen FWA, Vorst O, Dicke M, Bouwmeester HJ (2004) Combined transcript and metabolite analysis reveals genes involved in spider mite induced volatile formation in cucumber plants. *Plant Physiol* 135:2012–2024
- Ozawa R, Arimura G, Takabayashi J, Shimoda T, Nishioka T (2000) Involvement of jasmonate- and salicylate-related signaling pathway for the production of specific herbivore-induced volatiles in plants. *Plant Cell Physiol* 41:391–398
- Papaj DR, Lewis AC (1993) *Insect learning: ecology and evolutionary perspectives*. Chapman and Hall, NY
- Papaj DR, Snellen H, Swaans K, Vet LEM (1994) Unrewarding experiences and their effect on foraging in the parasitic wasp *Leptopilina heterotoma* (Hymenoptera, Eucilidae). *J Insect Behav* 7:465–481
- Paré PW, Lewis WJ, Tumlinson JH (1999) Induced plant volatiles: biochemistry and effects on parasitoids. In: Agrawal AA, Tuzun S, Bent E (eds) *Induced defenses against pathogens and herbivores*. APS, St. Paul, MN, pp 167–180
- Reymond P, Bodenhausen N, van Poecke RMP, Krishnamurthy V, Dicke M, Farmer EE (2004) A conserved transcriptional pattern in response to a specialist and a generalist herbivore. *Plant Cell* 16:3132–3147
- Roitberg B, Reid ML, Li C (1993) Choosing hosts and mates: the value of learning. In: Papaj DR, Lewis AC (eds) *Insect learning: ecology and evolutionary perspectives*. Chapman and Hall, NY, pp 174–194
- Sabelis MW, Bakker FM (1992) How predatory mites cope with the web of their tetranychid prey—a functional view on dorsal chaetotaxy in the Phytoseiidae. *Exp Appl Acarol* 16:203–225
- Sabelis MW, van de Baan HE (1983) Location of distant spider mite colonies by phytoseiid predators: demonstration of specific kairomones emitted by *Tetranychus urticae* and *Panonychus ulmi*. *Entomol Exp Appl* 33:303–314
- Sabelis MW, Afman BP, Slim PJ (1984) Location of distant spider-mite colonies by *Phytoseiulus persimilis*: localization and extraction of a kairomone. In: Griffiths DA, Bowman CE (eds) *Acarology VI*, vol 1. Halsted, NY, pp 431–440
- Sabelis MW, Diekmann O, Jansen VAA (1991) Metapopulation persistence despite local extinction: predator-prey patch models of the Lotka-Volterra type. *Biol J Linn Soc* 42:267–283
- Sabelis MW, Janssen A, Pallini A, Venzon M, Bruin J, Drukker B, Scutoreanu P (1999a) Behavioural responses of predatory and herbivorous arthropods to induced plant volatiles: from evolutionary ecology to agricultural applications. In: Agrawal AA, Tuzun S, Bent E (eds) *Induced plant defenses against pathogens and herbivores*. American Phytopathological Society, St. Paul, MN, pp 269–296
- Sabelis MW, van Baalen M, Bakker FM, Bruin J, Drukker B, Egas M, Janssen A, Lesna I, Pels B, van Rijn PCJ, Scutoreanu P (1999b) The evolution of direct and indirect plant defence against herbivorous arthropods. In: Olff H, Brown VK, Drent RH (eds) *Herbivores: between plants and predators*. Blackwell, Oxford, pp 109–166
- Sabelis MW, Janssen A, Bruin J, Bakker FM, Drukker B, Scutoreanu P, van Rijn PCJ (1999c) Interactions between arthropod predators and plants: a conspiracy against herbivorous arthropods? In: Bruin J, van der Geest LPS, Sabelis MW (eds) *Ecology and evolution of the acari*. Series entomologica, vol. 55. Kluwer Academic, Dordrecht, pp 207–230
- Sabelis MW, van Baalen M, Pels B, Egas M, Janssen A (2002) Evolution of exploitation and defence in plant–herbivore–predator interactions. In: Dieckmann U, Metz JAJ, Sabelis MW, Sigmund K (eds) *The adaptive dynamics of infectious diseases*. In pursuit of virulence management. Cambridge University Press, Cambridge, UK, pp 297–321
- Sabelis MW, Takabayashi J, Janssen A, Kant MR, van Wijk M, Sznajder B, Aratchige NS, Lesna I, Belliure B, Schuurink RC (2005a) Ecology meets plant physiology: herbivore-induced plant responses and their indirect effects on arthropod communities. In: Ohgushi T, Craig TP, Price PW (eds) *Indirect interaction webs: nontrophic linkages through induced plant traits*. Cambridge University Press, Cambridge

- Sabelis MW, Janssen A, Diekmann O, Jansen VAA, van Gool E, van Baalen M (2005b) Global persistence despite local extinction in acarine predator-prey systems: lessons from experimental and mathematical exercises. *Adv Ecol Res* 37:183–220
- Scutareanu P, Drukker B, Bruin J, Posthumus MA, Sabelis MW (1997) Isolation and identification of volatile synomones involved in the interaction between psylla-infested pear trees and two anthocorid predators. *J Chem Ecol* 23:2241–2260
- Shimoda T, Dicke M (2000) Attraction of a predator to chemical information related to nonprey: when can it be adaptive? *Behav Ecol* 11:606–613
- Shiojiri K, Takabayashi J, Yano S, Takafuji A (2001) Infochemically mediated tritrophic interaction webs on cabbage plants. *Popul Ecol* 43:23–29
- Shiojiri K, Takabayashi J, Yano S, Takafuji A (2002) Oviposition preferences of herbivores are affected by tritrophic interaction webs. *Ecol Lett* 5:186–192
- Storeck A, Poppy GM, van Emden HF, Powell W (2000) The role of plant chemical cues in determining host preference in the generalist aphid parasitoid *Aphidius colemani*. *Entomol Exp Appl* 97:41–46
- Takabayashi J, Dicke M (1992) Response of predatory mites with different rearing histories to volatiles of uninfested plants. *Entomol Exp Appl* 64:187–193
- Takabayashi J, Dicke M (1996) Plant-carnivore mutualism through herbivore-induced carnivore attractants. *Trends Plant Sci* 1:109–113
- Takabayashi J, Dicke M, Posthumus MA (1991) Variation in composition of predator-attracting allelochemicals emitted by herbivore-infested plants: relative influence of plant and herbivore. *Chemoecology* 2:1–6
- Thaler JS, Farag MA, Paré PW, Dicke M (2002) Jasmonate-deficient plants have reduced direct and indirect defenses against herbivores. *Ecol Lett* 5:764–774
- Turlings TCJ, Tumlinson JH (1992) Systemic release of chemical signals by herbivore-injured corn. *Proc Natl Acad Sci USA* 89:8399–8402
- Turlings TCJ, Tumlinson JH, Lewis WJ (1990) Exploitation of herbivore-induced plant odors by host seeking parasitic wasps. *Science* 250:1251–1253
- Turlings TCJ, Wäckers F, Vet LEM, Lewis WJ, Tumlinson JH (1993) Learning of host-finding cues by hymenopterous parasitoids. In: Papaj DR, Lewis AC (eds) *Insect learning: ecology and evolutionary perspectives*. Chapman and Hall, NY, pp 51–78
- Turlings TCJ, Loughrin JH, McCall PJ, Rose USR, Lewis WJ, Tumlinson JH (1995) How caterpillar-damaged plants protect themselves by attracting parasitic wasps. *Proc Natl Acad Sci USA* 92:4169–4174
- Van Poecke RMP, Dicke M (2003) Signal transduction downstream of salicylic and jasmonic acid in herbivory-induced parasitoid attraction by *Arabidopsis* is independent of JAR1 and NPR1. *Plant Cell Environ* 26:1541–1548
- Vet LEM, Dicke M (1992) Ecology of infochemical use by natural enemies in a tritrophic context. *Annu Rev Ecol Syst* 37:141–172
- Vet LEM, Lewis WJ, Cardé RT (1995) Parasitoid foraging and learning. In: Cardé RT, Bell WJ (eds) *Chemical ecology of insects 2*. Chapman and Hall, NY, pp 65–101
- Vos M, Berrocal SM, Karamaouna F, Hemerik L, Vet LEM (2001) Plant-mediated indirect effects and the persistence of parasitoid-herbivore communities. *Ecol Lett* 4:38–45
- Wang Q, Dorn S (2003) Selection on olfactory response to semiochemicals from a host-plant complex in a parasitic wasp. *Heredity* 91:430–435
- Wang Q, Gu H, Dorn S (2004) Genetic relationship between olfactory response and fitness in the *Cotesia glomerata* (L.). *Heredity* 92:579–584