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Mini review

Multitrophic effects of herbivore-induced plant volatiles in an evolutionary context

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Abstract

Herbivorous and carnivorous arthropods use plant volatiles when foraging for food. In response to herbivory, plants emit a blend that may be quantitatively and qualitatively different from the blend emitted when intact. This induced volatile blend alters the interactions of the plant with its environment. We review recent developments regarding the induction mechanism as well as the ecological consequences in a multitrophic and evolutionary context. It has been well established that carnivores (predators and parasitoids) are attracted by the volatiles induced by their herbivorous victims. This concerns an active plant response. In the case of attraction of predators, this is likely to result in a fitness benefit to the plant, because through consumption a predator removes the herbivores from the plant. However, the benefit to the plant is less clear when parasitoids are attracted, because parasitisation does usually not result in an instantaneous or in a complete termination of consumption by the herbivore. Recently, empirical evidence has been obtained that shows that the plant's response can increase plant fitness, in terms of seed production, due to a reduced consumption rate of parasitized herbivores. However, apart from a benefit from attracting carnivores, the induced volatiles can have a serious cost because there is an increasing number of studies that show that herbivores can be attracted. However, this does not necessarily result in settlement of the herbivores on the emitting plant. The presence of cues from herbivores and/or carnivores that indicate that the plant is a competitor- and/or enemy-dense space, may lead to an avoidance response. Thus, the benefit of emission of induced volatiles is likely to depend on the prevailing faunal composition. Whether plants can adjust their response and influence the emission of the induced volatiles, taking the prevalent environmental conditions into account, is an interesting question that needs to be addressed. The induced volatiles may also affect interactions of the emitting plant with its neighbours, e.g., through altered competitive ability or by the neighbour exploiting the emitted information.

Major questions to be addressed in this research field comprise mechanistic aspects, such as the identification of the minimally effective blend of volatiles that explains the attraction of carnivores to herbivore-infested plants, and evolutionary aspects such as the fitness consequences of induced volatiles. The elucidation of mechanistic aspects is important for addressing ecological and evolutionary questions. For instance, an important tool to address ecological and evolutionary aspects would be to have plant pairs that differ in only a single trait. Such plants are likely to become available in the near future as a result of mechanistic studies on signal-transduction pathways and an increased interest in molecular genetics.

Introduction

Arthropods live in a chemical world. Foraging herbivorous and carnivorous arthropods employ chemical information both prior to and after physical contact with their food (e.g., Bell & Cardé, 1984; Visser, 1986; Roitberg & Isman, 1992; Vet & Dicke, 1992; Cardé & Bell, 1995; Schoonhoven et al., 1998). Both herbivores and carnivores may exploit chemical information from plants when foraging for food. These chemicals may be produced constitutively by plants or they can be induced by herbivores. In this review we focus on herbivore-induced plant volatiles. The induction of plant volatiles potentially alters the interaction of the plant with its environment in many ways, e.g. by modified interactions with herbivores, carnivores and/or with competing plants. In this review we set out to identify major gaps in our knowledge and questions that should be answered to improve our understanding of the ecological costs and benefits of induced plant volatiles for plants and herbivores.

Characteristics of herbivore-induced plant volatiles and the induction process

Plants respond to herbivore feeding damage by producing mixtures of volatiles that not only differ in the quantity of volatiles released per unit of plant biomass but, more importantly, also in the composition of the volatile blend. The change in composition can be quantitative, i.e., changed ratios of the same components, or qualitative, by the release of compounds that do not occur in the blend emitted by the intact plant (e.g., Dicke et al., 1990b; Turlings et al., 1990; Takabayashi et al., 1991; De Moraes et al., 1998; Dicke & Vet, 1999). The release of herbivore-induced plant volatiles has in several cases been shown to constitute an active response of the plant, as is apparent from the *de novo* production of volatile compounds that are not released by intact or mechanically damaged plants (Dicke et al., 1990a, b; Turlings et al., 1990; Donath & Boland, 1994; Paré & Tumlinson, 1997; Tumlinson et al., 1999, Boland et al., 1999). Some steps in the biochemical pathways leading to induced homoterpenes as well as the enzymes involved have been elucidated (Donath & Boland, 1994, 1995; Bouwmeester et al., 1999; Degenhardt & Gershenzon, 2000). Moreover, the induced release of volatiles is not limited to the site of damage but can occur systemically (Dicke et al., 1990b; Turlings & Tumlinson, 1992; Potting et al., 1995; Röse et al., 1996). In addition, a considerable degree of specificity in blend composition has been documented in several, though not in all, tritrophic systems studied (for reviews see Dicke, 1999a, b). This specificity refers to consistent differences in volatile blends and/or discrimination by carnivores between plants of the same species that have been damaged by different herbivore species. The observation that such specificity has not been found for some plant-herbivore combinations may be interpreted to signify that specificity exists in some systems but not in others. Alternatively, it has been argued that specificity will be found with higher likelihood when the behavioural response of the carnivorous arthropod is studied (Dicke, 1999a, b). This can be understood from the observation that the chemosensory system of arthropods is able to detect volatile compounds at concentrations that are so low that they escape attention in gas-chromatographicmass spectrometric analyses (Pickett, 1990; Pickett et al., 1998).

The volatile blends that are released in response to herbivore feeding are not identical to those elicited by artificial damage done by mechanical means (reviewed by Turlings et al., 1995; Takabayashi & Dicke, 1996). Apart from crushing or puncturing of plant tissues, both mandibulate and haustellate herbivores produce oral secretions containing salivary components that come into contact with the wounded tissues. These secretions have been shown to contain substances that can elicit the herbivore-induced volatile production, when applied in combination with artificial damage or when fed systemically to the plant (Turlings et al., 1990; Mattiacci et al., 1995; Alborn et al., 1997). Only two such herbivore elicitors have thus far been characterized from two caterpillar species, and they turned out to be chemically unrelated. A β-glucosidase from regurgitant of *Pieris brassicae* (Lepidoptera: Pieridae) and the fatty acid – amino acid conjugate *N*-(17-hydroxylinolenoyl)-L-glutamine (volicitin) from regurgitant of *Spodoptera exigua* (Lepidoptera: Noctuidae) were reported to induce a volatile blend that is similar to that induced by herbivory (Mattiacci et al., 1995; Alborn et al., 1997). Recent investigations indicate that ion-channel-forming peptides from fungi may also be involved in volatile induction in plants (Engelberth et al., 2000). The discovery of elicitor molecules from herbivores gives a biochemical explanation for the differential effect of artificial and herbivore damage. Herbivory leads to the induction of signal-transduction pathways and the octadecanoid pathway appears to be central in the induction of volatile production (Hopke et al., 1994; Boland et al., 1995, 1999; Koch et al., 1999; Dicke et al., 1999; Gols et al., 1999). The application of jasmonic acid, an important product of the octadecanoid signalling pathway, to plants results in the induction of several biosynthetic pathways in an individual plant and in the emission of a volatile blend that is strikingly similar, though not identical, to the blend emitted by herbivore-damaged plants (Boland et al., 1999; Dicke et al., 1999; Gols et al., 1999). Terpenoids are an important group of herbivore-induced plant volatiles and their biosynthesis is induced by the application of jasmonic acid. Traditionally terpenoid biosynthesis has been considered to occur through the mevalonate pathway. Recently, an alternative biosynthetic route of terpenoids has been discovered that is mevalonate independent (Rohmer et al., 1993; Lichtenthaler, 1999). The alternative pathway is located in the plastids, whereas the mevalonate pathway is located in the cytosol. Among herbivore-induced terpenoid volatiles, the monoterpenes appear to be mainly produced through the alternative biosynthetic pathway, while sesquiterpenes may be produced through both pathways (Boland et al., 1999).

Carnivore responses to herbivore-induced volatiles

Although initially surprising, by now it has become well established that the plant under attack by a herbivore rather than the herbivore itself is commonly the source of the cues enabling orientation by the carnivore. This has set the stage for studying tritrophic interactions between plant, herbivore and carnivore at the informational level (Price et al., 1980; Vet & Dicke, 1992; Dicke & Vet, 1999; Sabelis et al., 1999). Involvement of first-third trophic level communication has been explained as the evolutionary outcome of a reliability-detectability problem faced by carnivores searching for herbivores: whereas cues provided by the herbivore itself are reliable indicators of herbivore presence, their detectability is low due to their small biomass relative to that of the plants they are feeding on; the argument runs *vice versa* for plant-produced cues (Vet & Dicke, 1992). Although intact plants constitutively produce volatiles (Visser, 1986; Schoonhoven et al., 1998) these generally do not provide reliable information to foraging carnivores. Herbivores are under selection not to convey their presence to enemies through e.g. volatile cues. The discovery of herbivore-induced plant volatiles described above has been central to understanding how foraging carnivores locate their herbivorous prey or host.

There is ample behavioural evidence that carnivores selectively exploit herbivore-induced plant volatiles during the location of their herbivorous hosts or prey (reviewed by Turlings et al., 1995; Takabayashi & Dicke, 1996; Sabelis et al., 1999; Dicke & Vet, 1999) and this includes field studies (e.g., Drukker et al., 1995; Shimoda et al., 1997; De Moraes et al. 1998). In very few cases, however, do we know the composition of the volatile blend to which the carnivores respond, the so-called ‘minimally effective blend’. Indeed, volatile blends collected from herbivore-damaged plants are commonly composed of 20 to over 200 compounds (e.g., Dicke et al., 1990a, 1999; Turlings et al., 1990, 1995; McCall et al., 1994; Krips et al., 1999). This extent of chemical diversity makes it difficult to establish which of the blend components evoke a response in the carnivore. As a consequence, at present only studies on two parasitoid wasps [*Cotesia marginiventris* (Hymenoptera: Braconidae) and *Aphidius ervi* (Hymenoptera: Aphidiidae)], one predatory mite [*Phytoseiulus persimilis* (Acari: Phytoseiidae)] and two anthocorid predatory bugs [*Anthocoris nemorum* and *A. nemoralis* (Heteroptera: Anthocoridae)] have explicitly addressed this issue by taking the plant-produced blend as starting point (Dicke et al., 1990a; Du et al., 1998; Turlings et al., 1991; Scutareanu et al., 1997; Turlings & Fritzsche, 1999). For the parasitoid *C. marginiventris* the complex natural blend was found to elicit a stronger attraction than the reduced synthetic blend, indicating that the complete signal is not yet known (Turlings et al., 1991). In fact, a detailed analysis to identify the minimal blend showed that some compounds in the complete blend may mask the attractive components (Turlings & Fritzsche, 1999).

Here exists an important gap in our knowledge. We consider it important, however laborious it will turn out to be, to establish the chemical nature of the behaviourally active induced volatiles for other tritrophic systems. This knowledge at the mechanistic level is essential to discern which major biosynthetic routes give rise to production of herbivore-induced plant volatiles that attract carnivores, and thus may contribute to indirect plant defence. A first step can be to elucidate which of the induced compounds are perceived by the carnivore, e.g., through an electrophysiological approach. To date, few studies have been devoted to an electrophysiological chemosensory analysis of carnivores, which strongly contrasts to the situation for herbivores (reviewed by van Loon & Dicke, 2000). A coupled electrophysiology – gas chromatography approach of the chemosensory system of carnivores allowing separation of the complex plant volatile blends into individual components, can be employed to identify on-line which individual volatiles elicit olfactory activity (Arn et al., 1975; Wadhams, 1984). The first attempts on carnivores have only recently proved successful (Du et al., 1996; Weissbecker et al., 2000). The electrophysiologically active components of induced plant odour blends that are thus identified need subsequently be tested for their possible behavioural effects. Carnivore chemosensory ecology is largely unexplored and conceivably a very fruitful field in which fundamental as well as applied advances lie ahead.

Not all predators that are attracted by herbivore-induced plant volatiles attack herbivores exclusively. Some predator species act as intraguild predators or hyperpredators. Some first studies on behavioural responses of these groups of predators are emerging (Janssen et al., 1998). It will be exciting to investigate whether specialist carnivores and generalists, that may act as intraguild predators or hyperpredators, respond to the same blend components. Data on behaviourally active components of a spider-mite induced blend of bean volatiles for a specialist and a generalist predator of spider mites indicate that although there are similarities in responses to blend components, there are also differences (Dicke et al., 1990a).

Herbivore-induced plant volatiles as component of indirect plant defence

From a phytocentric viewpoint, the attraction of carnivores to plants under attack by virtue of the plant's release of herbivore-induced volatiles has been classified as a form of (indirect) plant defence (Dicke & Sabelis, 1989; Karban & Baldwin, 1997; Dicke & Vet, 1999; but see van der Meijden & Klinkhamer, 2000). Under the definitions given for the term defence (Karban & Myers, 1989; Karban & Baldwin, 1997) this requires that the production of herbivore-induced plant volatiles decreases the negative consequences for plant fitness caused by herbivore attack. From the perspective of plant fitness the carnivores comprise two groups with very different strategies that at this stage need to be separated. The reduction in herbivore damage is obvious in the case of predators that kill their prey instantly, leaving little room for doubt on the benefit for the plant. In the case of parasitoids, especially koinobionts, however, the herbivorous host continues to feed on the plant until parasitoid egression and thus a reduction in plant damage may not result (Dicke & Sabelis, 1989). No studies have actually quantified the effect of carnivore attraction on plant fitness. In the case of plant – spider mite – predatory mite systems a benefit seems obvious as without predatory mites decimating the spider mite population, the plant is overexploited and may die before producing seeds. For other predators that feed on prey that do not overexploit their host plant, no indication of the benefit to the plant is known. A similar lack of information exists for parasitoids, the other major group of carnivorous arthropods. A dichotomy seems to occur in the effect that parasitoids exert on feeding by leaf-chewing insects. For all solitary dipteran and hymenopteran parasitoids studied in this respect, the parasitized host consumed less food than unparasitized hosts (e.g., Rahman, 1970; Guillot & Vinson, 1973; Harvey et al., 1999; Turlings & Fritzsche, 1999). For gregarious parasitoids very little information is available. There are only few studies available that addressed the effect of gregarious endoparasitoids on food consumption by their herbivorous hosts by the use of direct measurements of the amount of leaf tissue removed (Rahman, 1970; Slansky, 1978; Coleman et al., 1999). In these cases food consumption was either similar or slightly increased compared to unparasitized hosts, which indicates that a dichotomy between solitary and gregarious parasitoids might exist.

When the aim is to assess the benefit of herbivore parasitization in terms of plant fitness, measuring effects on herbivore food consumption does not provide the answer. An important next step is namely lacking, as the amount of leaf tissue removed cannot be simply translated into reproductive loss, among other reasons due to compensatory plant growth. A recent study that quantified plant fitness in terms of numbers of seed produced showed that parasitization of the caterpillar *Pieris rapae* (Lepidoptera: Pieridae), a specialist herbivore of Brassicaceae, by the specialized solitary braconid parasitoid *Cotesia rubecula* (Hymenoptera: Braconidae) resulted in a considerable fitness benefit for *Arabidopsis thaliana* plants (van Loon et al., 2000a). This analysis included seed production from regrown tissue and thus includes potential compensatory effects from plants damaged by unparasitized herbivores. Obviously, on the basis of this single study it is not possible to draw generalizations. Rather, this study should incite additional studies on other systems to substantiate the defensive function of herbivore-induced plant volatiles in plant – herbivore – parasitoid systems.

Induced plant volatiles: evolved plant defence or accidental release as consequence of damage? In a recent forum-paper van der Meijden & Klinkhamer

(2000) questioned whether herbivore-induced plant volatiles are an evolved defence. Their major concern is that 'evidence that plants actually benefit from the active attraction of natural enemies in the field is virtually absent' and they especially question whether parasitoids can benefit plants in terms of increased fitness. Their concern has three main components: (1) do plants *actively* attract carnivores rather than through an accidental release of volatiles as a consequence of damage, (2) does the attraction of carnivores exist under field conditions and (3) can parasitoid activity benefit individual plants in terms of fitness. The first question, whether the production of volatiles is an active response can definitely be answered positively for many plant species. New compounds in response to herbivory that are not produced in response to mechanical damage have been reported for many plant species (Dicke et al., 1990a; Turlings et al., 1990; Boland et al., 1992; see Dicke, 1999c, for review). These include a wide variety of species, including both agricultural and non-agricultural plant species. In addition, even for plants that do not produce novel compounds in response to herbivory, an active production has been recorded rather than a passive release caused by the rupture of plant cells (Paré & Tumlinson, 1997). Finally, induced volatiles are emitted systemically in response to herbivory, so cell damage at the emission site is not a prerequisite (Dicke et al., 1990b; Turlings & Tumlinson, 1992; Potting et al., 1995; Röse et al., 1996). The second question, on field studies, relates to an aspect that receives increasing attention. The attraction of carnivores to volatiles emitted from herbivore-infested plants has been demonstrated at several levels, ranging from closed system olfactometers and windtunnels (e.g., Sabelis & van de Baan, 1983; Dicke et al., 1990a; Turlings et al., 1990; van Loon et al., 2000b), to open semi-field setups (Steinberg et al., 1992; Sabelis & van der Weel, 1993; Janssen, 1999) and studies in the field (Drukker et al., 1995; Shimoda et al., 1997; De Moraes et al., 1998). Results from laboratory studies are confirmed by semi-field or field studies. The third question, on the benefits of parasitoid activity to plant fitness has been addressed above. The only study that has so far addressed this question by quantifying plant fitness, has shown that fitness reduction caused by caterpillar feeding was reduced by parasitization of the caterpillars (van Loon et al., 2000a). A final issue raised by van der Meijden & Klinkhamer (2000) is that the majority of studies relate to agricultural plants rather than to plants in natural ecosystems. Although this is true, our perception is that the fact that the widespread occurrence of active production of herbivore-induced plant volatiles among agricultural plants indicates that this phenomenon is not an artifact. After all, agricultural plants have not been selected for their ability to produce induced volatiles. Moreover, it is noteworthy that in all plant species studied so far, the release of carnivore attractants has been recorded. Yet, we agree with van der Meijden & Klinkhamer (2000) that field studies in natural ecosystems will be highly valuable to demonstrate the importance of herbivore-induced plant volatiles. We are aware of one study that addresses this. This is a study on wild tobacco, *Nicotiana attenuata*, that combines investigations in the laboratory with field tests (Kahl et al., 2000; Baldwin, 2000).

Responses of herbivores to induced plant volatiles

Attraction or repellence? Herbivores that search for suitable food plants can often exploit plant volatiles (Visser, 1986). However, volatiles are emitted at low rates from uninfested plants. In contrast, herbivore-infested plants emit volatiles in much larger amounts (e.g., Dicke et al., 1990a; Turlings et al., 1990). Thus, herbivore-infested plants are more easily perceived from a distance, although the cues emitted convey more information than only about the presence of a food plant. The volatiles may indicate that in the plants releasing them, defences have been induced. In contrast, the volatiles may also indicate that plant defence has been overcome by herbivores. Consequently, the cues may represent plants that have been weakened and are thus more susceptible to herbivores or offer less favourable nutrition. At any rate, herbivore-induced plant volatiles are indicators of the presence of feeding herbivores that may represent competitors. Furthermore, the cues also signify a potentially enemy-dense space because they will attract carnivorous arthropods if these are present in the habitat. In conclusion, to foraging herbivores the induced plant volatiles as such represent a complex information package and it will be difficult to predict whether herbivores are attracted to them or repelled. Indeed, both types of responses have been recorded. Attraction to volatiles from herbivore-infested plants has been recorded for herbivorous scarabeid and chrysomelid beetles (Harari et al., 1994; Loughrin et al., 1995; Bolter et al., 1997), for moths (Landolt, 1993; Anderson & Alborn, 1999; Rojas, 1999) and for spider mites

(Dicke, 1986; Pallini et al., 1997), while repellence has been recorded for moths (Landolt, 1993; Anderson & Alborn, 1999), aphids (Bernasconi et al., 1998) and spider mites (Dicke, 1986).

Plant species, herbivore species, and herbivore density are among the major variables influencing the behavioural responses recorded. For instance, Landolt (1993) found that cabbage looper moths were attracted to volatiles from cotton plants infested with conspecific caterpillars, while the moths were repelled when cabbage plants were used instead. In two-choice wind-tunnel experiments *Mamestra brassicae* (Lepidoptera: Noctuidae) females were attracted to cabbage plants infested with conspecific larvae, both when small and when large amounts of damage had been inflicted (Rojas, 1999). However, when the induced plants had a large amount of damage the differential attraction did not result in a larger number of eggs being laid on the damaged plants. Cabbage plants infested with locusts also attracted *M. brassicae* moths, but cabbage plants infested with aphids did not (Rojas, 1999). Chrysanthemum plants infested with *M. brassicae* larvae were not attractive to conspecific moths (Rojas, 1999). Spider mites (*Tetranychus urticae* – Acari: Tetranychidae) were attracted to volatiles from spider-mite infested bean leaves that were mixed with volatiles from uninfested bean leaves, representing a low spider mite density. In contrast, avoidance was recorded when only volatiles from spider-mite infested bean leaves were offered (Dicke, 1986). The spider mites were slightly attracted to spider-mite infested cucumber plants, whereas they were strongly repelled by cucumber plants infested with thrips (*Frankliniella occidentalis* – Thysanoptera; Thripidae) (Pallini et al., 1997).

The aphid *Rhopalosiphum maidis* (Homoptera: Aphididae) avoided the volatiles from maize plants treated with caterpillar regurgitant. This result may be explained by the emission of large amounts of (*E*)-β-farnesene, an aphid alarm pheromone, from the treated plants (Bernasconi et al., 1998), although it remains unknown how the other components of the plant blend affect the response of the aphids to this alarm pheromone.

Despite the variation within a herbivore species that has been recorded for responses to induced plant volatiles, it is striking to see that there are many more examples of attraction than of repellence. Attraction of herbivores to volatiles from herbivore-infested plants has been recorded when the attracted herbivores and the herbivores on the plants are conspecific (Dicke, 1986; Landolt, 1993; Harari et al., 1994; Loughrin et al., 1995; Bolter et al., 1997; Anderson & Alborn, 1999) as well as when they are heterospecific (Bolter et al., 1997; Rojas, 1999). An explanation for the frequent attraction may be that herbivore-induced plant volatiles are easier to detect than volatiles from uninfested plants because infested plants release larger amounts of volatiles (Vet & Dicke, 1992). With regard to the ecological costs of finding herbivore-infested plants, the costs related to competition are most likely smaller than those related to finding an enemy-dense space. Competition may result in low food intake, but as long as food intake is sufficient to support development and reproduction, it is better to compete for food than to have no food at all. In contrast, entering an enemy-dense space bears the risk of encountering an enemy which may result in death. One encounter with a competitor may result in less food ingested, whereas one encounter with a predator may result in the abrupt end of reproductive success. The presence of herbivore-induced plant volatiles, however, is a reliable indicator of the presence of competing herbivores, while it only represents a *potentially* enemy-dense space. After all, when there are no carnivores in the habitat, the induced volatiles will not turn the infested plant into an enemy-dense space. From the plant's point of view, it would be adaptive to reduce the emission of inducible volatiles under circumstances when carnivores are not present in the habitat or when it is no longer adaptive to attract carnivores. The latter situation has been reported for maize plants attacked by L5 instar caterpillars of *Pseudaletia separata* (Lepidoptera: Noctuidae) which do not attract *Cotesia kariyai* (Hymenoptera: Braconidae) parasitoids, in contrast to plants fed upon by L1-L3 instars. Although late-instar caterpillars can be successfully parasitized by *C. kariyai*, their parasitization hardly affects the amount of damage done to the plant. In contrast, the parasitization of young caterpillars results in a considerable reduction of feeding damage (Takabayashi et al., 1995). Plant responses may be more adaptively variable than is commonly considered. After all, the ample evidence on responses of plants to competitors, herbivores, and pathogens (Blaakmeer et al., 1994; Bruin et al., 1995; Karban & Baldwin, 1997; Shulaev et al., 1997; van Loon, 1997; Ballaré, 1999) should make us careful not to underestimate the potential of plants to respond to biotic components of the environment.

Integration with cues from herbivorous competitors and carnivorous enemies. In the previous section, it has been argued that there is a trade-off for herbivores: although volatiles from infested plants are much better detectable than volatiles from intact plants, they represent many risks. However, after localization of the source of the induced volatiles, the herbivores have additional selection phases. For instance female cabbage looper moths (*Trichoplusia ni* – Lepidoptera: Noctuidae) are attracted to cotton plants infested with looper larvae but once the females have located the infested plants they oviposit on nearby uninfested plants (Landolt, 1993). Females of *Spodoptera exigua* avoid laying eggs on plants contaminated with caterpillar faeces when non-contaminated plants are available as well (Hilker & Klein, 1989). *Pieris brassicae* females avoid oviposition on plants on which conspecifics have oviposited (Schoonhoven, 1990) and this behaviour is a response to herbivore-induced changes in plant chemistry that occur without tissue damage (Blaakmeer et al., 1994).

Herbivores may also avoid plants that are contaminated with cues related to carnivores. Spider mites prefer volatiles from plants infested with conspecific spider mites over volatiles from plants on which conspecific spider mites plus their predators are present (Pallini, 1998). This may be caused by an alarm pheromone produced by the spider mites that are exposed to predators (cf. Janssen et al., 1997). Moreover, spider mites avoid non-volatile cues deposited on the plant by carnivorous predators (Kriesch & Dicke, 1997; Grostal & Dicke, 1999). These cues remain active for at least four days after deposition by the predators (Kriesch & Dicke, 1997). An avoidance of cues from enemies has also been reported for the tephritid fruit fly *Rhagoletis basiola* (Diptera: Tephritidae) in response to cues from an egg parasitoid (Hoffmeister & Roitberg, 1997) and the parasitoid *Aphidius uzbekistanicus* (Hymenoptera: Aphidiidae) in response to cues from the hyperparasitoid *Alloxysta victrix* (Hymenoptera: Alloxystidae) (Höller et al., 1994).

In conclusion, the preference of herbivores for induced plant volatiles over volatiles from intact plants may reflect the difference in detectability. If subsequent information indicates that the food plant emitting the volatiles may not represent the best option available, the herbivores may avoid the infested plant. In fact, responses of herbivores to volatiles from herbivore-infested plants have so far received relatively little attention. More information is needed on these herbivore responses under varying conditions, represented by internal state (hunger, experience) and external conditions (availability of alternative options) (Dicke, 2000).

Herbivore induced plant volatiles and plant-plant interactions

In the 1980s, first indications appeared that plant volatiles can affect the defence of their neighbours (Baldwin & Schultz, 1983; Rhoades, 1985). Since the 1990s, several physiological and molecular studies demonstrated that defences could be induced in plants by exposure to volatiles from other plants (Arimura et al., 2000), or by exposure to gaseous methyl jasmonate (Farmer & Ryan, 1990) or gaseous methyl salicylate (Shulaev et al., 1997; but see Preston et al., 1999). For reviews, see Bruin et al. (1995), Shonle & Bergelson (1995) and Karban & Baldwin (1997). In addition, behavioural studies showed that plants that had been exposed to volatiles from spider-mite-infested conspecific or heterospecific plants became attractive to predatory mites that prey on the spider mites (Dicke et al., 1990b; Bruin et al., 1992; Oudejans & Bruin, 1995). The issue of whether the exposed plants are involved actively (exposed plants produce carnivore attractants) or passively (exposed plants are contaminated with carnivore attractants from their upwind neighbours) has not been resolved as yet (see Bruin et al., 1995, for discussion). It has been difficult to discriminate between the two with analytical chemical methods or through plant manipulations. A possibility would be to analyse the volatiles emitted by an undamaged plant from species A that has been exposed to volatiles from an infested plant of species B, with emphasis on induced volatiles from plant A that are not produced by plant B. However, undamaged plants exposed to volatiles from their neighbours emit low amounts of volatiles. This complicates such an approach. At the behavioural level it has been shown that exposure of bean plants to the volatile plant hormone methyl jasmonate results in attraction of predatory mites to the exposed plants. This induced attraction needed two days to become apparent, which supports the hypothesis that the production of the compounds is induced (Dicke et al., 1999). This is interesting because it demonstrates that carnivore attractants can be induced in plants by exposure to volatiles. The effect of methyl jasmonate can be understood from the role of jasmonic acid in the induction of volatile production. Jasmonic acid induces a volatile blend in bean or gerbera plants, that is quite similar to the blend induced in these plants by spider mite feeding (Hopke et al., 1994; Dicke et al., 1999; Gols et al., 1999), and the jasmonic acid-induced blend attracts predatory mites (Dicke et al., 1999; Gols et al., 1999). However, although indicating the potential for an active response in plants exposed to volatiles from infested neighbours, these data do not solve the issue of active versus passive involvement of the exposed plant in plant-plant interactions because methyl jasmonate itself is not known to be emitted by herbivore-infested plants (e.g., Dicke et al., 1990a; Turlings et al., 1990; McCall et al., 1994; Mattiacci et al., 1995; Bolter et al., 1997), except for mechanically damaged *Artemisia dentata* plants (Farmer & Ryan, 1990).

An interesting methodology to resolve the issue of active versus passive involvement of exposed undamaged plants in the attraction of carnivores may be found in the application of molecular techniques. These can be used to investigate whether the expression of genes involved in the production of herbivore-induced plant volatiles is induced by exposure to volatiles from infested neighbouring plants. This is an exciting option because such genes have been cloned for several plant species (Dudareva et al., 1996; Bohlmann et al., 1998). Gene-expression analyses have shown that plants can induce the expression of proteinase-inhibitor (PI)-genes, pathogenesis-related (PR)-genes or lipoxygenase, phenylalanine ammonia lyase or farnesyl pyrophosphate synthetase in response to volatiles from damaged neighbouring plants (Farmer & Ryan, 1990; Arimura et al., 2000). Demonstrating that such gene expression results in the production of carnivore attractants will be an exciting follow-up of this approach. This will allow for studies under field conditions that will yield important evidence to prove that the phenomenon observed in the laboratory also operates under natural conditions (Fowler & Lawton, 1985; Bruin et al., 1995; Shonle & Bergelson, 1995; Karban & Baldwin, 1997; Karban et al., 2000).

Even when volatiles from herbivore-infested plants do not induce defences in neighbouring plants, the herbivore-induced response in the infested plants may still affect plant-plant interactions. Induced defences may affect the competition among neighbouring plants (Augner, 1995; Dicke & Vet, 1999). For instance, induced resistance in tobacco plants affected the outcome of competition of the induced plants with their neighbours. Control plants grew better when competing with induced neighbours than when competing with uninduced neighbours (van Dam & Baldwin, 1998). Biosynthetic costs of herbivore-induced plant volatiles are very low, while ecological costs are considered very important (Dicke & Sabelis, 1989). The fact that costs of induced plant defences have almost exclusively been studied in the absence of competition among plants, may have resulted in a serious underestimation of costs (van Dam & Baldwin, 1998). More studies on interactions among induced plants and their neighbours are evidently needed.

Epilogue

The study of herbivore-induced plant volatiles has made tremendous progress within the last 15 years (for reviews, see Turlings et al., 1995; Takabayashi & Dicke, 1996; Tumlinson et al., 1999; Boland et al., 1999; Wadhams et al., 1999; Pickett et al., 1999; Sabelis et al., 1999; Vet, 1999; Dicke & Vet, 1999; Dicke, 1999a). After initial studies at the behavioural level that demonstrated that herbivore-induced volatiles attract carnivorous arthropods (e.g., Sabelis & van de Baan, 1983; Dicke & Groeneveld, 1986), analytical chemical investigations helped in elucidating the plant as the producer of the volatiles (Dicke et al., 1990a; Turlings et al., 1990). However, the chemical nature of the volatiles that are actually used by carnivores to orient to hosts and prey remains an enigma. Electrophysiological techniques linked to gas chromatography and subsequent chemical identification are likely to be very valuable to fill this gap in our knowledge. First empirical evidence demonstrating that the attraction of parasitoids benefits the reproductive success of plants has recently been obtained (van Loon et al., 2000a). At the mechanistic level, analytical chemical and biochemical approaches have provided information on signal transduction pathways involved and biosynthesis of the induced volatiles (Alborn et al., 1997; Boland et al., 1999; Koch et al., 1999; Tumlinson et al., 1999; Bouwmeester et al., 1999). Behavioural studies have demonstrated that the volatiles affect several other interactions in food webs, such as plant-plant and plant-herbivore interactions (Bruin et al., 1995; Janssen et al., 1998; Dicke & Vet, 1999; Sabelis et al., 1999; Dicke, 2000). At present several research groups have initiated studies using molecular approaches (e.g., Mitchell-Olds et al., 1998). In doing so, chemical ecology of induced plant volatiles will enter a new and exciting phase.

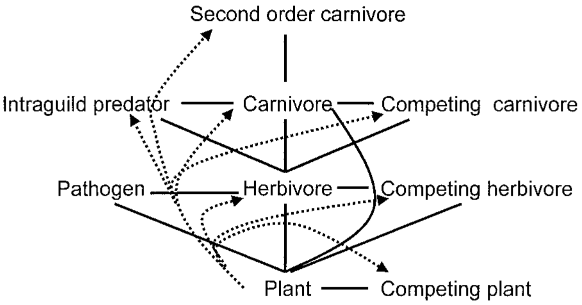

Figure 1. Herbivore-induced plant volatiles (dotted arrows) affect the behaviour or physiology of organisms at various trophic levels. As a result a variety of interactions in a food web are altered (continuous lines) which results in temporally and spatially variable multitrophic interactions.

Molecular approaches will allow carefully designed ecological comparisons, e.g. by comparing plants that are genetically identical apart from the expression of a single gene. This is likely to significantly increase our knowledge of the ecology and evolution of this intriguing plant response and to provide answers to several questions that lie ahead.

The issue of herbivore-induced plant volatiles has been subject to several recurring questions in the past 15 years. In the early days the major question brought up was whether indeed plants rather than herbivores produced the cues that attracted carnivores to herbivore-infested plants (Dicke et al., 1990a; Turlings et al., 1990). Currently, important issues are the evolution of the plant's response (e.g., Godfray, 1995; Sabelis et al., 1999; Dicke, 1999c; Dicke & Vet, 1999; van der Meijden & Klinkhamer, 2000), the variation in cue production and cue emission (Sabelis et al., 1999; Dicke & Vet, 1999), and their effects on plant fitness in natural ecosystems (van Loon et al., 2000a; van der Meijden & Klinkhamer, 2000; Baldwin, 2000). For evolutionary aspects a major breakthrough would be to have plant pairs that differ in only a single trait. Such plant pairs are currently not available with respect to volatile production, but it is anticipated that this will soon change. The increasing interest in molecular genetics in general, that also extends to the field of chemical ecology (Mitchell-Olds et al., 1998) is likely to provide new tools to address evolutionary questions accurately. The major questions to be addressed in the near future comprise the following: (1) What is the chemical blend that attracts a carnivore, and how does variation in blend composition affect responses by carnivores and herbivores. (2) To what extent are responses by carnivores and herbivores affected by the same components of the induced blend. (3) What is the effect of herbivore-induced plant volatiles on the composition of the animal community, both in terms of herbivores and different groups of carnivores, such as predators, parasitoids, intraguild predators, and hyperpredators or hyperparasitoids. (4) Can plants change the emission of induced volatiles depending on the environmental conditions such as the presence of carnivores. (5) What is the effect of carnivore attraction on plant fitness. (6) To what extent do herbivore-induced plant volatiles affect interactions among competing plants? (7) How important are herbivore-induced plant volatiles in natural ecosystems? These questions focus on interactions in plant-arthropod systems. In addition, plants are attacked by pathogens. Pathogen infection may lead to very different plant responses and in addition there may be 'cross-talk' between the signal pathways induced by pathogens and herbivores (Felton et al., 1999). Therefore, it is important to study the interactions of plant responses to pathogens and herbivores integratively (Agrawal et al., 1999). As a result the research of herbivore-induced plant volatiles will develop into the analysis of complex and temporally as well as spatially dynamic food webs (Figure 1). Although this development may seem to complicate the research, it should not be avoided as it will yield important progress in our understanding of the evolutionary aspects of arthropod-plant interactions. After all, temporally and spatially dynamic multitrophic systems are exactly the kind of conditions that have shaped the evolution of inducible plant volatiles.

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