

DO PLANTS CRY FOR HELP? EVIDENCE RELATED TO A TRITROPHIC SYSTEM OF PREDATORY MITES, SPIDER MITES AND THEIR HOST PLANTS

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ABSTRACT

Plants may defend themselves against herbivores by attracting predators as bodyguards. Release of infochemicals to do so bears costs in terms of energy and eavesdropping risks. Therefore, selection pressure on release of a bodyguard attracting synomone is expected to have a minimization component. Recent evidence for herbivore induced release of a synomone provides an intriguing example of bodyguard recruitment, in which release of the information is minimized. Features of this phenomenon are described and costs for the plants are discussed.

Key words: Acarina, Phytoseiidae, *Phytoseiulus persimilis*, predators, tritrophic interactions, infochemicals, synomone, indirect defence, induced defence, energetic costs, terpenes, methylene terpene, phenol, evolutionary aspects, volatiles.

INTRODUCTION

One of the defence mechanisms of plants against herbivores is promoting effectiveness of the herbivores' natural enemies: natural selection will favour (1) plant genotypes coding for traits that promote effectiveness of natural enemies and (2) predator genotypes that are better able to use the opportunities offered by the plant (Price et al., 1980). Mutualistic interactions between plants and their herbivores' enemies are therefore to be expected.

To promote effectiveness of predators, plants may provide shelter or alternative food in times of prey scarcity (e.g., Pemberton and Turner, 1989; Hagen, 1986). This may retain predators that are already present. In addition, plants may also produce volatiles to attract their herbivores' natural enemies as bodyguards (e.g., Williams et al., 1988).

Apart from costs related to production of bodyguard attractants, this defence mechanism also bears costs in terms of eavesdropping. Unauthorized users, such as herbivore species that are not affected by the recruited bodyguards, may use the released cues as a means of locating a food source. Thus, both energetic costs and eavesdropping risks may constrain the duration of release of bodyguard attractants. Recent investigations provide evidence for production of a bodyguard attracting

nature show a high degree of relatedness it is unlikely that the infested plant would produce the pheromone with the aim of informing conspecifics.

Costs of volatiles to plants. Chemicals used in defence have costs in terms of production, transport, storage, prevention of autotoxication, and release. In addition, there are also maintenance costs to synthesize enzymes needed in the above-mentioned processes. Calculation of overall costs is difficult, for several of the component costs. Biosynthetic costs are the component that can be usually quantified most reliably (Chew and Rodman, 1979). Intuitively, volatiles seem to constitute an extra cost for plants, since they are lost upon release and thus have to be renewed more often than non-volatiles. Several characteristics of volatile-release support this view:

(1) Plant volatiles are usually released in minute quantities and can only be analysed with very sensitive collection and analysis techniques (e.g., Buttery et al., 1984). The quantities released are in the ppm range, although upon damage, volatiles are generally released in much higher quantities (e.g., Dicke, 1988).

(2) Several volatiles are only released upon damage. For instance, precursors may be stored and degraded enzymatically when compartmentation is destroyed by herbivory, as is the case for production of volatiles from cyanogenic glycosides (Woodhead and Bernays, 1977; Conn, 1979).

(3) Release may be dependent on time of the day. For instance, some flower fragrances are produced exclusively during the day or the night, which is correlated with activity of their pollinators (Altenburger and Matile, 1988; Harborne, 1988). It would be a waste of energy for the plant to release volatiles while the pollinators are inactive and it would only increase chances of being located by herbivores.

These characteristics indicate that it is worthwhile for a plant to minimize its volatile release because of energetic costs and risks of use by "unauthorized receivers". The induced release of volatiles is a major means of reducing both types of costs. This is known for plant-herbivore interactions (Woodhead and Bernays, 1977; Harrison and Karban, 1986), but recently evidence was obtained that induced release of volatile infochemicals also occurs in plant-predator interactions (see below).

Induced indirect defence in a system consisting of predatory mites, herbivorous mites and their host plants. Spider mites are polyphagous herbivores that reach pest status in many agricultural crops (see Helle and Sabelis, 1985a for review). They insert their stylets in the leaves, inject saliva and ingest parenchymous cell contents. Spider mites are particularly ravenous herbivores, overexploiting their food source in the absence of predators. However, local populations are decimated, if discovered by predators such as predatory mites (see Helle and Sabelis, 1985b for review). Long-range dispersal by predatory mites occurs on wind currents. The aeronauts probably cannot control where they land and thus, chances of landing in a spider-mite colony or on a spider-mite infested plant will be small. However, after landing volatile infochemicals are used in making foraging decisions such as whether to stay or take off again, and where or how long to search (for review see Sabelis and Dicke, 1985). Because predatory mites overexploit their prey locally, it may be envisaged that any plant genotype that increases chances of predatory-mite invasion into spider-mite colonies will have a relatively higher fitness than conspecifics without this ability.

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Much research has been done on a tritrophic system consisting of the predatory mite *Phytoseiulus persimilis*, the spider mite *Tetranychus urticae* and its host plants. Predatory mites distinguish between clean plants and spider-mite infested plants by means of olfaction. The volatile allelochemical involved is mainly emitted from the leaves after infestation. Upon removal of spider mites and their visible products, previously infested leaves remained attractive to predatory mites for several hours, whereas the spider mites removed from the leaves were not attractive (Sabelis and Van de Baan, 1983; Sabelis et al., 1984a). The attractiveness is correlated with the amount of feeding by spider mites (Sabelis and Van de Baan, 1983; Sabelis et al., 1984a). Behavioural investigations in which the components of spider-mite infested plants were separately tested in an olfactometer showed that the volatile allelochemical is a product of the interaction between spider mites and host plant (Sabelis et al., 1984a). Chemical analysis revealed only compounds that are well-known from the plant kingdom, that are not known to be produced *de novo* by animals (Dicke et al., 1989). The allelochemical is spider-mite species specific (Sabelis and Van de Baan, 1983) but it is interesting to see that it is also plant-species specific (Takabayashi and Dicke, in prep). For example, cucumber plants infested by two-spotted spider mites are much less attractive than Lima bean plants infested by this herbivore species (Takabayashi et al., in prep). Different mixtures of volatiles are emitted by these plant species when infested by two-spotted spider mites. Four of the compounds emitted by infested Lima bean plants are attractive: the terpenes linalool and (*E*)- β -ocimene, the methylene terpene 4,8-dimethyl-1,3(*E*),7-nonatriene and the phenolic compound methyl salicylate (Dicke et al., 1989), whereas only two of these (β -ocimene and the methylene terpene) are emitted by infested cucumber plants (Takabayashi et al., in prep).

Apart from this evidence for plant involvement in production of the allelochemical (a synomone if plant-predatory mite interactions are regarded or a kairomone when spider mite-predatory mite interactions are regarded; cf. Dicke and Sabelis, 1988), behavioural investigations indicate that its production is not restricted to infested leaves but occurs plant-wide: uninfested leaves of infested plants are more attractive than uninfested leaves of uninfested plants. In these experiments adsorption of synomone to uninfested leaves of infested plants has been precluded (Dicke et al., in prep).

Effect of induced infochemical on spider-mite behaviour. *Tetranychus urticae* is repelled by leaves with a high density of conspecifics. The involved volatile infochemical overlaps with the synomone which attracts predatory mites, in at least one component: linalool (Dicke, 1986; Dicke et al., 1989). This interaction between spider mites raises the question whether (1) predatory mites spy on spider-mite communication or (2) spider mites leave as soon as the plant's cry for help gets too loud. This is essentially a question about who controls production and/or release of the chemicals.

1. The spider mites might control production of the infochemical to inform conspecifics about local density, and thus about food quantity and prospects for competition. But the spider mites would not need a volatile compound for this because information can also be conveyed by non-volatile chemicals or by contacts between

individuals, without the costs of volatiles or the associated risks of attracting predatory mites.

2. The plant might control production of volatiles to recruit bodyguards. The volatile nature of the chemicals is then indispensable for fast spread of the advertisement: success of *induced* indirect defence depends heavily on rapidly recruited defenders. In this case the spider mites would do best by using the volatiles as a dispersing pheromone. It seems unlikely that the mites could avoid the feeding-dependent release of the infochemical, unless they can make their feeding unrecognizable for the plant.

These considerations suggest that the volatile infochemical primarily functions in plant-predatory mite interactions and that the spider-mite response is secondary.

Bodyguard attracting synomone and spider mite extermination. Simulation models of the local population dynamics of the system consisting of predatory mites, spider mites and their host plants gave exceedingly bad predictions when the predators were assumed to search at random as they do in prey-infested leaf areas. However if the predators, upon leaving the prey-infested leaf area, are assumed to return immediately, the simulation models gave reasonably good predictions (Sabelis and Van der Meer, 1986). Behavioural studies have demonstrated that the volatile-synomone gradient present at the edge of the patch affects such returning behaviour (Sabelis et al., 1984b) and that, even when starved, the predatory mite *P. persimilis* did not take off on wind currents as long as the volatile infochemical was present (Sabelis and Afman, 1984). Because the volatile synomone appears to be essential in spider-mite extermination it is important to study the role of the plant in its production in more detail, thus improving knowledge of this indirect inducible defence mechanism.

Costs of bodyguard recruitment. In a first attempt to estimate biosynthetic costs of the synomone, Dicke and Sabelis (1989) reported a conservative estimate of 0.001% of leaf production costs per day. This value may seem to be low, but biosynthetic costs are but one of the costs made. Other costs may comprise e.g. maintenance costs for synthesizing enzymes, or costs of transport and storage of synomone (precursors). Moreover, even if overall costs are low indeed, their impact should not be overlooked since, given conditions of exponential leaf growth, small costs in an early phase may have large consequences for the production of reproductive tissue in the end (Gulmon and Mooney, 1986). It is also important to note that production of *volatile* infochemicals is much more expensive than production of non-volatiles, because volatiles have to be renewed constantly.

The view that costs are not negligible is strengthened by the fact that plants do not produce the infochemical non-stop. Eavesdropping risks may be responsible as well, but no evidence is available yet for this system.

When costs related to synomone production may be offset by saving the energy for other fitness-related purposes and by the probability of settlement close to a synomone producing plant, polymorphism is expected to occur under a wide range of conditions (Sabelis and De Jong, 1988).

Future investigations will concentrate on *how* plants contribute to synomone production, on cost-reducing mechanisms that plants may employ and on the use of the released information by each of the three trophic levels.

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