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PLANT STRATEGIES OF MANIPULATING PREDATOR- PREY INTERACTIONS THROUGH ALLELOCHEMICALS: PROSPECTS FOR APPLICATION IN PEST CONTROL

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Abstract—To understand the role of allelochemicals in predator-prey interactions it is not sufficient to study the behavioral responses of predator and prey. One should elucidate the origin of the allelochemicals and be aware that it may be located at another trophic level. These aspects are reviewed for predator-prey interactions in general and illustrated in detail for interactions between predatory mites and herbivorous mites. In the latter system there is behavioral and chemical evidence for the involvement of the host plant in production of volatile allelochemicals upon damage by the herbivores with the consequence of attracting predators. These volatiles not only influence predator behavior, but also prey behavior and even the attractiveness of nearby plants to predators. Herbivorous mites disperse away from places with high concentrations of the volatiles, and undamaged plants attract more predators when previously exposed to volatiles from infested conspecific plants

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rather than from uninfested plants. The latter phenomenon may well be an example of plant-to-plant communication. The involvement of the host plant is probably not unique to the predator-herbivore-plant system under study. It may well be widespread since it makes sense from an evolutionary point of view. If so, prospects for application in pest control are wide open. These are discussed, and it is concluded that crop protection in the future should include tactics whereby man becomes an ally to plants in their strategies to manipulate predator-prey interactions through allelochemicals.

Key Words—Predator, prey, host plant, tritrophic interactions, plant defense, allelochemicals, kairomone, pest control, behavior, chemical identification.

INTRODUCTION

Entomophagous arthropods use a wealth of chemical information when searching for hosts or prey (Nordlund et al., 1981a; Bell and Cardé, 1984; Haynes and Birch, 1985; Barbosa and Letourneau, 1988). Most of the published studies concern parasitoids; predators have been much less studied. Recently, however, data on the role of allelochemicals in predator foraging have increased for some groups such as predatory mites, bark beetle predators, and coccinellids (Billings and Cameron, 1984; Heuer and Vité, 1984; Payne et al., 1984; Sabelis and Dicke, 1985; Baisier et al., 1988; Dicke and Sabelis, 1988b; Hammond, 1988). This paper reviews that progress and presents new data. This is done with the aim of finding prospects for application of allelochemicals in pest control.

The focal points of this paper are the effect of allelochemicals on predator behavior and the origin and chemical nature of the allelochemicals. Application of allelochemicals in pest control is impossible without knowledge of the behavior induced by the chemicals (Lewis et al., 1975a,b, 1979; Gross, 1981). In addition, to manipulate predator-prey interactions with allelochemicals it is necessary to know the origin of the compounds, and thus the organism(s) that control their production. Finally, elucidation of the chemical structure is indispensable for synthesis of the allelochemicals.

Much of the research on allelochemicals affecting behavior of natural enemies of herbivores has been done in a bitrophic (predator-prey; parasitoid-host) context (Nordlund et al., 1981a; Bell and Cardé, 1984; Haynes and Birch, 1985), but since the papers by Price et al. (1980) and Price (1981) it is clear that plants are often an essential factor, either passive or active, affecting predator-prey interactions. Interactions mediated by allelochemicals are no exception and recent data, presented in this paper, reveal interesting plant activities such as beating the alarm or overhearing. Because plant activities seriously affect predator-prey interactions, it is essential to view the three focal points mentioned above in a tritrophic context.

ALLELOCHEMICAL TERMINOLOGY

Nordlund and Lewis (1976) presented a semiochemical terminology that was developed at a time when interactions were almost exclusively studied in a bitrophic context. Various semiochemical categories have been distinguished. They are based on: (1) whether or not the interaction is between conspecific individuals (pheromones vs. allelochemicals), (2) which costs and benefits fall to each of the two interacting organisms, and (3) which organism is the producer and which the receiver. Since tritrophic systems are of much greater complexity, several difficulties in using the terms have been encountered. In a reevaluation of this terminology, Dicke and Sabelis (1988a) argued that the producer criterion should be dropped. They presented several examples showing that organisms once thought to be producers later on appeared to be not the producers themselves, but rather to be associated with other organisms (e.g., microorganisms) that were responsible for allelochemical production or for induction of production in another organism. By taking the producer criterion strictly, terminology would exclude an important class of ecologically significant interactions (Dicke and Sabelis, 1988a). The terms in this paper are used according to this updated terminology: for any allelochemical the term used is based on the cost-benefit analysis for the two interacting organisms under consideration (see Table 1 for definitions).

In addition, Dicke and Sabelis (1988a) emphasized the special status of information-conveying chemicals: this category differs from toxins and nutrients in that they are not detrimental or beneficial themselves, but may be through the response they elicit. Information-conveying chemicals were termed infochemicals (Table 1) and constitute a subcategory of semiochemicals.

ROLE OF ALLELOCHEMICALS IN FORAGING BEHAVIOR OF PREDATORY ARTHROPODS

Predator foraging consists of a series of behaviors that are affected by information about the surroundings. Chemicals are among the main information-conveying agents available to predatory arthropods. They play an essential role in almost all stages of prey searching and prey selection. Predators may exploit chemical information in two main foraging strategies:

1. The predator lies in wait and attracts prey. This phenomenon has been studied in depth for bolas spiders. These predators produce allomones that are mimics of female moth sex pheromones and thus attract male moths of a restricted number of species that are caught by means of a sticky ball on the end of a silken thread (Eberhard, 1977; Stowe et al., 1987; Yeargan, 1988).

TABLE 1. INFOCHEMICAL TERMINOLOGY (DICKE AND SABELIS, 1988a)

Infochemical: A chemical that, in the natural context, conveys information in an interaction between two individuals, evoking in the receiver a behavioral or physiological response.

Pheromone: An infochemical that mediates an interaction between organisms of the same species whereby the benefit is to the origin-related organism [(+, -) pheromone], to the receiver [(-, +) pheromone], or to both [(+, +) pheromone].

Allelochemical: An infochemical that mediates an interaction between two individuals that belong to different species.

Allomone: An allelochemical that is pertinent to the biology of an organism (organism 1) and that, when it contacts an individual of another species (organism 2), evokes in the receiver a behavioral or physiological response that is adaptively favorable to organism 1, but not to organism 2.

Kairomone: An allelochemical that is pertinent to the biology of an organism (organism 1) and that, when it contacts an individual of another species (organism 2), evokes in the receiver a behavioral or physiological response that is adaptively favorable to organism 2, but not to organism 1.

Synomone: An allelochemical that is pertinent to the biology of an organism (organism 1) and that, when it contacts an individual of another species (organism 2), evokes in the receiver a behavioral or physiological response that is adaptively favorable to both organism 1 and 2.

2. The predator actively searches for prey. This strategy is the more common one, and allelochemicals play a role at several stages:

(a) In an initial phase of prey searching, predators may use plant volatiles as synomones in the selection of a suitable foraging habitat. It may be presumed that these synomones affect in-flight behavior of predators, but most behavioral assays have tested the animals in the ambulatory phase (Greany and Hagen, 1981; Vinson, 1981; Dwumfour, 1987; Reid and Lampman, 1989).

(b) Volatile prey-related chemicals may be used as kairomones in an early stage of prey searching (Vité and Williamson, 1970; Mpakagiannis, 1982; Aldrich et al., 1986; Sabelis and Afman, 1984; Sabelis and Dicke, 1985; Sabelis and Janssen, 1990). In-flight behavior may be influenced (Vité and Williamson, 1970), but alternatively, upon landing, the decision to stay or to continue aerial dispersal may be affected by volatile kairomones (Sabelis and Afman, 1984; Sabelis and Janssen, 1990). These compounds obviously provide more information about prey presence than plant volatiles and may function in distant prey selection (Sabelis and Van de Baan, 1983; Dicke et al., 1988).

(c) Once in a prey patch, predators may be arrested by volatile or non-volatile kairomones (Hislop and Prokopy, 1981; Hoy and Smilanick, 1981; Evans and Dixon, 1986; Sabelis et al., 1984b; De Moraes and McMurtry, 1985) through kinetic and tactic responses of the predator at the patch edge (Hislop and Prokopy, 1981; Sabelis et al., 1984b).

(d) Due to predator activity, prey density may decline locally and at some moment a predator decides to leave the patch to search for other, more rewarding, patches. Kairomones affect this decision (Sabelis and Afman, 1984; Sabelis and Janssen, 1990).

(e) Prey searching is not the only process affected by allelochemicals. For example, some predators use these cues to select oviposition sites (Hagen 1986; Evans and Dixon, 1986; Baisier et al., 1988). This is especially relevant when the larva is predacious and the adult is not, or consumes a different prey located elsewhere in the environment.

In conclusion, it is clear that allelochemicals affect many stages of predator foraging behavior through a variety of behavioral responses. As a consequence, thorough behavioral analysis is indispensable for drawing conclusions on the role of allelochemicals in predator foraging strategies and thus for possibilities to employ such chemicals in pest control.

ORIGIN OF ALLELOCHEMICALS INVOLVED IN PREDATOR FORAGING BEHAVIOR

Under the assumption that foraging behavior has a genetic basis, natural selection is expected to favor those predator genotypes that possess a foraging strategy that results in maximum reproductive success. Thus, the source of the allelochemicals used by predators may be expected to vary, under the condition that the chemicals involved increase the rate of prey finding. Indeed, foraging predators exploit allelochemicals from their prey, or prey activities, but also from the host plant, or from other organisms associated with the prey, such as microorganisms. Many examples exist for predators using prey-produced allelochemicals (for review, see Greany and Hagen, 1981), but fewer have been recorded for allelochemicals produced by the prey's host plant (Vinson, 1981; Nordlund et al., 1988) or associated microorganisms (Dicke, 1988a). However, this is presumably due to restricted efforts made to find the exact source of the allelochemical (for review, see Dicke and Sabelis, 1988a).

Elucidation of the origin of allelochemicals that affect predator foraging behavior is not only interesting from a theoretical point of view (Dicke and Sabelis, 1988a) but may also provide application possibilities. Identification of the origin of the allelochemical provides prospects for investigations aiming at finding ways to manipulate release rates. This will be illustrated in this paper.

CHEMICAL NATURE OF ALLELOCHEMICALS AFFECTING PREDATOR-PREY INTERACTIONS

Many allelochemicals that function in predator-prey interactions originally served as pheromones for the prey individuals: predators illegitimately use the chemicals either as receiver or as emitter. Thus, elucidation of the chemical

structures of allelochemicals has benefitted in many cases from studies on pheromone structures. This is most evident for predators of bark beetles. The wealth of knowledge on bark beetle pheromones (Wood, 1982; Birch, 1984; Borden, 1984) has caused a boom in chemical knowledge of kairomones that attract their predators (Vité and Williamson, 1970; Billings and Cameron, 1984; Chatelain and Schenk, 1984; Heuer and Vité, 1984; Payne et al., 1984). In addition, several tree terpenes whose release is increased by herbivore damage, and that function as synomones in plant-predator interactions, have been identified (Fitzgerald and Nagel, 1972; Baisier et al., 1988). Similarly, Aldrich et al. (1986) identified a pheromone of a stink bug and showed that it attracts its predator, the eastern yellowjacket. After good indications for the production of moth sex-pheromone components by bolas spiders to function as allomones in attracting male moths as prey (Eberhard, 1977), chemical investigations confirmed this (Stowe et al., 1987).

Pheromone identification has not always given the impetus to research aimed at structure identification. There are cases where the impetus came from investigations on predator-prey interactions. Lacewing adults (*Chrysopa carnea*), which feed on honeydew, are attracted to indole acetaldehyde, a breakdown product of the honeydew component tryptophan (Hagen et al., 1976; Van Emden and Hagen, 1976). The offspring produced on honeydew-contaminated plants feed on the aphids that deposited the honeydew. *Chrysopa* adults are also attracted to plant compounds such as caryophyllene, which presumably represents habitat location (Flint et al., 1979). Chemical analysis of volatile kairomones that attract predatory mites to prey-infested plants not only resulted in identification of kairomone structures but also revealed pheromonal and synomonal functions of these chemicals in a tritrophic context (Dicke, 1988c; Dicke et al., 1990a). Instead of being a consequence of pheromone identification, elucidation of allelochemical structures in this case was the first step in a process of unravelling interactions mediated by infochemicals, both pheromones and allelochemicals. Details of this example are given below (section "Allelochemicals in a tritrophic system consisting of predatory mites, spider mites, and their host plants").

FUNCTION OF ALLELOCHEMICALS IN A MULTITROPHIC CONTEXT

Once an infochemical is released, any organism that encounters it is a potential user and thus every infochemical may affect several interactions in a multitrophic system (Price et al., 1980; Price, 1981). Consequently, when considering the function of an allelochemical, care must be taken to investigate all components of the system. For instance, if a predator uses a volatile produced by its herbivorous prey as a kairomone in prey location, it is important to investigate what the function of this compound is to the prey (e.g., Bakke and

Kvamme, 1981; Payne et al., 1984; Dicke, 1986). Moreover, it appears to be also important to investigate the function of this infochemical to potential host plants of the herbivore: they may use the information to take defensive action. This was demonstrated for a system of cotton plants and a pathogenic fungus (Zeringue, 1987). However, the response of host plants to chemical information has as yet received limited attention (Baldwin and Schultz, 1983; Rhoades, 1985a,b; Bruin et al., 1990).

ALLELOCHEMICALS AFFECTING FORAGING BEHAVIOR OF NATURAL ENEMIES AND APPLICATION IN PEST CONTROL

Research on allelochemicals and natural enemies of herbivores has expanded enormously since the 1970s. This initiated many ideas about application of these infochemicals in pest control, such as: (1) enhancing searching efficiency of natural enemies (Lewis et al., 1975a,b, 1979; Gross, 1981); (2) bringing the natural enemies in a specific search mode (Gross, 1981; Vet, 1988); (3) making novel or artificial host-prey species acceptable in a mass rearing program (Vinson, 1986); (4) using the response to the allelochemical as a criterion in the selection of natural enemies for biological control (Janssen et al., 1990) or (5) as a criterion in quality control (Dicke et al., 1989c; Noldus, 1989); and (6) breeding plant cultivars that have an increased emission rate of natural-enemy-attracting synomones (Nordlund et al., 1981b, 1988).

The idea of enhancing search efficiency through application of allelochemicals has been seriously tested in laboratory and field situations with *Trichogramma* spp., egg parasitoids of moth species such as *Heliothis*. Although this work concerns parasitoids rather than predators, it is referred to in this paper because it is the best investigated system with respect to application of allelochemicals in pest control. The knowledge gained is thought to have profound implications for predator-prey interactions as well.

Initial tests showed that enhanced parasitization rates may be obtained by spraying an extract of moth scales or synthetic kairomone identified in these scales (Lewis et al., 1975a,b). However, subsequent testing revealed that, when using a blanket spray, this result could only be obtained at high host densities, not at natural densities. At low or intermediate densities, parasitization rates could be increased by applying kairomone or artificial moth scales (diatomaceous particles impregnated with kairomone) around the host eggs (Lewis et al., 1979; Gross, 1981). To understand these results, knowledge of the behavioral response induced in the parasitoid upon contacting kairomone is indispensable. Moth scales are present around oviposition sites and represent moth activity on a larger area than the egg alone. Upon contacting (kairomone in) moth scales, the parasitoids increase searching activities locally and are arrested (Beever et al., 1981; Noldus and Van Lenteren, 1985; Gardner and Van Len-

teren, 1986). Thus, when kairomone is applied on leaves without hosts, parasitoids waste time, which results in a reduction in the parasitization rate. At low ratios of host-containing leaves to leaves without hosts, this effect is most pronounced. At extremely high densities, there is a net positive effect, because there are no host-deficient leaves (Lewis et al., 1975a,b; 1979). This research led to the conclusion that kairomone distribution in combination with host distribution decisively affected the outcome of the experiments as a result of the behavioral response of the parasitoids. Increasing the parasitization rate under field conditions by increasing kairomone concentration at or in the neighborhood of oviposition sites is obviously not a practical solution for pest management, however. This research project demonstrated that knowledge of the foraging behavior is essential for successful employment of the allelochemical in pest control. Similar conclusions were obtained by Chiri and Legner (1983) in research on an egg-larval parasitoid of the pink bollworm.

The idea of applying allelochemicals in pest control through plant breeding has received increased interest in recent years because of biotechnological developments and their effects on plant breeding (Nordlund et al., 1988; Dicke et al., 1989a). Recent investigations of a tritrophic system consisting of predatory mites, spider mites, and their host plants indicate that plant breeding may solve problems about kairomone distribution, such as encountered for the *Heliothis-Trichogramma* system. This will be the subject of the remainder of this paper.

ALLELOCHEMICALS IN A TRITROPHIC SYSTEM CONSISTING OF PREDATORY MITES, SPIDER 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 (Tomczyk and Kropczynska, 1985). An adult female gives rise to a colony from which daughters disperse upon reaching adulthood to settle nearby and initiate new colonies. 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). Allelochemicals play an essential role in this process.

Allelochemicals and Predatory-Mite Behavior

Allelochemicals affect prey-searching and prey-selection behavior of predatory mites in several ways: (1) Predatory mites disperse on wind currents and probably exert little control on where they land. Thus, the chances of landing

in a spider-mite colony or on a spider-mite-infested plant are small. However, after landing, volatile kairomones are used in making foraging decisions such as whether to stay or to take off again, and where or how long to search (Sabelis and Afman, 1984; Sabelis and Dicke 1985; Sabelis and Janssen, 1990). The response to these volatile kairomones depends on quantitative and qualitative food history of the predatory mites (Sabelis and Van de Baan, 1983; Dicke et al., 1986, 1989c). (2) Once predatory mites are in a prey patch [a group of leaves infested by prey (cf. Sabelis, 1981; Sabelis and Dicke, 1985)], their behavior is affected by volatile and nonvolatile kairomones. These chemicals induce kinetic and tactic responses in the patch and at the patch edge (Hislop and Prokopy, 1981; Sabelis et al., 1984a; Sabelis and Dicke, 1985). As a result the predators stay in the patch as long as prey-related allelochemicals are present. (3) Predatory mites distinguish between volatile kairomones related to different prey species: they have kairomone preferences (Sabelis and Van de Baan, 1983; Dicke and Groeneveld, 1986; Dicke, 1988b; Dicke et al., 1988) that correlate to prey preferences as assessed in predation analyses under laboratory and field conditions (Dicke and De Jong, 1988; Dicke et al., 1988, 1989b). Thus, distant information about prey availability initiates prey selection decisions similar to those made in the prey patch.

Source of Volatile Allelochemical Affecting Predatory-Mite Behavior

Most research has been conducted on a system consisting of Lima bean plants (*Phaseolus lunatus*), the spider mite *Tetranychus urticae*, and the predatory mite *Phytoseiulus persimilis*. These predatory mites distinguish between *T. urticae*-infested and uninfested Lima bean plants by olfaction. The volatile kairomone involved in this predator-prey interaction 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). Several attempts have been made to gain more detailed knowledge of the origin of the kairomone by fragmentation of the spider mite colony or by extracting the leaf surface after spider-mite feeding had occurred (Sabelis et al., 1984a). The results show that all feeding spider-mite stages contributed to kairomone production and that the infested leaf was the main kairomone source. Very little kairomone activity was present in feces or in extracts of spider mites. No kairomone activity could be demonstrated in plants treated in several ways, unless spider-mite feeding had recently occurred. Although this investigation did not result in a final elucidation of the origin of the kairomone, it indicated that both spider mite and host plant are involved in its production. Note that we classify the allelochemical as a kairomone in this discussion as long as we deal with predator-prey interactions; in plant-predator interactions it is a synomone (Table 1).

Some further evidence for involvement of plant and spider mite in the production of kairomone is the following. Many different plant-spider mite combinations emit a volatile kairomone (Dicke and Sabelis, 1988b), and predatory mites distinguish between them (Sabelis and Van de Baan, 1983; Dicke and Groeneveld, 1986; Dicke et al., 1986; Dicke, 1988b). The volatile kairomone is spider-mite species specific: predatory mites distinguish between plants infested by different spider-mite species (Sabelis and Van de Baan, 1983). Moreover, recent experiments show that the kairomone is also plant species specific: *Phytoseiulus persimilis* females distinguish between *T. urticae*-infested Lima bean leaves and *T. urticae*-infested cucumber leaves. Predators from a stock culture on *T. urticae* on Lima bean leaves were transferred to either *T. urticae*-infested Lima bean leaves or *T. urticae*-infested cucumber leaves. After seven days, the predators were offered a choice between infested Lima bean leaves and infested cucumber leaves in a Y-tube olfactometer. The predators preferred the olfactometer arm with the odor source that they had experienced prior to testing (Figure 1). Because kairomone preference depends on predator experience, the discrimination is the result of a qualitative rather than a quantitative difference in kairomone (Dicke et al., 1990b).

Previously infested leaves are still highly attractive to predatory mites after removal of spider mites and their visible products. Thus, we investigated whether spider mites deposit the kairomone in invisible form on the leaf surface. For this, we studied whether kairomone activity on a spider-mite-infested plant is restricted to the infested leaves. Lima bean plants that had three or four leaves were infested on one of the primary leaves. Spider mites were prevented from leaving the leaf by applying Tanglefoot sticky material to the petiole. After six days at 25°C, uninfested leaves of infested plants were tested in a Y-tube olfactometer (see Sabelis and Van de Baan, 1983, for experimental setup) versus uninfested leaves of uninfested plants (equal leaf weights, in the range of 10–18 g, in both olfactometer arms). Uninfested plants were taken from the same batch as the plants that had been partly infested, and they had also been kept at 25°C for six days prior to the experiment. This was done in the same climate room as used for partly infested plants, but the air current in the climate room was such that uninfested plants did not receive air that had passed over partly infested plants. *Phytoseiulus persimilis* females preferred the odor of uninfested leaves of infested plants over the odor of uninfested leaves of uninfested plants (Figure 2A). This may be explained by either production of an allelochemical in uninfested leaves of infested plants or by adsorption and reemission of an allelochemical that was produced at the site of spider-mite infestation. To exclude adsorption, we carried out a similar experiment in which the infested leaves were enveloped in a Petri dish through which an airstream was generated to remove all emitted volatiles. In the Y-tube olfactometer experiment, the predator distribution was similar to that in the previous experiment (Figure 2B).

FIG. 1. Response of satiated *P. persimilis* females in a Y-tube olfactometer when offered *T. urticae*-infested Lima bean leaves vs. *T. urticae*-infested cucumber leaves. The ratio of spider-mite numbers of 1 : 10 was determined from preliminary experiments: the responses to each odor source were such that changes in preference were best detectable; at lower or higher ratios one of the odor sources evoked such a strong response that changes in preference were more difficult to detect (J. Takabayashi and M. Dicke, unpublished data). n: number of predators. Figure after data in Dicke et al. (1990b).

FIG. 2. Response of satiated *P. persimilis* females in a Y-tube olfactometer when offered uninfested leaves from infested Lima bean plants vs. uninfested leaves from uninfested Lima bean plants (equal leaf weights, within the range of 10–18 g, in both olfactometer arms). All plants were placed in a climate room (25°C) during six days, before uninfested primary leaves were picked to be used in the olfactometer. For further details see text. (A) Volatiles emitted from infested leaves may adsorb to uninfested leaves; (B) volatiles emitted from infested leaves are led to the vacuum system of the building to prevent adsorption to uninfested leaves. n: number of predators tested, P: critical level determined with sign test for differences from 50:50 distribution of predators over the two arms.

This indicates that an attractant is produced in uninfested leaves of infested plants. This is the first evidence that production of predator attractants and spider mite damage can be locally separated. Whether the same predator attractants are produced in spider-mite-infested leaves and in uninfested leaves of infested plants remains to be investigated.

Chemical Identification of the Kairomone

Chemical investigations (Dicke, 1988c; Dicke et al., 1990a) revealed that large amounts of volatiles are emitted from artificially damaged or *T. urticae*-infested Lima bean plants. Identification of these compounds revealed only chemicals that belong to classes that are well-known from the plant kingdom. Four of the compounds attracted *P. persimilis* females. These were identified in the headspace of *T. urticae*-infested Lima bean plants but were not found in

the headspace of undamaged or artificially damaged plants. These kairomone components are the terpenes linalool and (*E*)- β -ocimene, the methylene terpene 4,8-dimethyl-1,3(*E*),7-nonatriene, and the phenolic compound methyl salicylate (Figure 3). These classes of compounds are known to be produced by plants, but not by animals. Linalool, (*E*)- β -ocimene, and methyl salicylate are known from many plant species. However, the methylene terpene deserves special attention, because it has been identified only recently in plants (Maurer et al., 1986; Kaiser, 1987). It was not detected in steam distillates of uninfested Lima bean plants (H. van Bokhoven and T.A. van Beek, unpublished data).

While none of the four kairomone components was found in the volatile blend emitted by undamaged or artificially damaged Lima bean plants [many analyses during several years; (Dicke et al., 1990a)] and undamaged plants were not attractive to *P. persimilis* (Sabelis and Van de Baan, 1983), most recent analyses consistently revealed small amounts of the four predator-attracting compounds in the headspace of undamaged or artificially damaged Lima bean plants. The amounts are of the same order of magnitude for clean and artificially damaged plants, but much lower (up to 200 times) than in spider-mite-infested plants (Takabayashi, Dicke and Posthumus, in preparation). Also, a slight attractiveness of undamaged Lima bean to *P. persimilis* is recorded in

FIG. 3. Chemical structure of kairomone components identified in headspace of Lima bean plants infested by *T. urticae*.

recent experiments (Takabayashi et al., 1990, and in preparation). The plants used were never damaged by spider mites and have never been in the same room as spider-mite-infested plants. Thus, these recent data show that spider-mite damage is not necessary for the production of the allelochemicals, but that spider-mite damage, in contrast to artificial damage, increases the emission enormously. The discrepancy between recent data and those by Dicke et al. (1990a) for undamaged and artificially damaged plants is under investigation.

Recently, the headspace of *T. urticae*-infested cucumber plants (*Cucumis sativus* cv. Santo, F1) was analyzed (Takabayashi, Dicke, Posthumus, Van Beek, and De Bie, in preparation). Again, all compounds found were known to be produced by plants, and not by animals. The blend of volatiles emitted is different from the one emitted from *T. urticae*-infested Lima bean plants (Table 2). Of the four kairomone components emitted from infested Lima bean plants, only (*E*)- β -ocimene and 4,8-dimethyl-1,3(*E*),7-nonatriene were found in infested cucumber plants. In addition, some compounds that were discovered in the headspace of infested cucumber plants had not been found in infested Lima bean plants. Among these were two oxime ethers and two nitriles. The chemicals found in the headspace of infested cucumber plants are currently tested for attractiveness to predatory mites.

Although the chemical evidence corroborates the biological evidence that the plant is involved in kairomone production, it remains unknown how this is accomplished.

Is the Kairomone Important in Extermination of Spider Mites by Predatory Mites?

Simulation models of the local population dynamics of spider-mites (*T. urticae*) and predatory mites (*P. persimilis*) 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). Behavioral studies have demonstrated that the volatile-kairomone gradient present at the edge of the patch affects such returning behavior (Sabelis et al., 1984b) and that, even when starved, the predatory mite *P. persimilis* did not take off on wind currents as long as kairomone was present (Sabelis and Afman, 1984; Sabelis and Janssen, 1990). These investigations indicate that the volatile kairomone is essential in spider-mite extermination.

Effects of Predator-Attracting Allelochemical in Other Interactions in the Tritrophic System

So far, tritrophic aspects only referred to predatory mites as the organisms responding to the allelochemical of spider-mite-infested plants, but spider mites

TABLE 2. IDENTIFICATION OF CHEMICALS IN HEADSPACE OF LIMA BEAN PLANTS AND CUCUMBER PLANTS INFESTED BY SPIDER MITE *T. urticae*^a

Compound	Relative percentage in headspace of <i>T. urticae</i> infested	
	Lima bean leaves	Cucumber leaves
Aldehydes		
2-Hexenal	<1	
Ketones		
2-Butanone	3-7	
3-Pentanone	<1	
Alcohols		
2-Methyl-propan-1-ol	<1	
1-Butanol	<1	
1-Penten-3-ol	<1	
(Z)-3-Hexen-1-ol	1-10	<1
1-Octen-3-ol	1-10	
1-Hexanol	<1	<1
2-Ethyl-1-hexanol		2-10
2-Octene-1-ol		<1
Esters		
(Z)-3-Hexen-1-yl acetate	20-40	1-10
(Z)-3-Hexen-1-yl butyrate	<1	<1
Methyl salicylate	1-5	
Terpenoids		
(E)- β -Ocimene	10-30	20-50
(Z)- β -Ocimene	<1	<1
4,8-Dimethyl-1,3(E),7-nonatriene	10-30	20-50
Linalool	1	
4,8,12-Trimethyl-1,3(E),7(E),11-tridecatetraene	5-15	1-5
Limonene	tr	1-10
(E,E)- α -Farnesene		1-5
Nitriles		
2-Methylbutanenitrile		<1
3-Methylbutanenitrile		1-5
Oximes		
2-Methylbutanal, O-methyloxime		<1
3-Methylbutanal, O-methyloxime		5-15

^aFor methods see Dicke et al. (1990a).

respond as well. The spider mite *T. urticae* is attracted by a volatile kairomone of undamaged Lima bean plants, but the mites disperse from an odor plume of Lima bean plants infested by conspecifics (Dicke, 1986). In the context of intraspecific spider-mite interactions the volatile infochemical emitted from *T. urticae*-infested plants is a pheromone; in this case, a (+, +)-dispersing pher-

omone (Table 1) (Dicke and Sabelis, 1988a). The behavioral reaction depends on the ratio of pheromone to kairomone. At a low ratio (low degree of infestation), the mites are attracted; at a high ratio (high degree of infestation), they are repelled. From biological evidence alone, Dicke (1986) argued that the pheromone shares components with the predator-prey kairomone. Indeed, from the combined data of Dabrowski and Rodriguez (1971), Dicke (1986), and Dicke et al. (1990a), it can be deduced that at least one component of the spider-mite pheromone is also a component of the predator-prey kairomone linalool. Methyl salicylate is not, while no data are available for the response of *T. urticae* to (*E*)- β -ocimene and 4,8-dimethyl-1,3(*E*),7-nonatriene.

Thus, several interactions in this system are mediated by volatile infochemicals whose release is induced by spider-mite feeding activities. An important question is: do predatory mites "spy" on spider-mite communication or do 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 nonvolatile 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 predatory mites as "bodyguards." The volatile nature of the chemicals is then indispensable for fast spread of the advertisement: success of induced indirect defense (cf. Price et al., 1980, Dicke and Sabelis, 1988b) 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 to the plant.

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

New View on the Role of the Plant in the Tritrophic System of Predatory Mites, Spider Mites, and Their Host Plants

The role of the plant in this system appears to have unprecedented characteristics, and most recent data even add new aspects. It is important for plants to attract predatory mites at an early stage of spider-mite infestation. Kairomone emission occurs to a large extent upon spider-mite damage, but the emission of predator attractant is not restricted to the damaged tissue (Figure 2). This made

us wonder whether uninfested plants that are in the neighborhood of infested plants produce (increased amounts of) predator attractants. Such still-uninfested plants run high risks of becoming infested and might take preventive action. To investigate this, we used a three-compartment wind tunnel (Figure 4). Uninfested plants of one batch were placed in all three compartments. Spider-mites were released on the plants in compartment 2. Plants in compartments 1 and 3 remained uninfested. After several days the uninfested plants of compartment 1 and 3 were transferred to a Y-tube olfactometer setup to investigate the response of the predatory mite *P. persimilis*. After four to five days of incubation in the wind tunnel, the plants of compartment 3 (that had infested plants upwind) were more attractive than plants from compartment 1 (that had no plants upwind). This was done with Lima bean plants and cotton plants (Figure 5). When the setup was slightly modified so that the control plants had received the odor of uninfested plants, similar results were obtained, but the incubation time needed was somewhat longer (Figure 6).

Preliminary chemical investigations have revealed that the headspace of Lima bean plants from compartment B3 (Figure 6) contains relatively large amounts of (*E*)- β -ocimene and (to a lesser extent) 4,8-dimethyl-1,3(*E*),7-nonatriene: ca. 17 and 5 times more than in undamaged plants that had not been in the neighborhood of infested plants. Thus, the composition of the blend emitted by plants from compartment B3 is completely different from the blend of control plants. For instance, in analyses of the headspace of undamaged plants that never experienced *T. urticae* infestations, peak areas of (*E*)- β -ocimene and 4,8-dimethyl-1,3(*E*),7-nonatriene are smaller than or equivalent to that of (*Z*)-3-hexen-1-yl acetate, but in the headspace of plants from compartment B3, peak areas are up to five times [4,8-dimethyl-1,3(*E*),7-nonatriene] and up to 26 times [(*E*)- β -ocimene] larger than that of (*Z*)-3-hexen-1-yl acetate! These data may be explained by adsorption of 4,8-dimethyl-1,3(*E*),7-nonatriene and (*E*)- β -ocimene emitted from plants in compartment B2 on plants in compartment B3, but the amounts released from plants in compartment B3 are rather

FIG. 4. Three-compartment wind-tunnel.

Incubation period
of plants in wind tunnel

FIG. 5. Response of satiated *P. persimilis* females in a Y-tube olfactometer to plants from compartment 1 vs. plants from compartment 3 of the three-compartment wind tunnel. ** $P \leq 0.01$; * $0.01 < P \leq 0.05$; n.s.: $P > 0.05$, sign test for differences from 50:50 distribution of predators over the two arms.

FIG. 6. Response of satiated *P. persimilis* females in a Y-tube olfactometer to plants from compartment A3 vs. plants from compartment B3. ** $P \leq 0.01$; n.s.: $P > 0.05$, sign test for differences from 50:50 distribution of predators over the two arms.

high. The adsorption hypothesis also is not supported in control experiments in which uninfested plants were exposed to synthetic (*E*)- β -ocimene: only trace amounts of this compound were found in the headspace of the exposed plants. Alternatively, plants receiving information about nearby spider-mite infestations start producing the two bodyguard-attracting allelochemicals themselves. This can be interpreted as a strategy of "overhearing" other plants' cries for help and subsequently sounding the alarm. More detailed investigations into this strategy of plant defense are currently under way. In all these investigations, adsorption of allelochemicals to wind-tunnel walls as an explanation of the data has been precluded by taking plants out of the wind tunnel for behavioral or chemical investigations.

Differences between Plant Cultivars

Plant cultivars are known to differ in production of entomophage-attracting synomones (Van Emden, 1986; Elzen et al., 1985, 1986). For instance, genetically similar cotton cultivars and lines differ in quantities of parasitoid-attracting terpenes produced. Glanded cultivars produced ca. 100 times more terpenes than glandless cultivars (Elzen et al., 1985). For spider-mite-infested bean plants (*Phaseolus vulgaris*) differences in attractiveness for predatory mites have been found for two different cultivars. In a Y-tube olfactometer clean bean leaves were offered vs. spider-mite-infested leaves. *Phytoseiulus persimilis* females were attracted by pole bean leaves infested with 400 spider mites, but not by bush bean leaves infested by 400 spiders mites for the same period of time (two days). Bush bean leaves infested by 1000 spider mites are attractive to predators (Figure 7). Whether this is the result of quantitative or qualitative differences in the emitted blend of volatiles needs to be investigated.

ROLE OF PLANTS IN OTHER MULTITROPHIC SYSTEMS

So far, we have given details on the role of plants in the tritrophic system of predatory mites, spider mites, and several plant species. However, evidence for active involvement of plants in multitrophic interactions is appearing for other systems as well. Data supporting the idea of "talking plants" have been put forward by Rhoades (1983, 1985a,b) and Baldwin and Schultz (1983), although Fowler and Lawton (1985) criticized their results on methodological grounds. However, data on this issue are accumulating and recent research efforts have shown phenomena that are similar to those described for the mite-plant system.

Using an olfactometer, Nadel and Van Alphen (1987) showed that cassava plants infested by cassava mealy bug attract the parasitoid *Epidinocarsis lopezi*: not only the infested leaves are attractive but also uninfested leaves of infested

FIG. 7. Response of satiated *P. persimilis* females in Y-tube olfactometer experiments with different *Phaseolus vulgaris* cultivars infested by *T. urticae*. Infested leaves were offered vs. uninfested leaves of the same cultivar. *Phaseolus vulgaris* cultivars: (1) Bush bean 'dubbele zonder draad,' nr. 697 and (2) polen-bean 'Westlandse dubbele' nr. 671, Turkenburg Ltd., The Netherlands ** $P \leq 0.01$; n.s.: $P > 0.05$, sign test for differences from 50:50 distribution of predators over the two arms.

plants are more attractive than uninfested leaves of uninfested plants. Unfortunately, they did not try to avoid adsorption of volatiles emitted from the infested leaves. Thus, it remains unknown whether the uninfested leaves actually produce the allelochemical.

Turlings et al. (1990) reported behavioral and chemical data for a tritrophic system of the parasitoid *Cotesia marginiventris*, noctuid herbivores, and corn plants. It appears that phenomena that are quite similar to some of those reported here for the mite-plant system are found in their parasitoid-herbivore-plant system: after damage by the herbivore, plants emit chemicals of plant origin that attract parasitoids.

The most intriguing data on active involvement of plants in defense were published for a system of plants and their pathogens (Zeringue, 1987). It was shown that cotton plants that receive odors of conspecifics infested with a pathogen start production of phenols that hamper pathogen growth. This compares to the findings that plants that have been in the neighborhood of spider-mite-

infested plants attract more predatory mites than control plants that have not experienced spider-mite-infested plants.

PROSPECTS FOR APPLICATION

In the earlier section on application in pest control, we summarized the prospects for integrating the use of allelochemicals in pest management strategies. One may ask whether these prospects apply to the mite-plant system discussed subsequently and whether the results obtained in studying this system give rise to new avenues for pest control. Here, we will present our current thoughts.

1. Bringing the natural enemy in a specific search mode (Gross, 1981; Vet, 1988). The plant-related predator-attracting allelochemicals are involved in learning by predatory mites. Predators that have experienced *T. urticae*-infested Lima bean leaves prefer infested Lima bean leaves when given a choice between *T. urticae*-infested Lima bean and *T. urticae*-infested cucumber leaves. However, if these predators are given a seven-day experience on *T. urticae*-infested cucumber leaves they prefer infested cucumber leaves (Figure 1) (Dicke et al., 1990b). These recent data have not yet led to ideas for application.

2. Making artificial host-prey species acceptable in a mass rearing program (Vinson, 1986). Nonvolatile kairomones are involved in prey acceptance (Jackson and Ford, 1973), but no evidence for an effect of volatile allelochemicals on prey acceptance has been shown. Data on prey preference have shown that volatile kairomone preference is correlated with prey preference (Dicke et al., 1988), but no causal relationship has been reported. We do not expect applications in this context.

3. Using the response to the allelochemical as a criterion in selection of natural enemies for biological control. This valuable idea is being used to develop biological control of the cassava green mite in Africa (Janssen et al., 1990). Its contribution to a reduction in time needed for prerelease evaluation programs of predatory mites may be expected within five years. This application is not dependent on the detailed knowledge presented in this paper, however.

4. Using the response to the allelochemical as a criterion in quality control (Dicke et al., 1989c; Noldus, 1989). The response to volatile allelochemicals appears to be crucial in the ability of a predator to exterminate a prey population (Sabelis and Van der Meer, 1986), and thus incorporating this response in a quality control program may be worthwhile, the more so because data are available for loss of the response to volatile allelochemicals in small-scale laboratory rearings of predatory mites (Dicke et al., 1989c). This application may be manifest today, but so far quality control programs for natural enemies are scarce (Bigler, 1989).

5. Enhancing searching efficiency of entomophages (Lewis et al., 1975a,b, 1979; Gross, 1981). As shown above ("Allelochemicals affecting foraging behavior of natural enemies and application in pest control"), application of this idea in the *Heliothis-Trichogramma* system suffered from problems of distributing the allelochemical in the field (Gross, 1981). Compounds that inform beneficial arthropods about herbivore location should be applied according to the actual distribution of the herbivores and the behavioral response of the natural enemies, otherwise the beneficials are misled instead of supported. Our data for the mite-plant system show that plants are involved in production of volatile allelochemicals that attract predatory mites to and retain them in spider-mite patches. Because differences in attraction have been found for different bean cultivars infested by *T. urticae*, plant breeding may yield cultivars that emit higher concentrations of predator-attracting allelochemicals. Thus, enhancing predator efficiency by breeding plants for higher concentrations of allelochemicals (proposed for allelochemicals that are emitted without herbivore damage; Nordlund et al., 1981b; 1988) may bring new application possibilities. For these possibilities to become reality, it is necessary to convince plant breeders that plant resistance against herbivores has not only a direct component but also an indirect component, i.e., through the action of the third trophic level (Price et al., 1980). Neglecting the indirect component in a plant breeding program may lead to elimination of indirect defense and thus to selection of cultivars that have a reduced net resistance under field conditions, especially in those cases where natural enemies play a significant (but often unnoticed) role in reduction of herbivore populations (see Van Emden, 1986, for an example related to allelochemicals). Alternatively, plant breeders may aim at selecting a cultivar in which searching behavior of a natural enemy is not hampered, but rather improved. This has been done successfully for a morphological trait of cucumber plants in an attempt to have satisfactory control of whiteflies by the parasitoid *Encarsia formosa*. High hair densities on leaves of cucumber varieties used to date in horticulture impede host searching by the parasitoid, and, thus, biological control is not successful on these varieties (Hulspas-Jordaan and Van Lenteren, 1978; Van Lenteren et al., 1987; Li et al., 1987). Recently, new cucumber varieties with lower hair density have been selected in a cooperative effort of plant breeders and entomologists. Greenhouse experiments showed that parasitism of whiteflies by *Encarsia formosa* was significantly higher on a cucumber variety having a lower hair density than the variety used by growers (Van Lenteren and De Ponti, 1990). Such approaches to application may be feasible within 10 years.

We expect that taking indirect plant defense tactics more seriously will enable man to effectively cooperate with plants in the battle against herbivores. Allelochemicals will prove to be useful manipulators.

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