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Chemical cues mediating aphid location by natural enemies

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Abstract. There is increasing evidence that chemical cues play a pivotal role in host selection by the natural enemies of aphids. We use Vinson's (1976) division of the host selection process into habitat location, host location and host acceptance for both parasitoids and predators and review what is known about the role of semiochemicals in aphid selection by natural enemies. For habitat location (i.e. detection of the host plant), volatiles emitted by plants after aphid attack have been described for a number of plant-aphid interactions. These synomones indicate not only the presence of an aphid host plant to the predator or parasitoid, but also the presence of aphids. Volatiles emitted from undamaged host plants are often attractive to aphid parasitoids, but less so for predators. Host location by the natural enemy on the food plant is guided by semiochemicals that mostly originate from the aphids, in particular aphid alarm pheromone, honeydew, or the smell of the aphid itself. Host acceptance is guided by contact chemicals for both predators and parasitoids. In parasitoids, host recognition may be based on visual cues or on contact chemicals on the aphid's cuticle, whereas host acceptance is ultimately based on as yet unknown substances within the aphid's hemolymph. While it appears that many predators and parasitoids are attracted to the same semiochemicals, synergistic and antagonistic interactions among chemical substances have only rarely been investigated. More research into model systems is needed, not only to identify important semiochemicals, but also to determine their range of attraction. Recent progress in the development of analytical techniques has created new opportunities to improve our understanding of the chemical ecology of aphid-natural enemy interactions in the coming years.

INTRODUCTION

Prey location in a complex environment, filled with different plants and animal species, is a complex task. Predatory and parasitic insects have specialized sensory nervous systems that allow them to use a variety of cues to find and identify target organisms. Cues can be physical such as colour, sound, shape and size as well as chemical and these may be useful for long or short range attraction to prey. In this paper, we focus on the chemical cues used by aphid predators and parasitoids to detect their aphid (Hemiptera: Aphididae) prey or host. In recent years, much insight has been gained into the chemical ecology of aphid-natural enemy interactions and the large number of articles describing new findings suggests that a review on the current state of our knowledge would be useful. Reviewing physical cues is beyond the scope of the current paper, although we refer to these cues wherever appropriate.

For parasitoids, Vinson (1976) divided the host selection process into three different steps. The first step is habitat location and the second is host location. We define habitat location as finding the host plant of an aphid species and host location as locating the aphid when the natural enemy is already on the plant. Thus, in our terminology, habitat location is analogous to food plant location. Habitat location may also be defined as finding the habitat of the host plant, e.g. a meadow. However, we believe that for aphid natural enemies the distinction between finding a plant and finding an aphid on the plant is more useful, even though it is likely that for some natural enemies the search for hosts may start before landing on the plant. Because aphids only occupy a fraction of all host plants available, first finding a plant and then searching for aphids may not be a very efficient strategy. For this reason, many aphid natural enemies do not search for a "host habitat" but for a "habitat with hosts".

In Vinson's (1976) terminology, the final step in the host selection process is host acceptance, which is the proper act of oviposition or host/prey consumption (cf. Steidle & van Loon, 2002). For parasitoids, this final step has been divided into host recognition and host acceptance (Michaud & Mackauer, 1994; Muratori et al., 2006). A host may be recognized visually, or by antennal contact with chemical cues in the aphid cuticle. Final host acceptance depends on an assessment of host quality made during ovipositor probing, but a host may be rejected either after recognition or after ovipositor probing.

Although Vinson (1976) developed his framework to characterize the parasitoid search process, it can also be used for aphid predators. Whereas in aphid parasitoids the host is primarily used for oviposition, it may also be used for host feeding, or as a source of honeydew. Aphid predators need to find aphids for both feeding and oviposition, unless they obtain food from non-aphid prey or plant sources. In general, host/prey selection by both

aphid predators and parasitoids is a step-wise process consistent with Vinson's framework.

We start with a brief discussion of the particular challenges involved in the use of chemical cues for host selection and then review what is known about the importance of chemical cues in each step of the host selection process. We will not review the signal cascades within the organisms (plants, aphids or natural enemies) that are involved in the production and detection of chemical cues. The responses of plants to feeding by aphids and other insect herbivores and the activation of signalling pathways have been recently reviewed (Walling, 2000; de Vos et al., 2007; Kempema et al., 2007).

THE DETECTABILITY-RELIABILITY PROBLEM AND THE SEARCH FOR CHEMICAL CUES

In an ecological context, *semiochemicals* are chemical substances that convey information between two organisms, evoking a behavioural or physiological response that is adaptive to one of the organisms or both (Vet & Dicke, 1992). Semiochemicals are classified, not with respect to their chemical properties or source, but rather according to their ecological roles (Nordlund & Lewis, 1976; Dicke & Sabelis, 1988; Vet & Dicke, 1992). While *pheromones* are semiochemicals released by one individual and perceived by another of the same species, *allelochemicals* are perceived by individuals of a different species. Allelochemicals can be further subdivided into different categories depending on the beneficiary of the signal. If the only beneficiary is the perceiver, the allelochemical is termed an *allomone*; if only the fitness of the producer is increased, it is termed a *kairomone*, and if both producer and perceiver benefit from the information exchange it is termed a *synomone*. The classification of a chemical compound may thus change according to the studied interaction. Pheromones of herbivores, for example, that may be perceived by a natural enemy and used to locate it are, for this interaction, classified as kairomones (Gabrys et al., 1997; Glinwood et al., 1999; Al Abassi et al., 2000).

On searching for herbivores, natural enemies face the dilemma of reliability versus detectability (Vet & Dicke, 1992). Volatiles produced directly by herbivores give reliable information about their presence, but occur in low concentrations in the environment due to the low biomass of aphids. Plant volatiles, on the other hand, are easily detected because of their high biomass, but are less reliable since plants may or may not harbor herbivores. Vet & Dicke (1992) suggested that, in general, natural enemies might use the following strategies to overcome the reliability-detectability problem: (1) use more conspicuous semiochemicals from herbivore stages other than the one susceptible to attack, (2) focus responses on stimuli created by specific interactions between the herbivore and its plant, or (3) learn to link easy-to-detect stimuli to reliable but hard-to-detect stimuli. The first possibility is not useful for aphid natural enemies as aphid stages have such low biomass, but the other two are frequently used.

SEMIOCHEMICALS INVOLVED IN THE HOST SELECTION PROCESS

Habitat location

Aphid natural enemies must first locate aphid habitat, i.e. a host plant where aphids might be present. Attraction to (undamaged) host plants has been shown for a number of aphid parasitoids (Hymenoptera: Braconidae), e.g. *Diaretiella rapae* (M'Intosh) (Read et al., 1970), *Lysiphlebus testaceipes* (Cresson) (Schuster & Starks, 1974), *Trioxys indicus* Subba Rao and Sharma (Singh & Sinha, 1982), *Aphidius uzbekistanicus* Luzhetski, *Aphidius ervi* Haliday (Powell & Zhang, 1983), *Aphidius rhopalosiphi* De Stephani-Perez, *Lysiphlebus fabarum* (Marshall), *Praon* sp. (Van Emden, 1988), and *Aphidius funebris* Mackauer (Pareja et al., 2007) so that at first sight it appears to be a general phenomenon in aphid parasitoids. However, the parasitoid *Aphidius nigripes* Ashmead is not attracted to the odour of potato plants, the host plant of the aphid *Macrosiphum euphorbiae* (Thomas) (Bouchard & Cloutier, 1985). The aphids *M. euphorbiae* and *Myzus persicae* (Sulzer) are the most common hosts of *A. nigripes*, but are very polyphagous species. Thus, it is possible that generalist parasitoids, or those that attack aphids with a wide host range, are less likely to respond to cues from plants without any additional evidence that aphids are present. However, *A. ervi* is also quite polyphagous, but is attracted by uninfested plants of its aphid hosts (Powell & Zhang, 1983), suggesting more study is needed before generalisations can be drawn.

In contrast to parasitoids, aphid predators mostly appear not to use odours of undamaged plants to locate aphids. While ladybirds and other aphid natural enemies frequently visit plants for purposes such as nectar or pollen feeding, and may be attracted to these plants in the absence of aphids (e.g. Michaud & Qureshi, 2005), laboratory studies have often failed to show attraction to undamaged plants. For example, the ladybird (Coleoptera: Coccinellidae) species *Coccinella septempunctata* L. (Ninkovic et al., 2001) and *Adalia bipunctata* (L.) (Francis et al., 2004), and the hoverfly *Episyrphus balteatus* (DeGeer) (Diptera: Syrphidae) (Francis et al., 2005b) were not attracted to odours from their (undamaged) host plant. An exception is *Chrysoperla carnea* (Stephens) (Neuroptera: Chrysopidae) that is attracted to plant volatiles (Hagen et al., 1976). The number of predator species tested is still low, but it appears that aphid predators, which are usually more polyphagous than parasitoids, are generally not attracted by the odour of undamaged plants without evidence of aphids. There is need for more testing, in particular for those species that not only feed on aphids but also feed on plant pollen, nectar and other plant parts.

The first evidence that plants can modify their volatile emissions in response to aphid attack was given by Guerrieri et al. (1993) who found that the parasitoid *A. ervi* was attracted to plants damaged by aphids, but not to undamaged plants. In fact, early evidence that damaged plants emit allelochemicals only after herbivory was given by Read et al. (1970) who showed attraction of

TABLE 1. List of chemical compounds from different aphid-plant complexes and their effect on natural enemies responses.

HABITAT LOCATION	Plant	Aphid	Natural enemy	Effect	Reference
6-methyl-5-hepten-2-one (MHO)	*V. faba*	*A. pisum*	*A. ervi*	Attract	Du et al., 1998; Powell et al., 1998
	C. nigra	*U. jacea*	*A. funebris*	Attract	Pareja et al., 2007
	C. nigra	*U. jacea*	*A. uzbekistanicus*	Repel	Holler et al., 1994
	T. avestivum	*R. padi*	*A. rhopalosiphi*	None	Gonzales et al., 1999
(*Z*)-3-hexenyl acetate	*C. nigra*	*U. jacea*	*A. funebris*	Attract	Pareja et al., 2007
Allyl isothiocyanate	*B. oleracea*	*B. brassicae*	*D. rapae*	Attract	Read et al., 1970
Methyl salicylate	*G. max*	*A. glycines*	*C. septempunctata*	Attract	Zhu & Park, 2005
			Syrphid flies	Attract	
(Z)-jasmone			*A. ervi*	Attract	Birkett et al., 2000
			C. septempunctata	Attract	
Benzaldehyde	*C. sinensis*	*T. aurantii*	*C. sinica*	Attract	Han & Chen, 2002a, b
			C. septempunctata	Attract	
HOST LOCATION					
Indole acetaldehyde	Lucerne		*Hippodamia* spp.	Attract	van Emden & Hagen, 1976
			C. carnea	Attract	
(*E*)-β-farnesene		*M. persicae*	*H. convergens*	Attract	Acar et al., 2001
			C. septempunctata	Attract	Al Abassi et al., 2000
		M. persicae *A. pisum*	*A. bipunctata*	Attract	Francis et al., 2004
		M. viciae *A. pisum* *A. fabae*	*E. balteatus*	Attract	Francis et al., 2005b
			P. melanarius	Attract	Kielty et al., 1996
			H. rufipes	Attract	
			N. brevicollis	None	Kielty et al., 1996
		S. avenae	*A. uzbekistanicus*	Attract	Micha & Wyss, 1996
			P. volucre	Attract	
		S. avenae	*L. testaceipes*	None	Micha & Wyss, 1996
			C. cognata	None	Boo et al., 1998
HABITAT AND HOST LOCATION					
(4a*S*,7*S*,7a*R*)-nepetalactone			*C. cognata*	Attract	Boo et al., 1998
			A. ervi	Attract	Glinwood et al., 1999
			A. eadyi	Attract	
(1*R*,4a*S*,7*S*,7a*R*)-nepetalactol			*C. oculata*	Attract	Zhu et al., 2005
			P. volucre	Attract	Gabrys et al., 1997
			D. rapae	Attract	
HOST ACCEPTANCE					
long hydrocarbon chains, wax esters, alcohols, and aldehydes		*S. avenae*	*A. rhopalosiphi*	Accept	Muratori et al., 2006
		P. tessellatus	*F. tarquinius*	Accept	Lohman et al., 2006
		P. tessellatus	*C. slossonae*	Accept	Lohman et al., 2006
		P. tessellatus	*S. ribesii*	Accept	Lohman et al., 2006

Diaretiella rapae (M'Intosh) (Hymenoptera: Braconidae) to mustard oil, allyl isothiocyanate (Table 1), emitted by collard, *Brassica oleracea*, in response to damage by the aphid, *Brevicoryne brassicae* (L.) (Read et al., 1970). Thereafter, a number of studies reported attraction of both aphid parasitoids and predators to the "plant-aphid complex" (also "plant-host complex"). Because this term refers to a set-up where a natural enemy can choose between a plant where aphids have been feeding and a control, or clean plant, it is often not clear whether attraction is due to volatiles emitted by the plant, the aphid, or aphid residues on the plant. Guerrieri et al. (1993) tested plants where remains of aphids had been removed to show that the plant changed its volatile profile. A number of subsequent studies supported this result (Du et al., 1996, 1998; Guerrieri et al., 1999). For example, Du et al. (1996) used a no-choice wind-tunnel experiment to demonstrate that a higher percentage of naïve female parasitoids landed on broad beans, *Vicia faba* L., damaged by *Acyrthosiphon pisum* (Harris) than on undamaged plants or aphids alone. These experiments suggested that not only herbivore-induced plant volatiles can attract aphid parasitoids, but also that volatiles from exuviae and faeces do not influence parasitoid behaviour at long range, possibly because of their low detectability. It was clear from the results that the main stimuli attractive to parasitoids were released from the damaged plant and that

plants produce semiochemicals in concentrations sufficient to be detected by parasitoids.

Attraction to aphid-damaged plants has also been shown for predators such as *C. septempunctata and C. sinica* (Han & Chen, 2002a). Ninkovic et al. (2001) reported that *C. septempunctata* was attracted to odours from barley plants (*Hordeum volgare*) infested or previously infested by the aphid, *Rhopalosiphum padi* in a four-arm olfactometer assay, but not to volatiles from uninfested plants or undisturbed aphids. For both parasitoids and predators there is now increasing evidence for a role of plant-derived synomones in natural enemy habitat location.

The first study to identify aphid-induced volatiles was by Du et al. (1998), who tested the electroantennogram responses of *A. ervi* females to volatile compounds from broad bean, *V. faba*. Among the volatiles produced by the plant in response to aphid attack, 6-methyl-5-hepten-2-one (MHO) was identified to be mainly responsible for attraction of the parasitoid. A number of other compounds also elicited responses in an olfactometer, but only MHO elicited a parasitoid flight response (Powell et al., 1998). Since the seminal study by Du et al. (1998), a number of other model systems have demonstrated a special role for MHO (Table 1). It was even suggested that MHO acts as an elicitor of dispersal for the parasitoid *A. uzbekistanicus,* to avoid attack by the hyperparasitioid *Alloxysta victrix* (Westwood) (Hymenoptera: Alloxystidae), as MHO was detected in the headspace of the hyperparasitoid (Höller et al., 1994). MHO is, however, not attractive to all parasitoids. For example, MHO was detected among the entrained volatiles of wheat plants damaged by *R. padi*, but was not attractive to the parasitoid *A. rhopalosiphi* when offered alone (Gonzales et al., 1999). Interestingly, whereas MHO is induced in *V. faba* infested with *A. pisum* ostensibly to attract *A. ervi* females, *V. faba* infested with *Aphis fabae* Scopoli (Hymenoptera: Aphididae) does not produce this volatile chemical and attracts significantly fewer *A. ervi* females for which *A. fabae* is not a host (Du et al., 1996, 1998; Powell et al., 1998; Guerrieri et al., 1999). Clearly, the role of MHO needs to be investigated in more detail. Other compounds emitted from aphid-damaged plants that attract certain parasitoids are (Z)-3-hexenyl acetate and (Z)-jasmone (Table 1).

MHO appears to play no role in habitat location by aphid predators and other induced compounds have been implicated in guiding predator searching behaviour. Zhu & Park (2005) examined the volatile emissions of soybean plants, *Glycine max* L. and identified methyl salicylate (Table 1) as a compound induced by feeding of the aphid *Aphis glycines* Matsumura. When methyl salicylate was applied to the antennae of *C. septempunctata*, it elicited a positive EAG response and also attracted this predator and syrphid flies to traps (Zhu & Park, 2005). (*Z*)-jasmone (Table 1) is a volatile compound of plants known for activating plant defenses and will attract the predator *C. septempunctata* in a four-arm olfactometer and the parasitoid *A. ervi* in a wind tunnel (Birkett et al., 2000). Interestingly, (*Z*)-jasmone induced the emission of (*E*)-β-ocimene in *V. faba*, which also attracted the parasitoid (Birkett et al., 2000). Han & Chen (2002a, b) detected high amounts of benzaldehyde released from tea shoots, *Camellia sinensis* L., when damaged by *Toxoptera aurantii* (Boyer de Fonscolombe), which is probably formed from a cyanogenic glycoside hydrolyzed by salivary enzymes of the aphid (Table 1). Benzaldehyde elicited positive EAG responses and was attractive to *Aphidius* sp. parasitoids and the predators *Chrysopa sinica* Tjeder (Neuroptera: Chrysopidae) and *C. septempunctata* (Han & Chen 2002a, b). As in the case of parasitoids, the number of prey-predator systems investigated is increasing and it is likely that more compounds will be detected in the coming years.

One special case of habitat location semiochemicals are aphid sex pheromones. For many aphid species, sex pheromones were identified as a mixture of two monoterpenes, (+)-(4a*S*,7*S*,7a*R*)-nepetalactone and (-)-(1*R*,4a*S*,7*S*, 7a*R*)-nepetalactol (Table 1), in ratios that vary according to the species (Pickett et al., 1992). These volatile compounds have been shown to attract female parasitoids in the field (Hardie et al., 1991, 1994) and elicit oriented flights by *A. ervi* and *Aphidius eadyi* Starý females when they are added to a piece of filter paper next to *V. faba* plants in the lab (Glinwood et al., 1999). Other examples of attraction to aphid sex pheromones include the parasitoids *Praon volucre* (Haliday) (Hymenoptera: Aphidiidae) and *D. rapae* (Gabrys et al., 1997), and the predators *Chrysopa cognata* McLachlan (Neuroptera: Chrysopidae) (Boo et al., 1998), and *Chrysopa oculata* Say (Neuroptera: Chrysopidae) (Zhu et al., 2005). Although sex pheromones reliably indicate the presence of aphids, they are only useful foraging cues in autumn when sexual morphs are produced.

To summarize, the seminal study by Du et al. (1996) started the search for aphid-induced volatiles important for their location by predators and parasitoids. While such compounds are important for habitat location in many systems, many parasitoids are also attracted to host plants free of aphids. Further work is needed to (i) test attraction of predators to undamaged plants, (ii) identify volatile compounds from aphid-infested plants and (iii) test the range of attraction of these volatiles under field conditions.

Aphid location

Following habitat location, natural enemies use short range chemical and physical cues to search for a suitable herbivore on the host plant. Among physical cues, visual stimuli (colour and shape) and aphid movement have been shown to be important factors for a number of aphid parasitoids (e.g. Michaud & Mackauer, 1994, 1995) and predators (e.g. Harmon et al., 1998). For example, *A. ervi* prefers to oviposit into green rather than red clones of the aphid *A. pisum* (Michaud & Mackauer, 1994; Libbrecht et al., 2007). *Praon pequodorum* Viereck females rarely attack aphids when they are not moving (Michaud & Mackauer, 1995). The ladybirds (Coleoptera: Coccinellidae) *C. septempunctata*, *Hippodamia convergens* Guerin,

Harmonia axyridis (Pallas), and *Coleomegilla maculata* (DeGeer) selectively attack red and green clones of *A. pisum* (Harmon et al., 1998). Therefore, predators and parasitoids use a number of physical cues to locate aphids at short range and these may influence preferences for ovipositing or feeding on a particular species or clone.

Among the chemical cues used by natural enemies for aphid location, aphid honeydew was the first to be investigated (e.g. Bombosch & Volk, 1966). Initially considered to be an important kairomone for habitat location, studies with various parasitoids and predators have shown that it often acts as an arrestant, i.e. it increases the time that natural enemies search for aphids on plants. Often, the natural enemy needs physical contact with honeydew to change its behaviour (Dixon, 1959; Bombosch & Volk, 1966; Carter & Dixon, 1984; Budenberg, 1990; Budenberg & Powell, 1992; Budenberg et al., 1992; Ide et al., 2007). Aphid honeydew also acts as an oviposition stimulus for syrphid flies (Budenberg & Powell, 1992) and for the predatory gall midge, *Aphidoletes aphidimyza* (Rondani) (Diptera: Cecidomyiidae) (Choi et al., 2004). The spraying of artificial honeydew to increase numbers of *Hippodamia* spp. and *C. carnea* in lucerne fields in California is one well-known example of the use of kairomones in aphid control (Hagen et al., 1971). Predators respond positively to the odour of a breakdown product of tryptophane, probably indole acetaldehyde (Table 1, Van Emden & Hagen, 1976) and remain in the treated area even when aphids are absent. The usefulness of artificial honeydew in improving biological control has been repeatedly tested, for example to manipulate the spatial distributions of ladybirds (Ben Saad & Bishop, 1976; Evans & Richards, 1997). Hagen (1986) suggested that *C. carnea* detects a synonome from the crop before responding to the kairomone, but this has not yet been identified. Attraction to honeydew has been shown for the parasitoid *A. rhopalosiphi* (Gardner & Dixon, 1985; Hagvar & Hofsvang, 1989; Budenberg, 1990; Budenberg et al., 1992), although the range of detectability remains unclear. Recently, Choi et al. (2004) captured honeydew volatiles and found that the gall midge *A. aphidimyza* was attracted to them, suggesting that these may attract natural enemies from some distance. Results with the syrphid *E. balteatus* also suggest some attractant role of honeydew volatiles as females landed more frequently on corn ears contaminated with honeydew from *Metopolophium dirhodum* (Walker) (Hemiptera: Aphididae) than on clean ears (Budenberg et al., 1992). However, the amount of volatiles released is probably small and unlikely to be effective as a long range attractant until plants become heavily infested.

In addition to aphid honeydew, the aphid alarm pheromone, (*E*)-β-farnesene (EBF, Table 1) can be an important kairomone in aphid location. It is commonly released in the cornicle secretions of many aphid species (Francis et al., 2005a) to alert surrounding aphids of the presence of natural enemies (Grasswitz & Paine, 1992; Francis et al., 2004, 2005b; Kunert et al., 2005). However, EBF is a sesquiterpenoid which reacts quickly with ozone (Pinto et al., 2007). Single aphids have peak emissions of < 50 ng (Schwartzberg et al., 2008) and usually only the attacked aphid emits, whereas undisturbed aphids in the vicinity do not (Hatano et al., 2008). Thus, concentrations of EBF may be undetectable at a distance from the plant, likely limiting its usefulness to short range attraction. EBF is attractive to a number of aphid natural enemies such as the parasitoids *A. uzbekistanicus* and *P. volucre* (Micha & Wyss, 1996), the syrphid *E. balteatus* (Francis et al., 2005b), the ladybirds *A. bipunctata* (Francis et al., 2004), *C. septempunctata* (Al Abassi et al., 2000), *Harmonia axyridis* Pallas (Harmel et al., 2007) and *H. convergens* (Acar et al., 2001), and the ground beetles *Pterostichus melanarius* Illiger (Coleoptera: Carabidae) and *Harpalus rufipes* (DeGeer) (Coleoptera: Carabidae) (Kielty et al., 1996). Presumably as a consequence of EBF emission, disturbed or squashed individuals of *A. pisum* and *M. persicae* attracted significantly higher numbers of *A. bipunctata* than undisturbed aphids (Francis et al., 2004) and the same was observed for the parasitoid *A. uzbekistanicus* attacking *Sitobion avenae* (Fabricius) (Hemiptera: Aphididae) (Micha & Wyss, 1996). Interestingly, ladybird larvae can perceive EBF from an aphid captured by a conspecific larvae, alerting it to the presence of prey (Hemptinne et al., 2000). However, some aphid natural enemies are not attracted to EBF, including the predatory lacewing, *C. cognata*, and the parasitoid *L. testaceipes*, (Micha & Wyss, 1996; Boo et al., 1998). Francis et al. (2005a) analysed the volatiles emitted from squashed aphids and found 8 out of 23 species that emit other compounds in addition to EBF and two species that did not emit EBF. Thus, there are other volatiles emitted by aphids that are candidate compounds for host location.

It is important to point out that semiochemicals involved in host location do not necessarily lead the natural enemy directly to the aphid. Rather, substances indicating the presence of aphids may cue behaviours such as intensive local search which improve prey detection. For example, when perceiving aphid cues, or after capturing an aphid, ladybird larvae switch from an extensive search to an intensive, area-restricted search by increasing their frequency of turning and reducing their speed (Dixon, 1959, 2000).

To summarize, there is ample evidence for the involvement of chemical cues in host location but they remain poorly understood. The identity of the semiochemicals emitted by healthy or attacked aphids, or via honeydew, has not been established except for the aphid alarm pheromone, EBF, which appears to have broad activity. Detection distance appears to vary depending on the semiochemical and may also differ among species of predators and parasitoids.

HOST RECOGNITION AND ACCEPTANCE

Once an aphid is located, natural enemies have to recognize it as potential prey before they attack it. In addition, parasitoids use ovipositor probing to assess host quality before oviposition. For host recognition, chemical cues can be important, in particular contact kairomones

from the surface of aphid's cuticle. Most contact kairomones are not volatiles. Weinbrenner & Völkl (2002) showed that contact kairomones affect host recognition by the parasitoid *A. ervi*, since washed pea aphids were attacked less often than non-washed aphids. Shed exuviae of aphids often elicit oviposition responses by parasitoids e.g. *A. ervi* (Powell et al., 1998; Battaglia et al., 2000) and *A. rhopalosiphi* (Muratori et al., 2006).

Various isolation methods have been used to identify semiochemicals involved in host recognition. Han & Chen (2002a) used hexane and ether rinses of *T. aurantii* cuticles to test attraction of the parasitoid *Aphidius sp.*, and the predators, *C. sinica* and *C. septempunctata*. The hexane rinse was more attractive than the ether rinse, possibly because it contained benzaldehyde, but all cuticle rinses acted as short range cues or contact semiochemicals for all natural enemies tested. Chemical and physical characteristics of the exuviae of *S. avenae* were described by Muratori et al. (2006), who found a great variety of long hydrocarbon chains (C25 to C31), and a few wax esters, alcohols, and aldehydes (Table 1) in extractions. The extractions also elicited antennal contacts and attacks by *A. rhopalosiphi*, and heat treatment applied to destroy the structure of the epicuticular surface did not diminish responses, suggesting that wax structure *per se* does not determine host recognition. A similar role of hydrocarbons in aphid recognition was demonstrated for *Feniseca tarquinius* (Abbot) (Lepidoptera: Lycaenidae), *Chrysopa slossonae* Banks (Neuroptera: Chrysopidae), *Syrphus ribesii* (L.) (Diptera: Syrphidae), and for parasitoids of the genus *Lysiphlebus*, some of which chemically mimic the hydrocarbons of their prey to deceive aphid-tending ants (Völkl, 1992; Liepert & Dettner, 1993; Lohman et al., 2006).

Chemical and physical compounds in cornicle secretions are active at very short range or in direct contact with an aphid, usually stimulating attacks by parasitoids. This response to cornicle secretion appears to be innate and host specific (Battaglia et al., 1995, 2000). The parasitoid *L. testaceipes* responded differently toward *R. padi* homogenates and cornicle wax compared to those of the non-host *Aphis nerii* Boyer de Fonscolombe (Hemiptera: Aphididae). However, when the non-host was covered with *R. padi*'s cornicle wax, *L. testaceipes* increased its attack frequency (Grasswitz & Paine, 1992). Cornicle secretion is only produced by aphids during attack (Goff & Nault, 1974) and can be an effective defensive weapon against predators and parasitoids. However, when the secretion is hardened it poses no threat to natural enemies and may serve as a kairomone for host recognition.

Parasitoids also perceive the internal chemistry of their hosts via receptors on the ovipositor. Thus, probing ("test stinging") of the host, although indicative of attack, is also an investigatory behaviour (Grasswitz & Paine, 1992; Powell et al., 1998). Le Ralec & Rabasse (1988) studied the ovipositors of Aphidiinae and described three pairs of valvulae, in which the third valvulae surround the other two. Mechano- and chemoreceptors are present on the first and/or second valvulae depending on the species (Larocca et al., 2007). The internal cues within aphids that elicit oviposition remain unknown, but it is clear that not all probes result in oviposition. Thus ovipositor probing is the final stage of host selection and terminates with acceptance or rejection. In species that use no visual cues such as *Ephedrus californicus* (Michaud & Mackauer, 1994), host acceptance is entirely a function of stimuli perceived during ovipositor probing.

Many aphid predators probably assess the quality of their prey using receptors on the maxillae only after attack and following contact with body fluids (Nakamuta, 1984; Nakamuta & Saito, 1985). Dixon (1958) reported that larvae of *A. decempunctata* only reject the poisonous *Hyalopterus pruni* (Geoffroy) (Hemiptera: Aphididae) after piercing its cuticle. Moreover, the same predator also fed on *A. fabae* and *M. viciae,* but regurgitated and released them after two minutes (Dixon, 1958).

Predators also use host cues to decide whether to lay eggs at a given site. For example, aphid odours and cornicle secretions induce oviposition in *C. septempunctata* (Evans & Dixon, 1986). However, residues left by predators in previous visits to plants, in particular "larval tracks" may deter ovipositions by adults of the same or other species. Initially this was shown for green lacewings, *Chrysopa oculata* Say (Neuroptera: Chrysopidae) (Růžička, 1994), and for ladybirds including *C. septempunctata* (Růžička, 1997). Subsequently, it has been shown for a number of other species such as *H. axyridis* (Yasuda et al., 2000), *Cycloneda limbifer* Casey, *Ceratomegilla undecimnotata* (Schneider) (Růžička, 2003), *A. bipunctata* (e.g. Fréchette et al., 2004) and *H. convergens* (Michaud & Jyoti, 2007). Some predators such as the syrphid fly *E. balteatus* also react to the presence of conspecific eggs and their chemical residues (Scholz & Poehling, 2000). These responses are presumed to be adaptive because they reduce the risks of cannibalism and competition for offspring (Dixon, 2000)

To summarize, host recognition and acceptance by parasitoids and predators involve contact chemicals perceived after the aphid has been contacted with the antennae, probed with the ovipositor, or tasted with the mouthparts. Compounds present in the aphid cuticle are likely to be more important than components of cornicle secretion for host recognition. Understanding of the chemicals influencing host acceptance is still rudimentary, partly because of the large number of substances potentially involved, and the difficulty of constructing workable bioassays.

INTERACTION AMONG SEMIOCHEMICALS

Above we provided examples where a blend of volatiles was more important for habitat or host location than single compounds, i.e. where additive or synergistic interactions among semiochemicals occurred. However, there is also the possibility of antagonistic interactions among semiochemicals. A well-known example is the interaction between the aphid alarm pheromone EBF and β-caryophyllene, a sesquiterpenoid compound found in many plant species. β-caryophyllene is an EBF-inhibitor,

altering not only the behaviour of the aphids, but also that of predators (Dawson et al., 1984; Mostafavi et al., 1996; Zhu et al., 1999; Al Abassi et al., 2000). The ratio of EBF to β-caryophyllene is important here; a minimum ratio of 1 : 1 elicited a positive response by *C. septempunctata* in a Y-tube olfactometer, while a ratio of 1 : 3 did not significantly attract the predator. The importance of this ratio was also demonstrated for the aphid parasitoid *D. rapae* exposed to the odour of genetically modified *Arabidopsis thaliana* plants which produced increased amounts of EBF relative to β-caryophyllene (Beale et al., 2006).

A new hypothesis for the use of volatiles by insects foraging for their suitable prey was presented by Bruce et al. (2005). In addition to the use of combined compounds in specific ratios, insects appear to time the arrival of these different compounds on their chemical receptors. This could allow natural enemies to differentiate suitable targets from unsuitable ones if the latter emitted the same compounds but with different timing. However, this hypothesis has to be yet demonstrated for aphid natural enemies.

To summarize, both synergistic and antagonistic interactions among semiochemicals have been described and there are likely to be many more, given the fact that the same semiochemicals are involved in many aphid-natural enemy interactions. Testing combinations of semiochemicals for synergistic or antagonistic effect is laborious but would provide a fuller understanding of aphid chemical ecology.

CONCLUSIONS AND FUTURE DIRECTIONS

Plants produce volatile chemicals that are conspicuous to many insects including herbivores and their natural enemies. Chemicals from plants, although less reliable than chemicals from aphids, are important cues that elicit foraging behaviour in many aphid natural enemies, in particular more specialised parasitoids. Currently, there is increasing evidence that volatile blends from aphid-damaged plants play a pivotal role in habitat location by both parasitoids and predators, although only a few model systems have been investigated in detail. Plant changes are probably triggered by elicitors present in the aphid saliva (de Vos et al., 2007). Among the short range cues used by natural enemies are the pheromones of aphids (alarm and sex), and honeydew. For parasitoids, contact kairomones in the aphid cuticle, in particular waxes may be used for host recognition, whereas chemicals within the hemolymph are important for host acceptance. For predators, such compounds may act as a feeding stimulus.

In most cases, one or only a few semiochemicals of importance have been described for a particular system and these often differ among natural enemy species, suggesting that particular plant-aphid-complexes emit specific volatile chemicals. However, there are also examples of redundancy where the same compound is used by many natural enemies, e.g. MHO (Table 1). More studies are needed that submit a particular parasitoid species to different aphid-plant complexes to investigate whether natural enemy responses differ among complexes that produce similar volatile chemicals. Chemical analyses of these volatile blends are needed to investigate subtle differences. Finally, all species are embedded in a network of ecological interactions that shape the evolution of all traits. Understanding the evolution of the semiochemicals requires taking into account the interactions of aphids with plants, competitors, natural enemies and mutualists. For this, more field experiments are needed to unravel the true significance of semiochemicals under natural conditions.

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