THE ROLE OF SECONDARY PLANT COMPOUNDS IN APHID-HOST INTERACTIONS

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1. INTRODUCTION

The settling of an aphid on a proper host plant results from a sequence of steps which may be summarized as follows: 1) landing, 2) testing of the plant surface and the outer plant tissues, and 3) penetration and evaluation of the final feeding tissues (Hille Ris Lambers, 1979; Klingauf, 1987). The relative importance of these steps varies among different morphs of an aphid, and are dependent on factors such as environmental conditions and morphological and chemical features of the plant.

In this chapter, stimuli from secondary metabolites in the plant influencing aphid host-finding and feeding behaviour are examined.

2. LANDING

Evidence has accumulated on the importance of olfaction of plant volatiles in the orientation of an aphid to its host plant. Olfaction is performed by sensory organs located in the antennae. While their low number suggests that olfaction may become important only at short range (Anderson and Bromley, 1987), their distribution in different aphid morphs suggests the importance of olfaction in migration (Dunn, 1978; Shambaugh, 1978; Bromley et al., 1979; Bromley and Anderson, 1982). Two primary rhinaria in the two distal segments of the antennae are composed of placoid
sensilla structured as typical olfactory receptors. They are present in all instars and although fairly non-specific as receptors, they are the main receptors for an aphid alarm pheromone (E)-β-farnesene (Nault et al., 1973; Wohlers and Tjallingii, 1983) and also for plant volatiles (Pettersson, 1970a). Secondary rhinaria are only present in adults, in greater number in alate males and females, and in apterous males. They may be altogether lacking in apterous females of certain species. While in the males the secondary rhinaria are responsible for detection of the sex pheromone (Pettersson, 1970b), in alate females they have been associated with host selection.

Electrophysiological recordings of antennal receptors of Nasonovia ribis-nigri Mosley (Bromley and Anderson, 1982) and Sitobion avenae Fabrici (Yan and Visser, 1982), revealed their responses to various plant volatile compounds.

Using an olfactometer of simple design, it was shown that gynoparae and males of Rhopalosiphum padi L. were attracted to extracts of buds of Prunus padus, their primary host (Pettersson, 1970a). Alatae of non-migratory generations were not attracted (Pettersson, 1973). The receptors involved were shown to be the primary rhinaria. It was suggested that the principal compound involved in the attraction was benzaldehyde, arising from the enzymatic hydrolysis of prunasin, a glycoside characteristic of Prunus, followed by the decomposition of the aglycone. The importance of olfaction as opposed to tasting in host selection by gynoparae of R. padi was further supported by their non-random landing pattern on P. padus (Leather, 1986), in spite of the fact that they do not feed as adults (Leather, 1982; Walters et al., 1984).

Similar olfactometer experiments carried out with alate virgino paraphae of Brevicoryne brassicae L. showed that they were attracted to the scent of flowers and buds of Brassica plants, possibly in connection with higher concentrations of sinigrin and CO₂ (Pettersson, 1973).

Using an olfactometer of different design, it was shown that alate Aphis gossypii Glover were attracted selectively by the scent of their host plants Cucurbita pepo and Thunbergia laurifolia while being repelled by the scent of the non-host Lantana camara (Pospisil, 1972).
The orientation responses of Cryptomyzus korschelti Borner were studied using a locomotion compensator in front of a wind tunnel (Visser and Taamman, 1987). While still air, wind, and wind carrying the odour of the non-host plant Solanum tuberosum induced tortuous tracks, wind carrying the odour of the host plant Stachis sylvatica provoked a clear up-wind orientation, providing evidence for host plant odour-conditioned positive anemotaxis.

Attraction of flying Cavariella aegopodii Scopoli to traps baited with plant chemicals was demonstrated in field experiments (Chapman et al., 1981). Carvone, a compound frequently found in the umbelliferous summer hosts of C. aegopodii, was the most attractive compound tested.

On the other hand, evidence for olfactory reactions could not be proved during host finding by adult apterous Myzus persicae Sulzer or grass-colonizing virginoparvae of R. padi (Ahman et al., 1985), nor in the orientation of apterous M. persicae to target hosts in an artificial arena (Hodgson and Elbakhiet, 1985).

The data accumulated so far is still scarce, but there is indication that monophagous morphs of aphids tend to rely more heavily on olfactory cues than on visual cues for host finding. The inverse tendency would seem to prevail in polyphagous morphs. It is interesting to note in this context that aphids with specialized feeding behavior tend to develop annular rhinaria, an adaptation ideally suited for host finding without tasting (Shaposhnikov, 1987).

3. TESTING OF PLANT SURFACE AND OUTER PLANT TISSUES

Once an aphid has landed on a plant, it explores the plant surface with the antennae and engages in brief probes. This behavior is associated with the testing of the chemical nature of the surface and outer tissues of the plant.

Chemoreceptors are present in the antennae in the tip of the flagellum and sometimes lower down on the processus terminalis (Bromley et al., 1979). Sensilla located on the apex of the tibiae and the tarsi may also have a gustatory function (Anderson and Bromley, 1987). It should be noted that the short hairs or pegs on the tip of the labia, which were thought to be chemoreceptors, have been shown to correspond to mechanoreceptors (Wensler, 1977; Tjallingii, 1978).
The importance of surface testing was suggested by experiments with M. persicae males. They preferred to feed and tostay longer on peach (host) twigs than on pear, apricot or apple (non-host) twigs, and coating apple twigs with an extract of peach buds made them more attractive than untreated apple twigs (Tamaaki et al., 1970).

Leaf epicuticular waxes were shown to be important in host selection by Acyrthosiphon pisum Harris (Klingauf, 1971, 1975; Klingauf et al., 1978). Wax fractions of the host Vicia faba but not of the non-host Brassica napus stimulated walking of the aphid towards its feeding site. Mechanical destruction of the wax layer or inhibition of its biosynthesis increased the time needed for the aphid to find its feeding place on the host plant (Klingauf et al., 1978). Longer initial probes were obtained when non-host disks were treated with host wax extracts (Klingauf, 1975). Alkanes constituted the most active fractions (Klingauf et al., 1978).

The higher proportion of diketones in the wax of some wheat cultivars increased infestation by S. avenae (Lowe et al., 1985). The origin of the effect was not determined.

Leaf surface extracts of V. fabae and Beta vulgaris, host plants of the aphid Aphis fabae Scopoli, proved attractive to the aphid when added to an artificial diet. Low molecular weight phenols in the extract exhibited highest attractiveness, suggesting they may play a role in host selection (Jordens-Rottger, 1979).

Other surface chemicals which an aphid encounters while walking and probing are the secretions in the trichomes of some plants. Toxic alkaloids, the major one being nicotine, were isolated from the trichome secretions of several Nicotiana species. Contact with these secretions caused acute toxicity in Rhopalosiphum maidis Fitch and M. persicae (Thurston et al., 1966). As the plant aged, the amount of trichome exudates increased and toxicity to M. persicae increased concomitantly (Abernathy and Thurston, 1969). Trichome exudates of the wild tomato Lycopersicon hirsutum f. glabratum contain 2-tridecanone, shown to be toxic to A. gossypii (Williams et al., 1980).

Two types of foliar glandular trichomes may be found in potato plants: type A with a tetralobulate gland at its apex, and type B with an ovoid gland at its tip (Tingey, 1985). Trichomes
of type B in the wild potato *Solanum berthaultii* contain the aphid alarm pheromone (E)-β-farnesene, which is released in amounts capable of repelling the aphid *M. persicae* at a close range (Gibson and Pickett, 1983). Removal of droplets from trichomes resulted in a decrease in preprobe time by *M. persicae* compared with that on intact leaves (Lapointe and Tingey, 1984). Transfer of droplets to leaves of domestic potato *S. tuberosum*, lead to fewer probes, increased time to first probe and reduced total feeding activity compared with untreated leaves (Lapointe and Tingey, 1984). Furthermore, removal of exudates from trichomes of another wild potato species, *S. neocardenasii*, lead to a decrease in the length of developmental period and an increase in survival of *M. persicae* (Lapointe and Tingey, 1986).

Recently, trichomes of type A were also shown to contain (E)-β-farnesene. However, they did not hinder aphid attack, presumably due to the difficult detachment of the tetralobulate gland from the trichome stalk (Avé et al., 1987).

(E)-β-farnesene was also found in trichomes of *S. tuberosum* but did not show a repellent effect. This was attributed to the simultaneous presence of the aphid alarm pheromone inhibitor, (−)-α-caryophyllene (Avé et al., 1987). Similar effects had been observed in relation to the lupulin gland contents in hops *Humulus lupulus* (Dawson et al., 1984).

In view of the results presented, the importance of surface chemicals in the interaction between an aphid and a plant must be recognized. It is an area which deserves closer attention by both plant anatomists and chemists.

4. PENETRATION AND FEEDING

The final acceptance of a plant by an aphid is determined by the tasting of internal components. Gustation of ingesta is carried out by chemosensory structures in the food canal: an epipharyngeal organ possessing gustatory papillae has been described in *B. brassicae* and *Tuberolachrus salignus* Gmelin (Wensler and Filshie, 1969), and in *A. pisum* (Mc Lean and Kinsey, 1985).

The quality and quantity of plant compounds encountered by a feeding aphid depends on the path followed by the stylet on its way to the final feeding site, on the ingestion of plant
constituents during penetration and on the nature of the final feeding site.

While most aphids are phloem feeders, some feed in xylem or in mesophyll tissue (Pollard, 1973). The path followed by the styllets may be intracellular, intercellular or intramural (Kimmins, 1986). Recent studies indicate that intracellular pathways are more frequent than realized before (Spiller et al., 1985; Al-Mousawi et al., 1983; Tjallingii, 1985). There is also an indication that ingestion occurs before the aphid styllet has reached the final feeding site (Bradley, 1952; McLean and Kinsey, 1967; Lowe, 1967a,b; Henning, 1968; Scheller and Shukle, 1986; Brzezina et al., 1986). Thus, host discrimination may occur very early in the feeding approach (Adams and Wade, 1976).

Hence, although aphids tend to be selective in their feeding site, and thus be able to avoid toxic substances in certain tissues of the plant (Guthrie et al., 1962; Montgomery and Arn, 1974), the intake or contact with substances outside the vessels where they feed can not be dismissed a priori.

4.1. Alkaloids

Quinolizidine alkaloids produced by *Lupinus* spp. and other plant species are important in the interaction of legume feeding aphids with the plant. Polyphagous aphids, such as *A. pismum*, are able to colonize only sweet (alkaloid poor) lupines. The susceptibility of these hosts was reduced by infiltration of the alkaloids into them (Wegorek and Krzymanska, 1968, 1971). Some aphids however, are able to colonize alkaloid-rich plants. *Acyrthosiphon spartii* Koch lives on the spartine rich broom *Sarrothamnus scoparius*. The aphid migrates within developing plants following spartine rich tissue. Spartine was shown to be a feeding stimulant (Smith, 1966).

*Aphis cythiocrorum* lives on *Lupinus* and *Cytisus* species having relatively high alkaloid content. Alkaloids were found in the phloem of the plant (Wink et al., 1982; Wink and Witte, 1984). Aphids accumulated alkaloids. The composition of the alkaloid mixture in aphids was similar, but not the same, to that found in the plants (Wink et al., 1982; Wink and Witte, 1985).

Another aphid species which has specialized in feeding in certain alkaloid-rich plants is *Macrosiphon albifrons* Essig. The aphid does not infest alkaloid-free plants, and qualitative
alkaloid patterns as well as alkaloid content are important in determining the infestation levels of alkaloid-containing plants. Although the alkaloids ingested were found in the honeydew, aphids accumulated them in concentrations that proved toxic to predators (Wink and Romer, 1986).

Indole alkaloids, such as gramine, produced by *Hordeum* species, are important in the interaction of aphids with the plants. Infestation by the aphids *Schizaphis graminum* Rondani (Zúñiga et al., 1985) and *A. padi* (Zúñiga and Corcuera, 1986) were inversely correlated with gramine levels in barley plants. Older plants with lower gramine levels were more susceptible to infestation than younger ones. Gramine reduced survival and reproduction rate of both aphid species when added to artificial diets. Since gramine was not found in the vascular bundles, it was hypothesized that it could be encountered by aphids during their search for phloem tissue (Argandoña et al., 1987).

4.2. Phenolic compounds

Differences in ability to colonize different apple varieties and different parts of any one variety by the wooly aphid *Eriosoma lanigerum* Hausmann was found to be related to content of phenolics and α-amino nitrogen compounds. An inverse linear correlation was obtained between susceptibility and ratio of phenolics to α-amino nitrogen (Sen Gupta and Miles, 1975). This correlation was suggested to arise from the influence of the nutritional status of the plant on the ingestion of toxic compounds (Sen Gupta and Miles, 1975).

The phenolic compound phlorizin, characteristic of the apple genus, was found to be neutral as a probing stimulus to *Aphis pomi* DeGeer, an apple feeding aphid, but was a probing deterrent to the non-apple feeding aphids, *M. persicae* and *Amorphophora aphantorica* Hottes. Phlorizin was an ingestion deterrent to the three although the threshold was lower for *A. pomi*. The fact that apple is utilized as a host by *A. pomi* was associated with its feeding in the phloem, which appeared not to contain phlorizin (Montgomery and Arn, 1974).

The phenolic compound catechin was suggested as a factor in rose buds whose concentration increase as the sepals open, induces the aphid * Macrosiphum rosae* L. to walk off them (Miles, 1985).
Phenolic compounds play an important role in habitat selection by the galling aphid Pemphigus betae Auct. (Zucker, 1982). Inverse correlations were found between total phenols and suitability of a tree, leaf or leaf section for galling at the time of bud burst in Populus aqustifolia. The findings were consistent with the known biology and territorial behaviour of the aphids (Zucker, 1982).

4.3. Glucosinolates

Glucosinolates are important in host selection by the aphid B. brassicae. When the glucosinolate sinigrin was introduced via the cut petiole into leaves of the non-host plant Vicia faba, the leaves were preferred by B. brassicae over untreated ones. The compound was shown to increase probing and duration of probes into filter papers moistened with sinigrin solution as compared with filter papers moistened with water (Wensler, 1962). When incorporated into a diet containing sucrose, sinigrin rendered the diet more acceptable to B. brassicae (Moon, 1967). In agreement with these results, when a broad range of compounds were tested in artificial diets for effects on M. persicae in dual choice situations, all compounds with the exception of sinigrin (and tomatine) made the diet less acceptable (Schoonhoven and Derksen-Koppers, 1976). Interestingly, it was recently found that sinigrin made artificial diets less acceptable to a Beijing clone of M. persicae (Junde and Lidao, 1984). M. persicae and B. brassicae showed different strategies in dealing with glucosinolates ingested: while M. persicae excreted high concentrations of glucosinolates in the honeydew, B. brassicae retained high concentrations in the body (Weber et al., 1986).

Aphids such as B. brassicae and M. persicae, which have glucosinolate-containing crucifers as hosts, were more stimulated by sinigrin to take up a sucrose-containing diet than R. padi, A. fabae and A. pisum, for which crucifers are non-hosts (Klingauf et al., 1972). Similarly, whereas B. brassicae, M. persicae and Lipaphis erysimi Kaltenbach could be induced to feed on sinigrin-treated non-host leaves, A. fabae, A. pisum and Acyrthosiphon solani could not (Nault and Styer, 1972).

In addition to being phagostimulants, glucosinolates were antibiotics; they decreased survival of L. erysimi in diets (Dilawiri and Atwal, 1987), and positive correlations were
obtained between total glucosinolate content of various crucifers and resistance to L. erysimi (Malik, 1981; Gill and Bakhetia, 1985).

4.4. Hydroxamic acids

Hydroxamic acids (Hx) have been shown to play an important role in the interactions of cereals with aphids (Niemeyer, 1988b). Inverse correlations were obtained between Hx levels in maize and infestation by R. maidis, under field and greenhouse conditions (Long et al., 1977; Beck et al., 1983) and between Hx levels in wheat and infestation numbers of Metopolophium dirhodum Walker (Argandoña et al., 1980), S. graminum (Argandoña et al., 1981) and S. avenae (Bohidar et al., 1986) determined in the laboratory.

When DIMBOA (2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one), the main Hx in wheat and maize extracts, was infiltrated into barley leaves lacking Hx, the levels of DIMBOA in the leaves correlated inversely with infestation numbers of M. dirhodum (Argandoña et al., 1980).

Hx levels decreased with the age of the plant and the age of the tissue within a plant. Older plants and older leaves of wheat and maize were more heavily infested than younger ones (Argandoña et al., 1980, 1981).

When added to artificial diets, DIMBOA exhibited antibiotic (Zúñiga et al., 1983; Argandoña et al., 1980, 1981, 1983; Long et al., 1977; Corcuera et al., 1985) and antifeedant (Argandoña et al., 1983; Corcuera et al., 1985) effects towards various cereal aphids, the most sensitive being S. graminum and the least sensitive R. maidis. The 2-O-β-D-glucoside of DIMBOA, present in the uninjured plants, was less active than DIMBOA itself (Corcuera et al., 1985).

The toxicity of DIMBOA has been related to its inhibitory action over the mitochondrial energy transduction system (Niemeyer et al., 1986) and, more generally, to its capacity to inhibit various enzymes due to its reaction with nucleophiles such as cysteine and lysine residues (Pjérez and Niemeyer, 1985, 1989a, 1989b).

Higher levels of hydroxamic acids were found in the lateral veins than in the central vein of maize leaves (Argandoña and Corcuera, 1985). In wheat seedlings, the highest levels in the leaf were found in the vascular bundles (Argandoña et al., 1987).
Hydroxamic acids were not detected in the lower epidermis (Argandoña et al., 1987).

DIMBOA was present in aphids which had been feeding on DIMBOA-containing wheat plants (Niemeyer et al., 1989). Aphids feeding on plants with higher DIMBOA levels contained less DIMBOA, produced less honeydew and suffered less weight increase than those feeding on plants with lower DIMBOA levels, indicating a feeding deterrent effect of DIMBOA in the plant. Furthermore, it was found that aphid feeding provoked an increase in Hx levels in some wheat cultivars (Niemeyer et al., 1988). These results open the possibility of diminishing aphid-provoked viral infections in wheat. Screening of ancient and modern wheat germplasm has shown that potentially suitable material is available for breeding high Hx levels into agronomically relevant wheat (Niemeyer, 1988a; Thackray et al., 1989; Copaja and Niemeyer, unpublished results). A further advantage of Hx as a source of resistance in cereals is that its wide range toxicity might provide resistance against a large variety of organisms.

4.5. Other compounds

Benzyl alcohol was claimed to be involved in aphid resistance of barley (Juneja et al., 1972, 1975). However, the presence of benzyl alcohol could not be confirmed in a series of barley cultivars (Zūkiga et al., 1985).

Acceptability to *Aphis craccivora* Koch of *V. faba* over *Ternis lupinus* was associated with lower coumarin levels in the former. Systemic and spraying treatments of *V. faba* with coumarin diminished the performance of the aphid (Mansour et al., 1982).

Cardiac glycosides are important in the association of the aposenetic aphid *Aphis nerii* Boyer with asclepiadaceous plants. Plant-derived cardiac glycosides isolated from the aphid (Rothschild et al., 1970) were ingested by feeding preferentially from the internal primary phloem (Botha et al., 1977).

Numerous compounds of natural origin have been tested in artificial diets for effects on feeding preference and performance of aphids. The compounds tested have included flavonoids and phenolics (Todd et al., 1971; Dreyer and Jones, 1981; Jones and Klocke, 1987), terpenoids (Rose et al., 1981), coumarins (Dreyer et al., 1987), alkaloids (Dreyer et al., 1985) and a variety of other compounds (Herger, 1975; Schoonhoven and

In most cases, the ecological relevance of the results was not demonstrated, i.e., whether aphids encounter the compounds under natural conditions and whether effects in Nature parallel those obtained with artificial systems. Cyclitols from alfalfa were found in the honeydew of aphids fed with alfalfa (Campbell and Binder, 1984). Pinitol, the most abundant cyclitol in alfalfa showed, however, no effect on A. pisum when added to artificial diets (Campbell and Binder, 1984).

The feeding preferences of aphids is further complicated by variations that may be found among different clones (Weber, 1985 a,b,c), and by the occurrence of different biotypes (Wightman and Gibson, 1972; Eastop, 1973; Campbell et al., 1982; Montllor et al., 1983; Diehl and Bush, 1984; Srivastava et al., 1984; Ryan et al., 1987; Niassy et al., 1987)

5. CONCLUSIONS

The importance of plant volatiles in host selection by aphids is beginning to be recognized. Sophisticated instrumentation available for the observation of insect behaviour and for the analysis of minute amounts of volatiles in complex mixtures, make it possible to increase research efforts in this field. Similarly, the nature of plant surface chemistry should be further studied. Results in these two fields may be particularly beneficial in terms of possibilities of control of virus transmission by aphids.

In the area of internal plant constituents, efforts should be devoted to defining the precise location of secondary compounds in the plant, the chemical nature of phloem sap, the nature and quantity of materials ingested by aphids, and their fate in the aphid.

Secondary metabolites represent an interesting source of resistance in crop plants against aphids. Efforts should be directed towards understanding their mode of action on the recipient organism as well as their biosynthesis. This could lead to a more rational approach towards crop improvement, potentially allowing the attainment of more stable resistance and the use of genetic engineering techniques. The effect of an increase in levels of secondary metabolites in a crop plant on the
environment as well as on other potential consumers of the plant should also be considered.

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