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THE CHEMICAL ECOLOGY OF APHIDS

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Introduction

Insects are sensitive to chemical aspects of their environment, particularly with regard to host and mate location. Aphids can select individual or a few closely related host plant species from a wide range of nonhost vegetation (65, 71). This selection relies upon the detection of secondary plant compounds as well as primary metabolites associated with the physiological condition of the host plant (82). Use of long-range volatile chemical cues in aphid-plant and aphid-aphid interactions was formerly considered unlikely (78, 108). Nevertheless, recent work reviewed here demonstrates that olfaction plays a more extensive role in the chemical ecology of aphids than previously thought.

The study of aphid chemical ecology involving volatile semiochemicals, particularly pheromones, has been greatly enhanced by the development of electrophysiological recordings from aphid antennae, using the electroantennograph (EAG) and single-cell recording (SCR) methods. SCR directly coupled to high-resolution capillary column gas chromatography (GC-SCR) provides a powerful tool for locating the active components in behaviorally active samples (154). Analysis by other highly sensitive techniques such as

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combined GC-mass spectrometry (GC-MS) enables compounds to be identified, synthesized, and made available for use in further behavioral and ecological studies (125). These studies can then benefit from sophisticated behavioral assays employing alate or apterous aphids (22, 153).

Significant advances have been made in understanding the aphid chemical ecology relating to interactions with nonvolatile semiochemicals (82, 152). These compounds are involved in processes ranging from the detection of host plant acceptability prior to settling to determining appropriateness of the composition of the phloem.

Aphid pheromones were reviewed in 1977 (108). Since then, the study of pheromone-mediated aggregation has advanced little, and this review does not deal with this subject specifically. However, there has been considerable progress in understanding the nature and role of sex pheromones. Aphid alarm pheromones were fully reviewed in 1984 (110), so apart from introductory explanations, only developments made since then are discussed here. As is becoming apparent in other areas of chemical ecology (37), aphid pheromones often do not act alone. This review presents examples of the involvement of other semiochemicals, principally from the host plant.

The importance of chemical ecology in tritrophic interactions, particularly between aphids and aphidiid parasitoid wasps has also been demonstrated (15, 132, 133, 138). Although chemical studies are insufficient for a full review, some examples are presented of tritrophic interactions mediated by aphid semiochemicals.

Aphids are the major insect pests of temperate agriculture, causing damage either directly by feeding or by transmitting plant virus diseases (69). The study of aphid chemical ecology offers new opportunities for improvements in control (27), and where relevant, these aspects are described.

Perception of Semiochemicals

The aphid sensory system was reviewed recently (2). The olfactory nature of the placoid sensilla on the aphid antenna (Figure 1) was first suggested by ablation and behavioral experiments (107, 118) and confirmed by using electrophysiological recording techniques. However, because there are relatively few olfactory neurons, there has been limited success with the EAG. Thus, although stable preparations can be obtained that will survive for several hours, the amplitude of the response is small. Stimulation of the antennae of the pea aphid, *Acyrthosiphon pisum;* the vetch aphid, *Megoura viciae;* and the peach-potato aphid, *Myzus persicae*, with the alarm pheromone elicited EAGs of only 200–500 μV (154, 161, 162).

More detailed information can be obtained using SCR. This technique has demonstrated the response of antennal receptors to plant volatiles (13, 31) and to alarm and sex pheromones (25, 27, 31). Screening of more than 70 volatile compounds led to the belief that the primary rhinaria of the currant-lettuce aphid, *Nasonovia ribis-nigri*, were general odor receptors (13). However, studies on other aphids have not confirmed this hypothesis, and indeed many of these cells show a high degree of specificity for their key compounds. The high stimulus concentrations used in the lettuce aphid studies may account for the observed generalist responses, since at such levels, even specialized receptors may show some response to other compounds.

Figure 1 Diagram of an aphid antenna showing olfactory sensilla. (*A*) Distal primary rhinarium, (*B*) proximal primary rhinarium; (*C*) secondary rhinaria, (*D*) contact chemoreceptors (bar = 0.25 mm).

An important difference between alate and apterous aphids is the greater abundance of secondary rhinaria on the antenna of the alate morphs, suggesting their involvement in host location and mate selection. The secondary rhinaria of the male were proposed to be responsible for sex pheromone detection (44, 88, 120), and this has been confirmed by single cell recordings (SCR) (27). The secondary rhinaria of alate virginoparae have also been shown to respond to plant volatiles (L. J. Wadhams & C. M. Woodcock, unpublished data).

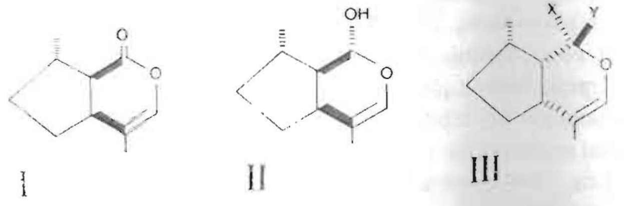
Once aphids have landed on a plant, selection or rejection may be associated with gustatory receptors. In addition to the trichoid sensilla on the terminal processes of the antenna (2) (Figure 1), sensilla located on the tarsi (J. Hardie & I. H. M. Fosbrooke, unpublished data) and the epipharangeal organs (93, 157) may be crucial. The labial tip pegs, once thought to have a gustatory role, are now known to be mechanoreceptors (148, 156). However, this area has received little attention. Preliminary studies have shown that electrophysiological responses to the antifeedant (−)-polygodial can be obtained from sensilla on the terminal process of the antenna (L. J. Wadhams, unpublished data).

Sex Pheromone

In the early 1970s, Pettersson (119, 120) demonstrated that oviparous females in the genus *Schizaphis* attracted males by means of a volatile sex pheromone released from the hind tibiae. Marsh (87, 88) later showed that sex pheromones are produced by *M. viciae* and *A. pisum*, and more recent studies have revealed their existence in several other aphid species (44, 121, 145).

The sex pheromone is produced and released by glandular cells underlying porous plaques on the tibiae of the metathoracic legs. For *M. viciae*, using solvent extracts of the tibiae, GC-SCR analysis on the secondary rhinaria of males, followed by GC-MS and synthetic studies, demonstrated that the sex pheromone of this aphid comprised a synergistic mixture of the monoterpenoids (+)-(4a*S*,7*S*,7a*R*)-nepetalactone (I) and (−)-(1*R*,4a*S*,7*S*,7a*R*)-nepetalactol (II) (Figure 2) (25, 34). These two compounds, in differing ratios, were also shown to be present in *A. pisum*; *M. persicae*; the black bean aphid, *Aphis fabae*; and the greenbug, *Schizaphis graminum* (26, 27). However, oviparae of the damson-hop aphid, *Phorodon humuli*, were found to produce only (4a*R*,7*S*,7a*S*)-nepetalactol (19). Although this pheromone has not yet been fully characterized at C1, researchers believe the aphid produces a mixture of the 1*S* and 1*R* diastereoisomers (III, Figure 2).

Volatiles collected from air above oviparous *M. viciae* by entrainment onto a porous polymer contained significantly greater proportions of nepetalactone I than were found in the leg extracts. In addition, while only a small amount of nepetalactone (1-2 ng/aphid) was obtained from these extracts (25), the amount produced by calling females exceeded 200 ng/day (67). Indeed, for some species, e.g. *Myzus persicae* and *S. graminum*, only the air entrainment method yielded detectable amounts of pheromone. This finding suggests that, during calling, production of nepetalactol is continuous, probably from a glycoside precursor, and that a proportion of the nepetalactol is sequentially oxidized to nepetalactone. Laboratory studies, using male behavioral responses to monitor pheromone release by oviparae, indicated that release is restricted to a specific part of the photophase (45, 87, 88, 120). This has been confirmed in *S. graminum*, for which only trace amounts of the lactol were found in air entrainment samples obtained when females were not calling (27). Pheromone release in *M. viciae* also appears to be age dependent, and both male response and pheromone release reach a maximum on the sixth day of adulthood (67, 87, 88). In addition, the ratio of the two compounds changes markedly on day six (Table 1), although the function of this change is unknown.



I

II

III

1S; X=H, Y=OH

1R; X=OH, Y=H

Figure 2 Structure of aphid sex pheromone components. I, (+)-(4a*S*,7*S*,7a*R*)-nepetalactone. II, (−)-(1*R*,4a*S*,7*S*,7a*R*)-nepetalactol. III, (4a*R*,7*S*,7a*S*)-nepetalactol

Table 1 Composition of aphid sex pheromones

Species	Ratio of I : II[a]
Aphis fabae	29 : 1
Megoura viciae (day 2–6)	4 : 1–6 : 1
(day 7–8)	12 : 1
Acyrthosiphon pisum	1 : 1
Sitobion avenae	1 : 0
Sitobion fragariae	1 : 0
Myzus persicae	1 : 2
Schizaphis graminum	1 : 8

[a] I = (+)-(4a*S*,7*S*,7a*R*)-nepetalactone; II = (−)-(1*R*,4a*S*,7*S*,7a*R*)-nepetalactol

Electrophysiological recordings from the secondary rhinaria of males of all the species studied, including *P. humuli*, have shown the presence of specialized olfactory cells that respond separately to compounds I and II (27), which would enable the insect to discriminate between different ratios of the two pheromone components. Although the role of these receptors in *P. humuli* is unclear, this aphid has other cells that respond to compound III in the secondary rhinaria. The ubiquity of compounds I and II in the sex pheromones of many aphids (Table 1) may give rise to interspecific mating behavior. Laboratory studies have shown that olfactory attraction of male aphids to calling oviparae was not necessarily species-specific (88, 120). However, male *S. graminum* could differentiate between different biotypes of the same species (46). Attraction of *S. graminum* and *M. viciae* males to oviparae from different species was also examined in the olfactometer. In many cases, the level of response correlated directly with the known ratios of compounds I and II, and there was a reduction in the interspecific interactions as the pheromone blend became less like the conspecific ratio (27). Similar results were obtained in mating assays using synthetic pheromone with *A. fabae*, *M. viciae*, and *A. pisum* (67).

Aphid sex pheromones were thought to act over only a short range and this belief, together with the observed interspecific interactions, led to the suggestion that, in order to provide a high degree of species specificity, males would first need to locate the primary host and then search locally for conspecific calling females (59, 60, 144). However, recent field trials have shown that males can be selectively attracted to pheromone-baited traps. Thus, water traps containing synthetic lactol (compound III) attracted only male *P. humuli*

(19). Similarly, compound I was an effective lure for the male blackberry-cereal aphid, *Sitobion fragariae* (J. Hardie & S. F. Nottingham, unpublished data). These results suggest that the early laboratory studies did not accurately reflect the situation in the field and that sex pheromones may be involved in long-range mate location. However, these field studies do not exclude a role for host plant volatiles in species discrimination during mate selection. Indeed, Campbell et al (19) have shown that an extract of the bark of the primary host *Prunus cerasifera* was an excellent synergist for pheromone III, both in the laboratory and in the field.

Dawson et al (25) suggested that aphid sex pheromones may also act as kairomones in attracting predators and parasitoids. In an experiment to observe the response of field-flying male aphids to synthetic sex pheromone, female braconid parasitoids (*Praon* spp.) were caught in the water traps, indicating that they use these compounds in host location (68).

Alarm Pheromone

The alarm pheromone is released from the cornicle secretion when aphids are attacked by predators or parasitoids and results in various types of defensive or avoidance behavior such as dispersal (110) or even attack (2a). As identified by independent groups, the pheromone for several aphid species comprises the sesquiterpene hydrocarbon (*E*)-*β*-farnesene (EBF) (8, 43, 158). The spotted alfalfa aphid, *Therioaphis maculata*, pheromone comprises another sesquiterpene hydrocarbon, (−)-germacrene A (10, 115), and for *M. viciae*, monoterpenes, particularly (−)-*α*-pinene, synergize the activity of EBF (128).

Excision studies indicated that the sixth antennal segment is involved in alarm pheromone response (107, 139), which has been confirmed for several aphid species by SCR studies on the distal primary rhinarium (Figure 3). The turnip or mustard aphid, *Lipaphis (Hyadaphis) erysimi*, responds to its own cornicle droplet but not to the EBF content alone (106, 109). A vacuum distillate from the aphid was highly active in causing dispersal of settled colonies (31). GC-SCR studies on the proximal primary rhinarium (Figure 4) showed cells that, although they did not respond to EBF, were stimulated by other components of the distillate. The additional components were identified as allyl, 2-butyl, 3-butenyl, and 4-pentenyl isothiocyanates, which presumably arose through action of thioglucosidase (myrosinase) enzymes by catabolism of glucosinolates sequestered from the cruciferous host plant. Indeed, this work showed that *L. erysimi* has its own thioglucosidase for this purpose. The isothiocyanates, although not active alone, gave full alarm activity when combined with EBF, even for single aphids, which do not readily become mobile under the influence of the natural pheromone. This suggests that the aphids can determine the proximity of others by the increased release of isothiocyanates caused by their feeding and, as a result, disperse more readily. For *A. fabae*, host-plant compounds have also been shown to synergize the activity of EBF (30).

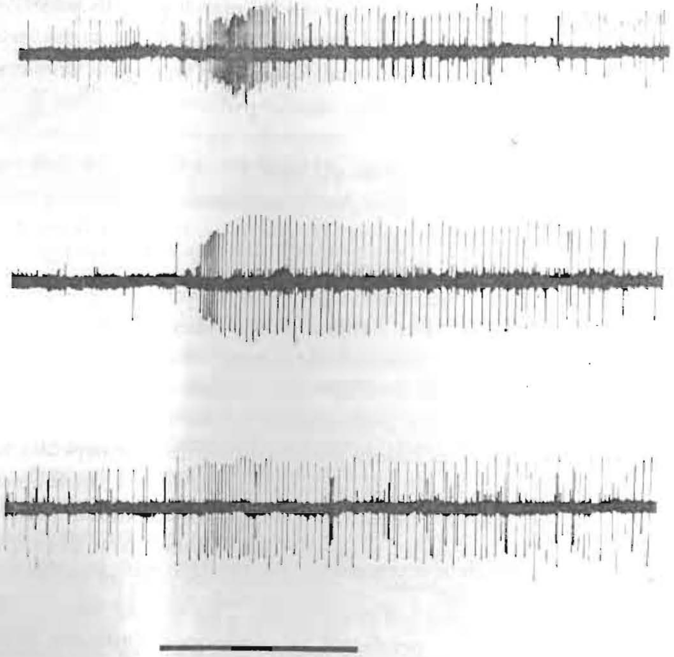


Figure 3 Response of olfactory cells from three aphid species to (*E*)-*β*-farnesene at 10[illegible] g (distal primary rhinaria): (*top*) *B. brassicae*; (*middle*) *A. fabae*; (*bottom*) *P. humuli* (C. M Woodcock, unpublished data). Black bar represents a 1-s stimulation

EBF is an ubiquitous plant component. The hop, *Humulus lupulus*, contains a relatively high proportion of EBF but, although *P. humuli* employs EBF as its alarm pheromone, this aphid colonizes hops and is a major pest. Examination of other volatile components of the hop plant revealed that several sesquiterpene hydrocarbons biosynthetically related to EBF, particularly (−)-*β*-caryophyllene, inhibit the activity of the pheromone (29). Thus, the aphid seemed to detect the difference between an aphid, which produces only EBF, and the plant, which produces the pheromone inhibitor as well. Investigations of a wide range of plants revealed a similar picture, although generally lower levels of these sesquiterpene hydrocarbons were found (126). Nonetheless, one plant, *Solanum berthaultii*, a close relative of the commercial potato *Solanum tuberosum*, was found to release EBF from its long foliar type B trichomes in such a way that the aphids perceived it separately

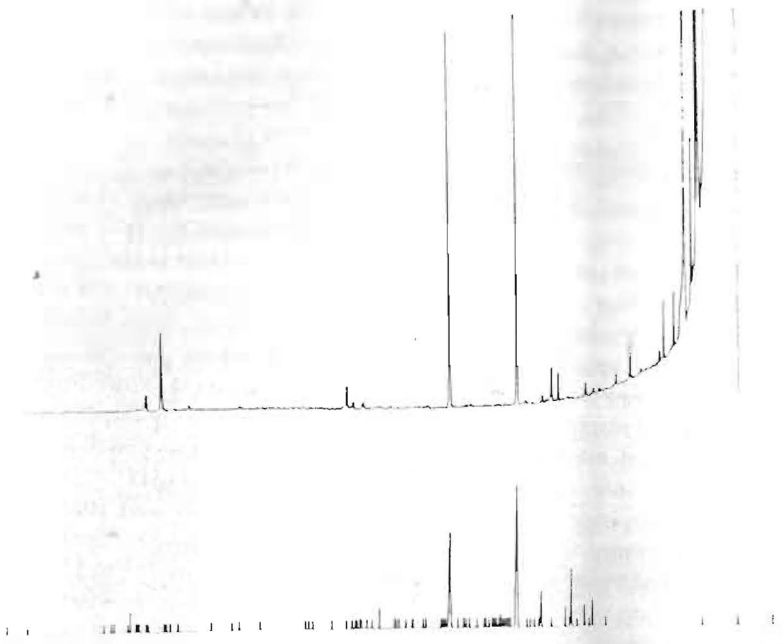


Figure 4 Coupled GC-SCR on *L. erysimi* proximal primary rhinarium. *(top)* gas chromatogram of a vacuum distillate of *L. erysimi*. *(bottom)* corresponding impulse frequency responses of olfactory cells.

from the caryophyllene produced in the rest of the leaf (48). Thus, the aphids responded by displaying typical alarm behavior and were repelled by the leaves, in agreement with earlier work in which plant leaves were treated with synthetic EBF (159, 160). Another study (53) showed that the total sesquiterpene fraction from *S. berthaultii* caused a general disturbance rather than the typical alarm response reported previously for the EBF from type B trichomes. A subsequent suggestion was that the content of EBF in type B trichomes arises from adsorption from type A trichomes, which contain large amounts of EBF together with the other sesquiterpenes (5). However, caryophyllene would then accompany EBF and inhibit any alarm response. A more likely explanation is, as reported originally (48), that the type B trichomes release low levels of EBF alone, while the main sesquiterpene content of the plant includes the alarm pheromone inhibitor (−)-β-caryophyllene, and that this mixture at high concentrations has other behavioral effects.

The prospect for improving aphid resistance in *S. tuberosum* by hybridization with *S. berthaultii* to increase levels of EBF has been considered (53).

The biosynthesis of EBF is presumably a simple enzymic step from farnesyl pyrophosphate, which is produced generally by plants. This process may offer a target for crop-plant modification by molecular genetics, but the site of production of the EBF would need to be separate from that of the endogenous generation of caryophyllene. For success against aphids, the type B trichome release system may also be required (124). Because the assumed precursor of EBF is present in plants, sequestration could provide an economic route to it for aphids. Indeed, aphids bred through many generations on artificial medium do not produce the alarm pheromone (H. van Emden, personal communication). However, farnesyl pyrophosphate, which is also highly unstable, would probably not be present in significant amounts in the phloem, and further studies indicate that addition of acetate to the artificial medium restores production of the pheromone (H. van Emden & J. A. Pickett, unpublished data).

The aphid alarm pheromone can probably attract predators or parasitoids, but this hypothesis has not been proven (105a). However, the inhibitor (−)-β-caryophyllene has been shown to attract the green lacewing, *Chrysoperla carnea*, (47) and may also enhance predation because it reduces aphid dispersal on attack (126). *A. pisum*, parasitized by *Aphidius ervi*, responded to the alarm pheromone or an approaching coccinellid predator to a lesser extent than when unparasitized. This is said to be the first practical example of adaptive host suicide behavior in connection with parasitism (38a, 90).

Other isomers are known to accompany EBF in aphids (128), and variations in ratios have been investigated in different morphs (64). This work, and the further finding that topical doses of EBF cause morphological changes, led to the suggestion that alarm pheromone components had additional hormonal functions (61a, 62). These functions have an endogenous nature and are not directly concerned in chemical ecology. However, aphids employ juvenile hormones (66) that are structurally related to EBF, and EBF and analogs are known to have juvenile hormone-like effects on aphids (89).

Soon after the first alarm pheromone identification, elegant structure activity studies demonstrated that EBF was substantially more active than any of the other farnesene isomers. However, the *(E)*-norfarnesene analog, which has similar stereochemistry but with one fewer carbon atom, was almost as effective as EBF (9). Replacement of hydrogen with fluorine in EBF gave a highly active and, in spite of the increase in molecular weight, more volatile analog, the 1,1,2-trifluorofarnesene, but this compound was chemically unstable (11). The stable and more easily synthesized 1,1-difluoronorfarnesene was also prepared, and its activity compared with the unfluorinated norfarnesene (Figure 5).

Although it was clearly demonstrated that the alarm effect of EBF alone would not be useful in crop protection (16, 72), laboratory studies sub-

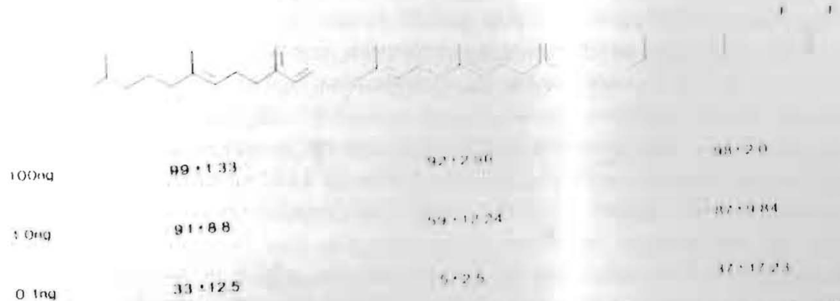


Figure 5 Activity of alarm pheromone (EBF) and analogs against *M. persicae*: percent of aphids responding after 1 min (*left*) (*E*)-β-farnesene, (*middle*) norfarnesene, (*right*) 1,1-difluoronorfarnesene (C. M. Woodcock, unpublished data).

sequently showed that the increased mobility caused by synthetic pheromone could improve the pick up of pesticides (55). Similar results were achieved in the field using a formulation comprising an emulsifiable concentrate of the pesticide together with the pheromone in a volatile hydrocarbon propellant, applied with an experimental electrostatic spraying system (56). In the glasshouse, EBF also improved control of the highly resistant cotton or melon aphid, *Aphis gossypii*, by increasing the pick up of spores from the fungal pathogen *Verticillium lecanii* (56, 73). In China, the addition of EBF to a commercial aqueous formulation of fenvalerate reportedly improved kill in field trials on an aubergine crop using a conventional hydraulic spraying system (163), but this formulation gave poor results in the United Kingdom (B. J. Pye, personal communication).

Laboratory studies indicate that just a few milligrams of EBF released within the crop are sufficient to elicit a maximum alarm response with an aphid such as *M. persicae*, but chemical detection of EBF at these levels within the canopy is extremely difficult. However, the fluorinated analog 1,1-difluoronorfarnesene can be detected at very low levels by means of an electron-capture detector with GC and may help in devising better formulations that could be used reliably with hydraulic systems (11). Further work on interactions between host plants and the alarm pheromone may also contribute; for example, although an aqueous formulation of EBF elicited no alarm response with *L. erysimi*, a high response was obtained when the formulation was combined with the plant-derived synergist allyl isothiocyanate (31).

Use of EBF in the field to control aphids by means of its reported toxicity has been suggested (64) and a related patent has been filed (63), but this use of EBF does not appear to exploit the promise of semiochemicals because treatment levels would be required well above those employed for conventional insecticides. A further complication in the use of EBF in aphid control is that the alarm response is greatly reduced in aphids resistant to insecticides (32). Although the reason for such a link is not obvious, commonly used aphicides such as pirimicarb reportedly induce alarm pheromone release. Again, however, insecticide-susceptible aphids respond more readily (134).

Host Location: Role of Plant Volatiles

Early studies suggested that chemical cues, detected only after visually mediated random landings on plants, resulted in selection of the host plant (78, 79, 105). However, the idea that olfactory cues play no part in host-plant selection prior to landing is now being questioned, and experimental evidence to support an olfactory role is accumulating. Several studies have demonstrated the response of aphids to plant volatiles in the laboratory, and although Jones (75) reported equivocal results with *A. fabae*, Alikhan (1) showed that this aphid did in fact respond to host-plant odors. Similarly, *A. gossypii* was attracted to host-plant material (*Cucurbita pepo* or *Thunbergia laurifolia*), while the nonhost *Lantana camara* appeared to be repellent (131).

The orientation responses of apterous *Cryptomyzus korschelti* were studied with a locomotion-compensator bioassay and demonstrated a positive upwind anemotaxis mediated by the odor of the summer host, *Stachys sylvatica* (153). Although the walking speed did not change, displacement from the starting point, track straightness, walking time, and distance moved upwind were significantly greater in the presence of host odor than in clean air or air carrying the odor of the nonhost, *S. tuberosum*. These authors concluded that olfactory cues are utilized in host-plant location. More recent work using a linear track olfactometer showed significant responses of apterous and alate *A. fabae* to the summer host *Vicia faba* (116). Alatae of the cabbage aphid, *Brevicoryne brassicae*, were also attracted to volatiles from their host plant *Brassica oleracea*. This result is in agreement with the previous findings (121) that *B. brassicae* summer alates responded to volatiles from *Brassica napus*. Although Pettersson (121) concluded that the volatile isothiocyanates were not the active factors, electrophysiological recordings from the proximal primary rhinaria of the crucifer specialists *B. brassicae* and *L. erysimi* have shown the presence of cells that respond specifically to these compounds (31, 116). Alate virginoparae of *A. fabae* also possess receptors sensitive to isothiocyanates, although these compounds are not associated with their host plants. However, while both *B. brassicae* and *L. erysimi* were attracted by 3-butenyl isothiocyanate, *A. fabae* was repelled (116). Thus, in *L. erysimi*, the isothiocyanates play a dual role in host location and as alarm pheromone synergists.

Pettersson (118), in a comprehensive laboratory study on gynoparae and males of the bird-cherry-oat aphid, *Rhopalosiphum padi*, demonstrated attraction to the winter host, *Prunus padus*, but not to the nonhosts *Prunus cerasus* and [illegible]s *ildaei*. Similarly, males of the hop aphid, *P. humuli*, responded to leaves and twigs from their primary host *P. cerasifera*, and an ether extract of the plant's bark was shown to be active. In addition, a mixture of the bark extract and synthetic sex pheromone was significantly more attractive than the pheromone alone (19). However, *A. fabae* gynoparae did not respond to volatiles from the primary host spindle, *Euonymus europaeus*, even after 72-h starvation (116).

Few field studies have examined the role of plant volatiles in host location by aphids. Pettersson (122) examined the effect of benzaldehyde on gynoparae of *R. padi* and of the glucosinolate sinigrin on summer alates of *B. brassicae* using baited water traps. In both instances, the results indicated an odor-enhanced catch. Presumably, the involatile sinigrin released volatile components by hydrolysis. Similar experiments with the willow-carrot aphid, *Cavariella aegopodii*, demonstrated a significantly greater catch in traps treated with the monoterpenoid (+)- or (−)-carvone (20). Simultaneous release of a biosynthetically related compound, linalol, significantly reduced trap catch, although linalol alone was inactive. Thus, the linalol apparently masked the attraction of the carvone. Interestingly, linalol was found to stimulate cells on the proximal primary rhinarium of *N. ribis-nigri* (13). Laboratory studies with *A. fabae* apterae and alatae have shown that isothiocyanates can mask the attractiveness of leaves of this species' host plant (116). *P. humuli* also possesses receptors on its antenna that respond to isothiocyanates (C. M. Woodcock, unpublished data), and in the field, application of a slow-release isothiocyanate formulation to hops decreased colonization by spring migrants (C. A. M. Campbell, personal communication). Recent field experiments showed significant catches of male *P. humuli* in water traps treated with an ether extract of *P. cerasifera* when the traps were placed 20 m outside the hop garden. Within the crop, the extract alone was not active but synergized the attractiveness of the sex pheromone (19). This effect was short lived, suggesting that the compounds involved were either highly volatile or unstable.

Thus, a role is being demonstrated for plant volatiles in long-range host location. However, during this phase of flight, aphids respond strongly to visual stimuli (84). The interaction of visual and odor cues was emphasized in the field study with *C. aegopodii* by the observation that carvone-baited yellow traps were more effective than transparent traps, which were in turn more effective than black traps (20). In addition, preliminary results suggest that approaches to plant-mimicking visual targets by flying aphids can be modified by olfactory stimuli (S. F. Nottingham & J. Hardie, unpublished data).

Host Selection—Settling and Feeding Behavior

Recent reports have extensively covered the effects of aphid feeding on plants (96–98). The sequence of behavioral events leading to settling and colonization has been reviewed (82), as has the location of the gustatory receptors involved in contact chemosensory interactions (2). However, a role for the antennal olfactory receptors in this phase must not be excluded because the compounds involved often have moderate volatilities.

Central to the investigation of aphid-plant interactions related to settling and feeding has been the development of electrical monitoring of probing activity. This technique was originally introduced by McLean & Kinsey (92), who used an AC amplifier to detect resistance changes in the plant-insect system as the stylets penetrated plant tissue. Further developments were made (149) in which changes in both resistance and electromotive force were measured with a DC amplifier, and the subject was recently reviewed (152, 152a). Various patterns in the electrical penetration graph (EPG) have been associated with different phases of stylet penetration, salivation, and feeding (80, 94, 143, 150, 151).

Electrical recording systems have been employed for investigating host-plant resistance to aphids. Early studies with *S. graminum* on resistant and susceptible sorghum, *Sorghum bicolor*, suggested resistance related to chemical composition of the phloem sap (18). Subsequent studies with this aphid on other cereals, e.g. wheat *(Triticum aestivum)*, obtained similar results and linked these to other manifestations of aphid resistance (112, 136). The effects of leaf excision, which increased feeding on resistant cultivars, were determined, and accompanying changes in chemical composition led to the conclusion that the amino acid content is not primarily involved in aphid resistance (103), although polysaccharide integrity or composition may have a bearing (155). Indeed, a role for plant matrix polysaccharides had already been evidenced by behavioral and electrical recording in artificial feeding studies with various polysaccharides (17). Recent work using the DC system with *M. persicae* and *N. ribis-nigri* on susceptible and resistant lettuce, *Lactuca sativum*, has examined fine aspects of the associated EPGs. In this case, resistance appears to involve both mesophyll and phloem components (104).

Aphid settling and feeding have also been widely studied without recourse to electrical monitoring systems. Indeed, the identification of the chemical components involved has mostly been accomplished in association with behavioral studies, whether they were related to resistance in plant cultivars or to general interactions with host plants (40, 50, 82). Although probing behavior can correlate well with cultivar resistance (52), this may not always be the case (61). Thus, there is considerable scope for linking chemical analysis with electrical recording.

Leaf-surface composition has long been known to influence aphid settling. For example, the flavonoid glucoside phlorizin from species in the apple genus *Malus* is a probing stimulant for the green apple aphid, *Aphis pomi*, and the apple grass aphid, *Rhopalosiphum insertum* (81), but was a probing deterrent to aphids such as *M. persicae* and the large American raspberry aphid, *Amphorophora agathonica*, which do not specialize on apple (102). Other groups of compounds have been implicated (76, 77), but work has mainly been directed at the secondary (summer) host, with few studies of the primary host, e.g. peach, *Prunus (Amygdalus) persica* for *M. persicae* (146).

Total extraction of plant tissues shows that a greater range of compounds is involved. Included here is the analysis of expressed sap, because unless scrupulous care is taken to eliminate contamination, one cannot define the origin of the compounds. Phenolic acids, particularly the caffeoylquinic acids, were investigated in lettuce cultivars susceptible and resistant to the lettuce root aphid, *Pemphigus bursarius*. Isochlorogenic acid levels and the activity of phenylalanine–ammonia lyase, a key enzyme in the biosynthesis of such phenylpropanoids, correlated with resistance to aphids (21).

Compounds isolated from whole tissue or expressed sap can be tested by incorporation into an artificial diet encapsulated by a synthetic membrane through which aphids can feed (100, 101). This approach was used to demonstrate feeding-deterrent activity of the flavon-3-ol catechin, a precursor of polyphenolic compounds such as the condensed tannins, against the rose aphid, *Macrosiphum rosae* (117). The level of catechin in buds from cultivars of its primary host genus *Rosa* had previously been found to correlate with reduced feeding (95).

Isothiocyanates and other compounds resulting from catabolism of glucosinolates, typical components of the Cruciferae, during damage have already been mentioned. This chemistry also has a role in settling and colonization. For example, sinigrin (allylglucosinolate), a powerful phagostimulant for the crucifer specialists *B. brassicae* and *L. erysimi*, could be tolerated by the polyphagous *M. persicae* but deterred the noncrucifer feeders *A. fabae* and *A. pisum* (111). Because contact chemosensory interactions are implicated at this stage, the nonvolatile glucosinolates are probably involved directly. However, the catabolites might be the active agents, by release at, or in the vicinity of, the aphid receptor. Indeed, thioglucosidase enzymes capable of releasing isothiocyanates are found in both *B. brassicae* (91) and *L. erysimi* (31). Preferences in aphid feeding may also occur within crucifer species (38) and cultivars (130), related to fine differences in glucosinolate levels.

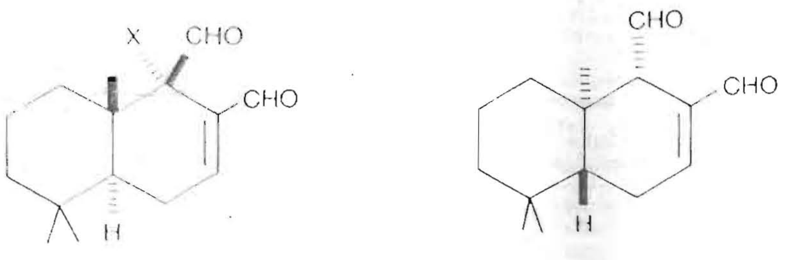
Hydroxamic acids, particularly 2,4-dihydroxy-7-methoxy-2H-1,4-benzoxazin-3(4H)-one from corn, *Zea mays*, and other cereals, have deleterious effects on the development of cereal aphids such as the rose-grain aphid, *Metopolophium dirhodum* (3). These compounds may act generally in

Gramineae (Poaceae) against this aphid (113). Some studies have examined the biochemical mode of action (114). A correlation between hydroxamic acid levels in cereals and resistance to *R. padi* and to the grain aphid, *Sitobion avenae*, has also been claimed (7, 147). However, further work is needed because no correlation was found between resistance of different maize cultivars to the corn leaf aphid, *Rhopalosiphum maidis* (6). Feeding deterrency of ellagitannins, phenolic acid hydrolysis products, and related compounds was also investigated through incorporation of these compounds into an artificial diet (74). *A. pisum* was least sensitive, *M. persicae* intermediate, and *S. graminum* most sensitive, particularly to ellagic acid. As a feeder on Gramineae, *S. graminum* is likely to be poorly adapted to defense systems based on polyphenolics, which are more pronounced in other plant families.

Various compounds with antifeedant activity have been identified from plants, particularly where the aphid is adapted to other unrelated species. Thus, several diterpenoid acids in the labdane class, e.g. 18-hydroxygrindelic acid from *Chrysothamnus nauseosus* (Compositae), were very active against *S. graminum*, which feeds on plants in the Gramineae (135). Also highly active against *S. graminum* was the spiroabietane diterpenoid, plectrin, from the labiate *Plectranthus barbatus* (85). However, some Gramineae produce potent defensive compounds, and the alkaloid gramine, produced in the genus *Phalaris*, is an antifeedant for both *S. graminum* and *R. padi* (164). In grasses such as *Lolium* spp. and *Festuca* spp., fungal endophytes of grasses in the genus *Acremonium* produce various alkaloids including peramine, which prevents survival of *S. graminum* (141).

When incorporated into an artificial diet, several potentially systemic quinolizidine alkaloids and the indolizidine alkaloid castanospermine were found to be antifeedants for *A. pisum* (42). However, since aphids would be expected to be more readily deterred from feeding on artificial diet than on plants, a range of general antifeedants was tested against *M. persicae* when these compounds were applied to leaf surfaces (57). At moderate application rates, several of these compounds, including hydroxamic acids, lipophilic amides, and β-tricarbonyl compounds, were inactive, as was the tetranortriterpenoid azadirachtin isolated from the neem tree, *Azadirachta indica* (14, 83). Indeed, the latter compound was only active when presented in an artificial diet and at levels that caused phytotoxicity when applied systemically to plants (54). Studies on a series of quassinoids showed quassin to have some activity, but the most active, isobrucein A, was phytotoxic (129).

Of the drimane antifeedants (Figure 6), (−)-polygodial from the water-pepper, *Polygonum hydropiper*, reduces settling by *M. persicae* as well as the acquisition of the semipersistent beet yellows virus and the nonpersistent potato virus Y (51). In structure-activity studies on a series of plant-derived



(−)-polygodial, X=H

(−)-warburganal, X=OH

(+)-polygodial

Figure 6 Structure of drimane antifeedants.

and synthetic drimanes. (−)-warburganal from the East African tree *Warburgia ugandensis* also showed high activity (4). Interestingly, the synthetic enantiomer (+)-polygodial had identical activity to that of the natural compound. The drimanes also show some phytotoxicity, but the possibility of such effects interfering with settling was eliminated by running parallel studies using artificial diets.

Extraction of (−)-polygodial from *P. hydropiper* by means of liquefied carbon dioxide yielded material for a field trial against the persistently transmitted barley yellow dwarf virus, principally vectored by *R. padi*. Under conditions of high pest and disease pressure, three two-weekly treatments of (−)-polygodial at 50 g/ha increased the yield by over 1 ton/ha, which was similar to that achieved by the conventional broad-spectrum insecticide cypermethrin (24, 127). As with EBF, the drimane antifeedants are biosynthesized from farnesyl pyrophosphate, and investigators are attempting to isolate the enzymes, particularly those involved in the cyclization reaction that produces the drimane skeleton. Molecular genetics could be used to develop these antifeedant effects (33).

The influence of the alarm pheromone on feeding has also been investigated. Although the insects continue to probe (58), probe duration is reduced (123). Attempts have been made to overcome the extreme volatility of the compound by producing derivatives that would release the pheromone by slow decomposition. However, although such compounds showed antifeedant activity, the most active were a series of high-molecular-weight derivatives that were in fact unable to release pheromone (12, 23). These compounds were also effective against transmission of non- and semipersistent plant viruses (49), and the most active derivative was used successfully against barley yellow dwarf virus transmission in the field (28).

Fatty acids, particularly dodecanoic acids, can reduce aphid settling on leaves (140). Acquisition (and thereby transmission) of semipersistent and persistent viruses is also decreased, but is increased for the nonpersistent potato virus Y. Unlike (−)-polygodial and the alarm pheromone derivatives, the fatty acids work slowly and allow virus to be transmitted before the aphid is deterred from feeding. This effect is also observed with certain aphid-resistant potato varieties (35). Nonetheless, under field conditions, the application of dodecanoic acid has been somewhat successful in reducing the level of *A. fabae* colonization on sugar beet (70). Certain mineral oils are also known to reduce aphid colonization of plants and virus disease transmission (36, 142).

Purely synthetic compounds can also indirectly affect aphid chemical ecology. For example, application of herbicides (86) or plant growth regulators (41) can reduce aphid colonization, the latter probably by increasing the pectin barrier to stylet penetration. Increased levels of nitrate caused reduced infestation of *S. graminum* on barley, probably by causing an increase in the alkaloid gramine (137). Also, the effects of air pollution, particularly sulfur and nitrogen dioxides, stimulate development of *A. fabae* (39).

Conclusions

The demonstration that aphids can respond to olfactory cues by orientated flight in the field is particularly exciting. Many of the recent advances involving aphid olfaction have been achieved by means of sophisticated sensory, chemical, and behavioral techniques requiring close interaction between the scientific disciplines. The future may see greater use of these approaches to investigate aspects of aphid chemical ecology involving gustatory cues.

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TACTICS FOR MANAGING PESTICIDE RESISTANCE IN ARTHROPODS: Theory and Practice

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PERSPECTIVES AND OVERVIEW

The evolution of resistance to insecticides and acaricides by arthropod pests can be viewed and studied from two contrasting perspectives. At a fundamental level, resistance provides an almost ideal model of adaptation to withstand severe environmental stress. Work on the genetic (127, 128), biochemical (30, 82), and more recently, the molecular basis of resistance mechanisms (32) has cast light on the nature of this adaptation in several insect species, leading in some cases to diagnostic assays for specific genes or gene products (3, 22, 45). Similarly, population geneticists have exploited opportunities to analyze the selection of resistance in laboratory and field experiments (94, 95), and to predict, using theoretical models, how fast resistance genes are likely to evolve under different pesticide exposure regimes (115, 120).

Unlike most evolutionary phenomena, however, resistance is also of great practical and economic significance. Not only have resistant species increased greatly in number (56), but the severity and extent of some resistance problems has increased alarmingly. For example, in some populations of the diamondback moth, *Plutella xylostella* (6), and Colorado potato beetle, *Leptinotarsa decemlineata* (50), resistance to virtually all available insecticides has