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Can aphid-induced plant signals be transmitted aerially and through the rhizosphere?

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Abstract

Aphids, through their close association with plants, cause systemic release of semiochemicals. These may have negative effects on subsequent aphid colonisation and can also have positive roles with insects that are antagonistic to aphid development, for example parasitoids. One of the semiochemicals involved in host selection by aphids is methyl salicylate, and since this compound was shown to have a role as a plant stress signal, the hypothesis that aphids might facilitate identification of new plant signals was examined. Confirmation was obtained during an investigation of avoidance of unsuitable hosts by the lettuce aphid, *Nasonovia ribisnigri*. (*Z*)-Jasmone was identified as a plant-derived semiochemical acting negatively for a number of aphid species, and positively for insect antagonists such as parasitoids and predators. However, when the compound was employed at 0.1 ppm in air above intact plants, these plants then attracted aphid parasitoids long after the (*Z*)-jasmone itself was no longer detectable. A specific interaction was proposed, since the (*Z*)-jasmone appeared to be selectively taken up by the plants. Aerial interactions between intact barley plants from different cultivars, which may be differentially releasing stress associated signals, can also influence acceptability to aphids. Furthermore, it has been shown that exudates from the roots

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of aphid-infested plants, grown hydroponically or in soil, cause intact plants to become more attractive to parasitoids.

Keywords: Induced defence; Aphids; Signals; Rhizosphere; Phytopheromones

1. Introduction

In exploring the title question, this study sets out the facts of aphid-related chemical ecology by which the hypothesis regarding associated plant/plant interactions can be tested and critically reviewed. Aphids (Homoptera: Aphididae) have particularly close interactions with plants, probably because of their highly adapted feeding mechanism which allows direct ingestion of phloem sap (Minks and Harrewijn, 1987). Although likely to be true for most aphids, those in the subfamily: Aphidinae, which comprise many pest species, are known to employ plant-derived signals, or semiochemicals, in interactions involved in the selection of prospective hosts (Pickett et al., 1992, 1995) and in acceptance after landing and during initial feeding behaviour (Tjallingii, 1990; Powell et al., 1999). Many species in the Aphidinae alternate between host plants, a woody species as their primary or winter host and an herbaceous annual as the secondary or summer host. Alternation can be determined by the generation of seasonal morphs and by the physiological state; for example, landing on a secondary host can be associated with the depletion of lipid reserves from migratory flight. Again, semiochemicals play an important role in selection or avoidance of the respective hosts (Pettersson et al., 1994; Birkett et al., 2000) and can also modify response to sex pheromones during the migration of sexual morphs to the primary host (Hardie et al., 1992; Guldemond et al., 1993). However, it is the ability of aphids to detect stress or induced defence in prospective host plants that provides an opportunity to look further at plant/plant interactions and this phenomenon will be considered in detail, particularly with regard to the production of semiochemicals by the plant as a consequence of aphid feeding. Such semiochemicals, as host or prey-related compounds, present an obvious evolutionary advantage to parasitoids and predators searching for aphids. Indeed, if the argument regarding "omniscience" by plants (Dicke and Bruin, 2001) is considered, then synomones caused to be released by aphid feeding, and employed by insects antagonistic to these herbivores, would also be candidate phytopheromones and would thus provide opportunities for induction of defence against aphid populations developing within the ecosystems.

Mechanisms by which phytopheromones could influence plant processes, specifically the inducible secondary metabolism associated with defence, are not known, so direct detection by plants as an identification tool is not yet available. However, use of electrophysiology in the identification of semiochemicals related to insect host location (Pickett et al., 1998), and particularly synomones active with the organisms antagonistic to aphids, is explored as an approach to identifying phytopheromones. Also considered are the opportunities offered by the rhizosphere for transmission, below ground, of signals conveying messages relating to aphid colonisation of nearby plants. Aphids, although comprising important pests, are here providing a model insect very closely associated with plants, largely through their intimate feeding mechanisms. The objective is to use the chemical ecology of these insects, and their parasitoids and predators where possible, to explore plant/plant interactions by means of phytopheromones. Knowledge of the molecular structures involved could, in the long term, be exploited to devise new approaches to "switching on" inducible defence mechanisms in crop plants prior to attack by pests and possibly pathogens.

2. Induction of plant-derived semiochemicals by aphids

After demonstrating that spring migrants of the bird cherry-oat aphid, *Rhopalosiphum padi*, were repelled from their primary host, bird cherry, *Prunus padus*, by volatile semiochemicals acting as non-host cues, active components were identified by use of electrophysiological recording techniques. Gas chromatography coupled to single cell (neuronal) recordings (GC-SCR) from olfactory organs on the antenna showed that methyl salicylate was a highly active component (Pettersson et al., 1994). This compound significantly reduced the attractiveness of secondary host semiochemicals in the laboratory, and also aphid colonisation of crops in the field (Pickett et al., 1995, 1997). However, in the field trials, it was observed that other cereal aphids which do not colonise primary hosts producing methyl salicylate were also repelled by this compound. Indeed, non-cereal aphids were found to be similarly affected; for example, in laboratory olfactometer assays, the black bean aphid, *Aphis fabae*, was no longer attracted to volatiles from its host plant when methyl salicylate, at physiologically relevant levels, was added (Hardie et al., 1994). As work proceeded with a greater range of aphid species, and with a wide range of other insects from five Orders, neurophysiological responses to this compound were shown to be widespread (Woodcock, unpublished). Methyl salicylate is known to be released from certain plants during herbivory (Bernasconi et al., 1998; Dicke et al., 1999) and to be directly related to salicylic acid, an internal plant stress signal derived from the inducible phenylalanine-ammonia lyase pathway. Thus, it was proposed that this compound might serve as a signal to aphids that the emitting plant may be undergoing stress through herbivory and may, as a consequence, be unsuitable, through feeding competition or induced chemical defence (Pettersson et al., 1994). At the same time, the suggestion was made that methyl salicylate might act as an external signal inducing defence pathways in intact plants, and subsequently Shulaev et al. (1997), presented evidence in favour of this proposal.

Although the link between plant stress and reduced aphid colonisation by means of methyl salicylate has not conclusively been demonstrated, such an association has been shown for the cereal/*R. padi* complex (Quiroz et al., 1997). Four compounds, 6-methyl-5-hepten-2-one, (−)- and (+)-6-methyl-5-hepten-2-ol and 2-tridecanone, were shown to be present in volatiles from aphid-infested wheat seedlings but not from intact plants. A mixture of the four compounds in the natural proportions counteracted the attractiveness of the volatiles from an intact wheat seedling. So far, we have no evidence that these compounds, at naturally occurring levels, are active as phytopheromones influencing subsequent colonisation attempts by aphids. However, it is known that the C_6 products of the lipoxygenase, or octadecanoid, pathway such as (*E*)-2-hexenal can induce expression of defence-related genes in intact plants (Bate and Rothstein, 1998).

Although there are obvious advantages in studying plant-derived semiochemicals arising directly from aphid feeding in the search for putative phytopheromone components, the next development arose again from interactions involved in aphid host alternation. The primary host of the currant-lettuce aphid, *Nasonovia ribis-nigri*, comprises principally the black currant, *Ribes nigrum*. Volatiles from intact black currant were investigated, this time using the chromatography coupled-electroantennogram system (GC-EAG). The EAG, although less sensitive than SCR, allowed detection of a range of putative semiochemicals characterising the black currant as a non-host for spring migrants searching for the secondary host, lettuce, *Lactuca sativa* (Birkett et al., 2000). A mixture of these compounds counteracted the attractiveness of lettuce plants in the laboratory and in the field (L.J. Wadhams, unpublished). However, one component, (*Z*)-jasmone (= *cis*-jasmone), was shown to repel not only spring migrants of *N. ribis-nigri* but also the hop aphid, *Phorodon humuli*, and cereal aphids in the field (Birkett et al., 2000). As a consequence of this more general activity, and because of its relationship with jasmonic acid, both compounds being produced by the lipoxygenase pathway, further investigations were made for semiochemical activity at higher trophic levels, and then as a putative phytopheromone component.

3. Systemic and species-specific release of semiochemicals evidenced by interactions with aphid parasitoids

In ecosystems containing leguminous (fabaceous) plants, the parasitoid *Aphidius ervi* (Hymenoptera: Braconidae) uses the pea aphid, *Acyrthosiphon pisum*, as one of its main hosts, but does not normally attack other legume-feeding aphids such as *A. fabae* or the vetch aphid, *Megoura viciae* (Starỳ, 1973). *A. ervi* is strongly attracted to bean plants, *Vicia faba*, infested with *A. pisum*, and this response is heightened following a successful oviposition experience on the plant (Du et al., 1997; Guerrieri et al., 1997; Powell et al., 1998). Furthermore, in wind tunnel bioassays, the parasitoids could discriminate between intact bean plants and those upon which the correct host was feeding (Guerrieri et al., 1993), and even between plants infested with *A. pisum* and those infested with the non-host *A. fabae* (Du et al., 1996; Powell et al., 1998). Host aphids feeding on a basal leaf of *V. faba*, which was subsequently removed before testing the plant, also caused increased attractiveness for up to 24 h after the aphids had been removed (Guerrieri et al., 1999). Thus, semiochemicals induced by aphid feeding can be produced systemically, with production continuing after feeding has ceased, and can be so specific as to denote the presence of a particular aphid species.

Using GC-EAG with *A. ervi*, electrophysiologically active components of volatiles entrained from infested bean plants were identified as comprising (*E*)-*β*-ocimene, 6-methyl-5-hepten-2-one, linalool, (*Z*)-3-hexen-1-ol, (*Z*)-3-hexenyl acetate and (*E*)-*β*-farnesene (Du et al., 1998). Some of these were also found in intact plants, but were released at higher levels from plants infested with the various aphid species. In wind tunnel bioassays, all six compounds had a significant effect on oriented flight by female *A. ervi*. However, none of the compounds elicited a response quantitatively comparable to that for the aphid-infested plant, and even a mixture of compounds did not account for its level of attractiveness. For five of the compounds, parasitoids with oviposition experience exhibited significantly stronger flight responses than naïve females. The exception was (*E*)-*β*-farnesene, which although in this context is plant-derived, is also generated by aphids as a component of their alarm pheromone (Pickett and Griffiths, 1980; Hardie et al., 1999). The most active compound in eliciting oriented flight, but also significantly more active with experienced parasitoids, was 6-methyl-5-hepten-2-one (Du et al., 1998). It has been proposed that parasitoids "learn" plant-derived chemicals but respond innately to host-derived cues, and the above results provide evidence for this hypothesis (Vet and Dicke, 1992).

6-Methyl-5-hepten-2-one was found to be specifically produced by bean plants on feeding by *A. pisum*, the host for *A. ervi* in this ecosystem. This compound is known to be biosynthesised oxidatively from the isoprenoid geraniol (Demyttenaere and DePooter, 1996) and is probably produced in the contexts described here through oxidation stimulated by aphid feeding. Another compound produced by oxidation of geraniol, geranic acid, was induced on feeding by *A. pisum* (Du et al., 1998), but no further role for this compound has yet been established. However, the systemic release of semiochemicals, and particularly where these relate selectively to particular herbivore species, presents another opportunity in which to investigate the effect on adjacent plants. Thus, not only in this system but also in others (De Moraes et al., 1998) showing similar parasitoid specificity, the induction of such specific effects in neighbouring plants should be tested.

4. (*Z*)-jasmone as a putative phytopheromone component

The discovery of high sensitivity and specificity of olfactory cells in aphids, and many other insects, to the stress-related compound methyl salicylate was seen as a prelude (Pettersson et al., 1994) to the identification of its role as a plant signal (Shulaev et al., 1997). (*Z*)-Jasmone was detected similarly by all the aphids investigated and was also found to be repellent for a number of species (Birkett et al., 2000). For *N. ribis-nigri*, there was a highly significant response to (*Z*)-jasmone from an olfactory cell in the proximal primary rhinarium (5th antennal segment), with the closely related methyl jasmonate giving virtually no response at a stimulus concentration two orders of magnitude higher. In addition, (*Z*)-jasmone was found to be attractive to an aphid predator, the seven-spot ladybird, *Coccinella septempunctata*, in the four-way olfactometer and to the parasitoid *A. ervi* in a wind tunnel. This activity, combined with the biosynthetic relationship to methyl jasmonate (Karban et al., 2000; Preston et al., 2001), suggested a possible role for (*Z*)-jasmone as a phytopheromone component. To test this hypothesis in the context of aphid chemical ecology, intact bean plants ($n = 9$) were treated with (*Z*)-jasmone at an initial concentration of 0.1 ppm in a closed glass vessel (25 l) for 24 h, after which time no remaining (*Z*)-jasmone could be detected. These plants were then tested in the wind tunnel, 48 h after initial exposure, and were significantly more attractive to female *A. ervi* than the control plants. Entrainment and analysis of volatiles released by the plants, for 48 h periods up to eight days after initial treatment, showed an increase in certain compounds, including (*E*)-*β*-ocimene, known to attract other parasitoids. However, when methyl jasmonate replaced (*Z*)-jasmone as the aerial treatment, although (*E*)-*β*-ocimene was produced in higher amounts than the control for the first 48 h period, the effect disappeared thereafter, whereas for (*Z*)-jasmone, the effect persisted significantly into the 144–192 h period (Birkett et al., 2000). Thus, a relatively low concentration of (*Z*)-jasmone causes an effect on an intact plant, giving rise to increased attraction of an aphid parasitoid.

Although aerially applied (*Z*)-jasmone has an effect on plants, the work here does not demonstrate unequivocally a phytopheromonal role, since we have been unable to detect sufficient (*Z*)-jasmone being released from aphid-damaged bean plants to cause this effect on neighbouring intact plants. However, (*Z*)-jasmone is widely considered not to have a hormonal effect in plants and may even be a sink for jasmonic acid which, because of the high volatility of the (*Z*)-jasmone, would thus be removed from the plant (Koch et al., 1997). Certainly, for (*Z*)-jasmone to be converted back into jasmonic acid would be unthinkable from a biosynthetic standpoint. The only real alternative explanation for the role of (*Z*)-jasmone not being a phytopheromonal one is that it is merely absorbed by the plant, as many other lipophilic and volatile compounds would be, and thereby exerts its effect as a general stress-related volatile. This is countered by the fact that some of the other compounds studied here do not appear to exert any such effects, and certainly at the relatively low level employed for (*Z*)-jasmone. However, a more compelling argument is that, although no (*Z*)-jasmone could be detected in the entrainments from plants after treatment with this compound, traces of related compounds were detected. These were found to be contaminants of the commercial (*Z*)-jasmone (Avocado Research Chemicals Ltd., Heysham, UK) employed in the work (Hick & Pickett, unpublished) and were identified from GC coupled-mass spectrometry as close structural analogues of (*Z*)-jasmone. The major component remaining after loss of (*Z*)-jasmone was identified from the mass spectral data as the known compound jasmolodione, or 4-methyl-5-(pent-2-enyl)-cyclopent-4-ene-1,3-dione (Crombie et al., 1971; Pattenden and Storer, 1974), this having been originally present in the (*Z*)-jasmone at less than 0.2%. [Mass spectral data: at 70 eV; m/z 178 (57%, M^+), 163 (7%), 150 (26%), 136 (21%), 135 (29%), 124 (42%), 121 (32%), 108 (26%), 96 (11%), 91 (41%), 79 (40%), 77 (39%), 55 (100%)]. Thus, although structurally very similar and biosynthetically closely related to the contaminants, (*Z*)-jasmone was taken up selectively by the bean plant, implying an active receptor mechanism and thereby adding weight to the argument for a phytopheromonal role.

None the less, this study should now be extended to use of isotopically labelled (*Z*)-jasmone and its precursors to explore, unequivocally, the transmission between plants and the fate in the recipient plants. Although here the effects of confining plants in a sealed vessel for aerial treatment with putative signals are taken into account by means of control experiments, in these further studies, elimination of such effects should be sought.

Recently, various defence genes have been shown to be expressed in leaves confined in a vessel containing plants infested with the spider mite *Tetranychus urticae* (Acarina: Tetranychidae) (Arimura et al., 2000). Also, Birkett et al. (2000), report that, by using differential display and confirmatory Northern blotting, (*Z*)-jasmone and methyl jasmonate were shown to have apparently distinct effects on plant gene expression. Therefore, the differentially displayed PCR product termed D251 was cloned and used to probe Northern blots from leaf or stem tissues of bean plants treated with air, (*Z*)-jasmone or methyl jasmonate. This clearly showed that, whereas the D251 sequence was up-regulated by treatment with both compounds in stem tissue, only (*Z*)-jasmone brought about an increase in the steady-state transcript level of this sequence in leaf tissue. Thus, the two compounds have distinct effects on plant gene expression and the response to these signalling compounds may be tissue-specific. The D251 sequence was identified as being derived from a gene encoding an α-tubulin isoform, based on the clear homology between the coding sequence contained in D251 and the α-tubulins.

5. Aerial interactions between barley cultivars affect subsequent aphid acceptance

An exciting development in the study of wound-induced signalling is the demonstration that intact plants can also produce semiochemicals associated with herbivore damage (Khan et al., 1997, 2000). The original study was related to feeding of noctuid and pyralid moth larvae on maize, where it was found that an intercrop comprising intact molasses grass, *Melinis minutiflora*, interfered with colonisation by adult moths and also enhanced parasitism by release of stress-related semiochemicals. This phenomenon was subsequently investigated for aphid/plant interactions. It was found that air passing over aggressive weeds such as couch grass, *Agropyron* (=*Elymus*) *repens*, caused cereal plants (barley, wheat and oats) situated downwind to become significantly less acceptable to *R. padi* than control plants (Pettersson et al., unpublished). In extension of this work, similar experiments were done using different barley cultivars, and very surprising results ensued (Pettersson et al., 1999). For example, when the cultivar Frida was placed downwind of the cultivar Hulda, the former became significantly less attractive to *R. padi* ($P<0.0001$). However, in a choice test, the two cultivars did not give statistically significant differences for acceptance by *R. padi* (Pettersson et al., 1999). The possibility that volatiles from one plant are adsorbed and then released by an adjacent plant is being investigated using cold isotopically labelled volatile compounds and their precursors. None the less, the likely explanation is that a form of phytopheromonal communication is involved, with the "provoking" cultivar simulating attack and releasing signals that affect the recipient cultivar. The test situation is artificial in that a wind tunnel is involved, but in this case the airflow is extremely low and so imitates field conditions more closely than many assays used elsewhere. Further experiments have shown that this type of aerially transmitted effect can also be demonstrated in the field (Ninkovic et al., in preparation).

6. Evidence for phytopheromones passed from aphid-damaged plants through the rhizosphere to intact plants

Recently, we have demonstrated that hydroponically grown bean plants infested with pea aphids, *A. pisum*, produce aphid-induced signals which attract parasitoids in the same way as similar plants grown in soil (Guerrieri and Pennacchio, unpublished). Significantly, when the infested plants were removed from the hydroponic medium, and intact plants were placed into this recently vacated solution, the intact plants then became attractive to parasitoids in wind tunnel bioassays. However, intact plants placed in a solution recently vacated by other intact plants did not undergo such a change and remained significantly less attractive to parasitoids ($P < 0.001$) (Fig. 1). This strongly suggests that root exudates from the infested plant contain compound(s) which are systemically translocated and elicit the release of the aphid-induced volatiles when taken up by an intact plant.

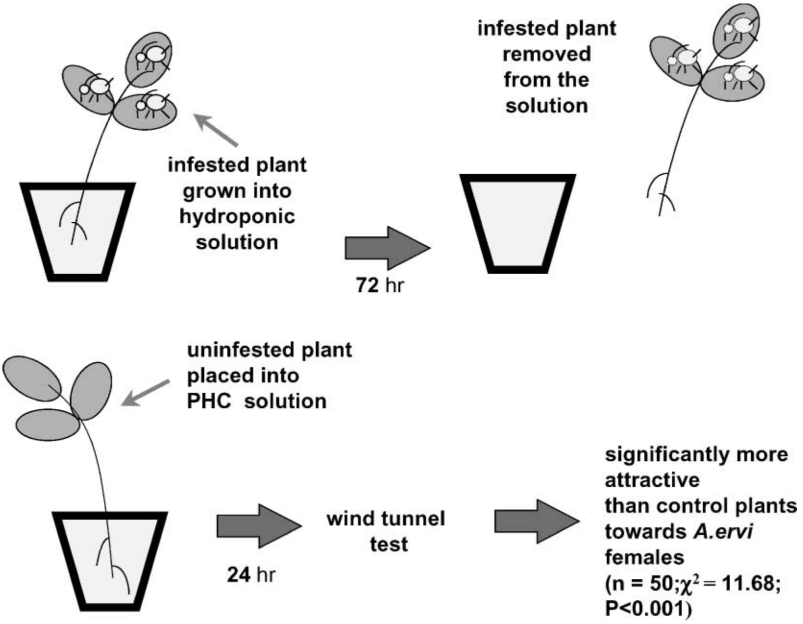

Fig. 1. Diagram illustrating an experiment, using broad bean plants growing in hydroponic solution, to demonstrate plant/plant transmission via root exudates of factors involved in the induction of plant volatiles associated with aphid damage, and which act as synomones for foraging parasitoids. PHC = plant/host complex.

These results were further supported by an experiment in which intact plants were maintained in soil in the same pot as infested plants, with the aerial parts of the infested plant caged to prevent contact with the intact plant. The latter, after the infested plant had been removed, was significantly more attractive to parasitoids in wind tunnel bioassays than intact plants which had shared pots with other intact plants ($P < 0.001$) (Fig. 2). A further experiment was undertaken to eliminate the possibility that aphid-induced volatiles, released from the infested plant, were adsorbed onto the foliage of the intact plant from which they were subsequently re-released, or alternatively that volatiles from the infested plant caused aerial induction of attractive volatiles in the intact plant. Thus, infested and intact plants were planted in separate pots to prevent root contact, but placed close together so that their foliage remained at the same distance apart for the same length of time as in the previous experiment (Guerrieri and Pennacchio, unpublished). In this case, the intact plants did not change in their attractiveness to parasitoids.

This work has strong parallels with that reported by Dicke and Dijkman, (2001) on spider mite-infested Lima beans, which also suggests that factors involved in herbivore-induced volatile release can be transmitted between plants via their roots. The possibility of rhizosphere transmission of factors inducing intact plants to release volatiles associated with aphid damage obviously requires further investigation. It has previously been shown that different aphid species feeding on bean plants

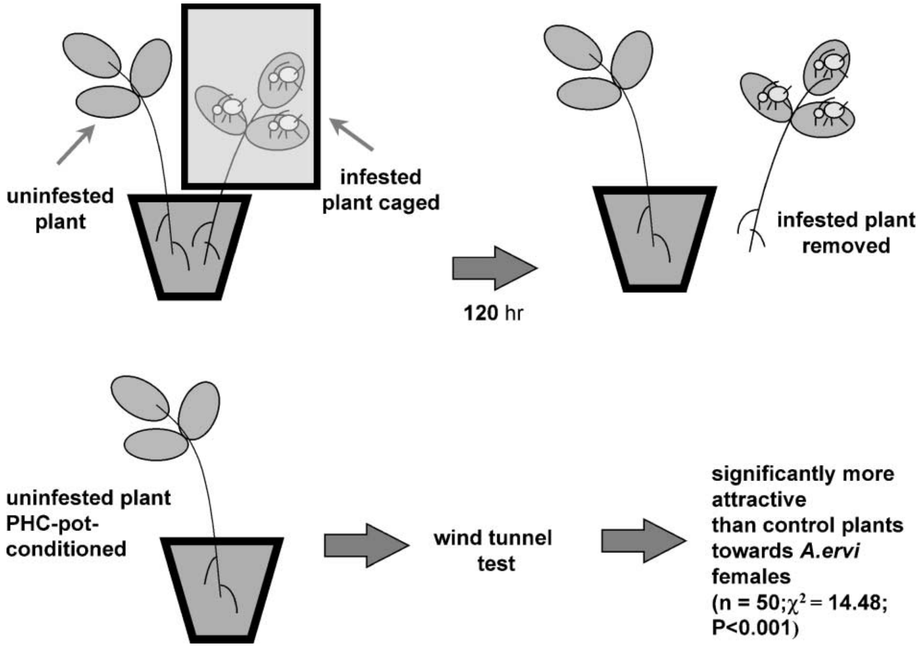

Fig. 2. Diagram illustrating an experiment, using broad bean plants growing in soil, to demonstrate plant/plant transmission via root exudates of factors involved in the induction of plant volatiles associated with aphid damage, and which act as synomones for foraging parasitoids. PHC = plant/host complex.

induce species-specific changes in plant volatile emission (Du et al., 1998; Powell et al., 1998) and it would be useful to determine whether such herbivore species-specificity is maintained in this plant/plant communication. Similarly, do root exudates from aphid-infested bean plants induce changes in the volatile profiles of other plant species, such as *Trifolium* spp., which are hosts to the same aphid. It is also important to investigate the spatial and temporal extent of the exudate effectiveness. Theoretically, it should be short-ranging and short-lived, unless it acts by priming plants to respond more quickly to herbivore damage when they themselves become infested. The ecological and evolutionary functions of such plant/plant interactions need to be elucidated.

7. Conclusions

At each stage, evidence for plant/plant communication is discussed critically, with specific experimental requirements for further elucidation suggested. However, the main objectives, given that aphid chemical ecology is providing model systems with which to investigate phytopheromonal effects, must be to account for the observed natural or semi-natural phenomena in qualitative and quantitative chemical terms. None the less, exploitation in crop protection represents an important goal. Intercropping (Khan et al., 1997, 2000) and mixed cultivars (Wolfe, 1985; Wiik, 1987; Gieffers and Hesselbach, 1988) have already been used successfully in reducing levels of pests and disease. Thus, studies must continue with these objectives and beyond, to elucidate phytopheromonal interactions which may be far more widespread than currently perceived.

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