

The chemical ecology of aphid host alternation: How do return migrants find the primary host plant?

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Abstract

The life cycle of some aphid species involves seasonal switches between unrelated summer (secondary) and winter (primary) host plants. Many of these “host-alternating” species, belonging to the sub-family Aphidinae, produce two return migrant forms on secondary host plants in autumn. Winged females (gynoparae) are produced first; these locate the primary host and deposit their sexual female offspring (oviparae). Later, males are produced on the secondary host and these locate the primary host independently before mating with the oviparae. The mechanisms of primary-host location by gynoparae and males are reviewed in this paper. Studies with several aphid species indicate that both forms are able to respond to volatile cues released by their specific primary host plant. Plant odours may also enhance or modify the responses of return migrants to the sex pheromone released by mature oviparae. Aphids are also able to sample non-volatile plant chemicals after landing, but there have been very few detailed investigations of the behaviour of return migrants at the primary-host-plant surface. Recent experiments with gynoparae of the black bean aphid, *Aphis fabae* Scopoli, show that these insects detect primary-host-specific cues during stylet penetration of peripheral plant tissues, and these stimuli promote settling and reproduction. Similar behavioural studies with males are required to shed light on the processes of speciation and reproductive isolation in host-alternating aphids.

Key words: Aphid-plant interactions, Aphidinae, autumn migration, host selection

INTRODUCTION

Aphid life cycles and host alternation. Aphids exhibit a variety of complex life cycles, with many species alternating between sexual and asexual reproduction (Moran, 1992). About 10% of extant aphid species host-alternate, spending autumn, winter and spring associated with a primary host plant (usually a woody tree or shrub) but switching to unrelated secondary hosts (often herbaceous plants) during summer. Figure 1 shows the complete life cycle (holocycle) of the host-alternating bird cherry-oat aphid, *Rhopalosiphum padi* (L.). In autumn, the wingless (apterous) sexual females (oviparae) mate with winged (alate) males on the primary host plant (in this case the bird cherry tree, *Prunus padus* L.) and produce cold-hardy, overwintering eggs. All other generations of the life cycle involve parthenogenetic, viviparous females. In spring, each individual that hatches from an egg (fundatrix) founds a clonal colony on new leaves. Descendants of the fundatrix (fundatrigeniae) re-

main on the primary host until the second or third generation develop wings; these ‘emigrants’ disperse as adults, colonising secondary host plants (cereal crops and other grasses in *R. padi*). Aphids remain on secondary hosts, producing alate and apterous summer females (virginoparae), until exposure to short days induces the production of ‘return migrants,’ the forms that relocate the primary host plant. The overwintering success of such holocyclic, host-alternating aphids therefore depends on dramatic changes in the host-selection behaviour of return migrants, which develop on a secondary host, but switch their preference to the primary host as adults. The aim of this review is to examine the mechanisms by which adult return migrants find their host plant.

Host-alternating aphids in three subfamilies (Anoeciinae, Eriosomatinae and Hormaphidinae) produce only one (female) return migrant form (sexuparae); these give birth to both oviparae and apterous males on the primary host plant. However, in the largest aphid subfamily (Aphidinae), which

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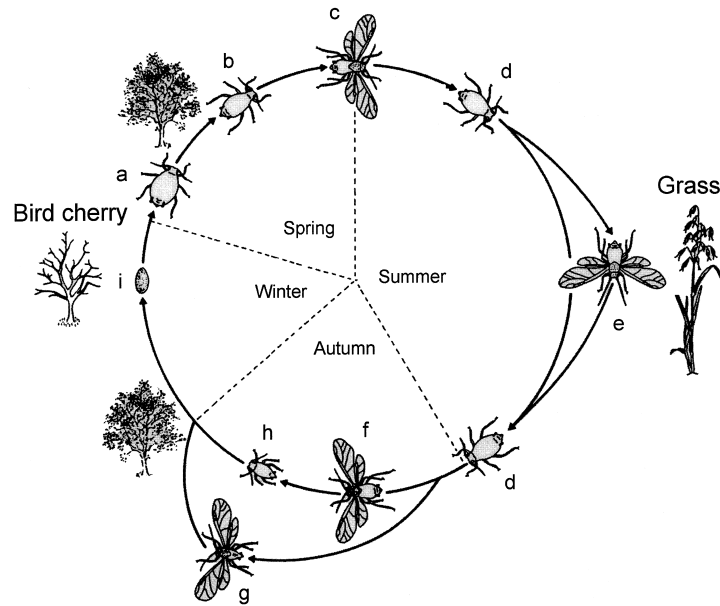


Fig. 1. Life cycle of the bird cherry-oat aphid, *Rhopalosiphum padi*; a) fundatrix, b) apterous fundatrigenia, c) spring migrant, d) apterous virginopara, e) alate virginopara, f) gynopara, g) male, h) ovipara, i) egg. Note that, in common with many host-alternating aphid species, some "anholocyclic" clones may remain on secondary hosts throughout the year, overwintering as asexual virginoparae with no egg stage. Modified from Carter et al. (1980) (with permission).

includes several economically-important host-alternating species (e.g. *R. padi*, Fig. 1), the return migration is carried out by two forms. Initially, short days trigger the production of gynoparae, winged females which fly to the primary host and give birth to oviparae. Later, winged males are also produced on secondary host plants, and these must also complete the return migration in order to mate with the oviparae. Virtually all studies of host location by aphid return migrants have examined species of Aphidinae; this review is therefore restricted to this subfamily.

Host location and plant-specific cues. The majority of host-alternating aphid species are highly specialised on both their primary and secondary host plants (Dixon, 1987). A few have a broader secondary host range, but even these species typically exploit only one or a few primary hosts. In addition, aphids are rather weak flyers, in that they are capable of controlled orientation only at relatively low wind speeds. The chances of return migrants locating their specific host are therefore very much dependent on the local abundance of the primary host plant species and will be extremely small in many cases. For example, Ward et al. (1998) estimated that less than 1% of the aerial population of *R. padi* gynoparae successfully lo-

cates and colonises a bird cherry tree. Studies carried out during the last 30 years indicate that, despite their relatively poor flight capability, aphids use plant-specific cues to increase their chances of host location. The host-selection behaviour of these small insects is largely based on plant chemistry.

Aphid responses to plant chemistry. Aphids are excellent phytochemists (van Emden, 1972; Pickett et al., 1992); their behaviour is influenced by plant metabolites that provide the insects with information concerning plant taxonomy and quality at various stages of the host-selection process. The landing response of flying aphids occurs as an attraction to non-specific visual stimuli (plant-reflected wavelengths; Hardie, 1989), but these responses may be modified by plant volatiles (Chapman et al., 1981; Nottingham and Hardie, 1993). In addition, laboratory experiments with several different designs of olfactometer show that walking aphids respond to the odours of host and non-host plants (Visser and Taanman, 1987; Nottingham et al., 1991; Pettersson and Stephansson, 1991; Visser and Piron, 1998; Hori, 1999). The above studies have all concerned the responses of summer female aphids (virginoparae); we will review the evidence that autumn return migrants (gynoparae and males) also show olfactory responses to their host plants.

Table 1. Evidence that return migrants of host-alternating aphids (Aphidinae) show a behavioural response (attraction/arrestment) to primary host-plant odour. Negative results are not listed here but are mentioned in the text.

Aphid species	Form showing a behavioural response	Test stimulus	Test method ^a	Reference
<i>Aphis fabae</i>	Gynoparae	Spindle leaves	Pettersson olfactometer	Isaacs, 1994
<i>Phorodon humuli</i>	Gynoparae	Plum and sloe leaf extracts	Water traps	Losel et al., 1996a
	Males	Myrobalan leaves, twigs	Pettersson olfactometer	Campbell et al., 1990
		Ether extract of myrobalan bark	Water traps	Campbell et al., 1990
<i>Rhopalosiphum padi</i>	Gynoparae and males	Bird cherry leaves/benzaldehyde	Pettersson olfactometer	Pettersson, 1970, 1993
	Males	Benzaldehyde	Linear-track olfactometer	Park et al., 2000
<i>Sitobion fragariae</i>	Gynoparae	Blackberry leaves	Linear-track olfactometer	Lilley and Hardie, 1996

^a Olfactometer studies were carried out in laboratory conditions; water traps were sited in the field.

After landing, a variety of chemical cues may be detected at the plant surface. Thus local odours (Storer et al., 1996), leaf trichome exudates (Neal et al., 1990; Rodriguez et al., 1993) and waxes (Powell et al., 1999) may all influence aphid behaviour. Stylet penetration of plant tissues includes regular brief cell punctures (Tjallingii, 1995), allowing assessment of internal plant chemistry. Even on a suitable host plant, aphids sample many plant cells (Tjallingii and Hogen Esch, 1993) before locating and accepting a food source (phloem sieve element). Investigations of aphid host selection and feeding have been heavily biased towards the economically important summer forms, but there is also some evidence that non-volatile cues are important in the recognition of primary host plants by autumn return migrants.

Interactions between plant chemicals and sex pheromone. Once the gynoparae settle on the winter host, their sexual female progeny (oviparae) mature and release a sex pheromone, which has a powerful influence on male behaviour. The sex pheromones of several species of Aphidinae have been identified, and their biology and chemistry were reviewed recently (Hardie et al., 1999). However, responses of male aphids to sex pheromone may be enhanced by specific chemical cues from the primary host. In addition, late-flying gynoparae may also utilise the sex pheromone (as an aggregation pheromone), enabling them to locate conspecific oviparae on suitable host plants. Plant volatiles may also synergise responses of gynoparae to sex pheromone.

RESPONSES TO VOLATILE CUES

Plant odours: gynoparae. Kennedy et al. (1959a, b) took advantage of extraordinarily heavy autumn migrations of the peach-potato aphid (*Myzus persicae* (Sulzer)) in 1947 and the black bean aphid (*Aphis fabae* Scopoli) in 1957, and observed the behaviour of gynoparae of these two species in field studies in southern Britain. *Myzus persicae* and *A. fabae* both have very broad summer host ranges, but specialise on particular overwintering hosts (especially peach, *Prunus persicus* L., and spindle, *Euonymus europaeus* L., respectively). Despite their extreme host-plant specificity, gynoparae of both species were equally likely to land on host and adjacent non-host plants. These observations led to the conclusions that there was “no evidence at all of olfactory discrimination at a distance” (Kennedy et al., 1959a), and that accumulation on appropriate host plants occurs as a reduced rate of departure, rather than increased arrival. However, subsequent laboratory and field studies have indicated that gynoparae may show a specific olfactory response to their primary host (Table 1).

Several studies have demonstrated the olfactory capabilities of *R. padi*. Experiments with a “Pettersson-style” olfactometer, where insects are free to move between four distinct odour zones (Pettersson and Stephansson, 1991), showed that *R. padi* gynoparae are attracted (or arrested) by the odour of their primary host plant. The insects contacted bird cherry leaf odour more frequently than clean air, but leaves of non-host plants had no such behavioural effects (Pettersson, 1970, 1993). One of

the major volatiles released by bird cherry is benzaldehyde. When *R. padi* gynoparae were tested in the same design of olfactometer, they contacted benzaldehyde-laden air more frequently than clean air (Pettersson, 1970). However, benzaldehyde had no behavioural effects when *R. padi* gynoparae were tested in a linear-track olfactometer, where the insects chose between turning into benzaldehyde-treated or clean air at a wire T-junction (Park et al., 2000). In an autumn field study, yellow water traps releasing benzaldehyde caught greater numbers of *R. padi* gynoparae than control traps with no chemical stimulus, but the difference was not statistically significant (Pettersson, 1979).

Another economically-important host-alternating species is the damson-hop aphid, *Phorodon humuli* (Schrank), which utilises several *Prunus* spp. as primary host plants, including sloe (*P. spinosa* L.) and plum (*P. domesticus* L.). In field experiments in Germany, steam-distilled extracts of the leaves of both of these plant species, as well as a chloroform epicuticular wax extract of plum leaves, were added to clear water traps within a hop garden. All three of these treatments attracted significantly more *P. humuli* gynoparae than control traps (Losel et al., 1996a).

Gynoparae of other host-alternating aphid species may also respond to the odour of their primary host plant. When blackberry-cereal aphids, *Sitobion fragariae* (Walker), were tested in a linear-track olfactometer, a greater number of gynoparae turned towards the odour of their blackberry (*Rubus fruticosus* L.) primary host plant when the choice was either clean air or the odour of a secondary host (barley, *Hordeum vulgare* L.) (Lilley and Hardie, 1996). Gynoparae of *A. fabae* may also be capable of responding to primary host (spindle) volatiles, but the evidence for such olfactory attraction is equivocal in this species. Although Isaacs (1994) reported that *A. fabae* gynoparae responded to spindle leaf odour in a Pettersson olfactometer, two other studies with gynoparae of the same laboratory aphid clone found no significant response to host odour in either linear-track (Nottingham et al., 1991) or Pettersson olfactometers (B. Donato, G. Powell and J. Hardie, unpubl.).

Plant odours: males. Volatiles from primary host plants may also attract male aphids (Table 1). Male *P. humuli* were attracted/arrested by the odour of myrobalan (*Prunus cerasifera* L.) leaves or

twigs in a Pettersson olfactometer, and an ether extract of the bark had similar behavioural effects (Campbell et al., 1990). In a field trial, the bark extract was released from yellow water traps placed outside an English hop garden, and lured greater numbers of *P. humuli* males than adjacent control traps (Campbell et al., 1990). However, the extracts of sloe and plum that attracted *P. humuli* gynoparae in the field trials in Germany did not increase catches of males in the water traps (Losel et al., 1996a).

Experiments with *R. padi* give further evidence that male aphids respond to primary-host-plant odour. Olfactometer tests indicate that males of this species are attracted/arrested by bird cherry volatiles, and also pure benzaldehyde (Pettersson, 1970; Park et al., 2000). However, olfactometer studies with *A. fabae* (Thieme and Dixon, 1996), *Cryptomyzus galeopsidis* (Kaltenbach) (Guldemond et al., 1993), and *S. fragariae* (Lilley and Hardie, 1996) found no evidence that males of these three aphid species respond to primary host odour.

Interactions between plant odours and pheromones. Although males of some aphid species respond to host-plant odour, a more important role of plant volatiles may be synergistic interactions with the sex pheromone. A steam-distilled bird cherry extract was not attractive to male *R. padi* when released on its own in a field trial, but enhanced the numbers of males caught in traps also releasing the sex pheromone for this species, (–)-(1R,4aS,7S,7aR)-nepetalactol (Hardie et al., 1994a; Fig. 2). Co-release of benzaldehyde with the pheromone had a similar effect on male catch (Hardie et al., 1994a). Field experiments with *P. humuli* also provide evidence for synergistic interactions between aphid pheromones and host-plant kairomones. Traps baited with sex pheromone plus extracts of primary host plants (*Prunus* spp.) caught more *P. humuli* males than traps releasing the pheromone or plant extract alone (Campbell et al., 1990; Losel et al., 1996a, b).

Catches of gynoparae in sex pheromone-treated water traps may also be enhanced by plant volatiles. Losel et al. (1996a, b) showed that gynoparae of *P. humuli* are attracted to traps by sex pheromone alone, but the additional release of primary host volatiles increased trap catches further. The aggregation of gynoparae on the primary host

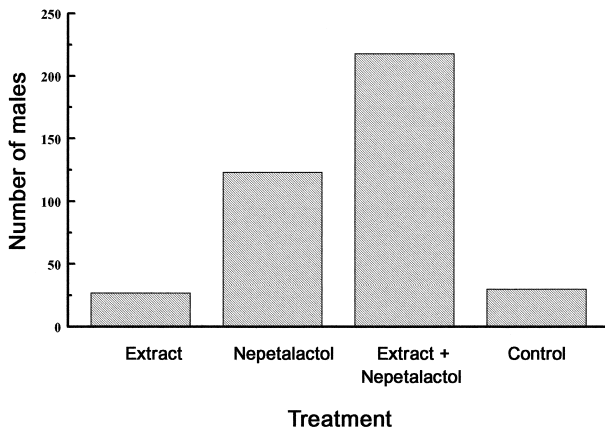


Fig. 2. Number of male *Rhopalosiphum padi* caught in transparent water traps releasing sex pheromone (nepetalactol), host volatiles (bird-cherry extract) or both during a 4-week field trial (data from Hardie et al. (1994a)).

may also be mediated by an additional, non-sexual pheromone. Pettersson (1993) has observed that, in *R. padi*, the gynoparae themselves release an aggregation pheromone. However, the chemical identity of such an aggregation pheromone is unknown.

Sensory aspects. The changes in plant preference by return migrants may be reflected by changes in the responses to plant volatiles by olfactory receptors on the aphids' antennae. Furthermore, since the phenotypes produced during other stages of aphids' life cycles do not respond behaviourally to sex pheromone, the males and gynoparae may also differ in their peripheral detection of sex pheromone components. Such phenotypic differences have been examined by comparing electroantennogram (EAG) responses of virginoparae, gynoparae and males of two aphid species. In a single clone of *A. fabae*, the three phenotypes had similar EAG sensitivities to plant volatiles but males were 1,000–10,000 times more sensitive to sex pheromone components (Hardie et al., 1994b, 1995). However, with a more sensitive whole-insect preparation (Park and Hardie, 1998), polyphenic differences were revealed when virginoparae, gynoparae and males of *R. padi* were stimulated by sex pheromone components and the primary host volatile benzaldehyde (Park et al., 2000).

RESPONSES TO NON-VOLATILE CUES

There have been very few studies of the behav-

iour of gynoparae and males after contact with plants, but the available evidence suggests that return migrants acquire plant-recognition information very quickly following plant contact. As phloem-feeders, aphids need to penetrate host plants for long periods (typically >30 min) before the stylets locate a food source (phloem sieve element) within the vascular tissues. However, when an aphid encounters a new plant, the first few stylet penetrations are usually brief (<1 min) 'probes' of the epidermis. Field observations showed that gynoparae of *A. fabae* and *M. persicae* discriminated their primary hosts from other plant species after making such brief probes (Kennedy et al., 1959a, b). Many aphids then flew from both host and non-host plants, but a slightly reduced rate of departure led to their accumulation on the appropriate winter host plant. Recent analysis of aphid behaviour in the laboratory supports the importance of probing for plant recognition by gynoparae. A close-up video technique (Hardie and Powell, 2000) was used to investigate detailed responses of *A. fabae* gynoparae during the first 5 min of contact with primary and secondary host plants. Gynoparae readily probed a secondary host plant (broad bean, *Vicia faba* L.), but most (63%) individuals took off very soon after withdrawing their stylets. On spindle, probing was very rarely (3%) followed by flight in these laboratory experiments (Fig. 3), indicating that plant-specific cues are detected early during penetration of the primary host and strongly inhibit the flight response (Powell and Hardie, 2000).

Stylet penetration processes can be monitored by making aphid and plant part of a DC circuit (Tjallingii, 1988). Aphids were therefore attached to fine gold wires so that their stylet activities could be electrically recorded during the first 5 min of plant access. Electrical recording of stylet activities on both spindle and bean showed that most (>65%) probes include brief (5–10 s) puncture of the epidermal plasmalemma and occurrence of waveforms associated with ingestion of intracellular contents. When gynoparae puncture spindle cells their behaviour is probably modified by intracellular metabolites detected via gustation of ingested epidermal cell sap. These cues inhibit the flight reflex which otherwise follows probing (Powell and Hardie, 2000).

Longer-term observations of *A. fabae* gynoparae

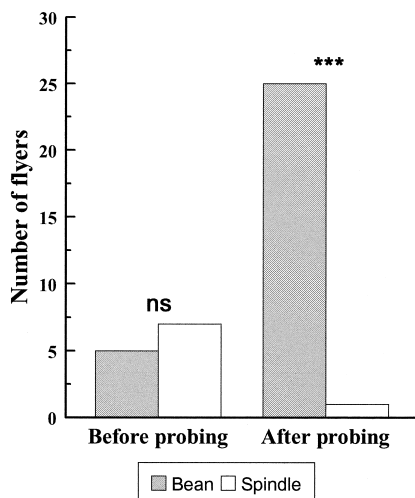


Fig. 3. Number of *Aphis fabae* gynoparae flying before/after probing bean/spindle during a 5-min, video-recorded plant access period ($n=40$; ns, not significant; *** $p<0.001$; χ^2 tests comparing total numbers flying before vs. after probing each plant species; data from Powell and Hardie (2000)).

on spindle leaves show that the first few brief superficial probes are typically followed by longer stylet penetration and the onset of reproduction. Such prolonged plant penetration may include ingestion from vascular tissues, but it has been suggested that the return migrants of some aphid species do not feed as adults. Both gynoparae and males are certainly more short-lived than virginoparae; the gynoparae also have a short reproductive period and therefore low fecundity, which may be unaffected by adult nutrition (Taylor, 1975; Dixon, 1976; Leather, 1982). Radioisotope experiments with *R. padi* indicated that gynoparae of this species did not ingest detectable levels of phloem sap during 17-h access to the primary host (Walters et al., 1984). However, survival studies with several aphid species provide evidence that return migrants feed as adults. For example, gynoparae and males of the willow-carrot aphid, *Cavariella aegopodii* (Scopoli), survive significantly longer when given access to leaves of their primary host (Willow, *Salix alba* L.) than when starved in humid conditions or confined to a non-host (Kundu and Dixon, 1994). Similar results were obtained in our laboratory, where survival of both *A. fabae* and *R. padi* gynoparae was extended by exposure to spindle and bird cherry respectively (J. Hardie and B. Donato, unpubl.). The experiments with *C. aegopodii* also showed that gynoparae of this species derive

reproductive resources from the primary host; those exposed to willow were able to ovulate and mature greater numbers of offspring (Kundu and Dixon, 1994).

In order to investigate whether gynoparae of *A. fabae* feed from their primary host, stylet activities were electrically-recorded during 6-h access to spindle leaves and then analysed for the occurrence and duration of waveforms with known behavioural correlations (Powell and Hardie, 2001). Several gynoparae (55%) showed phloem contact and sap ingestion on spindle. Moreover, 60% of insects ingested from xylem. Overall, the majority of aphids showed sustained ingestion from phloem, xylem, or both, indicating that *A. fabae* gynoparae often imbibe these sources of sap from the primary host. At the end of the 6-h recording period, 95% of the insects had produced one or more offspring on the spindle leaf.

A second group of *A. fabae* gynoparae were recorded on a secondary host plant (broad bean). However, even though the aphids on beans were confined to the plant (by the wire tether) for the full 6-h period, they rarely (10%) ingested from the phloem and never deposited offspring. Feeding and parturition by *A. fabae* gynoparae are probably inhibited unless spindle-specific compounds are detected during the stylet penetration process. Interestingly, several (47%) of the insects that deposited offspring on spindle had not shown phloem-associated electrical waveforms during the 6-h experiment. Furthermore, the numbers of offspring produced ($\text{mean} \pm \text{SE} = 4.2 \pm 0.6$; range=0–9) did not correlate with the occurrence or duration of ingestion from either phloem or xylem. These results suggest that parturition factor(s) are detected within spindle leaves during brief punctures of cells before sap ingestion is initiated. It is possible that the same compounds that inhibit the flight reflex following cell puncture are responsible for stimulating parturition (Powell and Hardie, 2001).

An aqueous extract of whole spindle leaves was prepared (0.5 g fresh weight of plant material per ml) and incorporated into artificial feeding chambers, where aphids were able to ingest it by penetrating a Parafilm membrane. Groups of adult *A. fabae* were confined to the feeding chambers, and the numbers of deposited offspring counted after 72 h. Exposure to the spindle extract had no effect on reproduction by alate virginoparae, compared

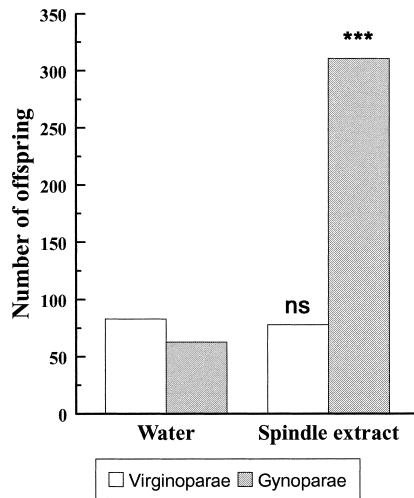


Fig. 4. Total offspring deposited by gynoparae and alate virginoparae of *Aphis fabae* ($n=30$) during 72-h access to an aqueous spindle extract or distilled water in artificial feeding chambers (ns, not significant; *** $p<0.001$; χ^2 tests comparing total numbers of offspring produced on extract vs. water for each aphid form; data from Powell and Hardie (2001)).

with aphids on distilled water controls but, when gynoparae were confined to the extract, larviposition was increased significantly ($p<0.001$) to four times control levels (Fig. 4). Dose-response properties of the extract were investigated in dilution experiments; activity was retained at a 1 in 4,000 dilution of the original extract (<10 ppm total extract present as determined by weight of the dried solid residue), but lost when diluted to 1 in 10,000. The leaves of spindle therefore contain a potent larviposition stimulant for *A. fabae* gynoparae which is a stable, water-soluble factor (Powell and Hardie, 2001).

These recent studies show that adult gynoparae are capable of feeding from primary host plants, but host-specific factors promoting settling and reproduction are encountered at an earlier stage, probably during stylet penetration of peripheral, non-vascular tissues. These conclusions are based on a series of experiments with a single aphid species; studies with other species are needed to test whether similar processes occur during host selection by gynoparae of other host-alternating aphids. It is possible that male aphids also probe the primary host plant as part of the plant recognition process, but there have been no detailed behavioural studies on the responses of males to plants. Hardie and Glascoine (1990) gave male *A.*

fabae access to spindle leaves in 48-h choice tests with broad beans. Whereas female forms of the aphid settled as expected, according to their seasonal plant preference, males were restless and reluctant to settle. However, in laboratory choice tests, male *M. persicae* preferred to settle on twigs of their primary host (peach), than on non-host twigs (Tamaki et al., 1970). An aqueous extract of peach, painted onto twigs of a non-host and allowed to dry, also enhanced settling, suggesting that non-volatile contact cues are involved in primary-host-plant recognition by males of *M. persicae*.

CONCLUSIONS

In host-alternating Aphidinae, the return migration commences when gynoparae fly from their natal (secondary) host plant and colonise the primary host. Studies with several aphid species indicate that gynoparae use host-specific olfactory cues to improve their chances of locating an appropriate plant. After plant contact, the settling response may be affected by a variety of non-volatile plant chemical cues. Recent behavioural studies suggest that gynoparae recognise the primary host very quickly, and that superficial probing is a very important host selection event. After settling on a senescing leaf of the host plant, gynoparae start to deposit their oviparous progeny. The signals that evoke the onset of reproduction may be potent, taxon-specific allelochemicals detected within the cells of non-vascular plant tissues.

The return migration is completed when males arrive at the primary host and inseminate the oviparae. Although sex pheromone has a powerful influence on male behaviour, host-plant cues undoubtedly play an important role in modifying these responses. Indeed, since many aphid species share the same two sex pheromone components (Hardie et al., 1999), responses to plant-specific cues may play a vital role in reproductive isolation. Host specificity of both gynoparae and males may therefore be as much a means of avoiding unsuitable mates as unsuitable plants (Ward, 1991). For males, the evidence for plant cues interacting with sex pheromone is currently limited to host-plant volatiles, which enhance responses to the pheromone during flight. However, males may also assess host-plant chemistry after landing, and such

“host”-selection behaviour may actually be an important component of mate selection. There have been very few studies of the precopulatory behaviour of male host-alternating aphids on the primary host (e.g. Steffan, 1990), and these have focussed on direct interactions with sexual females, rather than responses to plant stimuli. If, in common with gynoparae, males probe the plant surface and are able to detect the same host-specific cues, then these may provide a reliable means of detecting conspecific oviparae. Detailed studies of the behaviour of males at the plant surface are required to give a more complete picture of the role of host-plant stimuli in aphid speciation and reproductive isolation.

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