

Host selection by the generalist aphid *Myzus persicae* (Hemiptera: Aphididae) and its subspecies specialized on tobacco, after being reared on the same host

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Abstract

Decision-making during host selection by phytophagous insects has proved to be related to host range, with specialists taking faster decisions than generalists; however, this pattern fails to materialize in some host selection studies performed with aphids. Differences found in testing designs point to rearing effects on aphid host selection. To test whether specialization patterns derive from the nature of the aphid or as a consequence of rearing environment, host selection behaviours were compared between the generalist *Myzus persicae* (Sulzer) s.s. and its subspecies specialized on tobacco when reared on a common host and offered the choice of an alternative host and a non-host plant. Pre-alighting (host finding and attraction towards host volatiles) and post-alighting (leaf surface exploration and probing) behaviours did not differ between the generalist and the tobacco-specialist, except in the allocation of time to probing behaviour; furthermore, all specialists chose the host on which they performed best. Thus, although the specialist was not faster than the generalist, it showed a higher level of commitment to its preferred host plant.

Introduction

Herbivorous insects are frequently very selective feeders that choose their host plants based on visual, mechanical, and chemical stimuli (Prokopy, 1986; Bernays & Chapman, 1994; Price, 1997; Bernays, 1998). In aphids, the acceptance or rejection of a plant as a source of food involves the completion of behavioural patterns in which the plant's volatile chemicals, surface waxes, intercellular polysaccharides, mesophyll and phloem constituents are tested sequentially (Niemeyer, 1990; Caillaud & Via, 2000). Furthermore, host plant preference and discrimination has proved to be different between generalist and specialist aphids. The first example was provided by Bernays & Funk (1999) and Funk & Bernays (2001) in two races of *Uroleucon ambrosiae* (Thomas) (Hemiptera: Aphididae) which differed

in their host range, one being specialized on giant ragweed *Ambrosia trifida* L. (specialist race) and the other using several genera of Asteraceae (generalist race). These studies revealed behavioural differences in the detection of plant stimuli between races. The specialist race found its host plant faster, reached the phloem sooner, and spent more time feeding than the generalist one. Furthermore, a recent study that compared host selection behaviours between the generalist aphid *Myzus persicae* (Sulzer) (Hemiptera: Aphididae) and its subspecies specialized on tobacco, also found that the specialist subspecies performed more direct searching and acceptance behaviours than the generalist species (Vargas *et al.*, 2004). However, this pattern failed to show up in a study by Tosh *et al.* (2003), which compared host selection behaviours between specialist (gynoparae) and generalist (virginoparae) morphs of *Aphis fabae* Scopoli (Hemiptera: Aphididae).

The studies cited above involved subtle differences in the experimental design. Bernays & Funk (1999), Funk & Bernays (2001) and Vargas *et al.* (2004) tested aphid host preference on a range of plant species including that on

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which the aphid was reared, while Tosh *et al.* (2003) tested host preference on a range of plant species which excluded that on which the aphids were reared. Thus, it is possible that the patterns of plant preference observed (and presumably others found in nature), could have been the result of rearing experience. It is important then, to distinguish between patterns of specialization arising from adaptations that result from phylogenetic radiation (a species property) and specialization caused by ecological factors (a local population property) (Fox & Morrow, 1981).

The green peach aphid *M. persicae* uses more than 400 plant species from more than 40 families for parthenogenetic reproduction, and uses peach *Prunus persica* L. (Rosaceae), its primary host, for sexual reproduction (Van Emden *et al.*, 1969; Weber, 1986; Bernays & Chapman, 1994). The form of *M. persicae* specialized on tobacco (also known as the tobacco aphid) has been known for over 60 years (Brain, 1940), and exhibits clearly distinctive life history traits (only found on tobacco plants under natural conditions) and a sufficiently isolated tobacco-adapted genome to justify its status as a subspecies, *M. persicae nicotianae* (Blackman & Eastop, 2004). These characteristics of generalist and tobacco-specialist *M. persicae* provide a suitable scenario for testing whether specialization patterns derive from subspecies or local population properties. Following Blackman & Eastop (2004), we refer to the generalist and the specialist aphids as *M. persicae sensu stricto* and *M. persicae nicotianae*, respectively.

In this study, *M. persicae s.s.* and *M. persicae nicotianae* were reared on the same host and were offered the choice of two test hosts: an alternative host which is within their documented host range, and a non-host species. If host selection were a subspecies property, the expectation would be that *M. persicae s.s.* and *M. persicae nicotianae* should differ in their host selection behaviours, the generalist showing behaviours with no evident pattern, and the specialist being faster in finding the alternative host than the non-host despite being reared on another plant. On the other hand, if host selection were a local phenomenon influenced by rearing experience, the expectation would be for reduced behavioural differences between the generalist and the specialist when selecting the alternative host relative to the non-host. It should be noted that rearing experience encompasses both the influence of maternal effects and that of learning of host features (e.g. leaf surface characteristics, habituation to host volatiles), from the time of birth to maturity (Dixon, 1998).

Materials and methods

Both aphids were reared on the same plant species, and were offered the choice between an alternative acceptable host and a non-host. The generalist is known to accept sugarbeet, *Beta vulgaris* L. (Chenopodiaceae) (Williams *et al.*, 2000) and sweet pepper, *Capsicum annuum* L. (Solanaceae) (Margaritopoulos *et al.*, 2000; LaRock *et al.*, 2003; Nikolakakis *et al.*, 2003) but not tobacco, *Nicotiana tabacum* L. (Solanaceae) (Boiteau & Lowery, 1989; Blackman & Eastop, 2004), and the tobacco specialist, although showing best performance on tobacco, can also be reared on sweet pepper (Semtner *et al.*, 1998), but not on sugarbeet (personal observation). Therefore, in the experimental treatments, the rearing plant for both aphids was sweet pepper, and to compare host selection behaviours, generalist and specialist aphids were exposed to sugarbeet and tobacco in all behavioural tests.

Aphids and plants

Aphids were collected from parthenogenetic populations in the neighbourhood of Talca, Chile (35.5°S, 71.7°W). The generalist, which has a greenish colour, was collected from sugarbeet and the tobacco specialist, which has a pale red colour, was collected from tobacco (cv. BY 64). Monoclonal parthenogenetic colonies were reared for more than ten generations in the laboratory on sweet pepper at $21 \pm 2^\circ\text{C}$ and long day photoperiod (L:D 14:10).

The first two steps of the host selection process described for aphids are pre-alighting behaviour and leaf surface exploration (Niemeier, 1990; Caillaud & Via, 2000). Pre-alighting behaviour, aphid responses to plant volatiles, and leaf surface exploration behaviours were tested with wind tunnel, olfactometry bioassays and video-recording, respectively. All behavioural tests were performed with three-day-old alate virginoparae, between 0900 and 1500 h, in a room at $21 \pm 2^\circ\text{C}$.

Wind tunnel tests

A horizontal wind tunnel (215 × 82 × 82 cm) made of laminated wood (walls and floor) and Plexiglass (roof) was used. Air entered with a linear speed of 0.5 m s^{-1} and passed through air filters which cleaned it from impurities and exogenous volatiles, and ensured laminar flow across the test environment. The inner walls, floor and roof were covered with black non-reflective cardboard in order to ensure that plants were the only visual stimuli during tests. Light passed through a small uncovered area of the Plexiglass roof and shone only on the plants, with an intensity of 160 lux (measured at the leaf surface). Uninfected potted plants of tobacco and sugarbeet with similar leaf surface areas were placed near the point of air inlet, right under the light beam and equidistant from the aphid platform at the downwind end. The base of each plant pot was covered by double-sided adhesive tape in order to ensure that all aphids found on the plants had reached them through flight.

For each replicate, one alate virginopara was used and host selection after 1 h of testing was recorded. Fifty replicates were carried out for each aphid taxon. Data belonged to three categories: aphids of each taxon which did not select any host, those which selected the alternative host, and those which selected the non-host. Comparisons of the number of individuals among categories, and between the generalist and specialist aphids, were performed with a Chi-Square analysis of contingency tables (Zar, 1996). Proportions of individuals of each aphid taxon that landed on the acceptable host, were compared with the Z-test for proportions with the Yates correction for continuity (Zar, 1996).

Olfactometry

A four-arm Plexiglass olfactometer designed by Pettersson (1970) was used. Each pair of opposing arms was connected by Teflon tubing to a glass bell-jar (40 × 20 cm, height × diameter) containing a stimulus host. Air (80 ml min^{-1} through each bell-jar) was sucked out with a vacuum compressor connected to the centre hole of the olfactometer. To eliminate external odours, charcoal filters were placed at the air inlet of the bell-jars. The olfactometer was surrounded by a white paper cylinder (h = 10 cm) in order to eliminate visual stimuli from the surroundings.

Volatile stimuli consisted of uninfected potted plants of tobacco, sugarbeet and control pots (i.e. pots with soil but without plants). Three different treatments (combination of stimuli) were performed for the generalist and the specialist. Both the generalist and the specialist groups were independently exposed to volatiles of sugarbeet vs. tobacco, sugarbeet vs. control, and tobacco vs. control (with ten replicates for each comparison). A clean olfactometer was used for every replicate. One alate virginopara was used in each replicate and tested only once (Ramírez *et al.*, 2000). Time spent in each stimulus arm was recorded, and the data were analysed using the non-parametric Mann Whitney *U* test (Siegel & Castellan, 1988).

Video recordings

Leaf surface assessment behaviour of alate virginoparae was recorded with a close-up video system (Sony SSC-DC34 video camera connected to a Sony SVT-124 video recorder and a Sony SSM-14N1U colour video monitor for image output) coupled to a stereomicroscope for accurate monitoring of aphid movement (Hardie *et al.*, 1992; Powell & Hardie, 2000; Vargas *et al.*, 2004); recorded videotapes were later analysed using The Observer program (Noldus, 1995).

Recordings were performed on the surface of a freshly excised leaf which had a moistened cotton wool pad around its petiole, and was attached with a system of clamps that allowed easy orientation of the aphid rostrum with respect to the camera. Experiments began after placing a winged aphid on the centre of the adaxial surface of the leaf with the help of a fine hair paintbrush. In cases when the aphid walked off the leaf, it was returned immediately to continue recording. Following Vargas *et al.* (2004), recordings ended: (i) when an aphid took off; (ii) when it performed a probe for more than five minutes (a long-duration probe); (iii) when video recording was performed for more than 60 min; or (iv) when an aphid remained immobile for more than 30 min without performing a probe (in this case the individual was discarded and replaced by a new one).

The behavioural variables analysed were: time to first probe, first probe duration, time to long-duration probe, time spent probing before a long-duration probe, number of probes before a long-duration probe, proportion of time spent probing foliar tissues, proportion of individuals that achieved a long-duration probe, proportion of individuals which did not perform a long-duration probe and remained on the plant, and proportion of individuals which did not perform a long-duration probe and took off (see Vargas *et al.*, 2004). Twenty-five replicates of each subspecies/host combination were performed. For statistical analysis, a non-parametric two-way ANOVA (the Scheirer-Ray-Hare extension of the Kruskal-Wallis test, Sokal & Rohlf, 1998) was used to compare across aphid taxon/host combinations with the Dunnnett's test for *post hoc* comparisons for significant differences among treatments. Proportions were compared with the Z-test for proportions (Zar, 1996).

Results

Pre-alighting behaviour

A significantly higher number of individuals did not select any host during wind tunnel tests (fig. 1) ($X^2 = 27.04$; $P < 0.001$), and there were no statistical differences between

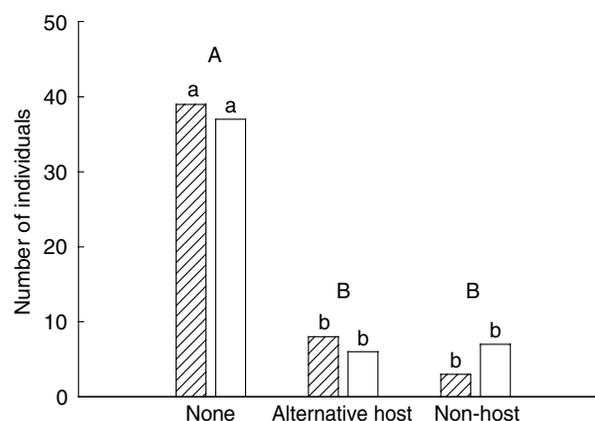


Fig. 1. Selection of landing surface by generalist, *Myzus persicae* s.s. (□) and the tobacco-specialist subspecies, *M. persicae nicotianae* (▨). Different letters show significant differences among groups as determined by a Chi-square analysis of contingency tables ($P < 0.05$).

M. persicae s.s. and *M. persicae nicotianae* in the frequency of individuals that did not select any host, selected the alternative host, or selected the non-host ($X^2 = 1.93$; $P > 0.50$).

Olfactometry tests revealed that neither *M. persicae* s.s. nor *M. persicae nicotianae* discriminated between volatiles from the alternative host and the non-host (fig. 2) (*M. persicae* s.s.: $U = 174$; $P = 0.96$; *M. persicae nicotianae*: $U = 172$; $P = 0.214$). Furthermore, no attraction to either tobacco or sugarbeet relative to control pots were found for *M. persicae* s.s. (sugarbeet vs. control: $U = 50$; $P = 0.10$; tobacco vs. control: $U = 39$; $P = 0.94$), or for *M. persicae nicotianae* (tobacco vs. control: $U = 39$; $P = 0.94$; sugarbeet vs. control: $U = 45$; $P = 0.38$).

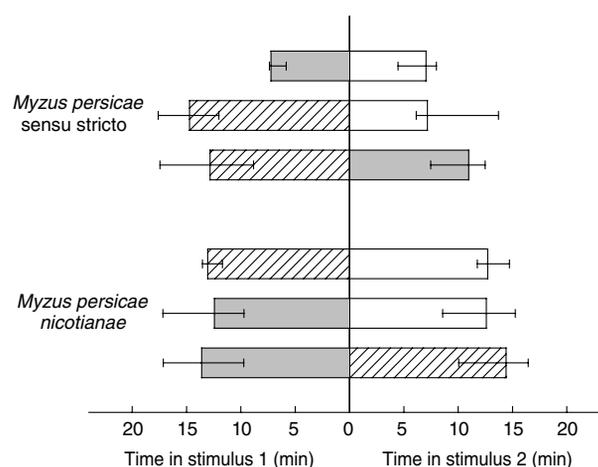


Fig. 2. Time (median and inter-quartile 25–75% range) spent by the generalist, *Myzus persicae* s.s. and its subspecies specialized on tobacco, *M. persicae nicotianae*, in the olfactometer zones permeated by stimuli 1 and 2. Stimuli were: sugarbeet (▨), tobacco (▧) and control pots (□). None of the treatments gave rise to significant differences between stimuli.

Video recordings on the leaf surface

Time to first probe and mean duration of a probe were significantly greater on tobacco than on sugarbeet (two-way non-parametric ANOVA, $H = 6.928$, $P < 0.01$ and $H = 7.989$, $P < 0.01$, respectively) (table 1), but there were no differences between *M. persicae* s.s. and *M. persicae nicotianae*. On the other hand, the proportion of total time spent probing was significantly greater for *M. persicae nicotianae* than for *M. persicae* s.s. (two-way non-parametric ANOVA, $H = 4.189$, $P < 0.05$), whereas a significant plant \times aphid interaction was found in time taken to perform a long-duration probe (two-way non-parametric ANOVA, $H = 4.873$, $P < 0.05$) whereby *M. persicae* s.s. was slower when performing a long-duration probe on tobacco. No differences between plants nor subspecies were found for the number of probes before a long-duration probe, whereas a significant aphid \times plant interaction for the total time spent probing before a long-duration probe (two-way non-parametric ANOVA, $H = 4.707$, $P < 0.05$) was found whereby *M. persicae* s.s. spent less time probing when on sugarbeet. The proportion of individuals that achieved a long-duration probe was significantly different among treatments, reaching its maximum in *M. persicae nicotianae* with 100% of aphids performing a long-duration probe on tobacco; overall, *M. persicae nicotianae* showed a significantly greater proportion of individuals that achieved a long-duration probe on both plants compared with *M. persicae* s.s. Only individuals of *M. persicae* s.s. failed to achieve a long-duration probe and remained on the plant, with a significant greater proportion on tobacco than on sugarbeet ($Z = 2.318$, $P < 0.05$). Taking-off only occurred on sugarbeet, and no differences were found between the aphid taxa ($Z = 1.719$, NS).

Discussion

Few individuals alighted on a host, despite the removal of all visual stimuli except the target plants inside the wind tunnel. Moreover, *M. persicae* s.s. and *M. persicae nicotianae* did not differ in their capacity to find their alternative host through flight behaviour. These latter results are similar to those found by Bernays & Funk (1999) and also by Vargas

et al. (2004) for the generalist aphid they studied, but different from those found for the specialist aphid.

Olfactometry bioassays revealed the inability of the aphids studied to discriminate between the alternative host and the non-host. Furthermore, when offered the choice between alternative host and control, there was no attraction towards the alternative host in either *M. persicae* s.s. or in *M. persicae nicotianae*. Interestingly, *M. persicae nicotianae* reared on tobacco clearly preferred tobacco volatiles when offered the choice between tobacco and control (Vargas *et al.*, 2004), suggesting that, at least during the volatile recognition stage, the aphid relied on rearing experience for its recognition abilities.

Host selection response to both visual and phytochemical stimuli can be modified by experience (see review in Papaj & Prokopy, 1989). Furthermore, environmental influences on alate host preference have been found for the aphid *Sitobion avenae* Fabricius (Hemiptera: Aphididae) (Lushai *et al.*, 1997). The absence of faster pre-alighting behaviour on tobacco than on sugarbeet by *M. persicae nicotianae* when not reared on tobacco, shows that integration of visual and olfactory stimuli for host finding depends on the aphid's prior experience.

Time to first probe and mean duration of the first probe can be considered as the first attempt of an aphid to evaluate internal subepidermic tissues. In the present study, both variables were affected by the nature of the plant but not by the nature of the aphid (table 1). Thus, regardless of the documented acceptance of tobacco and sugarbeet by *M. persicae nicotianae* and *M. persicae* s.s., respectively (Semtner *et al.*, 1998; Williams *et al.*, 2000), both aphids behaved in the same way when first evaluating tobacco and sugarbeet as potential hosts. Indeed, both aphids spent more time probing on tobacco than on sugarbeet, a fact most likely related to mobility difficulties on tobacco leaves due to the presence of trichomes and their sticky secretions. On the contrary, Vargas *et al.* (2004) found that both *M. persicae* s.s. and *M. persicae nicotianae* spent more time probing on their respective rearing host.

The allocation of time to probing behaviour when selecting a host varied between *M. persicae* s.s. and *M. persicae nicotianae* (table 1). Particularly, *M. persicae nicotianae*

Table 1. Summary of video recording results of host selection behaviour of *Myzus persicae* s.s. and *M. persicae nicotianae* on tobacco and sugarbeet.

Variables	Tobacco		Sugarbeet	
	<i>M. persicae</i> s.s.	<i>M. p. nicotianae</i>	<i>M. persicae</i> s.s.	<i>M. p. nicotianae</i>
Time to first probe (s)*	43.7 (19.7–133.2)a	40.6 (16.0–135.7)a	26.8 (13.7–38.0)b	20.3 (6.8–77.8)b
First probe duration (s)*	51.4 (26.4–69.3)a	27.0 (17.3–69.2)a	19.7 (13.7–25.7)b	24.2 (7.6–62.9)b
Proportion of total time spent probing foliar tissues*	0.2 (0.1–0.3)b	0.2 (0.1–0.4)a	0.2 (0.1–0.3)b	0.4 (0.2–0.5)a
Time to long duration probe (s)*	423 (321–825)b	340 (140–538)ab	186 (102–348)a	280 (118–778)a
Number of probes before a long duration probe*	1 (1–2)a	2 (0.8–2)a	1 (1–2.25)a	2.5 (1–5)a
Time spent probing before a long duration probe (s)*	100 (53.1–176.0)a	91.4 (47.3–201.9)a	32.7(20.0–45.2)b	92.3 (71.0–245.5)a
Proportion of individuals that achieved a long duration probe	0.60bc	1.00a	0.36c	0.72b
Proportion of individuals which did not perform a long duration probe but remained on the plant	0.40a	0	0.08b	0
Proportion of individuals which did not perform a long duration probe and flew from the plant	0	0	0.56a	0.28a

* Median (inter-quartile range 25–75%).

Note: Different letters in variables analysed by two-way non-parametric ANOVA show significant differences among treatments ($P < 0.05$) as determined by Dunnett's tests.

allocated a significantly higher proportion of time to probing behaviour than the *M. persicae* s.s. These differences are supported by ecological theories related to optimal diet models (MacArthur & Pianka, 1966; see review in Stephens & Krebs, 1986), whereby a specialist spends more time handling its prey (in the present case, probing and looking for nutritional tissues), whereas a generalist spends more time searching for its prey (in the present case, searching for alternative places to perform a probe). Interestingly, this tendency was not evident in the report by Vargas *et al.* (2004), where both aphid taxa spent more time probing on their respective host plant.

Variables related to a higher commitment of the aphid to the plant, such as number of probes before a long-duration probe, time to long-duration probe, and total time spent probing before a long-duration probe, led to variable results across the study, despite the differential time allocation to probing between the generalist and the specialist aphids. Thus, no evidence was found in variables related to commitment to the host between *M. persicae nicotianae* and *M. persicae* s.s. (table 1). However, despite the lack of evidence of a faster selection of their respective optimal hosts by both generalist and specialist aphids, all specialist individuals (100%) performed a long-duration probe on tobacco. These results indicate that, although the specialist was not faster than the generalist in all host selection behaviours (as found by Tosh *et al.*, 2003), the specialist made an optimal choice in terms of long-duration probes on tobacco, which contribute to its long term fitness.

Probing behaviour is known to be affected by previous experience, even for short periods of time, for *A. fabae* (Prado & Tjallingii, 1999), and for *Sitobion fragariae* (Walker) (Hemiptera: Aphididae) (Ramírez *et al.*, 1999; Ramírez & Niemeyer, 2000). Moreover, the present results suggest that post-alighting recognition relies mainly on abilities acquired during rearing. The effect of experience on host preference has also been described in other insect orders (see Szentesi & Jermy, 1990), and has been attributed to changes in chemoreceptors which affect further host selection (Renwick, 2001; Mustaparta, 2002; Chapman *et al.*, 2003). It is apparent from the above, that rearing experience enhances aphid recognition abilities when evaluating host features and deciding their suitability or unsuitability for further settlement.

This study, when compared with that of Vargas *et al.* (2004), has revealed that rearing experience affects pre-alighting behaviours and leaf surface evaluation by both *M. persicae* s.s. and *M. persicae nicotianae*, but not the final commitment to the plant (performance of a long duration-probe). Furthermore, the recognition abilities of the tobacco-specialized aphid appear as plastic traits, and host preference towards tobacco is not present in the tobacco specialist after its recent host shift (Landolt & Molina, 1996); rather it appears to retain the phenotypic plasticity of the generalist aphid from which it appears to have recently evolved. The ability to change preference is a form of phenotypic plasticity (Agrawal, 2002), and in specialists it is likely to be a residue from previous history (Pigliucci, 2001); moreover, a change of preference may also be beneficial for generalist herbivores by allowing them to become temporal specialists (Agrawal, 2002). Since the specialist on tobacco, *M. persicae nicotianae*, has evolved from the extremely polyphagous *M. persicae* s.s., the effect of development experience on host preference may be a residual consequence of its evolutionary history.

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