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Did *Myzus persicae* (Sulzer) from potato reared on a novel host for 15 years retain its host-related properties?

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Research Paper

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Abstract

Myzus persicae (Sulzer) is an important agricultural pest worldwide causing major economic losses due to its ability to transmit over 100 viruses including *Potato virus Y* (PVY). *Myzus persicae* shows considerable variation with respect to performance on its host plants. The objective of this study was to use a survival experiment, behavioural observations, including observations of probing and feeding behaviour obtained using the electrical penetration graph (EPG) technique, and a PVY acquisition experiment to determine whether or not potato was still the more suitable host for *M. persicae* originating on potato and reared on a novel host, table beet, for over 15 years. In a survival experiment, the pre-reproductive period was significantly longer while adult survival and whole longevity were significantly lower for *M. persicae* reared on beet fed beet leaves compared to *M. persicae* reared on potato fed potato leaves. The number of progenies produced and fecundity were both significantly reduced (90 and 85%, respectively) for *M. persicae* reared on beet fed beet leaves. Ethological observations and EPG assessment of *M. persicae* behaviour reared on beet placed on beet leaves showed significantly impaired behavioural responses compared to *M. persicae* reared on potato placed on potato leaves. The rate of PVY acquisition was the same for *M. persicae* reared on beet and on potato. These results indicate that after 15 years on table beet, *M. persicae* still performs better on its original host, potato, and appears to be a specialized potato-adapted genotype.

Introduction

The green peach aphid, *Myzus persicae* (Sulzer, 1776), is an important agricultural pest throughout the world causing major economic losses due to its ability to transmit over 100 viruses (Kennedy *et al.*, 1962; Mathers *et al.*, 2017). In North America, there are important economic losses in the potato crop production system due to this aphid's ability to transmit *Potato virus Y* (PVY). *Myzus persicae* is polyphagous, feeding on over 400 plant species in 50 families (Weber, 1985; Blackman and Eastop, 2000). This aphid's ability to colonize so many distantly related plant species makes it a highly destructive pest of several important crops (Mathers *et al.*, 2017). The primary hosts, where sexual reproduction occurs, are *Prunus* spp. trees (van Emden *et al.*, 1969; MacGillivray, 1979). The secondary hosts, where asexual reproduction occurs, include vegetable crops in the families Amaranthaceae, Brassicaceae, Asteraceae and Solanaceae, and field crops including table beet, sugar beet and tobacco (Heathcote, 1962; van Emden *et al.*, 1969; Weber, 1985; Blackman, 1987; Bell and Waters, 2021).

Myzus persicae shows considerable variation with respect to its performance on various host plants (Patch, 1938; Heathcote, 1962; Margaritopoulos *et al.*, 2003). Heathcote (1962) studied how suitable a number of hosts, including seven *Brassica* species, spinach, sugar beet and lettuce, were for the development of *M. persicae* and found that the aphid developed well on the *Brassica* species but much less well on sugar beet, spinach and lettuce. Wingless *M. persicae* differed greatly in their ability to colonize sugar beet plants depending on the host plant the aphid and previous generations of the aphid were reared on (Russell, 1966; Lowe, 1973). The findings of a study of over 1000 field sampled clones of *M. persicae* collected from various hosts, including potato, suggested a genetic fixation of the trait 'host plant adaption' (Weber, 1985). The results of the study also indicated that 10 generations of habituation or a year-round rearing on an alternative host did not alter the host plant adaptation trait. Nikolakakis *et al.* (2003) studied the performance of 18 clones of *M. persicae* on pepper and tobacco plants. All clones did well on both hosts, however, *M. persicae* originating from two tobacco growing regions in Greece performed significantly better on tobacco plants compared to pepper plants and aphids from a region of Greece where peppers were a common crop and tobacco was not grown performed better on pepper plants indicating a significant 'region/host plant origin effect' on aphid performance. Numerous studies have shown that a specific host-adapted form of *M. persicae* appears to

occur on tobacco and is distinct from populations occurring on other host plants (Blackman, 1987; Blackman and Spence, 1992; Margaritopoulos *et al.*, 2000, 2007*a*, 2007*b*; Blackman *et al.*, 2001). More recently, a study by Li *et al.* (2015) investigated the temperature-mediated effects of host alternation on the adaptation of *M. persicae* to oil seed rape and tobacco and found aphids habituated to rape performed well on tobacco under various temperatures while aphids originating from tobacco appeared more specialized to tobacco, particularly under less than optimal temperatures.

Several of the earlier laboratory and greenhouse studies on host adaptation for *M. persicae* reared on one host and transferred to another host have been carried out with aphid clones that were reared on the new host for relatively short periods of time; i.e. for a month (Heathcote, 1962), 10 generations, six months (Weber, 1985; Li *et al.*, 2015), eight months (Lowe, 1973). Blackman (1987) did rear *M. persicae* from tobacco on a non-tobacco host for a considerably longer period of time (seven years) and found that they were distinct from one another. In our study, *M. persicae* was reared on the new host, table beet (*Beta vulgaris* subsp. *vulgaris* 'Conditiva group'), for over 15 years (~500 generations).

PVY can be transmitted to potato by several aphid species, including non-colonizing aphids of potato (Kennedy *et al.*, 1962; van Hoof, 1980; Sigvald, 1984; Harrington and Gibson, 1989; de Bokx and Piron, 1990; Heimbach *et al.*, 1998). Colonizing aphids of potato are referred to as aphids that feed and reproduce on potato while those that do not feed and reproduce on potato are referred to as non-colonizing aphids of potato. Non-colonizing aphids land on a potato plant, perform test probes with their stylets and then leave the plant in search of their host plant (Boquel *et al.*, 2012, 2014). Boiteau *et al.* (1998) reported high virus infection rates in potato plots even when very low densities of potato-colonizing aphids were reported and DiFonzo *et al.* (1997) have suggested that massively trapped non-colonizing aphids may be responsible for the spread of PVY in the absence of potato-colonizing species. A study by Pelletier *et al.* (2008) showed that probing behaviour of aphids is a very important factor in the transmission of PVY. Species of aphids that do not colonize potato take more time to acquire PVY compared to *M. persicae* due to the increased time to the first puncture of a plant cell by the aphid's stylets (Boquel *et al.*, 2011). In our study, it was hypothesized that longer acquisition times for PVY by *M. persicae* reared on table beet compared to *M. persicae* reared on potato would indicate that *M. persicae* reared on table beet had adapted to table beet and become a non-colonizing aphid of potato whereas similar acquisition times would indicate that the *M. persicae* reared on table beet was still a potato-colonizing aphid.

The objective of this study was to use a survival experiment, behavioural observations, including observations of probing and feeding behaviour obtained using the electrical penetration graph (EPG) technique, and a PVY acquisition experiment to determine whether or not potato was still the more suitable host for *M. persicae* originating on potato and reared on a novel host, table beet, for over 15 years.

Materials and methods

Plants

All plants were grown from tuber seed pieces or beet seeds under greenhouse conditions (daytime: 22 ± 2°C, nighttime: 20 ± 2°C, L16:D8 photoperiod, supplemental lighting: 400-W high pressure sodium lights) in high porosity growing medium (Pro-Mix HP with Mycorrhizae, Premier Horticulture Ltd). Small beet leaves were collected from greenhouse-grown potted table beet plants 6–8 weeks after the seed was planted (cv. new crop) and seedling beet leaves were collected from trays of greenhouse-grown table beet seedlings just before transplantation, approximately four weeks after the seed was planted (cv. new crop). Since apterous adults preferred the young leaves at the centre of the plant (personal observation), two different types of leaves were used: small beet leaves located at the growing point of the plant and small seedling leaves. Seedling beet leaves were designated as the first pair of leaves that emerged after the cotyledons. Small beet leaves and seedling beet leaves were collected when they were 2.5 cm long and 1.25–2 cm wide. Healthy terminal potato leaflets were collected from greenhouse-grown potato plants (cv. Kennebec) when they were approximately 4.5 cm long and 2.5 cm wide, about twice the size of a beet leaf. The Kennebec variety was used in the survival, behaviour and EPG experiments because it was an elite grade potato seed low in diseases, including PVY. PVY^{NTN}-infected terminal potato leaflets were collected from greenhouse-grown potato plants (cv. Shepody). This variety was used in the PVY experiment because it is very sensitive to PVY (Young *et al.*, 1983; Singh and Somerville, 1987; Draper *et al.*, 2002). All terminal leaflets were collected 4–5 weeks after the seed pieces were planted.

Insects

Aphids used in this study were from two aphid colonies maintained at the Fredericton Research and Development Centre (FRDC). Virginoparous (asexually reproducing) *M. persicae* were collected from potato plants in a number of field plots surrounding the FRDC during the summer of 1999 and placed on potato plants under controlled conditions at the FRDC. Aphids were transferred from potato to a beet plant in late autumn 1999. Two weeks later, one aphid from this beet plant was transferred to a second beet plant to start a *M. persicae* colony on beet. Virginoparous *M. persicae* were collected as described above during the summer of 2000 and placed on potato plants under controlled conditions at the FRDC. Each aphid colony was reared on potted healthy host plants enclosed in wooden frame rearing cages (100 × 50 × 50 cm, all sides and ceiling screened) under controlled conditions (daytime: 24 ± 2°C, nighttime: 22 ± 2°C, L16:D8 photoperiod, supplemental lighting: 400-W high pressure sodium lights). *Myzus persicae* on potato was reared on potato plants (cv. Kennebec). Every 3–4 weeks, two new cages containing two to four potato plants (15–20 cm tall, 3–4 weeks after seed planting) were started. One or two small leaflets (approximately 3.5 × 2 cm) covered with nymphs were placed on plants in the new cage. *Myzus persicae* on beet was reared on table beet plants (cv. new crop). One or two cages containing six to eight beet plants were constantly maintained. Beet plants were replaced with new plants (12–18 cm tall, 6–7 weeks after sowing the seeds) as they senesced. Before removing the old plant from the cage, small beet leaves covered in nymphs were cut and placed onto small leaves at the centre of the new beet plants. Alate (winged) aphid production in the wooden cages was induced by crowding (Müller *et al.*, 2001) and approximately 1-day old alate aphids in their dispersal phase, flying or walking on the inner walls and ceiling of the rearing cage, were collected from the cages and used directly for the EPG and PVY acquisition experiments or placed in Petri dishes

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(Fisherbrand, 100 mm) with leaves to produce 1-day old nymphs that were used in the survival experiment. Apterous adult aphids in their reproductive stage were collected from their respective colonies and used for the behaviour experiment.

Aphid survival

To produce nymphs synchronized in age, alate aphids, in their dispersal phase, from the *M. persicae* on beet (MPB) and *M. persicae* on potato (MPP) colonies were placed respectively on beet leaves and potato leaflets in Petri dishes (Fisherbrand, 100 mm) containing 1.5% agar (Select, Sigma-Aldrich), the upper surface of leaves and leaflets against the agar. The tops of the dishes were lined with filter paper to absorb moisture and dishes were placed in a controlled environment cabinet (Conviron) overnight (20 ± 1°C, L16:D8 photoperiod) in an upside down position. The next day, 1-day old MPB and MPP nymphs produced by alate aphids were transferred singly onto potato leaflets, one leaflet per dish, in new tissue culture dishes (Sarstedt, 100 mm) containing 1.5% agar. One-day old MPB nymphs produced by alate aphids were also transferred to new dishes containing two beet leaves, a beet seedling leaf and a small beet leaf, touching along one edge. Nymphs were placed directly onto potato leaflets or beet seedling leaves. Dishes were placed in the controlled environment cabinet in an upside down position. The aphids were transferred to new dishes containing fresh potato leaflets or beet leaves every three or four days. The experiment was performed in two batches to obtain a total of 30 MPB on beet, 30 MPB on potato and 30 MPP on potato. Five biological parameters, pre-reproductive period (time from birth until onset of reproduction), adult survival (number of days the aphids survived after becoming adults), whole longevity (the number of days the aphids survived after birth), total progeny and daily fecundity were assessed each day (Alla *et al.*, 2003).

Aphid behaviour

Five small beet leaves, five beet seedling leaves and 10 healthy terminal potato leaflets were collected from greenhouse-grown plants, using a scalpel. The petiole of one small beet leaf, one beet seedling leaf or one potato leaflet was placed through a small hole in a Parafilm membrane stretched over a small plastic vial (50 ml) containing water. Fifteen apterous adult MPB and five apterous adult MPP were collected from their respective colonies, placed in separate snap-top vials (50 ml) and brought to the laboratory. An individual MPB or MPP was placed directly onto the upper surface of each beet leaf or potato leaflet using a small brush. Each leaf/leaflet and aphid was covered with a tubular cage made of a piece of Plexiglas tubing (30 cm long, 15 cm diameter), closed at one end with fine wire mesh screening. A total of 20 cages were set up, five cages with MPB on small beet leaves, five cages with MPB on beet seedling leaves, five cages with MPB on potato leaflets and five cages with MPP on potato leaflets. The cages were placed on a well-lighted laboratory bench (four T8 daylight fluorescent bulbs and four 500 W portable halogen work lights placed 125 cm over the bench) at room temperature (22 ± 2°C). The behaviour and position of the aphids were recorded every 5 min for a period of 2 h (120 min) with the four treatments being observed simultaneously to avoid any variation in aphid behaviour between replicates. The position of an aphid at each interval was designated as 'on the leaf/leaflet', or 'not on the leaf/leaflet'. The behaviour of the aphids was classified as 'walking', 'resting' if the aphid was immobile without the rostrum (feeding appendage) touching the leaf/leaflet or 'probing' if the aphid was immobile with the rostrum touching the leaf/leaflet. A magnifying glass was used to observe the contact of the rostrum with the leaflet. This protocol was replicated six times to bring the number of replicates for each treatment to 30.

EPG assessment of probing and feeding behaviour

Small beet leaves and terminal potato leaflets of the same age and size as those used for the behaviour observations were set up in plastic vials as described for the behaviour observations. The direct-current EPG technique (Giga 4 and Giga 8; EPG Systems, Wageningen, The Netherlands; Tjallingii, 1978, 1985, 1988; Pelletier *et al.*, 2008; Boquel *et al.*, 2012, 2016) was used to gather information on probing and feeding behaviour of MPB on small beet leaves and potato leaflets and MPP on potato leaflets. An alate aphid was immobilized on top of a small plastic tip set up under a dissecting microscope with the use of suction and was glued to a gold wire using water-based silver glue. The glue was made by mixing 2 g of water/detergent solution (100 ml of distilled water with one droplet of Triton X-100), 2 g of water-based paper glue (Ross Mucilage; Elmer's Products) and 2 g of fine-grain silver powder (0.4–1 µm; Inframat Advanced Materials). The gold wire was then glued onto a copper wire which was in turn soldered onto a brass nail. The brass nail was inserted into a head stage amplifier to form one end of an electrical circuit, and the aphid was set down on a small beet leaf or potato leaflet. A second electrode was placed in the plastic vial of water containing the petiole of the beet leaf or potato leaflet. When the aphid began to probe, the circuit was closed and waveforms, corresponding to previously described behaviours (Tjallingii, 1978, 1985), were recorded for a period of 8 h. Four to eight leaves/leaflets with one aphid per leaf/leaflet were set up inside a Faraday cage at room temperature (22 ± 2°C) each day EPG's were performed. Twenty recordings with MPB on small beet leaves, 20 with MPB on potato leaflets and 20 with MPP on potato leaflets were completed over a period of two weeks for a total of 60 recordings. Five MPB placed on beet did not probe at all. These five recordings were discarded since it was impossible to know whether 'not probing' was a true behaviour or the aphids did not probe because they were not well placed on the leaves. The acquisition and analysis of the EPG waveforms were performed with SCOPE v.2.2 software (Data Translation). Waveforms were interpreted according to Tjallingii and Esch (1993): 'non-probing' (NP), when the aphid was not inserting its stylets into the plant; 'potential drop' (pd) when aphids punctured plant cells with their stylets; 'xylem phase' (G), when the aphid was actively ingesting sap from the xylem; 'phloem sieve element phase' when the aphid was salivating into the phloem (E1), ingesting sap from the phloem (E2) and performing sustained phloem ingestion (Es; *i.e.* E2 lasting more than 8 min with E2 including Es); 'stylet pathway phase' (C), when the aphid was performing a behaviour eliciting one of three waveforms (A–C) interpreted as penetration (A), salivation (B) and other activities (C) in the mesophyll plant tissues. Forty-two behavioural response variables were selected to illustrate the effect of the host plant on the different behaviours, including the mean number and duration of events (per insect) and the total duration per insect (Backus *et al.*, 2007).

PVY acquisition by aphids

Two PVY^{NTN}-infected terminal potato leaflets were set up in plastic vials as described for the behaviour observations. Alate MPB

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and MPP were collected from their respective colonies in snap top plastic vials (50 ml). A group of approximately 15 MPB or 15 MPP was placed on the upper surface of each PVY^{NTN}-infected leaflet. A leaflet with aphids was covered with a tubular Plexiglas cage as described for the behaviour observations. After a period of 10 min, half of the aphids remaining on the leaflet were removed, placed in a 2 ml microcentrifuge tube containing 95% ethanol and stored at 4°C. At 20 min, the aphids remaining on the leaflet were collected in a separate microcentrifuge tube and stored as above. The acquisition assay was performed on two consecutive days with two replications with MPB and MPP on the first day and three replications on the second day. New PVY^{NTN}-infected leaflets were used on the second day. The first replication with MPB or MPP was performed on one leaflet and the second replication on the other leaflet. The leaves were switched again for the third replication on the second day. On the second day, seven aphids were used for the third replication with MPB and six aphids were used for the third replication with MPP. A total of 63 MPB and 63 MPP were assayed. Within one week of being collected, the stylets of each aphid stored at 4°C were removed from the aphid's body as described by Boquel *et al.* (2013). The dissected stylets were placed in their own 2 ml microcentrifuge tube and stored at −20°C. RNA was extracted from individual stylets using an RNeasy Mini kit (Qiagen) according to the manufacturer's instructions, and one-step reverse transcription polymerase chain reaction was carried out as described previously by Zhang *et al.* (2013) to assess the presence of PVY.

Data analysis

Ethographs for the behaviour experiment were constructed as stacked bar graphs of the percentage of aphids that performed a given behaviour at a given time during the experiment. Behaviours were grouped as, 'on leaf/leaflet probing', 'on leaf/leaflet resting or walking' and 'not on leaf/leaflet'. The 95% confidence interval was calculated for the proportion of aphids displaying a behaviour for each 5 min sampling time. The treatment was deemed to be different from the control if the confidence intervals for that sampling time did not overlap. Differences between treatment and the control were indicated at the top of the graph for each behaviour (Boquel *et al.*, 2015, 2016).

Analysis of variances using the general linear model (GLM) (Nelder and Wedderburn, 1972) were performed using SYSTAT v.13 (Systat Software). Data of the probing behaviour experiment (EPG) was log-(duration data) or $\sqrt{}$-transformed (frequency data) when necessary for normality and homogeneity of residuals (Backus *et al.*, 2007; Boquel *et al.*, 2016). Biological parameters measured during the survival experiment and behavioural response variables were analysed using the GLM and treatment as the main factor. The main effect was determined by performing post-hoc Tukey tests. Significance was accepted at P value of ≤ 0.05.

Percentages of acquisition were computed as the proportion of *M. persicae* stylets that had PVY compared to the number of aphids evaluated. Percentages of acquisition were analysed using a GLM with a binomial distribution of the error in R 4.0.3 (R Core Team, 2020). The main effects were the origin of the aphids (potato or beet), the period of PVY acquisition (10 or 20 min) and their interaction. Factors were tested using likelihood ratio tests. If an interaction was not significant, it was removed from the model.

Results

Aphid survival

The pre-reproductive period (fig. 1a) was significantly longer for MPB on beet (11 days) compared to MPP on potato (6.6 days) and MPB on potato (7.2 days). Adult survival was significantly lower for MPB on beet (4.7 days) compared to MPP and MPB on potato (15.7 and 11.6 days, respectively) (fig. 1b). Whole longevity was also significantly lower for MPB on beet compared to MPP on potato, and MPB on potato was not significantly different from the other treatments (fig. 1c). The total number of progenies produced was significantly different for all three treatments with aphids on potato producing 11 (MPP) and 7.5 (MPB) times more progenies compared to MPB on beet (fig. 1d). The daily fecundity was significantly lower for MPB on beet (0.5 nymph) compared to MPP on potato (3.4 nymphs) and MPB on potato (2.8 nymphs) (fig. 1e).

Aphid behaviour

The majority of the observed significant differences were for aphids in contact with beet leaves compared to aphids in contact with potato leaflets. The percentage of MPB that were not on the leaf/leaflet for small beet leaves was significantly higher for the first 65 min of the 2 h observation period compared to the percentage of MPP not on potato leaflets (fig. 2). This resulted in a significantly lower percentage of MPB probing small beet leaves over the same period of time. For the remaining 55 min, the percentage of MPB that were not on the leaf/leaflet for small beet leaves, therefore not probing, was significantly lower only between 85 and 100 min. No difference was observed for aphids on leaf/leaflet resting or walking. When MPB were placed on beet seedling leaves, the percentage of aphids that were not on the leaf/leaflet was significantly higher for the entire observation period compared to the percentage of MPP aphids not on potato leaflets. This resulted in a significantly lower percentage of aphids probing the beet seedling leaves for over 90% of the observation period. In contrast, similar proportions of MPB and MPP remained on potato leaflets and probed.

EPG assessment of probing and feeding behaviour

When MPB was placed on beet, a number of behavioural response variables differed significantly from the control, MPP placed on potato (table 1).

During the stylet pathway phase, where the aphid's stylet pierces the cuticle of the leaf and travels between the cells of the leaf, the number of penetrations of the cuticle (nP) and the number of short probes, less than 3 min (nc < 3), were increased compared to the control. There was also an increase in the average number of cell punctures (potential drops; avpd) per minute during this phase compared to the control. The number of penetrations before the first salivation in the phloem (n-P:E1) was also increased compared to the control.

In the phloem phase, where there is salivation in (E1) and ingestion from (E2) the phloem vessels, the number, average and total duration of salivation events in the phloem (nE1, avE1 and dE1) were reduced compared to the control. The number and total duration of salivation events before phloem consumption (n-E1:E2, d-E1:E2) were also reduced compared to the control. The time from the placing of the aphid on the leaf to the first salivation in the phloem (d-0:E1) was increased

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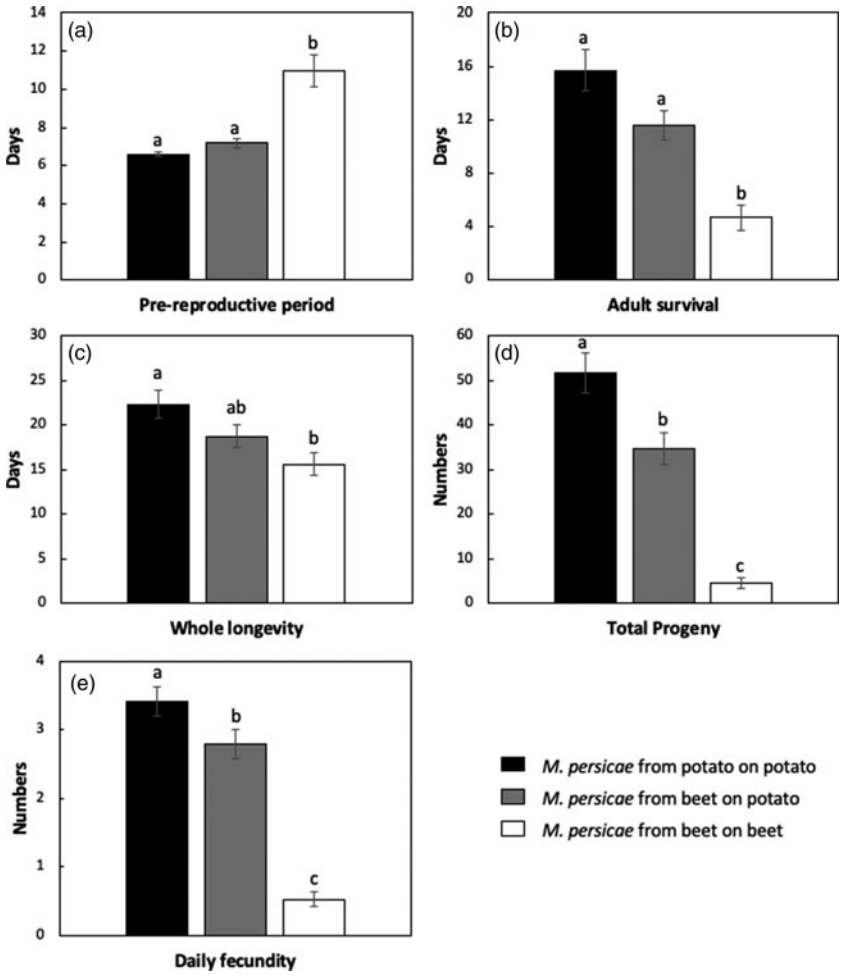

Figure 1. Pre-reproductive period (a), adult survival (b), whole longevity (c), total progeny produced (d) and daily fecundity (e) for *M. persicae* from potato on potato, *M. persicae* from beet on potato and *M. persicae* from beet on beet.

compared to the control, but not significantly (165 min compared to 101 min, respectively). With respect to phloem consumption, the number, average and total duration of phloem ingestion events (nE2, avE2 and dE2) and sustained phloem ingestion events (nEs, avEs and dEs) were reduced compared to the control, but not significantly. The total duration of phloem consumption before the first sustained phloem consumption (d-E2:Es) was increased compared to the control.

For the xylem phase, where hydration of the aphid occurs, the number of xylem consumption (nG) events was similar to the control while the total (dG) and average (avG) duration were increased compared to the control, but not significantly.

When MPB was placed on potato, there were no significant differences compared to the control, MPP placed on potato.

For MPB placed on potato compared to MPB placed on beet, the number of penetrations before the first salivation in the phloem (n-P:E1) and the average number of cell punctures per minute (avpd) were significantly increased on beet by an amount similar to that observed when MPB on beet was compared to the control. The time from the placing of the aphid on the leaf/leaflet to the first salivation in the phloem (d-0:E1) was significantly longer for MPB on beet compared to MPB on potato. The average duration of xylem consumption events (avG) increased significantly for MPB on beet compared to MPB on potato. The number, average and total duration of salivation events in the phloem (nE1, dE1 and avE1) and salivation events before phloem consumption (n-E1:E2, av-E1:E2 and d-E1:E2) were significantly reduced for MPB on beet compared to MPB on potato by an amount similar to that observed when MPB on beet was compared to the control.

Forty-four percent of MPP on potato and 56% of MPB on potato performed the first salivation in the phloem within the first hour after being placed on the potato leaflet while only 15% of MPB on beet performed the first salivation within the first hour (table 2). Sixty-two percent of MPB on beet took more than 2 h to perform the first salivation in the phloem while only 28% of MPP and 25% of MPB on potato took more than 2 h.

There were significant differences in the percentage of aphids performing four behaviours (table 3). The percentage of MPB on beet (87%) that performed salivation in the phloem before phloem consumption (E1:E2) and phloem consumption (E2) was significantly greater than that for MPB on potato (45%). A significantly lower percentage of MPB on beet (7%) performed salivation without subsequent phloem consumption (E1-E2) compared to MPB on potato (80%) and MPP on potato (85%). A significantly higher percentage of MPB on beet (87%) performed sustained phloem consumption (Es) compared to MPB on potato (35%) and MPP on potato (55%).

PVY acquisition by aphids

The percentages of MPP and MPB testing positive for PVY did not differ for the two host plants of origin ($X = 0.07$, *d.f.* = 1, P

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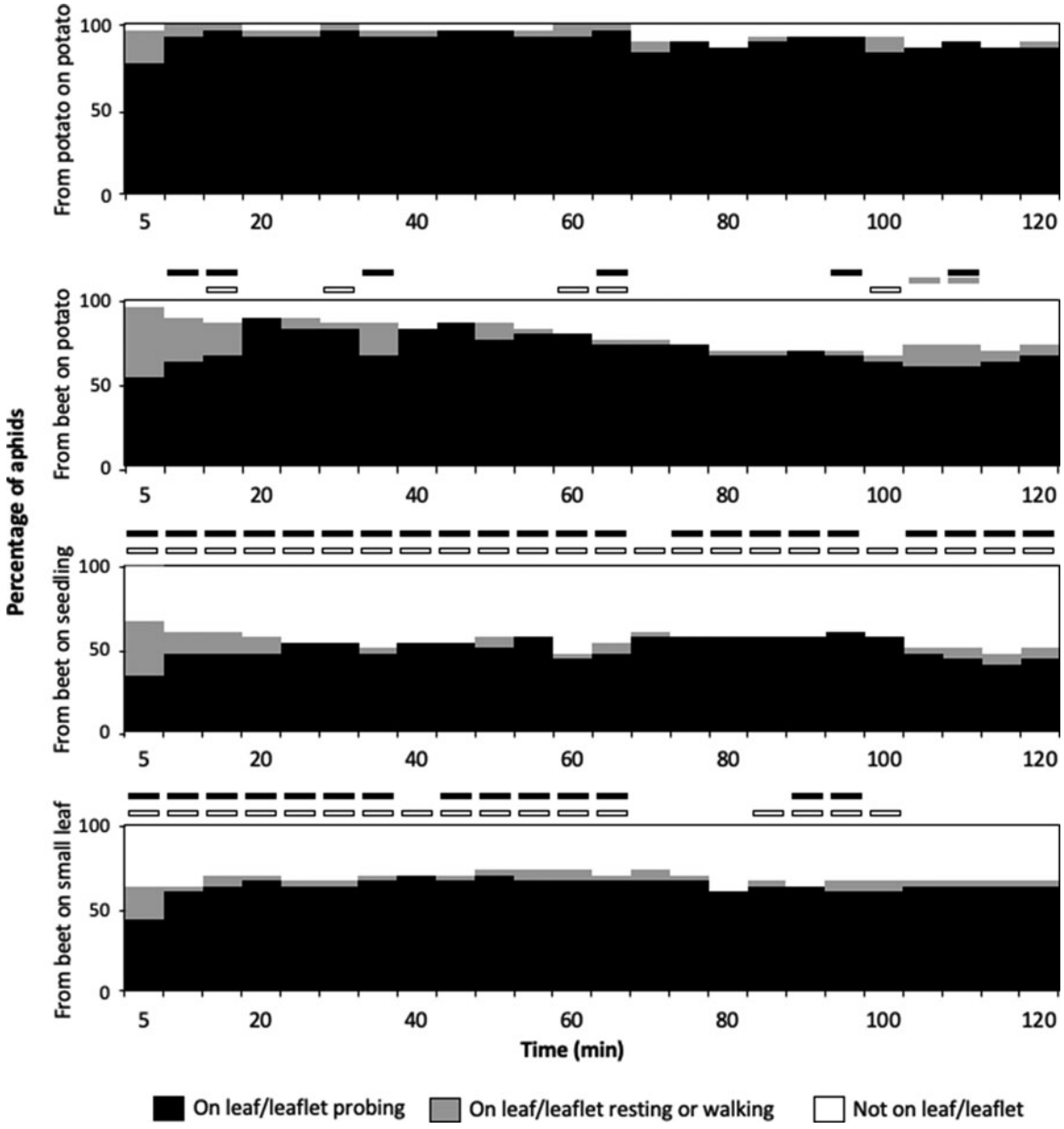

Figure 2. Ethographs showing the percentage of *M. persicae* aphids from beet and potato performing one of the three behaviours – on leaf/leaflet probing, on leaf/leaflet resting or walking and not on leaf/leaflet – on potato leaflets, on beet seedling leaves and on small beet leaves. The line pieces above the stacked bars indicate significant differences between *M. persicae* from potato on potato leaflets and *M. persicae* from beet on potato leaflets, on beet seedling leaves and on small beet leaves at a specific time, and their colour indicates the significantly different behaviour (based on non-overlapping 95% confidence intervals).

= 0.698) or the two periods of PVY acquisition ($X = 0.06$, $d.f. = 1$, $P = 0.897$) (table 4).

Discussion

Several studies have looked at the performance of *M. persicae* on a variety of host plants, including spinach, sugar beet, lettuce, various *Brassica* species, tobacco, potato and peppers (Heathcote, 1962; Weber, 1985; Nikolakakis *et al.*, 2003). To our knowledge, this is the first time the performance of *M. persicae*, originating on potato and reared on table beet, has been studied.

Myzus persicae reared on beet (MPB) performed much better on potato, the host it originated from, than it did on beet. MPB on beet exhibited a very large reduction in the number of progenies produced and a much longer pre-reproductive period compared to *M. persicae* reared on potato (MPP). The reduced number of progenies was contributed to by a highly significant reduction in the number of days MPB on beet survived after becoming adults resulting in MPB having fewer days to produce nymphs than MPP on potato. During behaviour observations when MPB was in contact with potato and beet, and MPP was in contact with potato, similar proportions of MPB and MPP remained on potato leaflets and probed while a higher proportion of MPB left beet indicating that beet may not be as suitable host as potato, it's host of origin. The findings of the EPG assessment of behaviour agreed with the behaviour observation findings with MPB on potato behaving very similarly to MPP on potato, and MPB on beet behaving differently than MPB and MPP on potato further

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Table 1. Probing and feeding behaviours (mean number of events, total duration of events (min) and mean duration of events (min) ± SEM) of *M. persicae* reared on potato and monitored on potato and *M. persicae* reared on table beet and monitored on potato and table beet

	M. persicae from:		
	Potato on potato Mean ± SEM	Beet on potato Mean ± SEM	Beet on beet Mean ± SEM
Stylet pathway phase – penetration of cuticle (P)			
d-0:P (min)	4.1 ± 1.2 (20)	4.1 ± 1.0 (20)	9.8 ± 6.2 (15)
nP	15.7 ± 2.5 b (20)	19.8 ± 2.3 ab (20)	28.1 ± 5.2 a (15)
dP (min)	357.2 ± 24.9 (20)	296.6 ± 26.4 (20)	351.8 ± 28.1 (15)
avP (min)	45.8 ± 12.0 (20)	20.8 ± 3.8 (20)	33.5 ± 14.2 (15)
n-P:E1	5.4 ± 0.7 b (18)	6.0 ± 0.9 b (16)	16.6 ± 3.4 a (13)
n-P:E2	9.9 ± 2.3 (14)	8.1 ± 1.4 (9)	16.6 ± 3.4 (13)
n-P:Es	10.4 ± 2.9 (11)	7.7 ± 1.7 (7)	16.6 ± 3.4 (13)
d-P:Es (min)	270.6 ± 136.3 (11)	65.8 ± 36.1 (7)	71.7 ± 16.9 (13)
Stylet activity in mesophyll (C)			
nC	20.6 ± 2.9 (20)	26.4 ± 2.3 (20)	30.3 ± 5.3 (15)
dC (min)	126.6 ± 16 (20)	141.1 ± 17.8 (20)	137.2 ± 20.0 (15)
avC (min)	6.5 ± 0.5 (20)	5.6 ± 0.9 (20)	5.3 ± 0.8 (15)
nC < 3	10.3 ± 1.9 b (20)	14.1 ± 1.6 ab (20)	21.3 ± 4.6 a (15)
npd	106.3 ± 16.4 (20)	104.3 ± 12.4 (20)	151.4 ± 23.8 (15)
Avpd	0.85 ± 0.06 b (20)	0.78 ± 0.05 b (20)	1.16 ± 0.07 a (15)
Xylem consumption (G)			
nG	1.3 ± 0.2 (11)	2.2 ± 0.6 (13)	1.1 ± 0.1 (9)
dG (min)	77.9 ± 18.9 (11)	67.3 ± 24.1 (13)	103.6 ± 43.3 (9)
avG (min)	71.1 ± 19.9 ab (11)	31.3 ± 9.1 b (13)	98.5 ± 43.8 a (9)
Salivation in phloem (E1)			
nE1	6.9 ± 1.2 a (18)	6.3 ± 1.1 a (16)	2.4 ± 0.4 b (13)
dE1 (min)	49.4 ± 9.3 a (18)	41.9 ± 8.6 a (16)	3.4 ± 0.6 b (13)
avE1 (min)	7.3 ± 1.4 a (18)	6.1 ± 0.7 a (16)	1.6 ± 0.3 b (13)
E1 bouts before E2			
n-E1:E2	3.5 ± 0.8 a (14)	5.0 ± 1.4 a (9)	1.0 ± 0.0 b (13)
d-E1:E2 (min)	19.0 ± 5.6 a (14)	32.5 ± 11.8 a (9)	2.0 ± 0.5 b (13)
av-E1:E2 (min)	4.4 ± 1.2 ab (14)	5.5 ± 0.7 a (9)	2.0 ± 0.5 b (13)
E1 bouts no E2			
n(E1-E2)	4.7 ± 0.8 (17)	5.6 ± 1.0 (16)	1.0 ± – (1)
d(E1-E2) (min)	31.7 ± 6.3 (17)	38.1 ± 8.4 (16)	1.4 ± – (1)
av(E1-E2) (min)	7.2 ± 1.3 (17)	6.1 ± 0.8 (16)	1.4 ± – (1)
E1 bouts before G			
n(E1-G)	3.0 ± 0.7 (5)	1.8 ± 0.2 (5)	2.0 ± 0.3 (5)
d(E1-G) (min)	7.4 ± 3.3 (5)	5.7 ± 1.4 (5)	2.2 ± 0.5 (5)
av(E1-G) (min)	2.2 ± 0.5 ab (5)	3.1 ± 0.6 a (5)	1.1 ± 0.1 b (5)
Aphid release to first E1			
d-0:E1 (min)	100.5 ± 19.7 ab (18)	92.1 ± 24.4 b (16)	164.9 ± 30.8 a (13)
Phloem consumption (E2)			
nE2	3.2 ± 1.3 (14)	1.2 ± 0.1 (9)	2.3 ± 0.4 (13)

(*Continued*)

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Table 1. (*Continued.*)

	M. persicae from:		
	Potato on potato Mean ± SEM	Beet on potato Mean ± SEM	Beet on beet Mean ± SEM
dE2 (min)	204.7 ± 44.4 (14)	173.9 ± 51 (9)	172.4 ± 31.1 (13)
avE2 (min)	110.7 ± 35.3 (14)	152.0 ± 44.6 (9)	96.0 ± 18.1 (13)
Sustained E2 (Es)			
nEs	2.0 ± 0.5 (11)	1.1 ± 0.1 (7)	1.6 ± 0.2 (13)
dEs (min)	254.9 ± 43.6 (11)	221.8 ± 53.0 (7)	168.6 ± 31.4 (13)
avEs (min)	174.8 ± 44.6 (11)	194.3 ± 45.4 (7)	116.6 ± 23.4 (13)
E2 before Es			
n-E2:Es	0.5 ± 0.2 (11)	0.0 ± 0.0 (7)	0.2 ± 0.2 (13)
d-E2:Es (min)	0.5 ± 0.2 b (11)	0.0 ± 0.0 (7)	1.3 ± 0.9 a (13)
Aphid release to first E2 and Es			
d-0:E2 (min)	192.2 ± 37.0 (14)	183.4 ± 51.0 (9)	166.9 ± 30.7 (13)
d-0:Es (min)	193.0 ± 39.7 (11)	125.7 ± 39.7 (7)	168.4 ± 30.4 (13)

Recordings were done for 8 h. Statistics are indicated only where there were significant differences ($\alpha \leq 0.05$). Number in brackets is the number of aphids performing the behaviour. Twenty MPP were monitored on potato, 20 MPB were monitored on potato and 15 MPB were monitored on beet.
Abbreviations: av refers to mean duration of events per insect (min), avpd refers to mean number of cell punctures per minute of pathway phase, C < 3 refers to short probes (less than 3 min), d refers to total duration of events per insect (min), d-0:P refers to time from placing of aphid on leaf/leaflet to first penetration (min), d-0:E1 refers to time from placing of aphid on leaf/leaflet to first salivation in phloem, d-0:E2 refers to time from placing of aphid on leaf/leaflet to first phloem consumption, d-0:Es refers to time from placing of aphid on leaf/leaflet to first sustained phloem consumption, d-P:Es refers to time to sustained phloem consumption from beginning of current probe, E1:E2 refers to phloem salivation events before phloem consumption, E1-E2 refers to phloem salivation events without subsequent phloem consumption, E1-G refers to salivation events before xylem consumption, Es refers to sustained E2 (>8 min) phloem consumption events, E2:Es refers to phloem consumption events before first sustained phloem consumption, n refers to number of events per insect, pd refers to cell punctures, P:E1 refers to penetration before first salivation, P:E2 refers to penetration before first phloem consumption, P:Es refers to penetration before first sustained phloem consumption. SEM refers to standard error of the mean.

Table 2. Percentage of *M. persicae* performing the first salivation in the phloem at seven time intervals between 1 and 420 min

	M. persicae from:		
Min	Potato on potato (%)	Beet on potato (%)	Beet on beet (%)
1–60	44.4	56.3	15.4
61–120	27.8	18.8	23.1
121–180	11.1	12.5	38.5
181–240	11.1	6.3	0.0
241–300	0.0	0.0	0.0
301–360	5.6	0.0	15.4
360–420	0.0	6.3	7.7

Recordings were done for 8 h. Eighteen MPP monitored on potato, 16 MPB monitored on potato and 13 MPB monitored on table beet performed the behavior.

indicating that potato is a more suitable host than beet. A study by Nikolakakis *et al.* (2003) showed there was a significant 'region/host plant origin effect' for *M. persicae* on pepper and tobacco from two regions of Greece. There appears to be a similar host plant effect for MPB on potato and beet, with *M. persicae* preferring potato, the plant from which it originated, even after being reared on beet for 15 years.

The EPG assessment of the behaviour of MPB on beet suggests that the aphids had difficulty finding a feeding site. After being placed on a beet leaf, the majority of MPB took much longer to find a feeding site and perform the first salivation in the phloem than MPP on potato. While trying to locate a feeding site, MPB on beet probed more often than MPP on potato, the probes were shorter and there was an increased number of cell punctures (potential drops), all indicating difficulty in finding a feeding site (Tjallingii and Esch, 1993; Ramírez and Niemeyer, 2000). This delay and difficulty in finding a feeding site suggests that several MPB on beet were not receiving cues to probe from beet. The five MPB on beet that did not probe at all may have not received cues from beet to probe, however, it is possible that the five aphids did not probe because they were not well placed on the leaves and for this reason no probing was recorded. The difficulty MPB appeared to have finding a feeding site could explain the reduction in the number of days the aphids survived after becoming adults leading to a reduction in the number of progenies as seen in the aphid survival experiment. Furthermore, if the aphid cannot find a feeding site it is less likely to probe and more likely to leave the beet leaf as observed in the behaviour experiment. The difficulty MPB has finding a feeding site on beet indicates beet is a less suitable host for *M. persicae* than potato.

For the MPB that found a feeding site on beet, almost all of them (87%) salivated into the phloem before consuming it while less than half of the MPB that found a feeding site on potato salivated into the phloem before consumption. Also, the first salivation into the phloem of beet was delayed compared to the first salivation into the phloem of potato. It is thought that saliva is added into the phloem to prevent phloem proteins from coagulating at the tip of the stylet's food canal and clogging it (Tjallingii, 2006; Will *et al.*, 2013). It is possible that beet phloem contains

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Table 3. Percentage of 20 *M. persicae* reared on potato and monitored on potato, 20 *M. persicae* reared on table beet and monitored on potato and 15 *M. persicae* reared on table beet and monitored on table beet performing four feeding behaviours, phloem salivation before phloem consumption, phloem consumption, phloem salivation without subsequent phloem consumption and sustained phloem consumption

	M. persicae from:			*Z*-test (*P*-values)		
Behaviour variable	P on P (%)	B on P (%)	B on B (%)	PonP vs. BonP	PonP vs. BonB	BonP vs. BonB
E1:E2	70	45	87	ns	ns	0.012
E2	70	45	87	ns	ns	0.012
E1-E2	85	80	7	ns	<0.001	<0.001
Es	55	35	87	ns	0.046	0.002

Recordings were done for 8 h. Only behaviour variables where there were significant differences in the percentage of aphids performing the behaviour were included in the table. Abbreviations: B refers to beet, BonB refers to *M. persicae* from beet on beet, E2 refers to phloem consumption, E1:E2 refers to phloem salivation before phloem consumption, E1-E2 refers to phloem salivation without subsequent phloem consumption, Es refers to sustained phloem consumption, P refers to potato, PonB refers to *M. persicae* from potato on beet, PonP refers to *M. persicae* from potato on potato.

Table 4. Percentages of *M. persicae* from potato and beet that tested positive for PVY after a 10 or 20 min acquisition period on PVY-infected potato leaves

	Acquisition time	
	10 min	20 min
M. persicae from potato	29% (9/31)	28% (9/32)
M. persicae from beet	30% (10/33)	33% (10/30)

Numbers within brackets are the number of aphids that tested positive for PVY followed by the total number of aphids tested for PVY.

more of the phloem proteins that could coagulate in the food canal than potato phloem and for this reason more MPB on beet salivate into the phloem than MPB on potato. The finding that several more MPB on beet salivated into the phloem than MPB on potato indicates that *M. persicae* still performs better on potato even after being reared on this host for over 15 years.

Species of aphids that do not colonize potato take much more time to acquire PVY compared to the potato-colonizing *M. persicae* due to the first probe being delayed, resulting in an increase in the total time required to acquire the virus (Boquel *et al.*, 2011). In this study, the rate of acquisition of PVY by MPB and MPP was the same for both the 10 and 20 min acquisition periods. It was initially hypothesized that an aphid that had shifted host (potato to beet) would become a non-colonizing aphid and would acquire PVY more readily after a 20 min acquisition period compared to a 10 min period. The absence of a difference in the acquisition rates for the two periods indicates that MPB has retained its host-related properties and potato is still a more suitable host.

The findings of this study suggest that the *M. persicae* reared on table beet for over 15 years was a potato-adapted form of *M. persicae* that had kept its host-related properties. Weber (1985) in a study on clones of *M. persicae* from Germany found that some clones of this aphid were adapted to potato. A tobacco-adapted form of *M. persicae* occurs in geographically separated areas of the world including North America, the Mediterranean region, the Middle East and Africa (Blackman, 1987; Margaritopoulos *et al.*, 2000). Clones of the *nicotianae* subspecies of *M. persicae* retained their host-related properties (morphological traits) even after long-term parthenogenetic rearing on other hosts (Blackman, 1987; Margaritopoulos *et al.*, 2000). The findings of this study contribute to the idea that within *M. persicae* there are specialist, host-adapted forms that retain their host-adapted genetic properties.

The differences in performance and behaviour for MPB placed on beet compared to MPP placed on potato, the similar performance and behaviour on potato for MPB and MPP and the similar PVY acquisition rates for MPB and MPP all strongly indicate that the original host, potato, was still the more suitable host for *M. persicae* reared on a novel host, table beet, for over 15 years. The *M. persicae* used in this study appears to be a specialized potato-adapted genotype of *M. persicae*.

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Conflict of interest. The authors declare none.

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