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Feeding Behavior of Two Exotic Aphid Species on their Original Hosts in a New Invaded Area

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Abstract

Greenidea ficicola Takahashi and *Greenidea psidii* van der Goot (Aphididae: Greenideinae) are Asian aphid species newly introduced in Brazil associated with Moraceae and Myrtaceae. The feeding behavior of *G. ficicola* and *G. psidii* was investigated on their respective host plants, *Ficus benjamina* (Moraceae) and *Psidium guajava* (Myrtaceae), using the Electrical Penetration Graph (EPG). Fifteen females of each aphid species were monitored during 24h using a DC-EPG GIGA-4 monitor. The time spent in phloem phase (waveforms E1 and E2) was 13.6% of the total recording time for *G. ficicola* and 0.8% for *G. psidii*. The average time in the pathway phase (waveforms C and pd) represented 50% of the total time for both species. Aphids spent more time in non-penetration and stylet pathway activities than in the phloem phase or actual feeding. The principal component analysis (PCA) showed that the two species formed different groups in relation to EPG parameters, despite some overlapping. The probing patterns with multiple penetrations of short duration in the sieve elements for both species may indicate apparent unsuitability for sustained feeding on their respective host plants. These results suggest that these two exotic species are in the process of adaptation to their host plants in their new environment and/or the plants may present either chemical or physical barriers against these insects.

Introduction

Dispersal is a basic life history process for all organisms, and all possess a life stage that is adapted in some way for dispersal. This process is of major importance for alien species to explore new environments where they will eventually establish and succeed (Cox 2004). Many species are dispersed by human action and may invade new areas. Physical and chemical factors act as selective elements for species adaptation to the new habitat. In some cases, abiotic and biotic pressures are relaxed, favoring rapid population growth, high reproductive success and new food resources exploitation by alien species (Dieckmann *et al* 1999, Cox 2004).

The development of new approaches in life-history theory may lead to predictions of species likely to become serious pests or may identify critical life history stages during which management will be the most successful. The key characteristics common to successful colonists (r-selected) are short generation time, high fecundity and growth rates (Sakai *et al* 2001), which are all found in aphids. The decision of aphids to colonize or not a plant is a complex process that involves a series of stimuli and responses (Klingauf 1987). The selection of the host plant is fundamentally affected by gustatory signals perceived during the penetration of stylets in peripheral tissues and vascular bundles of the potential host plant (Powell *et al* 2006).

Two exotic aphid species were recently introduced in Brazil, *Greenidea ficicola* Takahashi and *Greenidea psidii* van der Goot (Hemiptera: Aphididae), infesting, respectively, *Ficus benjamina* (Moraceae) and *Psidium guajava* (Myrtaceae) (Sousa-Silva *et al* 2005, Lazzari *et al* 2006). There is no information on how these two aphid species were introduced in the country, but probably with infested seedlings.

The genus *Greenidea* has its origin in Asia (Blackman & Eastop 1984), with *G. psidii* being distributed in Asia, Florida, Hawaii, California, Costa Rica, and Brazil (Blackman & Eastop 1984, Beardsley 1993, Halbert 2004, Lazzari *et al* 2006, Hidalgo *et al* 2009), feeding on leaves of *P. guajava* and other Myrtaceae (*Rhodomyrtus*, *Eugenia*, *Melaleuca*). *Greenidea ficicola* has been recorded from Asia, Australia, Florida, and Brazil (Blackman & Eastop 1984, Halbert 2004, Sousa-Silva *et al* 2005) feeding on *Ficus* spp.

As other aphids, these *Greenidea* species ingest phloem sap from their hosts through narrow piercing-sucking mouthparts and use the phloem as a feeding site mainly because this tissue has the greatest capacity for maintaining a supply of nutrient sap under pressure (Mittler 1957). During probing, the stylets of aphids transiently puncture epidermal, mesophyll, and parenchyma cells, and this mechanical damage may influence plant responses to infestation (Tjallingii & Esch 1993). Periods of phloem ingestion longer than approximately 10 min may represent phloem acceptance with phloem sap ingestion for a longer period, often several hours (Tjallingii 1994). Field and laboratory data indicated that the major factors influencing plant preference by aphids are recorded after stylet insertion (Powell *et al* 2006).

According to Schoonhoven *et al* (1998), plant acceptance by an insect can be defined in terms of food ingestion and/or reproduction. The growth rate of aphid populations depends on the quality and quantity of food consumed (Kordan *et al* 2008) and their ability to reach the phloem sieve element (Klingauf 1987). Using the Electrical Penetration Graph (EPG) technique, researchers have been studying aphid acceptance of host plants and defense mechanisms of susceptible and resistant plants to insects (Müller *et al* 2001, Tosh *et al* 2002, 2003, Kordan *et al* 2008). EPG recordings of 24h are suitable for best information on feeding behavior and studies involving plant resistance to homopterans, but recordings of 7h or 8h can be very informative as well (Reese *et al* 1994).

The EPG technique was used in here to characterize the feeding behavior and adaptive insect-plant interactions of *G. ficicola* and *G. psidii* on their respective host plants in Brazil, *F. benjamina* and *P. guajava*. Information on feeding adaptation of alien species to their host plants in the newly invaded area might be essential to understand the population biology and to successfully manage these invasive species.

Material and Methods

Aphids were collected from *F. benjamina* and *P. guajava* trees in Curitiba, Paraná state, Brazil. Fifteen parthenogenetic females of each aphid species from a single colony on their respective host plant were evaluated in the EPG system. Each aphid sample was monitored for 24h using a DC-EPG monitor, GIGA-4 model (EPG-Systems, Wageningen, The Netherlands) (Tjallingii 1978). Insects were attached to gold wire electrodes and placed onto the plant. For *P. guajava*, 20 cm-long branches with buds were kept in a pot with water, while 40 cm high, 1yr-old plants in a pot with soil were used for *F. benjamina*. A gold wire measuring 2 cm in length by 20 μm in diameter was glued to the dorsum of the aphid with a small drop of water-based colloidal silver glue (EPG-Systems, Wageningen, The Netherlands). The other end of this wire was attached to a copper wire of an electrode and this to the amplifier of the EPG equipment. A second electrode was inserted into the plant substrate, so the electrical circuit could be completed when the insect inserted the stylets into the plant tissues. The complete monitoring system was assembled inside a Faraday cage. Stylet penetration activities were recorded using PROBE 3.0 – Acq 3.2 software (EPG-System, Wageningen, The Netherlands) for the acquisition of digitized data. After recording, waveforms for each aphid were analyzed using PROBE 3.0 – Ana 3.2 software by type and time-marked, and the data were exported to Excel.

The following EPG events were recorded and recognized through waveforms: non-probing (np) – time that the insect is not piercing the plant tissues; C, pathway phase including primarily penetration through plant tissues, often with cell punctures, and salivation (when decision about acceptance or rejection of the host plant may occur); E1+E2, phloem phase - salivation into a sieve element plus ingestion from the sieve elements; and potential drops (pd) – brief insertions of the stylets into living cells during the pathway phase (Tjallingii 1978, 1988).

Timing the occurrence of each waveform allowed the evaluation of the following parameters: (1) number of np; (2) total duration of np; (3) np percent, compared with the total recording time (%); (4) time to first penetration within the experiment; (5) duration of first penetration; (6) total number of penetrations; (7) duration of C by insect (8) C percent, in relation to the total recording time (%); (9) time to first pd after each penetration; (10) time for reaching the phloem since the start of recording;

(11) time for reaching the phloem since the start of first penetration; (12) time for reaching the phloem since the start of the previous penetration; (13) time for sustained phloem ingestion (E2 > 10 min) since the start of recording; (14) time for sustained phloem ingestion since the start of the previous penetration; (15) mean time between phloem phase and sustained ingestion; (16) number of phloem phases; (17) number of np after the first phloem phase; (18) total duration of phloem phase by insect; and (19) phloem phase percent, compared with the total recording time (%).

The data were transformed to log (base-10 logarithm). Except for four parameters (number of np, duration of first penetration, time for reaching the phloem since the start previous penetration and phloem phase percent compared with the total time of recording), all the others showed normal distribution. The data were then subjected to one-way ANOVA using F-test for average comparison. Principal component analysis (PCA) was used to verify the distribution of the data recorded by EPG. For these analyses, we used STATISTICA 7.0 software (Statsoft 2004) and PAST 2.03 (Hammer *et al* 2001). Sustained phloem ingestion (parameters 13, 14, and 15 – Table 1) was excluded from statistical analysis because the time/activity relationship could be misinterpreted as zero, overestimating these parameters. The specimens that did not reach the phloem were excluded from the analysis, because they did not generate the waveforms related with most of the studied parameters (one out 14 specimens of *G. ficicola* and three out of 12 of *G. psidii*).

Results and Discussion

For *G. ficicola*, 97% of the insects reached the phloem of *F. benjamina* and 57% of them showed sustained phloem ingestion or actual feeding. For *G. psidii*, 80% reached the phloem of *P. guajava* and only 17% of them showed sustained phloem ingestion. The average time spent by aphids on non-probing (np) and pathway phase (C) was 20h for *G. ficicola* and 23h for *G. psidii*.

The results are summarized by the relative time (%) and absolute time (h) that aphids spent on non-probing, pathway and phloem phases. The percentage of time non-

Table 1 Mean (±SE) values for feeding parameters of *Greenidea ficicola* (*Gf*) and *Greenidea psidii* (*Gp*) on *Ficus benjamina* and *Psidium guajava*, respectively, obtained by the Electrical Penetration Graph (EPG) technique monitored during 24h and analyzed by one-way ANOVA.

Parameters[1,2]	Mean		ANOVA[4]	
	Gf (n = 15)	*Gp* (n = 15)	F	P-value
1. Number of non-probing (np)	24.3 (± 3.37)	25.7 (± 4.61)	0.001	0.971
2. Total duration of np	8.7 (± 1.29)	11.8 (± 1.31)	5.635	0.027*
3. % np in relation to total recording time	37.2 (± 5.49)	49.6 (± 5.45)	5.298	0.031*
4. Time to first penetration	0.9 (± 0.58)	1.8 (± 0.78)	6.289	0.021*
5. Duration of first penetration	0.7 (± 0.27)	1.6 (± 0.45)	1.898	0.182
6. Total number of penetration	23.3 (± 3.59)	25.0 (± 4.60)	0.070	0.793
7. Duration of the pathway phase (C)	11.4 (± 1.56)	11.7 (± 1.29)	0.279	0.602
8. % pathway phase (C) in relation to total recording time	46.6 (± 7.35)	49.4 (± 5.49)	0.903	0.352
9. Time to first potential drop (pd) after penetration	2.2 (± 1.09)	0.1 (± 0.04)	7.148	0.014*
10. Time for reaching the phloem (start recording)	7.5 (± 1.39)	6.9 (± 1.64)	0.377	0.545
11. Time for reaching the phloem (first penetration)	6.7 (± 1.39)	4.6 (± 1.48)	0.178	0.677
12. Time for reaching the phloem (previous penetration)	0.8 (± 0.15)	0.4 (± 0.09)	0.248	0.624
13. Time for sustained phloem ingestion (start recording)[3]	8.5 (± 1.39)	14.6 (± 2.46)	-	-
14. Time for sustained phloem ingestion (previous penetration)[3]	0.7 (± 0.04)	1.7 (± 0.55)	-	-
15. Mean time between phloem phase & sustained phloem ingestion[3]	0.9 (± 0.55)	9.9 (± 3.61)	-	-
16. Number of phloem phases	2.7 (± 0.68)	4.3 (± 1.10)	2.646	0.118
17. Number np after the first phloem phase	9.7 (± 1.20)	22.1 (± 4.30)	0.277	0.604
18. Total duration of phloem phase	3.2 (± 1.26)	0.2 (± 0.11)	1.63	0.215
19. % phloem phase compared with the total time of recording	13.6 (± 5.37)	0.9 (± 0.48)	1.106	0.304

[1] The first nine parameters indicate the attempts and initial probing pathway to recognize the host plant; the other parameters are related to the behavior after the stylets reach the phloem elements; [2] Time in hours; [3] *Gf* n = 8; *Gp* n = 2; [4] ANOVA analysis (*) α = 0.05.

probing (3) and in the pathway phase (8) and the phloem phase percentage compared with the total recording time (19) were not significantly different between the two species (Table 1).

By the one-way ANOVA analysis (Table 1), *G. ficicola* and *G. psidii* exhibited differences in feeding behavior regarding the following parameters: duration of np (2), np percent (3), time to first stylet penetration (4) and time to first pd (9).

Among the 16 parameters analyzed, the first five were sufficient to explain 90% of the distribution of the observations obtained by the PCA analysis. On Fig 1, the outlier (out of the ellipsis) corresponds to a single individual of *G. ficicola* that reached the phloem in the first penetration; however, it did not display sustained phloem ingestion. The other individuals penetrated the tissues in the first minutes, but failed to reach the phloem. The PCA graph (Fig 1) shows overlapping for several parameters of *G. ficicola* and *G. psidii*, corroborating the one-way ANOVA analysis that showed significant differences for only four parameters analyzed, as mentioned earlier.

In this study, the closely-related *G. ficicola* and *G. psidii* invested more time in the pathway phase than effectively ingesting phloem sap. The percentage of time spent in stylet pathway by *G. ficicola* and *G. psidii* was around 47% and 50% of the total recorded time, respectively (Table 1), more than twice the time registered for the pathway phase by *A. pisum* in two host plants (21.9%), record during approximately 7h (Caillaud & Via 2000). Kordan *et al* (2008) found that *A. pisum* possibly accepts or rejects non-host and/or host plants by the detection of chemical differences in the epidermis and mesophyll cells of plants without the need of reaching the phloem.

Aphids can be in contact with host plants that are nutritionally well supplied, but in the absence of attractants, the insects do not land, do not feed nor reproduce (Caillaud & Via 2000, Gabrys & Tjallingii 2002).

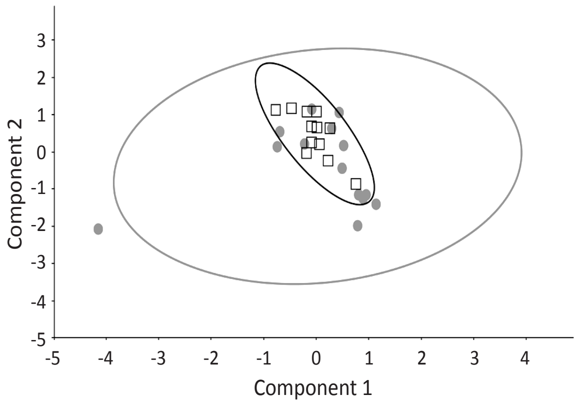

Fig 1 Principal Component Analysis (PCA) for *Greenidea ficicola* (●) and *Greenidea psidii* (□) feeding on *Ficus benjamina* and *Psidium guajava*, in relation to parameters analyzed by the Electrical Penetration Graph (EPG) technique.

Early probing activities are important, if not essential, for establishing plant suitability by aphids. The pathway phase includes intercellular stylet penetration from epidermis to phloem, during which aphids also puncture nearly every cell encountered (Prado & Tjallingii 2007). Among the indicators of plant quality, the most effective used by aphids lies in the intake of phloem sap (Tosh *et al* 2002). Prolonged phloem ingestion and reproductive performance, according to Klingauf (1987), indicates the acceptance of the host plant by aphids, what was not the case of the *Greenidea* species studied here.

The two *Greenidea* species spent short periods of time (<1-2h) in the first penetration in contrast to the records of host plant acceptance of the majority of aphids, which remain for longer periods of time in the first probe (Caillaud & Via 2000). The behavior observed for *G. ficicola* and *G. psidii* indicates certain difficulty to reach the phloem evidenced by some parameters analyzed (time required for reaching the phloem – around 7h; time for sustained phloem ingestion – more than 8h; duration of the pathway phase – around 11h) (Table 1). Klingauf (1987) mentioned that the acceptance of a host plant by an aphid depends on their ability to access and ingest in the phloem. Montllor & Tjallingii (1989) and Tjallingii (1995) add that short periods of pathway phase and long durations of sieve element (phloem) phase indicate plant acceptance by aphids, what was not the case of these two exotic species.

Multiple penetrations of short duration into the sieve elements by *G. ficicola* and *G. psidii* on *F. benjamina* and *P. guajava* may indicate apparent unsuitability of these plants for sustained phloem ingestion, in spite of being suitable host plants in the place of origin of these aphids. The high percentage of time spent in non-probing (np) and pathway phases in contrast with the limited time in the phloem phase by *G. ficicola* and *G. psidii* may suggest the presence of deterrent chemical compounds in the plant epidermis or along the stylet pathway through the mesophyl tissue, which might contribute for the long time required for reaching the sieve elements (pathway phase) and non-sustained phloem ingestion. Tosh *et al* (2001) confirmed, based on the short and unsustained feeding on the sieve elements, that certain host plants or varieties pose either chemical or physical barriers for some subspecies of *Aphis fabae* Scopoli, but not for others. These differences appear to be a function of individual plant species and not for all hosts, since some alternate plants could readily support a given aphid subspecies, showing an evolutionary role in the diversification of host plants for *A. fabae*.

The EPGs for *G. ficicola* and *G. psidii* showed several potential drops (pds) in the pathway phase (Fig 2) indicating relative acceptance of the host, despite the short sustained phloem ingestion, agreeing with Diaz-Montano *et al* (2007) who reported that the soybean

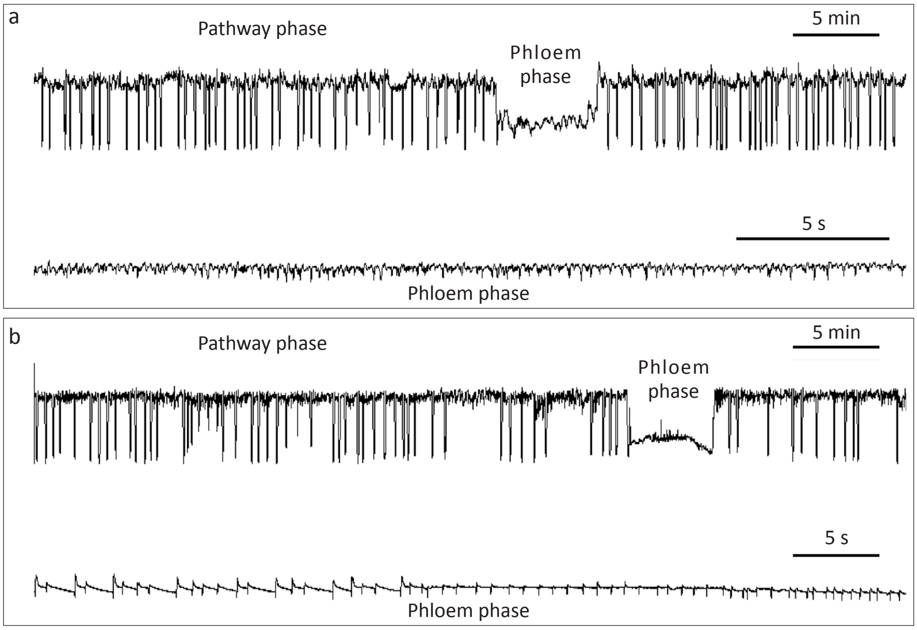

Fig 2 General scheme of pathway and phloem phases for *Greenidea ficicola* (a) and *Greenidea psidii* (b) feeding on *Ficus benjamina* and *Psidium guajava*, analyzed by the Electrical Penetration Graph (EPG) technique. Several pds (potential drops) were observed in the pathway phase.

aphid *Aphis glycines* Matsumura shows, on susceptible soybean genotypes, greater number of pds than those in resistant plants, as a sign of host plant acceptance, as well as much longer phloem feeding phase. In this study, 97% of *G. ficicola* reached the phloem and 57% showed sustained phloem ingestion, but with a total duration of only 3.2h, in average. For *G. psidii*, 80% reached the phloem and out of these, only 17% showed sustained phloem ingestion (0.2h, in average), indicating that some barriers, not elucidated in this study, are interfering in the interaction between *G. psidii* and its host *P. guajava*. This fact may explain the difficulty we found to rear this aphid species in the laboratory.

Other factors, such as the morphology and nutritional composition of host plants or their subspecies or varieties, as well as particular insect behaviors may have affected the feeding patterns of *G. ficicola* and *G. psidii*. For example, Morris & Foster (2008) report that the horned aphids (Cerataphidini) use the exact feeding site left by another individual of the same species to facilitate the pathway to reach the phloem, but this was not evaluated in our study.

In Fig 2, the waveforms and phases were similar for the two *Greenidea* species. The phloem phase longer than 10 min indicates sustained phloem ingestion and plant acceptance (Tjallingii & Mayoral (1992), what is expected when the insect is well-adapted to its host plant or if there is no resistance plant factor. In our experiment, the two species *Greenidea* showed reduced time in the phloem phase and only a few aphids showed sustained phloem ingestion.

The probing and feeding behavior patterns characterized by EPG we obtained suggest that these two newly introduced aphid species, *G. ficicola* and *G. psidii,* originally from Asia, are not yet adjusted to the new environment or to the host cultivar. According to Cox (2004), an alien or exotic species requires time to disperse throughout favorable habitat patches in a new area and to build up populations capable of producing abundant offspring, and eventually become a pest. Nevertheless, as many alien species do, these *Greenidea* species may be introduced into new areas where they are initially poorly adapted; with time, however, adaptation by a few populations may result in successful establishment in the same new areas. Knowledge of how genetic diversity, life-cycle, insect-plant and environment interactions of exotic species differ in their native and introduced areas may improve the understanding of population biology and provide a theoretical basis for successful management of invasive species.

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References

Beardsley JW (1993) *Greenidea formosana* (Maki), an aphid new to the Hawaiian islands (Homoptera:Aphididae: Greenideinae). Proc. Hawaiian Entomol Soc 32: 157-158.

Blackman RL, Eastop VF (1984) Aphids on the world's crop – an identification guide. Chichester, Wiley, 466p.

Caillaud MC, Via S (2000) Specialized feeding behaviour influences both ecological specialization and assortative mating in sympatric host races of pea aphids. Am Nat 156: 606-621.

Cox GW (2004) Alien species and evolution: evolutionary ecology of exotic plants, animals, microbes, and interacting native species. Washington, Island Press, 377p.

Diaz-Montano J, Reese JC, Louis J, Campbell LR (2007) Feeding behavior by the soybean aphid (Hemiptera: Aphididae) on resistant and susceptible soybean genotypes. J Econ Entomol 100: 984-989.

Dieckmann U, O'Hara B, Weisser W (1999) The evolutionary ecology of dispersal. Trends Ecol Evol 14: 88-90.

Gabrys B, Tajallingii WF (2002) The role of sinigrin in host plant recognition by aphids during initial plant penetration. Entomol Exp Appl 104: 89-93.

Halbert SE (2004) The genus *Greenidea* (Rhyncota: Aphididae) in the United States. Fla Entomol 87: 159-163.

Hammer O, Harper DAT, Ryan PD (2001) PAST: Paleontological statistics software package for education and data analysis. Palaeont Electron 4:1-9.

Hidalgo NP, Muller WV, Durante, MPM (2009) *Greenidea psidii* (Hemiptera: Aphididae: Greenideinae) new invasive aphid in Costa Rica. Fla Entomol 92: 396-398.

Klingauf FA (1987) Host plant finding and acceptance, p.209-223. In Minks AK, Harrewijn P (eds) Aphids, their biology, natural enemies and control, Vol. A, Amsterdam, Elsevier, 450p.

Kordan B, Gabrys B, Dancewicz K, Lahuta LB, Piotrowicz-Cieslak A, Rowiñska E (2008) European yellow lupine, *Lupinus luteus*, and narrow-leaf lupine, *Lupinus angustifolius*, as hosts for the pea aphid, *Acyrthosiphon pisum*. Entomol Exp Appl 128: 139-146.

Lazzari SMN, Zonta de Carvalho RC, Cardoso JT, Calado DC (2006) First record of *Greenidea psidii* van der Goot and comparison with *Greenidea ficicola* Takahashi (Hemiptera: Aphididae) in Brazil. Zootaxa 1235: 63-68.

Mittler TE (1957) Studies on the feeding and nutrition of *Tuberolachnus salignus* (Gmelin) (Homoptera, Aphididae). I. The uptake of phloem sap. J Exp Biol 34: 334-341.

Montllor CB, Tjallingii WF (1989) Stylet penetration by two aphid species on susceptible and resistant lettuce. Entomol Exp Appl 52: 103-111.

Morris G, Foster WA (2008) Dueling aphids: electrical penetration graphs reveal the value of fighting for a feeding site. J Exp Biol 211: 1490-1494.

Müller CB, Williams IS, Hardie J (2001) The role of nutrition, crowding and interspecific interactions in the development of winged aphids. Ecol Entomol 26: 330-340.

Prado E, Tjallingii WF (2007) Behavioral evidence for local reduction of aphid-induced resistance. J Insect Sci 7: 48.

Powell G, Tosh CR, Hardie J (2006) Host plant selection by aphids: behavioral, evolutionary, and applied perspectives. Annu Rev Entomol 51: 309-330.

Reese JC, Margolies DC, Backus EA, Noyes S, Bramelcox P, Dixon AGO (1994) Characterization of aphid host plant resistance and feeding behavior through use of a computerized insect feeding monitor. In Ellsbury MM, Backus EA, Ullman DL (eds) History, development and application of electronic monitoring and other techniques in the study of homopteran feeding behavior. Proceedings. Thomas Say Publications in Entomology, Entomological Society of America, Lanham, Maryland, USA, p.70-1001.

Sakai AK, Allendorf FW, Holt JS, Lodge DM, Molofsky J, With KA, Baughman S, Cabin RJ, Cohen JE, Ellstrand NC, McCauley DE, O'Neil P, Parker IM, Thompson JN, Weller SG (2001) The population biology of invasive species. Annu Rev Ecol Syst 32: 305-332.

Schoonhoven L M, Jermy T, Van Loon J J A (1998) Insect-plant biology: from physiology to evolution. London, Chapman & Hall, 409p.

Sousa-Silva CR, Brombal JC, Ilharco FA (2005) *Greenidea ficicola* Takahashi (Hemiptera: Greenideidae), a new aphid in Brazil. Neotrop Entomol 34:1023-1024.

Statsoft Inc. (2004) Statistica (data analysis software system). Version 7. www.statsoft.com.

Tjallingii WF (1978) Electronic recording of penetration behaviour by aphids. Entomol Exp Appl 24: 721-730.

Tjallingii WF (1988) Electrical recording of stylet penetration activities. In Minks AK, Harrewijn P (eds) Aphids, their biology, natural enemies and control. Amsterdam, Elsevier, 450p.

Tjallingii WF (1994) Sieve element acceptance by aphids. Eur J Entomol 91: 47-52.

Tjallingii WF (1995) Regulation of phloem sap feeding by aphids, UK, p.190-209. In Chapman RF, Boer G (eds) Regulatory mechanisms in insect feeding. London, Chapman & Hall, 398p.

Tjallingii WF, Esch TH (1993) Fine-structure of aphid stylet routes in plant-tissues in correlation with EPG signals. Physiol Entomol 18: 317-328.

Tjallingii WF, Mayoral A (1992) Criteria for host acceptance by aphids. In Menken SBJ, Visser JH, Harrewijn P (eds) Proceedings 8th Int. Symp. Insect-plant relationships Kluwer Acad. Publ. Dordrecht, Netherlands, p.280-282.

Tosh CR, Powell G, Hardie J (2002) Maternal reproductive decisions are independent of feeding in the black bean aphid, *Aphis fabae*. J Insect Physiol 48: 619-629.

Tosh CR, Powell G, Hardie J (2003) Decision making by generalist and specialist aphids with the same genotype. J Insect Physiol 49: 659-669.

Tosh CR, Walters KFA, Douglas AE (2001) On the mechanistic basis of plant affiliation in the black bean aphid (*Aphis fabae*) species complex. Entomol Exp Appl 99:121-125.