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Host preference and nymph performance of B and Q putative species of *Bemisia tabaci* on three host plants

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Abstract Host selection is central to understanding the evolution of the interaction between herbivorous insects and host plants. Most studies on host selection of herbivorous insects are focused on the optimal oviposition theory which posits that the herbivores preferentially oviposit on plants that provide optimal conditions for offspring development (preference–performance hypothesis). However, the positive correlation between female oviposition preference and offspring performance is not always observed. Here, we determined the relationship between whitefly settling and oviposition preference and nymph performance of B and Q putative species of *Bemisia tabaci* on three host plants, cotton *Gossypium hirsutum* L., tomato *Lycopersicum esculentum* Mill, and poinsettia *Euphorbia pulcherrima* Wild. We further investigated whether nutritional and defensive chemistry of the three host species shaped whitefly settling and oviposition preference of both putative species. Foliar chemistry differed significantly among the three host species. Compared to cotton and tomato foliage, poinsettia foliage was 8 % lower in nitrogen, 60 % higher in carbohydrate, and 90 % higher in phenolic compounds, respectively. When given a choice, B and Q putative species of *B. tabaci* preferred settling on nutritionally superior tomato, whereas both putative species preferentially oviposited on nutritionally inferior poinsettia. Nymph survivorship of B and Q putative species was substantially reduced and nymph developmental duration (egg-to-adult) was markedly prolonged on poinsettia relative to those reared on cotton and tomato. Therefore, our results are consistent with the optimal foraging theory, rather than the optimal oviposition theory. Females of B and Q putative species of *B. tabaci* preferentially ovipositing on poinsettia may be a trade-off between nymph performance and the avoidance of natural enemy.

Keywords *Bemisia tabaci* · Oviposition preference · Host suitability · Nymph performance

Introduction

Most research on host choice by arthropods is based on optimal oviposition theory, which is central to understanding the evolution of the interaction between herbivorous insects and host plants (Scheirs et al. 2000; Mayhew 2001; Scheirs and De Bruyn 2002). Female oviposition preference of the herbivorous insects correlates with host suitability for their offspring performance, since females are expected to oviposit on high quality hosts to maximize their fitness (Jaenike 1978). Numerous studies have investigated the relationship between female oviposition preference and offspring performance (Thompson 1988; Mayhew 1997; Berdegué et al. 1998; Gripenberg et al. 2010). In some cases, female oviposition preference, as expected, seems clearly adaptive, with offspring performing better on the host plants females preferred (Mayhew 1997; Gripenberg et al. 2010). However, such a positive relationship between

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female oviposition preference and offspring performance is not always observed (Mayhew 1997; Berdegué et al. 1998; Gripenberg et al. 2010). Several evolutionary and ecological explanations have been proposed to explain the apparent mismatch between female oviposition preference and offspring performance (Thompson 1988; Gripenberg et al. 2010). It is well documented that female oviposition preference in phytophagous insects may be shaped by numerous factors. These factors include the chemically mediated host suitability (defensive chemicals and/or nutritional quality), predators and parasites (Dicke 2000; Murphy 2004; Singer et al. 2004; Videla et al. 2006; Wiklund and Friberg 2008; Rodrigues et al. 2010), competitive interaction between interspecies and/or intraspecies (Mayhew 1997; Gripenberg et al. 2010), previous feeding experience (Papaj and Prokopy 1989) and spatial distribution of diverse host plants (Thompson 1988; Ballabeni et al. 2001). Therefore, the optimal oviposition theory seems inadequate for predicting the host selection of herbivorous insects (Mayhew 2001).

Apart from the optimal oviposition theory, the optimal foraging theory may to some extent play an important role in shaping host choice (Jaenike 1986; Scheirs et al. 2000; Scheirs and De Bruyn 2002; Scheirs et al. 2004). For example, females of the grass miner, *Chromatomyia nigra* (Scheirs et al. 2000), and the thistle-feeding beetle, *Altica carduorum* (Scheirs and De Bruyn 2002), oviposit where they feed, and they feed on the hosts that best enhance their performance rather than offspring. In some cases, herbivorous insects seem to be bad mothers (Mayhew 2001). Despite a range of literature on host choice, more attention is paid on the optimal oviposition theory (Scheirs et al. 2000; Mayhew 2001; Scheirs and De Bruyn 2002; Gripenberg et al. 2010). There still exists little evidence for a role of the optimal foraging in host choice of herbivorous insects (Scheirs et al. 2000; Scheirs and De Bruyn 2002; Scheirs et al. 2004).

The whitefly, *B. tabaci* (Gennadius), one of the most serious agricultural pests worldwide (Baldin and Beneduzz 2010), comprises a highly differentiated complex species that is yet to be fully resolved. Recent studies indicate that the *B. tabaci* species complex is composed of 11 well-defined high-level groups containing at least 24 morphologically indistinguishable species (Dinsdale et al. 2010; Xu et al. 2010; De Barro et al. 2011). The most widespread ones are the B (Middle East–Asia Minor 1) and Q putative species (Mediterranean), both of which are invasive pests on diverse vegetable, ornamental, and field crops throughout the world (Delatte et al. 2009; Dinsdale et al. 2010; Xu et al. 2010; De Barro et al. 2011). Although the performance of B putative species of *B. tabaci* has been investigated on several host plants (Bethke et al. 1991; Powell and Bellows 1992; Tsai and Wang 1996; Drost et al. 1998; Nava-Camberos et al. 2001; Zang et al. 2006; Islam and Ren 2007; Kakimoto et al. 2007; Baldin and Beneduzz 2010; Qiu et al. 2011), few studies have compared the differences in performance between B and Q putative species on various host species (Muñiz 2000; Muñiz and Nombela 2001; Iida et al. 2009; Tsueda and Tsuchida 2011). In particular, there exist few studies concerning the host choice (the optimal foraging and/or optimal oviposition theory) between B and Q putative species of *B. tabaci*.

According to the neural constraints hypothesis, it is possible that in the presence of various host species, the complex sensory environment may make it difficult for a generalist to make a choice (Bernays 2001; Janz 2003). In the case of polyphagous whiteflies, contrast results were made concerning whitefly host choice when various host species were presented (Bernays and Minkenberg 1997; Bernays 1999; Bird and Krüger 2006). When *B. tabaci* females were presented with a mixture of various host species, individuals moved more, switched between plants more frequently, and stayed feeding in one place for shorter periods of time, compared with the situation when single plant species were available (Bernays 1999). As expected, female whiteflies had a problem selecting a host species when given multiple choices, and their performance was similar to that obtained on the poorer hosts in no-choice experiment (Bernays 1999). Similarly, Bird and Krüger (2006) found that female whiteflies did appear to have difficulty in making a decision on host choice, when only low-ranking hosts were presented. In contrast, little difficulty in host choice was found by females when one high-ranking host was offered (Bird and Krüger 2006). It seems likely that the ranking ability of polyphagous female is at least in part dependent on the combinations of various host species (Ballabeni et al. 2001; Bird and Krüger 2006).

Here, we first investigated whether whitefly settling and oviposition preference differed between B and Q putative species of *B. tabaci* on the three common host plants, cotton *G. hirsutum* (var. BaolingDP99B), tomato *Lycopersicon esculentum* (var. Zhongza 9), and poinsettia *E. pulcherrima.* Second, we determined whether the differences in suitability among the three host plants contributed to the settling and oviposition preference and/or nymph performance of B and Q putative species of *B. tabaci*. Finally, we further tested whether the optimal foraging or optimal oviposition theory shaped female host choice between B and Q putative species of *B. tabaci* on three host plants. This information may contribute to developing suitable management tactics, such as trap cropping to control the whiteflies.

Materials and methods

Insect source and host plant production

The B putative species of *B. tabaci* were originally collected from cabbage (*Brassica oleracea* var. Jingfeng1) in

2004 in Beijing. The Q putative species of *B. tabaci* were originally obtained from poinsettia (*Euphorbia pulcherrima*) in 2008 in Beijing. To minimize any effects of the source plants on the experiments, we maintained the two putative species of *B. tabaci* on cucumber (*Cucumis sativa* var. Zhongnong12), the highly suitable host species in separate insect-proof screened cages (60 × 60 × 60 cm) for at least 20 generations under the laboratory conditions at 25 ± 1 °C, 60 ± 10 % RH and 14L:10D (Bird and Krüger 2006). The purity of the two cultures was monitored every 2–3 generations based on haplotypes of the DNA sequence obtained using the mtCOI primers (Zhang et al. 2005). For the experiments, the host plants of cotton, tomato, and poinsettia were established individually in 12-cm-diameter plastic pots and were used when they were 30-cm tall. Care was taken to select host plants of approximately the same size in each experiment.

Female whitefly settling and oviposition preference

Experiments of whitefly settling and oviposition preference were done as described by Omondi et al. (2005). Briefly, individual plants of cotton, poinsettia, and tomato of approximately the same size were arranged in the form of an even-sided triangle with a side length of 20 cm in a screen cage (60 × 60 × 60 cm). About 300 female whiteflies were collected from either putative species between 7:00–8:00 h, and released at the central of the screen cage above the plant canopy. The aspirator's sampling bottle component containing whiteflies was held inside a clear plastic tumbler hung at the centre of the cage, about 30 cm from the plant canopy. Whiteflies moved to the open top and flew away from the sampling bottle to approach the plants from above. The number of whiteflies on each plant was determined after 12, 24, 36, 48, 60, and 72 h, respectively. To avoid whitefly movement between leaves and plant species, counting was observed under dim torchlight just before 06:00 h, and just after 18:00 h. At the end of female settling preference bioassay, all leaves from each plant species were removed and examined under a dissecting microscope to count the numbers of eggs whiteflies laid. The experiments of whitefly settling and oviposition preference of either putative species (B and Q) replicated nine times, respectively.

Nymph survivorship and developmental duration

Nymph survivorship and developmental duration of B and Q putative species of *B. tabaci* on the three host species were measured under the laboratory conditions. Five insect-free host plants of each host species were placed in the insect-proof screened cages, of which B and Q putative species were maintained separately. After 8 h, the plants were removed from the cages. Three extended leaves per plant were selected and marked. The eggs distributed on the unselected leaves were removed under a binocular microscope. The abaxial surface of the selected leaves was drawn and the position of each egg was indicated. These drawings allowed us to follow each whitefly from egg until adult emergence. There were 30–50 eggs per selected leaf. The remaining eggs were also removed under a binocular microscope. Five plants of each host species were introduced into a separate climatic chamber at 27 °C, 60 ± 10 % RH, and a 14L:10D. When fourth-stage nymphs were observed on a specific leaf, the plant was introduced into an insect-proof net, and all of the emerged adults were collected and frozen two times a day. Nymph stages (eggs and nymphs by stage) and adults were recorded and counted daily for each plant. Nymph survivorship was expressed as the proportion of eggs that produced adults. Each selected leaf was considered a replicate in each treatment, and there were 15 replicates per treatment. Developmental time from egg-to-adult was determined for the eggs that developed into adults.

Host plant chemical analysis

Ca 50 g (fresh weight) foliar was randomly collected from three plants of each host species. Half of the fresh foliar dried at 80 °C for 72 h in drying oven for measuring the contents of total phenol, nitrogen, and carbohydrate, while the other half fresh foliar for measuring protein, total amino acid, and free fatty acid. Samples were analysed for total phenol concentration using the Folin–Ciocalteau method with tannic acid as a standard (Kerslake et al. 1998). Leaf water content, as a proportion of fresh weight, was calculated after drying at 80 °C for 72 h. Protein, total amino acid and free fatty acid were assayed according to the reagent label directions (Nanjing jiancheng Ltd Co., Nanjing, Jiangsu Province, China). Nitrogen content was measured using a CNH analyzer (Model ANCA-nt; Europa Elemental Instruments, Okehampton, UK). The total carbohydrates of the host tissues were estimated by the method of Yemm and Willis (1954). The measure of each biochemical components in each host species was repeated four times.

Data analysis

Data were first checked for normality and transformed when necessary to meet the assumption of normal distribution. The proportion of whiteflies (eggs) distributing on various host species was arcsine-square root transformed for analyses. The effects of putative species and host species on female host settling preference were tested by repeated-measures ANOVA, whereas the effects of putative species and host species on female oviposition preference, nymph survival, and developmental time were tested by generalized linear model (GLM, two-way ANOVA). Tukey's test was used to separate treatment means when the main effect was found to contribute significantly. Statistical analyses were performed with SPSS (version 13.0; SPSS Inc., Chicago, IL, USA).

Results

Female whitefly settling and oviposition preference

The dynamics of whitefly distributing on various host species are shown in Fig. 1. There was no significant difference in host settling preference between B and Q putative species ($F_{1,48} < 0.0001$, $P = 0.994$). Both B and Q females preferred settling on tomato over poinsettia and cotton (Fig. 1; $F_{2,48} = 22.24$, $P < 0.0001$). However, both putative species showed no significant difference in host settling preferences over poinsettia and cotton.

Although there was no significant difference in oviposition preference between B and Q putative species (Fig. 2; $F_{1,54} = 0.115$, $P = 0.736$), both putative species preferred ovipositing significantly more on poinsettia over those on tomato and cotton (Fig. 2; $F_{2,54} = 26.219$, $P < 0.0001$).

Nymph survivorship and developmental duration

Nymph survivorship (egg-to-adult) of *B. tabaci* differed greatly in putative species and host species (Fig. 3). Nymph survivorship was higher for Q than for B, regardless of host species ($F_{1,84} = 12.732$, $P = 0.001$). For both putative species, nymph survivorship reared on poinsettia was significantly lower compared to those reared on cotton and tomato ($F_{2,84} = 114.352$, $P < 0.0001$). However, there was no significant difference in nymph survivorship between cotton and tomato.

Nymph of B developed faster than Q (Fig. 4; $F_{1,597} = 9.29$, $P = 0.002$), regardless of the host species. For both putative species, nymph developed (egg-to-adult) slower on poinsettia than those on cotton and tomato (Fig. 4; $F_{2,597} = 173.593$, $P < 0.0001$).

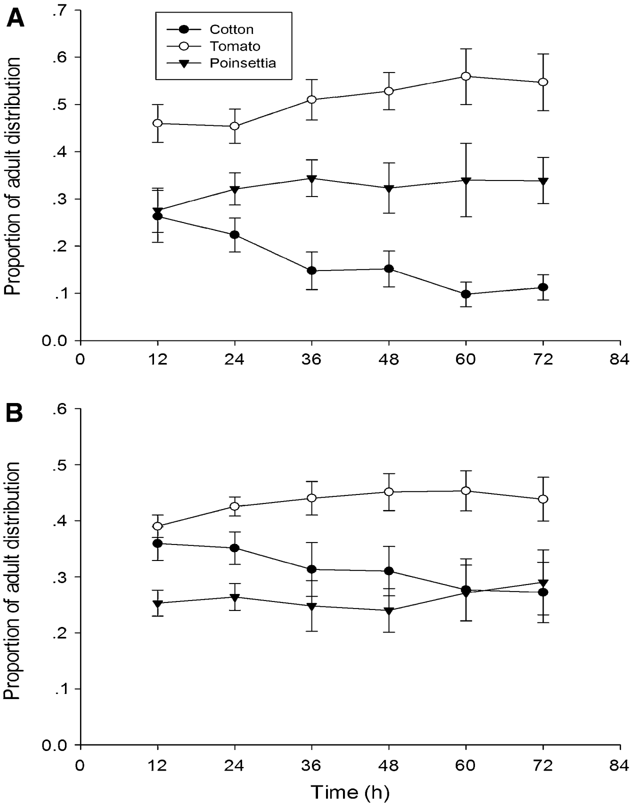

Fig. 1 Mean proportion (±SE) of *Bemisia tabaci* whiteflies settled on different host plants over time in choice test. **a** B putative species of *Bemisia tabaci*. **b** Q putative species of *Bemisia tabaci*

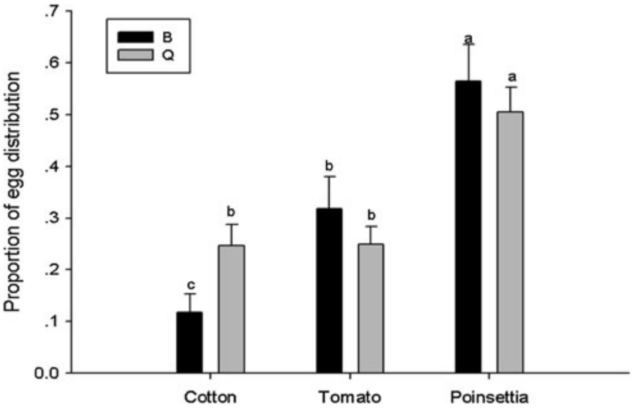

Fig. 2 Mean proportion (±SE) of eggs laid by B and Q putative species females of *Bemisia tabaci* on different host plants in choice test. *Different letters* above the *error bars* indicate significant difference (Tukey's test, $P < 0.05$)

Biochemical compositions of the three plant species

The biochemical compositions of the three plant species are provided in Table 1. The contents of nitrogen ($F_{2,9} = 9.618$, $P = 0.006$), protein ($F_{2,9} = 249.554$, $P < 0.0001$), and water contents ($F_{2,9} = 192.867$, $P < 0.0001$) in tomato were significantly higher than those in cotton and poinsettia, respectively. In contrast, the contents of carbohydrate ($F_{2,9} = 330.058$, $P < 0.0001$), total amino acid ($F_{2,9} = 311.637$, $P < 0.0001$), and total phenol ($F_{2,9} = 317.791$, $P < 0.0001$) in poinsettia were significantly higher than those in cotton and tomato, respectively. However, there was no significant difference in free fatty acid level among the three plant species ($F_{2,9} = 3.055$, $P = 0.097$).

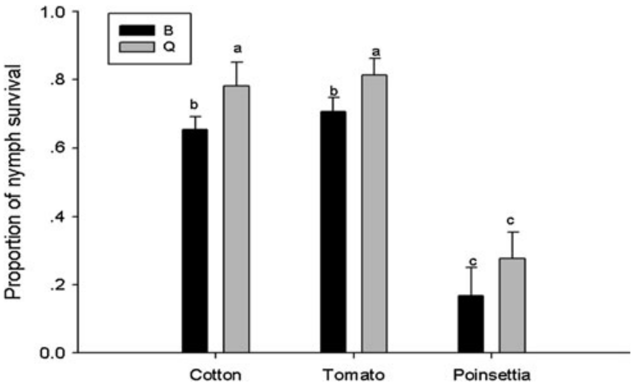

Fig. 3 Mean proportion (±SE) of nymph survival (egg-to-adult) of B and Q putative species of *Bemisia tabaci* on different host plants. *Different letters* above the *error bars* indicate significant difference (Tukey's test, $P < 0.05$)

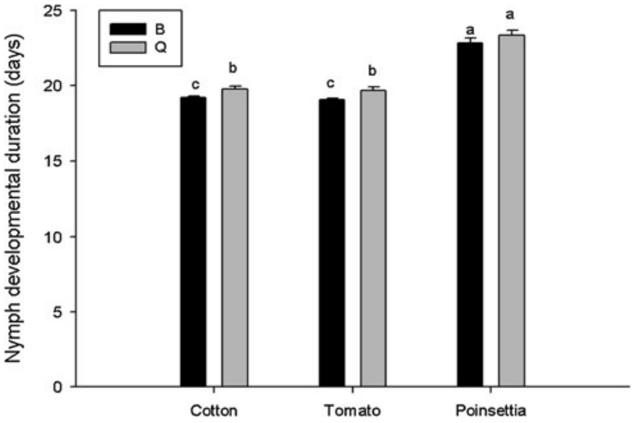

Fig. 4 Mean developmental duration (±SE) of nymph (egg-to-adult) of B and Q putative species of *Bemisia tabaci* on different host plants. *Different letters* above the *error bars* indicate significant difference (Tukey's test, $P < 0.05$)

Table 1 Mean content (±SE) of different biochemical components in cotton, tomato and poinsettia

Biochemical parameters	Cotton	Tomato	Poinsettia
Nitrogen (%)	3.82 ± 0.09b	4.32 ± 0.09a	3.98 ± 0.06b
Carbohydrate (%)	4.23 ± 0.16b	4.19 ± 0.15b	10.55 ± 0.27a
Free fatty acid (μmol/L)	301.65 ± 26.83	383.07 ± 7.80	398.93 ± 43.52
Soluble protein (g/L)	0.06 ± 0.01b	0.85 ± 0.05a	0.05 ± 0.01b
Total amino acid (μmol/L)	10.91 ± 0.62b	9.69 ± 0.32b	36.16 ± 1.29a
Water (%)	80.36 ± 0.31b	88.02 ± 0.43a	79.61 ± 0.23b
Total phenol (%)	3.77 ± 0.51b	2.19 ± 0.13b	22.47 ± 0.96a

The contents of protein, total amino acid, and free fatty acid were presented as the reagent label directions. Contents of total phenol, nitrogen, and carbohydrate were presented with dry mass of foliar. Water content was presented with fresh foliar. Within the row means followed by the same letter are not significantly different

Discussion

Host preference of phytophagous insect is often influenced by nutritional and defensive chemistry, which is one of diverse factors shaping herbivore insects host choice and fitness (Bernays and Chapman 1994). Considering the fact that plant chemistry with low nitrogen, high carbon, and high phenolics has commonly been shown to negatively affect phytophagous insects (Hartley and Jones 1997), in the present study, tomato appears to be the nutritionally superior host plant, followed by cotton, and poinsettia the most inferior host plant. Thus, whiteflies settling and feeding preference and nymph performance of B and Q putative species of *B. tabaci* are consistent with the rank in host plant quality. In contrast, B and Q putative species whiteflies unexpectedly preferred ovipositing and nymph performed poorer on nutritionally inferior poinsettia over cotton and tomato. Therefore, the present study demonstrates that whiteflies of B and Q putative species of *B. tabaci* could accurately rank the suitability of the three host plants for feeding rather than for ovipositing. Consequently, our results are consistent with the optimal foraging theory, rather than the optimal oviposition theory.

Although B and Q putative species of *B. tabaci* are extremely polyphagous, previous studies have shown that B and Q putative species vary substantially in many fitness parameters in response to various host species (Muñiz 2000; Muñiz and Nombela 2001; Iida et al. 2009; Tsueda and Tsuchida 2011). In the present study, whiteflies of B and Q putative species of *B. tabaci* preferred settling on nutritionally superior tomato, whereas both putative species preferentially oviposited on nutritionally inferior poinsettia. It seems likely that there is no significant divergence in whiteflies settling and oviposition preference over the three host species between B and Q putative species. Nevertheless, the nymph survivorship of Q putative species was significantly higher and developmental duration was substantially prolonged than those of B, regardless of host species. Therefore, nymph of Q putative species successfully matures at the expense of prolonged developmental duration. It seems likely that Q whiteflies have the capacity to adapt to a wider range of plant species relative to B whiteflies. Similar results are reported in previous studies (Muñiz 2000; Muñiz and Nombela 2001; Iida et al. 2009; Tsueda and Tsuchida 2011). The higher capacity of Q whiteflies to adapt to a wider range of plant species may to some extent contribute to the displacement of B by Q putative species in China and Japan (Chu et al. 2010; Pan et al. 2011; Tsueda and Tsuchida 2011).

In the present study, whiteflies of B and Q putative species preferred settling and feeding on nutritionally superior tomato over cotton and poinsettia. It seems likely that both B and Q whiteflies accurately rank the three host species, which is inconsistent with the neural constraints hypothesis (Bernays and Minkenberg 1997; Bernays 1999). In whiteflies, the conflicting results concerning whitefly host choice were made when various host species were presented (Bernays and Minkenberg 1997; Bernays 1999; Bird and Krüger 2006). The discrepancy may be due to the differences in taxonomy status of the whitefly and/or the combination of various host species (González-Zamora and Moreno 2011). Nevertheless, the differences in host quality among host species and/or different cultivars within a host species may be the most possible explanation for the discrepancy. Ideally, the larger the difference in quality among host species, the more likely are female herbivores to select high-ranking host species (Craig and Itami 2008). The neural constraints hypothesis may only operate when the differences in host quality are negligible (Bernays and Minkenberg 1997).

Even though we found that females of B and Q putative species of *B. tabaci* identically preferred ovipositing on poinsettia over cotton and tomato, nymphs of both putative species on poinsettia unexpectedly performed poorer (e.g. lower survival and slower development) than those reared on the other two host species. It is apparently inconsistent with the optimal oviposition theory (Jaenike 1978). Perhaps the poor performance of nymphs reared on poinsettia results from inadequate nourishment levels, as well as toxicity effects of host chemical defenses. The decision females make to oviposit on a particular host plant is a complex process that involves many factors (Shikano et al. 2010; Gripenberg et al. 2010). Several possible explanations, in the present study, are proposed to account for the poor relationship between whiteflies oviposition preference and nymph performance of B and Q putative species of *B. tabaci*. First, the evolutionary conflict between parent and nymph may at least partially explain the poor preference–performance correlation (Nylin and Janz 1996; Scheirs et al. 2000; Mayhew 2001; Scheirs and De Bruyn 2002; Scheirs et al. 2004; Gripenberg et al. 2010). In some cases, females lay eggs on host species that serve as food to the adult and confer them a better performance, being sub-optimal to offspring performance. In experiments with oligophagous species *Chromatomyia nigra*, females laid eggs where they fed, and such host conferred better performance to adults than to offspring (Scheirs et al. 2000). Ideally, females should try to maximize their fitness by optimizing adult and offspring performance. However, optimal resources for adults and offspring may be separated by some ecological and/or evolutionary factors, from which the parent-offspring conflict may arise (Nylin and Janz 1996; Mayhew 2001; Scheirs et al. 2004; Pöykkö 2006; Gripenberg et al. 2010). In the present study, the poor link between female oviposition preference and nymph performance may stem from the fact that the “selfish” females optimize their own fitness (survival and fecundity) on nutritionally superior tomato whereas oviposition on nutritionally inferior poinsettia at the expense of nymph survival and development. Second, patterns of host plant use by phytophagous insects, however, might result from tri-trophic interactions (Dicke 2000). This view invokes the concept of enemy free space, hypothesizing that phytophagous insects use particular host species in particular way to enhance survival via defense or refuge from their natural enemies (Singer et al. 2004). A trade-off between host suitability and avoidance of natural enemy may shape herbivores to prefer nutritionally inferior host plants on which the risk of being attacked is low, over superior host plants that are frequently visited by natural enemy (Dicke 2000; Murphy 2004; Singer et al. 2004; Videla et al. 2006; Wiklund and Friberg 2008; Rodrigues et al. 2010). In the case of whiteflies, whose nymphs have limited mobility that live closely within the sphere of the leaf’s microatmosphere, the importance of plant features is compounded. Whiteflies may prefer ovipositing on nutritionally inferior host plants if these hosts afford greater protection from natural enemies than on nutritionally superior hosts. For example, the thick trichomes, pubescence, and the relative abundance of vascular bundles of host leaves are positively related to female *B. tabaci* oviposition preference (Chu et al. 1995; McAuslane 1996; Khan et al. 2011). On the other hand, indirect (via the whiteflies) plant-mediated effects on natural enemies are common (Inbar and Gerling 2008). For example, predatory lacewings failed to reach pupation when feeding on *B. tabaci* that had reared on lima beans and poinsettia, probably because of their poor nutritional value (Legaspi et al. 1996). Similarly, significantly smaller and less fecund females *Eretmocerus mundus* were found when paratizising on *B. tabaci* nymphs that developed on sunflowers than on cabbage (Gerling et al. 2006). Under the natural conditions, it is expected that the increase in fitness resulting from enemy free space may compensate for any fitness reduction resulting from development on the nutritionally inferior host plants.

Third, we do not completely rule out the possibility that a poor relationship between female oviposition preference and offspring performance results from a lack of evolutionary history (Wiklund 1975; Legg et al. 1986; Thompson 1988; Berdegué et al. 1998). Herbivore populations that are undergoing rapid evolution in preferences may not show a correlation or concordance between preference and performance, but concordance between these traits is expected in stable populations (i.e., populations not undergoing rapid preference evolution, Singer et al. 1994).

For example, it is possible that the association of herbivore *Spodoptera exigua* with host plants *Apium graveolens* and *Chenopodium murale* is too recent for preference to correspond with performance (Berdegué et al. 1998).

Given the fact that nymph survival of B and Q putative species of *B. tabaci* was substantially reduced and nymph developmental duration (egg-to-adult) was markedly prolonged on poinsettia relative to those reared on cotton and tomato, both putative species preferentially ovipositing on poinsettia may reduce whitefly population build-up. Therefore, poinsettia may be developed as a trap "crop" system to control B and/or Q putative species in field.

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