Feeding Experience of *Bemisia tabaci* (Hemiptera: Aleyrodidae) Affects Their Performance on Different Host Plants

M. Mostafizur Rahman Shah^{1,2,3}, Tong-Xian Liu^{1,2*}

1 State Key Laboratory of Crop Stress Biology in Arid Areas, Northwest A&F University, Yangling, Shaanxi, China, 2 Key Laboratory of Integrated Pest Management on the Loess Plateau of Ministry of Agriculture, Northwest A&F University, Yangling, Shaanxi, China, 3 Wheat Research Center, Bangladesh Agricultural Research Institute, Dinajpur, Bangladesh

Abstract

The sweetpotato whitefly, Bemisia tabaci biotype B is extremely polyphagous with >600 species of host plants. We hypothesized that previous experience of the whitefly on a given host plant affects their host selection and performance on the plants without previous experience. We investigated the host selection for feeding and oviposition of adults and development and survival of immatures of three host-plant-experienced populations of B. tabaci, namely Bemisia-eggplant, Bemisia-tomato and Bemisia-cucumber, on their experienced host plant and each of the three other plant species (eggplant, tomato, cucumber and pepper) without previous experience. We found that the influence of previous experience of the whiteflies varied among the populations. All populations refused pepper for feeding and oviposition, whereas the Bemisia-cucumber and the Bemisia-eggplant strongly preferred cucumber. Bemisia-tomato did not show strong preference to any of the three host paints. Development time from egg to adult eclosion varied among the populations, being shortest on eggplant, longest on pepper, and intermediate on tomato and cucumber except for the Bemisia-cucumber developed similarly on tomato and pepper. The survivorship from egg to adult eclosion of all populations was highest on eggplant (80-98%), lowest on pepper (0-20%), and intermediate on tomato and cucumber. In conclusion, the effects of previous experience of whiteflies on host selection for feeding and oviposition, development, and survivorship varied depending on host plants, and host plants play a stronger role than previous experience. Preference of feeding and oviposition by adults may not accurately reflect host suitability of immatures. These results provided important information for understanding whitefly population dynamics and dispersal among different crop systems.

Citation: Shah MMR, Liu T-X (2013) Feeding Experience of *Bemisia tabaci* (Hemiptera: Aleyrodidae) Affects Their Performance on Different Host Plants. PLoS ONE 8(10): e77368. doi:10.1371/journal.pone.0077368

Editor: Nicolas Desneux, French National Institute for Agricultural Research (INRA), France

Received March 19, 2013; Accepted September 2, 2013; Published October 11, 2013

Copyright: © 2013 Shah et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Funding: This work was partially supported by the National Basic Research 359 Program of Ministry of Science and Technology, China (973 Program, 2012CB114105 and 2012CB017359), Special Fund for Agro-Scientific Research in the Public Interest (201303019), and China Agriculture Research System (CARS-25-B-06). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing interests: The authors have declared that no competing interests exist.

* E-mail: txliu@nwsuaf.edu.cn

Introduction

The sweetpotato whitefly, *Bemisia tabaci* Gennadius (*=Bemisia argentifolli* Bellows and Perring) (Hemiptera: Aleyrodidae) biotype B, is one of the most important pest insects of horticultural and some of agronomic crops in the tropics and subtropics of the world and in confined surroundings of other areas [1,2]. In 1949, *B. tabaci* was first documented in China [3], though it was not considered a pest until the mid 1990s [4,5]. In 1990s, it became a destructive pest in China that was recognized as an invasive new biotype, biotype 'B' [6-8]. Subsequently, the whitefly has been recorded injuring crops and ornamentals in most provinces in China and economic losses caused by this pest continuously increased

[9]. It has been recorded from a total of 361 plant species in 89 families in south, southeast, middle, north and northwest of China where many vegetables, filed crops and ornamental crops in the families of Compositae, Cruciferae, Cucurbitaceae, Solanaceae and Leguminosae were the most preferred hosts [8,10-12].

Bemisia tabaci shows dissimilar preference concerning their host suitability, oviposition, adaptation, and efficiency of virus transmission [7,13]. It has a diverse host range [14,15] and consequently easily adapts to new hosts and geographic regions. Apart from Antarctica, it has been recorded throughout the world [7,16], while it infests almost 600 plant host species, including eggplant, tomato, cucumber, and pepper [17,18].

These plant hosts could change the fitness of establishment of *B. tabaci* biotype B putative species [19,20].

Bemisia tabaci exhibited significant oviposition preference among plant hosts [21] and leaf surfaces of the same host [21,22]. Their oviposition preference is positively correlated with host quality for their offspring performance [23-25]. Nonetheless, prior feeding experience [26] and diverse plant distribution [27,28] might mediate the performance of phytophagous insects.

Although a large number of investigations have examined the performance of putative species of Bemisia tabaci biotype B on various plant hosts [15,29-35], few studies have compared the differences in fitness of B. tabaci populations with previous feeding experience on particular host species. We hypothesized that previous experience of the whitefly on a given host plant affects their host selection and performance on plants compared to populations without previous experience on that plant. We tested our hypothesis using three host-plantexperienced populations of B. tabaci, namely Bemisiaegoplant, Bemisia-tomato and Bemisia-cucumber, and determined host selection for feeding and oviposition of adults, and development and survival of immatures on their natal host plant and each of the three other plant species (tomato, eggplant, cucumber and pepper).

Materials and Methods

The study described was carried out in the Key Laboratory of Applied Entomology, Northwest A&F University, Yangling, Shaanxi, China from October 2011 to January 2013.

Host Plants

Eggplant, Solanum melongena L. (Solanaceae) cv. 'Zichanggie'; tomato, Solanum lycopersicum L. (Solanaceae) cv. 'Florida Lanai'; cucumber, Cucumis sativus L. (Cucurbitaceae) cv. 'Jinchun'; and pepper, Capsicum annuum L. (Solanaceae) cv. 'Qiemen-Tianjiao' were used. Plant seeds were germinated and seedlings were raised in plastic potting trays with a potting mix (a mixer of peat moss, vermiculite, and perlite at 5:1:1 ratio by volume) inside a growth chamber maintaining at 25±1°C, 75±5% RH, and a photoperiod of 16L: 8D h at a light intensity of 1400-1725 lux. The plant seedlings were individually transplanted in 15 diameter plastic pots with the same potting mix for mass-rearing of whiteflies. The plants with whiteflies were maintained inside air-conditioned insectaries at 25 ± 2°C, 65 ± 5% RH, and a photoperiod of 16L: 8D h at a light intensity of 1400-1725 lux. The plants used for bioassays were grown in 10 cm diameter plastic pots until five to six true leaves were present, and the second and third leaves from the top of the plant (the highest fully expanded leaves) were used for all tests. All plants were watered as per necessary and fertilized with "Harvest More 20-20-20+TE", a dry soluble fertilizer at a rate of 1 g/L water in seven-day intervals.

Whitefly culture

Bemisia tabaci culture originated from our insectaries at the Key Laboratory of Applied Entomology, Northwest A&F

University, Shaanxi, China, where it was previously cultured on tomato (*Solanum lycopersicum var.* 'Florida Lanai'). Adult *B. tabaci* used in this study was identified by mitochondrial COI gene as biotype B [36]. Later, the whiteflies were cultured separately (stock rearing) on eggplant, tomato and cucumber, namely Bemisia-tomato, Bemisia-eggplant and Bemisia-cucumber, for 8-10 generations, but did not have a pepper population due to high mortality [15,29,37]. The whiteflies were cultured in large screen cages ($65 \times 65 \times 65$ cm) inside air conditioned insectaries with the environmental conditions of 25 ± 2°C, RH 65 ± 5%, and a photoperiod of 16L:8D h at a light intensity of 1400-1725 lux. Newly emerged adult whiteflies were used for bioassays and tests were done at the same environmental conditions.

Host selection and oviposition of adults

Agar medium was prepared in 8.5 cm diameter sterilized clear plastic petri dishes. Leaf discs, 2 cm in diameter, were used to standardize the leaf area from each of the four plant species. Four leaf discs, one from each tested plant species, were placed randomly in a circle with equal distance among the leaf discs on the agar medium to keep the leaf discs fresh. The leaf discs were placed with the adaxial surface down on the agar and the abaxial surface up to examine feeding choice. Then the petri dishes with leaf discs were placed upside down to simulate leaves on the plants with the abaxial surface down. Twenty males and 20 females of adult whiteflies (10 adults/ disc) were released into each petri dish. The movement of adults among leaf discs for their feeding preference and behavior was recorded continuously for 24 h using a digital CCD camera (LX-IR920Y, 1/3" SONY 700TVL, Japan). Every test was initiated at 10:00 am each day. Video recording was aided with a 25-W lamp during the dark period. The recorded video was replayed continuously on a computer monitor to observe movement of whitefly adults for feeding and leaf disc selection. Then, number of whitefly eggs on each leaf disc was counted under a stereomicroscope. Eight replications were made with a completely randomized design.

No choice oviposition

A leaf clip-on cage was used in this bioassay, while the cage was made according to Mouttet et al. [38] with some modifications. In brief, the size of the clip cage was 3.5 cm in diameter × 4 cm in height and about 5.25 g weight, and was made of a plastic cup where a metallic clip was used to hold the cage on abaxial leaf surface. There had a circular opening (2.5 cm in dimater) at the bottom of the cage which was covered with nylon mesh netting for ventilation, and a small hole (2-3 mm in diameter) was made at the side of cage to introduce adult whiteflies. The leaf clip-on cage was attached on the abaxial surface of a leaf of each of the four plant species. One mated female (24-48 h old) was introduced into each clip-on cage, and numbers of eggs laid on abaxial surface of the leaf were counted after three days of female introduction. Four plants of each species and two top fully expanded leaves were used. Each leaf was considered as one replication.

Development and survivorship of whitefly

Four plants, one from each species were used, and two top fully expanded leaves were selected from each plant. Thirty couples of newly emerged adult whiteflies developed on each three colonies were confined in leaf-clip on cage onto the abaxial leaf surfaces of each of the four plant species. All whiteflies were removed from the cages 4 hours after adult introduction to get homogeneously aged eggs. Approximately 20-35 eggs were kept on each leaf which was considered as a replication of each treatment. Among them ten eggs were randomly selected and marked for developmental study (from egg to adult eclosion) while all eggs were monitored for survivorship. The immatures were exmined daily under a stereomicroscope until they either developed to adults or died.

Data Analysis

First, we tested the normality of all data using the Shapiro-Wilk test with the null hypothesis that all data were normally distributed; and we found that the P-values in all data sets were greater than 0.05, and then we accepted our null hypothesis that our data were normally distributed [39]. In the feeding choice bioassays, the data of the number of adults moved on different leaf discs were analyzed through linear mixed model with repeated measurements of time where the time factor resulted in significant differences only on Bemisia-cucumber population. Therefore, further factorial ANOVA with time factor was carried out for the Bemisia-cucumber (PROC MIXED; SAS Version 9.2) [40]. The data of number of eggs in both the choice and no choice bioassays for oviposition, development duration and survival of immature bioassays were subjected to factorial ANOVA to test the effect of whitefly populations, host plants and their interactions as well. Means were separated using the least significant difference test (LSD) at $P \leq 0.05$ when significant treatment effects were detected [40].

Results

Feeding and oviposition choice

Adult distribution dynamics in feeding choice of different whitefly populations on various host species are shown in Figure 1. The feeding choices of whitefly populations varied greatly ($F_{2,1008}$ = 10.16, P < 0.001) to their natal host and other offered host plants. The Bemisia-eggplant showed significant differences for feeding among the plants ($F_{3,336}$ = 199.60, P <0.001) but not with time factor ($F_{11,336}$ = 0.84, P = 0.605) and had no significant interactions ($F_{33,336}$ = 0.67, P = 0.922) (Figure 1A). However, cucumber attracted the highest number of adults among the four host plants at 4-24 h after adult introduction and pepper attracted the least number, whereas eggplant and tomato showed intermediate attraction. In case of Bemisiatomato, the adults attracted varied on different host plants $(F_{3,336} = 65.71, P < 0.001)$, but not either with time factor $(F_{11,336})$ = 1.87, P = 0.042) or their interactions ($F_{33,336} = 1.05$, P =0.393) as shown in Figure 1B. Tomato had more whiteflies than other host plants 4 and 6 hours after adult introduction, and eggplant had more adults 18, 20, 22 and 24 hours after adult introduction, whereas pepper had the lowest number of adults all over the time. In contrast, the Bemisia-cucumber showed

significant feeding preferences regarding plants ($F_{3,336}$ = 486.16, P < 0.001), times ($F_{11.336} = 3.63$, P < 0.001), and their interactions ($F_{33,336}$ = 3.15, P < 0.001) (Figure 1C). The greatest number of adults were found on cucumber at a 2-h interval for 24 h (2 h: $F_{3,28}$ = 14.317, P < 0.001; 4 h: $F_{3,28}$ = 16.568, P <0.001; 6 h: F_{3.28} = 19.955, P < 0.001; 8 h: F_{3.28} = 30.815, P < 0.001; 10 h: F_{3.28} = 44.451, P < 0.001; 12 h: F_{3.28} = 53.157, P < 0.001; 14 h: F_{3.28} = 62.596, P < 0.001; 16 h: F_{3.28} = 54.335, P < 0.001; 18 h: F_{3.28} = 53.764, P < 0.001; 20 h: F_{3.28} = 64.939, P < 0.001; 22 h: F_{3.28} = 65.922, P < 0.001; 24 h: F_{3.28} = 64.297, P < 0.001) (Figure 1C). Eggplant had the least number of adults at 2-8 hours, and pepper had the least number of adults at 14-24 h. The oviposition in choice tests varied significantly among the populations ($F_{2.84}$ = 3.74, P = 0.023), plants ($F_{3.84}$ = 32.99, P < 0.001) and their interactions ($F_{6.84}$ = 12.06, P < 0.001) (Figure 2.) For Bemisia-eggplant, the whiteflies oviposited the highest number of eggs ($F_{3,28}$ = 11.322, P < 0.001) on cucumber and eggplant whereas the whiteflies oviposited the lowest number of eggs on pepper (Figure 2A). The females of Bemisia-tomato oviposited similar numbers of eggs on eggplant, tomato and cucumber, and less on pepper than on those three plants ($F_{3,28}$ = 6.276, P < 0.002) (Figure 2B). The female adults of Bemisiacucumber oviposited significantly more eggs on cucumber ($F_{3,28}$ = 92.181, P < 0.001) among the four plants (Figure 2C).

No choice oviposition

The numbers of eggs laid in no choice oviposition bioassay significantly differed among whitefly populations ($F_{2,84} = 6.85$, P = 0.002), host plants ($F_{3,84} = 39.30$, P < 0.001), and their interactions ($F_{6,84} = 5.81$, P < 0.001) (Table 1). The female adults of Bemisia-eggplant laid the greatest number of eggs ($F_{3,28} = 24.022$; P < 0.001) on eggplant; whereas the females of Bemisia-tomato and Bemisia-cucumber laid the greatest number of eggs ($F_{3,28} = 21.403$; P < 0.001 and $F_{3,28} = 9.330$; P < 0.001, respectively) on cucumber. All *B. tabaci* populations deposited the least number of eggs on pepper.

Immature development duration

Development durations from egg to adult emergence of all three populations of whiteflies varied greatly among the four plant hosts ($F_{3,747}$ = 528.30, P < 0.001) and their interactions ($F_{6,747}$ = 46.23, P < 0.001) (Figure 3).

Bemisia-eggplant. The incubation period of eggs was shorter on eggplant ($F_{3,316} = 76.820$; P < 0.001), longer on tomato and cucumber, and intermediate on pepper (Figure 3A). Development times of nymphs on each of the four plants differed ($F_{3,271} = 194.393$; P < 0.001), and the development times of the nymphal stages can be ranked from shortest to longest as: eggplant < tomato < cucumber < pepper. The development time of the pupal stage was shortest on eggplant ($F_{3,271} = 49.039$; P < 0.001) and the longest on pepper whereas no difference between cucumber and tomato, showed intermediate (Figure 3A). The overall development time of the immature stages varied greatly among the four plants ($F_{3,271} = 252.857$; P < 0.001), and can be ranked from shortest to longest as: eggplant < tomato < cucumber < pepper (Figure 3A).

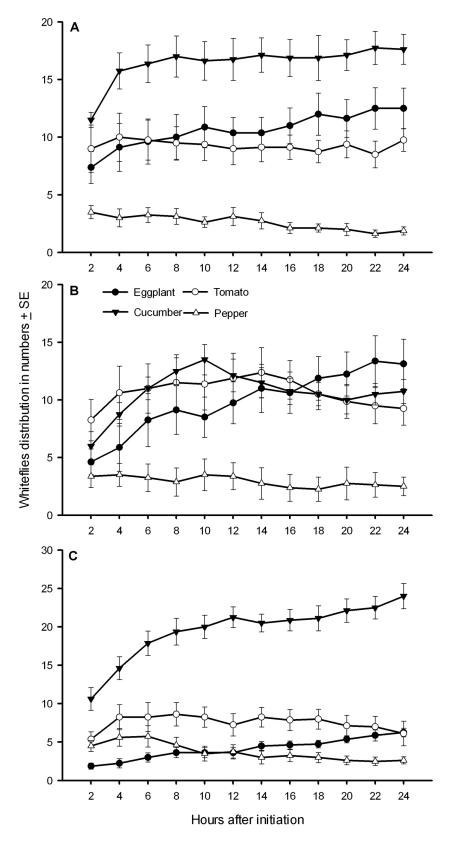


Figure 1. Numbers of *B. tabaci* adults (mean ± SE) on leaf discs of the four host plants at 2-h intervals for 24 h in a choice bioassay. A, B and C are denoted as Bemisia-eggplant, Bemisia-tomato, and Bemisia-cucumber, respectively. doi: 10.1371/journal.pone.0077368.g001

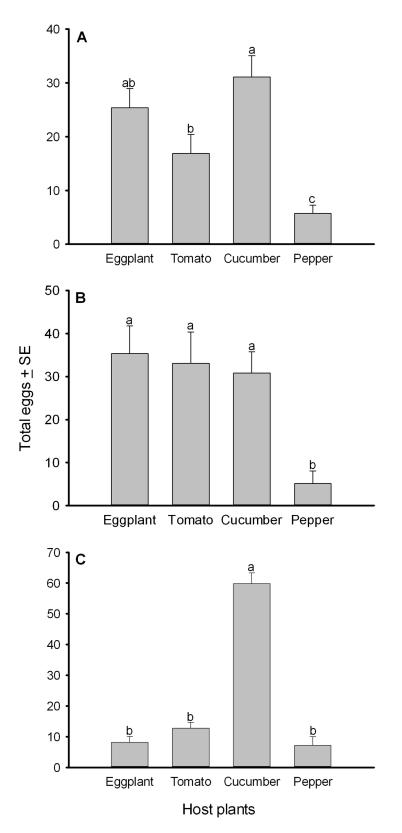


Figure 2. Number of *B. tabaci* eggs (mean ± SE) laid on leaf discs of the four host plants in a choice bioassay. A, B and C termed as total eggs laid by Bemisia-eggplant, Bemisia-tomato, and Bemisia-cucumber, respectively. Different letters above the error bars indicate significant difference at $P \le 0.05$, LSD. doi: 10.1371/journal.pone.0077368.g002

Table 1. Number of eggs per female deposited by the threewhitefly populations in no-choice bioassay, Bemisia-eggplant, Bemisia-tomato and Bemisia-cucumber, ondifferent host plants in 3 days.

Host plants	Mean number of eggs (± SE)		
	Bemisia-eggplant	Bemisia-tomato	Bemisia-cucumber
Eggplant	34.8 ± 2.9 a	14.6 ± 1.9 b	19.8 ± 2.8 b
Tomato	20.5 ± 2.0 b	17.9 ± 1.2 b	16.4 ± 3.1 bc
Cucumber	22.4 ± 2.6 b	24.9 ± 3.3 a	29.1 ± 2.8 a
Pepper	6.9 ± 1.6 c	2.4 ± 0.7 c	9.1 ± 2.1 c

Means having the same letter in the same column were not significantly different at $P \le 0.05$. LSD

doi: 10.1371/journal.pone.0077368.t001

Bemisia-tomato. The egg incubation period was longer on tomato than on other three hosts (Figure 3B). However, nymphal development time on each of the four plants differed ($F_{3,255} = 262.075$; P < 0.001), and the durations can be ranked from shortest to longest as: eggplant < tomato < cucumber < pepper (Figure 3B). The pupal development time was shortest on tomato and cucumber and the longest on eggplant and pepper ($F_{3,254} = 28.435$; P < 0.001). The overall durations of all immature stages differed among the four plants ($F_{3,254} = 151.599$; P < 0.001), the longest on pepper (28.3 ± 0.4 , days \pm SE), the shortest on eggplant (23.1 ± 0.1 , days \pm SE), and the intermediate on cucumber and tomato (Figure 3B).

Bemisia-cucumber. The egg incubation periods differed among the four plants ($F_{3,306} = 55.914$; P < 0.001), the longest on tomato, followed by that on cucumber, and the shortest on eggplant and pepper (Figure 3C). The development times of the nymphal stages differed on the four plants ($F_{3,223} = 137.390$; P < 0.001). The durations can be ranked from shortest to longest as: eggplant < cucumber < tomato < pepper (Figure 3C). The overall development times of all immature stages were significantly different ($F_{3,222} = 179.657$; P < 0.001); the longest on pepper and tomato, and the shortest on eggplant, and intermediate on cucumber (Figure 3C).

Immature survivorship

The overall immature survival rates varied significantly among the whitefly populations ($F_{2,84}$ = 21.92, P < 0.001) and among the plant species ($F_{3,84}$ = 220.51, P < 0.001) (Figure 4).

Bemisia-eggplant. The survival rate of eggs varied among the four hosts ($F_{3,28} = 7.004$; P < 0.001) (Figure 4A). All eggs developed to nymphs on eggplant (100.0 ± 0.0%), more than 95% on tomato and cucumber, and almost 89% on pepper. The survival of nymphs varied greatly among the plants ($F_{3,28} = 189.176$; P < 0.001). The greatest survival was found on eggplant (98.0% ± 0.9) as natal host and the least number survived on pepper (20.5% ± 3.1) and were intermediate on tomato and cucumber (Figure 4A). All pupae successfully developed to adults on all plants. The overall survival rates of immatures varied among the plant species ($F_{3,28} = 198.09$, P < 0.001) and can be ranked from the highest to the lowest as: eggplant > tomato and cucumber > pepper.

Bemisia-tomato. The survival of the eggs was similar on the four host plants. Although nymph survival rates differed significantly on the four plant hosts ($F_{3,28} = 140.854$; P < 0.001) (Figure 4B), only that on pepper was lower. Almost all pupae successfully developed to adults on all plants. The overall survival rates of Bemisia-tomato immatures also differed on various plant species ($F_{3,28} = 88.11$, P < 0.001) though there had no differences among eggplant, tomato and cucumber.

Bemisia-cucumber. There was no significant difference in egg survivorship among the four plant hosts ($F_{3,28} = 2.768$; P < 0.060) (Figure 4C). However, the survival of the nymphs of the Bemisia-cucumber varied significantly among the four plant hosts ($F_{3,28} = 134.403$; P < 0.001) (Figure 4C). The nymphal survival rates were highest on eggplant and cucumber, and lowest on pepper, and intermediate on tomato. Similar to other populations, almost all pupae successfully developed to adults on all plants. The survival rate of all immature stages (egg to adult) varied among the plant species ($F_{3,28} = 42.57$, P < 0.001) and can be ranked from the highest to the lowest as: eggplant and cucumber > tomato > pepper.

Discussion

Our data showed that the effects of previous host plant experiences of B. tabaci varied, and host plants played a more important role than previous experience. We found that the Bemisia-eggplant and Bemisia-cucumber preferred cucumber for feeding. Lei et al. [41] also stated that cucumber was more acceptable for probing and feeding. Our results show that the most preferred host plants for feeding might not be the best host for immature development and survival. For instance, B. tabaci immatures on eggplant had 80-98% survival and the shortest development duration, which were better than on any of host plants tested in this study. However, the whitefly populations with experience on eggplant preferred cucumber (eggplant ranked second) for feeding. In contrast, Bemisiacucumber preferred cucumber much better than any other host plants. This phenomenon has been thought to reflect the feeding experience recognition, i.e. whitefly population chose their natal host for feeding, and this is in agreement with the results of Lee et al. [42,43]. The preference of tomato for feeding by all whitefly populations ranked third, and our data of immature development and survival on tomato support that tomato is a poorer host plant than cucumber and eggplant. Perhaps tomato was a less attractive host for adult whiteflies in the presence of more preferred hosts. However, Bemisiatomato preferred tomato at earlier hours during feeding choice which reflects the effect of feeding experience. This might be due to long term association with specific host plant that mediates the behavior of whitefly.

Pepper is generally not a good host for B biotype of *B. tabaci* [15,29,37]. Our data showed that all populations of *B. tabaci* did not prefer pepper plant in the choice test, and the all populations on pepper gradually decreased. Through the video recording, we found that at earlier hours the adults landed on pepper, but after labial contact or feeding, the adults relocated to other hosts. This result suggests that further investigations on feeding behavior are needed to address this phenomenon

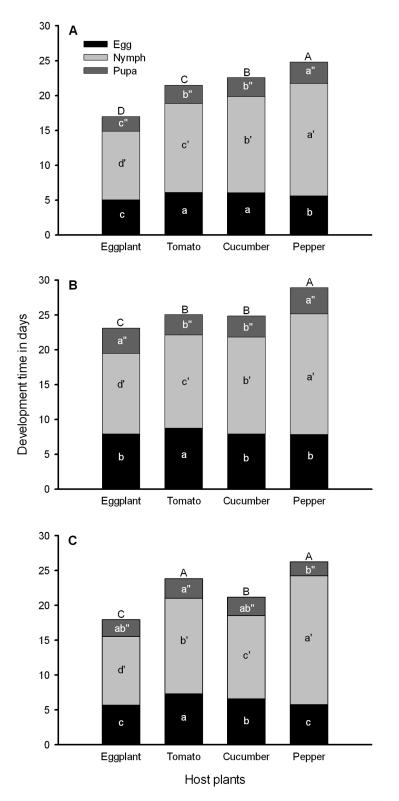


Figure 3. Development time (days ± SE) of *B. tabaci* immatures reared on four host plants. The bold A, B and C symbolized as immatures of Bemisia-eggplant, Bemisia-tomato, and Bemisia-cucumber, respectively. The regular A, B, C and D above the column symbolized for significant differences of overall development time among immatures on different host plants at $P \le 0.05$ (LSD). The letter on the columns a, b, c and d; a', b', c' and d'; a", ab", b" and c" indicate significantly difference of the development time among of egg, larval and pupal stages, respectively, at $P \le 0.05$ (LSD). doi: 10.1371/journal.pone.0077368.g003

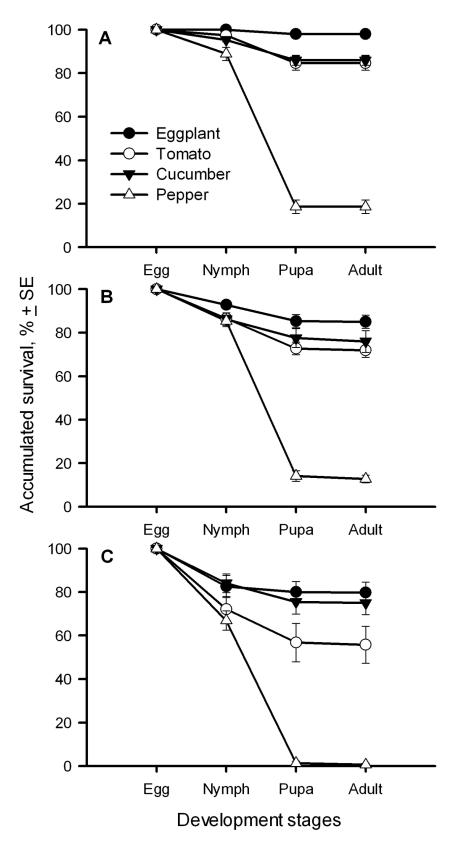


Figure 4. Survivorship (% ± SE) of *B. tabaci* immatures reared on four host plants. A, B and C represented for the immatures of Bemisia-eggplant, Bemisia-tomato, and Bemisia-cucumber, respectively. doi: 10.1371/journal.pone.0077368.g004

properly that could be done by the electrical penetration graph (EPG) technique [41]. In general, the host selection process of whiteflies is primarily by labial contact with host surface [41]. Our results suggest that whitefly populations affect on feeding choice but the host plant had stronger role than previous experience. This observation supports with the previous finding [41], which referred that the host plants had a stronger influence in feeding activities of the whiteflies than the whitefly strains.

In choice test, Bemisia-eggplant and Bemisia-cucumber deposited more eggs on cucumber than on other host plants, reflecting that host plant is a major factor for the manipulation of whitefly oviposition. The number of eggs laid on eggplant by Bemisia-eggplant did not differ from that on cucumber. On the other hand, number of eggs of Bemisia-cucumber on cucumber was much higher than on other host plants. These results demonstrate that previous host experience by whitefly populations can influence subsequent host plant selection. The Bemisia-tomato oviposited similar number of eggs on eggplant, tomato and cucumber though finally the adults preferred tomato plant thirdly among four plants. We observed that at earlier hours more adults of the Bemisia-tomato were found on tomato, assuming more adults laid more eggs; subsequently some of the adults relocated to other plants, and eventually there were similar numbers of eggs on eggplant, cucumber and tomato. However, all populations laid the lowest number of eggs on pepper. The number of eggs per adult was not significantly different among the plants for all populations of B. tabaci. This is due to the fact that adults landed on plants and laid eggs, but after contact the labial palps on the leaf surfaces they relocated and settled on their preferred hosts. This phenomenon has been assumed that adults laid eggs first, subsequently settled on leaves for feeding. Therefore, number of eggs per adult may not accurately reflect the host suitability of adults, when they have choice for feeding and settling. In the no choice test, Bemisia-eggplant and Bemisia-cucumber deposited the greatest number of eggs on their natal host plants which were in agreement with the result of Brown et al. [44]. This result also reflects the fact of feeding experience. In contrast, Bemisia-tomato laid more eggs on cucumber. These results showed that all B. tabaci populations did not prefer pepper. This might be due to the fact that pepper foliage was alabrous, whereas all others three host plants were pubescent because B. tabaci preferred the plants with pubescent leaves to the plants with glabrous leaves for feeding and oviposition. These results were similar to those reported by Gruenhagen and Perring [22], Mansaray and Sundufu [32], and Khan et al. [45].

The result of our study showed that developmental time from egg to adult eclosion of the Bemisia-eggplant, Bemisia-tomato and Bemisia-cucumber varied greatly when reared separately on eggplant, tomato, cucumber, and pepper. The incubation periods of all populations were always longer on tomato than on the other three hosts, indicating that tomato is a poorer host for eggs development than others. These results suggest that eggplant was better for development of *B. tabaci* immatures, and pepper was a poorer host plant, where tomato and cucumber were marginal, reflecting that host plant is a main

factor that influences the development of immature whiteflies. However, tomato ranked second for development of the Bemisia-tomato, and cucumber ranked second for Bemisiacucumber. These results clearly reflect the effect of whitefly populations of previous experience.

Nymphal survival was more significant among the host plants in all whitefly populations. The first and second instars on pepper plant had the lowest survival rate. The survival of the red-eyed nymphs or pupae was highest among other immature stages. The overall survival of all populations from egg to adult eclosion was highest on eggplant (80-98%) and lowest on pepper (0.6-20%). Similar results have been reported in previous studies [15,29,34,37]. Again, this result confirmed that host plant had the foremost effect on the survival of whitefly immatures. The immature survival of the Bemisia-cucumber on other three hosts (eggplant, tomato and pepper) was lower than the Bemisia-eggplant and Bemisia-tomato immature on those hosts. This might be due to the distant phylogenetic relation among cucumber and other three hosts, which supports the result reported by Carabali et al. [46].

In this study, Bemisia-eggplant performed better for their immature development as the shortest development duration and the highest survival on either natal or offered host plant. This result supports with the result of Enkegaard [47] who stated that the poinsettia strain performed better than the tobacco strain on poinsettia. Accordingly, adult feeding and egg laying preference and immature performance of *B. tabaci* mainly manipulated by plant features and partially by whitefly populations, supported by the results of Thomas [48] and Jiao [35]. The plant features include the nutrition of phloem sap, presence of secondary metabolites, and leaf surface characteristics [49,50].

In summary, the findings of our study can be stated as: firstly, feeding choice and oviposition of adults, and development and survival of immatures were mediated by both whitefly populations and host plants, though host plants had stronger effects. Secondly, whiteflies from different host plants performed differently on different host plants; *B. tabaci* adults may land on the plants that are not preferred and laid eggs first, and then relocate and settled on the plants they preferred. Therefore, numbers of adults that land on the plants may not be used to interpret for host suitability of immatures of *B. tabaci*. Thirdly, cucumber may be used as a trap crop for management of *B. tabaci*. Our findings will be useful for further understanding the population dynamics, dispersal and viral transmission in a landscape or large cropping system where *B. tabaci* on different crops spread around different crop systems.

Acknowledgements

We thank Yongmei Zhang for her technical instruction of culturing and data collection of whiteflies, and the assistance of all staff and students in the Key Laboratory of Applied Entomology, Northwest A&F University at Yangling, Shaanxi, China.

Author Contributions

Conceived and designed the experiments: MMRS TXL. Performed the experiments: MMRS. Analyzed the data: MMRS

References

- Dinsdale A, Cook L, Riginos C, Buckley YM, De Barro PJ (2010) Refined global analysis of *Bernisia tabaci* (Gennadius) (Hemiptera: Sternorrhyncha: Aleyrodoidea: Aleyrodidae) mitochondrial COI to identify species level genetic boundaries. Ann Entomol Soc Am 103: 196-208. doi:10.1603/AN09061.
- De Barro PJ, Liu SS, Boykin LM, Dinsdale AB (2011) *Bemisia tabaci*: A statement of species status. Annu Rev Entomol 56: 1-19. doi:10.1146/ annurev-ento-112408-085504. PubMed: 20690829.
- Chou I (1949) Listo de la konataj Aleurodoj "Homopteroj" en Cinio. J Chin Entomol 3: 1-18.
- Zhang LP, Zhang YJ, Zhang WJ, Wu QJ, Xu BY et al. (2005) Analysis of genetic diversity among different geographical populations and determination of biotypes of *Bemisia tabaci* in China. J Appl Entomol 129: 121-128. doi:10.1111/j.1439-0418.2005.00950.x.
- Chu D, Zhang YJ, Brown JK, Cong B, Xu BY et al. (2006) The introduction of the exotic Q biotype of *Bernisia tabaci* from the Mediterranean region into China on ornamental crops. Fla Entomol 89: 168-174. doi:10.1653/0015-4040(2006)89[168:TIOTEQ]2.0.CO;2.
- Wu XX, Li ZX, Hu DX, Shen ZR (2003) Identification of Chinese populations of *Bemisia tabaci* (Gennadius) by analyzing ribosomal ITS1 sequence. Prog Nat Sci 13: 276-281. doi: 10.1080/10020070312331343530.
- De Barro PJ, Trueman JWH, Frohlich DR (2005) *Bemisia argentifolii* is a race of *B. tabaci* (Hemiptera: Aleyrodidae): the molecular genetic differentiation of *B. tabaci* populations around the world. Bull Entomol Res 95: 193-203. doi:10.1079/BER2004351. PubMed: 15960874.
- Li SJ, Xue X, Ahmed MZ, Ren SX, Du YZ et al. (2011) Host plants and natural enemies of *Bemisia tabaci* (Hemiptera: Aleyrodidae) in China. J Insect Sci 18: 101-120. doi:10.1111/j.1744-7917.2010.01395.x.
- Wan FH, Zhang GF, Liu SS, Luo C, Chu D et al. (2009) Invasive mechanism and management strategy of *Bemisia tabaci* (Gennadius) biotype B: Progress report of 973 Program on invasive alien species in China. Sci China C 52: 88-95. doi:10.1007/s11427-008-0135-4. PubMed: 19152088.
- Zhao L, Zhang R, Xiao Y, Cui Y, Huang W (2000) Tobacco whitefly (*Bemisia tabaci*), a new insect pest was founded on cotton in Xinjiang. Xinjiang. J Agric Sci 1: 27-28.
- Luo C, Yao Y, Wang R, Yan Y, Hu D et al. (2002) The use of mitochondrial cytochrome oxidase I (mt COI) gene sequences for the identification of biotypes of *Bemisia tabaci* (Gennadius) in China. Acta Entomol Sin 45: 759-763.
- Lin K, Wu K, Wei H, Guo Y (2003) The effects of host plants on growth and development of *Bemisia tabaci* populations in China (Homoptera: Aleyrodidae). Acta Entomol Sin 23: 870-877.
- Perring TM (2001) The *Bernisia tabaci* species complex. Crop Protect 20: 725-737.
- Mayer RT, Inbar M, McKenzie CL, Shatters R, Borowicz V et al. (2002) Multitrophic interactions of the silverleaf whitefly, host plants, competing herbivores, and phytopathogens. Arch Insect Biochem Physiol 51: 151-169. doi:10.1002/arch.10065. PubMed: 12432517.
- Xu J, Lin KK, Liu SS (2011) Performance on different host plants of an alien and an indigenous *Bemisia tabaci* from China. J Appl Entomol 135: 771-779.
- Martin JH, Mifsud D, Rapisarda C (2000) The whiteflies (Hemiptera: Aleyrodidae) of Europe and Mediterranean Basin. Bull Entomol Res 90: 407-448. PubMed: 11082558.
- Oliveira MRV, Henneberry TJ, Anderson P (2001) History, current status, and collaborative research projects for *Bernisia tabaci*. Crop Protect 20: 709-723. doi:10.1016/S0261-2194(01)00108-9.
- Naranjo SE, Ellsworth PC (2009) The contribution of conservation biological control to integrated pest control of *Bemisia tabaci* in cotton. Biol Contr 51: 458-470. doi:10.1016/j.biocontrol.2009.08.006.
- De Barro PJ, Bourne A, Khan SA, Brancatini VAL (2006) Host plant and biotype density interactions-their role in the establishment of the invasive B biotype of *Bernisia tabaci*. Biol Invasions 8: 287-294. doi: 10.1007/s10530-005-1261-6.
- De Barro PJ, Bourne A (2010) Ovipositional host choice by an invader accelerates displacement of its indigenous competitor. Biol Invasions 12: 3013-3023. doi:10.1007/s10530-010-9691-1.

TXL. Contributed reagents/materials/analysis tools: TXL. Wrote the manuscript: MMRS TXL.

- Liu TX, Stansly PA (1995) Oviposition by *Bemisia argentifolii* (Homoptera: Aleyrodidae): Effects of tomato leaf factors and insecticidal residues. J Econ Entomol 88: 992-997.
- Gruenhagen NM, Perring TM (2001) Plant influences on silverleaf whitefly oviposition and development and the potential for enemy-free space. Entomol Exp Appl 99: 387-391. doi:10.1046/j. 1570-7458.2001.00839.x.
- Mayhew PJ (1997) Adaptive patterns of host-plant selection by phytophagous insects. Oikos 79: 417-428. doi:10.2307/3546884.
- Berdegue M, Reitz SR, Trumble JT (1998) Host plant selection and development in *Spodoptera exigua*: Do mother and offspring know best? Entomol Exp Appl 89: 57-64. doi:10.1046/j. 1570-7458.1998.00381.x.
- Gripenberg S, Mayhew PJ, Parnell M, Roslin T (2010) A meta-analysis of preference-performance relationship in phytophagous insects. Ecol Lett 13: 383-393. doi:10.1111/j.1461-0248.2009.01433.x. PubMed: 20100245.
- Papaj DR, Prokopy RJ (1989) Ecological and evolutionary aspects of learning in phytophagous insects. Annu Rev Entomol 34: 315-350. doi: 10.1146/annurev.en.34.010189.001531.
- Thompson JN (1988) Evolutionary ecology of the relationship between oviposition preference and performance of offspring in phytophagous insects. Entomol Exp Appl 47: 3-14. doi:10.1111/j. 1570-7458.1988.tb02275.x.
- Ballabeni P, Conconi D, Gateff S, Rahier M (2001) Spatial proximity between two host plant species influences oviposition and larval distribution in a leaf beetle. Oikos 92: 225-234. doi:10.1034/j. 1600-0706.2001.920204.x.
- Omondi AB, Obeng-Ofori Kyerematen RA, Danquah EY (2005) Host preference and suitability of some selected crops for two biotypes of *Bemisia tabaci* in Ghana. Entomol Exp Appl 115: 393-400. doi: 10.1111/j.1570-7458.2005.00296.x.
- Zang LŚ, Chen WQ, Liu SS (2006) Comparison of performance on different host plants between the B biotype and a non-B biotype of *Bemisia tabaci* from Zhejiang, China. Entomol Exp Appl 121: 221-227. doi:10.1111/j.1570-8703.2006.00482.x.
- Islam MT, Ren SX (2007) Development and reproduction of *Bemisia* tabaci on three tomato varieties. J Entomol 4: 231-236. doi:10.3923/je. 2007.231.236.
- Mansaray A, Sundufu AJ (2009) Oviposition, development and survivorship of the sweetpotato whitefly *Bemisia tabaci* on soybean, *Glycine max*, and the garden bean, *Phaseolus vulgaris*. J Insect Sci 9: 1-6. doi:10.1673/031.009.1001. PubMed: 19611218.
- Baldin ELL, Beneduzz RA (2010) Characterization of antibiosis and antixenosis to the whitefly silverleaf *Bemisia tabaci* B biotype (Hemiptera: Aleyrodidae) in several squash varieties. J Pest Sci 83: 223-229. doi:10.1007/s10340-010-0289-2.
- Chu D, Tao YL, Zhang YJ, Wan FH, Brown JK (2012) Effects of host, temperature and relative humidity on competitive displacement of two invasive *Bemisia tabaci* biotypes [Q and B]. J Insect Sci 19: 595-603. doi:10.1111/j.1744-7917.2011.01500.x.
- Jiao X, Xie W, Wang S, Wu Q, Zhou L et al. (2012) Host preference and nymph performance of B and Q putative species of *Bemisia tabaci* on three host plants. J Pest Sci 85: 423-430.
- Frohlich DR, Torres-Jerez I, Bedford ID, Markham PG, Brown JK (1999) A phylogeographical analysis of *Bemisia tabaci* species complex based on mitochondrial DNA markers. Mol Ecol 8: 1683-1691. doi: 10.1046/j.1365-294x.1999.00754.x. PubMed: 10583831.
- Tsueda H, Tsuchida K (2011) Reproductive differences between Q and B whiteflies, *Bemisia tabaci*, on three plants and negative interactions in mixed cohorts. Entomol Exp Appl 141: 197-207. doi:10.1111/j. 1570-7458.2011.01189.x.
- Mouttet R, Bearez P, Thomas C, Desneux N (2011) Phytophagous arthropods and a pathogen sharing a host plant: Evidence for indirect plant-mediated interactions. PLOS ONE 6: e18840. doi:10.1371/ journal.pone.0018840. PubMed: 21611161.
- Shapiro SS, Wilk MB (1965) An analysis of variance test for normality (complete samples). Biometrika 52: 591-611. doi:10.1093/biomet/ 52.3-4.591.
- 40. Institute SAS (2011) SAS/STAT® 9.2 User's Guide. NC, USA: Cary.

- 41. Lei H, Tjallingii WF, van Lenteren JC (1998) Probing and feeding characteristics of the greenhouse whitefly in association with host-plant acceptance and whitefly strains. Entomol Exp Appl 88: 73-80. doi: 10.1046/j.1570-7458.1998.00348.x.
- 42. Lee DH, Nyrop JP, Sanderson JP (2009) Attraction of *Trialeurodes* vaporariorum and *Bemisia argentifolii* to eggplant, and its potential as a trap crop for whitefly management on greenhouse poinsettia. Entomol Exp Appl 133: 105-116. doi:10.1111/j.1570-7458.2009.00920.x.
- Lee DH, Nyrop JP, Sanderson JP (2011) Avoidance of natural enemies by adult whiteflies, *Bemisia argentifolii*, and effects on host plant choice. Biol Contr 58: 302-309. doi:10.1016/j.biocontrol.2011.06.005.
- Brown JK, Frohlich DR, Rosell RC (1995) The sweetpotato or silverleaf whiteflies: biotypes of *Bemisia tabaci* or species complex? Annu Rev Entomol 40: 511-534. doi:10.1146/annurev.en.40.010195.002455.
- 45. Khan MR, Ghani IA, Khan MR, Ghaffar A, Tamkeen A (2011) Host plant selection and oviposition of whitefly *Bemisia tabaci* (Gennadius) in a mono and simulated polyculture crop habitat. Afr J Biotechnol 10: 1467-1472.

- Carabali A, Bellotti AC, Montoya-Lerma J, Cuellar ME (2005) Adaptation of *Bemisia tabaci* biotype B (Gennadius) to cassava, *Manihot esculenta* (Crantz). Crop Protect 24: 643-649. doi:10.1016/ j.cropro.2004.11.008.
- 47. Enkegaard A (1993) The poinsettia strain of the cotton whitefly, *Bemisia tabaci* (Homoptera: Aleyrodidae), biological and demographic parameters on poinsettia (*Euphorbia pulcherrima*) in relation to temperature. Bull Entomol Res 83: 535-546. doi:10.1017/ S0007485300039961.
- Thomas DC (1993) Host plant adaptation in the glasshouse whitefly. PhD thesis, Wageningen Agricultural University, The Netherlands. 129 pp.
- van Lenteren JC, de Ponti OMB (1991) Plant-leaf morphology, host plant resistance and biological control. Symp Biol Hung 39: 365-386.
- Noldus LPJJ, Xu R, van Lenteren JC (2009) The parasite-host relationship between *Encarsia formosa* Gahan (Hymenoptera, Aphelinidae) and *Trialeurodes vaporariorum* (Westwood) (Homoptera, Aleyrodidae). J Appl Entomol 101: 492-507.