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ORIGINAL PAPER

Lack of correlation between host choice and feeding efficiency for the B and Q putative species of *Bemisia tabaci* on four pepper genotypes

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Abstract The B and Q putative species of *Bemisia tabaci* are among the most invasive pests in the world. In China, Q is displacing B. Although this displacement is often attributed to the higher resistance of Q to insecticides, a higher tolerance of Q to low-quality host plants may also be important. In this study, we first determined the contents of main secondary insect-resistant compounds (total phenol and flavonoids) and nutrients (total amino acid, free protein, total nitrogen, phosphorus, and potassium) in four genotypes pepper (*Capsicum annuum*). We then conducted host choice and feeding behavior (EPG) experiments with B and Q on the four pepper genotypes. Zhongjiao4 was found to be the high-quality genotype (it had low levels of insect-resistance substances and high levels of nutrients), and Zhonghuahong was found to be the low-quality genotype (it had high levels of resistant compound and low levels of nutrients). EPG data indicated that both B and Q females fed more efficiently on high-quality Zhongjiao4 than on the other three pepper genotypes. In terms of settling and oviposition, however, B preferred the low-quality Zhonghuahong, and Q showed no preference among the four genotypes. We suggest that the lack of correlation between the results for feeding efficiency and settling/oviposition might be explained by repellent plant volatiles whose effects differ depending on pepper genotype and whitefly species.

Keywords *Bemisia tabaci* · Host choice · Plant defense · Resistance substances · Host nutrition · EPG

Key message

- B and Q putative species of *Bemisia tabaci* are two of the most invasive pests in the world.
- B whiteflies are quite sensitive to host quality and less tolerant and adaptive to low-quality hosts relative to Q whiteflies.
- These findings are consistent with the hypothesis that Q whiteflies can use a wider range of plant species than B whiteflies.

Introduction

The sweet potato whitefly, *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae), causes severe damage to more than 600 plant species (Brown et al. 1995; Perring 2001). Damage to host plants is caused by phloem-feeding (Byrne and Bellows 1991; Oliveira et al. 2001; Perring 2001), excretion of honeydew, induction of phytotoxic disorders (Costa and Brown 1991), and transmission of plant viruses (Brown 2000; Pan et al. 2012).

Bemisia tabaci is considered a species complex consisting of many biotypes and/or host races that differ

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greatly in host range, insecticide resistance, and ability to transmit plant viruses (Perring 2001). A recent phylogenetic analysis suggested that *B. tabaci* is a complex of 11 well-defined, high-level groups containing at least 24 morphologically indistinguishable putative/cryptic species (Dinsdale et al. 2010; De Barro et al. 2011). The two most widespread putative species are referred to as B (Middle East–Asia Minor 1) and Q (Mediterranean), both of which are highly invasive pests (Dinsdale et al. 2010; De Barro et al. 2011). B and Q putative species differ greatly in resistance to insecticides and stress temperatures. Q is less sensitive than B to common insecticides, which may help explain why Q has displaced B in China (Horowitz et al. 2005; Sun et al. 2013). In addition, Q is less sensitive than B to short periods of heat stress (Mahadav et al. 2009; Elbaz et al. 2011).

Although B and Q are polyphagous, they differ in their tolerance of low-quality hosts (Muñiz and Nombela 2001; Iida et al. 2009; Tsueda and Tsuchida 2011; Elbaz et al. 2012; Jiao et al. 2012, 2013, 2014; Sun et al. 2013). Q has a wider host range than B and a greater tolerance of low-quality host plants (Iida et al. 2009; Tsueda and Tsuchida 2011; Chu et al. 2012; Liu et al. 2012; Jiao et al. 2012, 2013, 2014; Sun et al. 2013). For example, many studies have demonstrated that B and Q differ greatly in their responses to pepper (*Capsicum annuum*) plants. All studies have indicated that Q can complete its development on pepper, but some studies differ about whether B can (Muñiz and Nombela 2001; Nava-Camberos et al. 2001; Kakimoto et al. 2007; Iida et al. 2009; Tsueda and Tsuchida 2011; Xu et al. 2011; Sun et al. 2013). The discrepancies in results for B may be due to the use of different pepper cultivars. Although the contrasting effects of pepper on B and Q have been widely reported, the mechanisms underlying the effects are largely unexplored.

Most research on host choice by arthropods is based on optimal oviposition theory, which posits that the female oviposition preference of herbivorous insects correlates with host suitability for their offspring, i.e., females are expected to oviposit on high-quality hosts in order to maximize offspring fitness (Jaenike 1978; Gripenberg et al. 2010). Gripenberg et al. (2010) performed a meta-analysis of the relationships between female preference and offspring performance in phytophagous insects. The authors found strong evidence for an effect of diet breadth on host choice: Female preference for high-quality plants was stronger in oligophagous insects than in polyphagous insects (Gripenberg et al. 2010). However, herbivorous insects often appear to make poor choices about where their offspring should develop (Mayhew 2001; Wise et al. 2008; Jiao et al. 2012). In addition to female feeding experience, the avoidance of predation risk and the trade-offs between larval and adult performance (Mayhew 2001; Jiao et al. 2012), the poor relationship between female preference and offspring performance may be due to the correlations between antixenosis and antibiosis in host plants against herbivores (Wise et al. 2008). The negative genetic correlations in antixenosis and antibiosis in plants may often result in zero or negative correlations between preference and performance in herbivores and thus may be an important reason why herbivorous insects often appear to be bad mothers (Wise et al. 2008). Although B and Q are both polyphagous, most reports indicate that the host range is wider for Q than B (Iida et al. 2009; Tsueda and Tsuchida 2011; Chu et al. 2012; Liu et al. 2012; Sun et al. 2013; Jiao et al. 2012, 2014). One might therefore hypothesize that discrimination among host plants is weaker for Q than B.

The suitability of hosts for herbivorous insects depends on both host nutrients and host insect-resistant compounds (Bernays and Chapman 1994; Awmack and Leather 2002). When consuming plants, herbivores must often deal with both nutritionally inferior quality and potentially toxic, plant secondary metabolites, and the contents of nutrients and toxic metabolites are often negatively related (Parikh et al. 2017). Herbivores generally face a trade-off between obtaining nutrients and avoiding toxic metabolites. Herbivores that consume a nutritionally superior but chemically defended plant may consume high levels of metabolites that require energy for detoxification (Parikh et al. 2017). Alternatively, herbivores may avoid consuming high levels of toxic metabolites by consuming a diverse diet that may be in nutritionally inferior quality (Parikh et al. 2017). Differences among host plants in their nutrients and toxic metabolites may shape host choice by herbivores (Bernays and Chapman 1994; Awmack and Leather 2002). In the case of whiteflies and other phloem-sucking insects, host choice is also affected by nitrogen fertilizer (Bentz et al. 1995; Bi et al. 2001, 2005; Rashid et al. 2017) and by phosphorus and potassium fertilizer (Cardoso et al. 2002; Myers et al. 2005; Myers and Gratton 2006; Rashid et al. 2017). In general, nitrogen contents in plants were positively related to the performance and host choice of phloem-sucking insects (Bentz et al. 1995; Bi et al. 2001, 2005; Rashid et al. 2017). However, the effects of phosphorus and potassium fertilizers on the performance of phloem-sucking herbivores were mixed. For example, host choice of brown planthopper, *Nilaparvata lugens,* for feeding and ovipositing was positively associated with plant tissue concentrations of N, but not with phosphorus (P) and potassium (K) (Rashid et al. 2017). The results of Cardoso et al. (2002) showed there was a tendency of population growth of small stink bug *Piezodorus guildinii* (Westwood) on the highest levels of P and K. In contrast, there was a significantly greater intrinsic rate of population increase and net reproductive rate of *Aphis glycines* in the low K treatments in comparison with the medium and high K treatments (Myers et al. 2005; Myers and Gratton 2006).

The electrical penetration graph (EPG) is a reliable tool for measuring the feeding behavior of sap-sucking insects. For such insects, EPG signals have been correlated with feeding activities as well as with the locations of the stylet tips in host tissues (Tjallingii and Hogen Esch 1993). EPG parameters can therefore be used to assess host suitability and to identify the host tissues in which resistance is expressed against aphids (Alvarez et al. 2006) and whiteflies (Liu et al. 2012; Jiao et al. 2014).

Here, we first measured the differences in contents of the main secondary insect-resistant compounds (total phenol and flavonoids) and nutrients (total amino acid, free protein, total nitrogen, phosphorus, and potassium) among four genotypes of pepper (*C. annuum*). We then conducted host choice experiments and feeding behavior (EPG) assays to determine why B and Q differ in their choice and tolerance of the four pepper genotypes.

Materials and methods

Insects and host plants

The B putative species of *B. tabaci* was originally collected from cabbage (*B. oleracea* var. Jingfeng 1) in 2004 in Beijing and was subsequently maintained on tomato (*Lycopersicon esculentum* var. Zhongza9) in a glasshouse. The Q putative species of *B. tabaci* was originally obtained from poinsettia (*Euphorbia pulcherrima*) in 2008 in Beijing and was subsequently maintained on tomato (*L. esculentum* var. Zhongza9) in a separate glasshouse. Stock cultures of B and Q were maintained on tomato (*L. esculentum* var. Zhongza9) in separate insect-proof screened cages (60 × 60 × 60 cm) in the greenhouse at 25 ± 1 °C, 60 ± 10% RH, and a 14L:10D photoperiod. The purity of the cultures was monitored every 2–3 generations based on determination of the DNA sequence of the haplotypes following amplification by mtCOI primers (Zhang et al. 2005). Four genotypes of pepper (Qianhong, Zhongjiao4, Hangjiao, and Zhonghuahong) were established individually in 12-cm-diameter plastic pots. All the plants from four genotypes of pepper were at the same level of fertilizer. Plants of similar size (20 cm tall) were randomly selected for each experiment. All the tested plants and whiteflies were free from pathogen.

Chemical analysis of four pepper genotypes

A 15-g sample (fresh weight) of leaves was randomly collected from three replicate plants of each pepper genotype. About one-third of the sample was dried at 80 °C for 72 h in a drying oven and was used for determination of total phenol and flavonoid contents. Another one-third of the sample was not dried and was used for determination of free protein and total amino acids. Total phenol, flavonoids, free protein, and total amino acids were assayed according to the reagent label directions (Nanjing Jiancheng Ltd. Co., Nanjing, Jiangsu Province, China). The remaining one-third of the sample was dried as above mentioned and was used for determination of nitrogen (N), phosphorus (P), and potassium (K) with a CNH analyzer (Model ANCA-nt; Europa Elemental Instruments, Okehampton, UK). The measure of each biochemical component was repeated five times for each pepper genotype.

Female settling and oviposition preference of B and Q females on four pepper genotypes

An experiment concerning whitefly settling and oviposition preference was conducted as described by Jiao et al. (2012, 2014). The choice experiments were carried out in the greenhouse at 25 ± 1 °C, 60 ± 10% RH, and a 14L:10D photoperiod. In brief, one plant of each of the four pepper genotypes was placed in a screen cage (60 × 60 × 60 cm). The four plants were spaced 20 cm apart so that their leaves did not touch. About 200 B or Q whiteflies (including females and males) emerged within 3 days were randomly collected between 07:00 and 08:00 h and released from an aspirator into the center of the screen cage above the plant canopy. The aspirator sampling bottle containing whiteflies was held inside a clear plastic tumbler that hung at the center of the cage, about 30 cm above the plant canopy. The females moved to the open top of the sampling bottle and flew away to approach the plants from above. The number of females on each plant was determined after 12, 24, 36, 48, 60, 72, 84, 96, and 108 h. To prevent females from moving between leaves and host genotypes during counting, the females were counted under dim light just before 07:00 and just after 19:00. At the end of the settling assay, all leaves from each genotypes pepper were removed and examined with a dissecting microscope; the number of eggs laid (an indicator of oviposition preference) was determined. The experiment was replicated seven times.

Feeding behavior of B and Q females on four pepper genotypes

EPG assays were carried out as described by Liu et al. (2012). In brief, adult females (2–3 days old) were immobilized on an ice-chilled glass dish (4 cm diameter). One pepper plant and one female were integrated in an electrical circuit by using a gold wire (12.5 μm in diameter and 1.5 cm long) that was glued to the immobilized female's dorsum (a conductive water-based silver glue was used) and a copper electrode that was inserted into the soil of the potted plant. The female was placed on the abaxial surface of a mature leaf. Host plant, females, and EPG probes were placed in electrically grounded Faraday cages to shield the setup from external electrical noise. Behavioral parameters of female feeding were monitored with a DC-EPG (Tjallingii 1988). The EPG signals, produced when the females inserted their stylets into the plant tissues, were digitized with a DI710-UL analog-to-digital converter (DATAQ Instruments, Akron, OH, USA). Digitized output was acquired with PROBE 3.4 software (Wageningen Agricultural University, The Netherlands). The recordings of female feeding were acquired during the day for 6 consecutive hours at 25 ± 1 °C and 70% RH. Each combination of pepper genotype and whitefly species was represented by 30 replicate females.

EPG waveforms were documented and categorized according to Jiang et al. (1999, 2000). Three waveforms were identified including C (stylet pathway phase), E(pd)1 (salivation into phloem), and E(pd)2 (ingestion of sieve element sap). Waveform pd (potential drop), F (presumed penetration difficulties), and G (ingestion of xylem sap) were rare and were grouped into waveform C (Liu et al. 2012). Eighteen EPG parameters (nine non-phloem-feeding and nine phloem-feeding parameters) belonging to three EPG waveforms (C, E1, and E2) (Tjallingii 1988) were calculated. The number of probes and total duration of probing by the females were considered as general probing behavior. The pathway phase (C), corresponding to foraging activities before the stylet reached phloem elements, included the number of pathway phases, the total duration of pathway phases, time from start to the first probe, time from the first probe to the first E(pd), and number of probes before the first E(pd).

The salivation phase in the phloem belonged to the E1 waveform. It included the number and total duration of single salivation periods not followed by sap ingestion and the mean duration of the first salivation periods. The phloem ingestion phase (E2) included the number and total duration of phloem ingestions and mean duration of phloem ingestion, which was considered as a successful feeding phase.

Statistical analyses

Statistical analysis was carried out with SPSS (version 13.0; SPSS Inc., Chicago, IL, USA). Homogeneity of variance was checked using the Levene test, and normality was checked using the Shapiro–Wilk test. Biochemical components (total phenol, flavonoids, total amino acid, soluble protein, total N, phosphorous, and potassium) were compared among the four pepper genotypes with one-way ANOVAs. The difference in female settling preference among the genotypes was tested by a repeated measures ANOVA (RMANOVA) for each whitefly species. The differences in female oviposition preference among four pepper genotypes were tested with a one-way ANOVA for each whitefly species. The differences in behavioral parameters associated with the feeding of the B and Q females on the four pepper genotypes were compared with two-way ANOVAs. Tukey's test was used to separate treatment means when the main effect was significant. For each whitefly species, successfully feeding was compared among the four genotypes with a Chi-square independence test.

Results

Biochemical properties of the four pepper genotypes

The biochemical properties of the pepper genotypes are shown in Table 1. The phenol content was markedly higher for Zhonghuahong than for Hangjiao or Qianhong, and the phenol content of the latter two genotypes was markedly higher than that of Zhongjiao4 ($F_{3,16} = 25.591, P < 0.001$). The flavonoid content was highest for Zhonghuahong ($F_{3,16} = 8.966$, $P = 0.001$). The contents of total amino acids and soluble protein were markedly higher in Zhongjiao4 than in the other three genotypes ($F_{3,16} = 7.603$ and $P = 0.002$ for amino acids; $F_{3,16} = 9.639$ and $P = 0.001$ for soluble protein). Total N content was significantly higher in Hangjiao than in Qianhong or Zhonghuahong ($F_{3,16} = 8.602$, $P = 0.001$). The potassium content was significantly higher in Zhongjiao4 than in Qianhong ($F_{3,16} = 3.829$, $P = 0.031$). The phosphorous content was significantly higher in Zhongjiao4 than in Hangjiao and was significantly higher in Hangjiao than in the other two genotypes ($F_{3,16} = 30.215$, $P < 0.001$).

Settling and oviposition preference of B and Q females on four pepper genotypes

B females preferred to settle on Zhonghuahong rather than on the other three pepper genotypes (RMANOVA, $F_{3,24} = 21.424$, $P < 0.001$, Fig. 1a). However, there were no significant difference in the settling preference of Q females among the four pepper genotypes (RMANOVA, $F_{3,24} = 0.712$, $P = 0.555$, Fig. 1b).

B females preferred to oviposit on Zhonghuahong rather than on the other three pepper genotypes (one-way ANOVA, $F_{3,24} = 19.401$, $P < 0.001$, Fig. 2a). However, oviposition by Q females did not significantly differ among the four pepper genotypes ($F_{3,24} = 0.029$, $P = 0.993$, Fig. 2b).

Table 1 Chemical components of four pepper genotypes

Component	Pepper genotype			
	Qianhong	Zhongjiao4	Hangjiao	Zhonghuahong
Total phenol (mg g^{-1} DW)	162.238 ± 2.259 b	111.223 ± 12.051 c	177.139 ± 8.379 b	225.625 ± 11.239 a
Flavonoids (mg g^{-1} DW)	4.115 ± 0.473 b	3.5383 ± 0.479 b	2.993 ± 0.412 b	6.831 ± 0.820 a
Total amino acid (mg g^{-1} FW)	4.960 ± 0.790 b	7.607 ± 0.714 a	3.607 ± 0.285 b	4.482 ± 0.584 b
Soluble protein (mg g^{-1} FW)	0.279 ± 0.052 b	0.468 ± 0.036 a	0.249 ± 0.014 b	0.235 ± 0.027 b
Total nitrogen (DW %)	5.038 ± 0.245 c	5.988 ± 0.127 ab	6.270 ± 0.246 a	5.372 ± 0.103 bc
P content (DW %)	0.444 ± 0.024 c	0.679 ± 0.027 a	0.542 ± 0.021 b	0.410 ± 0.011 c
K content (DW %)	5.348 ± 0.351 b	6.655 ± 0.339 a	6.096 ± 0.190 ab	5.868 ± 0.180 ab

Values are mean ± SE. Means in a row followed by different letters are significantly different ($P < 0.05$), and DW and FW refer to dry and fresh weight, respectively

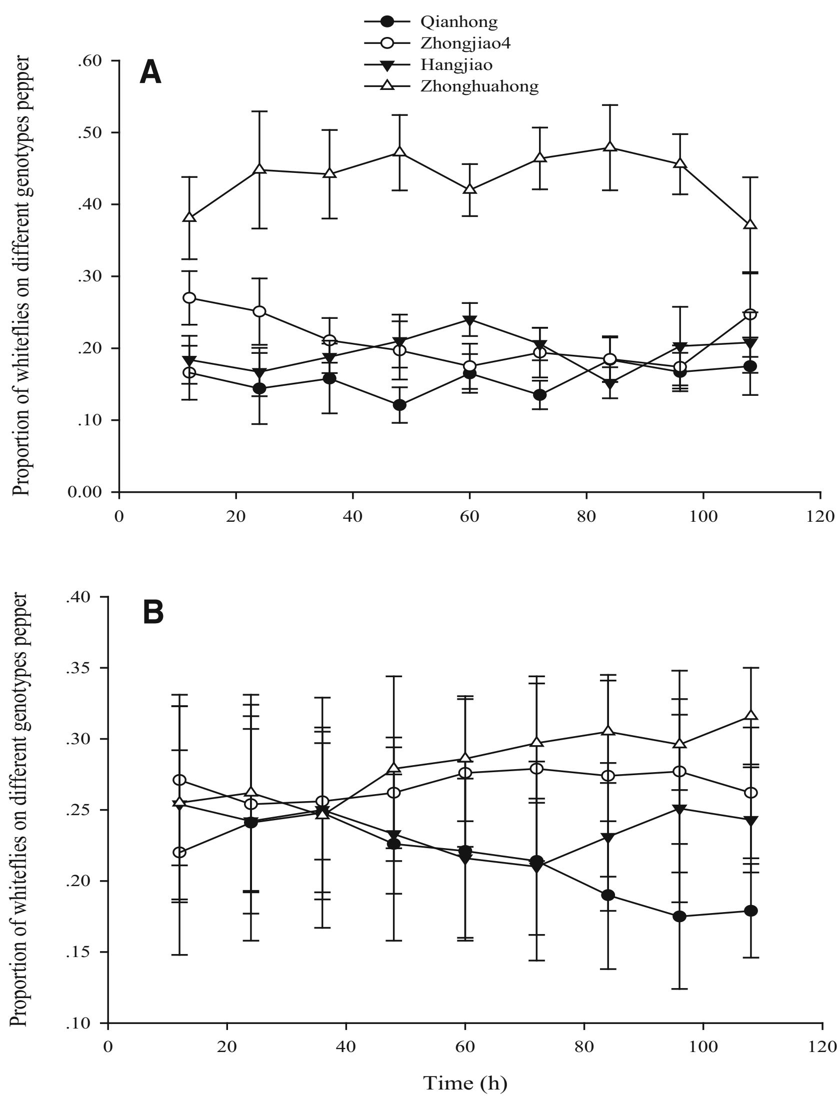

Fig. 1 Host choices (as indicated by settling) of B (**a**) and Q (**b**) putative species of *Bemisia tabaci* among four pepper genotypes. Values are mean ± SE

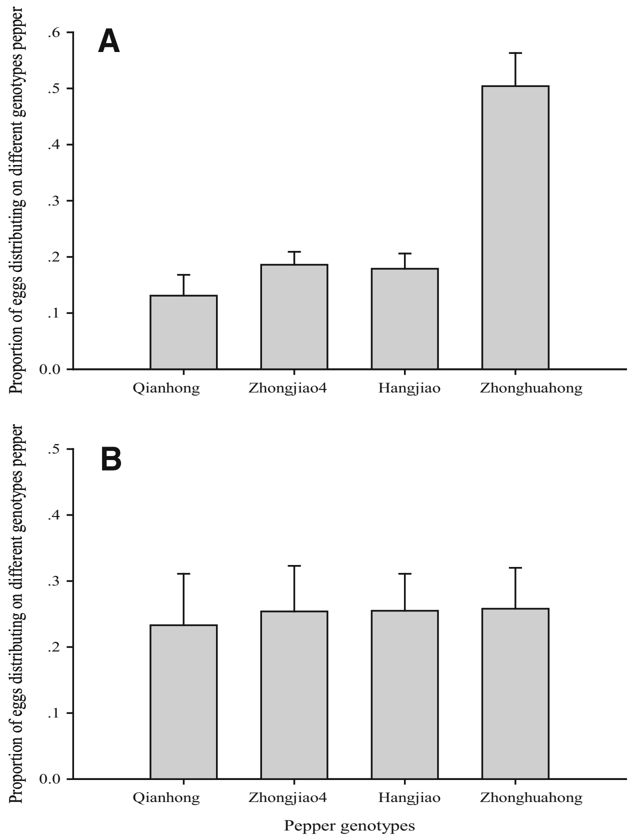

Fig. 2 Egg-laying choices of B (**a**) and Q (**b**) putative species of *Bemisia tabaci* among four pepper genotypes. Values are means + SE

Feeding behavior of B and Q females on four pepper genotypes

The proportions of B females that successfully fed on Qianhong, Zhongjiao4, Hangjiao, and Zhonghuahong were 66.7, 70.0, 66.7 and 70.0%, and the proportions of Q females were 70.0, 80.0, 56.7 and 73.3%, respectively. The proportion of B females or Q females that successfully fed on pepper plants was unaffected by pepper plant genotype ($\chi^2 = 0.154$, $df = 3$, and $P = 0.985$ for B; $\chi^2 = 4.127$, $df = 3$, and $P = 0.248$ for Q).

The nine non-phloem-feeding parameters of EPG were not significantly affected by whitefly species ($P > 0.05$) or pepper genotype ($P > 0.05$) (Fig. 3). However, the total number of probes, time from the first probe to the first E(pd), and number of probes before the first E(pd) were significantly affected by the whitefly × pepper genotype interaction (Fig. 3). Total number of probes ($F_{3,157} = 2.663$, $P = 0.05$, Fig. 3a), time from the first probe to first E(pd) ($F_{3,157} = 2.739$, $P = 0.045$, Fig. 3f), and number of probes before the first E(pd) ($F_{3,157} = 3.641$, $P = 0.014$, Fig. 3g) were significantly lower on Hangjiao than on the other three genotypes for B females but were significantly higher on Hangjiao than on the other three genotypes for Q females (Fig. 3a, f, g).

The phloem EPG feeding parameters for B and Q females on the four genotypes pepper are indicated in Fig. 4. The feeding parameters of total duration of E(pd)1 ($F_{1,157} = 3.969$, $P = 0.048$, Fig. 4a), total number of E(pd)1 ($F_{1,157} = 10.197$, $P = 0.002$, Fig. 4b), and total number of E(pd)2 ($F_{1,157} = 9.947$, $P = 0.002$, Fig. 4e) were significantly higher for B females than for Q females. Total duration of E(pd)2 ($F_{3,157} = 2.923$, $P = 0.036$, Fig. 4d), potential E(pd)2 index ($F_{3,157} = 2.772$, $P = 0.043$, Fig. 4g), and total duration E(pd) ($F_{3,157} = 2.902$, $P = 0.037$, Fig. 4h) were significantly higher on Zhongjiao4 than on Hangjiao, regardless of whitefly species.

Total duration of E(pd)1 and mean time of E(pd)1 were significantly affected by the whitefly × pepper genotype interaction. Total duration of E(pd)1 ($F_{3,157} = 5.459$, $P = 0.001$, Fig. 4a) and mean time of E(pd)1 ($F_{3,157} = 5.679$, $P = 0.001$, Fig. 4c) on Qianhong were significantly higher for B females than for Q females, whereas these feeding parameters on Zhonghuahong were significantly higher for Q females than for B females (Fig. 4a, c).

Discussion

Host choice by phytophagous insect is often influenced by host nutritional and defensive chemistry (Bernays and Chapman 1994; Awmack and Leather 2002). Based on the contents of total phenol, flavonoids, total amino acids, soluble protein, and total nitrogen, the lowest and highest quality pepper genotype in the current study was Zhonghuahong and Zhongjiao4, respectively. According to the EPG data, both B and Q females fed more efficiently on high-quality Zhongjiao4 than on low-quality Zhonghuahong.

According to the optimal oviposition theory, the oviposition preference of female herbivores is positively related to host suitability for offspring, i.e., females are expected to oviposit on high-quality hosts to maximize offspring fitness (Jaenike 1978; Gripenberg et al. 2010). However, Q females did not show any preference for settling and ovipositing on any of the four pepper genotypes, and B females preferred to settle and lay eggs on the low-quality Zhonghuahong.

That Q females did not prefer the high-quality Zhongjiao4 and that B females preferred the low-quality Zhongjiao4 might be due to the quality and quantity of repellent volatiles released from the pepper genotypes. Repellent volatiles from host plants can substantially affect *B. tabaci* host choice and fitness (Bleeker et al.

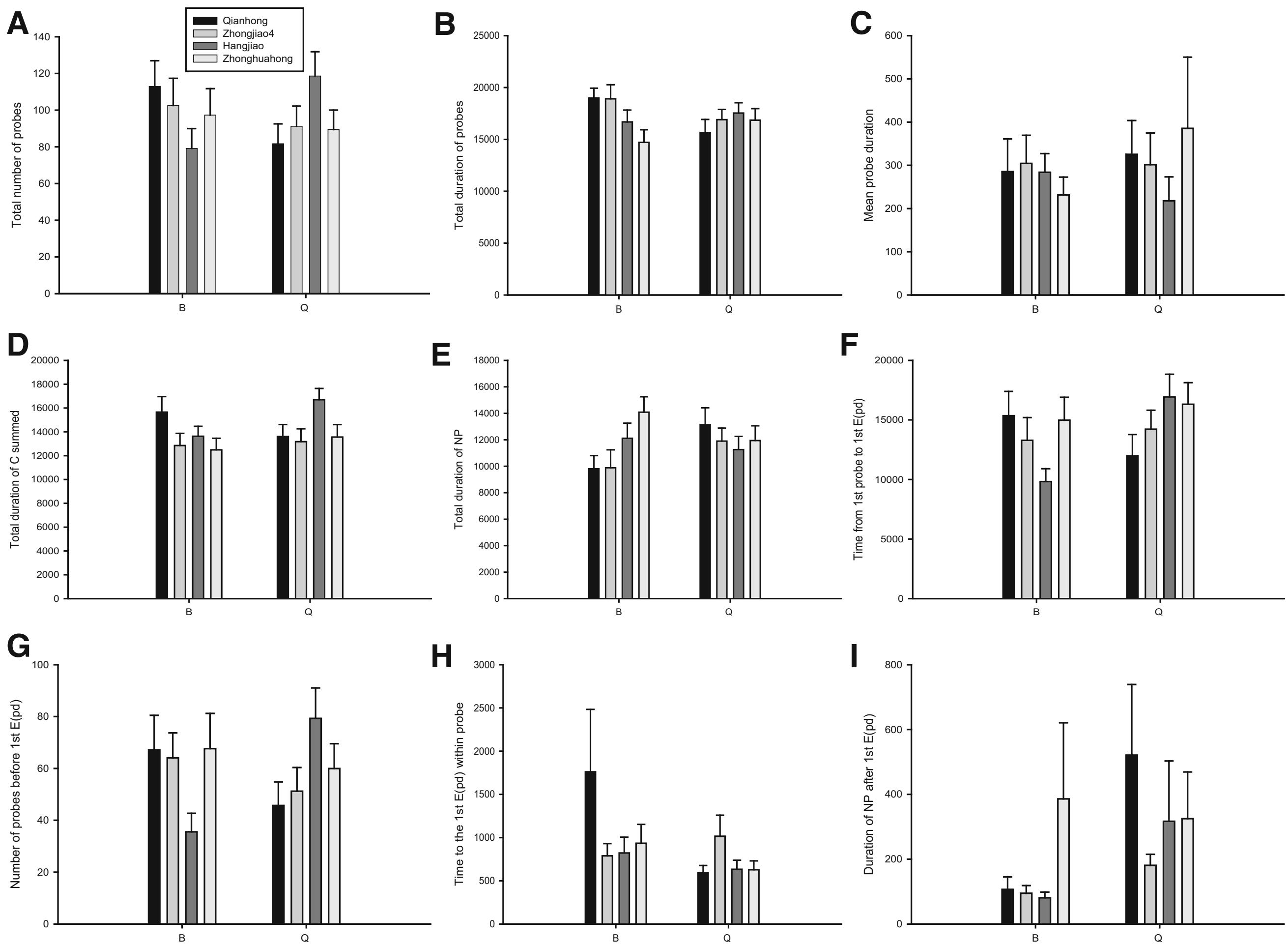

Fig. 3 Non-phloem EPG feeding behaviors of B and Q putative species of *Bemisia tabaci* on four pepper genotypes. Probe numbers are per female. Durations are in seconds. Values are means + SE

2009, 2011, 2012; Shi et al. 2016; Chen et al. 2017). For example, tomato-produced 7-epizingiberene and R-curcumene act as repellents to whiteflies (Bleeker et al. 2009, 2011, 2012). Shi et al. (2016) found that the volatiles methyl salicylate and δ-limonene from tomato repelled Q. The results of Chen et al. (2017) indicated that Q preferred to settle and oviposit on Tomato spotted wilt virus (TSWV)-infected *Datura stramonium* and *Capsicum annuum*, even though the offspring performed better on TSWV-free plants. The latter authors also determined that the lower levels of the repellent volatiles o-xylene and α-pinene from TSWV-infected than from TSWV-free *D. stramonium* explain the preference of Q females for TSWV-infected host plants. It therefore seems that repellent volatiles released from host plants (antixenosis) can affect host choice by phytophagous insects and can result in an inconsistency between host choice and offspring performance (Wise et al. 2008). In support of the possibility that B females preferred the low-quality Zhonghuahong because the volatiles from that genotype were less repellent than the volatiles from the other genotypes, more B females were observed resting on the cage wall than on the pepper plants in our study (*unpublished observation*). Our results are consistent with the hypothesis that most pepper plant genotypes have antixenosis resistance to B whiteflies (Jiao et al. 2014). For example, the negative genetic correlations between antixenosis and antibiosis in tall goldenrod, *Solidago altissima*, result in the negative correlation between preference and performance in spittlebug *Philaenus spumarius* (Wise et al. 2008).

As noted earlier, Q displayed little preference for settling and ovipositing among the four pepper genotypes, even though the four genotypes differed greatly in quality. This unexpected result has at least two possible explanations. First, the ability to distinguish low- and high-quality plants may be low in Q. According to the neural constraints hypothesis, generalist herbivores differ from specialists in being deficient in decision-making and in choosing high-quality food (Bernays and Minkenberg 1997; Bernays 1999; Wise et al. 2008; Gripenberg et al. 2010). Although

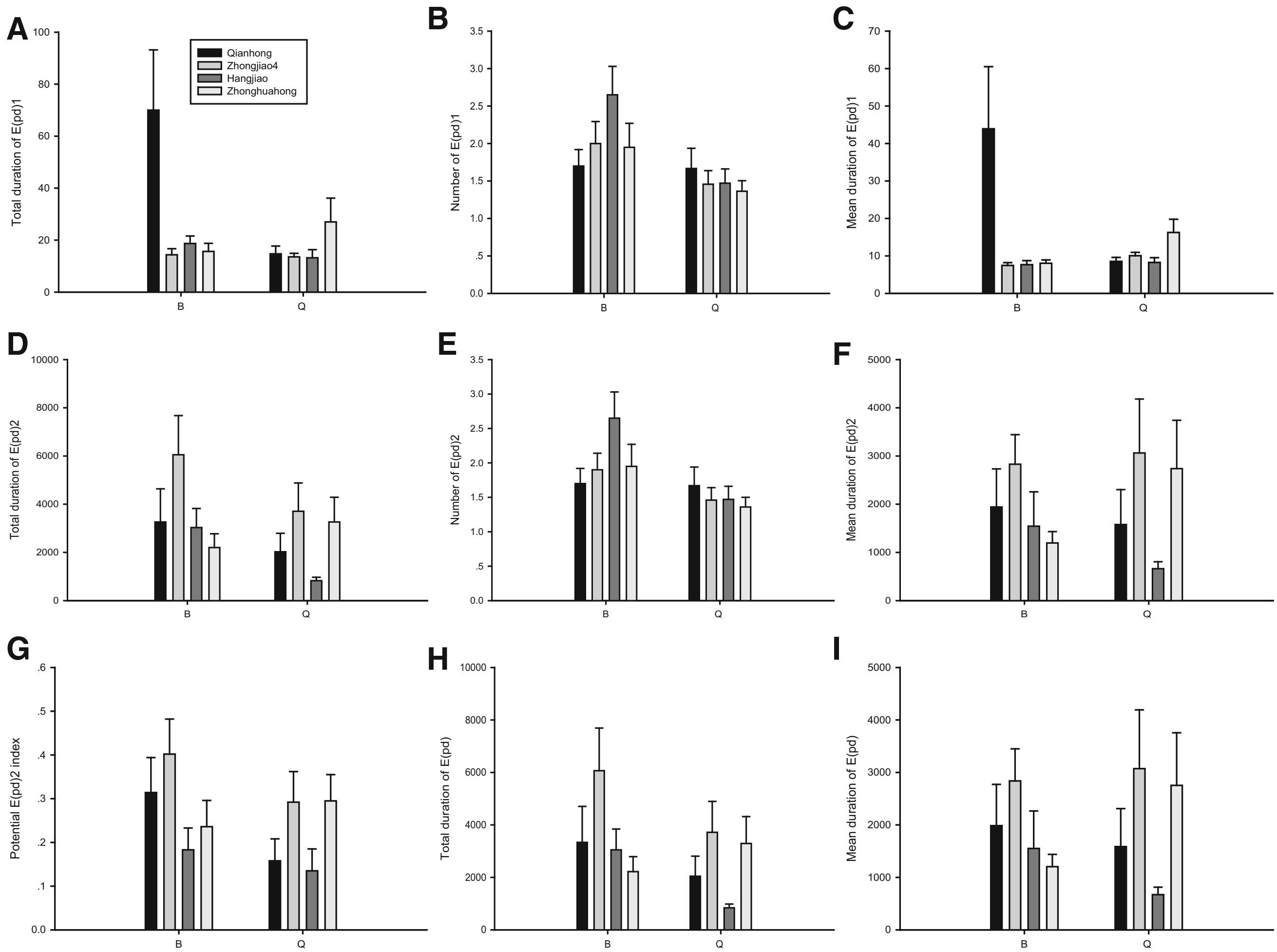

Fig. 4 Phloem EPG feeding behaviors of B and Q putative species of *Bemisia tabaci* on four pepper genotypes. Probe numbers are per female. Durations are in seconds. Values are means + SE

B and Q whitefly species are generalist herbivores, B whitefly species may be a more specialist relative to Q species. Second, Q may be highly resistant to the repellent volatiles released from pepper plants. Many studies have documented that Q is more tolerant than B of the low-quality host plants (Muñiz 2000; Iida et al. 2009; Tsueda and Tsuchida 2011; Chu et al. 2012; Sun et al. 2013; Jiao et al. 2014).

The two possible explanations for why Q showed no preference for any of the four genotypes are not mutually exclusive. Q relies on two strategies to adapt to low-quality host plants. On the one hand, the high activities of Q's main metabolic enzymes efficiently detoxify the high levels of toxins in low-quality hosts (Guo et al. 2014). On the other hand, Q's efficient feeding may help it compensate for feeding on low-quality hosts (Liu et al. 2012).

EPG has often been used to study the feeding behavior of phloem-feeding pests and host resistance mechanisms (Alvarez et al. 2006; Liu et al. 2012; Jiao et al. 2014). The present study showed that both B and Q females fed more efficiently, in terms of phloem-feeding parameters, on high-quality Zhongjiao4 than on the other three pepper genotypes (Fig. 4). Our EPG data provided strong evidence that the phloem-feeding behaviors of B and Q females are positively related to host quality. Because Zhongjiao4 had higher contents of nitrogen (total amino acid, soluble protein), phosphorus, and potassium than the three other genotypes, it is difficult to determine which component(s) of nutrition most affected feeding efficiency. In the future, we intend to separate the effects of nitrogen, phosphorus, and potassium contents on B and Q feeding efficiency.

In contrast to the phloem-feeding parameters, the nine non-phloem-feeding parameters were not significantly affected by whitefly species or pepper genotype (Fig. 3). However, the total number of probes, the time from the first probe to the first E(pd), and the number of probes before the first E(pd) were significantly affected by the interaction between whitefly species and pepper genotype. In addition, two phloem-feeding parameters, the total duration of E(pd)1 and the mean time of E(pd)1, were also significantly affected by the interaction between whitefly species and pepper genotype (Fig. 4a, c). This indicates divergence in the feeding behaviors of B and Q females on pepper genotypes.

As noted earlier, the results showed that B females are quite sensitive to host quality but Q females are not. These findings are consistent with the hypothesis that Q whiteflies can use a wider range of plant species than B whiteflies. Similar results have been reported in previous studies (Muñiz 2000; Muñiz and Nombela 2001; Iida et al. 2009; Tsueda and Tsuchida 2011; Chu et al. 2012; Xu et al. 2011; Sun et al. 2013; Jiao et al. 2012, 2013, 2014). Elbaz et al. (2012) showed that B and Q species differ in their 'optimal defense strategy.' B uses inducible defenses that are profitable if the probability of experiencing stress is small and if stress severity is low, while Q invests significant resources in always being 'ready' for a challenge. The higher capacity of Q whiteflies to adapt to a wider range of plant species may play a certain role in the displacement of B by Q in China and Japan (Chu et al. 2010; Pan et al. 2011; Tsueda and Tsuchida 2011).

In considering the differences in B and Q geographic origins (Boykin et al. 2007), Elbaz et al. (2012) hypothesized that the past experience of Q may have mainly involved natural and agricultural habitats with host plants that were chemically heterogenous, unpredictable, and often toxic; the past experience of B, in contrast, may have mainly involved more predictable habitats with a relatively low percentage of toxic hosts. The results of the current study are consistent with that hypothesis.

Author contribution statement

XGJ and YJZ designed the experiment. WX, YZ, and CW performed the experiments. XGJ and WX analyzed the data. BML, SLW, and QJW contributed reagents/materials. XGJ and YJZ wrote the paper. All authors read and approved the manuscript.

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Compliance with ethical standards

Conflict of interest The authors declare no conflict of interest.

Ethical approval This article does not contain any studies with human participants or animals performed by any of the authors.

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