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Host selection of the tobacco whitefly *Bemisia tabaci* (Hemiptera: Aleyrodidae) among four pepper cultivars (*Capsicum* spp.), Thailand

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ABSTRACT: The tobacco whitefly *Bemisia tabaci* (Gennadius) causes yield loss of a variety of plants by infesting and transferring viruses. Host-plant resistance to *B. tabaci* could potentially reduce its impact. However, resistance is low in most Thai pepper (*Capsicum* spp.) cultivars. In this study, we evaluated host-plant resistance of four common pepper cultivars in Thailand, including *C. annuum* cv. Jinda, *C. annuum* cv. Yuak, *C. frutescens* cv. Keenu (= Khinu), and *C. chinensis* cv. Karang (= Kareang or Kariang), by quantifying plant attraction, egg-laying preference, feeding activity, and growth performance of *B. tabaci* in relation to the four cultivars. Our results showed that *C. annuum* cv. Jinda and *C. annuum* cv. Yuak are less attractive to *B. tabaci* adults, which had a significantly lower egg-laying preference and less feeding activity in relation to *C. annuum* cv. Jinda. No difference in total growth duration of *B. tabaci* was found in regards to the different cultivars. We believe that *C. annuum* cv. Jinda has traits that deter or repel the *B. tabaci* adults and inhibit their feeding activities.
Keywords: *Bemisia tabaci*; *Capsicum* spp.; host-plant resistance; insect-plant interactions

Introduction

The tobacco whitefly *Bemisia tabaci* (Gennadius) is a well-known 'pest' and vector of a broad range of crop species, such as lettuce, cantaloupe, tomato, eggplant, and pepper (Costa et al., 1991; Darshanee et al., 2017; Lei et al., 1999; Polston and Anderson, 1997). It has caused serious economic loss toward the production of these crops. Major portions of yield loss have been attributed to viruses transmitted by the whitefly. Loss caused by whitefly in the United States from 1991–1992 was estimated to cost around 111 million USD (Gonzalez et al., 1992). For example, Thresh et al. (1994) reported that the loss caused by geminivirus may have reached 95% of the total yield. Wisler et al. (1998) reported that the whitefly-transmitted closteroviruses caused a loss of ~20 million USD in the production of lettuce, sugar, beets, and melons in one single growing season.

The selection of a host is a determining factor of phytophagous insects' fitness (Mayhew, 1997). The resistance of plants affects host selection and fitness of insects (Follett, 2017). Moreover, improving host-plant resistance could be a low-cost and environmentally friendly approach to combating phytophagous pests (Sharma and Ortiz, 2002). For example, the chemical resistance of plants against aphids involves a variety of allelochemicals, such as growth inhibitors, toxins, and repellents or deterrents (Smith and Chuang, 2013). The physical resistance of plants against aphids, such as glandular trichomes, thick stem cortexes, and glossy leaves, also function as deterrents or repellents and affect host selection and feeding preferences (Smith and Chuang, 2013). One example of a whitefly

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resistant cultivar of cassava reportedly extends larval duration and causes 72.5% larval mortality of the cassava whitefly *Aleurotrachelus socialis* Bondar (Bellotti and Arias, 2001). Soybean cultivars with high trichome erectness are thought to be more resistant to *B. tabaci (*Lambert et al., 1995*).*

Peppers, particularly the varieties and cultivars of five *Capsicum* spp. (Solanales: Solanaceae), *C. annuum* L., C. *baccatum* (Willd.), *C. chinense* Jacq., *C. frutescens* L., and *C. pubescen* R. et P., are economically important crops cultivated with an annual yield of more than seven millions tons around the world (Fári, 1986). FAO (2018) reported that pepper production is around 732,524 tons and is harvested from ~30,899.68 hectares globally.

Different varieties and cultivars of pepper have different morphology and chemical composition, including the color and shape of the pods, the nutrients, antioxidant compounds, and allelochemicals (Bosland and Votava, 2000; Guil-Guerrero et al., 2006). This subsequently affects the yield, flavor, and resistance against phytophagous insects (Babu et al., 2011; Maharijaya et al., 2011; Meresa et al., 2017). Various pepper cultivars have been reported as being resistant to *B. tabaci* because of their unattractive egg-laying properties for adult insects, thereby reducing the rate of infection and inducing nymph mortality *(* Jeevanandham et al., 2018; Pantoja et al., 2018*)*. In Thailand, whitefly, especially *B. tabaci* biotype Asia1 (Götz and Winter, 2016), is considered to be a super-spreader that transmits begomoviruses, causing chilli leaf curl virus disease (ChiLCVD) and yield loss in Thai peppers (Laprom et al., 2019). Understanding whitefly resistance of Thai pepper cultivars would benefit resistance trait selection and whitefly population management.

In this study, we evaluated whitefly resistance of four commonly cultivated *Capsicum* spp. cultivars in Thailand, including *C. annuum* cv. Jinda, *C. annuum* cv. Yuak, *C. frutescens* cv. Keenu (= Khinu), and *C. chinensis* cv. Karang (= Kareang or Kariang) (Benchasri and Pruthikanee, 2018; Kaewdoungdee and Tanee, 2013; Nantachit and Winijkul, 2007). To do so, we quantified plant attraction, egg-laying preferences, and feeding activity of *B. tabaci* adults, as well as the survival and growth performance of *B. tabaci* nymphs.

Materials and Methods

Whitefly and host plants

Whitefly in this study were obtained from an eggplant-infesting colony in Upper Northeastern Regional Center of National Biological Control Research Center (NBCRC, Khon Kaen University, 40002 Khon Kaen, Thailand). At the NBCRC, eggplant seedlings were sown into 104-well plates that were filled with soil and watered daily for 20 days. Then, the seedlings were transplanted into pots (diameter: ~12.7 cm) filled with soil and were grown for two months before being introduced to whitefly. There were 250 pairs of wild-type whitefly adults that were collected in the fields surrounding the NBCRC. To collect eggs from the wild-type whitefly, the adults were released into a nylon cage with a single eggplant. After five days, the eggplant with wild-type eggs was moved and kept in another nylon cage. Individual insects grown from the wild-type eggs were called the 1st laboratory generation. The same methodology was applied to collect eggs of the 2nd and 3rd generations. The 4th laboratory generation of whitefly reared at the NBCRC was used for the experiments in this study, totaling 250 eggs, or 125 male adults and 125 female adults. Different growth stages of *B. tabaci* were identified by body length and body width based on Sripontan and Siri (2006).

Four pepper cultivars, including *C. annuum* cv. Jinda, *C. annuum* cv. Yuak, *C. frutescens* cv. Keenu, and *C. chinensis* cv. Karang were used for testing whitefly resistance. The plant seeds were sown in 104-well plates filled with soil and were watered daily for 20 days. Then, the seedlings were transplanted into pots (diameter: ~12.7 cm) filled with soil and were grown for another 30 days before experiments began. To prevent insect infestation, each pot was covered by a nylon cage (Mosquito net) for protection. Both the whitefly and plants were kept in rooms with a temperature of 31.7±3.1°C and a relative humidity of 62.0±17.0%.

Plant attraction and egg-laying preference

The selection probability of the four pepper cultivars by *B. tabaci* adults was quantified using choice and non-choice tests. In each choice test, fifteen males and fifteen females of *B. tabaci* were released into a cage (60×60×90 cm). The four pepper cultivars were placed in different corners of the cage (**Fig. 1A**). The choice test was replicated five times, and the distribution of pepper cultivars was changed in each replication, with clockwise and counterclockwise rotations, as shown in **Fig. 1B.** Totally, one-hundred fifty individuals of whitefly adults were used in choice tests.

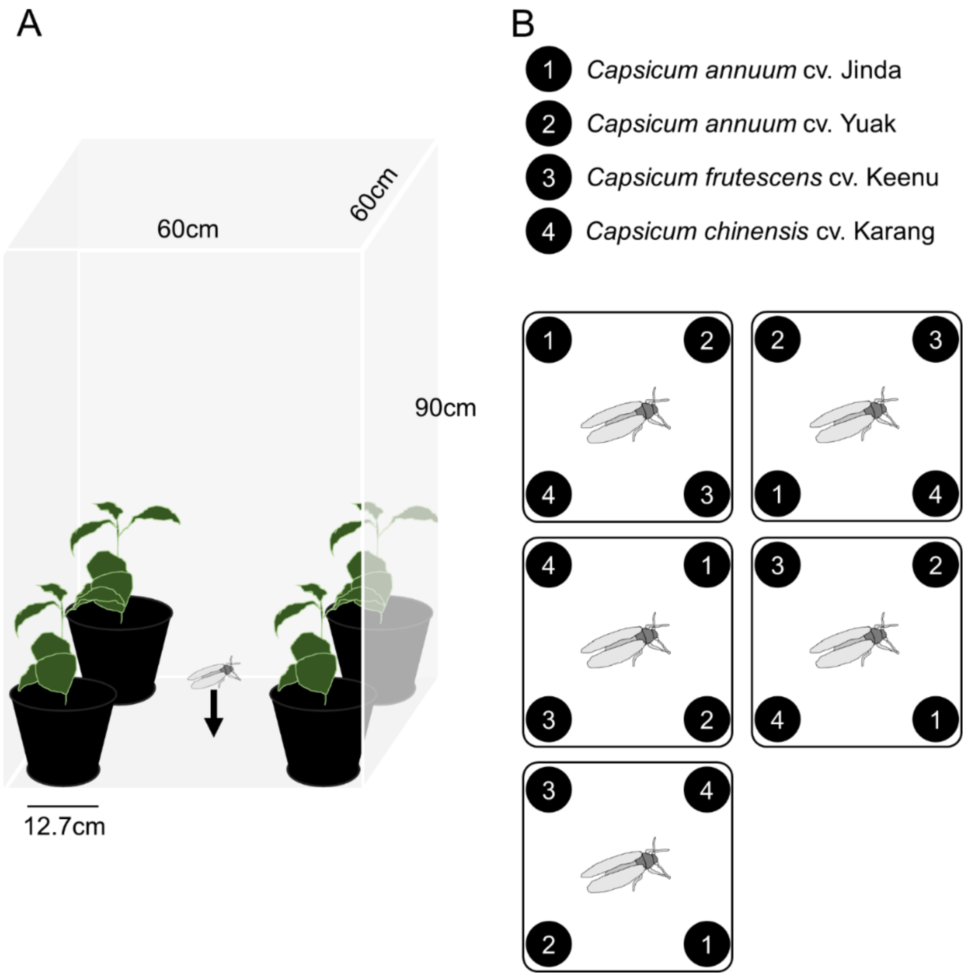

Fig. 1 The scale of the rearing cage (A) and the relative distribution of pepper cultivars (B); *Capsicum annuum* cv. Jinda, *C. annuum* cv. Yuak, *C. frutescens* cv. Keenu, and *C. chinensis* cv. Karang were used in each of the five replications of host selection bioassay. In each replication, adults of *Bemisia tabaci* were released in the center of the cage (arrowed in Fig. 1A). The locations of the different cultivars were rotated clockwise or

counterclockwise to ensure the distribution of cultivars was different in all five replications. The net opening was rolled and directed to face one side of the cage for releasing whitefly adults. After the release, the caged was immediately closed by tying up the net opening.

Non-choice tests were conducted using cylindrical cages (diameter: ~12.7cm, height: ~45cm) with a single pepper cultivar, which reduced the foraging space for whitefly adults and made the adults and larvae more visible. In each non-choice test, five males and five females of *B. tabaci* were released and confined in a cylindrical cage. The non-choice test was repeated five times for each pepper cultivar, and a total of 25 whitefly adults were used for each pepper cultivar. To test the preference of whitefly adult in the choice test, the number of adults on each cultivar was counted in one and 24 hours after the release of *B. tabaci*. For both choice and non-choice tests, the number of eggs on each plant was counted 24 hours after the release of *B. tabaci*.

Nymph survival and growth performance

The eggs observed in the choice and non-choice tests were kept on the plants, and their survival and growth were monitored daily for 20 days. Recognizing that the number of whiteflies on a plant may affect the survival rate, only 10 whitefly eggs were kept on each single plant, the other eggs were manually removed. To prevent the escape of whiteflies or interactions between different cultivars, each plant in the choice and non-choice test was moved to a separate cage. Five replications were conducted for each pepper cultivar.

Feeding activity of adults

To test whether the pepper cultivars inhibited the feeding activity of the whitefly, the feeding activity of *B. tabaci* on each cultivar was quantified based on the quantity and volume of honeydew excreted. The method of Pollard (1955) was used to collect honeydew. In each trial, one male and one female whitefly adult were confined to a single leaf on a plant by removing the other leaves. Filter paper stained with 0.4% bromocresol green was placed under the leaf to collect the honeydew. The filter paper was replaced daily, and the amount of honeydew excreted was measured until one of the two whiteflies died (6–8 days). The trial was replicated five times for each pepper cultivar.

Leaf morphology

To examine whether whitefly resistance was associated with leaf morphology of the cultivars, we measured length, width, and thickness of the third leaf of each pepper cultivar. The leaf length was measured from leaf base to tip, and the leaf width was measured from the middle of the leaf. Leaves were cut off at the middle and the leaf thickness was measured using a USB microscope (Model: UM12, Microlinks Technology Corp., Taiwan) with photo-capture analysis software UM12-CAM Viewer (Version 2.507, Microlinks Technology Corp.).

Statistical analysis

The experimental design of choice test and no-choice test are Completely Randomized Design (CRD). To test whether or not any of the pepper cultivars deter or repel *B. tabaci*, the number of adults and eggs on the four pepper cultivars were analyzed using a chi-square test of homogeneity. The residual results of each cultivar in the chi-square tests were calculated for comparison. For each cultivar, the number of adults and eggs in different replications were pooled for analysis. To test whether the pepper cultivars inhibited the growth and feeding activity of *B. tabaci*, the growth duration at different stages (egg, 1–4 instars, total growth duration), the amount of honeydew excreted, and the diameter of excreted honeydew were compared among the four pepper cultivars using an analysis of variance (ANOVA) with Tukey's HSD test.

Results

Plant attraction and egg-laying preferences

In the choice test, one hour after release, the number of *B. tabaci* adults was 12, 19, 19, and 14 on the four pepper cultivars *C. annuum* cv. Jinda, *C. annuum* cv. Yuak, *C. frutescens* cv. Keenu, and *C. chinensis* cv. Karang, respectively (**Fig. 2A**). No significant difference was found among the different cultivars (Chi-square test for homogeneity: χ^2 = 0.53, p = 0.91). After the insects had been released for 24 hours, 18, 27, 50, and 32 *B. tabaci* adults were observed on pepper cultivars *C. annuum* cv. Jinda, *C. annuum* cv. Yuak, *C. frutescens* cv. Keenu, and *C. chinensis* cv. Karang, respectively (**Fig. 2B**). The number of adults was significantly different among cultivars (χ^2 = 8.26, $p < 0.05$); in addition, negative residuals were found on *C. annuum* cv. Jinda (-1.38) and *C. annuum* cv. Yuak (-0.04), a strong positive residual was found on *C. frutescens* cv. Keenu (1.43), and nearly no residual appeared on *C. chinensis* cv. Karang (0.02).

In the choice test, a total of 16, 21, 47, and 47 *B. tabaci* eggs were found on pepper cultivars *C. annuum* cv. Jinda, *C. annuum* cv. Yuak, *C. frutescens* cv. Keenu, and *C. chinensis* cv. Karang, respectively (**Fig. 2C**). The number of eggs on different pepper cultivars was significantly different (χ^2 = 13.42, $p < 0.01$). Negative residuals were found on cultivars *C. annuum* cv. Jinda (-1.70) and *C. annuum* cv. Yuak (-1.13), while positive residuals were found on *C. frutescens* cv. Keenu (1.13) and *C. chinensis* cv. Karang (1.13). In the non-choice test, there were 9, 41, 50, and 53 eggs on the pepper cultivars *C. annuum* cv. Jinda, *C. annuum* cv. Yuak, *C. frutescens* cv. Keenu, and *C. chinensis* cv. Karang, respectively (**Fig. 2D**). The number of eggs was significantly different among pepper cultivars (χ^2 = 22.15, $p < 0.0001$). Negative residual was found on *C. annuum* cv. Jinda (-3.01), and positive residuals were found on *C. annuum* cv. Yuak (0.22), *C. frutescens* cv. Keenu (0.88), and *C. chinensis* cv. Karang (1.09).

The high number of *B. tabaci* adults and eggs found on *C. frutescens* cv. Keenu and *C. chinensis* cv. Karang showed that these two cultivars do not have traits that deter or repel the *B. tabaci* adults or their egg-laying behavior. In contrast, a lower number of *B. tabaci* adults were found on *C. annuum* cv. Jinda and *C. annuum* cv. Yuak, indicating that both of these cultivars had less attractive traits for *B. tabaci.* Moreover, the smallest number of *B. tabaci* eggs was found on *C. annuum* cv. Jinda in both the choice and non-choice tests. This shows that *C. annuum* cv. Jinda has traits that inhibit the egg-laying behavior of *B. tabaci.*

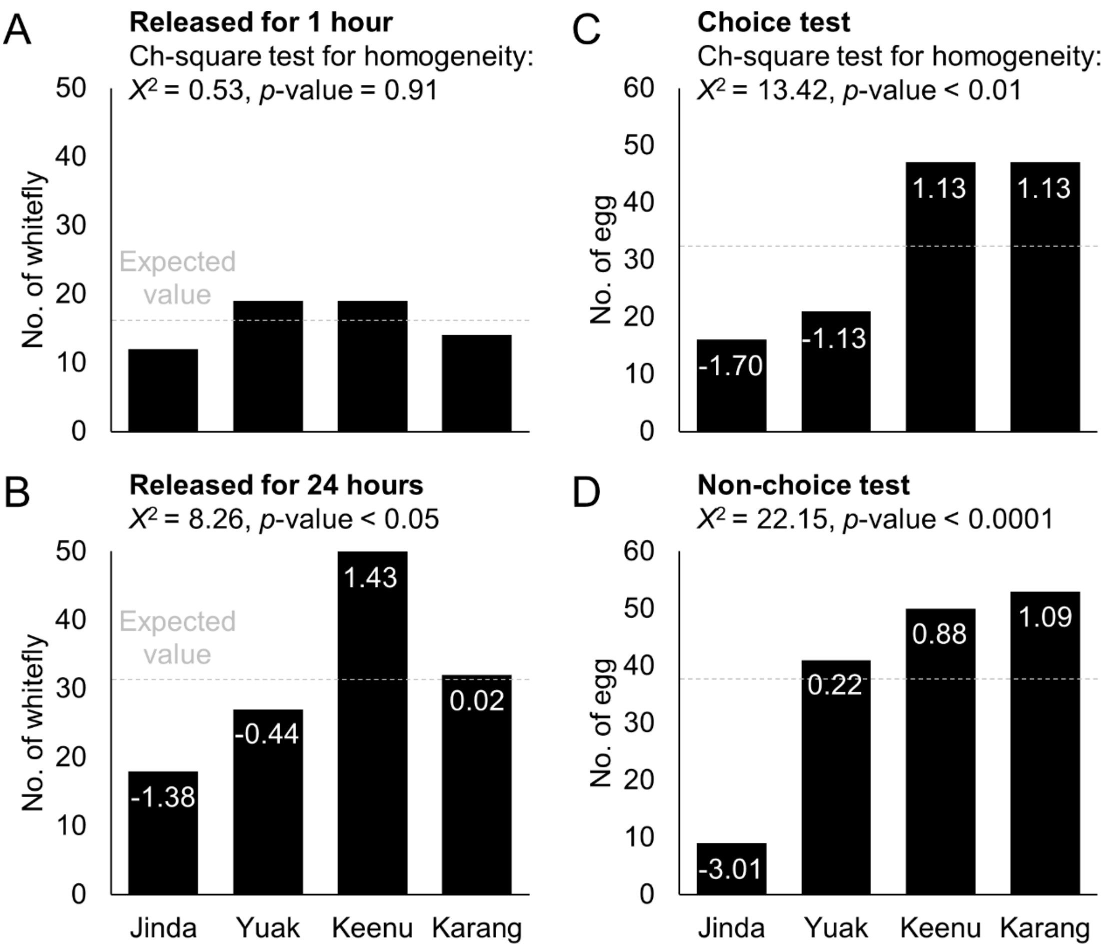

Fig. 2 Quantifying the attraction and egg-laying preference among *Bemisia tabaci* for pepper cultivars *Capsicum annuum* cv. Jinda, *C. annuum* cv. Yuak, *C. frutescens* cv. Keenu, and *C. chinensis* cv. Karang based on the distribution of *B. tabaci* adults one hour (A) and 24 hours (B) after release in the choice test and based on the distribution of eggs in the choice (C) and non-choice test (D) after 24 hours. Differences among cultivars were examined using a Chi-square test for homogeneity, which tested an equal hypothesis (gray dotted lines) among treatments. Values on the top of the bars are residual values in the Chi-square tests.

Survival and growth duration

For all pepper cultivars, 100% of whitefly eggs and nymphs survived and emerged into adults, No difference of survival rate was observed during the choice test or the non-choice test. The trials reared an equal number of individuals. Significant differences of growth duration were observed in terms of the eggs (ANOVA: $F = 34.5$, $p < 0.0001$), and the 1st instar ($F = 14.2$, $p < 0.0001$), 2nd instar ($F = 9.9$, $p < 0.0001$), 3rd instar ($F = 23.9$, $p < 0.0001$), and 4th instar of the nymph ($F = 6.7$, $p < 0.001$) **(Fig. 3)**. Egg duration was significantly shorter in *C. chinensis* cv. Karang; 1st instar growth duration was shorter in pepper cultivars *C. annuum* cv. Jinda and *C. frutescens* cv. Keenu; 2nd instar growth duration was shorter in *C. annuum* cv. Jinda; and 3rd instar growth duration was shortest in *C. annuum* cv. Yuak, followed by cultivars *C. frutescens* cv. Keenu, *C. chinensis* cv. Karang, and *C. annuum* cv. Jinda**.** Growth duration of the 4th instar was shorter in cultivars *C. annuum* cv. Yuak, *C. frutescens* cv. Keenu, and *C. chinensis* cv. Karang**.** Despite these differences, there were no differences in total growth duration among the different pepper cultivars ($F = 2.19$, $p = 0.09$) **(Fig. 3)**.

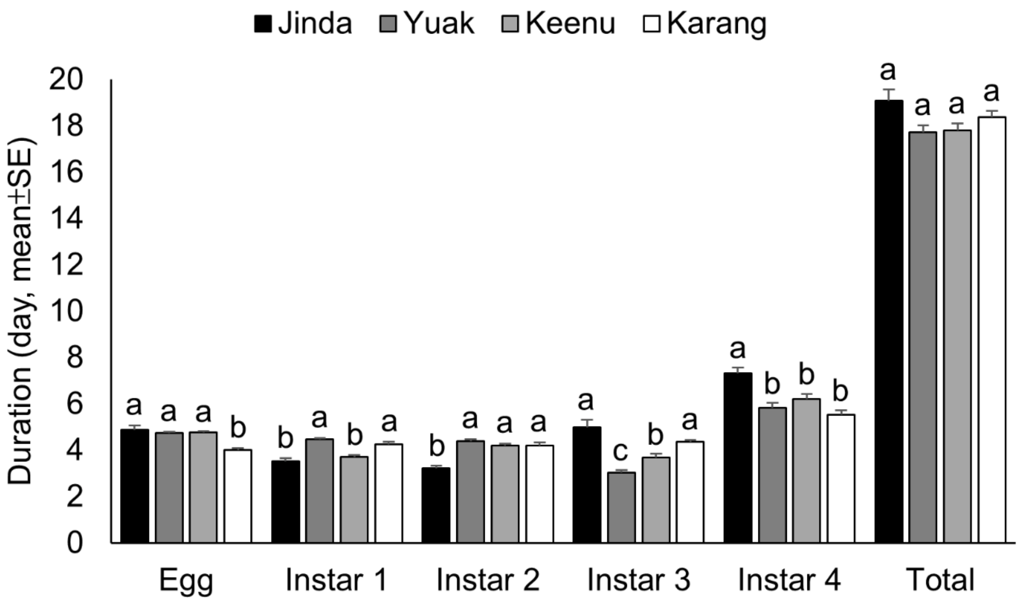

Fig. 3 Comparing the growth duration of different stages of *Bemisia tabaci* growth when occupying pepper cultivars *Capsicum annuum* cv. Jinda, *C. annuum* cv. Yuak, *C. frutescens* cv. Keenu, and *C. chinensis* cv. Karang. The means followed by the same lowercase letter within the same column are not significantly different at alpha=0.05.

Feeding activity

The amount of honeydew excreted per day and its diameter were both significantly different among *B. tabaci* occupying the different pepper cultivars (ANOVA: Amount of honeydew excreted: $F = 21.0$, $p < 0.0001$; diameter of honeydew: $F = 32.7$, $p < 0.0001$). The highest amount of honeydew excreted was 4.2±0.1 per day, found among *C. chinensis* cv. Karang, followed by *C. frutescens* cv. Keenu (3.6±0.2) and *C. annuum* cv. Yuak (3.3±0.1), and the lowest amount was found among *C. annuum* cv. Jinda (2.6±0.1). The honeydew diameter was largest among *C. chinensis* cv. Karang (0.210±0.002 mm), followed by *C. frutescens* cv. Keenu (0.200±0.002 mm), and *C. annuum* cv. Yuak (0.193±0.001 mm) and *C. annuum* cv. Jinda (0.190±0.001 mm). Based on these results, *C. annuum* cv. Jinda and *C. annuum* cv. Yuak are the most likely cultivars to inhibit the feeding activity of adult *B. tabaci*, while *C. frutescens* cv. Keenu and *C. chinensis* cv. Karang are more susceptible **(Fig. 4)**.

Leaf morphology

Observations on the leaf morphology of the four pepper cultivars showed that *C. annuum* cv. Jinda has a smaller leaf area (22.9±10.7 cm^2) than the other cultivars (mean leaf area: 30.1–56.5 cm^2) (**Table 1**). This may indicate that *B. tabaci* prefers plants with bigger leaves. We also observed that *C. annuum* cv. Jinda and *C. annuum* cv. Yuak have tough leaves, and the leaves of *C. annuum* cv. Jinda (0.21±0.03 cm) and *C. annuum* cv. Yuak (0.27±0.08 cm) are thicker than those of *C. frutescens* cv. Keenu (0.18±0.04 cm) and *C. chinensis* cv. Karang (0.18±0.04 cm) (**Table 1**).

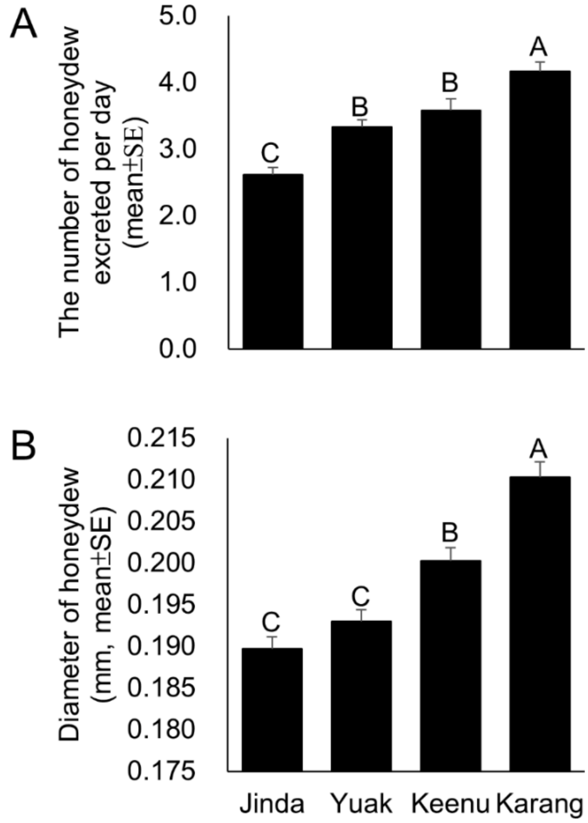

Fig. 4 Comparing the feeding activity of adult *Bemisia tabaci* among pepper cultivars *Capsicum annuum* cv. Jinda, *C. annuum* cv. Yuak, *C. frutescens* cv. Keenu, and *C. chinensis* cv. Karang by measuring the amount of honeydew produced per day (A) and the mean diameter of the honeydew (B). The means followed by the same lowercase letter within the same column are not significantly different at alpha=0.05.

Table 1 Leaf measurements of nine leaves taken from the pepper cultivars *Capsicum annuum* cv. Jinda, *C. annuum* cv. Yuak, *C. frutescens* cv. Keenu, and *C. chinensis* cv. Karang

Cultivar	Leaf measurements (mean±SD)		
	Length (cm)	Width (cm)	Thickness (cm)
Capsicum annuum cv. Jinda (n = 9)	7.4±1.8	2.9±2.6	0.21±0.03
Capsicum annuum cv. Yuak (n = 9)	7.8±1.6	4.4±2.5	0.27±0.08
Capsicum frutescens cv. Keenu (n = 9)	9.0±1.7	6.1±2.4	0.18±0.04
Capsicum chinensis cv. Karang (n = 9)	6.6±1.5	4.3±1.9	0.20±0.03

Discussion

Host selection of phytophagous insects is generally considered to be related not only to the preferences of adults, but also to the fitness of their offspring (Thompson, 1988; van Lenteren and Noldus, 1990). For example, Islam et al. (2010) reported that the eggplant cultivars that adults found attractive also reduced the growth duration of *B. tabaci* nymphs. In the present study, the high survival rates and homogeneous growth durations of *B. tabaci* on *C. annuum* cv. Jinda, *C. annuum* cv. Yuak, *C. frutescens* cv. Keenu, and *C. chinensis* cv. Karang showed that none of the cultivars have traits that efficiently inhibit the growth of *B. tabaci* nymphs. In contrast to van Lenteren and Noldus (1990) and Islam et al. (2010), we found no associations between offspring fitness and adult attraction or egg-laying preference. However, our results showed that *C. frutescens* cv. Keenu and *C. chinensis* cv. Karang are more attractive to *B. tabaci*. The selection on *C. frutescens* cv. Keenu and *C. chinensis* cv. Karang are more likely related to other cues, such as the color and morphology of leaves, or food cues (Berlinger, 1986), rather than offspring performance. Leaf toughness and thickness as seen in *C. annuum* cv. Jinda and *C. annuum* cv. Yuak may negatively affect the feeding activity of *B. tabaci*, which is consistent with the results of their honeydew excretions. Host selection by *B. tabaci* from among the four pepper cultivars may also relate to food cues.

Conclusion

C. annuum cv. Jinda was shown to be the least attractive and least preferred for egg-laying and feeding activity among the whitefly *B. tabaci.* This cultivar showed a higher resistance than the other pepper cultivars, which were *C. annuum* cv. Yuak, *C. frutescens* cv. Keenu, and *C. chinensis* cv. Karang. The host selection preference from among the four pepper varieties is most likely associated with cues related to feeding behavior rather than nymph survival and growth rates.

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