

Impacts of Cucurbit Chlorotic Yellows Virus (CCYV) on Biological Characteristics of Its Vector *Bemisia tabaci* (Hemiptera: Aleyrodidae) MED Species

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Abstract

Plant viruses can change the phenotypes and defense pathways of the host plants and the performance of their vectors to facilitate their transmission. Cucurbit chlorotic yellows virus (CCYV) (*Crinivirus*), a newly reported virus occurring on cucurbit plants and many other plant species, is transmitted specifically by *Bemisia tabaci* MEAM1 (B biotype) and MED (Q biotype) cryptic species in a semipersistent manner. This study evaluated the impacts of CCYV on *B. tabaci* to better understand the plant-virus-vector interactions. By using CCYV-*B. tabaci* MED-cucumber as the model, we investigated whether or how a semipersistent plant virus impacts the biology of its whitefly vector. CCYV mRNAs were detectable in nymphs from first to fourth instars and adults of *B. tabaci* with different titers. Nymph instar durations and adult longevity of female whiteflies greatly extended on CCYV-infected plants, but nymph instar durations and adult longevity of male whiteflies were not significantly influenced. In addition, the body length and oviposition increased in adults feeding on CCYV-infected plants, but the hatching rates of eggs and survival rates of different stages were not affected. Most interestingly, the sex ratio (male:female) significantly reduced to 0.5:1 in whitefly populations on CCYV-infected plants, while the ratio remained about 1:1 on healthy plants. These results indicated that CCYV can significantly impact the biological characteristics of its vector *B. tabaci*. It is speculated that CCYV and *B. tabaci* have established a typical mutualist relationship mediated by host plants.

Key words: *Crinivirus*, insect vector, whitefly-virus interaction, fitness, cucurbit plant

The plant viruses have developed specific relationships with insect vectors in the long course of coevolution. Approximately 80% of the phytovirus depend on vectors for transmission (Andretlink and Fuchs 2005, Hohn 2007). Virus infection may change not only the phenotypes and volatiles of the host-plants, but can also modify the behaviors of their insect vectors (Maluta et al. 2014, 2017, 2019, Mauck 2016, Fereres et al. 2016, Chesnais et al. 2017, Pereira et al. 2019).

Studies have shown that after carrying tobacco curly shoot virus (TbCSV) or tomato yellow leaf curl China virus (TYLCCNV), the fecundity and longevity of *Bemisia tabaci* MEAM1 species were significantly increased (Jiu et al. 2007). *B. tabaci* MEAM1 and MED species feeding on TYLCCNV-infected tobacco plants increased its egg production and realized fecundity (Guo et al. 2010), and the feeding behaviors were promoted in *B. tabaci* MEAM1 and MED species when feeding on tomato yellow leaf curl virus (TYLCV)-infected plants, for example, the viruliferous *B. tabaci* spent more time in salivating into sieve elements of plants than did nonviruliferous whiteflies, a behavior essential for viral inoculation

of uninfected hosts, indicating that the altered behavior of whiteflies seems likely to increase TYLCV transmission rates (Liu et al. 2013). Increasing researches have shown that plant viruses can regulate the growth, mating, immunity, feeding, fecundity, survival, host selection, gene expression, and other characteristics of their insect vectors (Moreno-Delafuente et al. 2013, Su et al. 2015, Chen et al. 2016, Kaur et al. 2017, Maluta et al. 2017, Safari et al. 2019, Wan et al. 2020, Chen et al. 2021).

Bemisia tabaci (Gennadius) (Hemiptera: Aleyrodidae) is one of the most important agricultural pests and the most efficient vectors for the transmission of plant viruses in the world (De Barro et al. 2011). Previous studies have reported that more than 500 species of plant viruses from 5 families and 5 genera are transmitted by *B. tabaci* (Jones 2003, Bragard et al. 2013, Polston et al. 2014, He et al. 2021), and some of these viruses have caused serious damage and economic losses to agricultural production.

Cucurbit chlorotic yellows virus (CCYV) (*Closteroviridae: Crinivirus*), as an emergent plant virus, was firstly identified in melon (*Cucumis melo*) in Japan in 2004 (Gyoutoku et al. 2009). CCYV is

composed of two single-stranded RNA, and transmitted specifically by Middle East Asia Minor 1 (MEAM1, formerly biotype B) and Mediterranean (MED, formerly biotype Q) cryptic species of *B. tabaci* in a semipersistent manner (Okuda et al. 2010, Li et al. 2016). CCYV can systematically infect melon plants such as watermelon, luffa, and pumpkin and non-melon plants such as beet, quinoa, datura, and *Nicotiana benthamiana* (Gyoutoku et al. 2009), causing chlorotic leaf spots and complete yellowing of leaves. CCYV seriously affects the yield and quality of melons in most parts of China and many other countries (Gu et al. 2011, Wintermantel et al. 2018).

Recent studies suggest that CCYV had impacts on the feeding behavior of *B. tabaci*, and the degree of influence depends on the gender (male and female) and the cryptic species of *B. tabaci* (Lu et al. 2017, 2019). In this study, the effects of CCYV on the nymph development, reproduction, and other biological characteristics of *B. tabaci* were studied in order to evaluate the impacts of CCYV on *B. tabaci* to better understand the plant-virus-vector interactions and provides new ideas for the management of viruses.

Materials and Methods

Insect and Plants

The colony of *B. tabaci* Mediterranean (MED, Q biotype) was maintained on cucumber plants (*Cucumis sativus* L.cv. Bojie-107) in cages (60 cm × 60 cm × 80 cm) in the greenhouse at 28 ± 1°C, photoperiod of 16:8 L:D, and 75 ± 1% relative humidity. The genetic purity of *B. tabaci* Q biotype cultures was monitored every 3 generations using the random amplified polymorphic DNA polymerase chain reaction (RAPD-PCR) technique combined with the sequencing of *mtCO1* gene (Chu et al. 2010). To obtain CCYV-infected plant cultures, cucumber plants at the two-true-leaf stage were inoculated with *Agrobacterium tumefaciens*-mediated CCYV clones (Shi et al. 2016). Healthy and CCYV-infected cucumber plants were separately kept under above-mentioned conditions.

Quantification of CCYV in Cucumber Plants and Whiteflies

A pair of adults (a male and a female) were placed with a clip cage (radius: 2.5 cm × height: 2 cm) on a leaf of CCYV-infected cucumber plant for oviposition. After 24 h, the adults were removed. Observations were taken every day under the ultra-depth-of-field microscope (Keyence digital microscope VHX-600E) until eclosion. Ten individuals of each stage of first to fourth instar nymphs and adults (48 h after eclosion) were collected for RNA extraction. Total RNA of whiteflies or infected cucumber plants (100 mg) was extracted using TRIzol Reagent (Invitrogen Carlsbad, CA) following the manufacturer's instructions. RNA concentration and purity were measured in a NanoDrop spectrophotometer (Thermo Scientific Wilmington, DE) and stored at -80°C for subsequent analysis. Total RNA (1 µg) from each sample was reverse transcribed to generate the first-strand cDNA using the PrimeScript RT reagent Kit (Takara, Dalian, China).

Primers were designed based on coding sequences of CCYV coat protein (CP) by using primer premier 5 software and the nucleotide sequence in GenBank (Accession No: HM581658.1). The primers used are shown in Table 1. Subsequent primer-blast searches showed that they had a high specificity towards CCYV. PCR products were connected with pMD18-T vector to construct standard recombinant plasmids. Six gradients (3.40 × 10³–3.40 × 10⁸ copies/µl) of standard recombinant plasmids were set up as a template for real-time qRT-PCR, with three replicates for each concentration, meanwhile, blank controls and negative controls were also set up.

Table 1. PCR primers for CCYV detection

| Primers | Positions | Sequence (5'-3') | Size (bp) |
|---------|-----------|-----------------------|-----------|
| CCYV-F | 548-567 | GCGACCATCATCTACAGGCA | 152 |
| CCYV-R | 679-699 | CCGACTTGTTCCTTTCAGAGC | |

Primers were designed based on coding sequences of CCYV coat protein (CP) by using primer premier 5 software and the nucleotide sequence in GenBank (Accession No: HM581658.1).

Amplification reactions were performed as follows: 94°C for 2 min, 40 cycles of 94°C for 15 s, 60°C for 20 s, 72°C for 20 s. According to the standard curve automatically generated by the instrument, the correlation coefficient $R^2 = 0.9984$, the amplification efficiency $E = 95\%$, and the standard curve equation is $Y = -3.33961 \lg X + 27.8480$ (Supp Fig. 1 [online only]). C_t value of each sample was detected by qRT-PCR with replicates, and the absolute CCYV mRNA molecules in cucumber plants or *B. tabaci* were quantified.

Impacts of CCYV on Biology of *B. tabaci*

A pair of nonviruliferous adults of 3-d were placed with a clip cage on a leaf of a healthy cucumber plant for oviposition. After 24 h, the adults were transferred to CCYV-infected cucumber plant for another 24 h for oviposition, then the adults were removed from plants. Thirty eggs on each leaf were marked under the ultra-depth-of-field microscope and other eggs were removed with a small brush. Three replicates were used for each treatment. Observations were taken every day under the microscope until the nymphs hatched from the eggs, and the number of hatched and unhatched eggs were recorded. Locations of the first-instar nymphs were marked. The survival number and development time of each instar were recorded and wait until the nymph has emerged as an adult to distinguish its gender. The hatching rates (P_0), nymph survival rates (P_n), and sex ratio (P) of newly emerging adults were calculated with the following equations:

$$P_0 = \frac{N_1}{K} \times 100\% \quad (1)$$

$$P_n = \frac{N_{n+1}}{N_n} \times 100\% \quad (2)$$

$$P = \frac{M}{F} \times 100\% \quad (3)$$

where N_1 is the number of first-instar nymphs; K is a constant of 30; P_n is the survival rates of each instar nymphs ($n = 1, 2, 3, 4$); M is the number of males and F is the number of females. The nymph duration and adult longevity were recorded separately. Sizes of adult individuals were measured under the ultra-depth-of-field microscope.

In another set of experiments, a couple of newly emerged adults were placed with a clip cage on a leaf of healthy or CCYV-infected cucumber plant. The insects were moved to a new plant every 24 h. Eggs on all leaves were counted, and dead male adults were replaced with new males until the female adults died. Ovipositional capacity was calculated and 58 samples were analyzed for each treatments.

Data Statistics

IBM SPSS Statistics 21.0 was used to conduct data analyses. Comparisons in body size, oviposition as well as sex ratio of insects

on healthy and CCYV-infected cucumber plants were made using Independent-Samples *t*-test; median-based statistics test was used to analyze nymph duration and adult longevity; and one-way ANOVA, LSD test was used to analyze fertility rate, nymph survival rates and the amount of CCYV mRNA molecules among all instar nymphs and adults. Significant differences were tested at the 0.05 or 0.01 level. All data were expressed as mean \pm SE.

Results

Detection of CCYV in Cucumber

The cucumber plants at two-true-leaf stage were inoculated with *A. tumefaciens*-mediated CCYV clones. After 25 d postinfiltration, leaves of *C. sativus* plants agroinfiltrated developed yellowing symptoms, typical CCYV infection in plants (Fig. 1A), whereas no symptoms were observed on healthy leaves. Analysis by RT-PCR using the primers is specific to the CP coding sequence (Table 1). All samples displayed amplification products of the expected sizes (Fig. 1B). The amplification products were sequenced, which verified CCYV infection. qRT-PCR was used to quantify CCYV mRNA molecules in healthy and CCYV-infected *C. sativus*. The results showed that the amount of CCYV mRNA molecules were only found in leaves of CCYV-infected *C. sativus* with 87,114.56 copies, while amount was undetectable in healthy *C. sativus* (Fig. 1C).

Absolute Quantification of CCYV mRNA Molecules in Individual Whiteflies

We used qRT-PCR to detect the absolute quantification of CCYV mRNA molecules in individual *B. tabaci* at different stages (first to fourth instars and adult) having fed on CCYV-infected cucumber plants for 48 h. The results showed that the amount of CCYV mRNA molecules were detectable in all instars of nymphs as well as in adults of *B. tabaci*, with 21360.08 copies in adults, followed by 1,424.54 copies in the second-instar nymphs, 300.71 copies in the

third-instar nymphs, 125.26 copies in the first-instar nymphs and 112.34 copies in fourth-instar nymphs (Fig. 2).

Effects of CCYV on Nymphal Stage Durations and Adult Longevity of *B. tabaci*

B. tabaci nymph instar duration and adult longevity were shown in Fig. 3. The nymph instar duration of females on the healthy plants and on the CCYV-infected plants were 13.83 ± 0.29 d and 16.00 ± 0.50 d, respectively ($F_{1,4} = 0.40$, $P < 0.01$). The nymph instar duration of males on the healthy plants and on the CCYV-infected plants were 14.00 ± 0.50 d and 13.67 ± 0.29 d, respectively ($F_{1,4} = 0.40$, $P = 0.37$). These results showed that CCYV significantly extended the developmental duration of female nymphs, but had no significant effect on duration of male nymphs (Fig. 3A).

The developmental duration of *B. tabaci* female adults on the healthy plants and on the CCYV-infected plants were 12.50 ± 0.50 d and 14.08 ± 0.14 d, respectively ($F_{1,4} = 1.73$, $P < 0.01$), and male adults on the healthy plants and on the CCYV-infected plants were 14.00 ± 0.50 d and 14.75 ± 0.25 d, respectively ($F_{1,4} = 0.80$, $P = 0.08$). The results showed that CCYV significantly extended the female adult longevity of *B. tabaci*, but had no significant effect on longevity of male adult *B. tabaci* (Fig. 3B).

Effects of CCYV on Body Length and Oviposition of Adult *B. tabaci*

As shown in Fig. 4A, the body lengths of *B. tabaci* female adults on healthy cucumber plants and the CCYV-infected plants were $1,066.30 \pm 5.04$ μ m and $1,091.02 \pm 4.05$ μ m, respectively ($F_{1,423} = 0.32$, $P < 0.01$). The body lengths of *B. tabaci* male adults on healthy cucumber plants and the CCYV-infected plants were 895.70 ± 4.13 μ m and 913.52 ± 3.18 μ m, respectively ($F_{1,285} = 2.40$, $P < 0.01$). Independent Sample *t*-test showed that CCYV could significantly increase the body lengths of both female and male adults. Amount of eggs laid by females on healthy plants were 105.03 ± 4.13

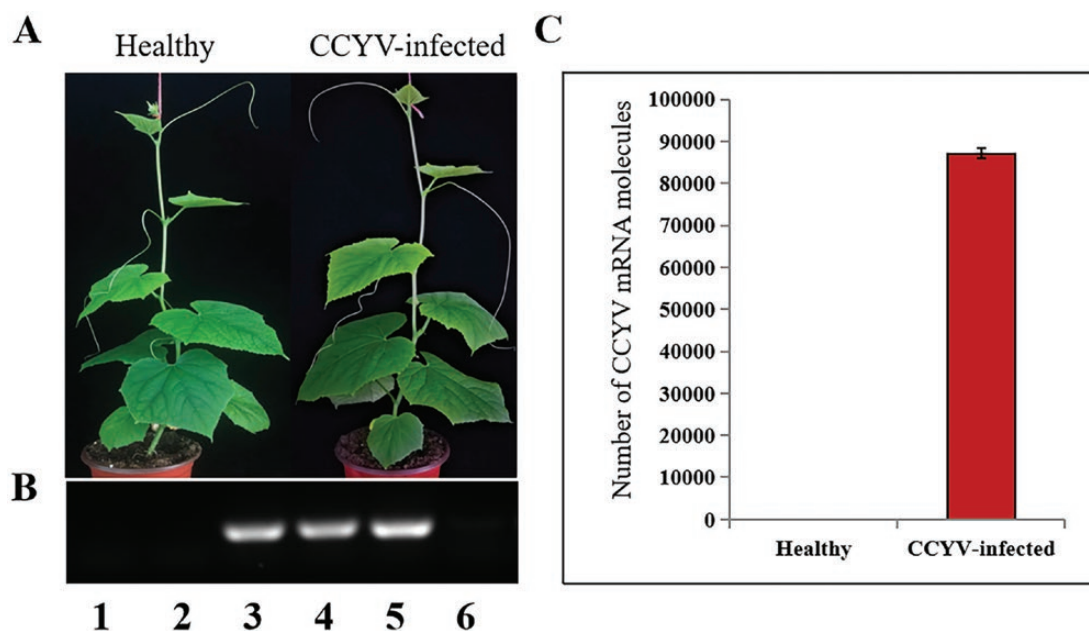


Fig. 1. Determination of CCYV infection after agroinoculation in *C. sativus*. A. Symptoms displayed on the systemic leaves of *C. sativus* at 25 d postagroinoculation. Yellowing was observed on the systemic leaves of *C. sativus*. B. RT-PCR detection of CCYV in the systemic leaves of *C. sativus*. Lane 1 and lane 2, healthy *C. sativus*; Lane 3 and lane 4, CCYV-infected *C. sativus*; Lane 5, positive control; Lane 6, negative control. C. Absolute quantification of CCYV mRNA molecules in healthy and CCYV-infected *C. sativus*. Mean \pm SE of three independent experiments.

on average, while on the plants infected with CCYV, the amount of oviposition of individual female adults were 125.22 ± 3.31 (Fig. 4B). Independent Sample *t*-test results showed that CCYV could significantly increase oviposition of female adults of *B. tabaci* ($F_{1,114} = 0.37$, $P < 0.01$).

Effects of CCYV on Hatching Rate and Nymphal Survival Rates of *B. tabaci*

The egg hatching rate and nymph survival rates of *B. tabaci* at various instars on healthy and CCYV-infected cucumbers were shown in Table 2. The egg hatching rate of *B. tabaci* on healthy cucumber plants was $91.10 \pm 2.20\%$, and that was $85.53 \pm 3.99\%$ on CCYV-infected cucumber plants. Independent Sample *t*-test shown that CCYV had no significant effect on the egg hatching rate of *B. tabaci*. The survival rates from first to fourth-instar nymphs on healthy cucumber plants were 98.25 ± 1.75 , 99.25 ± 0.75 , 100 ± 0.00 , and

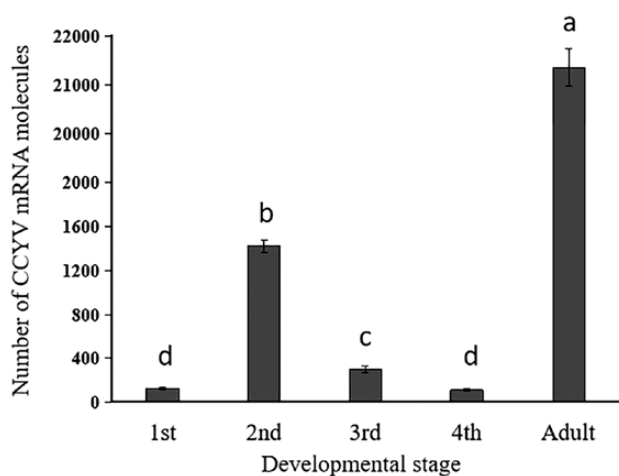


Fig. 2. Absolute quantification of CCYV mRNA molecules in individual whiteflies of *B. tabaci* obtained by amplifying portions of the CP genes using qRT-PCR. Whiteflies of the same colony were fed on CCYV-infected cucumbers for 48 h, and were collected in group of 10 individuals of each stage of first to fourth instar nymphs and adults for RNA extraction. Total RNA (1 μ g) from each sample was reverse transcribed to generate the first-strand cDNA for qRT-PCR. Mean \pm SE of three independent experiments is shown. $P < 0.05$ (one-way ANOVA, LSD test).

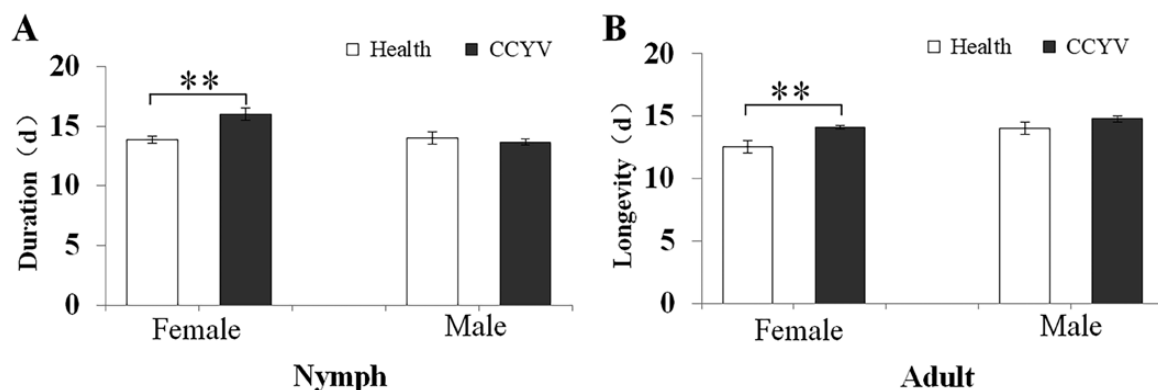


Fig. 3. Impact of CCYV on the nymph duration (A) and adult longevity (B) of *B. tabaci*. Health: whiteflies on healthy cucumbers; CCYV: whiteflies on CCYV-infected cucumbers; nymph duration include stages from first to fourth instar. For each treatment, 30 samples were analyzed, median-based statistics test were used. Mean \pm SE of three independent experiments is shown. * $P < 0.05$; ** $P < 0.01$ (independent-sample *t* test).

$100 \pm 0.00\%$, respectively, and the survival rates on CCYV-infected cucumber plants were 97.57 ± 1.59 , 96.00 ± 2.12 , 100 ± 0.00 , and $99.25 \pm 0.75\%$, respectively. The nymph survival rates of *B. tabaci* on healthy cucumber plants were all higher than those on CCYV-infected plants, but the difference did not reach a significant level.

Effect of CCYV on Sex Ratio of *B. tabaci*

The effect of CCYV on the sex ratio of *B. tabaci* is shown in Fig. 5. On the healthy cucumber plants, the sex ratio was 1:1, but on the CCYV-infected cucumber plants, the sex ratio was 0.5:1. *B. tabaci* had a higher percentage of females on the CCYV-infected cucumber plants than on the healthy plants ($F_{1,4} = 0.04$, $P < 0.01$).

Discussion

Vector-borne pathogens can alter the phenotypes of their hosts and vectors in ways that influence the frequency and nature of interactions between them, with significant implications for the transmission and spread of diseases (Mauck et al. 2010). Plant viruses can manipulate vector insects by directly influencing the feeding behavior. For example, *B. tabaci* carrying CCYV increased non-phloem probing and phloem salivation (Lu et al. 2019). *Bemisia tabaci* with TYLCV spend more time in phloem salivating and ingesting sap (Moreno-Delafuente et al. 2013). Plant viruses can also affect behaviors of vector insects indirectly via regulating host plant metabolism. For instance, terpenoid synthesis is suppressed in begomovirus-infected plants, leading to reduced plant resistance or modulated plant volatile production to influence vector behaviors (Li et al. 2014, Luan et al. 2013, Zhang et al. 2012). In this study, whiteflies were developed on CCYV-infected plants, so the indirect effects of CCYV on biological characteristics of its vector *B. tabaci* were mainly investigated.

Previous studies have shown that plant viruses can affect insect vectors, but the degrees of influence of different virus-vector combinations are not identical. There have been many reports on alteration of biology and behaviors in insect vectors by persistently transmitted plant viruses, for example, *Begomovirus* on *B. tabaci* (Jiu et al. 2007, Guo et al. 2010, Liu et al. 2013, Maluta et al. 2014, 2017, 2019), and more and more studies have been available on impact of semipersistent viruses on vectors in recent years (Lu et al. 2017, 2019, Pereira et al. 2019). These results suggested that different transmission types of viruses have different effects on vectors (Maluta et al. 2017, Chesnais et al. 2017).

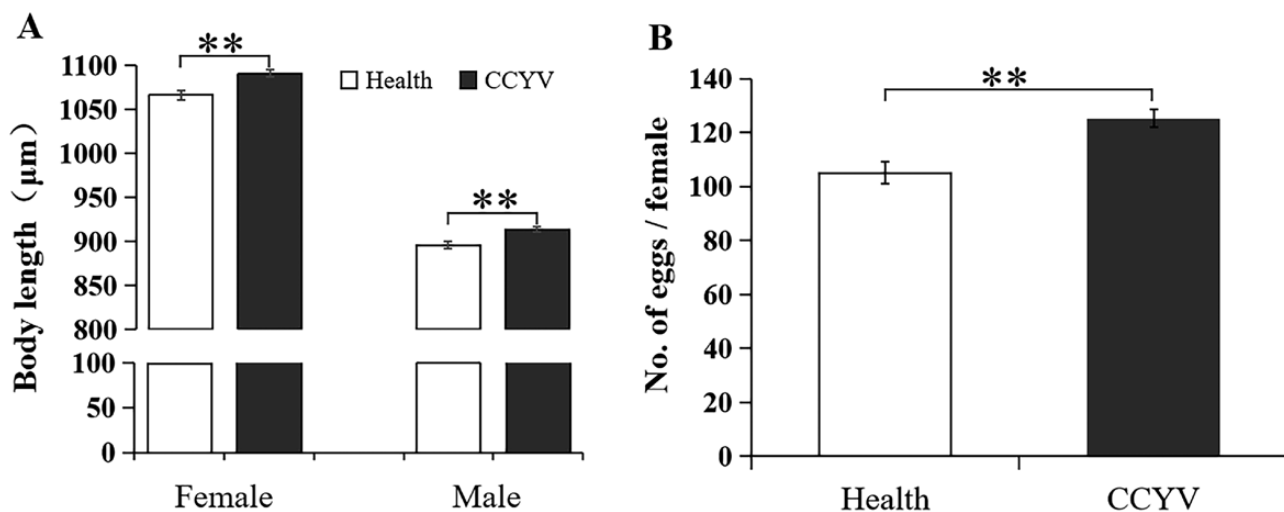


Fig. 4. Impact of CCYV on the body length (A) and oviposition (B) of *B. tabaci*. Health: whiteflies on healthy cucumbers; CCYV: whiteflies on CCYV-infected cucumbers; 177 and 135 samples were analyzed for the nonviruliferous females and males, respectively; 248 and 152 samples were analyzed for the viruliferous females and males, respectively; 58 samples were analyzed for the oviposition. Mean \pm SE is shown. * $P < 0.05$; ** $P < 0.01$ (independent-sample *t* test).

Table 2. Fertility rates and nymph survival rates of *B. tabaci* on healthy and CCYV-infected cucumber plants

| Developmental stage | Healthy plants | CCYV-infected plants | Sig. |
|---------------------|-------------------|----------------------|-------|
| egg | 91.10 \pm 2.20a | 85.53 \pm 3.99a | 0.184 |
| First instar | 98.25 \pm 1.75a | 97.57 \pm 1.59a | 0.831 |
| Second instar | 99.25 \pm 0.75a | 96.00 \pm 2.12a | 0.109 |
| Third instar | 100 \pm 0.00a | 100 \pm 0.00a | — |
| Fourth instar | 100 \pm 0.00a | 99.25 \pm 0.75a | 0.109 |
| Egg + nymphs | 88.84 \pm 1.60a | 79.52 \pm 2.09a | 0.184 |

Mean \pm SE of three independent experiments is shown, and same letters in the same line indicate that survival rate of the *B. tabaci* on CCYV-infected and healthy cucumber plants was not significantly different at the 0.05 level (one-way ANOVA, LSD test).

Although the nymphs of *B. tabaci* play no roles in virus transmission, their immobile stages (esp. second to fourth instar) encounter the plant viruses when feeding on the plant. Nymphs can be affected, more or less, by virus particles taken with plant sap, and thereby may affect the status of the adults responsible for virus transmission. The results in the present study indicated that all nymph instars were affected by CCYV, and the viral mRNA accumulation varied with instars. The second-instar has the highest viral mRNA accumulation (1,424.54 copies) among all the instar nymphs, followed by the third instar and the first instar, and the fourth instar (112.34 copies) has the lowest viral mRNA accumulation, which may be related to the behavior characteristics of each instar nymph. The first-instar nymphs have tentacles and feet, and can crawl over a short distance to find a suitable feeding site and then settle down and start feeding. The tentacles and feet of the second- and third-instar nymphs are atrophy, and they have no crawling ability. They are fixed on the back of the leaves for feeding with the stylets (Yang et al. 2016). The fourth-instar nymphs, also known as ‘pseudo pupal’ stage, basically stop feeding (Chandi et al. 2014, Yan and Bai 2017), which may be the reason for the low viral mRNA accumulation in the fourth-instar nymphs. The viral mRNA accumulation of the adults was much greater than those of the nymphs, and the viral mRNA

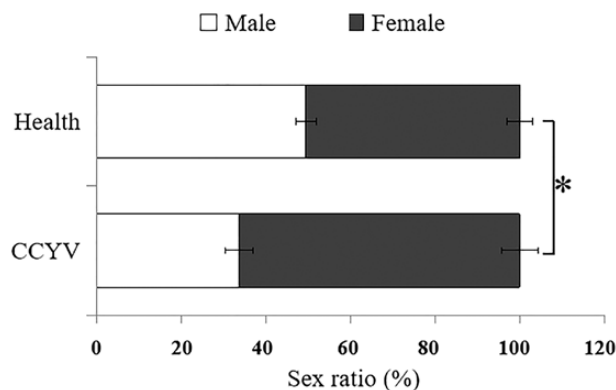


Fig. 5. The sex ratio of *B. tabaci* on the healthy cucumbers (Health) and CCYV-infected cucumbers (CCYV). Thirty eggs from a couple of 3-d adults on a leaf of healthy cucumber plant and CCYV-infected cucumber plant were marked under the super-depth microscope. The sex ratio of newly emerging adults were calculated, Mean \pm SE of three independent experiments is shown. * $P < 0.05$; ** $P < 0.01$ (independent sample *t* test).

accumulation of the individual adult was up to 21,360.08 copies. Adult *B. tabaci* is highly active and can even migrate over long distances with the assistance of air currents, becoming the main cause of the CCYV pandemic.

By comparing the developmental periods of *B. tabaci* on healthy and CCYV-infected plants, it was found that CCYV could significantly extend the developmental period of female nymphs ($P < 0.01$) and the longevity of female adults ($P < 0.01$), but not significantly affect the development period of male nymphs ($P = 0.37$) and the longevity of male adults ($P = 0.08$). The influence of CCYV on the growth and development of females was much greater than that of males. Longer development period and longevity mean more possibility for virus transmission. Therefore, we speculate that females are more conducive to the transmission of CCYV virus than males.

Through a comparative analysis of the body length and oviposition of *B. tabaci*, we found that CCYV significantly increased the body length of female adults ($P < 0.01$) and male adults ($P < 0.01$),

and increased the oviposition of individual female adult ($P < 0.01$). It may be due to an extended developmental period and a higher intake of nutrients. The size of an insect is an important factor affecting population development potential as well as community structure and function (Siemann et al. 1996, Whitman et al. 2008, Henri et al. 2011). Relevant studies have shown that, compared with smaller individuals within the same species, larger insects often have advantages in reproduction, flight, competition, stress resistance, and other aspects, contributing to the improvement of population fitness (Huang et al. 2017).

CCYV significantly increased the proportion of female adult from 50.53% on healthy plants to 66.40% on CCYV-infected cucumber plants. There are two reproductive modes of *B. tabaci*, including parthenogenesis and amphigenesis. The female offsprings of *B. tabaci* are all developed from fertilized eggs, while the male offsprings may come from fertilized eggs and parthenogenesis (Byrne et al. 1991). The increase of female proportion of whitefly may be due to the increase of body length caused by CCYV, which enables it to have comparative advantages in mating process and obtain more mating opportunities, so as to increase the proportion of female offsprings by increasing the number of fertilized eggs, thus ensuring the reproduction of its offspring population.

Conclusions

In conclusion, our results confirmed that CCYV, a semipersistently transmitted plant virus, could manipulate the growth and development of its vector, *B. tabaci*. CCYV had more effects on female than male in development duration by increasing duration of female nymphs and adults. Interestingly, CCYV could significantly increase the body length and oviposition of *B. tabaci* and the ratio of females became higher on CCYV-infected cucumber plants, which will undoubtedly increase the population fitness and beneficial to its population reproduction, and thereby it is beneficial to the transmission of CCYV. These results clearly indicated that the biological characteristics of *B. tabaci* Q biotypes changed greatly when feeding on CCYV-infected plants, and the effects on females were much greater than on males. Based on the above results, we can infer that CCYV and *B. tabaci* have a typical mutualist relationship, and this plays an important role in *B. tabaci* outbreak. Studies in this paper on the effects of a semipersistent virus on the biological characteristics of its vectors may enrich our understanding of the plant-virus-vector interactions.

Supplementary Data

Supplementary data are available at *Journal of Insect Science* online.

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Author Contributions

HH: Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Visualization; Writing—original draft; Writing—review & editing. FY and JL: Conceptualization; Project administration; Resources; Supervision; Validation; Visualization; Writing—review & editing. ZZ, XT and DS: Data curation; Investigation; Writing—original draft.

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