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Effects of *Tomato chlorosis virus* on the performance of its key vector, *Bemisia tabaci*, in China

J. Li[1] | T. B. Ding[1] | H. Chi[2] | D. Chu[1]

[1]Key Laboratory of Integrated Crop Pest Management of Shandong Province, College of Agronomy and Plant Protection, Qingdao Agricultural University, Qingdao, China

[2]Department of Plant Production and Technologies, Faculty of Agricultural Sciences and Technologies, Niğde Ömer Halisdemir University, Niğde, Turkey

Correspondence
Dong Chu, Key Lab of Integrated Crop Pest Management of Shandong Province, College of Agronomy and Plant Protection, Qingdao Agricultural University, Qingdao, China.
Email: chinachudong@sina.com

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Abstract

Tomato chlorosis virus (ToCV), which is a newly emerged and rapidly spreading plant virus in China, has seriously reduced tomato production and quality over the past several years. In this study, the effect of ToCV on the demography of the whitefly, *Bemisia tabaci* biotype Q (Hemiptera: Aleyrodidae), fed on infected and healthy tomato plants was evaluated using the age-stage, two-sex life table. When reared on ToCV-infected tomato plants, the fecundity, length of oviposition period and female adult longevity of *B. tabaci* biotype Q decreased significantly, while the pre-adult duration significantly increased compared to controls reared on healthy tomatoes. Consequently, the intrinsic rate of increase (r) and finite of increase (λ) of *B. tabaci* biotype Q on ToCV-infected tomato plants significantly decreased compared to those on healthy tomatoes. Population projection predicted that a population of *B. tabaci* biotype Q fed on ToCV-infected tomatoes increases slower than on healthy plants. These findings demonstrated that ToCV infection decreased the performance of *B. tabaci* biotype Q on tomato plants.

KEYWORDS
Bemisia tabaci, life table, *Tomato chlorosis virus*, vector performance

1 | INTRODUCTION

The sweet potato whitefly, *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae), which is considered to be one of the most economically important crop pests worldwide, has invaded over 60 countries during the past decades (De Barro, Liu, Boykin, & Dinsdale, 2011; Dinsdale, Cook, Riginos, Buckley, & De Barro, 2010). *Bemisia tabaci* is a species complex composed of at least 34 morphologically indistinguishable cryptic species, among which *B. tabaci* biotype B (also known as MEAM1 putative species) and *B. tabaci* biotype Q (also known as MED putative species) are the two most invasive and destructive forms (Boykin & De Barro, 2014; De Barro et al., 2011). *Bemisia tabaci* biotype Q was first detected in Yunnan Province, China, in 2003 (Chu et al., 2006) and has since displaced *B. tabaci* biotype B, which was introduced in the 1990s. In recent years, *B. tabaci* biotype Q has become the dominant whitefly in the field, becoming a major crop pest in China (Pan et al., 2011; Rao, Luo, Zhang, Guo, & Devine, 2011). The whitefly causes severe crop damage through direct feeding, excretion of honeydew and transmission of numerous plant viruses (Jones, 2003). Two hundred and twelve virus species are known to be transmitted by *B. tabaci*, of which 90.6% belong to the genus *Begomovirus*, 5.7% in the genus *Crinivirus* and the remaining 3.7% distributed among several minor genera, including *Closterovirus*, *Ipomovirus* and *Carlavirus* (Polston, De Barro, & Boykin, 2014).

Tomato chlorosis virus (ToCV) (genus *Crinivirus*, family Closteroviridae) is one of the most devastating tomato pathogens in subtropical regions worldwide and is responsible for severely decreasing tomato production wherever it becomes established (Navas-Castillo, Fiallo-Olive, & Sanchez-Campos, 2011; Tzanetakis, Martin, & Wintermantel, 2013). ToCV is a phloem-limited virus transmitted by several whitefly species including *B. tabaci*, *Trialeurodes vaporariorum* (Westwood) and *T. abutilonea* (Haldeman) in a semi-persistent, non-circulative manner (Chen et al., 2016; Wintermantel & Wisler, 2006). The relationship between the virus and vector can significantly

impact transmission efficiency (Wintermantel, Cortea, Anchieta, Gulati-Sakhuja, & Hladky, 2008). ToCV outbreaks are frequent in many parts of the world including the Americas, Europe, Africa and its adjacent islands, the Middle East, and Asia (Wintermantel & Wisler, 2006; Wintermantel et al., 2008). ToCV was first recorded in Taiwan in 2004 (Tsai, Shih, Green, & Hanson, 2004), and outbreaks of ToCV disease with severe symptoms occurred in several regions of Beijing, Tianjin and Shandong between 2012 and 2016 (Wang et al., 2016). Afterwards, *B. tabaci* biotype Q was found to be the major vector in ToCV-infected fields in China (Dai, Liu, Zhu, Liu, & Zhao, 2016).

Increased incidences of ToCV and its whitefly vectors in greenhouse and field production systems across numerous agricultural crops have emphasized the need for additional efforts towards managing ToCV and its whitefly vectors. Efforts to elucidate factors contributing to the emergence and prevalence of ToCV are important for explaining ToCV epidemiology and developing effective management strategies for ToCV control. The relationship between pathogen, vector and host plant is important in understanding the epidemiology of all insect-transmitted plant pathogens. Construction and interpreting life tables is an indispensable tool in generating an overall assessment of fitness of a vector on a host plant, traditional female-based, age-specific life tables (Birch, 1948; Carey, 1993; Leslie, 1945; Lewis, 1942), however, are inherently incapable of properly describing a population, because they ignore the male component of a population and stage structure in metamorphosing species. Age-stage, two-sex life table construction is a comprehensive method for summarizing the survival, development and reproductive potential of a population (Chi, 1988). Because this method can readily portray stage differentiation and includes both sexes, it can accurately depict the actual life history of an insect species. This life table, which has been widely utilized in the measurement of various ecological aspects of interest in relation to insect pests and their natural enemies, is helpful to the development of integrated control strategies (Chi & Su, 2006; Reddy & Chi, 2015; Saska et al., 2016; Yin, Sun, Wu, & Ge, 2010).

The interactions between host plant–plant virus–arthropod vectors are characterized by complex direct or indirect interactions, with many studies having shown that such complex interactions may play important roles in the abundance and distribution of arthropod vectors and the epidemiology of plant virus diseases (Stout, Thaler, & Thomma, 2006). A plant virus can affect the arthropod vector directly by influencing physiological functions or indirectly by influencing host plant nutrient exchanges. These changes can alter the vector's development, life cycle, fertility and other life history parameters (Jiu et al., 2007; Li, Liu, & Liu, 2011; Matsuura & Hoshino, 2009; Rubinstein & Czosnek, 1997; Sidhu, Mann, & Butter, 2009; Su et al., 2015).

The goal of this study was to understand the potential effects of ToCV infection on performance of *B. tabaci* biotype Q. In this study, the differences of performance of *B. tabaci* biotype Q on ToCV-infected and healthy tomato plants were first evaluated using the age-stage, two-sex life table with a simplified method (Chi, 1988; Zheng, Tao, Chi, Wan, & Chu, 2017). The differences in the growth potential of *B. tabaci* biotype Q on ToCV-infected and healthy tomato plants were also demonstrated using population projections.

2 | MATERIALS AND METHODS

2.1 | Insects

The stock population of *B. tabaci* biotype Q was obtained from a laboratory colony established from Jina, Shandong, China, in 2012. The whiteflies were cultured on cotton plants, *Gossypium hirsutum* M. cv. Lu-Mian 21, a common host plant of *B. tabaci* biotype Q. Experimental whitefly adults were transferred to tomato plants and reared for five generations prior to being used. Tomato plants were grown in insect-proof screen cages placed in climate-controlled cubicles at 27 ± 2°C, 60 ± 10% RH and a photoperiod of 16:8 (L:D) hr. All experiments were conducted under identical environmental conditions. The purity of the *B. tabaci* biotype Q population was maintained by monitoring it every 30 days using the *Vsp* I-based mtCOI PCR-RFLP method (Chu et al., 2012).

2.2 | Plants and ToCV

Tomato plants, *Solanum lycopersicum* Mill. Cv. Zhongza 9, a host of ToCV, were used in this study. Virus-free tomato plants were grown in a potting mix (a mixture of humus soil, vermiculite, organic fertilizer and perlite in a 10:10:10:1 ratio by volume) in 10-cm diameter plastic pots in climate-controlled chambers. The ToCV was obtained from Qingdao, Shandong, China, in 2014 and maintained on tomato plants from the above culture. ToCV-infected tomato plants were obtained by male whitefly inoculation (male whiteflies were transferred and allowed to feed on ToCV tomato plants for 48 hr and then 30 male whiteflies were transferred onto healthy tomatoes for 5 days). Healthy tomato plants were used as controls exposed to feeding by non-viruliferous male whiteflies (30 non-viruliferous male whiteflies were transferred onto healthy tomato plants for 5 days). All tomato plants were inoculated at the 4th–5th true-leaf stage. Virus-infected and healthy tomato plants were used in the age-stage, two-sex life table experiments approximately 4 weeks after inoculation. The virus infection status of test plants was visually determined when the plants showed typical symptoms and then verified using reverse transcription-PCR (RT-PCR) as described by Dovas, Katis, and Avgelis (2002). All plants were watered every 5–7 days as necessary.

2.3 | Detection of ToCV in tomato plants using the RT-PCR method

Total RNAs from inoculated and control tomato plants were extracted from 100 mg of leaf tissue per plant using Trizol reagent following the manufacturer's protocol (Invitrogen, Carlsbad, CA, USA). The resulting total RNA was resuspended in nuclease-free water and quantified with a NanoPhotometer N50 (Implen Scientific, Munich, Germany). Reverse transcription was then performed on 2.0 μg of each RNA sample. The first-strand cDNA was synthesized using the PrimeScript™ RT reagent Kit according to the manufacturer's protocol (TaKaRa Biotechnology, Dalian Co., Ltd, Liaoning, China). Specific primers (forward primer ToC-5: 5′-GGTCAATTATGAGGTCGTGAA-3′and reverse primer ToC-6: 5′-CTCTGCCCAGACTTGTAATCA-3′) were used to detect ToCV

(Dovas et al., 2002). PCR amplifications were performed in 20 μl of a mixture containing 1.4 μl of cDNA, 0.3 μl of each primer (10 μM each) and 18 μl of Premix Taq (TaKaRa Biotechnology Corporation Co. Ltd, Dalian, China). Simultaneously, PCR amplifications with the negative controls (template was ddH_2O) and positive controls (template was the tomato plant cDNA containing ToCV) were also performed. The cycling conditions were as follows: 4 min of activation at 94°C, followed by 35 cycles of 30 s at 94°C, 30 s at 55°C, 30 s at 72°C, and a final extension of 10 min at 72°C. The PCR products were electrophoresed on a 1.2% agarose gel in a 0.5× TBE buffer and were visualized by *Gelview* staining.

2.4 | Population parameters of *B. tabaci* biotype Q on ToCV-infected and healthy tomato plants

To determine differences in the population parameters of *B. tabaci* biotype Q on ToCV-infected and healthy tomato plants, we analysed the population parameters using the age-stage, two-sex life table method (Chi, 1988; Chi & Liu, 1985). For the life table study, the rearing containers (Fig. S1) were made of plastic pots. A small pot (7 cm top diameter, 4.5 cm bottom diameter and 7.5 cm height), which was used as the bottom container, was covered with plastic wrap to isolate the whiteflies from groundwater. An inverted plastic pot (7.5 cm top diameter, 5 cm bottom diameter and 11 cm height) was used as the cover. The top of the plastic pot cover was cut out and covered with fine mesh cloth for ventilation. Tomato seedlings at the 7th–9th leaf stage were used in this study. A single true leaf (third to seventh leaf from the bottom) was detached from the tomato seedling, and the stem of the true leaf immersed in 1-naphthylacetic acid (50 ppm) for 10 min, rinsed with water and then maintained in a separate container with nutrient solution (Lv, Sang, Li, & Li, 2010).

Life table experiments were conducted in climate-controlled chambers at 27 ± 2°C, 60 ± 10% relative humidity and a photoperiod of 16:8 (L:D) hr. Approximately 10 pairs of whitefly adults (randomly selected from the culture population maintained on tomato plants) were transferred into rearing containers containing a single tomato seedling. The same process was repeated on healthy tomato and ToCV-infected tomato plants. Each treatment contained four replicates. After 24 hr, all of the adults were removed, and the numbers of eggs counted under a stereomicroscope (Nikon SMZ 745T). There were 155 and 125 eggs used for the life table studies on healthy and ToCV-infected tomato plants, respectively. The seedlings in the rearing containers were checked daily for newly emerged adults beginning at the 15th day (corresponding to the day prior to eclosion). Date for the pre-adult duration and pre-adult survival was recorded for all individuals. Newly emerged female and male adults resulting from the treatment were paired and transferred to a new rearing container with containing a tomato leaf and allowed to mate and oviposit. The adult whitefly individuals were checked daily for survival. To record egg production, each pair of the whiteflies was transferred into a new rearing container with one tomato leaf every 5 days (corresponding to the time period prior to nymph emergence). The daily fecundity was calculated as the mean number of eggs laid within each 5-day period.

2.5 | Statistical analysis

The raw life history data of all the whitefly individuals were analysed based on the age-stage, two-sex life table (Chi, 1988; Chi & Liu, 1985) using the computer program TWOSEX-MSChart (Chi, 2017). The program is available for no cost at http://140.120.197.173/Ecology/download/TWOSEX-MSChart.rar. The population parameters included the age-stage specific survival rate (s_{xj}, the probability that a newborn will survive to age x and stage j), the age-specific survival rate (l_x, the probability of a newly laid egg surviving to age x), the age-stage-specific fecundity (f_{xj}, the mean number of offspring produced by a female at age x), the age-specific fecundity (m_x, the mean fecundity of individuals at age x), the age-stage life expectancy (e_{xj}, the length of time that an individual of age x and stage j is expected to live) and the reproductive value (v_{xj}, the contribution of an individual to the future population).

In the age-stage, two-sex life table (Chi & Liu, 1985), m_x and l_x are calculated as:

$$m_x = \frac{\sum_{j=1}^{k} s_{xj} f_{xj}}{\sum_{j=1}^{k} s_{xj}} \quad (1)$$

$$l_x = \sum_{j=1}^{k} s_{xj} \quad (2)$$

where k is the number of stages. The net reproductive rate (R_0) is calculated as:

$$R_0 = \sum_{x=0}^{\infty} l_x m_x \quad (3)$$

The intrinsic rate of increase (r) is determined using the Euler–Lotka equation

$$\sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_x = 1 \quad (4)$$

with age is indexed from 0 (Goodman, 1982). The finite rate of increase (λ) is calculated as $\lambda = e^r$. The mean generation time T is defined as the length of time that a population needs to increase R_0 fold of its size (i.e., $e^{rT} = R_0$ or $\lambda^T = R_0$) at a stable age-stage distribution and is calculated as:

$$T = \frac{\ln R_0}{r} \quad (5)$$

The life expectancy e_{xj} is calculated as described by Chi and Su (2006) as:

$$e_{xj} = \sum_{i=x}^{\infty} \sum_{y=j}^{k} s'_{iy} \quad (6)$$

where s'_{iy} is the probability that an individual of age x and stage j will survive to age i and stage y and is calculated by assuming $s'_{xj} = 1$ (Chi & Su, 2006). The reproductive value (v_{xj}) is calculated according to Tuan, Lee, and Chi (2014a,b) as:

$$v_{xj} = \frac{e^{r(x+1)}}{s_{xj}} \sum_{i=x}^{\infty} e^{-r(i+1)} \sum_{y=j}^{k} s'_{iy} f_{iy} \quad (7)$$

The standard errors of all life table parameters, including r, λ, R_0, T, adult longevity and fecundity, were estimated using the bootstrap procedure with 100,000 resampling. A paired bootstrap test was used to detect the difference between treatments based on the confidence interval of differences (Polat-Akköprü, Atlihan, Okut, & Chi, 2015; Efron & Tibshirani, 1993; Huang & Chi, 2012). SigmaPlot v.12.0 software was used to prepare the graphs.

2.6 | Population projection

We projected the population growth to illustrate the predicted population size and age-stage structure of a *B. tabaci* population by incorporating developmental rate, survival rate and fecundity data (Chi, 1990; Chi & Liu, 1985) using the TIMING-MSChart program (http://140.120.197.173/ecology/Download/TIMING-MSChart.rar) (Chi, 2016).

3 | RESULTS

3.1 | Detection of ToCV in tomato plants using RT-PCR method

The primers Toc-5 and Toc-6 amplified a fragment of expected size from extracts from individual tomato plants that had been inoculated with ToCV (Figure 1a). No product was obtained from the non-inoculated tomato plants (Figure 1b).

3.2 | Population parameters of whiteflies on ToCV-infected and healthy tomato plants

Whitefly pre-adults developed slower on ToCV-infected tomato plants than on healthy tomato plants. The pre-adult duration, 26.6 ± 0.37 days when reared on ToCV-infected tomato plants, was significantly longer than that observed on healthy plants (23.65 ± 0.31 days, $p < .0001$) (Table 1). However, the longevity of female adults was significantly shorter when reared on ToCV-infected tomato plants (20.6 ± 0.94 days) than on healthy plants (23.84 ± 0.81 days) ($p = .0098$) (Table 1). The mean fecundity of females was 92.10 ± 6.55 eggs on ToCV-infected plants, a significant decrease when compared to the mean fecundity of 130.37 ± 4.34 eggs on healthy tomato plants ($p < .0001$) (Table 1). There were no significant differences in the pre-adult survival rate and male longevity between ToCV-infected and healthy tomato plants ($p = .3903$ and $p = .7381$, respectively) (Table 1).

The relatively slow development of *B. tabaci* biotype Q on ToCV-infected plants could also be observed in the age-stage survival rate (s_{xj}), where adults of both sexes began to emerge after 21 days (Figure 2b) on ToCV-infected tomato plants versus 19 days on uninfected plants (Figure 2a). The female age-stage specific fecundity (f_{xj}) and age-specific fecundity (m_x) on ToCV-infected tomato plants began on the 20th day (Figure 3b), only 1 day later than on healthy plants (at day 19) (Figure 3a). All m_x, $l_x m_x$ and f_{xj} values on ToCV-infected tomato plants were lower than those on healthy tomato (Figure 3).

The intrinsic rate of increase (r), finite rate (λ) and net reproductive rate (R_0) of whiteflies reared on ToCV-infected tomato plants were 0.10 ± 0.005 d^{-1}, 1.11 ± 0.005 d^{-1} and 34.63 ± 4.68 eggs, respectively, and all of which were significantly lower values ($p < .0001$) than those on healthy tomato plants (0.13 ± 0.003 d^{-1}, 1.14 ± 0.004 d^{-1} and 67.29 ± 5.70 eggs, respectively) (Table 2). The mean generation time (T) on ToCV-infected tomato plants (34.41 ± 0.72 days) was longer than that on healthy tomato plants (31.55 ± 0.42 days) ($p = .0007$) (Table 2).

The mean longevity of the whiteflies, that is, the life expectancy at age zero (e_{01}), was 41.7 days on ToCV-infected tomato plants, which was similar to that on healthy plants (41.3 days) (Figure 4). At age zero, the reproductive values (v_{01}) were equivalent to the finite rates on both plants, that is, 1.1085 d^{-1} on ToCV-infected tomato and 1.1427 d^{-1} on healthy tomato (Figure 5). The v_{xj} values jumped to 45.2845 d^{-1} on day 19 when female adults emerged on healthy tomato plants, and 47.5343 d^{-1} when they emerged later (on day 20) when reared on ToCV-infected plants (Figure 5).

3.3 | Population projection of the whitefly on ToCV-infected and healthy tomato plants

The population sizes of the different stages simulated from an initial population of 10 eggs using the TIMING-MSChart program are shown in Figure 6. The whitefly population increased much slower on ToCV-infected tomato plants than on healthy plants (Figure 6). After 60 days on ToCV-infected tomato plants, there were 1,318 individuals in various pre-adult stages, 49 female and 57 male adults; while on healthy

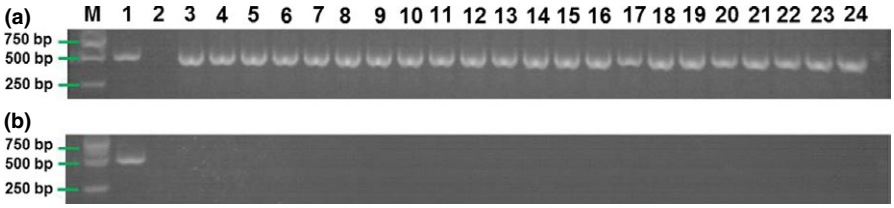

FIGURE 1 Detection of ToCV in tomato plants by RT-PCR and agarose gel electrophoresis with Gelview staining. Each lane is a PCR amplification from the RNA extraction of one leaf of each tomato plant. (a) Samples were from tomato plants inoculated with ToCV after 3 weeks (lanes 3-24); (b) Samples were from healthy tomato plants (lanes 3-24). lane M: 2000bp marker; lane 1: a positive sample of ToCV-infected tomato plant; lane 2: a non-inoculated control tomato plant

TABLE 1 Means and standard errors of pre-adult developmental time (days), pre-adult survival rate (%), adult longevity (days), oviposition days (days) and fecundity (eggs) of *B. tabaci* Q on healthy and ToCV-infected tomato. Standard errors were estimated using 100,000 bootstrap resampling. The differences between two treatments were evaluated using paired bootstrap test

	Host plant				
Basic statistic	*n*	Healthy tomato	*n*	ToCV-infected tomato	*p*
Pre-adult duration (days)	128	23.65 ± 0.31	98	26.66 ± 0.37	.0001
Pre-adult survival rate (%)	155	82.58 ± 3.04	125	78.40 ± 3.7	.3903
Female longevity (days)	80	23.84 ± 0.81	47	20.60 ± 0.94	.0098
Male longevity (days)	48	20.51 ± 1.37	51	19.94 ± 1.02	.7381
Oviposition days (days)	80	22.06 ± 0.72	47	18.87 ± 0.91	.0062
Fecundity (eggs per female)	80	130.37 ± 4.34	47	92.10 ± 6.55	.0000

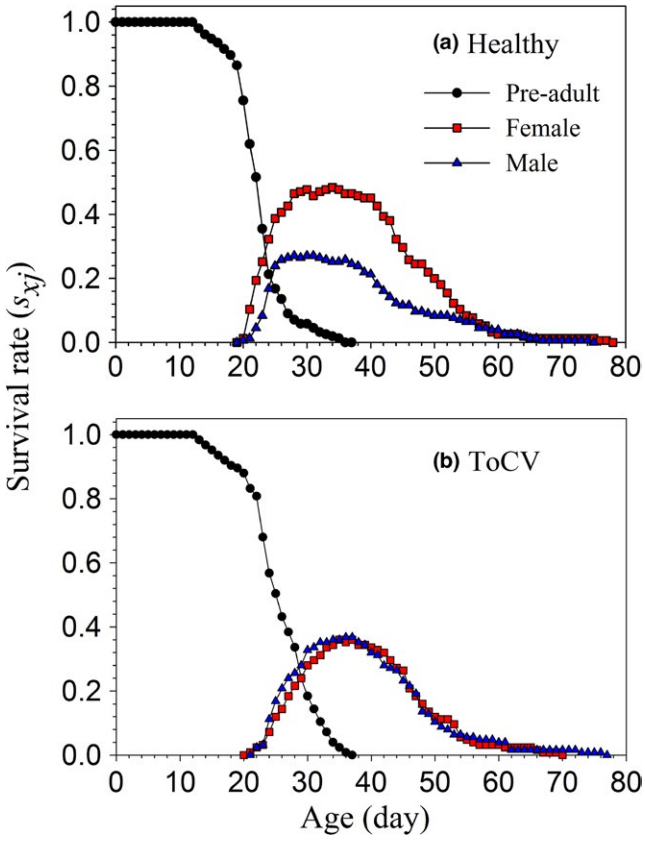

FIGURE 2 Age-stage-specific survival rate (s_{xj}) of the *B. tabaci* biotype Q on healthy and ToCV-infected tomato plant

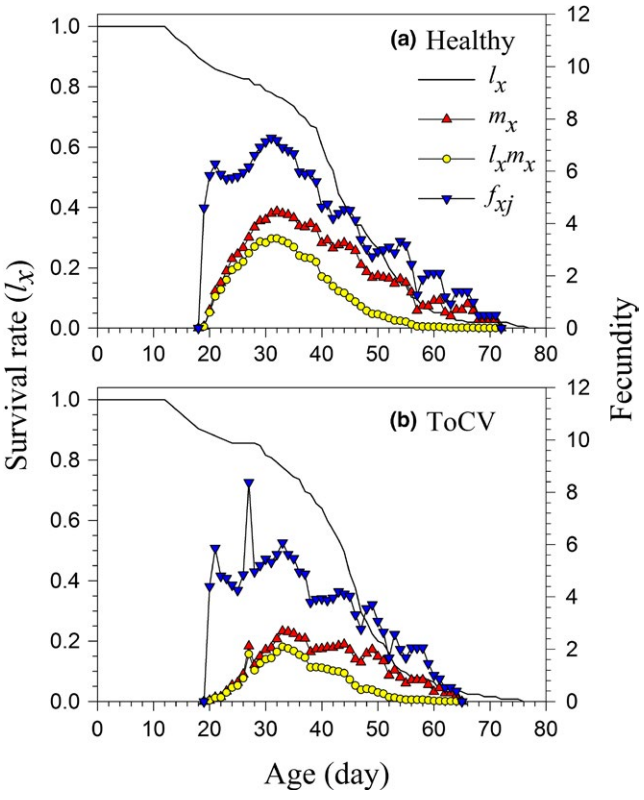

FIGURE 3 Age-specific survival rate (l_x), female age-specific fecundity (f_{xj}), age-specific fecundity of the total population (m_x) and age-specific maternity ($l_x m_x$) of the *B. tabaci* biotype Q on healthy and ToCV-infected tomato plant

tomato plants, there were 9,752 individuals in the pre-adult stages, 171 female and 116 male adults (Figure 6).

4 | DISCUSSION

In this study, the impact of ToCV infection on population parameters of *B. tabaci* biotype Q was examined using the age-stage, two-sex life table. This method was chosen because, contrary to traditional female-based life tables, it is capable of precisely describing the population parameters, stage differentiation and variation among individuals, by taking both sexes into consideration (Chi, 1988; Chi & Liu, 1985). Our results showed that the fecundity and female adult longevity of *B. tabaci* biotype Q were significantly decreased, while the pre-adult duration (from egg to adult) was significantly extended when reared on ToCV-infected tomato plants compared with their counterparts reared on healthy tomato plants (Table 1). Mann, Sidhu, Butter, Sohi, and Sekhon (2008) and Sidhu et al. (2009) reported similar

TABLE 2 Means and standard errors of the intrinsic rate of increase (r), finite rate (λ), net reproductive rate (R_0) and mean generation time (T) of *B. tabaci* Q on healthy and ToCV-infected tomato. Standard errors were estimated using 100,000 bootstrap resampling. A paired bootstrap test was used to detect differences between treatments

	Host plant		
Parameters	Healthy tomato	ToCV-infected tomato	*p*
r (d^{-1})	0.1334 ± 0.0033	0.1030 ± 0.0046	.0001
λ (d^{-1})	1.1427 ± 0.0037	1.1085 ± 0.0051	.0001
R_0 (offspring/individual)	67.29 ± 5.70	34.63 ± 4.68	.0001
T (days)	31.55 ± 0.42	34.41 ± 0.72	.0007

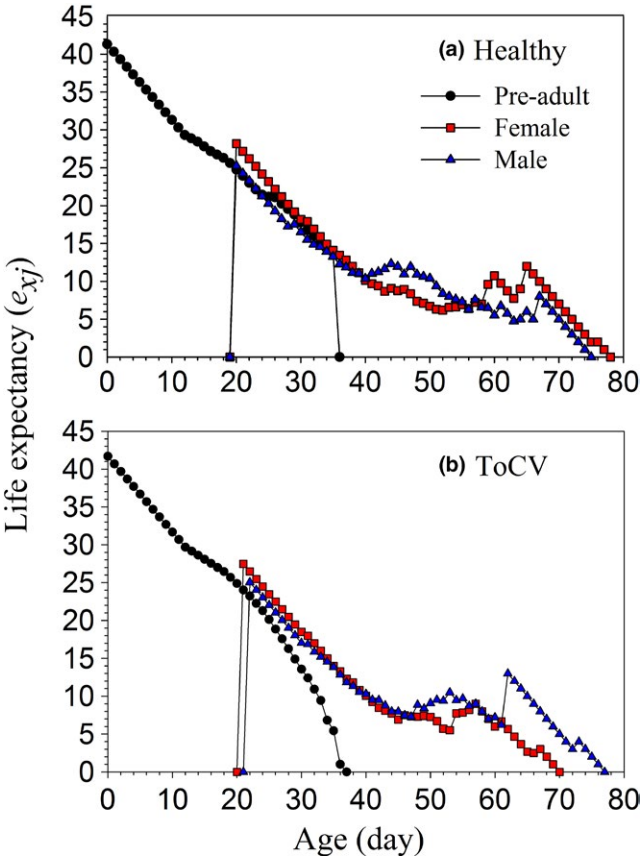

FIGURE 4 Age-stage-specific life expectancy (e_{xj}) of the *B. tabaci* biotype Q on healthy and ToCV-infected tomato plants

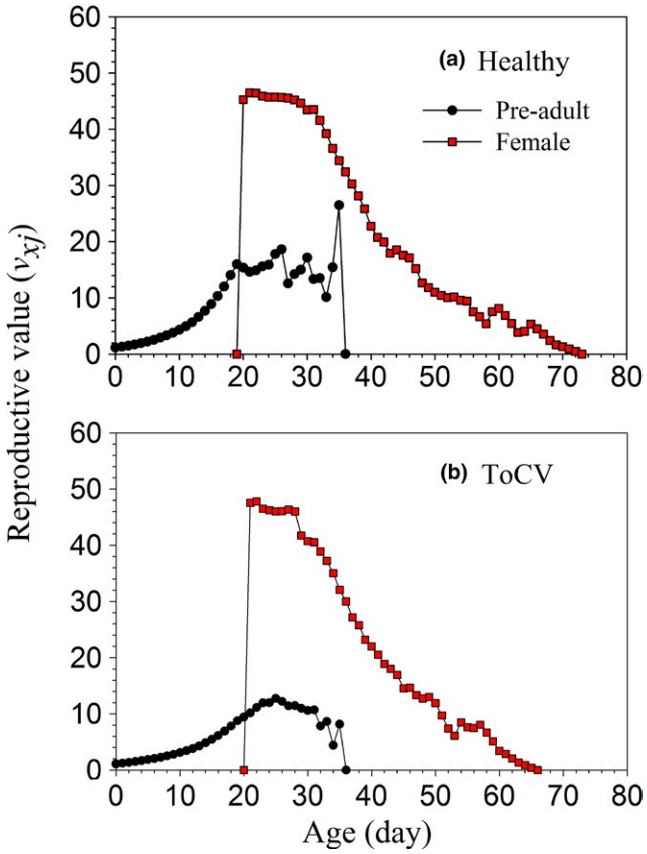

FIGURE 5 Reproductive value (v_{xj}) of the *B. tabaci* biotype Q on healthy and ToCV-infected tomato plants

results for *B. tabaci* ovipositing fewer eggs and having a shorter longevity on plant infected with *Cotton leaf curl virus* (CLCuV). Rubinstein and Czosnek (1997) also demonstrated that *Tomato yellow leaf curl virus* (TYLCV) had adverse effects on *B. tabaci* causing reduced fecundity and longevity. Jiu et al. (2007) also reported similar effects in *B. tabaci* caused by *Tomato yellow leaf curl China virus* (TYLCCV). All of the above studies demonstrated negative effects that viruses had on their vectors. However, Pan et al. (2013) demonstrated the opposite occurred when TYLCV-infected whiteflies developed a higher fecundity and longer longevity. Several previous reports have shown that circulative viruses could increase the quality of the host plants and have a positive impact on the vector fitness through downregulation of defence pathways, reduced callose deposition, altered amino acid content of the sap, etc. (Casteel et al., 2015; Su et al., 2015; Xu, He, Zheng, Yang, & Lu, 2014). In contrast, the effect of non-circulative viruses on vector growth is much less clear. Based on the assumption that viruses can affect the interaction between host plants and their vectors, plants infected by non-circulative viruses should rapidly deter vectors, forcing migration onto neighbouring healthy plants (Blanc & Michalakis, 2016). Thus, a decrease in the fitness of the whitefly on its ToCV-infected tomato plant may be associated with a decrease in the quality of the host plant.

Comparisons of the population parameters, especially the r, λ and R_0 values, have been generally used to detect differences between populations or treatments. Because traditional female age-specific life tables ignore stage differentiation and the male population, their application to species with bisexual populations will often result in errors (Huang & Chi, 2011). In this study, we analyzed and compared life tables of *B. tabaci* biotype Q reared on healthy tomato plants and on ToCV-infected tomato plants using the age-stage, two-sex life table. The r, λ and R_0 values showed that *B. tabaci* biotype Q survived better on healthy tomato plants than on ToCV-infected tomato plants (Table 2). Population

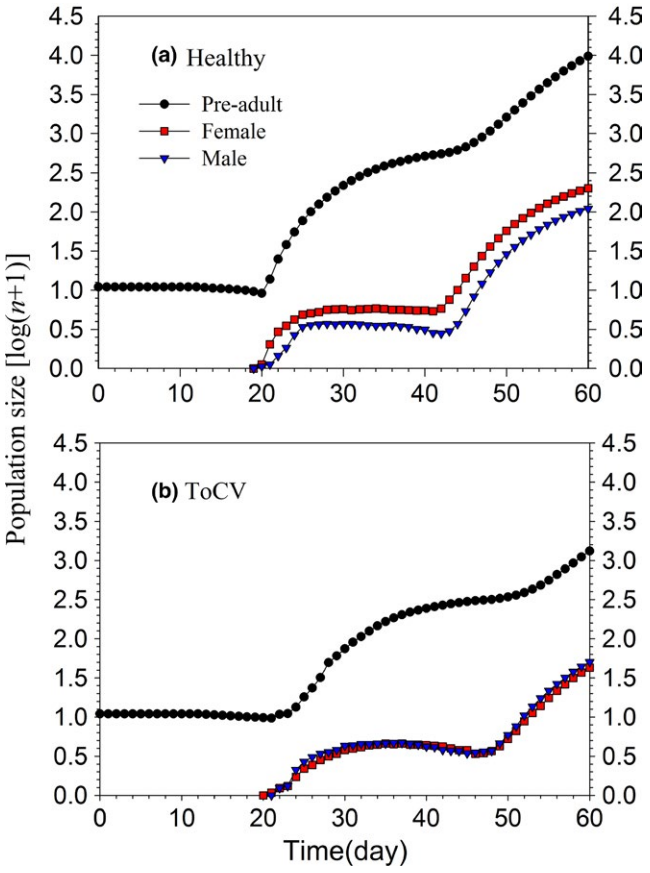

FIGURE 6 Population projection of the *B. tabaci* biotype Q on healthy and ToCV-infected tomato plants. An initial population of 10 eggs was used in each projection

projections based on the age-stage, two-sex life table can predict changes in population size and stage structure through time. These can be useful in providing valuable information on the trends and emergence timing of not only the pre-adult stages but the female and male adult emergences as well (Chi, 1990). Our projections demonstrated the diminished growth of a *B. tabaci* population on ToCV-infected tomato plants compared to a population growing on healthy plants (Figure 6). Earlier studies by Donaldson and Gratton (2007) also reported that soybean plants infected with the potyvirus *Soybean mosaic virus* (SMV, a non-persistent virus) reduced the population growth of its vector aphid *Aphis glycines*. This information is also useful for implementing and timing pest and plant virus control schedules.

The present study demonstrates that ToCV infections in tomato plants have detrimental effects on *B. tabaci* biotype Q. This is consistent with the results published by Fereres et al. (2016) that ToCV infection promoted a sharp increase in the emission of some tomato terpenes, and non-viruliferous whiteflies avoided the volatiles from the ToCV-infected plants. All of these findings suggest that ToCV infection is detrimental to further spread of the ToCV, which would seem contradictory to the observed epidemics of the ToCV in the field. For example, in a field survey conducted in 2014, we observed *B. tabaci* biotype Q outbreaks on ToCV-infected tomato plants in Qingdao, Shandong Province of China (J. Li, unpublished data). Dai et al. (2016) also found *B. tabaci* biotype Q outbreaks on ToCV-infected tomato plants in Shouguang, Shandong, China. Possible explanations for this are as follows: ToCV infection in tomato plants can lower the performance of *B. tabaci* biotype Q, but it may not affect the efficiency of virus acquisition, virus retention and/or virus transmission. Similar results have been observed in aphids. Peñaflor, Mauck, Alves, De Moraes, and Mescher (2016) found that although SMV is detrimental to the performance of *A. glycines*, it did not affect the transmission of SMV. In addition, some studies reported that the visual stimuli of the ToCV-infected tomato plant may positively affect whitefly preference, irrespective of their infectious status, they always preferred to land on ToCV-infected rather than on mock-inoculated leaves (Fereres et al., 2016), which would be beneficial to the spread of ToCV. Because of the complicate interactions among virus, insect vectors and host plants, the mechanism underlying the epidemics of ToCV in China should be further explored.

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AUTHOR CONTRIBUTION

DC and JL contributed to experimental design and management. JL performed the experiments, analyzed the data and drafted the manuscript. TBD helped with the experiments. HC and DC edited and revised the manuscript. All authors read and approved the final manuscript.

ORCID

J. Li http://orcid.org/0000-0002-9013-6862

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