Effects of Plant Virus and Its Insect Vector on Encarsia Formosa, a Biocontrol Agent of Whiteflies

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Effects of plant virus and its insect vector on *Encarsia formosa*, a biocontrol agent of whiteflies

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In this study, we investigated the tritrophic interactions among a persistently transmitted plant virus, *Tomato yellow leaf curl virus* (TYLCV), its insect vector, the sweetpotato whitefly *Bemisia tabaci*, and a parasitoid, *Encarsia formosa* Gahan, one of the most extensively used biological control agents. As an emerging invasive pest worldwide, the two most damaging whiteflies are *B. tabaci* B and Q cryptic species. On healthy tomato plants, parasitoid-induced mortality was significantly higher in *B. tabaci* B than in Q. In contrast, similar mortality levels of B and Q were observed on TYLCV-infected plants. A higher rate of parasitism was consistently observed in *B. tabaci* B, independent of the TYLCV infection. Similarly, the life history traits of *E. formosa* were influenced by both TYLCV and the two cryptic species of *B. tabaci*. Specifically, *E. formosa* parasitizing *B. tabaci* B had a greater adult longevity and shorter developmental time on healthy plants, whereas the parasitoids developing from Q has a greater adult longevity on TYLCV-infected plants. The emergence rate of *E. formosa* was unaffected by either *B. tabaci* cryptic species or the virus. These results suggest that the vector-borne pathogen can manipulate the host suitability of a parasitoid and hence the parasitoid-host interactions.

The sweetpotato whitefly, *Bemisia tabaci* (Gennadius) (Homoptera: Aleyrodidae), attacks many economically important crops, including vegetables, cotton, and ornamentals. Recent studies suggest that *B. tabaci* is a species complex containing at least 24 morphologically indistinguishable cryptic species1–3. The two most invasive and widespread groups of *B. tabaci* are the Middle East-Asia Minor I species (referred to as B hereafter) and the Mediterranean species (referred to as Q hereafter)1–3. The *B. tabaci* B was first recorded in China in the early 1990s, and it subsequently spread throughout much of the country, but has been recently displaced by Q in many areas4,5.

Although *B. tabaci* can damage crops directly by feeding, it causes greater damage by transmitting over 100 begomoviruses that can have catastrophic impacts on plant growth and survival6. *Tomato yellow leaf curl virus* (TYLCV) is a single-stranded DNA plant virus that originated in the Middle East7. TYLCV is transmitted by *B. tabaci*, the only known vector, in a circulative, persistent manner7. TYLCV was first detected in Shanghai, China in 20068 and then quickly spread from the Southern to Northern parts of China9. Although both B and Q can vector TYLCV horizontally, Q exhibited a much higher efficiency than B; as a result, Q appears to be a more competent viral vector than B10–12. The spread of TYLCV coincided with the rapid displacement of the *B. tabaci* B by Q in China9. Because both cryptic species have developed resistance to various synthetic insecticides, especially in Q12,13, biological control is one of the best alternatives available for the sustainable management of *B. tabaci* populations.

*Encarsia formosa* Gahan (Hymenoptera: Aphelinidae) is a solitary endoparasitoid that has been used commercially for the biocontrol of whiteflies, including the sweetpotato whitefly *B. tabaci* and the greenhouse whitefly *Trialeurodes vaporariorum*, worldwide14. As one of the most extensively used natural enemies, *E. formosa* parasitizes at least fifteen species of whiteflies in eight genera14. Specially, adult females parasitize and kill whitely nymph, although the developmental time of *E. formosa* depends on the developmental stage of *B. tabaci* nymph15. 

*Bemisia tabaci* Q has now become the primary whitely cryptic species in China14,15, and as noted, the rapid spread of Q has been accompanied by the recent outbreaks of TYLCV9. Information regarding the tritrophic interactions among TYLCV, a persistently transmitted plant virus, *B. tabaci*, the only known insect vector, and *E. formosa* are scarce.
formosa, the primary biocontrol agent for whiteflies, are grossly lacking. In this study, we are specifically investigating the impacts of this virus and its insect vector on the performance and life history traits of E. formosa. A better understanding of such interactions will, in turn, offer valuable insight into the long-term sustainable control of whiteflies, with or without the occurrence of epidemic plant virus.

**Results**

Biocontrol properties of *E. formosa* on the sweetpotato whitefly *B. tabaci*. The 3rd instar nymphs of *B. tabaci* B and Q cryptic species were reared on healthy (NV) and TYLCV-infected tomato plants (V), respectively, before submitting them to a hymenopterous parasitoid, *E. formosa*. The percent mortality (A) and the parasitism rate (B) of *B. tabaci* were documented. Values (means ± SE) are from three biological replications. Within each panel, different letters indicate significant differences among treatments (P < 0.05).

The impacts of *TYLCV* and *B. tabaci* cryptic species on the life history traits of *E. formosa*. The developmental time of *E. formosa* was significantly affected by the virus infection status (F$_3$, 236 = 34.759, P < 0.0001), virus infection status (F$_3$, 236 = 34.759, P < 0.0001), and the interaction between the two (F$_3$, 236 = 23.432, P < 0.0001). The mortality rate was significantly lower in Q reared on healthy plants than in B reared on healthy plants or in either B or Q reared on TYLCV-infected plants (Figure 1A, Figure S1).

The parasitism rate was significantly affected by the *B. tabaci* cryptic species (F$_3$, 236 = 190.939, P < 0.0001), virus infection status (F$_3$, 236 = 15.896, P < 0.0001), and the interaction between the two (F$_3$, 236 = 27.190, P < 0.0001). The parasitism rate was significantly lower in Q reared on healthy plants than in B reared on healthy plants or in either B or Q reared on TYLCV-infected plants. In addition, the parasitism rate was lower in Q reared on TYLCV-infected plants than in B reared on healthy or TYLCV-infected plants (Figure 1B, Figure S1).
10.960, \( P = 0.001 \) and the interaction between \( B. \) tabaci cryptic species and virus infection status (\( F_3, 236 = 11.954, P = 0.001 \)), but was not significantly affected by \( B. \) tabaci cryptic species (\( F_3, 236 = 3.640, P = 0.058 \)). Developmental time was shorter in \( B \) reared on healthy plants than on TYLCV-infected plants or \( Q \) reared on either healthy plants or TYLCV-infected plants. But it was not significantly different among \( B \) reared on TYLCV-infected plants or \( Q \) reared on either healthy plants or TYLCV-infected plants (Figure 2A, Figure S2).

The emergence rate of \( E. \) formosa, i.e., the percentage of pupae from which adult wasps emerged, was not significantly affected by \( B. \) tabaci cryptic species (\( F_3, 236 = 0.723, P = 0.396 \)), virus infection status (\( F_3, 236 = 0.238, P = 0.626 \)), or the interaction between the two (\( F_3, 236 = 2.239, P = 0.136 \)) (Figure 2B, Figure S2).

The longevity of \( E. \) formosa was significantly affected by the \( B. \) tabaci cryptic species (\( F_3, 236 = 6.086, P = 0.014 \)), virus infection status (\( F_3, 236 = 80.644, P < 0.0001 \)), and the interaction between the two (\( F_3, 236 = 294.839, P < 0.0001 \)). Longevity was significantly shorter in \( Q \) reared on healthy plants than on TYLCV-infected plants or \( B \) reared on either healthy plants or TYLCV-infected plants. In addition, the longevity of \( E. \) formosa parasitizing \( B. \) tabaci \( Q \) from the TYLCV-infected tomato was significantly higher than those wasps parasitized whiteflies from the TYLCV-free tomato. In case of \( B. \) tabaci \( B \), however, the trend was reversed (Figure 2C, Figure S2).

**Discussion**

The influence of insect vector on the performance and fitness of \( E. \) formosa. Although parasitism of \( B. \) tabaci by \( E. \) formosa has been studied previously\(^{19-18} \), none of them has been focused on the potential impact of cryptic species. As the most invasive and destructive \( B. \) tabaci cryptic species, \( B \) and \( Q \) vary in their mating and feeding behavior and prefer different host plants\(^{10,19,20} \). On healthy tomato plants, \( E. \) formosa performed better (higher mortality and parasitism rates) on \( B. \) tabaci \( B \) than on \( Q \) (Figure 3). This is consistent with the results from a congeneric parasitoid, \( E. \) sophia\(^11 \). In regard to fitness, the developmental times of \( E. \) formosa on the 3rd instar nymphs of \( B. \) tabaci were 14.16 and 14.52 days, respectively for \( B \) and \( Q \). A similar trend was documented in \( E. \) sophia, in which the developmental time of the parasitoid on \( B. \) tabaci \( B \) and \( Q \) were not significantly different\(^{11} \). Similarly, the emergence rate of \( E. \) formosa was not significantly affected by the two cryptic species. As for adult longevity, however, \( E. \) formosa lived longer in \( B \) than in \( Q \). The combined results from parasitoid’s performance and fitness indicate that \( B. \) tabaci \( B \) is a more suitable host for the \( Encarsia \) spp. than \( Q \), although the underlying mechanisms are largely unknown. The \( E. \) formosa colony was obtained initially from the United Kingdom and was introduced into the vegetable-growing areas in China to control whiteflies in the 1980s. \( E. \) formosa has been acclimated into the field conditions in China for over 30 years, and experienced the invasions of \( B. \) tabaci \( B \) and \( Q \) in the 1990s and 2000s, respectively\(^{22} \). By 2011, \( Q \) had displaced \( B \) and \( Q \) in China. In the present study, when infected, the fitness level of \( E. \) formosa decreased in \( B \), whereas both fitness and performance of the parasitic wasp were significantly improved in \( Q \).

**Conclusion**. A persistently transmitted virus, like TYLCV, can enhance the quality of host plant to attract insect vector and increase the viral transmission\(^{23} \). The quality of the insect vector, the host for parasitoids, can be improved accordingly. Higher quality of the host, consequently, can impact the performance of parasitoids and can, potentially, shift their host preference (Figure 3). Previous study showed that TYLCV-infected plants improved the growth, development, and fitness of \( Q \) but decreased the fitness of \( B \). In this study, when infected, the fitness level of \( E. \) formosa decreased in \( B \), whereas both fitness and performance of the parasitic wasp were significantly improved in \( Q \).

The present work showed the improved parasitism of \( E. \) formosa on the host of \( B. \) tabaci \( Q \) when the virus factor was added. The combined results suggest that the parasitoids may contribute to the suppression of TYLCV in the field by disproportionately influencing the vectors feeding on the infected plants. In addition, for the concurrent control of \( B. \) tabaci \( B \) and \( Q \) in the field, our results are encouraging in the context of integrated pest management, because they suggest that the current biological practice with parasitoids may contribute indirectly to the management of TYLCV by impacting on more competent virus-carrying vectors, \( B. \) tabaci \( Q \), and consequently reducing the proportion of vectors in the population that are infectious.
Figure 2 | The impact of TYLCV and *B. tabaci* cryptic species on the life history traits of *E. formosa*. To evaluate the potential impacts of plant virus and insect vector on a primary whitefly parasitoid, life history traits, including the developmental time (A), emergence rate (B), and longevity (C), of *E. formosa* were recorded. The 3rd instar nymphs of *B. tabaci* B and Q cryptic species were reared on healthy (NV) and TYLCV-infected tomato plants (V), respectively. Values (means ± SE) are from three biological replications. Within each panel, different letters indicate significant differences among treatments (P < 0.05).
Methods

Insect and parasitoid cultures. *Bemisia tabaci* B population was originally collected from an infested cabbage field in Beijing, China in 2004\(^1\), and the Q population was collected from a poinsettia plant in Beijing, China in 2009. Their identities were confirmed by random amplified polymorphic DNA polymerase chain reaction (RAPD-PCR)\(^2\). Both *B. tabaci* populations were maintained on tomato plants in a growth chamber at 27 ± 1°C, 70 ± 5% RH, and a 16/8 L/D photoperiod.

*Encarsia formosa* culture was a gift from the Beijing Academy of Agriculture and Forestry Sciences. The parasitic wasp had been maintained on *B. tabaci* B on tobacco plants for more than five generations. Upon arrival in our laboratory, the original plant was from an infested cabbage field in Beijing, China in 2004\(^3\), and the Q population was confirmed by random amplified polymorphic DNA polymerase chain reaction (RAPD-PCR)\(^4\). Both *B. tabaci* populations were maintained on tomato plants in a growth chamber at 27 ± 1°C, 70 ± 5% RH, and a 16/8 L/D photoperiod.

Plant materials. Tomato (*L. esculentum* Mill, No. 9 Zhongza) was used as the host plant for *B. tabaci* B and Q. The tomato plants were grown in the greenhouse and covered with 100-mesh insect-proof screen to exclude whitewalls and other pests.

TYLCV-infected tomato plants were obtained by *Agrobacterium tumefaciens* TYLCV-mediated inoculation using a cloned TYLCV genome (GenBank accession ID: AM282874). The plants were inoculated at the 3 to 4 true-leaf stage. TYLCV infection of the inoculated tomato plants was confirmed in the laboratory. The effects of *B. tabaci* cryptic species, virus infection status of the tomato plant, and experimental conditions. The endpoint measurements, including parasitism rate, mortality, and emergence rate were determined for each cohort of 30 *B. tabaci* nymphs in their respective clip-cage after 6–10 days assay period.

A second experiment was carried out to determine the impact of *B. tabaci* cryptic species and plant virus on *E. formosa* longevity. This experiment used the same conditions and materials as described in the previous paragraph. One newly emerged *E. formosa* female adult was introduced into a clip-cage on a tomato leaf (infected or not infected with TYLCV) infested with 30 3rd-instar nymphs of *B. tabaci* (B or Q). Each of the four treatments (two cryptic species and two virus conditions) was represented by 20 replicate clip-cages. Each day until the wasp died, the wasp in each clip-cage was transferred to a new leaf with 30 3rd-instar nymphs. The longevity of each *E. formosa* adult was recorded. Both experiments have been independently replicated three times.

Data analysis. Data were first checked for normality and transformed when necessary to meet the assumption of normal distribution. The data for parasitism rate, *B. tabaci* mortality rate, and *E. formosa* emergence rate were arcsine-square root transformed for analyses. The generalized linear model (GLM, two-way ANOVA) was used to test the effects of *B. tabaci* cryptic species, virus infection status of the tomato plant, and the interaction of cryptic species and virus infection status on the following parameters: *B. tabaci* mortality rate, the percentage of *B. tabaci* parasitized by *E. formosa*, the emergence rate of *E. formosa* adults from pupae, the longevity of *E. formosa* adults, and *E. formosa* developmental time. SPSS (version 13.0; SPSS Inc., Chicago, IL, USA) was used for statistical analyses (one-way ANOVA, Tukey’s test).

**Figure 3** | Patterns of parasite behavior in relation to plant pathogen and insect vectors. In this schematic, the parasitoid is an endoparasitoid, *E. formosa*, the pathogen is a plant virus, *Tomato yellow leaf curl virus* (infected plant is discoloured in yellow), and the vector is the sweetpotato whitefly *B. tabaci* B and Q cryptic species. Both insect vector and plant virus have a significant influence on the performance and fitness of *E. formosa*. Parasitic wasp performed better on *B. tabaci* B than on Q on healthy plants. Whereas, virus induced plant responses influences the behavior and physiology of the insect vector, and consequently exerts its impact on the parasitoids indirectly. For *B. tabaci* Q, TYLCV had a positive effect on both performance and fitness of *E. formosa*. In contrast, a negative impact on the life history traits of *E. formosa* was observed when B was fed on the infected tomato plants. Please note the number of *B. tabaci* nymphs infected with *E. formosa* is purely hypothetical, implicating either positive (more) or negative (less) effects.
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**Author contributions**

S.L.W., Y.J.Z., X.G.Z. and X.G.L. designed the experiment. X.Y.L. performed the experiment. Q.J.W., S.L.W., W.X. and W.S.X. contributed reagents/materials. X.Y.L., S.L.W., X.J.G. and X.G.Z. wrote the paper. All authors reviewed the manuscript.

**Additional information**

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