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Intra- and Interspecific Competition Between Western Flower Thrips and Sweetpotato Whitefly

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Subject Editor: Inon Scharf

J. Insect Sci. 14(187): 2014; DOI: 10.1093/jisesa/ieu049

ABSTRACT. The western flower thrips, *Frankliniella occidentalis* (Pergande), and the sweetpotato whitefly, *Bemisia tabaci* (Gennadius), are both invasive insect pests and are present in most of the same agricultural crops without a clear dominance of either species. Here, intra- and interspecific competition in *B. tabaci* and *F. occidentalis* was determined under controlled experiments. The results showed that intraspecific competition was distinct in *F. occidentalis* and that the co-occurrence of *B. tabaci* had a strong effect on *F. occidentalis*, resulting in a decrease in oviposition. Significant intraspecific competition was found in *B. tabaci*, and the coexistence of *F. occidentalis* had limited effect on the oviposition of *B. tabaci*. In a selective host plant preference experiment, both *F. occidentalis* and *B. tabaci* preferred eggplants most, followed by cucumbers and tomatoes. On cucumber plants, *B. tabaci* was predominant, whereas on eggplant and tomato plants, *F. occidentalis* and *B. tabaci* exhibited comparative competitive abilities during the initial stage. However, over time, higher numbers of *B. tabaci* than that of *F. occidentalis* were found on the two host plants. Our in vitro and potted plant experiments indicate that *B. tabaci* is competitively superior to *F. occidentalis*, which might help to explain their differential distribution patterns in China.

Key Words: *Frankliniella occidentalis*, *Bemisia tabaci*, intraspecific competition, interspecific competition

The western flower thrips, *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae), was reported in China for the first time in 2003 (Zhang et al. 2003). The sweetpotato whitefly, *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae), was first recorded in China in 1949, but no significant damage was caused by this insect until the late 1990s, when a new B-biotype from Middle East-Minor Asia 1 invaded China (Luo et al. 2002). Since then, this B-biotype and a later invasive Q-biotype of the Mediterranean group have become the dominant *B. tabaci* biotypes in China (Chu et al. 2006, Pan et al. 2011). *F. occidentalis* and *B. tabaci* are small hypermetamorphic insects with many common characteristics. The adults mainly reproduce sexually but also by parthenogenesis. Both species are globally distributed invasive insect pests (CABI 2012). They both feed directly on leaves and have an adverse impact on leaf size and photosynthesis. Both can cause indirect damage, which is especially important due to the transmission of plant viruses, such as tomato yellow curl virus by *B. tabaci* (Jones et al. 2003) and tomato spotted wilt virus by *F. occidentalis* (Whitfield et al. 2005). Furthermore, they have a wide range of host plants and favor various horticultural crops, and can be found on vegetable crops such as tomatoes, cucumbers, peppers, and melons.

Generally, two species with highly similar fundamental niches would often compete strongly with each other upon first encounter. Interspecific competition is defined as a reduction in individual fecundity, survival, or growth as a result of exploitation of resources or by interference with individuals of another species. Some studies have shown that interspecific competition is widespread among insects (Denno et al. 1995, Stewart 1996, Reitz and Trumble 2002). The most severe outcome of interspecific competition is competitive displacement, about 78% of which is triggered by introduction or invasion of an exotic species (Reitz and Trumble 2002). Well-documented cases of competitive displacement have occurred after the importation of *Aphytis* spp. parasitic wasps (DeBach 1966). The introduced *Aphytis melinus*, the most widespread natural enemy of the California red scale (*Aonidiella aurantii*) and a superior competitor, has displaced the native

Aphytis chrysomphali from most citrus areas of the Mediterranean basin and other citrus areas across the globe (Sorribas et al. 2010). Moreover, competitive displacement mediated by different mechanisms also takes place between invasive insects, such as beetles (Lee et al. 2010), leaf miner flies (Gao et al. 2011), and whiteflies (Liu et al. 2012). More commonly, different phytophagous insect species usually co-occur, although interspecific competition is often asymmetrical, so that the effect of one species on another is much more prominent than the reverse (Lawton and Hassell 1981). For instance, the current distribution of *Aedes albopictus* and *Aedes japonicus* in the United States overlaps considerably, and *A. albopictus* has a competitive advantage over *A. japonicus* (Armistead et al. 2008). Peixoto and Benson (2009) reported the co-occurrence of two tropical satyrine butterflies through completely different daily activity patterns to avoid stressful climatic conditions. Klapwijk and Lewis (2011) investigated the spatial ecology of multiple parasitoids. Venner et al. (2011) observed four competing weevil sister species to commonly co-occur on the same oak trees. Here, the marked time partitioning of the resource use appeared as a keystone of their coexistence.

As invasive insect pests, both intra- and interspecific competition between *F. occidentalis* or *B. tabaci* and native species has been widely studied and discussed (Brown et al. 1995, Pascual and Callejas 2004, Painsi et al. 2008). However, it is not clear whether interspecific competition exists between the invasive *F. occidentalis* and *B. tabaci*. In China, invasive *F. occidentalis* has been reported from Beijing, Yunnan, Shandong, and Guizhou (Wu et al. 2007, Zheng et al. 2007, Yuan et al. 2010), whereas *B. tabaci* has been found almost everywhere (Pan et al. 2011). We speculate that apart from other factors affecting the different range of their distribution, *B. tabaci* might outcompete *F. occidentalis*. During indoor rearing of *F. occidentalis* and *B. tabaci* on host plants, we found that *F. occidentalis* on some seedlings were often contaminated with or sometimes replaced by *B. tabaci*, and vice versa, which seems to indicate that the competition between the two species is host plant dependent. The coexistence of *F. occidentalis* and *B. tabaci*

on the same vegetable crops might result in them competing for similar resources. Therefore, the major objective of this study was to determine whether both intra- and interspecific competition would occur between *F. occidentalis* and *B. tabaci* under controlled experimental conditions. The fecundities of *F. occidentalis* and *B. tabaci* at different densities were compared in the laboratory, and their host preference was compared in a cage experiment.

Materials and Methods

Insect Pests. *F. occidentalis* and *B. tabaci* B-biotype were used in this study. *F. occidentalis* has been reared on bean pods in our laboratory since 2003 (Zhang et al. 2007). *B. tabaci* B-biotype was originally collected on cabbage plants from a field of the Institute of Vegetables and Flowers, Chinese Academy of Agricultural Sciences, China, in 2000, and has subsequently been maintained on cabbage plants in a glasshouse (Feng et al. 2009).

Competition Experiment on Cut Leaves.

Intraspecific Competition Within *F. occidentalis*. The experiment containers consisted of agar tubes and were prepared as follows: agar was diluted with distilled water into a concentration of 15–17 g/ml in a triangle flask and then heated in a microwave oven at medium level for 3–4 min. The agar was allowed to cool down, and 5 ml of liquid agar was transferred to a flat-bottomed glass tube (78 mm length, 22 mm diameter) by using a micropipettor (Eppendorf AG, Germany). Great care was taken to avoid liquid tainting of the inner tube wall or producing air bubbles. Leaf discs (22 mm diameter) were cut from *Phaseolus vulgaris* leaves and placed with their abaxial side down on the agar bed. One-day-old female and male adults of *F. occidentalis* with densities of 3, 6, and 10 pairs, respectively, were placed into each tube with an aspirator. Each density had 15 replicates. The open ends of the tubes were sealed with cotton plugs, and the tubes were placed in growth chambers upside down at a photoperiod of 14:10 (L:D) h at 26°C. The leaves were changed daily after the *F. occidentalis* on the leaves had been carefully removed by an aspirator. The displaced leaves were put in Petri dishes (10 cm diameter) filled with moistened filter papers. The Petri dishes were maintained in the same growth chambers. Because eggs are laid inside the leaf and are not visible, the number of the first instars hatching on replaced leaves was counted and used to calculate the daily fecundity of females (Watts 1934, Zhang et al. 2007). The observation lasted for 7 d.

Intraspecific Competition Within *B. tabaci*. The experimental containers were similar to the agar tubes described earlier. Newly emerged female and male adults of *B. tabaci* with densities of 3, 6, and 10 pairs, respectively, were placed into each tube with an aspirator. Each density had 10 replicates. The open ends of the tubes were sealed with cotton plugs, and the tubes were placed in growth chambers upside down at a photoperiod of 14:10 (L:D) h at 26°C. The leaves were changed daily after the *B. tabaci* on the leaves had been carefully removed by an aspirator. The displaced leaves were placed in Petri dishes (10 cm diameter) filled with moistened filter papers. The eggs on leaves were counted under a stereomicroscope. The observation lasted for 7 d.

Interspecific Competition Between *F. occidentalis* and *B. tabaci*. The experimental containers were similar to the agar tubes described earlier. *B. tabaci* were first inoculated, followed by *F. occidentalis*. The *B. tabaci* used in this experiment were the newly emerged female and male adults, and the *F. occidentalis* were 1-d-old female and male adults. All insects were transferred to the tubes by using an aspirator. The procedure was similar to that described in the previous section. The densities were 3 pairs of *B. tabaci* with 3 pairs of *F. occidentalis*, 6 pairs of *B. tabaci* with 6 pairs of *F. occidentalis*, and 10 pairs of *B. tabaci* with 10 pairs of *F. occidentalis*, respectively. Each density had 10 replicates. The number of the first instars of *F. occidentalis* and the number of eggs of *B. tabaci* on leaves were counted under a stereomicroscope. The observation lasted for 7 d.

Host Plant Preference Experiment. Eggplants (*Solanum melongena*) with three to four leaves, cucumber (*Cucumis sativus*) plants with three to four leaves, and tomato (*Solanum lycopersicum*) plants with three to four compound leaves were used in the experiment.

Multiple Choice Experiment. Two plants of each of the three plant species (*S. melongena*, *C. sativus*, and *S. lycopersicum*) were placed in one cage (60 by 60 by 60 cm) in an alternating arrangement, i.e., six host plants were placed in one cage in this experiment. Fifteen pairs of newly emerging female and male adults of *F. occidentalis* and 15 pairs of 1-d-old female and male adults of *B. tabaci* were collected with an aspirator. The insects were put in Eppendorf tubes and then simultaneously released onto plant leaves in the cage. The experiment was conducted in three replicates, and the cages were placed in a glasshouse. The numbers of *B. tabaci* and *F. occidentalis* on every plant were investigated for a month at a 5-d interval. The plants were watered when necessary.

Nonchoice Experiment. Three plants of *S. melongena*, *C. sativus*, or *S. lycopersicum* were placed in a cage, i.e., only one species of host plant was used per cage. Five pairs of *F. occidentalis* and five pairs of *B. tabaci* were collected and released by using the same method as described earlier. The experimental conditions and investigation methods were the same as in the previous section.

Statistical Analysis. Statistical analyses were performed with SPSS (version 13.0; SPSS, Chicago, IL). In the intraspecific competition experiments, the effect of densities on female fecundity was tested by one-way Analysis of Variance (ANOVA). In the interspecific competition experiments, the effects of densities and insect species on female fecundity were tested by two-way ANOVA. In the multiple-choice experiment, the effects of insect species and host plants on insect settling preferences were tested by repeated-measures ANOVA. In the nonchoice experiment, the effect of mutual interferences between *F. occidentalis* and *B. tabaci* on insect feeding was tested by repeated-measures ANOVA. Tukey's test was used to separate treatment means when the main effect or the interaction was significant.

Results

Fecundity of *F. occidentalis* Alone and Coexisting With *B. tabaci*.

For intraspecific competition in *F. occidentalis*, the number of eggs laid per *F. occidentalis* per day decreased with increased density (Fig. 1A), resulting in a significant decrease in the total fecundity (one-way ANOVA: Fig. 1B, $F_{2,42} = 47.119$, $P < 0.0001$). The highest fecundity (19 eggs per *F. occidentalis*) was observed under the density of three pairs, whereas only eight eggs per *F. occidentalis* at the density of 10 pairs. When *F. occidentalis* coexisted with *B. tabaci*, its fecundity was gradually decreased with the increased density of *B. tabaci* (two-way ANOVA: Fig. 1C and D, $F_{1,69} = 380.486$, $P < 0.0001$). The total fecundity of *F. occidentalis* at a density of 10 pairs was significantly lower than that at six and three pairs (Fig. 1D, $F_{2,27} = 11.785$, $P < 0.0001$).

Fecundity of *B. tabaci* Alone and Coexisting With *F. occidentalis*.

For intraspecific competition in *B. tabaci*, the fecundity was uncorrelated with densities (Fig. 2A). The total fecundity at a density of 10 pairs was significantly lower than that at six pairs (one-way ANOVA: Fig. 2B, $F_{2,27} = 4.974$, $P = 0.014$). The existence of *F. occidentalis* resulted in significant decreased fecundity of *B. tabaci* and higher density of *F. occidentalis* had a stronger effect on the fecundity of *B. tabaci* (two-way ANOVA: Fig. 2C and D, $F_{1,54} = 36.142$, $P < 0.0001$). The total fecundity of *B. tabaci* gradually decreased with densities ($F_{2,27} = 64.743$, $P < 0.0001$).

Selective Host Plant Preferences of *F. occidentalis* and *B. tabaci*.

Equal numbers of eggplant, tomato, and cucumber plants were placed in one cage, and at the same time, equal numbers of *F. occidentalis* and *B. tabaci* were released onto the plants in the cage. Insect settling preference was significantly affected by insect species (repeated-measures ANOVA: $F_{1,12} = 265.186$, $P < 0.0001$), by host plant (repeated-measures ANOVA: $F_{2,12} = 50.092$, $P < 0.0001$), and by the

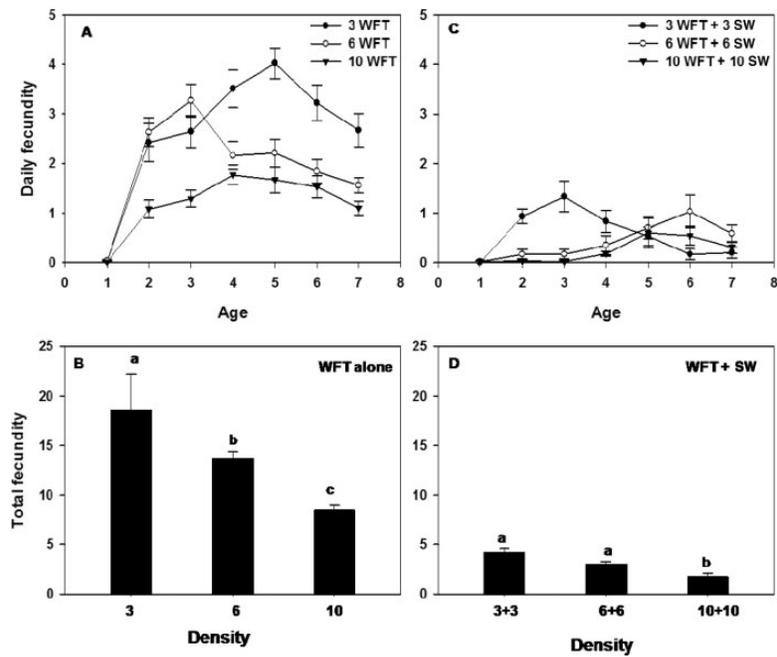


Fig. 1. Daily and total fecundity per *F. occidentalis* alone (A, B) or coexisting with different densities of *B. tabaci* (C, D). WFT: western flower thrips, *F. occidentalis*; SW: sweetpotato whitefly, *B. tabaci*. Bars represent mean \pm SE. Different lowercase letters above the error bars in (B) or (D) indicate significant difference (Tukey's test, $P < 0.05$).

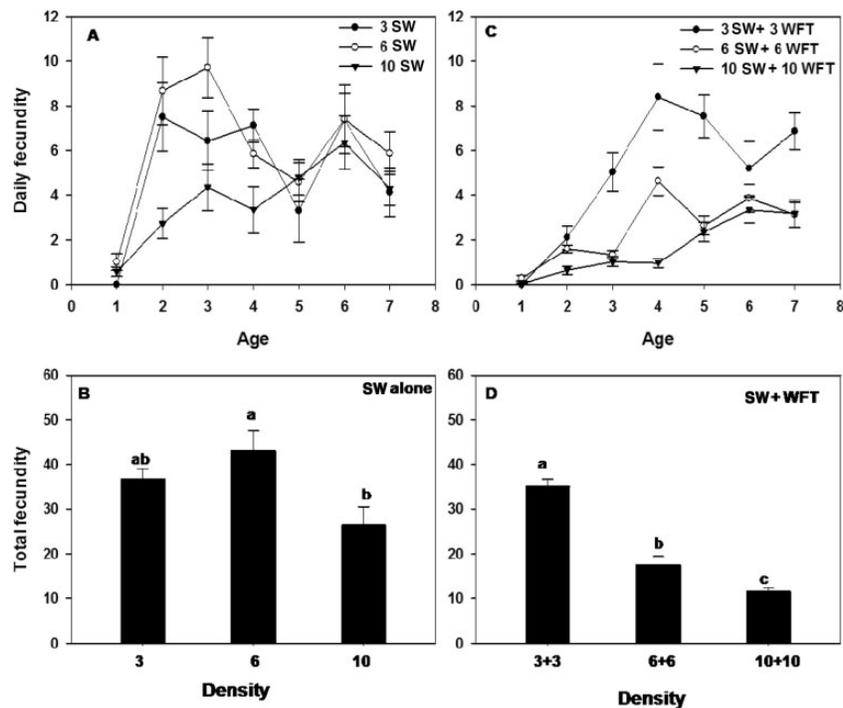


Fig. 2. Daily and total fecundity per *B. tabaci* alone (A, B) or coexisting with different densities of *F. occidentalis* (C, D). WFT: western flower thrips, *F. occidentalis*; SW: sweetpotato whitefly, *B. tabaci*. Bars represent mean \pm SE. Different lowercase letters above the error bars in (B) or (D) indicate significant difference (Tukey's test, $P < 0.05$).

interaction between insect species and host plant (repeated-measures ANOVA: $F_{2,12} = 50.349$, $P < 0.0001$). Among the three tested host plants, the total numbers of *B. tabaci* were significantly higher than that of *F. occidentalis* (Fig. 3). In addition, significant higher numbers of insects (both *F. occidentalis* and *B. tabaci*) were observed on eggplants than on tomato or cucumber plants (Fig. 3). Furthermore, *F.*

occidentalis preferred cucumber plants over eggplant and tomato plants, whereas *B. tabaci* preferred eggplants over cucumber and tomato plants (Fig. 3).

Nonselective Host Plant Performance of *F. occidentalis* and *B. tabaci*. On eggplant and tomato plants, the population increases of *F. occidentalis* and *B. tabaci* showed a similar trend. The *F. occidentalis*

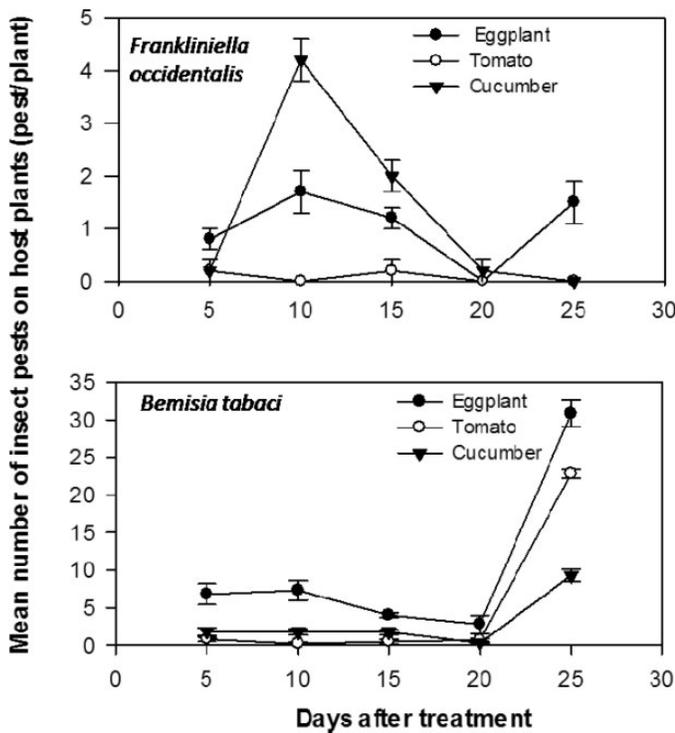


Fig. 3. Mean number of *F. occidentalis* and *B. tabaci* settled on different host plants over time in choice experiment.

population increased faster than that of *B. tabaci*, although at 5 d after treatment its size was smaller (Fig. 4). However, the mean total numbers of *F. occidentalis* and *B. tabaci* on eggplants and tomato plants were not significantly different (repeated-measures ANOVA: eggplant, $F_{1,4} = 0.018$, $P = 0.90$; tomato, $F_{1,4} = 3.875$, $P = 0.120$). On cucumber plants, the numbers of *F. occidentalis* and *B. tabaci* increased slowly for 15 d after inoculation. *F. occidentalis* showed the same trend during the entire test, with a mean total number of 0.8 individuals per plant. *B. tabaci* exhibited a different trend and increased quickly to a mean number of 23.7 individuals per plant at 20 d after treatment (Fig. 4). The mean total number of *B. tabaci* individuals on cucumber plants was significantly higher than that of *F. occidentalis* (repeated-measures ANOVA: $F_{1,4} = 488.058$, $P < 0.0001$). The results indicate that on eggplants and tomato plants, *F. occidentalis* and *B. tabaci* have a similar population increase potential, whereas on cucumber plants, *B. tabaci* might be stronger.

Discussion

Invasion success and spread of nonnative species can be enhanced by superiority in interspecific competition, particularly when similar species and limited resources are encountered (Williamson 1996). *F. occidentalis* and *B. tabaci* are superior competitors compared with some native species, which is often cited as the main reason for their invasive success (Kirk and Terry. 2003, Chu et al. 2010). Our results indicate that under the conditions of limited food and space (such as a glass tube), the daily reproduction and the total mean reproduction of *F. occidentalis* decrease with increasing density, and that the intraspecific competition is distinct in *F. occidentalis* (Fig. 1A and B). The coexistence of *B. tabaci* had great effect on *F. occidentalis*, resulting in a decreased fecundity (Fig. 1C and D). Although significant intraspecific competition was found in *B. tabaci* (Fig. 2A and B), the coexistence of *F. occidentalis* had limited effect on the reproduction of *B. tabaci* (Fig. 2C and D). Intraspecific competition is a particular form of competition in which members of the same species vie for the same resource in an ecosystem. Our results indicate that for *F. occidentalis*,

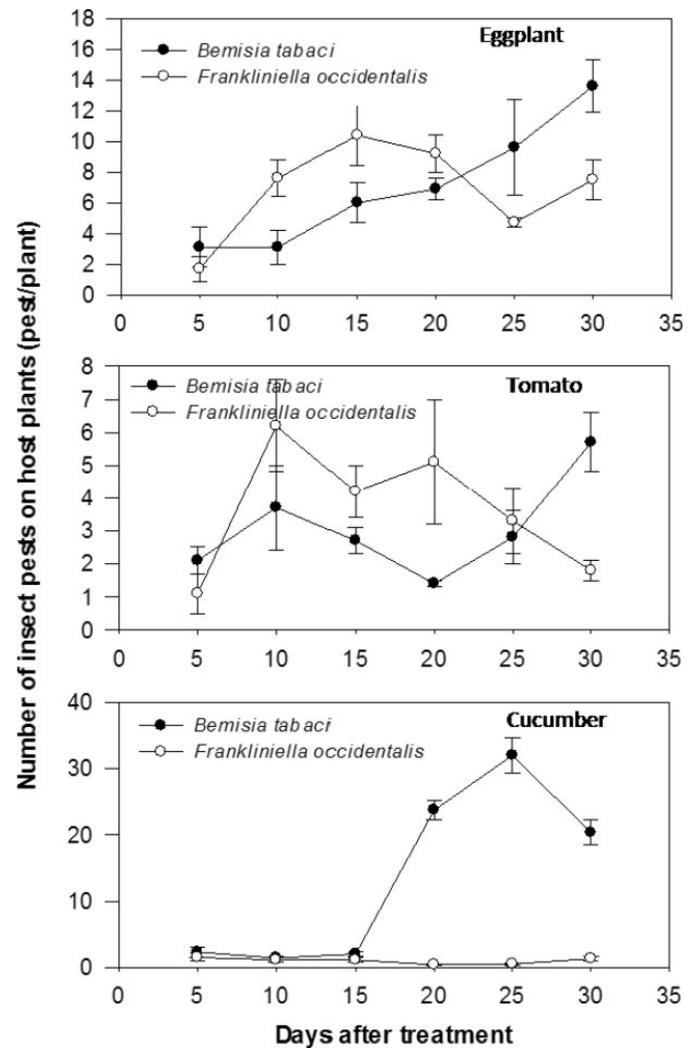


Fig. 4. Mean number of *F. occidentalis* and *B. tabaci* settled on different host plants over time in nonchoice experiment.

both the intraspecific competition and the interspecific competition from *B. tabaci* were stronger. In *B. tabaci*, on the other hand, the interspecific competition from *F. occidentalis* was a little stronger than the intraspecific competition, in which the egg-laying amount decreased more in interspecific than in intraspecific competition. Northfield et al. (2011) reported significant intraspecific competition occurring in *F. occidentalis*. A likely explanation might be that *F. occidentalis* is a facultative predator of spider mites (Wilson et al. 1996) and that higher densities could cause it to become more aggressive. In *B. tabaci*, however, intraspecific competition occurred among immature insects rather than among adults (Pascual and Callejas 2004).

Both *F. occidentalis* and *B. tabaci* are small-size insects and have a close relationship with plants (Morse and Hoddle 2006, Inbar and Gerling 2008). They both have a wide range of host plants but different host preferences. Our multiple-choice experiment showed that *F. occidentalis* and *B. tabaci* favored eggplants over cucumber and tomato plants (Fig. 3). On cucumber plants, *B. tabaci* was predominant, whereas on eggplant and tomato plants, the *F. occidentalis* populations increased faster than those of *B. tabaci*. The *F. occidentalis* population also showed a stronger capacity of population growth during the initial stage. However, over time, higher numbers of *B. tabaci* than *F. occidentalis* were found on the two host plants (Fig. 4). This difference might be due to the biological differences between the two insect species. *F. occidentalis* develops faster but has a lower fecundity than *B. tabaci*.

On average, the generation time of *B. tabaci* is about 25 d, and its lifetime fecundity is about 100 eggs per female (Mansaray and Sundufu 2009), whereas for *F. occidentalis*, the mean generation time is about 15 d, and the lifetime fecundity is 70–80 eggs per female (Zhang et al. 2007). The crop growth period could be another possible reason. Some studies have reported that pollen can have a positive effect on growth, development time, and fecundity of *F. occidentalis* (de Jager and Butôt 1993, Hulshof et al. 2003). The host plants used in this experiment were at the stage of vegetative growth and not many flowers were present. The fewer flowers might affect the population growth of *F. occidentalis* but not of *B. tabaci*.

It is possible that competition from *B. tabaci* reduced *F. occidentalis* density on the plants. The mechanisms that lead to the competitive superiority of *B. tabaci* over *F. occidentalis* are yet unclear. Interference-type competitive interactions could have occurred between the two species, thus showing that the presence of *B. tabaci* resulted in the absence of an oviposition peak in *F. occidentalis*, whereas the presence of *F. occidentalis* resulted in a decreased reproduction time in *B. tabaci*. Thus, our in vitro and potted plant experiments contribute to explaining their different distribution patterns in China.

Acknowledgments

We thank Prof. X. Jiao (Hubei University) for assistance with the statistical analysis. This work was supported by grants from the National Technology Support Program (2012BAD19B06), the Special Fund for Agro-scientific Research in the Public Interest (201103026), and Beijing Leafy Vegetables Innovation Team of Modern Agro-industry Technology Research System (blvt-15).

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