

## **Behavioral Interactions between *Bemisia tabaci* (Homoptera: Aleyrodidae) and *Tetranychus truncatus* (Acarina: Tetranychidae)**

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BEHAVIORAL INTERACTIONS BETWEEN *BEMISIA TABACI*  
(HOMOPTERA: ALEYRODIDAE) AND *TETRANYCHUS TRUNCATUS*  
(ACARINA: TETRANYCHIDAE)

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ABSTRACT

Interspecific interactions between *Bemisia tabaci* (Gennadius) and the spidermite *Tetranychus truncatus* Ehara were evaluated by observation of behavioral responses over 30 min intervals on cowpea leaves. The response of adult female whiteflies was observed on 4 classes of leaf: (1) uninfested (2) previously fed upon by spidermite nymphs, (3) spidermite nymphs and webbing present, and (4) spidermite adults present. Likewise, adult female spidermite response was observed on (1) leaves uninfested with whiteflies, (2) leaves previously fed upon by whitefly nymphs, (3) leaves with whitefly nymphs present, and (4) leaves with whitefly adults present. Spidermites generally had a greater effect on whitefly behavior than *vice versa*. Whitefly feeding duration decreased while labial tapping duration and frequency increased on all 3 types of mite-infested leaves compared to uninfested leaves. Although whitefly oviposition duration and frequency did not change on leaves infested with spidermite nymphs, whitefly fecundity decreased compared to untreated leaves. Although whitefly effects on spidermite behavior were less marked, nevertheless, duration and frequency of cheliceral tapping by spidermites did increase in the presence of whiteflies, although duration or frequency of feeding did not. Thus, one would predict that spidermites would win out in competition with whiteflies on a common host plant. Behavioral observations of interactions between herbivores can provide valuable insight into competitive relationships which should, however, be verified by field studies.

Key Words: *Bemisia tabaci*; Behavior; Host Plant; Interspecific Interaction; *Tetranychus truncatus*

RESUMEN

Interacciones interespecíficas entre hembras adultas de la mosca blanca *Bemisia tabaci* y el ácaro *Tetranychus truncatus* fueron evaluados mediante observaciones durante intervalos de 30 minutos en las hojas de caupí. Las respuestas de la mosca blanca se observó en 4 clases de hoja: (1) no infestadas (2) anteriormente alimentado por ninfas del ácaro, (3) con ninfas y telaraña del acaro presentes, y (4) con adultos del ácaro presentes. Del mismo modo, la respuesta de las crías de araña se observó que (1) hojas no infestadas, (2) hojas previamente alimentado por ninfas de mosca blanca, (3) hojas con ninfas de mosca presentes, y (4) hojas con los adultos de mosca presentes. Los ácaros en general tuvieron un mayor efecto sobre el comportamiento de la mosca blanca que a la inversa. Duración en alimentación de la mosca blanca se disminuyó, mientras que la duración y frecuencia de pulsaciones labiales aumentaron en presencia de los tres tipos de hojas infestadas por ácaros en comparación con hojas no infestadas. A pesar de la duración y la frecuencia de ovoposición de mosca blanca no ha cambiado en las hojas infestadas con ninfas de las crías de araña, la fecundidad de la mosca blanca se disminuyó en comparación con las hojas no tratadas. Aunque los efectos sobre el comportamiento de las crías de araña mosca blanca fueron menores, sin embargo, la duración y frecuencia de pulsaciones chelicerales por los ácaros se incrementó en presencia de la mosca blanca, aunque no hubo cambio en la duración o frecuencia de la alimentación. Por lo tanto, se podría predecir que se ganaría los ácaros en una competencia con la mosca blanca cuando compartiendo una planta huésped. Aunque observaciones del comportamiento pueden proporcionar información valiosa sobre relaciones de competencia entre herbívoros, sin embargo, sería siempre necesario verificarlas por estudios de campo.

Translation provided by authors.

Herbivores that share a common host plant can interact with each other positively or negatively in different ways. Negative interactions are most often thought of as competition, which can be direct (exploitation of a common limited food resource) or indirect (mediated by the host plants, even for spatially or temporally-separated competitors (Wise & Weiberg 2002; Hunt-Joshi & Blossey 2005; Lynch et al. 2006). Many studies on competition conclude that previous feeding by one species induces nutritional and allelochemical changes in the plant that adversely affect the performance of another species feeding subsequently on the same host (Petersen & Sandström 2001; Awmack & Leather 2002; Bezemer et al. 2003; Denno & Kaplan 2007). The ability of phloem-feeders to induce changes in their host plants is well documented, including galling, chlorotic lesions and necrosis, and reduction in the size of roots and leaves. These alterations might be associated with changes in the composition of phloem (Telang et al. 1999; Sandström et al. 2000) that would affect other phloem-feeders as well. Prior feeding by one herbivore has been seen to prolong development, reduce body size and survival, and affect behavior of potential competitors (Inbar et al. 1999a; Gianoli 2000; Ferrenberg & Denno 2003).

Herbivore feeding behavior varies based on quality of host plants. For instance, a mobile herbivore should move when a nutrient is needed, but rest when satiated. Locomotion should follow feeding if a full meal is obtained that is deficient in any nutrient, but rest should follow a nutritionally adequate meal (Bernays 1998). Leaf-surface features have been seen to affect behavior of phytophagous insects, including Acrididae (Blaney & Chapman 1970), whiteflies (Aleyrodidae) (Walker 1987) and Coleoptera (Harrison & Mitchell 1988). Isaacs et al. (1999) reported that behavior was similar on untreated leaves and leaves whose foliage was treated imidacloprid, but markedly different on plants drenched with the systemic insecticide, indicating that the behavioral sequence was affected significantly by ingestion rather than direct contact with the compound.

*Bemisia tabaci* is a highly polyphagous pest, infesting more than 600 plant species including a great variety of vegetable, ornamental and agronomic host plants in the tropics and subtropics (Secker et al. 1998). Damage is caused directly by feeding on phloem or deposition of honeydew, or indirectly by physiological disorders and transmission of more than 150 plant viruses (Oliveira 2001; Perring 2001; Jones 2003). *Tetranychus truncatus* is a major pest of cotton (*Gossypium hirsutum* L.), corn (*Zea mays* L.), soybean (*Glycine max* (L.) Merr.), cucumber (*Cucumis sativus* L.), kidney bean (*Phaseolis vulgaris* L.) and eggplant (*Solanum melongena* L.) in China (Li et al.

1998; Pang et al. 2004; Qui et al. 2009). The mites feed on the epidermis and puncture parenchyma cells, leaving light-colored stipples on the leaf surface and interfering with photosynthesis (Tomczyk & Kropczyńska 1985). *T. truncatus* often occurs simultaneously in the field with *B. tabaci* on bean, eggplant, tomato (*Solanum esculentum* L.) and cucumber.

Wide distribution of the B biotype of *B. tabaci* with its severe effects on plants provides many opportunities to study intra- and interspecific interactions with conspecifics and other herbivores (Rosell et al. 2010). Intraspecific competition between B biotype and other biotypes of *B. tabaci* (De Barro et al. 2006; Pascual 2006; Liu et al. 2007) has been well studied with indications that intraspecific competition plays an important role in whitefly biology and evolution (De Barro 2005; De Barro et al. 2006; Jiu et al. 2007). Interspecific competition between *B. tabaci* and other herbivores has also been investigated. Inbar et al. (1999b) reported that first instar cabbage looper *Trichoplusia ni* (Hübner) switched to the adaxial (whitefly-free) side of collard leaves that were previously infested with *B. tabaci*. Negative effects on host preference and performance of *Liriomyza trifolii* Burgess and *Liriomyza sativae* Blanchard were observed in the presence of *B. tabaci* on tomato, pumpkin and cucumber (Inbar et al. 1999a; Zhang et al. 2005).

In this study, we investigated interspecific competition between *B. tabaci* and *T. truncatus* by observing various behaviors on cowpea, *Vigna unguiculata* (L.) Walp). We show that cohabitation by *T. truncatus* and *B. tabaci* on cowpea leaves results in increased labial/cheliceral tapping suggesting reduced host suitability. Furthermore, we observed reduced fecundity in whitefly, indicating negative interspecific interactions. We hypothesize that the observed interspecific interactions between *B. tabaci* and *T. truncatus* evolved as a result of overlap in host range, high population densities, and similar feeding habits.

## MATERIALS AND METHODS

### Plants and Herbivores

Cowpea (*V. unguiculata*) seedlings were grown in plastic pots (diam 20 cm), fertilized with approximately 2 g of complete slow release fertilizer (Guifeng, Huazhou Guifeng Chemicals Inc. Guangdong China) mixed into loamy soil (84% sand, 7% silt, 6% clay, 3% organic matter) at planting. Pots were incubated in a glass greenhouse (25-30 °C) with natural light and ventilation until plants grew to 20-25 cm height and had 3-5 compound leaves. Plants were then maintained in insect cages (60cm × 60cm × 60cm) in an air-conditioned room at 25 ± 1 °C, 65 ± 10% RH, and a photoperiod of 14:8 (L:D) h by a daylight

lamp (9,000 lux) in the laboratory of the Department of Insect Ecology, South China Agricultural University (SCAU), Guangzhou, China. Insect cages consisted of stainless steel frames with acrylic walls containing 2 nylon mesh screens for ventilation.

Whiteflies, *B. tabaci* (Gennadius) biotype B and spidermites, *T. truncatus* were collected from cucumber (*Cucumis sativus* L.) and eggplant (*Solanum melongena* L.), respectively in the SCAU Farm and then maintained on cowpea plants in a separate glass greenhouse (25-30 °C) with natural light and ventilation for more than 10 generations.

Approximately 300 whitefly and 100 spidermite adults were introduced into a separate cage for 24 h to deposit eggs and then removed. The resulting eggs were reared to adults in an air-conditioned room at  $25 \pm 1$  °C,  $65 \pm 10\%$  RH, and illuminated with a daylight lamp (9,000 lux) and a photoperiod of 14:10 (L: D) h. Three- to 4-day-old whitefly adults were used in the experiments, as most are mated 48h after emergence (Musa & Ren 2005). Most spidermites were mated 24 h after emergence, so 1- or 2-days old spidermite adults were used. Whitefly and spidermite adults were starved for 2 h before initiation of the experiments.

#### Direct Observations of *B. tabaci* and *T. truncatus* Feeding Behavior on the Leaf Surface

Four treatments were used for behavioral observations of whitefly: (1) cowpea leaves with no spidermites; (2) leaves fed upon by 5-8 protonymphs for 5-6 days that were then removed along with their webbing; (3) as above but with spidermites nymphs and webbing left over approximately 60% of the leaf surface; and (4) leaves infested with 5 pairs of spidermite adults per leaf.

Spidermite behavior was also observed on four kinds of cowpea leaves: (1) leaves uninfested with whiteflies; (2) leaves fed upon by  $10.2 \pm 2.3$  third or fourth instar whitefly nymphs per cm<sup>2</sup> of leaf surface then removed; (3) leaves as above but with whitefly nymphs left on; (4) leaves each infested with 5 pairs of whitefly adults.

Six specific elements of whitefly behavior were noted - feeding, grooming, walking, resting, labial tapping, and oviposition (Isaacs et al. 1999) (Table 1). The first 5 of the specific behavioral elements listed above were noted for *T. truncatus* except that tapping was with the chelicerae (Table 1). We defined feeding as the whitefly adult not moving across the leaf surface while holding the labial tip stationary.

The experimental leaf disc (diam 4 cm) was placed on a single wet filter paper (diameter 5 cm) in a Petri dish (diam 5.5 cm, ht 1.2 cm). A hardened 0.5 cm thick disk of 2% agar into which a 1.5 cm observation hole had been cut out in the cen-

TABLE 1. DESCRIPTION OF DIFFERENT BEHAVIORS OF *BEMISIA TABACI* AND *TETRANYCHUS TRUNCATUS* ON COWPEA LEAF SURFACE.

Behavioral element	<i>B. tabaci</i>	<i>T. truncatus</i>
Feeding	Standing motionless with stylets penetrating into the leaf.	Standing motionless with the chelicerae penetrating into the leaf.
Grooming	Wings rapidly shaking and rubbing across the two sides of the body or the abdomen; standing on the prothoracic legs and the rubbing meso- and meta-thoracic legs together or rubbing the wings; standing on the meso- and meta-thoracic legs and rapidly rubbing the prothoracic legs together.	The middle and back legs standing on the leaf surface, the front legs and chelicerae rubbing the leaf surface from right to left.
Walking	Walking across the leaf surface	Walking across the leaf surface
Resting	Standing motionless, with the labium retracted under the head.	Standing motionless, with the chelicerae retracted under the head.
Labial/ cheliceral tapping	Standing motionless, labium rapidly tapping the leaf surface.	Standing motionless, chelicerae rapidly tapping the leaf surface.
Oviposition	The abdominal tip dabbing the leaf surface and laying an egg.	—

ter using a test tube was then placed on the leaf disk. During observations, the agar was covered with a piece of clear plastic film to prevent the herbivore's escape. The film was punctured 10 times using an insect pin (No. 1) to provide ventilation (Fig. 1).

For observations on whitefly, a single mated female adult was starved for 2 h, cooled for 1 min at -4 °C, and then placed gently onto the surface of test leaf. For spidermite observations, a single mated female adult was placed on leaf surface using a fine brush. Observations were made in an air-conditioned room at 25 ± 1 °C, 65±10% RH under a cool light source using a stereoscopic microscope (Zeiss Stermi 2000-cs). A continuous observation period of 30 min was initiated once the subject took a normal stance on the leaf surface. Start times and durations of each specific behavioral element were recorded. Two sets of observations were made for each treatment in random order during the morning until a total of 30 replicates were obtained for each treatment.

Statistical Analysis

Data on the duration and frequency of each behavioral element were first subjected to the Leven test for homogeneity of variances (SPSS 10.0). For data conforming to the assumptions of ANOVA, multiple comparisons among groups were made contingent on a significant treatment effect using Tukey's test in SPSS 10.0. Non-normally distributed data were analyzed using the Kruskal-Wallis test.

RESULTS

Effect of *T. truncatus* on the Feeding Behavior of *B. tabaci*

Total duration of whitefly feeding on uninfested leaves was 1263 s, which was significantly greater than on mite-infested leaves with webbing (318 s) and leaves infested with adult mites (966 s), but not compared to leaves with nymphs alone (1052 s) ( $F_{3,116} = 39.55, P < 0.0001$ ; Fig. 2).

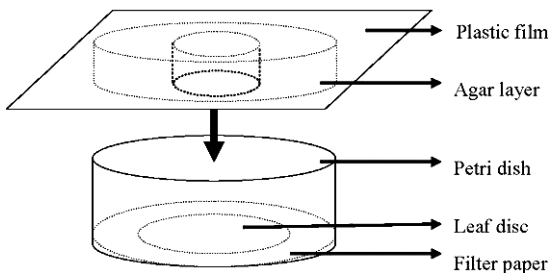


Fig. 1. Bioassay arena used for observation of *Bemisia tabaci* and *Tetranychus truncatus* on cowpea leaves.

Whiteflies also fed more frequently on uninfested leaves (10.6 times per 30 min) compared to nymph-infested leaves with webbing (1.3 times per 30 min), but not significantly different from the other 2 treatments ( $F_{3,116} = 44.19, P < 0.0001$ ; Fig. 3). While these differences were observed in total time, the mean duration spent in feeding was not significantly different among the four treatments ( $F_{3,116} = 1.89, P = 0.1350$ ; Table 2).

Duration and frequency of labial tapping by whitefly adults on mite-free leaves was significantly less than on leaves infested with mite nymphs or adults ( $F_{2,87} = 7.31, P = 0.001$ , and  $F_{2,87} = 6.97, P = 0.002$ , respectively; Fig. 2). Mean duration of labial tapping by whitefly was only 2 s on uninfested leaves, significantly less than the time spent on nymph or adult-infested leaves (25 s and 20 s, respectively) ( $F_{2,87} = 11.68, P < 0.0001$ ; Table 2). Labial tapping by whiteflies was not observed on nymph-infested leaves with webbing.

Oviposition time of whiteflies on mite-free leaves was 39 s, with no significant difference compared to leaves infested with mite nymphs or adults (43 s and 66 s, respectively) ( $F_{2,87} = 2.55, P = 0.084$ ; Fig. 2). Oviposition occurred 2.8 times on mite-free leaves, which was not different from that seen on nymph-infested leaves (1.9 times) or adult-infested leaves (3.8 times). However, the mite nymphs or adults significantly depressed whitefly oviposition frequency ( $F_{2,87} = 2.55, P = 0.045$ ; Fig. 3). Nevertheless, there was no treatment effect on mean duration of oviposition ( $F_{2,87} = 1.54, P = 0.219$ ; Table 2). Average whitefly fecundity during 30 min on mite-free leaves was 2.8 eggs, significantly more than that on nymph-infested leaves (1.0 eggs), but not significantly more than on adult-infested leaves (2.1 eggs) ( $F_{2,87} = 6.90, P = 0.002$ ; Table 2). No oviposition was observed on mite nymph-infested leaves with webbing.

Effect of *B. tabaci* on the Feeding Behavior of *T. truncatus*

Spidermites spent a total of 1176 s feeding on whitefly-free leaves, not significantly different leaves infested by adults (933 s) or by nymphs that had been removed (1122 s), or not removed (1033 s) ( $F_{3,116} = 1.91, P = 0.132$ ; Fig. 3). There were also no significant differences between the frequency or mean duration of feeding on the four kinds of cowpea leaves ( $F_{3,116} = 0.54, P = 0.655$ , Fig. 3 and  $F_{3,116} = 0.75, P = 0.524$ , Table 3, respectively).

Spidermites spent 33 s and 35 s, respectively, tapping on leaves previously or actually infested with whitefly nymphs, which was significantly more than that on whitefly-free leaves (10 s) or whitefly adult-infested leaves (1 s) ( $F_{3,116} = 128.75, P < 0.0001$ ; Fig. 3). Cheliceral tapping on whitefly-free leaves occurred 1.5 times, which was significantly less than on leaves previously or actu-

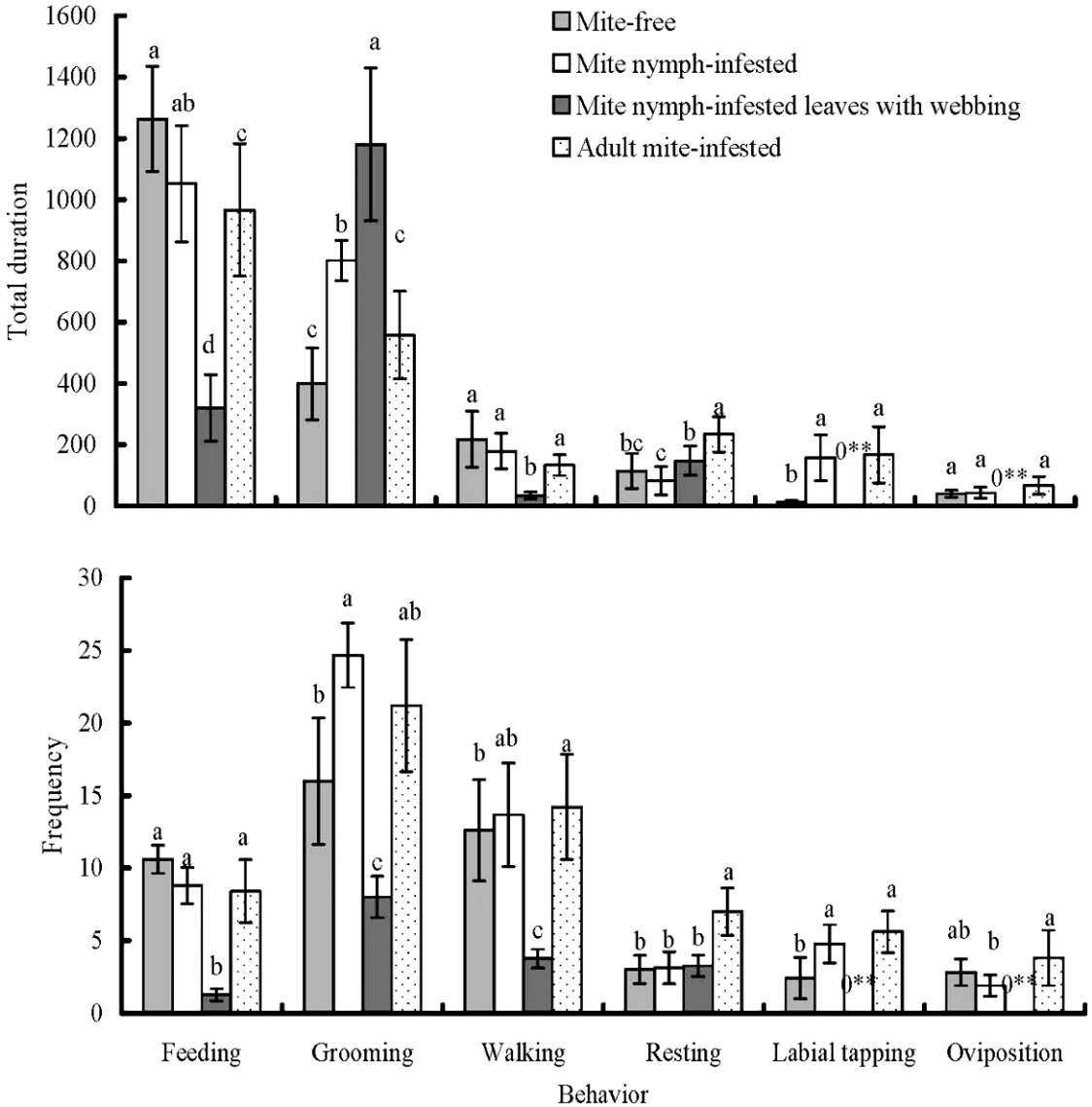


Fig. 2. Duration and frequency ( $M \pm SE$ ) of different behaviors of *Bemisia tabaci* on four kinds of cowpea leaves. For feeding, grooming, walking and resting behaviors, means were analyzed using ANOVA. Total durations of labial tapping and oviposition on three treatments with non-zero means were calculated using ANOVA and then tested for differences between zero and all the other values with a *t*-test ( $P < 0.01$ ). Bars within each behavior with the same letter above are not significantly different from each other (Tukey's test,  $P < 0.05$ ).

ally infested with whitefly nymphs but more than on whitefly adult-infested leaves ( $F_{3,116} = 55.03, P < 0.0001$ , Fig. 3 and  $F_{3,116} = 31.27, P < 0.0001$ , Table 3, respectively).

DISCUSSION

Most studies on interspecific interactions have focused on outcomes in terms of survival, development or reproduction of 2 competing species (Gi-

anoli 2000; Wise & Weinberg 2002; Ferrenberg & Denno 2003; Hunt-Joshi & Blossey 2005; Lynch et al. 2006). Here we investigated how whiteflies and spidermites modified their behaviors in response to each other's presence. Our data indicated that initial behavioral responses of both herbivores were significantly affected by the other competitor. Our data showed that whitefly adults fed less, spent more time tapping and laid fewer eggs on mite-infested leaves. Spidermites

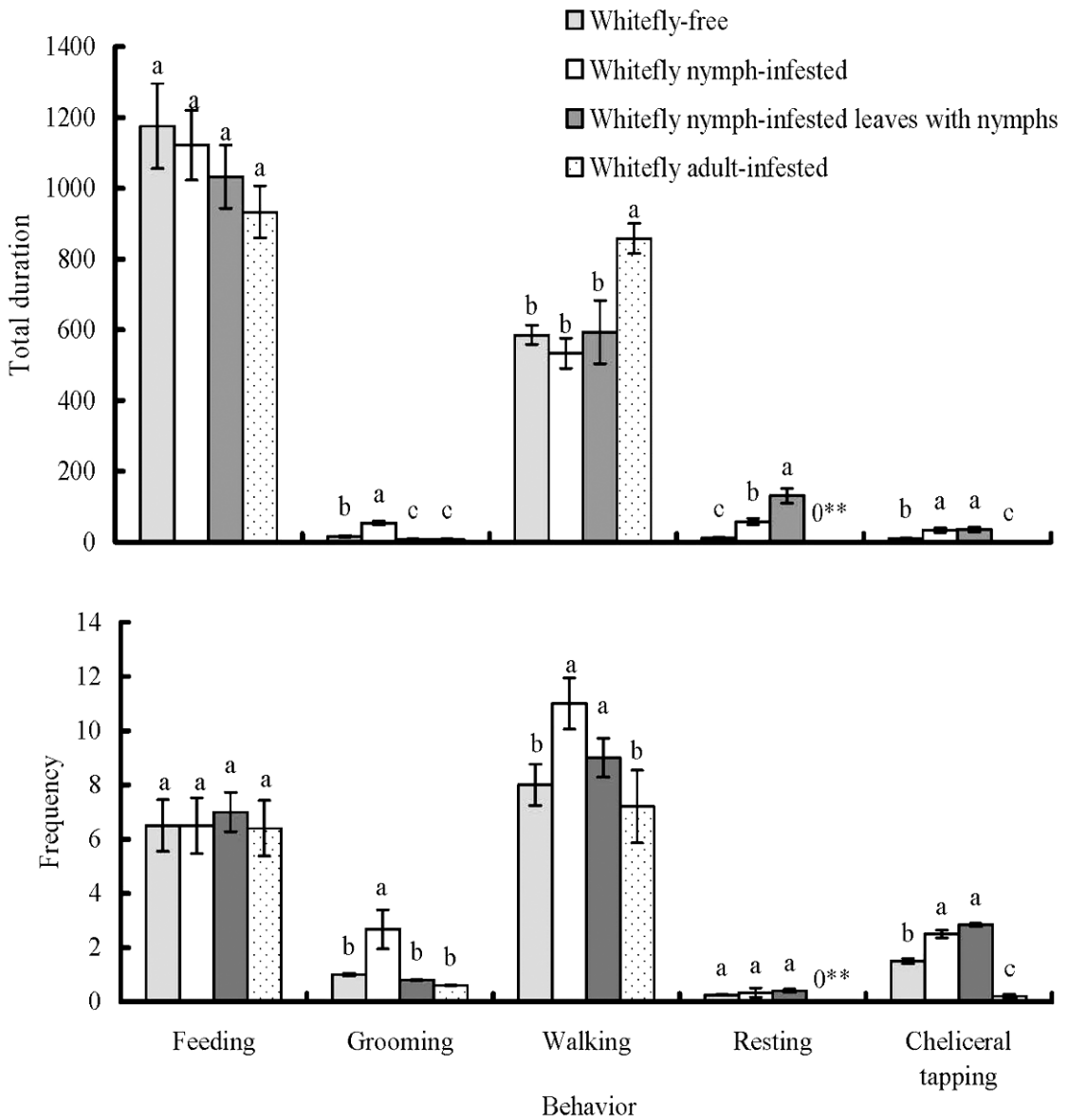


Fig. 3. Total duration and frequency ( $M \pm SE$ ) of different behaviors of *Tetranychus truncatus* on four kinds of cowpea leaves. For feeding, grooming, walking and cheliceral tapping behaviors, means were analyzed using ANOVA. Total durations of resting on three treatments with non-zero means were calculated using ANOVA and then tested for differences between zero and all the other values with a *t*-test ( $P < 0.01$ ). Bars within each behavior with the same letter above are not significantly different from each other (Tukey's test,  $P < 0.05$ ).

spent more time tapping on whitefly infested leaves compared to uninfested leaves, even if the whiteflies were no longer present. Nevertheless, long-term negative interactions cannot be assumed because changes in fitness were not assessed. Thus further research is needed.

Labial tapping is regarded as a way whiteflies use to evaluate host plant palatability (Isaacs et al. 1999). The fact that tapping was significantly

increased on mite-infested leaves indicates reduced palatability. Similarly, duration and frequency of cheliceral tapping by spidermites was also significantly increased on whitefly nymph-infested leaves, even when the nymphs were no longer present, indicating again that palatability may have declined in response to whitefly feeding. Furthermore, whitefly fecundity decreased on leaves in the presence of spidermites compared

TABLE 2. MEAN DURATION OF FEEDING, LABIAL TAPPING AND OVIPOSITION BY *BEMISIA TABACI* ( $M \pm SE$ ) ON FOUR KINDS OF COWPEA LEAVES. MEAN DURATIONS OF FEEDING OF WHITEFLY WERE ANALYZED USING ANOVA. MEAN DURATIONS OF LABIAL TAPPING, OVIPOSITION AND FECUNDITY OF WHITEFLY ON THREE TREATMENTS WITH NON-ZERO MEANS WERE CALCULATED USING ANOVA AND THEN TESTED FOR DIFFERENCES BETWEEN ZERO AND ALL THE OTHER VALUES USING THE *T*-TEST ( $P < 0.01$ ). VALUES WITHIN A ROW FOLLOWED BY THE SAME LETTER ARE NOT SIGNIFICANTLY DIFFERENT FROM EACH OTHER (TUKEY'S TEST,  $P < 0.05$ ).

	Mite-free	Mite nymph-infested	Mite nymph-infested leaves with webbing	Adult mite-infested
Feeding (s)	129 ± 14 a	167 ± 21 a	214 ± 46 a	166 ± 11 a
Labial tapping (s)	2 ± 0 b	25 ± 5 a	0** <sup>1</sup>	20 ± 3 a
Oviposition (s)	13 ± 1 a	14 ± 2 a	0** <sup>2</sup>	16 ± 0 a
Fecundity (eggs)	2.8 ± 0.9 a	1.1 ± 0.3 b	0** <sup>3</sup>	2.1 ± 0.9 a

<sup>1</sup>Highly significant differences compared to mite-free leaves ( $t_{58} = 4.27$ ,  $P < 0.0001$ ).

<sup>2</sup>Highly significant difference compared to mite-free leaves, mite nymph-infested leaves and mite adult-infested leaves ( $t_{58} = 8.74$ ,  $P < 0.0001$ ;  $t_{58} = 2.43$ ,  $P = 0.018$ ;  $t_{58} = 5.03$ ,  $P < 0.0001$ ).

<sup>3</sup>Highly significant difference compared to mite nymph-infested leaves ( $t_{58} = 6.59$ ,  $P < 0.0001$ ).

with uninfested leaves. Changes in nutrient content and increases in allelochemical concentrations in plant host quality can affect survival, reproduction, behavior, and population dynamics of co-occurring or later arriving herbivores (Gianoli 2000; Wise & Weinberg 2002; Ferrenberg & Denno 2003; Hunt-Joshi & Blossey 2005; Lynch et al. 2006). We propose that reduced whitefly oviposition on spidermite-treated leaves may have been a result of perceived and/or actually reduced host quality.

Spidermite webbing may play an important role in competition with other herbivores. Morimoto et al. (2006) reported that competition between different spidermite species was partly mediated by webbing. All whitefly behaviors we observed were significantly affected by nymphs + webbing compared to nymphs alone (Figs. 2 and 3). Feeding duration and frequency were decreased, while grooming duration was increased and frequency decreased. Walking increased in duration and frequency, resting in duration, while labial tapping and oviposition ceased entirely. All these whitefly responses to webbing could be considered deleterious. In addition, we have observed increased mortality of whitefly nymphs and adults in the presence of spidermite webbing (unpublished data). Therefore, the presence of spidermite webbing may negatively affect whitefly fitness. Further detailed work is required to determine whether this also occurs in the field.

Asymmetry is a common characteristic of interspecific competition among herbivores (Hunt-Joshi & Blossey 2005; Lynch et al. 2006; Kaplan & Denno 2007). In this case, it appears that spidermites had greater influence on whitefly behavior than *vice versa*. On the one hand, feeding duration decreased, labial tapping duration and frequency increased and fecundity decreased on all three kinds of mite-treated leaves, compared to untreated leaves. On the other hand, while duration and frequency of cheliceral tapping by spidermites increased on whitefly infested leaves, no effect on feeding duration and frequency was observed. This asymmetry may relate to the tissues fed on by two herbivores. Whiteflies feed on phloem sap without causing visible damage to cowpea leaves. Spidermites remove the contents of parenchyma cells, leaving light-colored stippling on the leaf surface (Tomczyk & Kropczyńska 1985) that may not be acceptable to whitefly adults for feeding.

While whitefly feeding does not produce visible damage, the plant response, especially to nymphs, is similar to the response to pathogens, in that high levels of defensive proteins are induced, which may play defensive roles against other insect feeders (Inbar et al. 1999a, b; Mayer et al. 2002). Whether spidermite feeding induces similar plant defenses is unknown. Karban & English-Loeb (1988) indicated that *Tetranychus urticae* Koch can induce chemical changes in host plants

TABLE 3. MEAN DURATION OF FEEDING AND CHELICERAL TAPPING BY *TETRANYCHUS TRUNCATU* ( $M \pm SE$ ) ON FOUR KINDS OF COWPEA LEAVES. VALUES WITHIN A ROW FOLLOWED BY THE SAME LETTER ARE NOT SIGNIFICANTLY DIFFERENT FROM EACH OTHER (TUKEY'S TEST,  $P < 0.05$ ).

	Whitefly-free	Whitefly nymph-infested	Whitefly nymph-infested Leaves with nymphs	Whitefly adult-infested
Feeding (s)	21139 a	16720 ab	15729 b	17131 ab
Cheliceral tapping (s)	31 b	81 a	92 a	10 c



that affect later attackers. Agrawal et al. (2000) found that resistance induced by the spidermite *Tetranychus turkestanii* Ugarov and Nikolskii feeding in cotton seedlings reduced whitefly densities. However, the reciprocal effects of whiteflies on mites were not tested. We conclude that both herbivores have their own specific biological characteristics, contributing to their predominance in competition. The outcome of interspecific competition between *B. tabaci* and *T. truncatus* may depend on the host plant, the mode of feeding of the competitor, population density, and the timing of interactions (Inbar et al. 1999a).

The presence of spidermite adults influenced whitefly oviposition behavior. Whiteflies spent more time on oviposition but laid fewer eggs on spidermite-infested leaves compared to clean leaves. We observed that spidermites disturbed oviposition of whiteflies through direct contact while wandering the leaf surface. Limited space in our bioassay arena may have intensified direct contact. The effect of these interactions in the field requires further investigation.

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