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RESEARCH

An Evaluation of *Frankliniella occidentalis* (Thysanoptera: Thripidae) and *Frankliniella intonsa* (Thysanoptera: Thripidae) Performance on Different Plant Leaves Based on Life History Characteristics

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ABSTRACT. To compare the performance of *Frankliniella occidentalis* (Pergande) and native *Frankliniella intonsa* (Trybom) on cucumber and tomato leaves in laboratory, life history characters were investigated, and life tables were constructed using the method of agestage, two-sex table life. Compared with tomato leaf, there were shorter total preoviposition period (TPOP), higher fecundity, longer female longevity, and higher intrinsic rate of increase (r) of both F. occidentalis and F. intonsa on cucumber leaf. Meanwhile, on cucumber leaf, the shorter TPOP, higher fecundity, longer female longevity, and higher value of r were found on population of F. intonsa but on tomato leaf which were found on population of F. occidentalis. From above, cucumber leaf was the preference to population development of both F. occidentalis and F. intonsa compared with tomato leaf. Nevertheless, on cucumber leaf, population of F. intonsa would grow faster than that of F. occidentalis, which was the opposite on tomato leaf. As to the population development in fields, much more factors would be taken into account, such as pollen, insecticide resistance, and effects of natural enemies etc.

Key Words: Frankliniella occidentalis, Frankliniella intonsa, cucumber leaf, tomato leaf, life history

The western flower thrips, *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae), was first described in California in 1895, and since the 1970s, it had invaded much of the world and became dominant population in most of the areas where it had been introduced (Kirk and Terry 2003, Morse and Hoddle 2006).

F. occidentalis has a wide host-plant range including more than 250 species of vegetables and ornamental crops (Zhi et al. 2005). Even though F. occidentalis is prevalent in flowers (Salguero Navas et al. 1991a, Riley and Batal 1998), it can also be found on crop foliage (Todd et al. 1995, Joost and Riley 2004) and fruit (Salguero Navas et al. 1991b), which reduce photosynthetic capacity (Shipp et al. 2000) and cause fruit surface dimpling. F. occidentalis also transmitted plant virus, such as tomato spotted wilt virus (TSWV), impatiens necrotic spot virus (INSV), chrysanthemum stem necrosis virus (CSNV), groundnut ring spot virus (GRSV), and tomato chlorotic spot virus (TCSV) (Riley et al. 2011). Meanwhile, F. occidentalis is considered to be the predominant vector of TSWV worldwide (Peters et al. 1996, Sherwood et al. 2000), a serious virus for wide range of crop and noncrop hosts and causes billions economic losses worldwide (Prins and Goldbach 1998, Riley et al. 2011).

In China, *F. occidentalis* was first found in 2003 in Beijing (Zhang et al. 2007) and then has caused serious damage in several provinces (Lu et al. 2011). In some area, *F. occidentalis* occurred with native *Frankliniella intonsa*, the predominant thrips population in horticultural ecosystems (Gai et al. 2011). *F. occidentalis* has replaced *Thrips tabaci* as the dominant species in European greenhouses (van Rijn et al. 1995) and has also been implicated in the displacement of *F. intonsa* in Turkey (Atakan and Uygur 2005) and the displacement of *Frankliniella gemina* (Bagnall) in Argentina (de Borbon et al. 2006). However, *F. occidentalis* has failed to replace of *Frankliniella tritici* (Fitch) as the dominant species in the eastern United States (Salguero Navas et al. 1991a, Reitz 2002, Reitz et al. 2003, Paini et al. 2007, Northfield et al. 2008) and in central and southern Florida where

Frankliniella bispinosa (Morgan) dominates (Childers et al. 1990, Hansen et al. 2003, Frantz and Mellinger 2009).

Life history characteristics were the important factors leading an organism being a successful invader (Morse and Hoddle 2006). In this study, we investigated the life-history characteristics of *F. occidentalis* and native *F. intonsa* on cucumber and tomato leaves, which are the important vegetables in greenhouse around year and was to evaluate the population growth of these two thrips species and the invasion ability of *F. occidentalis*.

Materials and Methods

Insects and Plants. Population of F. occidentalis was originated collected from melon Cucumis melo L. in a greenhouse at the Institute of Vegetables and Flowers, Chinese Academy of Agricultural Sciences, in Beijing 2007, then was mass reared with fresh bean pods in the climate room with $27 \pm 1^{\circ}\mathrm{C}$ and $16\,\mathrm{h}$ light photoperiod. Population of F. intonsa was collected from the vegetable flowers in Hangzhou suburb field and then was mass reared in laboratory as the method of F. occidentalis in another climate room.

Commercial cucumber (*Cucumis sativus* (L.), zhexiu203) and tomato (*Lycopersicon esculintum* (Mill.), hezuo903) were planted in greenhouse with regular management of fertilizer and water, and no pesticides were applied. Fresh leaves were collected for experiments.

Development and Juvenile Survival. Cohorts of eggs were obtained by allowing about 300 female adults to oviposit on leaves of cucumber and tomato for 8 h. Then, each leaf was transferred into one plastic Petri dish (40 by 15 mm) covered with Parafilm (Bemis Company INC, Neenah, WI) membrane to prevent larvae from escaping, the leaf was observed with 12 h interval until eggs hatched. Once the newly hatched larvae emerged, they were individually transferred into the new plastic Petri dish with new leaf disk (1-cm diameter). As eggs are laid inside the leaf tissue and not visible, the duration of the egg stage was recorded from eggs laid to larvae emerged.

The juveniles of both thrips were observed every day until died or matured, and the leaf disks were changed daily to keep the fresh diet for larvae. Juvenile stages of two thrips were divided as first-instar larva, second-instar larva, prepupa, and pupa. The morphology of second instar was determined from the individual size, and the molted skin of the first instar, prepupa was determined with their short wing sheaths and erect antennae, and pupa has long wing sheaths almost reaching the end of the abdomen with the antennae is bent backwards along the head. The experiment was conducted in the growth chambers with $27 \pm 1^{\circ}$ C, 16 h light photoperiod, and $65 \pm 5\%$ relative humidity (RH).

Oviposition and Adult Survival. Newly emerged female and male adults were paired in glass bottles (30 by 40 mm), and one leaf disk was offered to every couple daily. The replaced disc was individually transferred into the new Petri dish for another 5 d cultivation until all eggs hatched, and the spawned larva were counted as the daily offspring of each female adult because of the difficulty to detecting eggs in plant tissue. If any individual died earlier than its mate, a replacement would be supplied from the mass rearing colony, and the data of these recruited individuals were excluded from analysis.

Life Tables. The raw data were analyzed based on the theory of the age-stage, two-sex life table (Chi and Liu 1985, Chi 1988). The mean of the development periods for each development stage, the longevity for adult female and male, the adult preoviposition period (APOP), the total preoviposition period (TPOP), and the female fecundity of F. occidentalis and F. intonsa were calculated. The age-specific survival rate (L_x) and the age-specific fecundity (M_x) were calculated from the daily records of the survival and fecundity of all individuals in the cohort. The intrinsic rate of increase (r) was estimated by using the iterative bisection method from the Euler-Lotka formula: with age indexed from 0.

$$\sum_{x=0}^{\infty} e^{-r(x+1)} L_x M_x = 1 \tag{1}$$

The finite rate λ is calculated as $\lambda = e^r$. The net reproductive rate is the total offspring that an individual can produce during its life time. The mean generation time (T) is defined as the time that a population needs to increase by a factor of R as the stable age-stage distribution and the stable increase rate (i.e., r and λ) are reached. The formula for R_0 and T is as follows:

$$R_0 = \sum_{x=0}^{\infty} L_x M_x$$

$$T = \frac{\ln R_0}{r}$$
(3)

$$T = \frac{\ln R_0}{r} \tag{3}$$

The gross reproductive rate (GRR) was calculated as GRR = $\sum M_x$. An analysis of the raw data and an estimation of the life table parameters were performed with a user-friendly computer program, TWOSEX-MSChart (Chi 2009). This program is available at http:// 140.120.197.173/Ecology/Download/Twosex-MSChart.zip.

Statistical Analysis. One-way analysis of variance and Student's t-test (SAS Institute 2005) were used to test for significant difference in development times of each stages, APOP, TPOP, adult longevity, fecundity, and population life-table parameters including the intrinsic rate of increase (r), the net reproduction (R_0) , the finite rate (λ) , the mean generation time (T), and the GRR were compared with bootstrap technique (Huang and Chi 2012).

Results

Development and Juvenile Survival. The immature stages period of two thrips on different plant leaves were stated in Table 1. On cucumber leaf, total development time from egg to adult of F. occidentalis was longer than that of F. intonsa, and the development time was about 5 d longer in F. occidentalis compared with F. intonsa, the longer immature

Table 1. Mean (\pm SE) preadult stages (d) of *F. occidentalis* and F. intonsa on different plant leaves

Stages		Cucumber	Tomato	t	df	P	
Egg	F. occidentalis	$\textbf{3.37} \pm \textbf{0.07}$	4.10 ± 0.05	8.80	130.0	0.0000	
	F. intonsa	3.19 ± 0.05	3.06 ± 0.04	1.97	134.0	0.0572	
	t	2.12	17.17				
	df	145	119				
	P	0.0349	0.0000				
First instar	F. occidentalis	1.00 ± 0.00	1.17 ± 0.05	3.09	130.0	0.0008	
	F. intonsa	1.03 ± 0.02	1.19 ± 0.05	3.08	134.0	0.0013	
	t	1.42	0.32				
	df	145	119				
	P	0.1594	0.7474				
Second instar	F. occidentalis	6.34 ± 0.26	5.02 ± 0.09	4.78	123.0	0.0000	
	F. intonsa	2.53 ± 0.07	6.64 ± 0.22	18.11	130.0	0.0000	
	t	14.19	6.86				
	df	143	110				
	P	0.0000	0.0000				
Prepupa	F. occidentalis	1.06 ± 0.03	1.04 ± 0.03	0.47	122.0	0.6593	
	F. intonsa	1.05 ± 0.03	1.11 ± 0.04	1.10	127.0	0.2511	
	t	0.07	1.45				
	df	131	89				
	P	0.9432	0.1520				
Pupa	F. occidentalis	2.16 ± 0.07	2.35 ± 0.08	1.76	116.0	0.0818	
	F. intonsa	1.11 ± 0.04	1.78 ± 0.06	9.22	126.0	0.0000	
	t	13.51	5.55				
	df	139	103				
	P	0	0				
Egg to adult	F. occidentalis	14.54 ± 0.29	14.38 ± 0.17	0.28	116.0	0.7961	
	F. intonsa	9.77 ± 0.08	14.47 ± 0.26	17.87	126.0	0.0000	
	t	16.0918	0.2401				
	df	139	103				
	P	0.0000	0.8131				

P < 0.05 for a significant difference and P < 0.01 for a highly significant difference.

development time was caused by the longer egg period, second-instar period, and pupa period. On tomato leaf, the development time from egg to adult of two thrips was not significant different, though the longer egg period but the shorter second-instar period of *F. occidentalis*.

As for F. occidentalis, there was no difference on the total development time from egg to adult between cucumber leaf and tomato leaf, though the shorter period of egg and first instar, but longer period of second instar in cucumber leaf. For F. intonsa, the development time from egg to adult is shorter on cucumber leaf than that on tomato leaf, which was caused by the shorter first instar, second instar, and pupa period on cucumber leaves (Table 1).

Because the eggs invisibly developed in the tissues of plants, the survival rate of preadult of two thrips was recorded only from the newly hatched larvae to the emergence of adult, and they were 86.4% and 91.8% on tomato and cucumber plants, respectively, for F. occidentalis and were 87.1% and 100% for F. intonsa.

Adult Longevity and Reproduction. In cucumber, the female longevity of F. intonsa was about 2.5 d longer than that of F. occidentalis. meanwhile, the time of the APOP and the TPOP of F. intonsa were shorter than that of F. occidentalis, and the time of TPOP was about 6 d shorter in F. intonsa. Although there was no significant difference, the fecundity per F. intonsa was more than that per F. occidentalis in all their life time. In tomato, there were all not significant different in adult longevity, APOP and TPOP, but the fecundity per F. occidentalis was more than that of *F. intonsa*.

For different plant leaves, adult longevity of F. occidentalis and F. intonsa and male longevity of F. intonsa were longer in cucumber leaf than in tomato leaf. APOP of F. occidentalis and F. intonsa and TPOP of F. intonsa were all shorter in cucumber leaf than in tomato leaf. Moreover, the fecundity of F. occidentalis and F. intonsa were both more in cucumber leaf than in tomato leaf, which was high to 17 times of F. intonsa (Table 2).

The age-specific survival rate (L_x) is the probability that an egg will survive to age x. The pattern of L_x curves of F. occidentalis and F. intonsa were similar on cucumber and tomato leaves, they began to sharply declined at 10 d (F. intonsa in cucumber leaf) or 15 d (F. occidentalis and F. intonsa in tomato leaf and F. occidentalis in cucumber leaf) from the age 0 of egg stage, the decline time was relative to the immature stage period of two thrips on two plant leaves. The area of L_x curves surround from time of adult emergence of F. intonsa in cucumber leaf was larger of F. occidentalis and was larger of F. occidentalis in tomato leaf. These mean the longer female longevity of F. intonsa in cucumber leaf and F. occidentalis in tomato leaf.

The age-specific fecundity (M_x) was the number of offspring by one female every day. From M_x curves, it was shown that the time began to

Table 2. Longevity and fecundity of F. occidentalis and F. intonsa adults on different plant leaves

		Cucumber	Tomato	t	df	P
Longevity						
Female	F. occidentalis	14.82 ± 0.89	11.33 ± 1.04	2.56	94	0.0122
	F. intonsa	17.30 ± 0.74	8.87 ± 0.90	7.25	91	0.0000
	t	2.13	1.78			
	df	108	77			
	P	0.0355	0.0784			
Male	F. occidentalis	10.18 ± 1.43	6.91 ± 1.06	1.84	20	0.0801
	F. intonsa	12.65 ± 1.41	5.33 ± 0.57	4.80	33	0.0002
	t	1.13	1.40			
	df	29	24			
	P	0.2678	0.1735			
APOP ^a	F. occidentalis	2.11 ± 0.14	3.04 ± 0.30	2.79	78	0.0002
	F. intonsa	0.72 ± 0.09	4.60 ± 0.73	5.29	72	0.0000
	t	8.19	1.98			
	df	108	42			
h	P	0.0000	0.0416			
TPOP ^b	F. occidentalis	15.98 ± 0.32	16.88 ± 0.35	1.65	78	0.1038
	F. intonsa	9.67 ± 0.12	18.15 ± 0.75	11.14	72	0.0000
	t	18.31	1.54			
	df	108	42			
- 11.	P	0.00	0.1111			
Fecundity	F. occidentalis	27.45 ± 3.05	15.15 ± 3.33	2.69	94	0.0086
	F. intonsa	34.76 ± 2.78	2.23 ± 0.74	11.29	91	0.0000
	t	1.77	3.79			
	df	108	77			
	P	0.0802	0.0040			

^aAPOP, time between adult emergence and first oviposition.

oviposit of two thrips were earlier on cucumber leaf than on tomato leaf, and the M_x values of both thrips were higher on cucumber leaf than that on tomato leaf, especially the peak value was 4.7 and the average value was 1.4 in F. intonsa on cucumber leaf but were 1.1 and 0.4 on tomato leaf. On the other hand, the M_x values of F. occidentalis were higher all over the female life time than that of F. intonsa on tomato, and the reproduction period was 5 d longer in F. occidentalis females, on cucumber leaf; however, the M_x values were higher in F. intonsa and the time began to oviposition of F. intonsa was 5 d earlier than on tomato leaf (Fig. 1).

Life Table Parameters. Life table parameters of F. occidentalis and F. intonsa on different plants were listed in Table 3. Intrinsic rate of increase (r), net reproductive rate (R_0) , finite rate of increase (λ) , and GRR of F. occidentalis and F. intonsa were significant higher on cucumber leaf than on tomato leaf, but the generation time (T) was the opposite. The more obvious difference was on the values of r, R_0 , and GRR of F. intonsa between two plant leaves, e.g., they were 0.21, 25.35, and 44.33, respectively, on cucumber leaf but only 0.01, 1.42, and 6.35 on tomato leaf. As to different thrips, there were higher r, R_0 , λ , and GRR values and lower T value of F. intonsa than that of F. occidentalis on cucumber leaf, but it was the opposite on tomato leaf, especially on the r, R_0 , and GRR, which were 0.10, 10.28, and 27.78 of F. occidentalis but only 0.01, 1.42, and 6.35 of F. intonsa as mentioned above.

Discussion

Performance of insect (including development, longevity, and oviposition) depends on the quality of food ($Br\Phi dsgaard$ 1987, Brodbeck et al. 2002). The faster developmental rates and the higher fecundity of insects indicate a better suitability of a host plant (van Lenteren and Noldus 1990). Life history characteristics of *F. occidentalis* and *F. intonsa* were investigated on cucumber and tomato leaves.

Immature duration of *F. occidentalis* was similar on cucumber and tomato leaves, which were 14.53 and 14.38, respectively. Soria and Mollema (1995) reported the duration from egg to adult of *F. occidentalis* ranged from 12.6 to 17.8 d on susceptible and resistant cucumber genotypes, the result 14.53 in this study was within the range above,

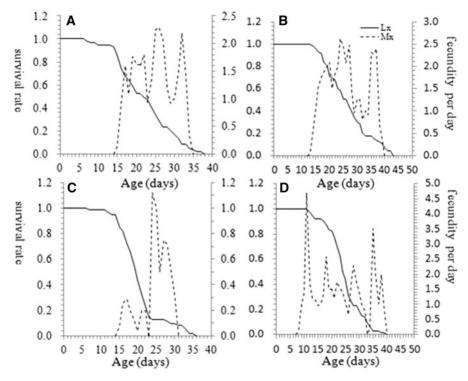


Fig. 1. Age-specific survival rate (L_x) and age-specific fecundity (M_x) of F. occidentalis (A) and F. intonsa (B) in tomato leaf and in cucumber leaf (F. occidentalis (C) and F. intonsa (D)).

^bTPOP, time from birth to first reproduction in female.

Table 3. Life table parameters (mean \pm SE) of *F. occidentalis* and *F. intonsa* on different plants leaves

Parameter		Cucumber	Tomato	t	df	P
r	F. occidentalis F. intonsa t df P	0.14 ± 0.00 0.21 ± 0.00 247.62 145 0.0000	0.10 ± 0.00 0.01 ± 0.00 142.43 119 0.0000	91.49 347.03	130 134	0.0000 0.0000
R ₀	F. occidentalis F. intonsa t df P	21.23 ± 0.09 25.35 ± 0.08 33.03 145 0.0000	10.28 ± 0.08 1.42 ± 0.02 111.62 119 0.0000	93.40 279.10	130 134	0.0000 0.0000
λ	F. occidentalis F. intonsa t df P	1.15 ± 0.00 1.24 ± 0.00 245.86 145 0.0000	1.11 ± 0.00 1.01 ± 0.00 145.43 119 0.0000	92.62 372.43	130 134	0.0000 0.0000
GRR	F. occidentalis F. intonsa t df P	41.52 ± 0.09 44.33 ± 0.19 13.37 145 0.0000	27.78 ± 0.17 6.35 ± 0.06 118.48 119 0.0000	70.88 191.77	130 134	0.0000 0.0000
T	F. occidentalis F. intonsa t df P	21.56 ± 0.01 15.08 ± 0.01 460.9 145 0.0000	22.02 ± 0.02 22.11 ± 0.05 1.78 119 0.0765	21.77 145.51	130 134	0.0000 0.0000

and the similar duration 12.39 d was also found in F. occidentalis on cucumber leaf, but the shorter duration 9.22 d was found by Zhang et al. (2007), the difference may caused by the cucumber genotypes. The result 14.38 d on tomato leaf was the similar as 12.91 d on tomato leaf on Zhang et al. (2007). For F. intonsa while, the immature duration was shorter on cucumber than on tomato and the difference was caused by the duration of the second instar. The duration of the second instar was the most vulnerable by different plants, it was found that the second instar duration ranged from 4.3 to 9.1 d according the resistance of cucumber genotypes and which also resulted in prolonged developmental period of F. occidentalis on the resistant genotypes (Soria and Mollema 1995). Moreover, the duration of preadult of F. intonsa was shorter than that of F. occidentalis on cucumber leaf in this study, which also was mainly caused by the duration of the second instar. For immature development, the cucumber leaf and tomato leaf were similar suitable to F. occidentalis and F. intonsa with similar duration from egg to adult.

Higher fecundity, longer female longevity, shorter APOP, and TPOP were found on cucumber leaf compared with tomato leaf, this means that cucumber leaf was more suitable for reproduction of F. occidentalis and F. intonsa, on cucumber leaf, it is also reported that cucumber leaf was more suitable for reproduction of F. occidentalis than tomato leaf with higher fecundity and shorter APOP (Zhang et al. 2007). As to different thrips, there were different suitable of two plant leaves for them, i.e., there were higher fecundity, longer female longevity, shorter APOP, and TPOP of F. occidentalis on tomato leaf and that is the opposite on cucumber leaf, this means that compared with F. occidentalis, the population of F. intonsa would develop faster on cucumber leaf, but population of F. occidentalis would develop faster on tomato leaf. It is reported that food quality and different leaf morphology, affected the adult longevity, adult behavior during oviposition, and the rate of egg hatching (Scott Brown et al. 2002, Zhang et al. 2007), thus the performance of adult and offsprings may affected by food quality and leaf morphology of two plants.

As the intrinsic rate of increase (*r*) is a reflection of many factors, such as fecundity, survival, and generation time, it adequately summarizes the physiological qualities of an animal in relation to its capacity to increase. Therefore, it is the most appropriate index to evaluate performance of an insect on different host plants and the host plant's suitability on different herbivores (Smith 1989, Southwood and Henderson 2000, Murai 2001, Wang et al. 2011).

The r value of F. occidentalis was 0.10 on tomato, which was the same as the result of Zhang et al. (2007), on cucumber, it was 0.14 of

F. occidentalis, which was the similar to the result of the value of F. occidentalis on cucumber leaf (van Rijn et al. 1995) but was lower than the value of 0.3 in Gaum et al. (1994) and 0.21 in Zhang et al. (2007), the reason may be the different genotypes of cucumber (Soria and Mollema 1995) or the difference of experiment temperature, which was 27°C on the experiment of Gaum et al. (1994). As the results of history characteristics, on cucumber leaf, the r value of F. intonsa was higher compared with F. occidentalis and which was higher of F. occidentalis on tomato leaf. The higher intrinsic rate of increase value integrated with the higher fecundity and the shorter development period of preadult, the lower mortality, and the shorter TPOP (Jha et al. 2012).

In this study, the *r* value of *F. occidentalis* and *F. intonsa* was higher on cucumber leaves than that on tomato leaves, especially for *F. intonsa*, which is low to 0.01 on tomato leaf, this means the not suitable of tomato leaf for population development, but slowly population development would be improved in fields when added with pollens as reported in *F. occidentalis* (Gerin et al. 1999, Hulshof et al. 2003, Zhi et al. 2005).

Although the important effect of pollens on individual growth and population development of flower visiting thrips, such as *F. occidentalis* (Hulshof et al. 2003, Riley et al. 2011), plant leaves also offered sufficient nutrition when flower were scare, e.g., *F. occidentalis* caused severe damage on the seedling stages and young leaves (Olson et al. 2006), and in laboratory, the intrinsic rate of *F. occidentalis* on cucumber leaf were 0.3 in Gaum et al. (1994) and 0.21 in Zhang et al. (2007) as was 0.21 of *F. intonsa* in cucumber in this study which mean the suitability for population development of thrips. The plant leaves also be used to evaluate the performance of *F. occidentalis* on different plants and performance of *F. occidentalis* compared with other thrips such as *F. bispinosa* (Northfield et al. 2011) and *T. tabaci* (van Rijn et al. 1995) on the same plant. However, the effects of pollens on life history character should be done in the future experiments to know the comprehensive influence of plants on different thrips.

Although the important of life history characteristics on biological invasion, the pesticide resistance, host range, symbiotic virus, and other competitive mechanism also influenced successful invasion and outburst (Reitz 2009). For example, in spite of the disadvantage of history parameters compared with indigenous species T. tabaci (van Rijn et al. 1995), F. occidentalis invaded successfully into the Europe and displaced T. tabaci become the dominate species, whereas F. occidentalis appears to be competitively excluded by the native F. tritici of eastern states of the United States because of the biotic resistance (Paini et al. 2008), further, even if the inferior competitor of F. bispinosa with F. occidentalis on adult reproduction, F. bispinosa still established dominance over F. occidentalis in Florida because of climate or natural enemy (Northfield et al. 2011). The performance of F. occidentalis and F. intonsa depend on the kind of host plant, so more work about the performance of these two thrips on different important economical plants also should be done in the future, to evaluate the invasion of F. occidentalis.

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