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Interference and exploitation competition between *Frankliniella occidentalis* and *F. intonsa* (Thysanoptera: Thripidae) in laboratory assays

*Mohammad Mosharof Hossain Bhuyain[1], and Un Taek Lim[2,]**

Abstract

Recently, the native species *Frankliniella intonsa* (Trybom) (Thysanoptera: Thripidae) has been found to be regionally dominant over its invasive congener *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae) in Korea. To understand the variation in patterns of occurrence in the field, the effect of competition on the biological attributes of the 2 thrips species was assessed in the laboratory. In a behavioral study, the effect of inter- and intraspecific competition in honey or pollen feeding was observed in a glass-slide arena, and we found both reproduction and longevity to be more reduced in *F. occidentalis* than in *F. intonsa* by competition. However, the extent of feeding marks on bean leaves made by both species (in competition) was not significantly different from that made by each species separately, except in the case of the *F. intonsa* larvae. In an experiment on potted bean plants, competition caused a greater reduction in numbers of *F. occidentalis* progeny than that of *F. intonsa* progeny. In behavioral observations, guarding and feeding times of adult *F. intonsa* were 8.5 and 1.5 times longer on honey, and 42.8 and 1.3 times longer on pollen than *F. occidentalis*, respectively. However, in intraspecific competition, none of the behavioral parameters in pollen feeding showed significant differences in either species, except for the "confronting" behavior. In conclusion, both interference and exploitation competition exist between the 2 thrips species, and in laboratory studies *F. intonsa* was more persistent, not only at feeding and guarding food sources, especially in the adult stage, but also in displaying higher reproduction and longevity. These may be the underlying mechanisms for the asymmetrical pattern of occurrence of the 2 thrips in the field.

Key Words: flower thrips; food guarding; inter- and intraspecific competition; invasive species; species dominance

Resumen

Recientemente, se ha encontrado que la especie nativa, *Frankliniella intonsa* (Trybom) (Thysanoptera: Thripidae), es regionalmente dominante sobre su congénero invasor *F. occidentalis* (Pergande) (Thysanoptera: Thripidae) en Corea. Para comprender la variación en los patrones de ocurrencia en el campo, se evaluó en el laboratorio el efecto de la competencia de los atributos biológicos de las 2 especies de trips. En un estudio de comportamiento, se observó el efecto de la competencia inter e intraespecífica en la alimentación con miel o polen en una pecera de arena, y encontramos que tanto la reproducción como la longevidad se redujeron más en *F. occidentalis* que en *F. intonsa* por competencia. Sin embargo, la extensión de las marcas de alimentación en las hojas de frijol hechas por ambas especies (en competencia) no fue significativamente diferente de la que hicieron cada especie por separado, excepto en el caso de las larvas de *F. intonsa*. En un experimento con plantas de frijol en maceta, la competencia causó una reducción en los números de producción de progenie de *F. occidentalis* mayor que en la producción de progenie de *F. intonsa*. En observaciones de comportamiento, los tiempos de guarda y alimentación de *F. intonsa* en adultos fueron 8.5 y 1.5 veces más largos en miel y 42.8 y 1.3 veces más en polen que en *F. occidentalis*, respectivamente. Sin embargo, en la competencia intraespecífica, ninguno de los parámetros de comportamiento en la alimentación con polen mostró diferencias significativas en ninguna de las especies a excepción del comportamiento de "confrontación." En conclusión, tanto la competencia de interferencia como la de explotación existen entre las dos especies de trips, y en los estudios de laboratorio, *F. intonsa* fue más persistente no solo en la alimentación y la protección de las fuentes de alimentos, especialmente en el estadio del adulto, pero también mostró una mayor reproducción y longevidad. Estos pueden ser los mecanismos subyacentes para el patrón asimétrico de ocurrencia de los 2 trips en el campo.

Palabras Clave: trips de flores; custodia de alimentos; competencia inter e intraespecífica; especies invasivas; dominancia de las especies

Frankliniella occidentalis (Pergande) and *Frankliniella intonsa* (Trybom) (both Thysanoptera: Thripidae) are sympatric thrips species found on many flowering plants, making them important agricultural pests (Murai 1988; Atakan et al. 1999). Thrips damage plants directly by sucking plant cell contents, and indirectly by transmitting tospoviruses such as tomato spotted wilt virus and impatiens necrotic spot virus, causing significant economic losses worldwide (Lewis 1997). *Frankliniella occidentalis* is an invasive species in Korea, where it has spread throughout Korea since its first appearance on Jeju Island in 1993, whereas *F. intonsa* is a native species, and widely distributed in the Palearctic and part of the Oriental regions. *Frankliniella intonsa* has itself invaded both North America (Nakahara & Foottit 2007) and New Zealand (Teulon & Nielsen 2005). In Korea, no consistent pattern has been observed regarding the occurrence of these 2 thrips (Table 1).

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Table 1. The pattern of relative occurrence of *Frankliniella occidentalis* (FO) and *Frankliniella intonsa* (FI) in fields and greenhouses in Korea.

Survey dates	Relative occurrence (FO/FI)	Methods of sampling	Location	Host plant	References
14 Jul–25 Aug 2002	< 0.85 [a]	Sticky trap	Jeongeup	Pepper (field)	(Moon et al. 2006)
14 Jul–25 Aug 2002	< 0.41 [a]	Sticky trap	Geochang	Pepper (field)	(Moon et al. 2006)
30 Apr–13 May 2007	< 2.6 [a]	Sticky trap	Andong	Strawberry (greenhouse)	(Mainali & Lim 2008)
12 May 2007	2.0 [a]	Sticky trap	Andong	Strawberry (greenhouse)	(Mainali & Lim 2010)
16 May–6 Jun 2008	0.01 (6/521) [b]	Direct flower collection	Andong	Strawberry (greenhouse)	(Lim & Mainali 2009)
16 May–6 Jun 2008	< 0.01 (3/783) [b]	Sticky trap	Andong	Strawberry (greenhouse)	(Lim & Mainali 2009)
20 Jul 2012	0.26 [a]	Sticky trap	Youngyang	Pepper (field)	(Kwon et al. 2013)
20 Jul 2012	0.34 [a]	Sticky trap	Uiseong	Pepper (field)	(Kwon et al. 2013)
12 Sep–Oct 18 2013	0.02 (10/536) [b]	Direct flower collection	Andong	Pepper (field)	Unpublished

[a]Calculated by dividing the average number of FO with the average number of FI recorded.
[b]Calculated by dividing the total number of FO with the total number of FI recorded.

However, the native *F. intonsa* has recently been found to be regionally dominant in Korea, although the invasive *F. occidentalis* is generally considered to be the more common thrips (Table 1). Our preliminary laboratory assays (unpublished) indicate that interspecific competition occurs between these 2 species.

Interspecific competition can be an important factor in determining insect population size and structure. Under interspecific competition, individuals of 1 species will suffer resource restriction due to the presence of individuals from the other species. Interspecific competition is often highly asymmetrical, with the consequences differing between the 2 species. Interspecific competition also can be a factor determining geographic ranges of thrips (van Rijn et al. 1995; Kirk & Terry 2003; Deligeorgidis et al. 2006). In European greenhouses, *F. occidentalis* replaced *Thrips tabaci* Lindeman (Thysanoptera: Thripidae), but van Rijn et al. (1995) suggested that *F. occidentalis* is the superior competitor, because they could find no differences in other potential explanations, including the intrinsic rate of increase, net reproductive time, or development time. In contrast to outcomes in European greenhouses, *F. occidentalis* has failed to establish as the dominant species in the eastern US, despite repeated accidental introductions (Kirk & Terry 2003). Paini et al. (2008) demonstrated that *F. occidentalis* larvae are competitively inferior to the congeneric *Frankliniella tritici* (Fitch) (Thysanoptera: Thripidae), a species endemic to most of the eastern US. The authors speculated that interspecific larval competition between *F. occidentalis* and *F. tritici* possibly contributes to the biotic resistance limiting the spread of *F. occidentalis* in the eastern US. Therefore, interspecific competition is an important factor that should be considered when assessing any invasive species' spread and success, but there is no information available on the competition between *F. occidentalis* and *F. intonsa*. In this study, we conducted both biological and behavioral studies to explain the different pattern of occurrence in the field between these 2 anthophilous thrips in recent yr.

Materials and Methods

INSECT REARING

Collections of *F. occidentalis* and *F. intonsa* were made from a strawberry greenhouse in 2012, in Songcheon, Andong, South Korea, and thrips were reared in plastic containers (24 cm L × 17 cm W × 8 cm H) containing 8 excised, rooted (on water-soaked cotton) red kidney bean (*Phaseolus vulgaris* L.; Fabaceae) stems with cotyledonous leaves. A mixture of pure honey and pine pollen was streaked along the principal vein of each leaf using a fine brush. For ventilation, two 6 cm diam holes were cut in the lid of each container, and the holes were covered with thrips-proof fabric (196 mesh count, Saatilene Hi-tech, Zurich Co., Como, Italy). The containers were kept at 24 °C and 16:8 h (L: D) photoperiod in a growth chamber, and water was added when needed. To initiate new generations, 30 newly emerged adult thrips were transferred to a new plastic container with the same food sources as needed.

EFFECT OF INTERSPECIFIC COMPETITION ON REPRODUCTION

Unmated adult females (< 24 h old) were used for this experiment. A leaf cage arena was constructed of cotton with a 0.7 cm diam hole attached to a red kidney bean leaf. The cotton with the hole was covered with thrips-proof fabric. A mixture of honey and pollen was provided inside the arenas, inside of which we placed either 1 individual of 1 of the 2 thrips or a single pair of thrips, with 1 individual of each species. Thrips were kept in the leaf cages for 24 h at 28 °C in an incubator, after which adults were removed. The leaf arena exposed to thrips was detached, placed on water-soaked cotton, and examined daily for larval hatch and adult emergence.

EFFECT OF INTERSPECIFIC COMPETITION ON LONGEVITY

We assessed the effect of competition on adult longevity using Eppendorf tubes (2 mL) as an experimental arena. In these tubes, we placed either a single 1-d-old individual of 1 of 2 species or 1 pair (1 female of each species). A 4 mm diam hole was made in the cap, then covered with thrips-proof fabric. As a food source, we placed a fresh leaf disc (5 mm L × 2 mm W) of red kidney bean on water-soaked cotton, and a drop of mixed honey and pollen on the inside the tube. Leaf discs were changed daily. Each treatment was replicated 10 times. The experiment was conducted inside a growth chamber at 30 °C, 70–75% RH, and a 16:8 h (L:D) photoperiod, and data were recorded daily until all adults died.

EFFECT OF INTERSPECIFIC COMPETITION ON EXTENT OF LEAF FEEDING

Female adults (< 24 h old) and second instar larvae (48 h old after molt from the first instar) were used to measure feeding activity on kidney bean leaves in a leaf-cage arena. For both life stages (adults or larvae), 1 individual of 1 of the 2 species or a pair of thrips (1 individual each from the 2 species) were kept in an arena, which was made of a cotton pad with a 5 mm diam hole space placed over the bean leaf. A piece of thrips-proof fabric was attached to the arena using a clip to fix the cotton ring to the leaf, and the arena was kept at 24 °C in an incubator after adding sufficient water to the bean plant to keep the plant fresh during the experimental period. Adults were removed after 24 h,

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and feeding marks on the leaf were photographed under a dissecting microscope (10×) with a digital camera (DS-Fi 1, Nikon Corporation, Kanagawa, Japan). Sigma Scan Pro (SPSS Science, Chicago, Illinois, USA) was then used to measure the area of leaf with thrips damage.

DEMONSTRATION OF INTERSPECIFIC COMPETITION ON POTTED BEAN PLANTS

Interspecific competition between *F. occidentalis* and *F. intonsa* on whole plants was demonstrated using a cylindrical cage (30 cm H × 16 cm D), with 1 end covered by thrips-proof fabric, that covered a potted red kidney bean plant with 2 cotyledonous leaves. Ten females and 5 males (all 5–7 d old) of either 1 or both of the test species were released into test cages, which were then held at 28 °C in an incubator. The 3 treatments, each with 10 replicates, included in the experiment were (i) *F. occidentalis* only, (ii) *F. intonsa* only, and (iii) *F. occidentalis* and *F. intonsa* together. Data were first recorded from 14 d after treatments and continued up to 7 d. For easier collection, each plant was placed under a fluorescent light, causing thrips to aggregate at the top of the cylinder, where they were collected using an aspirator into a centrifuge tube (about 50 mL). Species and sex were identified under the dissecting microscope. Mean generation time was calculated as the date of introduction of thrips to the cylindrical cage until the date of adult emergence in the next generation.

BEHAVIORAL OBSERVATIONS ON INTERSPECIFIC ADULT COMPETITION

For this experiment, we used an experimental arena formed by 2 microscope glass slides sandwiched together (Lim et al. 2001), after inserting a flattened piece of cotton (1.5 cm L × 1.5 cm W × 0.2 cm H) with an internal hole (5 mm diam) between the 2 slides as a spacer. A droplet of honey or a lump of powdered pine pollen were placed in the center of the arena as a food source. Unmated, unfed females of *F. occidentalis* and *F. intonsa* (< 1 d old) were paired in an arena, and replicated 20 times for each food source (honey or pollen). Thrips behaviors were observed for 20 min, and were classified into categories as follows: (1) confrontation (when 2 thrips face each other without any movement); (2) food guarding (when either *F. occidentalis* or *F. intonsa* remain very close to food, sometimes feeding and sometimes quiescent); (3) feeding (when an individual stood still with its forelegs apart, antennae still, usually nodding its head up and down, and probing with its mandible); (4) wandering (random movement); and (5) resting (no movement of any body parts). Data were recorded either as number of events observed (for confrontation) or number of s when the thrips were engaged in a particular behavior (all other behaviors).

BEHAVIORAL OBSERVATIONS ON INTERSPECIFIC IMMATURE COMPETITION

The same procedures and treatments were used to observe the behavior of second instar larvae (< 48 h old after molting from the first instar) of the 2 species of thrips. Each arena contained 2 individuals, i.e., 1 of each test species. There were 30 and 20 replications for honey and pollen as a food source, respectively. Behavioral parameters, including confrontation, food guarding, feeding, wandering, and resting also were measured as mentioned above.

BEHAVIORAL OBSERVATIONS ON INTRASPECIFIC ADULT COMPETITION

The same procedures as above were used to observe intraspecific behavioral parameters to assess the effects within each thrips species of intraspecies competition of adults. A total of 10 and 15 pairs of individuals were observed for *F. occidentalis* and *F. intonsa*, respectively, when honey was provided as a food source, whereas 20 pairs of individual *F. occidentalis* or *F. intonsa* were replicated on pollen. Behavioral parameters, including confrontation, food guarding, feeding, wandering, and resting also were measured as mentioned above. The value of each individual in each parameter in each species was averaged and used for further analysis.

STATISTICAL ANALYSIS

All data analyses were performed in SPSS (SPSS Inc., Chicago, Illinois, USA). Before analysis, all data sets were tested for normality using a Kolmogorov-Smirnov test ($P < 0.05$), and a Levene test was applied to test the data for homogeneity of variance using SPSS version 22. A nonparametric 2-way ANOVA was used according to Scheirer et al. (1976) if data did not meet the assumptions of parametric ANOVA and could not be adequately transformed. Pairwise comparisons were performed using the nonparametric Mann-Whitney *U* test ($P < 0.05$).

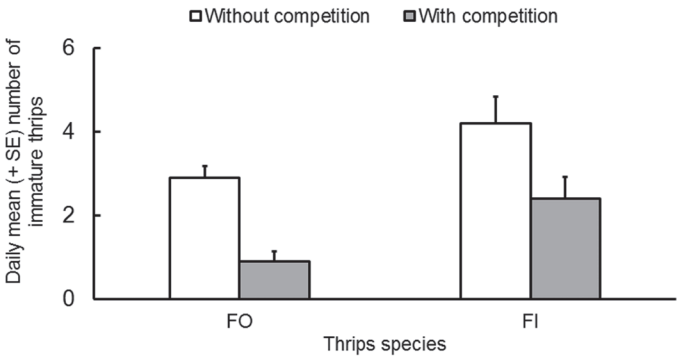
Results

EFFECTS OF INTERSPECIFIC ADULT COMPETITION ON REPRODUCTION

We found a significant difference in progeny production between the 2 species. In competition, the number of progeny were reduced by 79.0% in *F. occidentalis* and 43.0% in *F. intonsa* (species $H = 18.249$; df = 1; $P < 0.001$; competition $H = 39.649$; df = 1; $P < 0.001$; species × competition $H = 2.051$; df = 1; $P = 0.099$) (Fig. 1).

EFFECTS OF INTERSPECIFIC ADULT COMPETITION ON LONGEVITY

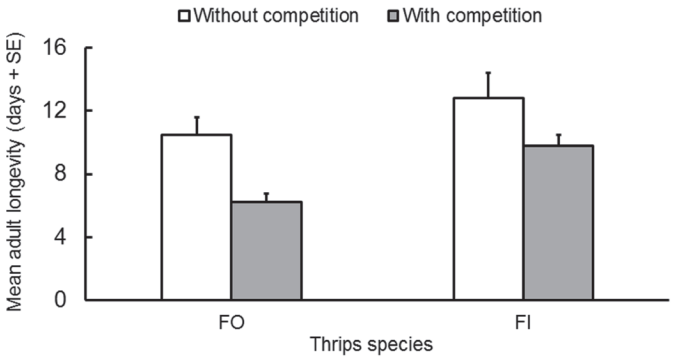
There also were significant effects of competition on adult longevity. *Frankliniella intonsa* lived 1.22 times longer than *F. occidentalis* when not in competition, but this increased to 1.58 times when in competition with *F. occidentalis*. Under competition conditions, the longevity of both species was reduced compared to when there was no competition. Longevity under competition was reduced by 41.0% and 23.0% for *F. occidentalis* and *F. intonsa*, respectively (species $H = 17.210$; df = 1; $P < 0.001$; competition $H = 29.512$; df = 1; $P < 0.001$; species × competition $H = 6.981$; df = 1; $P = 0.005$) (Fig. 2).



"Species: $P < 0.001$, Competition: $P < 0.001$, Species × Competition: $P = 0.009$"

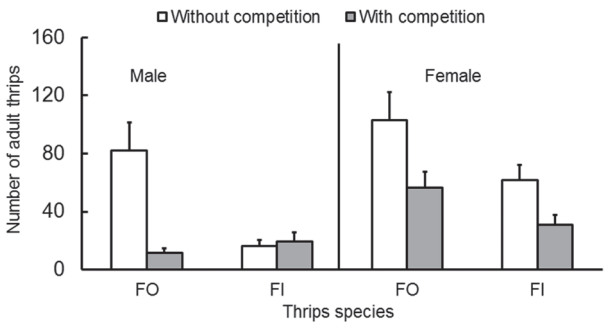
Fig. 1. Effect of competition between *Frankliniella occidentali*s (FO) and *Frankliniella intonsa* (FI) on progeny production (mean + SE) in a leaf cage (hole covered with thrips-proof fabric in 0.7 cm diam cage).

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"Species: $P < 0.001$, Competition: $P < 0.001$, Species × Competition: $P = 0.005$"

Fig. 2. Effect of competition between *Frankliniella occidentalis* (FO) and *Frankliniella intonsa* (FI) on adult longevity (mean d + SE) in a micro-tube arena (2 mL capacity).



"Male: Species: $P = 0.001$, Competition: $P < 0.001$, Species × Competition: $P < 0.001$"

"Female: Species: $P < 0.001$, Competition: $P < 0.001$, Species × Competition: $P = 1.308$"

Fig. 4. Number (mean + SE) of next generation thrips progeny produced by *Frankliniella occidentalis* (FO) or *Frankliniella intonsa* (FI) female adult under competitive conditions in a cylindrical cage arena.

EFFECTS OF INTERSPECIFIC ADULT AND IMMATURE COMPETITION ON AREA OF LEAF FEEDING

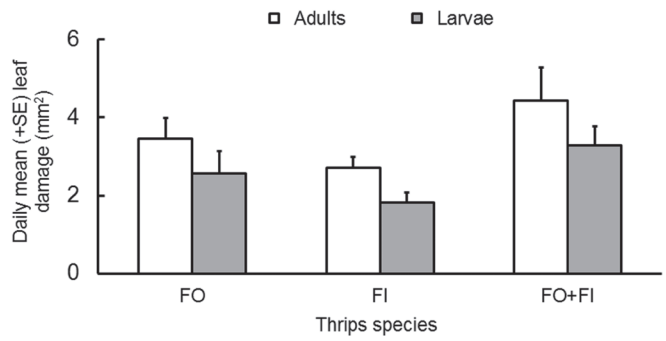
We found significant differences in the area of leaf feeding between the 2 life stages, i.e., adult and larvae, and between the interspecific competition and no-competition treatments (life stage $H = 16.400$; df = 1; $P < 0.001$; competition $H = 11.035$; df = 2; $P < 0.002$). However, no significance was found in the interaction of species and competition ($H = 1.295$; df = 2; $P = 0.262$). In both adults and larvae of the 2 thrips species, the area of feeding damage on leaves made by 1 individual of either species of *F. occidentalis* or *F. intonsa* alone (without competition) was not significantly different than that made by 2 individuals (1 each from the 2 species, in competition) as determined by post-hoc *t*-tests, except in the case of *F. intonsa* larvae (*F. occidentalis* adults $t = 0.995$; df = 18; $P = 0.333$; *F. intonsa* adults $t = 1.940$; df = 18; $P = 0.068$; *F. occidentalis* larvae $t = 0.974$; df = 18; $P = 0.343$; *F. intonsa* larvae $t = 2.671$; df = 18; $P = 0.016$) (Fig. 3). Also, when we summed the areas of feeding made by 1 individual from each species without competition, they were not significantly different from that made by 2 individuals (1 each from the 2 species) in competition (adults $t = 1.607$; df = 18; $P = 0.126$; larvae $t = 1.306$; df = 18; $P = 0.208$ in a post-hoc *t*-test) (Fig. 3).

EFFECTS OF INTERSPECIFIC COMPETITION ON PROGENY PRODUCTION ON POTTED BEAN PLANTS

There were significant effects on progeny production in terms of both male offspring (species: $H = 9.414$; df = 1; $P = 0.001$; competition: $H = 17.488$; df = 1; $P < 0.001$; species × competition: $H = 19.240$; df = 1; $P < 0.001$) and female offspring (species: $H = 16.182$; df = 1; $P < 0.001$; competition: $H = 24.444$; df = 1; $P < 0.001$; species × competition: $H = 0.085$; df = 1; $P = 1.308$) under competition in the cylindrical cage experiment. When in a competitive environment, the number of *F. occidentalis* male progeny produced was significantly reduced (by 85.8%), whereas numbers of *F. intonsa* male progeny produced were significantly increased (by 15.9%) (Fig. 4). When under competition, female progeny numbers were significantly reduced by 45.3 and 49.9% in *F. occidentalis* and *F. intonsa*, respectively (Fig. 4). Competition had no significant effect on male generation time in either *F. occidentalis* or *F. intonsa* (species: $H = 0.074$; df = 1; $P = 1.416$; competition: $H = 0.088$; df = 1; $P = 1.288$; species × competition: $H = 0.088$; df = 1; $P = 1.288$) (Fig. 5). However, competition significantly reduced the female generation time in both *F. occidentalis* and *F. intonsa* (species: $H = 7.245$; df = 1; $P = 0.004$; competition: $H = 8.927$; df = 1; $P = 0.002$; species × competition: $H = 2.195$; df = 1; $P = 0.090$) (Fig. 5).

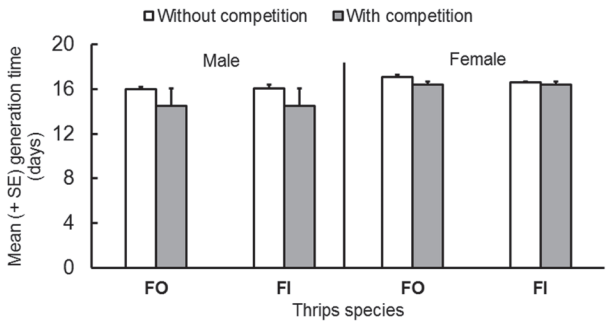
INTERSPECIFIC BEHAVIOR OF ADULT FEMALES FEEDING ON HONEY

Frankliniella occidentalis and *F. intonsa* adult females showed different feeding behavior when provided with honey as the only food source. Significant differences between the species were observed in food guarding, feeding, and wandering (Table 2). *Frankliniella intonsa* guarded the honey 8.5 times longer ($U = 128.500$; $P = 0.017$) and fed 1.5 times longer ($U = 127.000$; $P = 0.048$) than did *F. occidentalis*. Also, *F. intonsa* wandered 40.4% as much as *F. occidentalis* ($U = 107.000$; $P = 0.012$). There were no significant differences in resting behavior between the 2 species ($U = 158.500$; $P = 0.257$).



"Life stage: $P < 0.001$, Competition: $P = 0.002$, Species × Competition: $P = 0.262$"

Fig. 3. Effect of competition between *Frankliniella occidentalis* (FO) and *Frankliniella intonsa* (FI) on leaf feeding in a leaf cage.



"Male: Species: $P = 1.416$, Competition: $P = 1.288$, Species × Competition: $P = 1.288$"

"Female: Species: $P = 0.004$, Competition: $P = 0.002$, Species × Competition: $P = 0.090$"

Fig. 5. Generation time (mean d + SE) of males and females of *Frankliniella occidentalis* (FO) and *Frankliniella intonsa* (FI) reproducing in a cylindrical cage arena.

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INTERSPECIFIC BEHAVIOR OF ADULT FEMALES FEEDING ON POLLEN

There was also a significant difference in food guarding behavior when pine pollen was provided as a food source (Table 2). *Frankliniella intonsa* guarded the pollen 42.8 times longer (U = 75.500; P = 0.000) than *F. occidentalis* (Table 2). No significant difference was found between species in feeding (U = 150.500; P = 0.180) or resting time (U = 152.500; P = 0.196). *Frankliniella intonsa* wandered only 39.8% as long as *F. occidentalis* (U = 95.500; P = 0.005).

INTERSPECIFIC BEHAVIOR OF IMMATURES FEEDING ON HONEY

Food guarding, feeding, and wandering times differed significantly between immature stages of the 2 species (Table 3). *Frankliniella intonsa* guarded 14.5 times longer (U = 344.000; P = 0.012), fed on honey only 32.2% as long as *F. occidentalis* (U = 252.500; P = 0.003), and wandered 1.78 times longer (U = 234.000; P = 0.001) than *F. occidentalis*. Resting time was not different between the species (U = 368.000; P = 0.223).

INTERSPECIFIC BEHAVIOR OF IMMATURES FEEDING ON POLLEN

None of the behaviors, i.e., food guarding (U = 180.500; P = 0.311), feeding (U = 165.500; P = 0.343), wandering (U = 169.000; P = 0.402), or resting (U = 195.500; P = 0.903) were significantly different between immature stages of the 2 species when feeding on pollen (Table 3).

INTRASPECIFIC BEHAVIOR OF ADULT FEMALES FED HONEY

Frankliniella occidentalis females engaged in 2.5 times more bouts of confrontation (U = 39.500; P = 0.044) than *F. intonsa* (Table 4). *Frankliniella intonsa* guarded honey 4.7 times longer than *F. occidentalis* (U = 50.500; P = 0.047). None of the other behaviors were significantly different between females of the 2 species feeding on honey (feeding U = 70.000; P = 0.782; wandering U = 62.000; P = 0.471; resting U = 57.000; P = 0.316).

INTRASPECIFIC BEHAVIOR OF ADULT FEMALES FED POLLEN

Among females provided with pollen, none of the behaviors measured showed any significant differences between species except for bouts of confrontation. No significant differences were found for other behaviors (food guarding U = 180.000; P = 0.152; feeding U = 188.500; P = 0.756; wandering U = 162.500; P = 0.310; resting U = 159.000; P = 0.257) (Table 4). *Frankliniella occidentalis* engaged in 2.6 times more bouts of confrontation (U = 90.500; P = 0.002) than did *F. intonsa*.

Discussion

Interspecific competition refers to competition for limiting resources such as food, nutrients, space, mates, or nesting sites between 2 or more species (Begon et al. 1996). Interspecific competition often negatively affects inferior species by reducing their population and growth rates, which in turn influences the population dynamics of both the superior and inferior species (Booth & Murray 2008). The competition can be either direct interference (contest) competition or indirect exploitative (scramble) competition. In interference competition, 1 conspecific or heterospecific organism prevents other organisms from using the resource, whereas organisms use up a limited resource in exploitation competition (Nicholson 1954). Interference competition includes direct killing, aggressive displacement behavior, and the production of chemicals (deterrents and pheromones) that hinder colonization, feeding, or oviposition (Kaplan and Denno 2007). On the other hand, exploitative competition includes resource depletion with severe consequences for most or all of the competing individuals, resulting in high density-dependent mortality and reproductive failure, drastic population crashes, and unstable population dynamics (Nicholson 1954). This study confirms that both interference and exploitation competition may occur between the 2 flower thrips *F. occidentalis* and *F. intonsa*, and *F. intonsa* seems to be a superior competitor to *F. occidentalis*. Adult *F. intonsa* guarded both honey and pollen longer, and fed longer on honey than *F. occidentalis*, and this dynamic may have led to lower reproduction and longevity in *F. occidentalis* than in *F. intonsa* in leaf cage and micro-tube arena experiments, respectively. These behaviors also may be the underlying reason for the competitive dominance of *F. intonsa* under field conditions. Adult *F. intonsa* may consume more food due to its higher reproductive activity compared to *F. occidentalis*. Ullah and Lim (2015) found that *F. intonsa* produced 46% more offspring per female than did *F. occidentalis* under fluctuating temperatures. As Murai (1988) reported, pollen feeding increases the number of eggs produced by *F. intonsa*, and therefore nutrients ingested during the adult stage might affect certain life table parameters, such as fecundity. This relationship between the populations of *F. occidentalis* and *F. intonsa* could be an example of the more general situation in which populations subjected to interference competition benefit from competition with another species. Food guarding is described here for the first time in thrips, although mate guarding has been documented in phlaeothripid thrips (Mound 1991; Tsuchida & Ohguchi 1998; Morris et al. 2002; Ullah & Lim 2015).

Resource guarding has been studied extensively in different insect taxa. Social insects have a division of labor in which individuals specialize in reproduction, feeding, or guarding. Many terrestrial hemipterans exhibit maternal guarding behavior of eggs and young nymphs (Eickwort 1981). Eberhard (1975) found a pentatomid bug defending her eggs against the scelionid egg parasitoid. In dung beetles, male beetles guard dung balls while the female excavates sites for oviposition (Kanta 2013). Guarding behavior also has been observed in a female earwig, cockroaches, crickets, bugs, web spinners, and book lice (Kanta 2013).

Table 2. Interspecific behavior between *Frankliniella occidentalis* and *Frankliniella intonsa* female adults when either honey or pollen was provided as food in an experimental arena. Confronting behavior (mean ± SE) was recorded as number of confrontation bouts, but duration (mean s ± SE) was recorded for all other behaviors.

			Behavior				
Treatments	Species	n	Confronting	Food guarding	Feeding	Wandering	Resting
Honey	*F. occidentalis*	20	1.0 ± 0.2 (0.1)	3.5 ± 2.1 a (0.3)	409.4 ± 52.6 a (34.1)	541.9 ± 56.7 a (45.2)	237.7 ± 50.2 a (19.8)
	F. intonsa	20		29.7 ± 8.3 b (2.5)	594.1 ± 63.0 b (49.5)	367.9 ± 48.9 b (30.7)	199.8 ± 59.2 a (16.7)
Pollen	*F. occidentalis*	20	1.7 ± 0.2 (0.1)	2.5 ± 2.5 a (0.2)	234.5 ± 75.6 a (19.5)	825.1 ± 70.5 a (68.8)	133.1 ± 44.7 a (11.1)
	F. intonsa	20		106.9 ± 25.5 b (8.9)	311.3 ± 66.1 a (25.9)	546.5 ± 54.8 b (45.5)	229.5 ± 61.8 a (19.1)

Means for a column within a diet with the same letter were not significantly different between the 2 species (α = 0.05).
Values in the parentheses indicate the percent (%) time spent for each behavioral parameter tested.

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Table 3. Interspecific behavioral observation between *Frankliniella occidentalis* and *Frankliniella intonsa* larvae when either honey or pollen was provided as food in an experimental arena. Confronting behavior (mean ± SE) was recorded as number of confrontation bouts, but duration (mean s ± SE) was recorded for all other behaviors.

			Behavior				
Treatments	Species	n	Confrontation	Food guarding	Feeding	Wandering	Resting
Honey	*F. occidentalis*	30	0.9 ± 0.2 (0.1)	1.7 ± 1.7 a (0.1)	589.9 ± 74.3 a (49.2)	334.7 ± 53.0 a (27.9)	273.0 ± 66.9 a (22.8)
	F. intonsa	30		24.6 ± 9.9 b (2.1)	280.3 ± 44.2 b (23.4)	596.7 ± 57.3 b (49.7)	295.9 ± 53.8 a (24.7)
Pollen	*F. occidentalis*	20	1.6 ± 0.2 (0.1)	1.3 ± 1.3 a (0.1)	497.0 ± 62.8 a (41.4)	498.0 ± 45.5 a (41.50)	204.1 ± 45.2 a (17.0)
	F. intonsa	20		3.3 ± 1.8 a (0.3)	387.8 ± 62.0 a (32.3)	566.9 ± 43.4 a (27.24)	237.4 ± 61.8 a (19.8)

Means for a column within a diet with the same letter(s) were not significantly different between the 2 species (α = 0.05).
Values in the parentheses indicate the percent (%) time spend for each behavioral parameter tested.

Interestingly, the greater guarding behavior of *F. intonsa* larvae did not translate into more food consumed. On pollen, no statistical difference was found in any of the other parameters we assessed in the presence of competition. Although the underlying mechanism responsible for the asymmetry in competitive dominance between adult and larval stages is not known, larvae of *F. occidentalis* did better in competition with *F. intonsa* than did adults. Although *F. occidentalis* larvae did not guard food resources to any great extent, they fed on honey for a longer period of time than did larvae of *F. intonsa* (Table 3). Sometimes, confrontation also occurred close to a food source, and such behavior was especially severe on pollen among both adults and larvae. However, we observed that *F. occidentalis* larvae did not abandon a honey source when confronted by *F. intonsa* larvae, but rather made quick forays into the food. The reason for the more frequent confrontation on pollen than on honey can be explained by the fact that pollen is an important food source for thrips. Pollen is known to enhance survival and fecundity, and shorten development time (Abdullah et al. 2001), although pollen from different plant species varies in nutritional value (Lundgren 2009).

Interspecific competition of insects is 1 component of the biotic resistance of ecosystems (Northfield et al. 2011), and is affected by the availability of resources. Thus, the impact of invasive species may be reduced through competitive interactions with native species (Levine et al. 2004). In this study, we found that adults of the invasive *F. occidentalis* were inferior competitors to adults of the native *F. intonsa* on both food sources tested, and this competitive asymmetry may lead to the exclusion of *F. occidentalis* from some areas. Similar results were found by Paini et al. (2008), who showed that the native *F. tritici* is competitively superior to the invasive *F. occidentalis* in the eastern states of the US. In contrast, Northfield et al. (2011) reported that *F. occidentalis* is competitively superior to *Frankliniella bispinosa* (Morgan) (Thysanoptera: Thripidae), a common thrips in southern Florida, and suggested this greater competitive ability of *F. occidentalis* was a cause of its invasiveness. Increasing densities of *F. occidentalis* lowered the average reproductive success of *F. bispinosa* females, which may have caused *F. occidentalis* to be the better competitor (Northfield et al. 2011). Nevertheless, competition can be affected by other external factors, such as weather condition and insecticide application, and pesticide-mediated interspecific competition has recently been reported between local and invasive thrips species in China (Zhao et al. 2017).

Interspecific competition also can be important in other insects, such as the competitive superiority of the invasive mosquito *Aedes albopictus* (Skuse) (Diptera: Culicidae) over several native species, which appears to have aided the spread of this invasive pest (Levine 2004). Likewise, the invasive fire ant *Solenopsis invicta* Buren (Hymenoptera: Formicidae) has extirpated many native ant species in the southeastern US due to the former species' superiority in both resource exploitation and aggressiveness. Based on both empirical evidence and model prediction, Amarasekare (2002) suggested that successful invasive species should be superior at both exploitation and interference competition. Thus, our study suggests that the native *F. intonsa* provide resistance to invasion by *F. occidentalis*, because the invasive thrips is inferior at both interference and exploitation in the adult stage, although not in the larval stage. In interspecific competition, adult *F. intonsa* guarded the honey 6.3 times and pollen 71.3 times longer than in intraspecific competition, suggesting that it performs better in the presence of the opponent species *F. occidentalis* on both food sources, relative to competition from its own species.

In conclusion, when native *F. intonsa* in the adult or larval stage feed on honey, they are better at exploitation and interference competition than the invasive *F. occidentalis*. However, when the larval stages feed on pollen, this difference was not always observed between the 2 species. Interspecific competition between the 2 thrips species may be 1 of the underlying mechanisms explaining patterns of occurrence in the field. If the factors affecting the spread of invasive species can be better understood, invasions might be better predicted and pest management programs could be improved (Yasuda et al. 2004).

Table 4. Intraspecific behavioral observation between *Frankliniella occidentalis* and *Frankliniella intonsa* female adults when either honey or pollen was provided as food in an experimental arena. Confronting behavior (mean ± SE) was recorded as number of confrontation bouts, but duration (mean s ± SE) was recorded for all other behaviors.

			Behavior				
Treatments	Species	n	Confrontation	Food guarding	Feeding	Wandering	Resting
Honey	*F. occidentalis*	10	3.2 ± 0.8 a (0.3)	0.0 ± 0.0 a (0.0)	399.5 ± 64.2 a (33.3)	646.3 ± 76.8 a (53.9)	146.3 ± 54.3 a (12.2)
	F. intonsa	15	1.3 ± 0.3 b (0.1)	4.7 ± 2.5 a (0.4)	419.6 ± 55.9 a (35.0)	700.7 ± 60.8 a (58.4)	72.5 ± 20.1 a (6.0)
Pollen	*F. occidentalis*	20	2.9 ± 0.5 a (0.2)	0.0 ± 0.0 a (0.0)	533.7 ± 75.9 a (44.5)	521.3 ± 70.1 a (43.4)	141.0 ± 39.1 a (11.8)
	F. intonsa	20	1.1 ± 0.2 b (0.1)	1.5 ± 1.1 a (0.1)	501.2 ± 36.2 a (41.8)	611.6 ± 36.3 a (51.0)	84.6 ± 26.8 a (7.1)

Means for a column within a diet with the same letter(s) were not significantly different between the 2 species (α = 0.05).
Values in the parentheses indicate the percent (%) time spend for each behavioral parameter tested.

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