Laboratory Assays of Density-Dependent Interspecific and Intraspecific Competition between *Aphis gossypii* and *Acyrthosiphon gossypii* (Hemiptera: Aphididae)[1]

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Abstract *Aphis gossypii* Glover and *Acyrthosiphon gossypii* Mordvilko (Hemiptera: Aphididae) are important pests of cotton (*Gossypium hirsutum* L.) in Xinjiang, China, that reduce yield and lint quality. We studied competition between the two aphid species in laboratory arenas to better understand population change and competitive advantage between the two and to provide a theoretical basis for the observed population outbreak of aphids in cotton fields. To study intraspecific competition, densities of 5, 10, and 15 aphids per 5-cm-diameter leaf disc were established in individual 6-cm-diameter arenas. Equal numbers of each species were placed on leaf discs in the arenas to establish densities of 3, 5, and 10 aphids of each species per leaf disc to assess interspecific competition. In intraspecific competition assays, the mean generation time (T) and the net reproductive rate (R_o) of both species decreased as aphid density increased, while the intrinsic rate of increase (r) and finite rate of increase (λ) of *Acy. gossypii* increased as density increased. In interspecific competition assays, population growth of *A. gossypii* was higher than with *Acy. gossypii* at the same density, while the mean generation time of *A. gossypii* was less than with *Acy. gossypii*. The net reproductive rate, intrinsic rate of increase, and finite rate of increase were higher in *A. gossypii* than in *Acy. gossypii*. Density is a key factor affecting competition between *A. gossypii* and *Acy. gossypii*. The higher the density, the more intense the interspecific competition, with interspecific competitiveness of *A. gossypii* stronger than that of *Acy. gossypii*.

Key Words density restriction, aphids, competition, age-stage, population parameters

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Due to food and space constraints, insects have competitive, reciprocal, partial, or neutral relationships (Denno et al. 1995). In these relationships, competition is an important factor affecting community structure (Iwabuchi and Urabe 2012; Soares 2013; Utsumi et al. 2010). This competition may occur between individuals of the same species, e.g., intraspecific competition, or between individuals of different species, e.g., interspecific competition (Barabas et al. 2016; Reitzl and Trumble 2002; Zhao et al. 2017). Multiple factors influence interspecific and intraspecific competitive relationships during competition in insect populations (Duan et al. 2016; Gergs et al. 2013; Jordan and Tomberlin 2017). Generally, external factors such as temperature, humidity, light, precipitation, and pesticides are considered to have an

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important impact on insect competition (Marchioro and Foerster 2011, 2016; Mohammed et al. 2019; Qu et al. 2020; Savopoulou-Soultani et al. 2012). However, the key role of density-dependent effects in population regulation in competition cannot be ignored (Li and Akimoto 2021; Magneville et al. 2018). Density directly affects population growth rate, development duration, life span, and offspring production, and ultimately affects population quantity change (Naselli et al. 2017; van Veen et al. 2006).

Intraspecific and interspecific density-dependent effects are common in most herbivorous insects, especially in Hemiptera and Homoptera with piercing-sucking mouthparts (Denno and Roderick 1992). Density-dependent effects directly affect population life parameters in the competitive relationships of aphids, such as *Acyrthosiphon pisum* (Harris), *Myzus persicae* (Sulzer), and *Lipaphis erysimi* (Kaltenbach), and the planthoppers such as *Nilaparvata lugens* (Stal), *Sogatella furcifera* (Horváth), and *Laodelphax striatellus* (Fallén) (Hu et al. 2004; Li and Akimoto 2021; Lü et al. 2011; Zhao et al. 2001). For these insects with similar ecological habits and niches, the constraint of density effect in competition will be more prominent (Chongrattanameteekul et al. 1991; Gonzalez-Megias and Gomez 2003). These insects consume available resources in limited space and increase intraspecific and interspecific competition (Klepsatel et al. 2018; Reis et al. 1999; Villemereuil and Lopez-Sepulcre 2011). As individuals with insufficient resources die, population density decreases with heightened risk of population collapse (Karban 1986; Thirakhupt and Araya 1992). At the same time, population growth strategies of individuals may adjust to compensate. These include development period, body weight, life span, and others (Morimoto et al. 2019; Than et al. 2020; Tsurim et al. 2018). Therefore, the density effect not only restricts population size (Mueller et al. 1991) but also affects individual growth and reproduction (Diamantidis et al. 2020; Henry et al. 2018; Kaplan and Denno 2007; Morimoto et al. 2016,).

The primary aphid pests of cotton (*Gossypium hirusutum* L.) grown in Xinjiang, China, are *Aphis gossypii* Glover and *Acyrthosiphon gossypii* Mordvilko (Hemiptera: Aphididae). Feeding by both species causes leaf curling, delays budding and flowering, causes abscission of buds and bolls, and reduces cotton yield and quality (Gao et al. 2013; Hullé et al. 2020; Moran and Whitham 1990). *Aphis gossypii* and *Acy. gossypii* can occur at the same time in cotton fields, but the two have different temporal characteristics (Lü et al. 2002; Yao 2017). In normal years, the temperature is relatively low before and after cotton seedling emergence to the budding period when *Acy. gossypii* is the dominant species of the two; *A. gossypii* is the dominant species in the middle and late stages of cotton growth (Gao et al. 2012; Li et al. 2008; Yao 2017). *Aphis gossypii* and *Acy. gossypii* have similar niche and living habits in cotton, so there is a strong competitive relationship in the dynamic changes of population structure (Gao et al. 2013; Lü et al. 2002). Previously, interspecific and intraspecific competition between *A. gossypii* and *Acy. gossypii* were studied in response to temperature, natural enemies, cotton–host-plant resistance, pesticide stress, and other external factors (Feng et al. 2015; Gao et al. 2012; Yao 2017). In our previous study, we confirmed that the feeding behavior of *A. gossypii* and *Acy. gossypii* also was an important factor in mediating the competition between the two species (Deng et al. 2013; Wu et al. 2020; Yan et al. 2019, 2020; Zhang et al. 2020). These studies have helped us to better understand the competition between the two species. However, no study has yet investigated the intraspecific and interspecific competition in response to density of *A. gossypii* and *Acy. gossypii*.

Therefore, in this study, *A. gossypii*, *Acy. gossypii*, and their mixed populations were established at different densities in laboratory arenas. The effects of density on the growth and development, population number, and life parameters of *A. gossypii* and *Acy. gossypii* were thus observed and calculated to clarify intraspecific competition and interspecific competition in response to density.

Materials and Methods

Insects. Colonies of *A. gossypii* and *Acy. gossypii* were initially established from aphids collected from cotton fields growing in Shihezi University fields. Over 30 generations of each species had been maintained in the laboratory on cotton in an environmentally controlled chamber at 26 ± 1°C, 70 ± 5% relative humidity, and a photoperiod of 16 h:8 h (L:D).

Assay arenas. Five-centimeter-diameter circular discs were cut from newly emerged cotton leaves that had been excised from the plant, washed, and air dried. The discs were inverted with abaxial surface facing up and placed onto 1% agar gel that had been previously poured and allowed to cool in 6-cm-diameter Petri dishes.

Assay design. We used the leaf disc method to measure population production time, duration, quantity, and life span in response to intraspecific and interspecific competition. For intraspecific competition, aphid nymphs obtained from the respective laboratory colonies were placed individually on leaf discs to a total of 5, 10, and 15 aphids per disc for each species. The arenas were covered, and the aphids were observed for 20 d. We observed and recorded aphids on leaf discs at 8:00 a.m. and 8:00 p.m. each day. In recording the immature stages of aphids, we determined the age of aphids according to the number of molts, and the molted exuviae were removed after each observation. The period from the molting of fourth instar nymphs to appearance of adult aphids was recorded at the prereproductive period. We recorded the daily aphid production, survival number, and population number. The three treatments for each species were replicated 10 times with one arena representing a replicate.

Interspecific competition responses were measured by placing both *A. gossypii* and *Acy. gossypii* nymphs on individual leaf discs. The treatments were (a) 3 *A. gossypii* and 3 *Acy. gossypii* nymphs per disc; (b) 5 *A. gossypii* and 5 *Acy. gossypii* nymphs per disc, and (c) 10 *A. gossypii* and 10 *Acy. gossypii* nymphs per disc. We observed and recorded aphids on leaf discs at 8:00 a.m. and 8:00 p.m. each day. We recorded the molting of aphids, daily aphid production, survival number, and population number. Each treatment was replicated 10 times with one arena representing a replicate. Nymphs were obtained from the respective laboratory colonies and observed for 15 d.

Calculations and analyses. Using the age-stage, two-sex life table theory (Chi 1988; Chi and Liu 1985), the data recorded from the various treatments were used to calculate developmental duration of nymphs plus prereproductive adults. The age-specific survival rate (l_x) and age-specific fecundity (m_x) were calculated according to the survival of aphids at different developmental stages and the nymph production by females as recorded daily. Net reproductive rate (R_0), or the total number of offspring produced by an individual, was then calculated by the formula,

$$R_0 = \sum_{x=0}^{\infty} l_x m_x.$$

An R_0 value of 1.0 indicates that a population is neither increasing nor decreasing. Likewise, the intrinsic rate of increase (r) was estimated by the Euler–Lotka formula,

$$\sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_x,$$

and provides an estimate of continuous population growth when environmental resources are hypothetically unlimited. The finite rate of increase of the population (λ) was calculated as $\lambda = e^r$, which indicates population increase over time, with $\lambda = 1$ being a stable population. The mean generation period (T) refers to the time required to increase R_0 when the population reaches a stable age-stage distribution and a stable growth rate, namely $e^{rT}=R_0$ or $\lambda^T = R_0$. The formula for calculating T was $T = \ln R_0/r$.

Calculations were conducted using the program TWOSEX-MSChart (Chi 2022). The least significant differences (LSD) multiple comparison method of the statistical software SPSS (Statistical Package for the Social Sciences, Version 18.0, Chicago, IL) was used to identify treatment differences in developmental duration. The mean values of life table parameters were estimated using the bootstrap method of Akkopru et al. (2015), and LSD was used to separate treatment means.

Results

***Acyrthosiphon gossypii* density-dependent response to intraspecific competition.** The population growth curves (Fig. 1) of *Acy. gossypii* at the three aphid densities were similar in shape and appearance. During the 20 d of observation, the numbers of aphids remained constant initially, then increased to respective peaks and quickly declined. As might be expected, we observed differences in the timing of these phases of the curve with respect to initial aphid density. Numbers of aphids increased and peaked earlier in the observation period in the initial 15 aphids/disc than in the treatments with 10 and 5 aphids/disc.

We found no significant influence on the duration of the individual nymphal stages in response to initial aphid density, but mean (±standard deviation) duration of the prereproductive period in the treatment of 5 aphids/disc (2.85 ± 0.88 d) was significantly longer than either the 15 (1.30 ± 0.80 d) or 10 (1.75 ± 0.72 d) aphids/disc treatments ($F = 21.59$; df = 2, 279; $P < 0.0001$; Table 1). With respect to the life table parameters, the mean generation time (T) was longer in the treatment with 5 aphids/disc than in the other two treatments, while the intrinsic rate of increase (r) was significantly lower than either the 15 or 10 aphids/disc treatment ($F = 131.28$; df = 2, 29; $P < 0.0001$; Table 2). We found no significant differences in the net

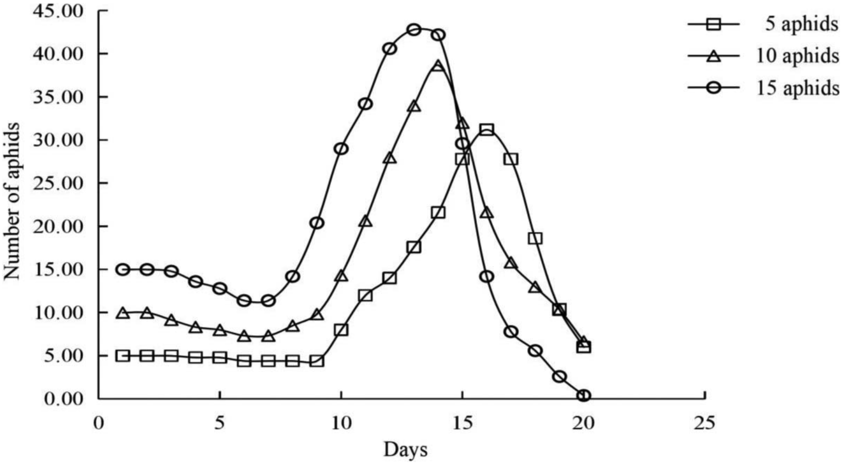

Fig. 1. Population growth of *Acyrthosiphon gossypii* in response to densities of 5, 10, and 15 aphids per 5-cm leaf disc.

reproductive rate (R_0) or the finite rate of increase (λ) among the density treatments for *Acy. gossypii* ($P > 0.05$; Table 2). The population doubling time was significantly higher in the treatment with 10 aphids/disc (12.41 ± 1.23 d) than in either the 15 aphids/disc (2.85 ± 1.08 d) or the 5 aphids/disc (3.76 ± 0.91 d) treatments ($F = 67.29$; df = 2, 29; $P < 0.0001$; Table 2).

***Aphis gossypii* density-dependent response to intraspecific competition.** The population growth curves for the *A. gossypii* density treatments were similar to those of *A. gossypii* (Fig. 2). In the treatment with 15 aphids/disc, the increase in aphid numbers occurred earlier in the observation period than the treatments with 10 and 5 aphids/disc. The 20-d observation period was not sufficiently long to note population collapse in any of the treatments. The duration of the immature stages of *A, gossypii* did not differ among the density treatments ($P > 0.05$; Table 1).

Of the life table parameters, mean generation time (T) and net reproductive rate (R_0) were not significantly affected by aphid density ($P > 0.05$; Table 2). The intrinsic growth rate (r) was significantly lower in the treatment with 15 aphids/disc in comparison to the treatments with either 10 or 5 aphids/disc ($F = 35.70$; df = 2, 29; $P = 0.0016$; Table 2), while the finite rate of increase (λ) when compared among treatments was highest in the treatment with 10 aphids/disc ($F = 114.59$; df = 2, 29; $P < 0.0001$; Table 2). As with *Acy. gossypii*, the doubling time of *A. gossypii* was significantly longer in the 10 aphids/disc treatment (10.02 ± 1.35 d) in comparison to either the 5 (2.28 ± 0.53 d) or 15 (2.18 ± 0.97 d) aphids/disc treatments ($F = 45.17$; df = 2, 29; $P < 0.0001$; Table 2).

***Acyrthosiphon gossypii* and *A. gossypii* responses to mixed population density.** When aphids of both species were placed on the same leaf disc, the numbers of *A. gossypii* increased to higher levels than did *Acy. gossypii*, regardless of the initial density of the mixed population (Fig. 3). For example, in the arenas with an initial density of three *A. gossypii* and three *Acy. gossypii* aphids per disc, the numbers of *A. gossypii* increased 13-fold, while the numbers of *Acy. gossypii*

Table 1. Duration in days (mean±standard deviation) of immature stages of development of *Acyrthosiphon gossypii* and *Aphis gossypii* in response to intraspecific competition at three densities of aphids per 5-cm leaf disc.*

Initial Density (aphids/disc)	First Instar	Second Instar	Third Instar	Fourth Instar	Prereproductive Adult
Acyrthosiphon gossypii					
5	2.00 ± 0.56a	1.60 ± 0.50a	1.45 ± 0.51a	1.70 ± 0.47a	2.85 ± 0.88a
10	1.90 ± 0.72a	1.65 ± 0.49a	1.70 ± 0.73a	2.00 ± 0.73a	1.75 ± 0.72b
15	1.85 ± 0.67a	1.60 ± 0.50a	1.70 ± 0.73a	1.95 ± 0.60a	1.30 ± 0.80b
Aphis gossypii					
5	1.15 ± 0.37a	1.10 ± 0.31a	1.15 ± 0.37a	1.20 ± 0.41a	1.50 ± 0.51a
10	1.10 ± 0.31a	1.05 ± 0.22a	1.10 ± 0.31a	1.15 ± 0.37a	1.15 ± 0.37a
15	1.05 ± 0.22a	1.10 ± 0.31a	1.05 ± 0.22a	1.15 ± 0.31a	1.05 ± 0.22a

* Treatment means within columns and aphid species followed by the same lowercase letter are not significantly different ($P < 0.05$; least significant difference).

Table 2. Estimated (mean ± standard deviation) life parameters of *Acyrthosiphon gossypii* and *Aphis gossypii* in response to intraspecific competition at three densities of aphids per 5-cm leaf disc.*

Initial Density (aphids/disc)	Mean Generation Time (days)	Net Reproductive Rate (R_0)	Intrinsic Rate of Increase (r)	Finite Rate of Increase (λ)	Doubling Time (days)
Acyrthosiphon gossypii					
5	16.69 ± 0.79a	21.55 ± 3.44a	0.18 ± 0.0048b	1.20 ± 0.0050a	3.76 ± 0.91b
10	12.41 ±0.55b	18.25 ± 4.70a	0.23 ± 0.0022a	1.26 ± 0.0052a	12.41 ± 1.23a
15	11.86 ± 1.20b	17.95 ± 4.32a	0.24 ± 0.0041a	1.28 ± 0.0050a	2.85 ± 1.08b
Aphis gossypii					
5	10.59 ± 0.37a	25.00 ± 4.07a	0.30 ± 0.0051b	1.36 ± 0.0063b	2.28 ± 0.53b
10	10.03 ± 0.30a	24.15 ± 3.91a	0.32 ± 0.0050b	2.18 ± 0.0060a	10.02 ± 1.35a
15	9.83 ± 0.41a	22.85 ± 4.82a	0.18 ± 0.0063a	1.38 ± 0.0060b	2.18 ± 0.97b

* Treatment means within columns and aphid species followed by the same lowercase letter are not significantly different ($P < 0.05$; least significant difference).

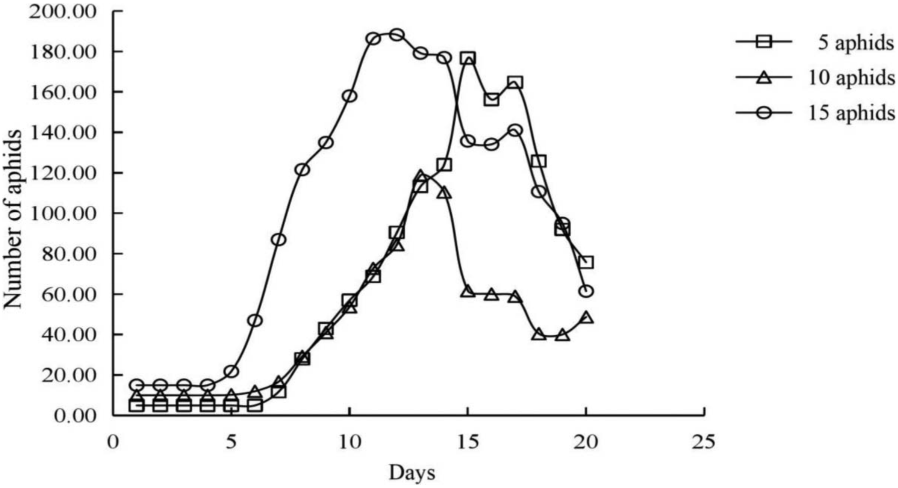

Fig. 2. Population growth of *Aphis gossypii* in response to densities of 5, 10, and 15 aphids per 5-cm leaf disc.

increased 4.3-fold (Fig. 3A). Likewise, in the treatment with five aphids of each species per leaf disc, the numbers of *A. gossypii* increased 18.8-fold at peak numbers, while *Acy. gossypii* numbers increased only 5.6-fold before declining after the 10th day (Fig. 3B). Increases were 5.6-fold in *A. gossypii* numbers and 2.7-fold in *Acy. gossypii* numbers in the treatment with 10 aphids of each species per leaf disc (Fig. 3C).

We also compared responses in duration of developmental stages and life table parameters to the three mixed population densities within each species. There were no significant differences ($P > 0.05$) in the duration of the four nymphal stages of *Acy. gossypii* among the mixed population densities, but the duration of the prereproductive period in the lowest density (three aphids of each species) was significantly longer than in the other two density levels ($F = 31.32$; df = 2, 157; $P <$

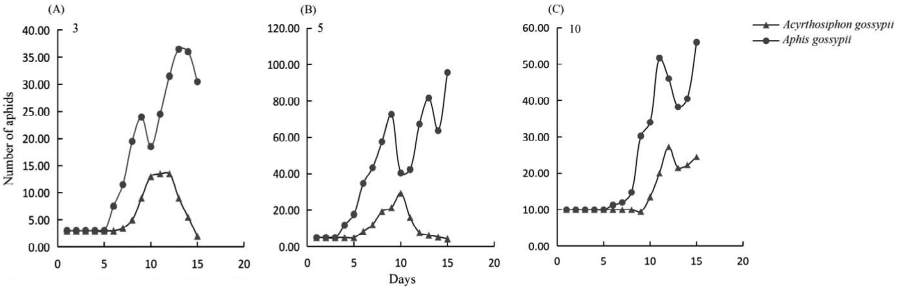

Fig. 3. Population growth of *Acyrthosiphon gossypii* and *Aphis gossypii* in response to combined densities of 3 (A), 5 (B), and 10 (C) aphids of each species per 5-cm leaf disc.

0.0001; Table 3). No significant differences ($P > 0.05$) were detected in the duration of the first, second, and third instars of *A. gossypii* among the density treatments, but the duration of the fourth instar ($F = 14.50$; df = 2, 170; $P < 0.0001$) and the prereproductive period ($F = 9.49$; df = 2, 165; $P = 0.0008$) were significantly longer in the lowest density treatment than in the higher two densities (Table 3).

For *Acy. gossypii*, the mean generation time (T) was significantly longer ($F = 12.51$; df = 2, 29; $P = 0.0037$) and the intrinsic rate of increase (r) was significantly lower ($F = 49.36$; df = 2, 29; $P < 0.0001$) in the lowest density (3 aphids of each species) of the mixed population treatment than in either of the other density treatments (5 aphids of each species and 10 aphids of each species (Table 4). In comparing the three density treatments, the net reproductive rate (R_0) was significantly lower in the treatment of five aphids of each species in the mixed population than in other treatments ($F = 5.56$; df = 2, 29; $P = 0.0095$; Table 4). There were no significant differences among the treatments in finite rate of increase (λ) and doubling time ($P > 0.05$; Table 4).

With *A. gossypii*, no significant differences were detected in mean generation time (T) or doubling time ($P > 0.05$; Table 4). The net reproductive rate (R_0) ($F = 16.73$; df = 2, 29; $P < 0.0001$), intrinsic rate of increase (r) ($F = 43.33$; df = 2, 29; $P = 0.0021$), and finite rate of increase (λ) ($F = 34.31$; df = 2, 29; $P < 0.0001$) in the highest density treatment were significantly lower than those of the other two density treatments (Table 4).

In comparing each of the immature stages calculated for the two species in mixed populations, there were no significant differences in the duration of the first instar stage in the lowest density (3 aphids of each species) and prereproductive period in the treatment of 5 aphids of each species ($P > 0.05$), second (3 aphids of each species: $F = 21.88$; df = 1, 56; $P = 0.0097$; 5 aphids of each species: $F = 13.49$; df = 1, 97; $P = 0.0043$; 10 aphids of each species: $F = 8.36$; df = 1, 195; $P = 0.0012$) , third (3 aphids of each species: $F = 10.20$; df = 1, 54; $P = 0.0050$; 5 aphids of each species: $F = 38.05$; df = 1, 92; $P < 0.0001$; 10 aphids of each species: $F = 35.41$; df = 1, 193; $P = 0.0087$), and fourth stages (3 aphids of each species: $F = 30.43$; df = 1, 54; $P < 0.0001$; however, 5 aphids of each species: $F = 116.00$; df = 1, 92; $P < 0.0001$; 10 aphids of each species: $F = 32.26$; df = 1, 187; $P < 0.0001$) were significantly shorter for *A. gossypii* than *Acy. gossypii* at each of the aphid densities (Table 5).

In comparing each of the life table parameters calculated for the two species in mixed populations, we found that the mean generation time (T) (3 aphids of each species: $F = 12.96$; df = 1, 19; $P < 0.0001$; 5 aphids of each species: $F = 61.19$; df = 1, 19; $P < 0.0001$; 10 aphids of each species: $F = 60.15$; df = 1, 19; $P < 0.0001$), and the generation doubling time (3 aphids of each species: $F = 37.64$; df = 1, 19; $P < 0.0001$; 5 aphids of each species: $F = 20.86$; df = 1, 19; $P < 0.0001$; 10 aphids of each species: $F = 6.39$; df = 1, 19; $P = 0.0211$) were significantly shorter for *A. gossypii* than for *Acy. gossypii* at each of the aphid densities (Table 6). Furthermore, the net reproductive rate (R_0) (3 aphids of each species: $F = 32.08$; df = 1, 19; $P < 0.0001$; 5 aphids of each species: $F = 45.95$; df = 1, 19; $P < 0.0001$; 10 aphids of each species: $F = 7.60$; df = 1, 19; $P = 0.0130$) , intrinsic rate of increase (r) (3 aphids of each species: $F = 15.22$; df = 1, 19; $P = 0.0011$; 5 aphids of each species: $F = 9.43$; df = 1, 19; $P < 0.0001$; 10 aphids of each species: $F = 29.33$; df = 1, 19; $P < 0.0001$), and finite rate of increase (λ) (3 aphids of each

Table 3. Duration in days (mean ± standard deviation) of immature stages of *Acyrthosiphon gossypii* and *Aphis gossypii* in response to interspecific competition at three densities of mixed populations of aphids per 5-cm leaf disc.*

Number Aphids of Each Species	First Instar	Second Instar	Third Instar	Fourth Instar	Prereproductive Period
Acyrthosiphon gossypii nymph development					
3	1.55 ± 0.51a	1.75 ± 0.44a	1.45 ± 0.51a	1.65 ± 0.49a	4.65 ± 0.59a
5	1.50 ± 0.51a	1.65 ± 0.49a	1.70 ± 0.47a	1.55 ± 0.51a	0.70 ± 1.17b
10	1.20 ± 0.41a	1.35 ± 0.49a	1.75 ± 0.44a	1.55 ± 0.51a	2.15 ± 0.75b
Aphis gossypii nymph development					
3	1.10 ± 0.31a	1.10 ± 0.31a	1.15 ± 0.37a	1.15 ± 0.36a	1.15 ± 0.36a
5	1.15 ± 0.37a	1.10 ± 0.31a	1.15 ± 0.37a	0.60 ± 0.75b	0.60 ± 0.75b
10	1.10 ± 0.31a	1.10 ± 0.31a	1.15 ± 0.37a	1.00 ± 0.73b	1.00 ± 0.73b

* Treatment means within columns and aphid species followed by the same lowercase letter are not significantly different ($P < 0.05$; least significant difference).

Table 4. **Estimated (mean ± standard deviation) life parameters of *Acyrthosiphon gossypii* and *Aphis gossypii* in response to interspecific competition at three densities of mixed populations of aphids per 5-cm leaf disc.***

Number Aphids of Each Species	Mean Generation Time (days)	Net Reproductive Rate (R_0)	Intrinsic Rate of Increase (r)	Finite Rate of Increase (λ)	Doubling Time (days)
Acyrthosiphon gossypii					
3	15.14 ± 0.72a	17.00 ± 4.29a	0.19 ± 0.0068b	1.21 ± 0.0050a	3.70 ± 0.63a
5	11.32 ± 0.60b	14.30 ± 3.06b	0.24 ± 0.0043a	1.27 ± 0.0061a	2.95 ± 0.71a
10	12.32 ± 1.25b	16.40 ± 4.59a	0.23 ± 0.0040a	1.25 ± 0.0061a	3.06 ± 0.79a
Aphis gossypii					
3	10.22 ± 0.89a	24.10 ± 3.40a	0.31 ± 0.0051a	1.37 ± 0.0063a	2.23 ± 0.35a
5	9.84 ± 1.11a	22.50 ± 4.83a	0.32 ± 0.0045a	1.37 ± 0.0059a	2.19 ± 0.40a
10	10.15 ± 1.40a	19.10 ± 4.21b	0.29 ± 0.0057b	1.34 ± 0.0066b	2.39 ± 0.92a

* Treatment means within columns and aphid species followed by the same lowercase letter are not significantly different ($P < 0.05$; least significant difference).

Table 5. Comparison of *Acyrthosiphon gossypii* and *Aphis gossypii* immature stages (mean±standard deviation) in response to interspecific competition at three densities of mixed populations of aphids per 5-cm leaf disc.*

Number Aphids of Each Species	Aphid Species	First Instar	Second Instar	Third Instar	Fourth Instar	Prereproductive Period
3	*Acy. gossypii*	1.55 ± 0.51b	1.75 ± 0.44b	1.45 ± 0.51b	1.65 ± 0.49b	4.65 ± 0.59b
	A. gossypii	1.10 ± 0.31a	1.10 ± 0.31a	1.15 ± 0.37a	1.15 ± 0.36a	1.15 ± 0.36a
5	*Acy. gossypii*	1.50 ± 0.51b	1.65 ± 0.49b	1.70 ± 0.47b	1.55 ± 0.51b	0.70 ± 1.17a
	A. gossypii	1.15 ± 0.37a	1.10 ± 0.31a	1.15 ± 0.37a	0.60 ± 0.75a	0.60 ± 0.75a
10	*Acy. gossypii*	1.20 ± 0.41a	1.35 ± 0.49b	1.75 ± 0.44b	1.55 ± 0.51b	2.15 ± 0.75b
	A. gossypii	1.10 ± 0.31a	1.10 ± 0.31a	1.15 ± 0.37a	1.00 ± 0.73a	1.00 ± 0.73a

* Treatment means within columns and aphid density followed by the same lowercase letter are not significantly different ($P < 0.05$; least significant difference).

Table 6. Comparison of *Acyrthosiphon gossypii* and *Aphis gossypii* life parameters (mean±standard deviation) in response to interspecific competition at three densities of mixed populations of aphids per 5-cm leaf disc.*

Number Aphids of Each Species	Aphid Species	Mean Generation Time (days)	Net Reproductive Rate (R_0)	Intrinsic Rate of Increase (r)	Finite Rate of Increase (λ)	Doubling Time (days)
3	*Acy. gossypii*	15.14 ± 0.72a	17.00 ± 4.29b	0.19 ± 0.0068b	1.21 ± 0.0050b	3.70 ± 0.63a
	A. gossypii	10.22 ± 0.89b	24.10 ± 3.40a	0.31 ± 0.0051a	1.37 ± 0.0063a	2.23 ± 0.35b
5	*Acy. gossypii*	11.32 ± 0.60a	14.30 ± 3.06b	0.24 ± 0.0043b	1.27 ± 0.0061b	2.95 ± 0.71a
	A. gossypii	9.84 ± 1.11b	22.50 ± 4.83a	0.32 ± 0.0045a	1.37 ± 0.0059a	2.19 ± 0.40b
10	*Acy. gossypii*	12.32 ± 1.25a	16.40 ± 4.59b	0.23 ± 0.0040b	1.25 ± 0.0061b	3.06 ± 0.79a
	A. gossypii	10.15 ± 1.40b	19.10 ± 4.21a	0.29 ± 0.0057a	1.34 ± 0.0066a	2.39 ± 0.92b

* Treatment means within columns and aphid density followed by the same lowercase letter are not significantly different ($P < 0.05$; least significant difference).

species: $F = 25.17$; df = 1, 19; $P < 0.0001$; 5 aphids of each species: $F = 63.70$; df = 1, 19; $P = 0.0022$; 10 aphids of each species: $F = 7.09$; df = 1, 19; $P = 0.0003$) of *A. gossypii* were significantly lower than with *Acy. gossypii* at all aphid densities (Table 6).

Discussion

Intraspecific density effects are common in herbivorous insects, but there are some differences in strength of response (Chongrattanameteekul et al. 1991). As numbers increase to a point of limiting resources, the population will reach an equilibrium or experience a decline in numbers, or both (Karban 1986; Thirakhupt and Araya 1992). Our results with single populations of *A. gossypii* and *Acy. gossypii* (i.e., intraspecific competition) well illustrated these observations and results. At initial densities of 5, 10, and 15 aphids per 5-cm leaf disc, numbers of aphids initially remained relatively constant for several days, then increased exponentially until reaching a level at which undefined density-dependent factors limited population growth, resulting in a rapid decline in numbers (Figs. 1, 2). Regardless of our initial treatment densities, the numbers of *A. gossypii* increased to higher levels than *Acy. gossypii* in these tests, thus indicating that the threshold for tolerance of population growth limiting factors is greater for *A. gossypii* than for *Acy. gossypii*.

When the insect population density reaches or exceeds this threshold, limiting factors associated with density can reduce survival rate, change sex ratio, reduce fertility and resistance to disease, and induce diapause, dormancy, and developmental deformity, thus affecting population growth (Xu 1987). For example, the larval density of the leafminers *Liriomyza trifolii* (Burgess) and *Liriomyza sativae* Blanchard significantly affects survival rate, mean pupal weight, pupation rate, emergence rate, adult longevity, and fecundity per female (Yi et al. 2014). In our study, the mean generation time (T) of *Acy. gossypii* significantly decreased with increased aphid density, while the intrinsic rate of increase (r) value increased with higher density levels (Table 2). Of the aphid densities tested, the intermediate density of 10 aphids/leaf disc had a significantly longer population doubling time than did the 5 and 15 aphids/leaf disc densities. We saw a similar response in doubling time for *A. gossypii* at the intermediate density in comparison to the low and high densities tested (Table 2). Other significant differences among the density treatments were recorded with intrinsic rate of increase (r) (e.g., high density level significantly higher) and finite rate of increase (λ) (e.g., intermediate density level significantly higher).

Inherent competitiveness of insects varies among species. In interspecific interactions, the species with strong competitive advantages can exploit niche factors to displace the weaker species, as reported for *Bemisia tabaci* (Gennadius) biotypes (Pan et al. 2010) and *Liriomyza* spp. (Yi et al. 2014). This phenomenon is also evident in interspecific competition among herbivorous insects such as thrips (Wang et al. 2011), mites (Yan et al. 2010), and whiteflies (Zheng et al. 2012).

Our results appear to corroborate those results when *A. gossypii* and *Acy. gossypii* aphids are in a mixed populations for 15 d. As previously noted, when *A. gossypii* and *Acy. gossypii* aphids were placed on the same leaf disc, the numbers of *A. gossypii* increased to higher levels than did *Acy. gossypii*, regardless of the initial density of the mixed populations (Fig. 3). The ecological equilibrium of *A. gossypii* in our test arenas is higher than that of *Acy. gossypii*, which might be attributed to differences in life parameters, differences in tolerance of undefined limiting factors, differences in capabilities to exploit the ecological niche created in the arena, or any combination of those factors. Furthermore, we postulate that these factors operate in Chinese cotton fields where *A. gossypii* tends to become the dominant aphid species as the growing season progresses. Our life parameters data show that *A. gossypii* possesses several characteristics that contribute to its competitive success over *Acy. gossypii*. Regardless of aphid density, the mean generation time (T) of *A. gossypii* was significantly shorter than that of *Acy. gossypii*, and the net reproductive rate (R_0), intrinsic rate of increase (r), and finite rate of increase (λ) of *A. gossypii* were significantly lower than for *Acy. gossypii* (Table 6). These contributed to the significantly lower population doubling time of *A. gossypii* than of *Acy. gossypii*.

When challenged by abiotic or biotic limiting factors (e.g., temperature, pesticides, host plant resistance, population density, food availability) (Feng et al. 2015; Gao et al. 2012; Meng and Li 2000; Yao 2017), *A. gossypii* adapts more readily than does *Acy. gossypii*. This is at least one explanation of how *A. gossypii* becomes the dominant aphid species when *A. gossypii* and *Acy gossypii* occupy the same cotton plants in production fields. We also postulate that this observed competitive advantage evolved through interspecific competition for the same resources.

Admittedly, the design of this study in closed arenas had some limitations, especially with regard to movement of aphids to and from host plants that commonly occurs in natural environments. However, analyses using the age-stage, two-sex life table effectively reflected the intraspecific and interspecific competition dynamics of *Acy. gossypii* and *A. gossypii*. Future studies should be designed and conducted in larger spaces to better simulate field conditions.

Data Availability

The raw data from this study that support the conclusions of this paper will be made available by the authors upon request, without undue reservation.

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