Life Table Analysis and Development of Singhiella simplex (Hemiptera: Aleyrodidae) Under Different Constant Temperatures

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ABSTRACT Singhiella simplex (Singh) (Hemiptera: Aleyrodidae) is a newly invasive pest of several species of Ficus plants in the United States. Very little is known about its biology and life history. Here, we studied its development and reproduction at 15, 20, 25, 27, 30, and 35°C. No immatures survived the 35°C treatment. Stage-specific duration times are presented for the other temperatures. Total duration of immature stages varied from 97.1 d at 15°C to 25.2 d at 30°C. Linear functions were used to describe development rates for eggs, instars and pupal stages. Total immature development also was modeled using a nonlinear Briere-1 function: \( r(T) = aT(T - T_0) \), where \( r(T) \) is developmental rate at temperature \( T \), \( a = 0.0000146 \), \( T_0 = 7.310084 \) and \( T_L = 45.9512202 \) (constant, lower developmental threshold, and lethal temperature, respectively). The thermal requirement for development from eggs to pupae was estimated to be 487.8 degree-days. S. simplex reproduction was highest at 27°C, where \( R_0, \) GRR, \( T, r, \) and \( DT \) were 23.114 \( \uparrow / ? \), 24.25 \( \uparrow / ? \), 31.413 \( \downarrow / ? \), 0.099 \( \downarrow / ? \), 1.105 \( \downarrow / ? \), and 6.93 \( \downarrow \), respectively. The combined effect of temperature and female adult age on daily oviposition rate was modeled using the Enkegaard equation: \( \text{eggmean} = (p + qT) d \exp(-wTd) \), where \( T \) is temperature. Parameter estimates were \( p = -30.21, q = 2.62, \) and \( w = 0.034 \). Duration of female adulthood was 9 d at 15°C, significantly longer than 2.5–4.2 d at the higher temperatures. At 25 and 27°C, lifetime fecundity per female averaged 37.9 and 46.2, respectively.

KEY WORDS life history, reproduction, survivorship, Ficus benjamina, fecundity

The whitefly Singhiella simplex (Singh) (Hemiptera: Aleyrodidae), is an economic pest of Ficus plant species in India, Burana, and China (Hodges 2007). This whitefly has been most commonly found infesting weeping fig (Ficus benjamina L.) (Moraceae). However, it has been reported on Ficus altissima Blume (lofty fig, false banyan tree), Ficus bengalensis L. (“banyan tree”), Ficus microcarpa L.f. (Cuban laurel), Ficus aurea Nutt. (strangler fig), Ficus lyrata Warb. (fiddle-leaf fig), Ficus racemosa L. (cluster fig, Indian fig), and Ficus macelldulli King (banana-leaf fig) (Mannion et al. 2008). Severe infestations result in leaf dropping or shedding and defoliation. S. simplex can cause serious injury to host plants by sucking sap, resulting in wilting, yellowing, stunting, leaf drop, or even death (Osborne 2008). Very little is known about its biology and life history. Like other species of Singhiella in Florida, S. simplex is assumed to have at least three generations per year (Hodges 2007). The life cycle of this whitefly is \( \approx 1 \) mo (Mannion et al. 2008). The adult whitefly head, thorax, and abdomen are yellow, and the wings are white with a faint gray band toward the middle. Immature stages are located on the undersides of leaves. Crawlers are mobile on the leaf until they start to feed. The nonmobile feeding nymphs are usually flat and oval (Mannion et al. 2008). Pupae measure \( \approx 1.3 \) mm in length and are tan to light green discs with red eyes (Hodges 2007, Mannion et al. 2008). Some biological studies have been conducted on this whitefly under different temperature regimens (Mannion, unpublished data). Known natural enemies include Encarsia tricolor Foerster (Hymenoptera: Aphelinidae) (Hodges 2007). The first U.S. record of S. simplex was made on F. benjamina in Miami, FL, on 3 August 2007 (Hodges 2007). Since then, its geographic range has increased to include most of southern Florida, as well as along both coasts of Florida up to central Florida (Hodges 2007).

Here, we studied life history and reproduction of S. simplex in the laboratory under different constant temperatures.
Materials and Methods

Test Colony And Experimental Protocol. A colony of S. simplex was maintained at the USDA–ARS–CMAVE Center for Biological Control in Tallahassee, FL. The colony was initiated from S. simplex immatures collected from ficus plants in Homestead, FL, in May 2009. S. simplex were continuously reared on 3.78-liter (1-gal) potted F. benjamina plants (50 cm in height) in cages (61 by 61 by 61 cm) screened with ultrafine screen under ambient laboratory conditions at 25–28°C. Cages were kept near a window in the laboratory where they were exposed to natural light in addition to a photoperiod of 14:10 (L:D) maintained with fluorescent lamps (Sylvania Gro-Lux, Osram, Sylvania, Ltd. Mississauga, ON, Canada).

Studies of immature development and adult fecundity were made on individual 2.5-cm F. benjamina leaves housed in enclosures made from plastic petri dishes (90 by 15 mm in diameter). The dishes were positioned vertically and placed on top of plastic tubes (55 by 35 mm in diameter) containing water. A hole was cut into the side of the dish to allow the leaf petiole to pass into the watering tube and modeling clay was used to seal the dish enclosure to the water container. Two 1-cm holes were cut in the lid of each enclosure. One hole was covered with ultrafine screen mesh to provide ventilation, whereas the other hole was plugged with the cut top from a plastic microcentrifuge tube to provide access for introducing insects. Dish enclosures were sealed with Parafilm to prevent insects from escaping. In this arrangement, leaves would grow roots into the water and could remain alive for several months.

In studies of immature development, pairs of male and female adult whiteflies were transferred into the leaf enclosures and were kept in growth chambers at constant temperatures (15, 20, 25, 27, and 30°C) and photoperiod (14:10 [L:D] h). After 24 h, the adult whiteflies and eggs were removed except for a single egg on each leaf (for temperatures from 15 to 35°C; N = 14, 16, 16, 20, 14, and 14, respectively). Daily observations were made on the survival and development of these whiteflies at each temperature until they reached adult eclosion. Individuals that died or failed to eclose were omitted from analysis. Studies of adult fecundity were conducted using adult whiteflies that had completed their immature development in leaf enclosures at constant temperatures (15, 25, 27, and 30°C; N = 10, 17, 13, and 12, respectively). On the day of eclosion, these adults were paired and placed in new enclosures where oviposition and survival were recorded each day until death.

Analysis of Whitefly Development. Developmental rate of immature S. simplex was analyzed as the reciprocal of total immature duration. Individuals that did not survive to adulthood were excluded from analysis. Both linear and nonlinear regression models were fitted to developmental rate as a function of temperature. The linear equation was as follows:

\[ v = a + bT, \]

where \( v \) is developmental rate (reciprocal of mean developmental time), \( T \) is temperature, and \( a \) and \( b \) are constants. Accumulated effective temperature (Kelvin [K]) was estimated as \( K = \frac{1}{b} \) (Bergant and Trdan 2006, Pandey and Johnson 2006, Grout and Stoltz 2007, Haghani et al. 2007).

For the nonlinear model, we used the simple function of Briere et al. (1999) (i.e., Briere-1 model):

\[ r(T) = a(T - T_0) \sqrt{T_L - T}, \]

where \( a \) is an empirical constant, \( r \) is developmental rate, \( T \) is temperature, \( T_0 \) is the lower developmental threshold, and \( T_L \) is lethal temperature. (In the Briere-2 model, the last term of the equation is generalized to \((T_L - T)^{1/m}\), where \( m \) is a shaping parameter and Briere-1 is a special case when \( m = 2 \)). Whereas the Briere models explicitly estimate \( T_0 \), the linear equation allows a calculation of \( T_0 = -\frac{a}{b} \).

Nonlinear regression also was used to estimate mean numbers of whitefly eggs as a function of time and temperature, resulting in three-dimensional surfaces (Engesaard 1993). Numbers of eggs laid over time was modeled according to the equation \( \text{eggnum} = (p + qT) \exp(-eT/d) \), where \( T \) is temperature (Celsius). The parameters \((p + q)\) describe how quickly maximal oviposition is reached as a function of temperature, and \( e \) how quickly it returns to zero (Drost et al. 1998, Greenberg et al. 2000, Legaspi et al. 2008).

Duration of developmental times at each stage was recorded separately for each temperature. Stages considered were egg, first–fourth instars, prepupaee, and pupae; we also recorded total immature duration from egg to pupae. The insects were observed daily, and the occurrence of molting was used to distinguish between nymphal instars. The fourth-instar stage is translucent and flat and the characteristic red eyes begin to form in the prepupaee. The pupal stage is more opaque, and the red eyes are more prominent.

Life Table Analysis. Standard life table parameters were calculated at 15, 25, 27, and 30°C (e.g., Southwood and Henderson 2000): net reproductive rate (\( R_0 \), mean number of female progeny produced by a single female during its mean lifetime, expressed in \( \varphi/\varphi \)); gross reproductive rate (\( GRR \), in \( \varphi/\varphi \)); generation time (\( T \), mean period between birth of the parents and that of the offspring, in days); intrinsic rate of increase (\( r \), in \( \varphi/\varphi/d \)); finite rate of increase (\( \lambda \), in \( \varphi/\varphi/d \)); and doubling time (\( DT \), time for population to double, in days). Eggs were not reared to adulthood, so 1:1 sex ratio was assumed and numbers of female eggs was estimated by dividing total eggs by two (Wittmeyer and Coudron 2001, Legaspi et al. 2008).

Statistical Analysis. Nonlinear regression was performed using the NONLIN command (Least Squares Estimate) and the Gauss–Newton method. Life stages were analyzed separately as one-way analyses of variance, where duration was the response variable and temperature was treatment. Statistical analyses and life table calculations were performed using Systat 12 (Systat Software Inc., Chicago, IL).
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Results and Discussion

Analysis of Whitefly Development. Total immature developmental rate is shown as a function of temperature, together with linear regression and the nonlinear development function (Fig. 1). No individuals survived the 35°C treatment and were excluded from statistical analysis. Linear functions were used for eggs (Fig. 1A), instars (first-fourth; Fig. 1B) and pupal stages (prepupae and pupae; Fig. 1C) because nonlinear model estimates did not converge for these stages. For the combined immature stages (eggs to pupae, Fig. 1D), the linear model estimate for $T_0$ was 10.6°C ($x$-intercept in Fig. 1D), which is higher than the estimate of the Briere model at 7.3°C. However, $T_0$ estimate is comparable with that of 10.32°C reported for Bemisia argentifolii Bellows & Perring by using similar methods (Greenberg et al. 2000) and is close to that of 10.2 estimated for sweetpotato whitefly, Bemisia tabaci (Gennadius) (Q-biotype) on tomato, Solanum lycopersicum L. (Bonato et al. 2007). The thermal requirement for development from eggs to pupae was estimated as 487.8 degree-days (DD) ($K = 1/0.0020499$). By comparison, mean DD requirements for egg to adult were estimated at 483.4 for T. vaporariorum and 319.7 for B. argentifolii on sweetpotato, Ipomoea batatas (L.) Lam. (Greenberg et al. 2000). A thermal requirement for egg-to-adult development of 307 DD was calculated for B. tabaci on beans based on a lower developmental threshold of 11.53°C (Bosco and Caciagli 1998).

Briere-1 and -2 models were assessed as accurately predicting lower and upper threshold temperatures of codling moth, Cydia pomonella (L.) (Lepidoptera: Tortricidae), in apple (Malus spp.) orchards in Iran (≈8 and 34°C, respectively; Aghdam et al. 2009). In this study, the lethal temperature estimate of 45.9°C by the Briere model is similar to estimates obtained by Liu and Ye (2009) by using the same model on the fruit fly Bactrocera correcta (Bezzi) (Diptera: Tephritidae). The estimate of lethal temperature may be high in light of the observation that no insects survived the 35°C treatment. In some studies (Roy et al. 2002, Zamani et al. 2007), individuals that did not survive a temperature treatment are included in the analysis and developmental rate is set to zero. Applying this method here would have resulted in a lethal temperature estimate of 35°C. Bergant and Trdan (2006) discuss problems in using laboratory-derived estimates for describing biological thermal constants.

The Briere nonlinear models compare favorably when evaluated against linear and other nonlinear models such as those by Logan et al. (1976) and Lactin et al. (1995). One linear and three nonlinear models, including Briere-1, adequately described development of three economically important species of Ceratitis (Diptera: Tephritidae) in southern Africa (Grout and Stoltz 2007). Compared against several linear and nonlinear models, Briere-1 was recommended for describing development of the parasitoid Diadegma anurum (Thomson) (Hymenoptera: Ich-
neunonid) attacking the diamondback moth, *Plutella xylostella* (L.) (Golizadeh et al. 2008). Similar conclusions were reached regarding both Briere models on the leafminer parasitoid *Diglyphus isaea* (Walker) (Hymenoptera: Eulophidae) (Haghani et al. 2007). The Lactin and Briere-1 models were found to have excellent goodness-of-fit to data and were strongly recommended for describing development of the aphid parasitoids *Aphidius colemani* Viereck and *Aphidius matricariae* (Haliday) (Hymenoptera: Braconidae) (Zamani et al. 2007). Finally, the Briere-1 model was used to estimate lower developmental threshold (*T₀*) for the encyrtid endoparasitoid *Anagyrus anamatis* Gahan (Hymenoptera: Encyrtidae) (Pandey and Johnson 2006). The estimate of ∼12°C was in agreement with estimates obtained using the alternative method of Ikemoto and Takai (2000). In summary, the Briere models compare favorably with other nonlinear development models in goodness-of-fit to experimental data, and simplicity (having only three or four parameters), and clear biological meaning of those parameters (Roy et al. 2002, Smits et al. 2003).

Immature developmental durations for *S. simplex* are similar to those of other whitewells. Total duration of immature stages from eggs to pupae varied from 97.1 d at 15°C to 25.2 d at 30°C. Higher temperatures resulted in significantly shorter developmental times (Table 1).

Much of the work on life history in whitewells has been done on *B. tabaci*, which we use as a basis of comparison, given the lack of data on *S. simplex*. Development of an Italian colony of *B. tabaci* on beans varied from 70 d at 16°C to 22 d at ≥26°C (Bosco and Caciagli 1998), whereas development for the Q-bio-

### Table 1. Effect of temperature on immature survival (days) of *S. simplex*

<table>
<thead>
<tr>
<th>Life stage</th>
<th>Temp (°C)</th>
<th>Statistics</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>15</td>
<td>20</td>
</tr>
<tr>
<td>Egg</td>
<td>36.00 ± 0.82a</td>
<td>21.00 ± 0.26b</td>
</tr>
<tr>
<td>First instar</td>
<td>1.56 ± 0.18ab</td>
<td>1.00 ± 0.00b</td>
</tr>
<tr>
<td>Second instar</td>
<td>18.78 ± 1.34a</td>
<td>11.12 ± 0.18b</td>
</tr>
<tr>
<td>Third instar</td>
<td>11.67 ± 0.5a</td>
<td>6.18 ± 0.30b</td>
</tr>
<tr>
<td>Fourth instar</td>
<td>22.56 ± 0.62a</td>
<td>12.58 ± 0.34b</td>
</tr>
<tr>
<td>Prepupae</td>
<td>3.67 ± 0.64a</td>
<td>1.75 ± 0.23b</td>
</tr>
<tr>
<td>Pupae</td>
<td>3.67 ± 0.71a</td>
<td>2.38 ± 0.39b</td>
</tr>
<tr>
<td>Total immatures</td>
<td>97.11 ± 2.11a</td>
<td>56.31 ± 0.69b</td>
</tr>
</tbody>
</table>

Insects in 35°C treatment did not survive and are excluded from analysis; each stage analyzed separately for effects of temperature on life stage duration (means ± SE); Numbers in parentheses for total immatures indicates sample size; within each row, means followed by different letters are significantly different Tukey’s HSD test (*P* < 0.05).

### Table 2. Life history parameters for *S. simplex*

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Temp (°C)</th>
<th>15</th>
<th>20</th>
<th>25</th>
<th>27</th>
</tr>
</thead>
<tbody>
<tr>
<td>Generation time (<em>T</em>)</td>
<td>99.3</td>
<td>35.48</td>
<td>31.413</td>
<td>26.56</td>
<td></td>
</tr>
<tr>
<td>Intrinsic rate of increase (<em>r</em>)</td>
<td>0.0258</td>
<td>0.0864</td>
<td>0.0999</td>
<td>0.0978</td>
<td></td>
</tr>
<tr>
<td>Finite rate of increase (<em>λ</em>)</td>
<td>1.0262</td>
<td>1.0902</td>
<td>1.105</td>
<td>1.103</td>
<td></td>
</tr>
<tr>
<td>Doubling time (<em>DT</em>)</td>
<td>26.57</td>
<td>5.922</td>
<td>6.93</td>
<td>7.087</td>
<td></td>
</tr>
</tbody>
</table>

* R₀ = Σ *m₀*; summation of survivorship multiplied by age-specific fecundity per female, expressed in units of *μ* *μ*; *R₀* egg numbers divided by 2 assuming 1:1 sex ratio.

* GRR = Σ *S*; summation of age-specific fecundity per female in *μ* *μ*.

* T = (Σ *xₙ* *mₙ*) / R₀ in days.

* r = (ln R₀) / T in *μ* *μ* / d.

* λ = e⁺ in *μ* *μ* / d.

* DT = ln (2) / r in days.

Life Table Analysis. Reproductive parameters for *S. simplex* at each temperature are shown in Table 2. *S. simplex* reproduction was highest at 27°C where *R₀* = 23.114; GRR = 24.25; *T* = 31.413 d, 0.0999; *r* = 0.0978; *λ* = 1.103; *DT* = 6.93 d, and 6.93 d, respectively. The calculations are based on the assumption of a 1:1 sex ratio (e.g., Wittmeyer and Coudron 2001). However, they may underestimate actual reproductive values because sex ratios of immatures that successfully emerged as adults was female-biased (79.4%; 15:5:58).
loftini (Dyar) (Harbison et al. 2001); the generalist predators Delphastus catalinae (Horn) (Coleoptera: Coccinellidae) (Legaspi et al. 2008) and Podisus maculiventris (Say) (Heteroptera: Pentatomidae) (Legaspi 2004; Legaspi and Legaspi 2005) and the cactus moth, Cactoblastis cactorum (Berg) (Lepidoptera: Pyralidae) (Legaspi and Legaspi 2007).

As in the case for life history studies, much of the work on life tables in whiteflies has involved B. tabaci. Adult longevity of B. tabaci on soybean (15.3 ± 4.6 [mean days ± SE]) was significantly longer than on garden bean (10.6 ± 3.2) (Mansaray and Sundufu 2009). For Q-biotype on tomato, total fecundity per female ranged from 105.3 at 21°C to 41 at 35°C, whereas the intrinsic rate of increase ranged from 0.0450 at 17°C to 0.123 at 30°C (Bonato et al. 2007). R₀, T, r, λ, and DT values for B. tabaci on soybean were 82.69, 23.89, 0.18, 1.69, and 3.38, respectively (Mansaray and Sundufu 2009). On garden bean, these values were 54.98, 25.92, 0.15, 1.87, and 4.48, respectively.

The Enkegaard model did not provide a very good fit to the observed data (Fig. 2). Parameter estimates were $p = -30.21$, $q = 2.62$, and $w = 0.034$ (±SE = 8.83, 0.556, and 0.0038, respectively; $R^2 = 0.16$), where $T$ is temperature and $d$ is time (Enkegaard 1993).

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0.556, and 0.0038, respectively; $R^2 = 0.16$). The poor fit may be attributed to high variability in fecundity, and having relatively few data points because only four temperatures were studied, and adult duration was short. Nevertheless, the surface shows the expected combined effects of temperature and insect age on fecundity, i.e., asymptotic increases with temperature and decreases with time. The Enkegaard model has been applied to the alfalfa weevil, *Hypera postica* (Gyllenhal) (Coleoptera: Curculionidae) (Zahiri et al. 2010) and the pseudococcid predators *Nephus includens* (Boheman) and *Nephus bisignatus* (Kirsch) (Coleoptera: Coccinellidae) (Kontodimas et al. 2007). In both studies, the model results were in reasonable statistical agreement with experimental data.

Female adult survivorship was plotted on a linear scale (Fig. 3A) and shows the expected decline in adult longevity at increased temperatures. Numbers of individual females tested were 10, 17, 12, and 12 at 15, 25, 27, and 30°C, respectively. Duration of adulthood was significantly longer at 15°C compared with all other temperatures tested ($F = 20.61; df = 3, 48; P < 0.01; R^2 = 0.57$; Tukey’s honestly significant difference [HSD], $P < 0.05$) (Fig. 3B). At 15°C, adult longevity averaged 8.0 d, compared with ~2.5–4.2 d at the higher temperatures.

Daily and lifetime fecundity are shown as affected by temperature (Fig. 4). Temperature was not found to significantly affect lifetime fecundity ($F = 1.60; df = 3, 48; P = 0.20; R^2 = 0.09$) (Fig. 4E). At temperatures of 25 and 27°C, lifetime fecundity per female averaged 37.9 and 46.2, respectively. The temperature effect was not significant, probably due to high variability. Also, lower daily fecundity at lower temperatures may have been compensated by longer ovipositional periods (Fig. 4A–D).

*S. simplex* is a newly invasive pest of several species of *Ficus* plants in Florida. Because very little is known about the biology of *S. simplex*, the information presented herein will be useful in determining potential impact and control in Florida and possibly some other states, including more distant areas in California and Hawaii. The developmental data also may be useful in parameterization of insect phenology models such as the North Carolina State University–APHIS Plant Pest Forecast (NAPPFAST) program (Nietschke et al. 2007).
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