Life Table of *Tamarixia radiata* (Hymenoptera: Eulophidae) on *Diaphorina citri* (Hemiptera: Psyllidae) at Different Temperatures

Author(s): Mariuxi Lorena Gómez-Torres, Dori Edson Nava, and José Roberto Postali Parra


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ABSTRACT  Tamarixia radiata (Waterston, 1922) is the main parasitoid of Diaphorina citri (Kuwayama, 1907) and has been used in classical biological control programs in several countries. The current study investigated the biology and determined the fertility life table of T. radiata in different temperatures, to obtain information to support the establishment of a biological control program for D. citri in Brazil. Fifth-instar nymphs of D. citri were offered to females of T. radiata for parasitism, for 24 h. Then, the parasitoid was removed and the nymphs were placed in incubators at 15, 20, 25, 30, or 35 ± 1°C, 70 ± 10% RH, and a 14-h photophase. The percentages of parasitism and emergence, the sex ratio, and the preimaginal period of T. radiata were determined. The fertility life table was developed from the biological data. The highest parasitism rate (77.24%) was obtained at a temperature of 26.5°C, and the lowest parasitism rates occurred at 15 and 35°C (23.1 and 40.2%, respectively). The highest percentages of emergence of the parasitoid occurred at 25, 30, and 35°C (86.7, 88.3, and 78.8%, respectively), with the calculated peak at 30.8°C (89.90%). The duration of the preimaginal developmental period for both females and males of T. radiata was inversely proportional to temperature in the thermal range of 15–35°C. The development of T. radiata occurred at all temperatures studied, and the highest viability of the preimaginal period occurred at 25°C. The highest values of net reproductive rate and finite growth ratio (λ) were observed at 25°C, so that in each generation the population of T. radiata increased 126.79 times, higher than the values obtained at the other temperatures.

KEY WORDS  citrus, parasitism, life cycle, net reproductive rate

Diaphorina citri (Kuwayama, 1907) (Hemiptera: Psyllidae) has been associated with citrus in Brazil since the 1940s (Costa Lima 1942) and now occurs in most of the country. In Brazil until 2004, insecticide control of D. citri was carried out sporadically, that is, only when population outbreaks occurred. The only injuries caused by the pest had been leaf curling and shoot deformation, which prevented normal growth. These injuries were caused by a toxin released by D. citri as it feeds on sap (Fundecitrus 2004). In 2004, Huanglongbing (HLB), also known as citrus greening pathogen, was first detected in Brazil, specifically in citrus groves in the state of São Paulo, and D. citri was identified as the vector of the disease (Teixeira et al. 2005).

Insecticide control of D. citri became the principal strategy for HLB management in orchards in Brazil. The consequent frequent use of insecticides has caused a series of problems, including the destruction of the natural enemies of other major citrus pests, which had been kept below the economic threshold level through biological control, in accordance with the principles of integrated pest management (IPM) (Yamamoto and Parra 2005). The wide geographical distribution of D. citri in Brazil and its potential as a vector of HLB may negatively affect citrus crops, as has been reported in other countries (Fundecitrus 2004, Parra et al. 2010).

Alternatives for management of D. citri are currently being studied, and include biological control with Tamarixia radiata (Waterston, 1922) (Hymenoptera: Eulophidae). T. radiata is an idiobiont ectoparasitoid that has been used in classical biological control programs, significantly reducing D. citri populations in several parts of the world (Aubert and Quilici 1984, Chien and Chu 1996, Étienne et al. 2001, Hoy and Nguyen 2000, Skelley and Hoy 2004). In Brazil, T. radiata was first identified in 2006 in the state of São Paulo (Gómez Torres et al. 2006). However, T. radiata is not found in all regions of Brazil, and the parasitism rate is highly variable.

The success of a biological control program depends on factors that affect the field efficiency of organisms raised under laboratory conditions (Bigler 1986). Climate is probably the most important of these factors, given that a complex set of meteorological variables...
affects the development, emergence, survival, activity, and fecundity of the parasitoids released; temperature and relative humidity are the most influential factors (King et al. 1985, Fauvergue and Quilici 1991). A life table is extremely useful for understanding the population dynamics of the target species, because it provides an integrated view of the biological characteristics of a given population under defined environmental conditions, as well as showing the development rate, longevity, and fecundity, all of which are expressed in terms of population means (Coppel and Mertins 1977, Silveira Neto et al. 1976).

The objective of the current study was to investigate the biology of *T. radiata* and to construct life tables at different temperatures, to determine the possible impacts of this factor on parasitism, emergence, development, and the growth potential of the population of this parasitoid, envisaging its mass production. This study will contribute to the establishment of a biological control program for *D. citri*, as a component of IPM in different citrus-growing regions of Brazil.

**Materials and Methods**

We collected adults of *D. citri* and *T. radiata* from citrus groves in the state of São Paulo. The insect populations were maintained at the Insect Biology Laboratory of the Department of Entomology and Acarology of the Luiz de Queiroz School of Agriculture, University of São Paulo, Piracicaba.

**Rearing *D. citri***. *D. citri* was reared by a technique adapted from those proposed by Skelley and Hoy (2004) and Nava et al. (2007). We used seedlings of the orange jasmine *Murraya paniculata* (L.) Jack, 25–30 cm in height. The plants were grown in a substrate of vermiculite and compost (1:1), and maintained in incubators (30 ± 1°C, 60 ± 10% RH, and a 14-h photophase), until new shoots emerged. No pesticides were used. The plants were then transferred to acrylic cages (34 × 34 × 40 cm) containing adult *D. citri* females, from which eggs were collected for up to 5 d. After the eggs were laid, the nymphs were transferred to rearing cages (70 × 50 × 50 cm) and maintained in incubators (25 ± 1°C, 70 ± 10% RH, and a 14-h photophase).

**Rearing *T. radiata***. To rear *T. radiata*, we used fourth- and fifth-instar *D. citri* (Chu and Chien 1991, Skelley and Hoy 2004). *T. radiata* populations were maintained in rearing cages measuring 60 × 50 × 52 cm, in incubators (25 ± 1°C, 70 ± 10% RH, and a 14-h photophase). Fourth- and fifth-instar *D. citri* nymphs, which remained attached to the plants, were parasitized by *T. radiata* for a period of 24 h in cages measuring 45 × 35 × 37 cm. The nymphs were then transferred, together with the plants, to rearing units, where they remained for the duration of the preimaginal period. After the adults emerged, we collected 80% of them for use in the experiments, leaving the remaining adults in the rearing units for use in rearing and maintaining additional *T. radiata* populations.

**Development of *T. radiata* on *D. citri* at Different Temperatures**. Recently emerged females and males of *T. radiata* were kept for 24 h in cages measuring 60 × 50 × 50 × 52 cm, to mate. During this period the insects were fed with a mixture of pure honey and pollen (Chien et al. 1994), provided on small plates in the upper part of the cage, which was made of glass. Afterwards, the females were placed in individual cages consisting of plastic cylinders (15.5 × 5.5 cm), with their openings covered with voile for ventilation. Each female *T. radiata* was offered a myrtle plant with 30 fifth-instar nymphs of *D. citri*, according to Chu and Chien (1991) (Gomez-Torres, 2009). Parasitism was allowed for 24 h, in incubators at temperatures of 15, 20, 25, 30, and 35 ± 1°C, RH 70 ± 10%, and a 14-h photophase. After, the female was removed from the cage with the use of a glass tube (12 × 75 mm), and the parasitized nymphs of *D. citri* were maintained in the same temperatures until the adults emerged.

For each of the temperatures (treatment), four replicates were used, each consisting of five myrtle plants with 30 nymphs, totaling 150 nymphs/replicate and 600 nymphs/treatment. The following biological parameters were evaluated: percentage of parasitism, duration of the preimaginal (egg-adult) period, percentage of emergence, and sex ratio. The percentage of parasitism was determined on the fifth day after the nymphs were offered to the parasitoids, evaluating the formation of mummies. The sex ratio was defined as the number of females divided by the total number of individuals.

**Life Table of *T. radiata* at Different Temperatures**. Ten pairs of 24-h-old individuals, fed with pure honey and pollen (Chien et al. 1994), were placed in individual cylindrical plastic cages (15.5 × 5.5 cm) with the openings covered with voile (for ventilation). To each female parasitoid, 30 fifth-instar nymphs of *D. citri* reared on myrtle plants were offered daily. After 24 h, the plants containing the parasitized nymphs were placed in climate-controlled chambers maintained at the temperatures of 15, 20, 25, 30, and 35 ± 1°C, RH 70 ± 10% RH, and 14-h photophase. Longevity and fecundity were evaluated daily; fecundity was determined on the fifth day after parasitism, based on the number of mummified nymphs.

Each treatment (temperature) consisted of ten replicates (pairs), and the adults were observed daily until they died. Subsequently, we calculated the mean number of parasitized nymphs per female (nx) on each date of parasitism (x), based on the total number of females, the cumulative survival rate of females (Ix) during the oviposition period, and the number of descendants that survived to age x. The survival- and fecundity-related data were summarized in a life table, in accordance with the model proposed by Maia et al. (2000). We calculated the net reproductive rate, the estimated intrinsic rate of increase, the (observed) intrinsic rate of increase, the interval between generations, and the finite rate of increase using the equations from Southwood (1978).

**Statistical Analysis**. To determine the relationship between temperature and the percentages of parasit-
ism, emergence, and the duration of the preimaginal period, the data were analyzed by the nonlinear polynomial fit model. For the sex ratio, the data were submitted to analysis of variance (ANOVA), and the means were compared by Tukey test ($P < 0.05$). The life table parameters and their respective standard errors were estimated according to the method proposed by Meyer et al. (1986). The means were compared by the two-tailed Student’s $t$-test ($P < 0.06$) with the lifetable.sas files (Maia et al. 2000). The analyses were carried out with the use of the program SAS (Statistical Analysis System), version 9.2, 2002–2008 (SAS Institute, Inc., Cary, NC).

**Results**

**Biology.** Temperature influenced the rates of both parasitism and emergence ($F = 92.20, P < 0.01$; and $F = 25.29, P < 0.01$, respectively) (Fig. 1A, B). The parasitism rate was highest at the temperatures of 25 and 30°C, corresponding to 85.50 and 72.80%, respectively. At 15 and 35°C the parasitism rates were 23.1 and 40.2%, respectively. The optimum temperature at which the highest parasitism occurred was 26.3°C, which corresponded to the predicted value of 77.26% parasitism. For emergence, the highest percentages occurred at the temperatures of 25, 30, and 35°C, varying from 88.30 to 78.80%, with the estimated maximum at 30.8°C with an emergence of 84.91%. The lowest emergence rates were recorded at 15 and 20°C (Fig. 1). Temperature had no significant effect on temperature, with $P$ values below 0.5 ($F = 1.731; df = 4; P = 0.196$).

The mean duration of the preimaginal developmental period of $T. radiata$ on fifth-instar nymphs of $D. citri$ was inversely proportional to temperature for both females ($F = 191.21; P < 0.01$) and males ($F = 82.02; P < 0.01$) (Fig. 2A, B). For females of $T. radiata$, the duration varied from 489.60 h at 15°C to 247.20 h at 35°C; for males, the duration varied from 343.20 h at 15°C to 146.40 h at 35°C. This demonstrated that the preimaginal development period of the males is more rapid than the females. That is, within the temperature range studied (15–35°C), for each degree-centigrade increase in temperature, there was a reduction in the development period of $\approx 10$ h for males and $13$ h for females (Fig. 2A, B).

**Fertility Life Table.** The mean duration of one generation ($T$) varied with the temperatures in which the parasitoid developed. The variation was from 10.43 d at 35°C to 20.32 d at 15°C (Table 1). The net reproduction rate ($Ro$) differed significantly as a function of temperature, with the highest fecundity at 25°C, 12.83 times higher than the lowest Ro, obtained at 15°C (Table 1).

All the values of the intrinsic rate of increase ($r_m$) were positive, indicating an increase in population at the temperatures evaluated; this parameter varied from 0.1828 to 0.3742, and was highest at 25°C. For the finite rate of increase ($\lambda$), the values obtained at 25°C was the biggest and differ from the other values (Table 1). The maximum rate of increase varied in concordance with the previous results, according to temperature, with the first peaks at the temperatures of 25, 30, and 35°C, and was more delayed at 15 and 20°C (Fig. 3). These values are directly correlated with the duration of the insect’s cycle, because the cycle was shortest at 35°C and prolonged at 15°C (Table 1).

The net reproduction rate ($Ro$) was highest at 25°C, because in each generation the population of $T. radiata$ will increase 126.79 times, more than the rates obtained at the other temperatures (Table 1).
Discussion

The results obtained in this study demonstrate that the development of *T. radiata* is influenced by temperature, showing that 25°C is the optimum temperature for growth of this parasitoid, and is where the highest reproduction rate occurs, although the point of maximum emergence is close to 30°C.

The values of parasitism, emergence, and sex ratio observed in this study are similar to those obtained by Chu and Chien (1991), who studied the biology of *T. radiata* in laboratory conditions at 25°C, 100% RH, and a 14-h photophase. In this context and taking as a reference that the mean annual temperature in the state of São Paulo oscillates between 20 and 25°C, it is important to note that the results obtained in the current study, at the temperatures of 15, 20, 25, 30, and 35°C, provide basic information for better understanding of the dynamics and performance of *T. radiata* in citrus-growing regions of São Paulo. Similar results have been obtained for other species of the family

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**Table 1.** Characteristics of *T. radiata* reared at various temperatures, under controlled conditions (relative humidity 70 ± 10% and a 14 h photophase)

<table>
<thead>
<tr>
<th>Temp (°C)</th>
<th>T (days)</th>
<th>( R_o )</th>
<th>( r_m )</th>
<th>( \lambda )</th>
</tr>
</thead>
<tbody>
<tr>
<td>15</td>
<td>20.32 ± 0.24a</td>
<td>9.88 ± 1.05d</td>
<td>0.1826 ± 0.008d</td>
<td>1.2003 ± 0.010d</td>
</tr>
<tr>
<td>20</td>
<td>16.84 ± 0.12ab</td>
<td>23.62 ± 2.48c</td>
<td>0.2531 ± 0.013c</td>
<td>1.258 ± 0.016c</td>
</tr>
<tr>
<td>25</td>
<td>15.53 ± 0.21bc</td>
<td>126.79 ± 0.23a</td>
<td>0.3742 ± 0.002a</td>
<td>1.4538 ± 0.004a</td>
</tr>
<tr>
<td>30</td>
<td>11.78 ± 0.13c</td>
<td>55.63 ± 0.23b</td>
<td>0.3378 ± 0.002b</td>
<td>1.4919 ± 0.012b</td>
</tr>
<tr>
<td>35</td>
<td>10.43 ± 0.35c</td>
<td>21.27 ± 2.01c</td>
<td>0.2526 ± 0.009c</td>
<td>1.2839 ± 0.014c</td>
</tr>
</tbody>
</table>

\( T \), mean generation time; \( R_o \), net reproductive rate; \( r_m \), intrinsic rate of increase; \( \lambda \), finite rate of increase. Values followed by the same lower-case letter are not significantly different, as assessed by two-tailed Student’s t-test (\( P \leq 0.06 \)).

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**Fig. 3.** Age-specific survival rate (\( l_x \)) and age-specific fecundity (\( m_x \)) for *T. radiata* on *D. citri* at temperatures of 15, 20, 25, 30, and 35 ± 1°C, 70 ± 10% RH, and 14 h photophase.
Eulophidae. According to Wang et al. (1999), temperatures ranging from 20 to 30°C favor the development, survival, and reproduction of members of Eulophidae. Although parasitism occurs at high temperatures, the emergence rate decreases drastically at temperatures above 32.5°C. In contrast, the parasitoids do not emerge at 15°C. Those authors found that the number of hosts parasitized by eulophid females, and the eulophid fertility rates were higher at 25°C than at other temperatures studied, a similar finding to our observations for *T. radiata*.

Hondo et al. (2006) evaluated, on the basis of thermal tolerance, the development, efficiency, and reproduction of seven species of the family Eulophidae and concluded that all the species were adapted to high temperatures, their reproductive capacity decreasing in the 15–20°C range. Our findings regarding *T. radiata* show that it is important to evaluate thermal tolerance, particularly in relation to the effects on development and reproduction, before choosing a biological control agent for a given pest.

Minkenberg (1989), Bazzocchi et al. (2003), and Duale (2005) also reported that temperature influences the rate at which Eulophidae develop. However, the findings of the current study have more in common with those obtained by Chu and Chien (1991), who studied *T. radiata* under similar conditions. Chu and Chien reported an interval between generations of 17.8 d, a net reproductive rate of 285 female offspring/female, an intrinsic rate of increase of 0.31, and a finite rate of increase of 1.37.

Other studies involving Eulophidae have underscored the importance of temperature for development and reproduction (Acosta and O’Neil 1999, Castillo et al. 2006). The findings reported by Castillo et al. (2006) are similar to those of the current study. Those authors demonstrated that the eulophid preimaginal development time decreased as the temperature increased from 20 to 33°C. They also found that the parasitoids did not develop at temperatures below 15°C; that fecundity was greatest at 25°C and 30°C; and that development decreased sharply at temperatures ≥33°C.

Acosta and O’Neil (1999) developed life tables for eulophid populations from Honduras, Colombia, and Mexico, testing at 15, 24, and 30°C. The authors concluded that the discovery of biotypes adapted to low temperatures is important to the understanding of the biogeography of parasitoids, their hosts, and host plants, as well as of the population dynamics in geographically distinct regions. They also noted that such variability might serve as the basis for the selection of populations adapted to the climate conditions common to the regions where they would be used to control the target insect. Viggiani et al. (2000) discussed the importance of understanding the biological parameters of Eulophidae under different temperature regimes. The authors demonstrated, under field conditions, that these parasitoids are inefficient when the climate conditions were less than ideal for phytophagy.

A complex set of meteorological variables can affect the development, emergence, survival, activity, and fecundity of *T. radiata*. Among these variables, temperature occupies a prominent position, because it has a direct influence on these parasitoids.

The information obtained in the current study facilitates the understanding of the influence of temperature on the physiological and ethological parameters studied. These data will allow laboratory rearing of *T. radiata* as well as its release in the field, thus making it possible to deploy an additional strategy to manage *D. citri* at the different times of year, as well as its eventual establishment as another tactic among the measures to be applied in the different climate regions of Brazil for the control of HLB in citrus-growing areas.

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