INTEGRATED PEST CONTROL IN CITRUS-GROVES
Demographic parameters of the Mediterranean fruit fly at various laboratory conditions

A. Gil
Center for Information Sciences, Superior Council for Scientific Research, Madrid, Spain

M. Muñiz
Institute of Edaphology and Plant Biology, Superior Council for Scientific Research, Madrid, Spain

Summary

Demographic parameters and their standard errors have been estimated for females of Ceratitis capitata (Wied.) at 31.28, 25, 22 and 19°C. Highest mortalities were obtained during the larval stage and, generally, the lowest mortalities occurred at 22°C. Intrinsic rate of increase (r) varied from 0.103 at 19°C to 0.237 at 31°C. The longest mean generation time (T) ranged from 22.97 days at 31°C to 55.57 days at 19°C. The highest net reproductive rate (R₀ = 308.72 days) was obtained at 19°C.

A new mathematical methodology to estimate demographic parameters and their standard errors is reported.

1. Introduction

During the last ten years it has been pointed out the significance of biological studies on the species of economic importance in order to acquire basic scientific knowledge of the insect pest (5). So, it will possible to apply the different programmes and techniques with an adequate level of efficiency.

Ceratitis capitata (Wied.) is a highly destructive pest in the Mediterranean basin. In Spain the direct and indirect damage is nearly 1% of the citrus fruit production. However, as Carey pointed out, little work has been done on the demography of this species (3). Rössler used the net reproductive rate and the generation time for determining the quality of lab-reared fruit flies (13). In other cases, more extensive studies have been done, but regarding one specific temperature (3, 4, 15); however, errors of such a parameters, a very important topic in statistical works, were not included.

Using data from earlier studies on daily reproductive activity of Ceratitis at various experimental conditions (12), we report here a new mathematical methodology and some results on the demography of this insect. In this manner, we collaborate to increase the basic knowledge of this major pest in many tropical and subtropical countries.

2. Material and methods

2.1. Laboratory methodology

In the before mentioned studies, one day old males and females of the Medfly were removed from a very well adapted population to lab rearing conditions and then were introduced in specially designed cages with adult
food and water at the rate of one couple per cage (9,10). Each cross was carried out in 20 replicates consisting of 1 male and female each for all environmental conditions of this work.

Eggs were collected once daily and transferred to a Petri dish in the bottom of which, a black filter paper was placed in order to maintain an optimal level of moisture. Neonatal larvae were daily seeded in vials (5 cm dia x 9 cm long) containing 5 grs of a new larval diet (1.11) and provided with a porous stopper to get an adequate aeration.

The following data were daily collected: Oviposition, egg hatch, larval development time, pupal and adult production, mortality of eggs, larvae, pupae and adults, sex segregation of the newly emerged adults and longevity of females. In this study food was unlimited and there were no mortality factors other than physiological ones.

2.2. Mathematical methodology

For the sake of simplicity we assume that a lot of individuals increases or decreases with an intrinsic rate \( r \) of increase, positive or negative. The deterministic model is

\[
N_t = N_0 \cdot e^{rT}
\]

where \( N_t \) is the number of individuals at time \( t \). We are also assumed that adult female populations of Ceratitis have reached a stable age distribution; so, if a such population is divided into classes, according their age, each of them has its own growing law, but the proportion between the number of individuals of two different classes is a constant.

Now, let \( B_t \) the number of emergencies per unit of time in the \((0,t)\) interval. The birth rate in the population is

\[
\lambda = \frac{B_t}{N_t}
\]

Furthermore, if \( p_x \) is the probability of surviving to age \( x \), the proportion of individuals, aged between \( x \) and \( x+1 \) in the stable population is

\[
c_x = \frac{B_{t-x} \cdot p_x}{N_t} = \frac{\lambda p_x \cdot N_{t-x}}{N_t} = \lambda p_x \cdot e^{-rx}
\]

Thus, \( \sum c_x = 1 \) and then

\[
\lambda = 1 / \sum p_x \cdot e^{-rx} \quad (1)
\]

The death rate is defined by

\[
\mu = \lambda - r \quad (2)
\]

Also, if \( m_x \) is the mean number of female offspring produced in a unit of time by a female aged \( x \), then

\[
B_t = \sum_x N_t \cdot c_x m_x = \lambda N_t \sum_x p_x m_x e^{-rx}, \text{ so that } \\
\sum_x p_x m_x e^{-rx} = (1/\lambda) \cdot (B_t/N_t) \quad \text{ or } \\
\sum_x p_x m_x e^{-rx} = 1 \text{ (Lotka equation)} \quad (3)
\]

As Birch pointed out (2), usual methods of calculation of \( r \) may be found in Dublin and Lotka (6) or Lotka (7). However, these conventional calculations don't offer adequate solutions for high values of this parameter. We have preferred to start from the following initial value:

\[
r_0 = \frac{1}{n} \sum \ln \frac{N_{t+1}}{N_t}
\]
where the sum is extended to a sufficient number of days \( n = 3\omega \); \( \omega \) is the extinguished time. So, it will be possible to estimate the standard errors of \( r \), as we do later.

From (3), we derived the recurrent equation:

\[
\begin{align*}
    r_{i+1} = \ln\left[\frac{\sum k p_x m_x e^{-r_i(x-1)}}{\sum k p_x m_x x^{-r_i}}\right]
\end{align*}
\]

The process is finished when one of the following conditions results:

a) The absolute value of two consecutive terms, \( r_i \) and \( r_{i+1} \), is less than \( 5.10^{-6} \), in which case we take \( r = r_i \).

b) \( |r_i| > 5.10^{-6} \) and sign \( r_i \) \# sign \( r_0 \). In this case \( r = r_0 \).

c) If the number of iterations is greater than 50, then \( r = r_{50} \).

We have considered that \( r \) is the basic parameter, so that, both, the mean generation time \( (T) \) and the net reproductive rate \( (R_0) \) are functions of \( r \). The former is defined as

\[
T = \frac{TF + TG}{2}
\]

where

\[
TF = \sum x p_x m_x / \sum x p_x m_x \quad \text{and}
\]

\[
TG = \sum x p_x m_x e^{-rx} / \sum x p_x m_x e^{-rx}
\]

Last expressions are the age of females at time in which they produce female offspring.

Net reproductive rate is the factor by which one generation is multiplied to obtain the next one:

\[
R_0 = N_{t+1} / N_t = e^{rT}
\]

In particular, for \( T = 1 \), expression (5) is known as finite rate of increase.

The method of calculating \( R_0 \) allows us to estimate the standard error \( (S) \) of \( r \):

\[
SE(r) = \sqrt{\frac{\text{Var}(r)}{n}}
\]

Taking derivatives in (4) and (5) with respect to \( r \), we obtained the standard error of \( T \) and \( R_0 \):

\[
SE(T) = T \cdot r \left( \frac{\text{Var}(r)}{n} \right)
\]

In like manner, from (1) and (2):

\[
SE(\lambda) = \lambda^2 \sum x p_x e^{-rx} \cdot SE(r)
\]

\[
SE(\mu) = \lambda^2 \sum x p_x e^{-rx} - 1 \cdot SE(r)
\]

A programme named TYVI was written in FORTRAN IV language to estimate \( r, T, R_0, \lambda \) and \( \mu \), as well as their standard errors. For this purpose, it is necessary to know the daily emergence rate and mortality in the \((x, x+1)\) interval.

3. Results and discussion

Highest mortalities of 54, 42, 40, 33 and 40, for 31, 28, 25, 22 and 19°C, respectively, were obtained during the larval stage (Table 1). Lowest mortalities occurred during the pupal stage, except for 19°C. At this temperature, egg mortality was 48% and larval mortality was 40%.

153
### Table I. Life table of *Ceratitis capitata* (Wied.) (12 : 12 hrs L : D)

<table>
<thead>
<tr>
<th>Experimental conditions</th>
<th>x</th>
<th>1_x</th>
<th>d_x</th>
<th>100q_x</th>
<th>s_x</th>
<th>Gen.mort. (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>T: 31 ± 1ºC, RH: 73 ± 3%</td>
<td>Egg</td>
<td>1179</td>
<td>302</td>
<td>25,61</td>
<td>25,61</td>
<td>71,08</td>
</tr>
<tr>
<td></td>
<td>Larvae</td>
<td>877</td>
<td>476</td>
<td>54,28</td>
<td>65,99</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Pupae</td>
<td>401</td>
<td>60</td>
<td>14,96</td>
<td>71,08</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Adult</td>
<td>341</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>T: 28 ± 1ºC, RH: 67 ± 2%</td>
<td>Egg</td>
<td>1340</td>
<td>269</td>
<td>20,07</td>
<td>20,07</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Larvae</td>
<td>1071</td>
<td>452</td>
<td>42,20</td>
<td>53,81</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Pupae</td>
<td>619</td>
<td>24</td>
<td>3,88</td>
<td>55,60</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Adult</td>
<td>595</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>T: 25 ± 1ºC, RH: 57 ± 4%</td>
<td>Egg</td>
<td>1731</td>
<td>538</td>
<td>31,08</td>
<td>31,08</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Larvae</td>
<td>1193</td>
<td>475</td>
<td>39,82</td>
<td>58,52</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Pupae</td>
<td>718</td>
<td>16</td>
<td>2,23</td>
<td>59,45</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Adult</td>
<td>702</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>T: 22 ± 1ºC, RH: 67 ± 4%</td>
<td>Egg</td>
<td>1831</td>
<td>494</td>
<td>26,98</td>
<td>26,98</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Larvae</td>
<td>1337</td>
<td>447</td>
<td>33,43</td>
<td>51,39</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Pupae</td>
<td>890</td>
<td>11</td>
<td>1,24</td>
<td>51,99</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Adult</td>
<td>879</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>T: 19 ± 1ºC, RH: 78 ± 3%</td>
<td>Egg</td>
<td>1777</td>
<td>855</td>
<td>48,11</td>
<td>48,11</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Larvae</td>
<td>922</td>
<td>365</td>
<td>39,59</td>
<td>68,66</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Pupae</td>
<td>557</td>
<td>37</td>
<td>6,64</td>
<td>70,74</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Adult</td>
<td>520</td>
<td></td>
<td></td>
<td></td>
<td>70,74</td>
</tr>
</tbody>
</table>

x = Stage of life cycle; l = Number living at beginning of stage in the x column; d = Number dying within stage in the x column; 100q_x = Percentage mortality of the stage in the x column; s_x = Percentage mortality of the generation after stage in the x column. Gen.mort. = Generation mortality. Symbols given by Micinski et al. (8).

Generation mortality (egg to adult) varied from 71% at 31ºC and 19ºC to 52% at 22ºC. Note that, in general, the lowest mortalities were obtained at 22ºC. At this temperature and 67% RH we obtained the optimal reproductive parameters of this insect (12). In this Table, the number living are referred to the mean total production in each stage and are related to the whole fertility period of females.

Table II shows the values of the various demographic parameters and their standard errors. The highest intrinsic rate of increase was obtained at 31ºC with the shortest mean generation time, but the shortest net reproductive rate. The highest net reproductive rate was obtained at 19ºC.

Values of these parameters at 25ºC and 57% RH are similar to those reported by Rössler (13) and Carey (3) with data taken from Shoukry and Hafez (14). This fact is a result of the different methodology and lab-rearing.
<table>
<thead>
<tr>
<th>Experimental conditions</th>
<th>Intrinsic rate of birth ($\lambda$)</th>
<th>Intr. rate of death ($\mu$)</th>
<th>Intr. rate of increase ($r$)</th>
<th>Finite rate of increase ($e^r$)</th>
<th>Mean generation time ($T$)</th>
<th>Net reproductive rate ($R_0$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>$T = 31 \pm 1^\circ C$</td>
<td>$0.272 \pm 0.015$</td>
<td>$0.035 \pm 0.003$</td>
<td>$0.237 \pm 0.012$</td>
<td>$1.27 \pm 0.015$</td>
<td>$22.97 \pm 0.35$</td>
<td>$233.15 \pm 61.82$</td>
</tr>
<tr>
<td>RH = $73 \pm 3%$</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$T = 28 \pm 1^\circ C$</td>
<td>$0.262 \pm 0.013$</td>
<td>$0.034 \pm 0.002$</td>
<td>$0.228 \pm 0.011$</td>
<td>$1.26 \pm 0.014$</td>
<td>$25.12 \pm 0.43$</td>
<td>$306.69 \pm 81.89$</td>
</tr>
<tr>
<td>RH = $67 \pm 2%$</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$T = 25 \pm 1^\circ C$</td>
<td>$0.236 \pm 0.015$</td>
<td>$0.025 \pm 0.003$</td>
<td>$0.211 \pm 0.012$</td>
<td>$1.24 \pm 0.015$</td>
<td>$26.64 \pm 0.42$</td>
<td>$277.59 \pm 88.99$</td>
</tr>
<tr>
<td>RH = $67 \pm 4%$</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$T = 22 \pm 1^\circ C$</td>
<td>$0.169 \pm 0.007$</td>
<td>$0.015 \pm 0.001$</td>
<td>$0.154 \pm 0.006$</td>
<td>$1.17 \pm 0.007$</td>
<td>$36.34 \pm 0.50$</td>
<td>$274.01 \pm 61.90$</td>
</tr>
<tr>
<td>RH = $67 \pm 4%$</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$T = 19 \pm 1^\circ C$</td>
<td>$0.109 \pm 0.004$</td>
<td>$0.005 \pm 0.0004$</td>
<td>$0.103 \pm 0.004$</td>
<td>$1.11 \pm 0.004$</td>
<td>$55.57 \pm 0.62$</td>
<td>$308.72 \pm 60.42$</td>
</tr>
<tr>
<td>RH = $78 \pm 3%$</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

(12 : 12 hrs. L : D regime; Mean ± SE)
REFERENCES


