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Effects of temperature on biology and life table parameters of the Asian citrus psyllid, *Diaphorina citri* Kuwayama (Homoptera: Psyllidae)

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Summary

The development, survivorship, longevity, reproduction, and life table parameters of the Asian citrus psyllid, *Diaphorina citri* Kuwayama were evaluated at 10°C, 15°C, 20°C, 25°C, 28°C, 30°C and 33°C. The populations reared at 10°C and 33°C failed to develop. Between 15°C and 30°C, mean developmental period from egg to adult varied from 49.3 days at 15°C to 14.1 days at 28°C. The low-temperature developmental thresholds for 1st through 5th instars were estimated at 11.7°C, 10.7°C, 10.1°C, 10.5°C and 10.9°C, respectively. A modified Logan model was used to describe the relationship between developmental rate and temperature. The survival of the 3rd through 5th nymphal instars at 15-28°C was essentially the same. The mean longevity of females increased with decreasing temperature within 15-30°C. The maximal longevity of individual females was recorded 117, 60, 56, 52 and 51 days at 15°C, 20°C, 25°C, 28°C and 30°C, respectively. The average number of eggs produced per female significantly increased with increasing temperature and reached a maximum of 748.3 eggs at 28°C ($P < 0.001$). The population reared at 28°C had the highest intrinsic rate of increased (0.199) and net reproductive rate (292.2); and the shortest population doubling time (3.5 days) and mean generation time (28.6 days) compared with populations reared at 15-25°C. The optimum range of temperatures for *D. citri* population growth was 25-28°C.

Key words: Asian citrus psyllid, life table, temperature effect

Introduction

Citrus is one of the most important economic crops in the USA with about 500 000 ha in citrus groves mostly in California, Florida, Texas and Arizona. In Florida alone, citrus encompasses 857 687 planted acres with a total of 107 million trees in the 33 citrus producing counties. The annual earning on citrus is estimated at $1.1 billion (Tsai & Wang, 1999). Citrus greening disease or Huanglungbin is the most serious disease of citrus in the world (Aubert, Grisoni, Villemin & Rossolin, 1996; Su & Huang, 1990; Tsai, Chen, Shen & Jin, 1988). The Asian citrus psyllid (*Diaphorina citri* Kuwayama) is the most efficient vector of citrus greening bacterium (*Liberobacter asiaticum*) throughout Asia and the Far East (Catling, 1970; Pande, 1971; Tsai *et al.*, 1988). The combined presence of psyllid vector and greening agent has been the limiting factor in citrus production in these areas. On 3 June 1998, the Asian citrus psyllid was first found in South Florida. The subsequent finding of *D. citri* widespread in Broward, Palm Beach, Martin, Dade, St. Lucie, Hendry and Collier Counties in a 3-month period has been reported (Halbert, Brown & Dixon, 1998). Given high reproductive potential of this vector during favourable conditions of weather and food availability (Catling, 1970; Mead, 1977; J H Tsai, unpublished data), this pest is expected to spread throughout citrus producing areas in Florida in 2-3 years. It poses a serious threat to other citrus producing states in the near future.

The Asian citrus psyllid is of known Far Eastern origin (Mead, 1977). In the last three decades, research reports on Asian citrus psyllid have mainly focussed on the transmission of citrus greening agent (Salibe & Cortez, 1966; Martinez & Wallace, 1967; Su & Huang, 1990; Capoor, Rao & Viswanath, 1974). Only a few researches related to the field biology of this pest (Catling, 1970; Capoor *et al.*, 1974; Pande, 1971; Yang, 1989). Little is known of the biology of *D. citri*, especially about its developmental rate, temperature threshold, age-specific fecundity, and survival in the Western Hemisphere. A thorough understanding of pest biology and population dynamics is essential for development of a reliable pest population prediction system and management strategies. Therefore, we initiated a study to quantify the Asian citrus psyllid development, reproduction and longevity in relation to temperature and to provide an experimental basis for developing an overall psyllid population model.

Materials and Methods

Psyllid and host sources

A stock culture of Asian citrus psyllid (*Diaphorina citri* Kuwayama) originated from the orange jessa-

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mine [*Murraya paniculata* (L.) Jack] plants in Pompano Beach, Broward County, Florida, USA. The culture was maintained on potted orange jessamine plants (40-50 cm tall), in a walk-in insect rearing room at 28 ± 1°C, 75-80 r.h., and a photoperiod of 13:11 (L:D) h. After a 4-month rearing period, the ensuing colonies were used for the tests. The identity of *D. citri* was confirmed by S E Halbert at the Division of Plant Industry (DPI), Florida Department of Agriculture and Consumer Services (FDACS), Gainesville, FL. Voucher specimens were deposited at the collection of the DIP, FDACS. Seedlings of orange jessamine at the two to three leaf stage, grown singly from seed, in plastic containers (6 cm × 6 cm × 8 cm), served as test plants in various temperature experiments.

Development and survivorship of immatures

For each experiment, ≈ 400-500 adults from the stock colonies were transferred to a group of 12-15 orange jessamine seedlings for a 6-h oviposition period. At the end of this period, the adults were removed and plants with eggs were checked and eggs counted under a stereomicroscope. They were placed in growth chambers (Percival, Boone, IA) at 10°C, 15°C, 20°C, 25°C, 28°C, 30°C and 33°C, 75-80% r.h., and a photoperiod of 13:11 h for daily observation on incubation period. First instars collected within 4 h of egg hatch were transferred individually to an orange jessamine seedling using a camel s-hair brush and covered with a cylinder cage (8 cm × 4 cm diameter with a nylon cloth top). Covered plants were placed in the growth chambers at 10°C, 15°C, 25°C, 28°C, 30°C and 33°C, 75-80% r.h., and a photoperiod of 13:11 h. Individual insects were checked daily for ecdysis and survivorship. The exuviae were used to determine moulting.

Adult longevity and reproductive capacity

Two to 300 matured nymphs reared from the stock culture were collected and caged on potted orange jessamine plants. Adult females emerged within 6 h were singly aspirated into cylinder cages as described above. Two adult males were also introduced into each cage. At least 18 pairs were tested for each temperature. The caged adults were kept in growth chambers at 10°C, 15°C, 25°C, 28°C, 30°C and 33°C with 75-80% r.h. and a photoperiod of 13:11 (L:D) h. The paired adults were moved to new seedlings every 24 h and the eggs were counted under a stereomicroscope. Observations were made daily until the last female died.

Data analysis

Life table parameters at five temperatures were analysed using general linear model procedures (Anon., 1988). The adults that died within 12 h of emergence or produced no eggs were excluded from the analysis. The rate of development of each life stage was calculated as the reciprocal of days of developmental time. A linear regression analysis was used for computing the lower developmental threshold of immatures by using growth rate data as dependent variable (*y-axis*) and constant temperature treatments of 15-28°C as independent variable (*x-axis*). Development at 30°C was outside the linear segment of the growth curve and therefore not included in the linear regression. The lower developmental threshold was determined as the *x*-intercept of the linear equation (Campbell *et al.*, 1974). The degree-day requirements for nymphal development were determined as the value of the inverse of the linear equation slope.

A modified Logan model (Logan, Wallkind, Hoyt & Tanigoshi; 1976) as described by Lactin, Holliday, Johnson & Craigen (1995) was used to describe temperature-dependent developmental rate of different stages: $r(T) = e^{pT} - e^{[pT_{\max} - (T_{\max} - T)/\Delta]} + \lambda$ where $r\ (T)$ is mean developmental rate at temperature T in centigrade, *þ, Tmax,* λ, and Δ are fitted parameters. The adjusted coefficient of determination was calculated using the equation of Kvalseth (1985).

Life table statistics were calculated for the populations at different temperatures as described by Hulting, Orr & Obrycki (1990). The sex ratio of 0.5224 based on laboratory reared 3500 adults (J H Tsai, unpublished) was used to calculate the statistics.

Results

Development and survivorship of immatures

Asian citrus psyllid failed to develop beyond third instar stage at 10°C and fourth or fifth instar stages at 33°C. For this reason, 10°C and 33°C were excluded from analysis.

Eggs

Temperature had a significant effect on egg incubation period (Table 1; $P < 0.001$). The average incubation period varied from 9.7 days at 15°C to 3.5 days at 28°C. The egg survivorship was also affected by temperature. The highest survival (96.2%) was recorded at 28°C, but significantly lower survivals (84.5%, 89.4% and 93.2%) were recorded at 15°C, 20°C and 30°C (Table 2). Low (< 20°C) and high temperature (> 28°C) caused a slight decline in the egg survivorship compared with moderate temperatures (Table 2). A linear regression analysis was applied to the developmental points within 15-28°C, within which the developmental rates of *D. citri* increased linearly with the increase of temperature (Table 3). The theoretical developmental threshold for eggs was estimated at 9.0°C (Table 3). The nonlinear modified Logan model gave a good fit to the data set within the range of 15-30°C (Fig. 1A).

Table 1. *Mean ± SE developmental periods of immature stages (in days) of* D. citri *at five constant temperatures*

Temp (°C)	n	Egg	1st instar	2nd instar	3rd instar	4th instar	5th instar	Total Nymphs	From egg to adult
15	35	9.74 ± 0.23	6.54 ± 0.09	5.54 ± 0.09	6.46 ± 0.09	7.26 ± 0.09	13.80 ± 0.11	39.60 ± 0.26	49.34 ± 0.39
20	33	7.03 ± 011	3.67 ± 0.09	2.67 ± 0.09	3.36 ± 0.11	5.09 ± 0.15	6.97 ± 0.17	21.76 ± 0.44	28.79 ± 0.46
25	34	4.15 ± 0.07	2.00 ± 0.06	1.59 ± 0.09	1.68 ± 0.08	2.36 ± 0.08	5.21 ± 0.10	12.82 ± 0.17	16.97 ± 0.16
28	35	3.46 ± 0.09	1.57 ± 0.08	1.43 ± 0.08	1.91 ± 0.09	2.29 ± 0.08	3.40 ± 0.09	10.60 ± 0.18	14.06 ± 0.21
30	31	3.29 ± 0.06	1.74 ± 0.08	1.54 ± 0.10	1.77 ± 0.11	2.52 ± 0.10	5.42 ± 0.16	13.00 ± 0.29	16.29 ± 0.29
	F	438.8	640.3	368.3	464.6	456.7	938.6	1895.3	2247.8
	df	4, 163	4, 163	4, 163	4, 163	4, 163	4, 163	4, 163	4, 163
	P	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001

Table 2. *Survivorship (%) of immature stage of* D. citri *at five constant temperatures*

Temp (°C)	Egg	1st instar	2nd instar	3rd instar	4th instar	5th instar	From egg to adult
15	84.5	83.9	92.2	98.6	99.5	96.5	61.9
20	89.4	85.4	93.9	99.4	99.4	98.7	69.8
25	95.5	87.2	96.8	97.0	99.4	97.0	75.4
28	96.2	93.4	96.2	99.4	99.1	98.7	83.9
30	93.2	91.1	96.0	97.7	96.1	96.5	73.7
F	11.6	3.9	2.8	0.8	2.9	1.5	16.2
df	4, 15	4, 15	4, 15	4, 15	4, 15	4, 15	4, 14
P	<0.001	0.02	0.06	0.53	0.06	0.27	<0.001

Table 3. *Developmental threshold and degree-day required for* D. citri

Stages	Intercept	Slope	R^2	θ, °C	Degree-day
Egg	-0.1326	0.0148	0.97	8.96	67.57
1st instar	-0.4415	0.0378	0.98	11.68	26.46
2nd instar	-0.4429	0.0415	0.99	10.67	24.10
3rd instar	-0.3364	0.0332	0.87	10.13	30.17
4th instar	-0.2702	0.0258	0.92	10.47	38.76
5th instar	-0.1761	0.0158	0.94	10.86	63.29
Nymph	-0.0584	0.0054	0.99	10.81	185.19
Egg to adult	0.0418	0.0040	0.99	10.45	249.88

The linear model ($y = a + bx$) was employed to describe the relationship between developmental rate (y) and temperature (x) within the temperature range of 15-28°C. Developmental threshold (θ) = -a/b. Degree-day = 1/b.

Nymphs

The effects of temperature on nymphal developmental periods were highly significant (Table 1; $P < 0.001$). The average developmental period for combined nymphal stages ranged from 10.6 days at 28°C to 39.6 days at 15°C. The developmental rate of five stadia increased with increasing temperature until they reached the maximum developmental rates at 28°C. High temperature (> 28°C) caused a significant decline in the developmental rate of combined nymphal stages (Table 1; $P < 0.001$).

Temperature had relatively less effect on the nymphal survivorship except for the first two nymphal stages. Again, high temperature (> 28°C) caused a decline in nymphal survivorships (Table 2; $P < 0.001$). *Diaphorina citri* required 49.3 days to complete development from egg to adult at 15°C, but only 14.1 days at 28°C. Development thresholds for 1st through 5th instars were estimated at 11.7°C, 10.7°C, 10.1°C, 10.5°C and 10.9°C, respectively. It required 26.5, 24.1, 30.2, 38.8, 63.3 degree-days for the development of 1st through 5th instars, respectively. Two hundred and fifty degree-days were required for an egg to become an adult based on 10.5°C developmental threshold for whole life stage (Table 3). The nonlinear modified Logan model gave a good fit to the data sets within the range of 15-30°C (Fig. 1B, C). Parameters and R^2 for the modified Logan model are shown in Fig. 1.

Adult longevity and reproductive capacity

Temperature also affected female longevity and fecundity significantly ($P < 0.001$) (Table 4; Fig. 2). Within 15-33°C, the mean longevity of females increased with decreasing temperature and a record of 88.3 days was recorded at 15°C. Mortality occurred from 22 to 25 days after emergence of females at 28-30°C (Fig. 2D, E). A rapid decline on the survival curve appeared after 30 days when the populations were exposed to 20-30°C (Fig. 2B, C, D, E). The longest longevity of individual females was 117, 60,

Table 4. Oviposition (eggs per female, mean ± SE) and longevity (days, mean ± SE) of female D. citri *at six temperatures*

Temp. (°C)	*N*	Mean longevity of female	Mean no. eggs per female
15	18	88.3 ± 4.31	171 ± 25.1
20	22	50.6 ± 2.61	494 ± 50.5
25	25	39.7 ± 1.39	626 ± 22.3
28	21	34.7 ± 1.13	748 ± 34.7
30	25	33.5 ± 1.08	316 ± 30.9
33	23	28.7 ± 1.38	67 ± 10.3
	F	98.4	70.2
	df	5, 128	5, 128
	P	<0.001	<0.001

56, 52 and 51 days at 15°C, 20°C, 25°C, 28°C and 30°C, respectively (Fig. 2).

Fecundity was significantly affected by temperature. The average number of eggs laid per female significantly increased with increasing temperature and reached a maximum of 748 eggs at 28°C ($P <$ 0.001) (Table 4; Fig. 2). A rapid decline in egg production was noted as temperature increased from 28°C to 33°C. The preoviposition period varied with temperature. The shortest period occurred at 28°C, the longest was at 15°C. The reproduction peaks appeared on 82, 20, 18, 12, and 34 days at 15°C, 20°C, 25°C, 28°C and 30°C, respectively (Fig. 2).

The intrinsic rate of increase (r_m), net reproductive rate (R_0), mean generation time (*MT*), and population doubling time (*t*) were calculated for the populations at different temperatures and presented in Table 5. The population reared at 28°C had the largest r_m (0.199) and R_0 (292.2), as well as shortest *MT* (28.6 days) and *t* (3.5 days) compared with the populations reared at other temperatures. In contrast, the populations reared at the low temperatures of 15°C and 20°C had a significantly smaller r_m (0.036 and 0.092), R_0 (63.8 and 169.7), and a relatively large value of *MT* (116.8 and 55.8 days), and *t* (19.5 and 7.5 days).

Discussion

Temperature is one of the most important factors affecting the growth of arthropods. The developmental rate relative to constant temperature tends to be nonlinear. Development ceases below a low-temperature threshold; above this the rate of development increases with temperature until an optimum is reached. At the upper limit the rate decreases rapidly to zero (Briere, Pracros, Roux & Pierre, 1999). Even though insects are not always subject to constant temperatures in nature; a controlled study can provide a valuable insight into the population dynamics of a particular species (Summers, Coviello & Gutierrez, 1984). Our results clearly showed the effects of temperature on the development, survival, longevity and reproduction of *D. citri*. Within 20-28°C, overall nymphal developmental periods ranged from 10.6 to 21.8 days and mean adult longevity varied from 33.5 to 50.6 days. Pande (1971) also reported that nymphal developmental periods of *D. citri* varied from 10 to 30 days and adult longevity varied from 25 to 30 days depending on the season. Catling (1970) reported that an average egg incubation period of 3 days was required at a mean temperature of 25-26°C, and nymphal development was completed in 11 to 15 days. In our study, the average egg incubation period was 4.2 days, and the mean nymphal developmental period was 12.8 days at 25°C (Table 1). These minor variations are expected as these observations were made at different temperatures. We applied the modified Logan model (Lactin *et al.*, 1995) to

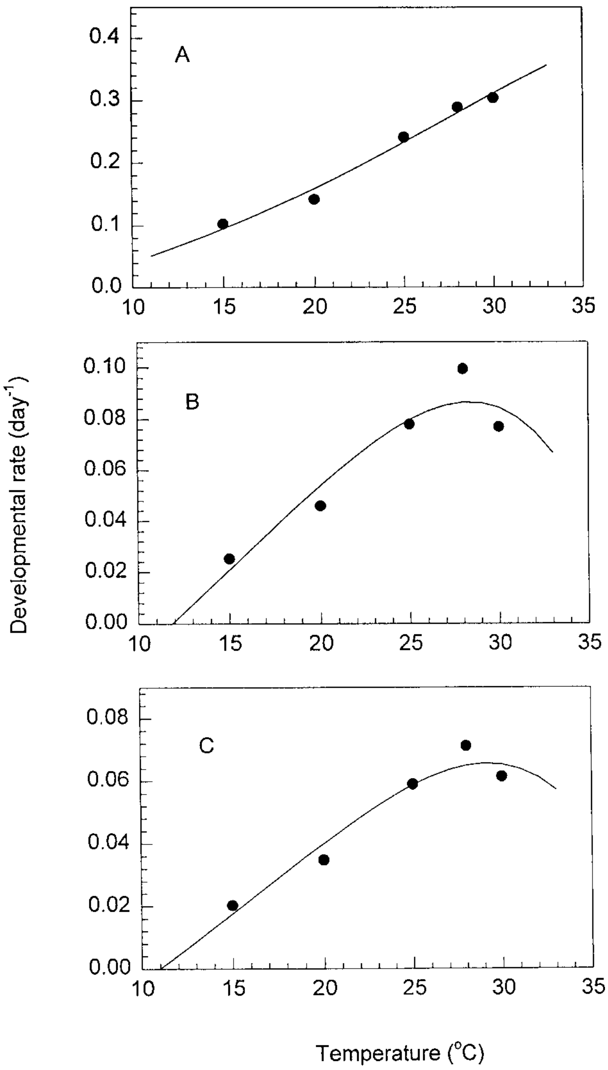

Fig. 1. Development rate (*r*) of egg (A), total nymphs (B), and combined immature stages (C) of *D. citri*, as a function of temperatures (*T*) in centigrade. Dots are observed rates. Curve is the modified nonlinear model for the ranges of 15-30°C (Lactin *et al.*, 1995). The parameter estimations were: Egg (A), þ = 0.0758, T_{max} = 53.5144, Δ = 12.8513, λ = -0.1377, R^2 = 0.90; Total nymphs (B), þ = 0.0772, T_{max} = 41.1246, Δ = 12.6104, λ = -0.1476, R^2 = 0.92; Combined immature stages (C), þ = 0.0777, T_{max} = 41.9700, Δ = 12.6581, λ = -0.0914, R^2 = 0.94.

Table 5. Comparison of life table parameters of D. citri *at five constant temperatures*

Temp (°C)	*n*	r_m	*Ro*	*MT*	*t*
15	18	0.036 ± 0.003	63.8	116.8	19.5
20	22	0.092 ± 0.002	169.7	55.8	7.5
25	25	0.162 ± 0.002	245.6	33.9	4.3
28	21	0.199 ± 0.002	292.2	28.6	3.5
30	25	0.130 ± 0.003	123.8	37.2	5.4

n, Number of females in analysis. r_m, Jackknife estimate of the intrinsic rate of increase (per capita rate of population growth). *Ro,* net reproductive rate. *MT,* mean generation time (in days). *t,* doubling time (in day) for population.

describe the relationship between developmental rate and temperature and to reflect the adverse effect of extreme temperature on developmental rate. The nymphs of *D. citri* failed to develop at the extreme temperatures (10°C and 33°C). The modified Logan model gave a good fit to the data sets covering the range of 15-30°C (Table 1; Fig. 1). High temperature (30°C) caused a decrease in developmental rate for combined immature stages from a linear trend (Table 1; Fig. 1), and a high mortality (26.3%) of combined immature stages (Table 2), as well as significantly lower production of 316 eggs per female (Table 4; $P < 0.001$) resulting in a significantly lower r_m (0.130). Yang (1989) reported that *D. citri* reared at 30°C had a shorter total nymphal period (10.8 days) than this study and a variable rate of nymphal mortality ranging from 9.8% to 43% depending upon the relative humidity. High temperature had another effect on the physiology of *D. citri*. It was noticed that the population (30 nymphs) reared at 33°C

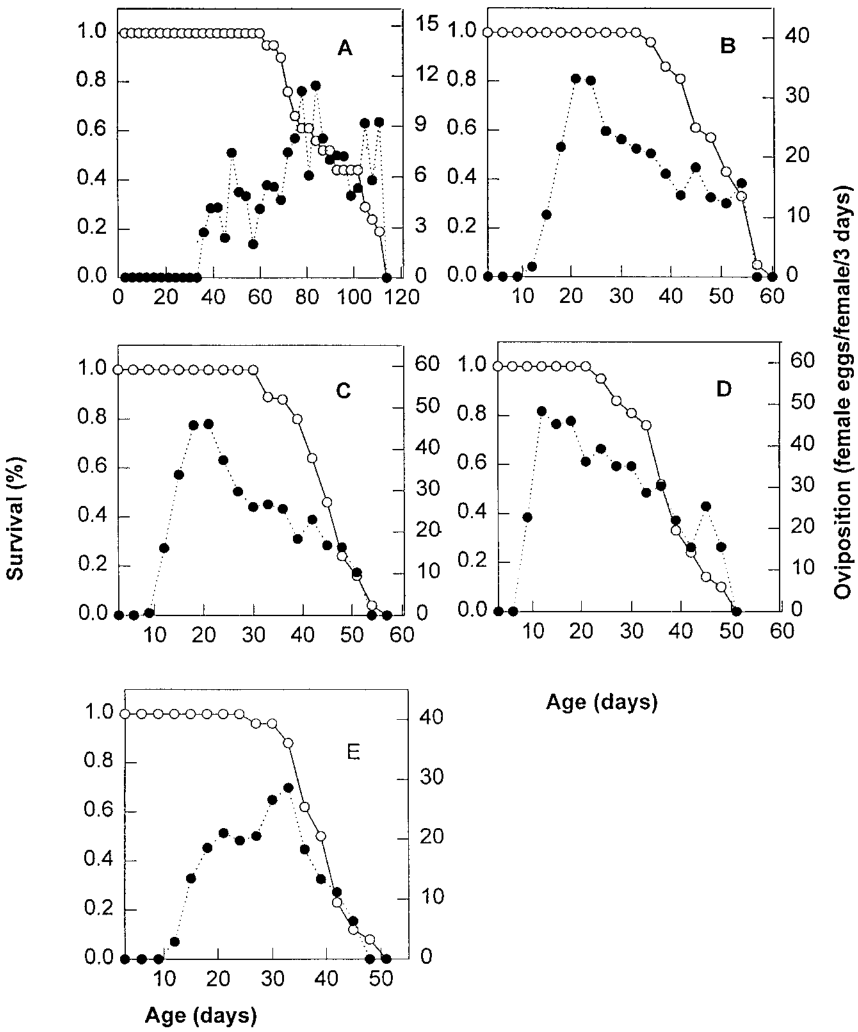

Fig. 2. Age-specific survivorship (circles and curve) and oviposition (dots and dotted line) for *D. citri* female at 15°C (A), 20°C (B), 25°C (C), 28°C (D), and 30°C (E).

remained in a state of aestivation for over 3 months. Those aestivated individuals did not proceed to develop when they were returned to 25°C.

The r_m is a good indicator of the temperature at which the growth of a population is most favourable, as it reflects overall effect of temperature on development, survival and reproduction characteristics of a population. The populations reared at 25°C and 28°C had a higher r_m due to higher rate of development (Table 1) and higher survivorship of immature stages (Table 2), and higher fecundity (Table 4). The populations reared at 15°C and 20°C had a much smaller r_m than those of other populations (Table 5). The reduction in r_m could be due to longer immature developmental time (Table 1) and a longer reproductive period (Fig. 2A, B) that had resulted in a considerably longer mean generation time (Table 5). The population exposed to high temperature (30°C) had fewer eggs than the populations reared at 20-28°C (Table 4), but had a significantly higher r_m than those at 15°C and 20°C (Table 5). The increase in r_m could be caused by the significantly faster development of immatures stages and shorter reproductive period, which in turn resulted in the shorter mean generation time (37.2 days) (Table 5).

In summary, temperature has a significant effect on developmental rate, survivorship, reproduction and longevity of *D. citri*. A temperature range of 25-28°C appears to be most suitable for the population growth and for rearing of this insect in the laboratory. This agrees with the report of the suitable temperature (25-26°C) for the development of *D. citri* (Catling, 1970). The use of life table statistics such as intrinsic rate of natural increase and approaches used to model patterns of *D. citri* survivorship and reproduction should provide a better means to quantify the effect of environmental factors such as temperature on this important pest.

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