

Full Length Research Paper

Effect of temperature on development and survival of *Bactrocera correcta* (Diptera: Tephritidae)

Liu, Xiaofei and Ye, Hui*

School of Life Sciences, Yunnan University, Kunming, Yunnan, China.

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The effect of temperature on the development and survival of the guava fruit fly, *Bactrocera correcta* (Bezzi) (Diptera: Tephritidae) from egg to adult's pre-ovipositional stage was studied in laboratory under 5 different constant temperatures: 18, 24, 30, 33 and 36 °C. The developmental time of the egg, larva and pupa significantly decreased with increasing temperature from 18 to 33 °C. The developmental rate of the pre-oviposition stage reached physiological maximum at the higher temperature (36 °C). At 18 °C, no female oviposited. The survival rate reached maximum at 24 - 33 °C and decreased at higher or lower temperature. The lower developmental thresholds, thermal constants and lethal high temperatures for different life stages of the fly were also estimated. The results will be useful for the predicting the fly's population dynamics and geographical distribution, which would help develop the fly management strategies.

Key words: Guava fruit fly, temperature-dependent development, lower developmental threshold, thermal constant, lethal high temperature.

INTRODUCTION

The guava fruit fly, *Bactrocera correcta* (Bezzi) (Diptera: Tephritidae), is one of the most destructive pests in the genus *Bactrocera* (Wang, 1996). The fly was first recorded in 1916 at Bihar, India (Bezzi, 1916) and is now distributed throughout most countries of south East Asia, including Pakistan, India, Nepal, Burma, Thailand, Sri Lanka, Vietnam and China (Wang, 1996; Drew and Raghu, 2002). The fly is polyphagous with wide range of tropical and subtropical fruits and melons belonging to 30 plant families (Allwood et al., 1999; Maynard et al., 2004). Of particular concern is its feeding on economically valuable fruits and vegetables, such as mango, citrus fruits and banana (White and Elson-Harris, 1992). In Vietnam and central to northern Thailand, serious infestation by this fly causes great loss in fruit and vegetable production (Drew and Raghu, 2002). *B. correcta* is listed as a quarantine pest by most countries worldwide (White and Elson-Harris, 1992).

B. correcta as an adventive insect to China was first recorded in 1986 in Yuanjiang, Yunnan province (Liang et al., 1996). Over past 20 years of dispersing, the fly is found in more than 11 counties of Yunnan (Liu et al., 2005). In

recent years the fly's infestation has become more and more serious. In Yuanjiang where *B. correcta* was first discovered, this fly has become a dominant pest causing great loss to the local fruit productions (Liu, 2007).

Temperature plays a vital role in development, survival and reproduction of tephritid species and other insects (Davidson, 1944; Fletcher, 1987; Fletcher, 1989). As little is known regarding this important environmental factor on *B. correcta*, the objective of this study was to assess the development and survival of the fruit fly at various temperatures. The results will be useful for prediction of the fly's occurrence and geographical distribution, which would help develop better management strategies for this important pest.

MATERIALS AND METHODS

B. correcta larvae and pupae were collected from the infested guava in June 2005 in Yuanjiang, Yunnan, China. The laboratory culture was kept at 25 - 30 °C with 50 - 80% RH and photoperiod of L13: D11. The rearing method developed by Jaldo et al. (2001) was used. Studies were conducted on the F2 of the laboratory-reared flies in artificial climate chambers (RQH-250, Jing Hong laboratory instrument Co., Ltd. China). 5 constant temperatures were used: 18, 24, 30, 33 and 36 °C, with a variation of ± 1 °C, $80 \pm 10\%$ RH and L13: D11 photoperiod. The developmental duration was determined by the time required for 50% of individuals to complete the development of a particular stage (Vargas et al., 1984).

*Corresponding author. E-mail: yehuikunming@gmail.com. Tel.: +86-871-5032363.

Egg stage

Eggs were collected from an artificial egg-laying device offered to a stock colony within 1 h. The device consisted of a plastic cup with small holes, fresh mango juice was placed inside the cup in order to stimulate egg-laying. The 100 randomly selected eggs were placed on wet filter paper in a petri dish. The eggs were then observed hourly under a stereo-microscope to determine the status of hatching.

Larval stage

1 hundred newly hatched larvae (age < 1 h) were carefully transferred to a petri dish that contained artificial diet (Jaldo et al., 2001). The petri dish was then placed inside a larger plastic container. Wet sand had been spread on the bottom of the container to allow pupation of jumping larvae. Observations were performed 3 times a day by sifting the sand and recording the number of pupae recovered.

Pupal stage

As soon as pupation was completed, 100 pupae (age < 3 h) were randomly selected and transferred into a plastic box containing wet sand. At the end of the pupal stage, the number of emerged adults was recorded 3 times a day.

Pre-oviposition stage

Newly emerged male and female flies that had emerged on the same day were confined in a transparent meshed plastic cage (40 × 15 × 15 cm) at a ratio of 1 male to 1 female to allow for mating. Adult flies had free access to a diet of sugar, enzymatic yeast hydrolysate (Oxoid Ltd., Basingstoke, England) and water. Eggs were collected daily and the date of the first laying was recorded.

Survival rate

Stage-specific survival was calculated for each temperature by dividing the number of flies still alive at the end of each life stage by the original number of specimens. The number of emerged adults per 100 eggs was also calculated as the product of survival rates.

Statistical analyses

Test of developmental time for each life stage was replicated 4 times. Standard analyses of variance (ANOVA) were used to test the effect of treatments on developmental time or survival rate. Means were compared when necessary by Fisher's protected LSD tests ($P = 0.05$). All statistical analyses were carried out using SPSS software (version 11.5; SPSS Inc., Chicago, IL, USA).

The lower threshold temperature for development (t_{\min}) and the thermal constant (K) could be calculated from the linear model:

$$\frac{1}{D} = bT + a \quad (1)$$

Where D is the duration of development (in days) of a particular stage and a and b are the regression parameters (Wagner et al., 1984). Based on the regression parameters a and b , the threshold temperature or developmental zero t_{\min} and the thermal constant or physiological time K can be calculated with the following equations:

$$t_{\min} = -\frac{a}{b} \quad (2)$$

and

$$K = \frac{1}{b} \quad (3)$$

The threshold temperature t_{\min} is the temperature below which the regression predicts that no development occurs and the thermal constant K is the physiological time in degree-days above t_{\min} required to complete the development stage. Standard errors in these estimates were calculated using the method given by Campbell et al. (1974):

$$SE_t = \frac{1/D}{b} \sqrt{\frac{s^2}{N(1/D)^2} + \left[\frac{SE_b}{b}\right]^2} \quad (4)$$

and

$$SE_K = \frac{SE_b}{b^2} \quad (5)$$

The term $1/D$ is the mean developmental rate of a particular life stage, s^2 is the residual mean square of the developmental rate and SE_b is the standard error of the regression parameter b .

The recent nonlinear function proposed by Briere et al. (1999) was also used in the study. The mathematical expression of this model is:

$$r(T) = aT(T - T_0)\sqrt{T_L - T} \quad (6)$$

where a is an empirical constant, T_0 is the lower temperature developmental threshold and T_L lethal temperature.

The estimates of model parameters for the linear and nonlinear regression models were obtained using the Table Curve 2D (version 5.01; SYSTAT software Inc., Richmond, VA, USA).

RESULTS

Developmental time

The developmental times of various *B. correcta* stages were significantly temperature dependent (Table 1). Mean developmental time required for eggs to hatch decreased with increasing temperatures from 18 up to 33°C ranging from 26.5 to 66.75 h. At temperatures higher than 33°C, the egg developmental time increased with temperature increasing.

At larval stage, the trend was similar to egg stage. The developmental time decreasing from 17.56 days at 18°C to 7.56 days at 33°C and then increased to 7.96 days at 36°C.

However, the developmental time of pupa decreased with increasing temperature within the whole temperature range tested in this study. The developmental time at 33 and 36°C was not significantly different.

No mating and oviposition was observed for adult *B. correcta* at 18°C, although the adults were able to survive prolonged periods at this temperature. The adult's pre-oviposition duration was 38.75 days at 24°C and decreased with increasing temperature from 24 to 36°C.

Table 1. Mean developmental time of various life stages of *Bactrocera correcta* at 5 constant temperatures.

Temperature °C	Egg development	Larval development	Pupal development	Pre-oviposition
	Mean ± SE. (h)	Mean ± SE. (days)	Mean ± SE. (days)	Mean ± SE. (days)
18	66.75 ± 0.14a	17.59 ± 0.15a	18.47 ± 0.19a	No emergence
24	41.50 ± 0.16b	12.05 ± 0.11b	11.24 ± 0.19b	38.75 ± 0.13a
30	28.50 ± 0.10c	8.28 ± 0.07c	7.45 ± 0.13c	23.25 ± 0.20b
33	26.50 ± 0.10d	7.56 ± 0.11e	7.00 ± 0.14d	20.50 ± 0.31c
36	26.75 ± 0.11d	7.96 ± 0.10d	6.76 ± 0.25d	15.75 ± 0.14d

Means followed by different letters in the same column are significantly different according to ANOVA and LSD test ($P < 0.05$).

Table 2. Lower developmental threshold (t_{min}), thermal constants (K) and regression equations estimated by linear regression for *Bactrocera correcta*.

Developmental stages	Regression equation	Regression statistics		$t_{min} \pm SE_{tmin}$	$K \pm SE_K$
		P	R^2		
Egg	$Y = 0.038x - 0.322$	0.003	0.994	8.5 ± 1.1	26.3 ± 1.5
Larval	$Y = 0.005x - 0.038$	0.004	0.993	7.6 ± 1.2	200 ± 11.4
Pupal	$Y = 0.006x - 0.057$	0.005	0.989	9.5 ± 1.3	166.7 ± 11.9
Pre-oviposition	$Y = 0.003x - 0.047$	0.010	0.978	15.7 ± 0.8	333.3 ± 35.0

The linear model is for the range of 18-33°C for egg, larval and pupal stages, 24 - 36°C for pre-oviposition stage.

Temperature-dependent developmental rate models

The relationship between the developmental rates of *B. correcta* and temperatures was described with linear and nonlinear models (Figure 1).

Estimated parameter values of the linear models are presented in Table 2. The low developmental thresholds were estimated to be 8.5, 7.6, 9.5 and 15.7°C for egg, larval, pupal and pre-oviposition stages respectively and the effective cumulative temperatures were 26.3, 200, 166.7 and 333.3 degree-days for the 4 life stages. Apparently, both the low developmental threshold temperature and thermal constant required for the pre-oviposition stage were higher than other stages in *B. correcta*. The low threshold temperature of all generation was determined by the temperature requirement of the pre-oviposition stage.

Plots of the fitted nonlinear model and observed data for egg, larval and pupal stages are also shown in Figure 1 and their estimated parameter values are presented in Table 3. The low developmental threshold estimated by the Briere model for egg, larva and pupa was 6.0, 4.6 and 6.7°C respectively. The low developmental thresholds estimated by this model were lower than those estimated by the linear regression model. The lethal high temperatures were estimated to be 42.56, 42.39 and 43.75°C for egg, larva and pupa.

Survival rates

Survival rates of the immature stages (egg to adult emergence) of *B. correcta* varied at the 5 temperatures ($F = 64.7$; $df = 4$; $p = 0.003$) (Table 4). Survivor rates of egg and larval stages was highest at 33°C and decreased significantly at higher and lower temperatures (Table 4). At the pupal stage, the highest survivorship was 97.25% at 30°C. The percentage of adults emerging from 100 eggs peaked at 77% at 30°C compared to 47% at 18°C.

DISCUSSION

Temperature is one of the most important factors affecting the developmental rate through the various life stages of fruit fly (Fletcher, 1987). One of the most commonly used models for describing a relationship between temperature and development rate in insects is the linear approximation (Uvarov, 1931; Wagner et al., 1984). However, insect development is non-linear at the extremes of high and low temperature and several non-linear models are available to describe developmental rate and estimate temperature thresholds more precisely. In this research the linear model was used because the temperatures under examination lie, for the most part, within the linear portion of development and it provides a straightforward comparison of physiological time with previous work on fruit flies (Vargas et

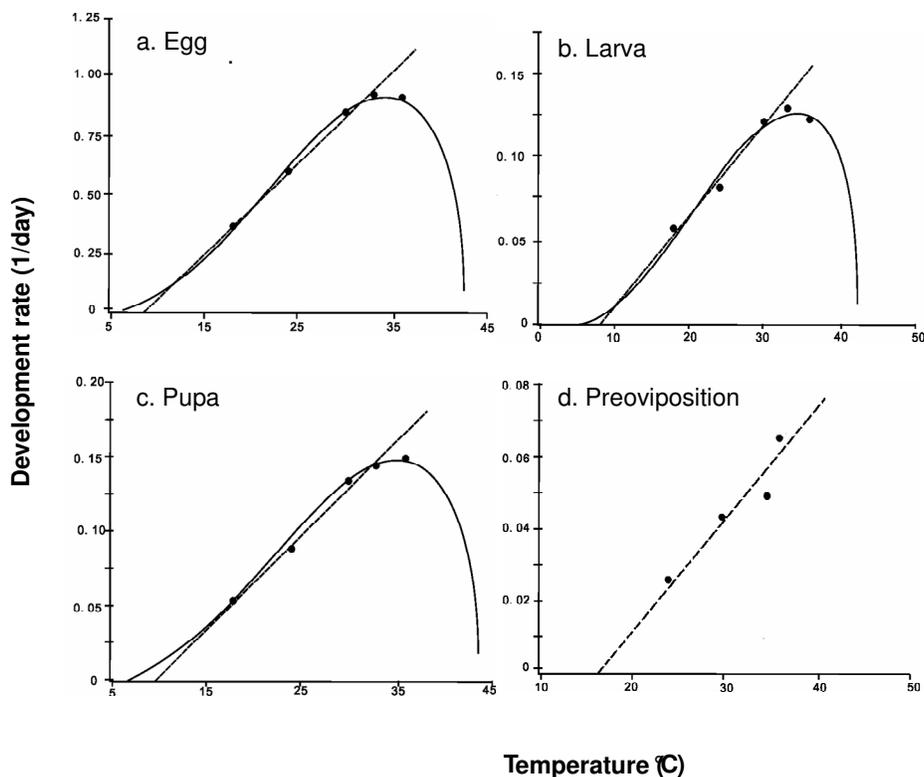


Figure 1. Influence of temperature on the developmental rate of different life stages of *Bactrocera correcta*. (a) Egg. (b) Larva. (c) Pupa. (d) Pre-oviposition. The dotted line represents the regression line fit to Equation (1); the solid line represents the regression line fit to Equation (6)

Table 3. Parameter estimates for nonlinear model describing the relationship between temperature and development rates of immature stages for *Bactrocera correcta*.

Parameter	Life stage		
	Egg	Larva	Pupa
a	0.0003	0.00004	0.00005
T_0	6.0438	4.6119	6.6936
T_L	42.5598	42.3933	43.7530
R^2	0.9975	0.9828	0.9949

al., 1996; Thierry and Serge, 2000; Yuan et al., 2005). Meanwhile, the non-linear model was used for egg, larval and pupal stages because the developmental time increased when the temperature was above 33°C and the linear equation would not account for this.

B. dorsalis is another prevalent fruit fly whose pest infestations occur all year round in most of Yunnan, China (Ye, 2001). Both *B. dorsalis* and *B. correcta* are found in mixed infestations, predominantly at lower elevation and attack generally similar hosts (Liu et al., 2005). Vargas et al. (1996) estimated from linear regression the thermal constant for total development of *B. dorsalis* to be 358

degree-days and the lower temperature threshold of eggs, larvae and pupae to be 11.8, 5.6 and 9.3°C. The lower temperature threshold of pre-oviposition in *B. dorsalis* was reported to be 12.44°C (Yuan et al., 2005). The present study demonstrated that the temperature requirement seems much higher through all the life stages for *B. correcta*, especially for the pre-oviposition stage (Table 2).

Biological parameters like developmental zero and the thermal constant are supposed to be the limit factors in the geographic distribution for the fruit flies (Ye, 2001). In Yunnan, *B. correcta* only occurs in low-altitude areas under 1500 m altitude, where the annual average temperatures of these areas are all over 15.8°C (Liu, 2007; Lu, 1982). By contrast, *B. dorsalis* could be trapped at an elevation of above 2000 m (Ye, 2001). Therefore, thermal requirement explain the reason that distribution range for *B. correcta* is much narrower in comparison with *B. dorsalis* (Liu et al., 2005).

The results may also help to understand the life cycle strategy of *B. correcta* in its breeding areas. No oviposition was observed at 18°C, even at this temperature the adult fly remains surviving. The evidence proved that thermal requirement is higher for oviposition than for development. However, at the lower temperature like 18°C, development period for the adults is much prolonged. Similar phenomenon is commonly found in other *Bactrocera* fruit flies, which was regarded to be reproductive “diapause” (Fletcher, 1987).

Table 4. Stage-specific survivorship (%) of *Bactrocera correcta* at 5 constant temperatures.

Temperature (°C)	Stage viability (Mean ± SE)			Emerging adults /100 eggs
	Egg	Larva	Pupa	
18	91.50 ± 1.26b	62.75 ± 1.25c	81.25 ± 5.85b	47
24	91.75 ± 1.84ab	81.50 ± 4.73ab	93.00 ± 5.69ab	70
30	93.25 ± 0.85a	85.00 ± 4.10a	97.25 ± 0.85a	77
33	93.50 ± 2.18a	85.75 ± 7.40a	93.00 ± 4.34ab	75
36	91.50 ± 1.44b	66.50 ± 8.09bc	89.75 ± 5.27ab	55

Means followed by different letters in the same column are significantly different according to ANOVA and LSD test ($P < 0.05$).

Probably, *B. correcta* adults take the similar strategy to overcome somewhat lower temperatures.

Establishment of experimental populations is essential for laboratory studies (Yuan et al., 2003) and temperatures play a key role in the insect breeding process (Thierry and Serge, 2000). According to the results of this study, the temperatures from 30 to 33°C appear to be the most suitable for egg, larva and pupa development. The pre-oviposition time is shortened greatly with the temperature higher than 33°C.

The development, survival and reproduction of fruit flies are also influenced by the species and quality of hosts, especially at the larval stage. Carey (1984) reported that larval development of *Ceratitidis capitata* increased from 1 week in favorable hosts such as mango and tomato to more than 3 weeks in quinces. Kamala and Abraham (2002) noticed that the developmental time of *B. dorsalis* varies with the host fruit species. Compared with the artificial diet, the development of larva is slow in natural hosts, because of the quick depletion of food material due to faster ripening and subsequent spoilage of fruit (Kamala and Abraham, 2002). The study results were obtained in the base of breeding with artificial diet. Therefore, these biological parameters for the fly will be changed when it feed with other type of host food. However, it provides us the basic information on the bionomics of the fruit fly.

This study constitutes a first step before analyzing more complex ecological relations. For example, these data, combined with results of other studies on trapping and population fluctuations, should be useful in the construction of computer simulation models of fruit fly population dynamics that will enable better monitoring and management of this destructive pest.

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