

# Life table determination of thermal requirements of the tomato borer *Tuta absoluta*

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**Abstract** Temperature is one of the main factors affecting insect populations. The models used for studying the effect of temperature on insects are usually based on insect developmental rates. However, life table parameters such as the (intrinsic) population rate of increase ( $r_m$ ), which reflect the overall effect of temperature on the development, reproduction, and survival of the insect, should also be considered. The leaf miner *Tuta absoluta* (Lepidoptera: Gelechiidae) is an invasive tomato pest across several regions of the world with its range currently expanding because of its spread into the Middle East and Asia. Thus, this study aimed to assess the impact of temperature on *T. absoluta* and to determine the thermal requirements for this pest based on life table parameters. For this purpose, bioassays of the development and reproduction of *T. absoluta* under constant temperatures (17, 22, 26, 28, 30, and 33 °C) were performed. The thermal requirements of *T. absoluta* were assessed from  $r_m$ . We found that the immature mortality of *T. absoluta* was lowest at 28 and 30 °C and highest at 17 °C. The optimum temperature for *T. absoluta* was 30 °C with upper and lower developmental

thresholds of 34.6 and 14 °C, respectively. These thermal requirements were different from those that can be estimated from the rate of insect development. The results of this study would be helpful toward developing phenological, spatial, and temporal distribution models for *T. absoluta* and toward determining optimal management strategies for this pest species.

**Keywords** Modeling · Thermal requirements · *Tuta absoluta* · Tomato leaf miner

## Key messages

- This study assessed the impact of temperature on *T. absoluta* and its thermal requirements based on its intrinsic population growth rate ( $r_m$ ) and net reproductive rate ( $R_0$ ), contrasting with the prevalent use of the developmental rate for the same purpose.
- The optimum temperature for *T. absoluta* was 30 °C with upper and lower developmental thresholds of 34.6 and 14 °C, respectively.
- These thermal requirements were different from those that can be estimated from the rate of insect development.
- Our study provides useful data for developing predictive models of the population density and spatial-temporal distribution of *T. absoluta*.

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## Introduction

Insect populations are affected by environmental factors such as climatic variables, which may directly or indirectly affect their abundance and geographical distribution (Estay

et al. 2009). Climatic variables directly affect the egg-laying, feeding, growth, development, reproduction, and migration of pest insects (Lam et al. 2001). Moreover, climatic variables indirectly affect insect pests with respect to biochemical and physiological changes in the host plant and also affect the fitness, feeding, appearance, and abundance of their natural enemies (Harrington et al. 2001; Thomson et al. 2010).

Among the climatic variables, temperature is the main factor affecting insects' biological characteristics including the survival, longevity, development, phenology, sex ratio, fecundity, and fertility (Wallner 1987; Cui et al. 2008; Zheng et al. 2008; Ju et al. 2011). The survival, fecundity, and hatching rates of some insect species may decline significantly under high temperatures (Cui et al. 2008). In contrast, progeny sex ratios tend toward a high proportion of males under low temperatures (Nigro et al. 2007). The colonization, geographical distribution, abundance, behavior, life history, and performance of insects are affected by temperature indirectly based on their biological characteristics (James et al. 2002). Therefore, information about the impact of temperature and the thermal requirements for insect pests has significant implications for pest ecology and management (Kang et al. 2009).

The determination of temperature impact on insects is usually performed using models of thermal requirements based on the species rate of development (Lactin et al. 1995; Briere et al. 1999; Sreedevi et al. 2013; Liu et al. 2015). These models estimate the optimum temperature for development, lower developmental threshold (the temperature below which the development is arrested), and upper developmental threshold (the temperature above which development stops). However, the overall effect of temperature on the survival and reproduction of insects is not considered in these models. In contrast, life table parameters, such as the net reproductive rate ( $R_0$ ) and intrinsic rate of increase ( $r_m$ ) calculated on the basis of survival, fertility, developmental time, and sex ratio, more comprehensively reflect the overall effect of temperature on insects. The  $R_0$  is the average number of female offspring produced by a female during her lifetime and expresses the population growth rate per generation (i.e., the replacement rate), while the  $r_m$  is the instantaneous rate of change of population size (i.e., the change in population size per individual per unit of time). When  $R_0$  is less than 1 and  $r_m$  is less than 0, the members of the population are not replacing themselves (i.e., the population is declining). However, when  $R_0$  is greater than 1 and  $r_m$  is positive, the population is increasing. Finally, an  $R_0$  equal to unity and  $r_m$  equal to zero indicate a stationary or "stable" population (Carey 1993; Krebs 1994).

The tomato leaf miner *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) is one of the main pests of tomatoes

in South America (Desneux et al. 2010, 2011; Guedes and Picanço 2012). Since its detection in Spain, *T. absoluta* has caused losses in several European countries and in North Africa (Desneux et al. 2010, 2011). Recently, an analysis using microsatellite markers provided evidence that the origin of the populations of this invasive species that is now in Afro-Eurasia stems from the central region of Chile (Guillemaud et al. 2015). The losses caused by this pest species change with their host plants' phenological stages and throughout the year and may reach 100 % because the insects attack the leaves, flowers, stems, and fruits of tomato plants (Picanço et al. 1995; Chermiti et al. 2009; Balzan and Moonen 2012; Harbi et al. 2012). The losses caused by *T. absoluta* and its rapid expansion in several tomato-producing areas of the world are possibly due to the high adaptability of this species to different environmental conditions. Therefore, studies that evaluate the effects of weather variables on *T. absoluta* are important to provide comprehensive data on its demographic parameters, allowing for a better design and timing of management strategies against this pest species on tomato crops.

Curiously, until now, no study has evaluated the overall effect of temperature on the biological performance of *T. absoluta*. Therefore, the objective of this study was to assess the impact of temperature on *T. absoluta* on tomato crops and to determine the thermal requirements for *T. absoluta* based on its net reproductive rate and intrinsic rate of population growth. The proposed approach allows for a more comprehensive assessment of the overall effect of temperature on the species, contrasting with the prevalent use of developmental rate for the same purpose.

## Materials and methods

### Study site, insect colony, and host plant

The experiments were performed at the Federal University of Viçosa, Viçosa, Minas Gerais, Brazil (20°48'45"S, 42°56'15"W, altitude 600 m, and highland tropical climate) in 2011 and 2012. *T. absoluta* were obtained from a laboratory colony established from at least 400 field-collected individuals to minimize the loss of genetic variability. The insect colony was maintained under controlled conditions of  $25 \pm 0.5$  °C,  $75 \pm 5$  % relative humidity (RH), and a 12-h photophase. The insects were reared in individual wooden cages as described elsewhere (Silva et al. 2011). Commercial tomato plants (*Solanum lycopersicum* L. var. Santa Clara), which were grown without applying insecticide, were used for colony maintenance and in the laboratory experiments. Tomato cultivation was performed in 5-l pots under greenhouses conditions (Silva and Vale 2007). The plants were fertilized with cattle

manure, superphosphate (125 g plant<sup>-1</sup>), ammonium sulfate (34 g plant<sup>-1</sup>), and potassium chloride (23 g plant<sup>-1</sup>) during the seedling transplant process. As top dressing, the plants were fertilized weekly with 30 g of a mixture of ammonium sulfate and potassium chloride (3:1 ratio). Other cultural practices, such as staking and irrigation, were performed daily throughout the tomato plant development area.

## Experimental procedure

The experiments were performed under constant temperatures (17 °C, 22 °C, 26 °C, 28 °C, 30 °C, and 33 ± 1 °C), 70 ± 5 % RH, and a 12-h photoperiod in incubators (model 347 CDG; FANEM, SP, Brazil). The range of temperatures used was selected based on preliminary field data following the population fluctuation of the tomato borer and on previous studies that used only biological responses (e.g., developmental time) to determine the insect's thermal requirements (Betancourt et al. 1996; Barrientos et al. 1998). The temperature intervals used allowed for the intended estimates and trend determinations. Smaller time intervals would compromise the range of temperatures used. This experiment was performed in two steps: (1) an assessment of the development and survival of the egg, larvae, and pupal stages of *T. absoluta* and (2) an assessment of the second aimed at assessing the fecundity and longevity of *T. absoluta* during its adult stage. The experimental design was completely randomized and used nine replicates, each containing an experimental unit (i.e., one leaf for the first experiment and one cage for the second experiment).

## Egg, larvae, and pupae survival and development assessment

In this experiment, each replicate consisted of a tomato leaf from the fifth-node leaves (counted from the plant apex). The leaf petiole was inserted into a 100-ml glass vial containing distilled water to maintain turgescence and viability as described by Silva et al. (2011). Each leaf was placed into a 2-l transparent plastic bottle, which had a side opening covered by organza cloth to allow ventilation. The leaves were placed into plastic bottles to prevent insect escape. At least 180 newly laid eggs were used at each temperature condition. To obtain the eggs, the tomato leaves were placed into adult cages from the laboratory colony for 6 h, the time necessary to obtain at least 20 newly laid eggs per leaf. To ensure exactly 20 eggs on each leaf, the leaves were inspected under a stereomicroscope, and excessive eggs were removed with a light brush tip.

The number of live and dead insects and their developmental stages were monitored daily until adult emergence. A new leaf was added into each plastic bottle every 5 days throughout the experimental period to ensure that the detached leaves did not impair insect performance. Five days is the period during which a detached tomato leaf remains green and turgid (Galdino et al. 2011). The insects were sexed upon reaching the pupal stage as described by Coelho and França (1987).

## Fecundity and longevity assessment

In this experiment, each replicate consisted of a wooden cage (30 × 30 × 30 cm) covered with an organza cloth containing one tomato leaf and ten newly emerged (<12 h) adult pairs of *T. absoluta*. A piece of cotton saturated with 10 % honey solution was placed at the top of the cage as a food source for the adults. Egg-laying capacity and adult survival rate were recorded daily until the death of all adults. Dead adults were removed from the cage, and the number of dead females was recorded. Dead males were replaced with others from the laboratory colony to prevent female infertility, which may be affected by lack of copulation. The tomato leaves were replaced daily in the wooden cages to allow egg-laying by females.

## Life history parameters

Fertility life tables were built for each replicate following the method by Krebs (1994). For the construction of the fertility life table, the following parameters were determined from the biological data of *T. absoluta*:  $x$ , the average age of the insects since emerging from egg stage;  $ax$ , the number alive at the beginning of each age;  $lx$ , the proportion surviving to each life stage  $x$  obtained by dividing the number of individuals living at the beginning of each age ( $ax$ ) by the initial number of eggs;  $mx$ , the specific fertility or number of descendants per female produced at age  $x$  that resulted in females;  $lx \cdot mx$ , the total number of females born at age  $x$ . Using these life table parameters, the following parameters of population growth were estimated: the net reproductive rate ( $R_0$ ), duration of each stage of the life cycle, generation time ( $T$ ), rate of development (number of generations year<sup>-1</sup>), survival, reproductive rate (total number of eggs female<sup>-1</sup>), age-specific fertility (number of eggs female<sup>-1</sup> days<sup>-1</sup>), and intrinsic rate of increase ( $r_m$ ).

The net reproductive rate ( $R_0$ ) was estimated by the following equation:  $R_0 = \sum l_x m_x$ , where  $l_x$  is the probability at birth of being alive at the age ( $x$ ) in days, and  $m_x$  is the number of female offspring produced by age  $x$ . The generation time ( $T$ ) was estimated by the equation  $T = \sum x l_x m_x / \sum l_x m_x$ . The intrinsic rate of natural

increase ( $r_m$ ) was estimated by the equation  $\sum l_x m_x e^{-r_m x} = 1$ . A 1:1 sex ratio was used to estimate of the reproductive parameters of population growth. This sex ratio assumption was made from the data obtained in this study. Thus, the number of eggs laid was divided by two to exclude male offspring.

## Data analysis

All data were checked for normality and homoscedasticity by using the UNIVARIATE procedure (PROC) (SAS Institute 2008). One-way analysis of variance (ANOVA,  $P < 0.05$ ) (PROC ANOVA, SAS Institute 2008) was performed to examine the significance of the effects of temperature on *T. absoluta*. Developmental time and mortality data at each life stage and over the total cycle, as well as the life table population parameters and female fecundity, were analyzed by regression analyses. To fit regression curves, the data were plotted for the temperatures tested and for the distribution found; we then attempted to find an equation that best described the relationship between the variables (i.e., the temperature and life history parameters of *T. absoluta*). Regression curves were fitted and model parameters estimated using the Table Curve 2D software (Systat Software Inc, TableCurve 2D 2002). The model selection was based on the following criteria: F-value and significance of the model ( $P < 0.05$ ), steep increase of the determination coefficient with model complexity ( $R^2$ ), and parsimony. The survival curves and lethal time (LT<sub>50</sub>) for *T. absoluta* at each temperature were estimated using the Kaplan-Meier estimators and the nonparametric LIFETEST procedure from SAS (SAS Institute 2008). The curves of  $r_m$  as a function of temperature were used to estimate the upper and lower temperature thresholds ( $r_m = 0$ ), while the optimal temperatures (maximum point of the curves) were determined from the  $r_m$  regression curves with temperature as the independent variable. An additional experiment was subsequently performed to examine the accuracy of the temperature threshold. Two temperature thresholds were used: one below the lower developmental threshold (13 °C) and the other slightly above the upper developmental threshold (35 °C). This experiment was performed and analyzed as previously described in the sections experimental procedure and data analysis.

## Results

The developmental times of eggs, larva, and pupa, as well as the egg-to-adult emergence, were significantly affected ( $P < 0.05$ ) by temperature (egg,  $F_{5,48} = 103.18$ ;  $P < 0.0001$ ; larva,  $F_{5,48} = 893.97$ ;  $P < 0.0001$ ; pupa,

$F_{5,48} = 198.09$ ;  $P < 0.0001$ ; egg-to-adult emergence,  $F_{5,48} = 1130.46$ ;  $P < 0.0001$ ). The duration of the egg, larva, pupa, and egg-to-adult stages decreased by 2.9, 3.5, 3.2, and 3.3 times, respectively, as the temperature increased from 17 to 33 °C. The mortalities of *T. absoluta* for egg, larva, pupa, and egg-to-adult emergence were all significantly affected by temperature (egg,  $F_{5,48} = 3.57$ ;  $P = 0.008$ ; larva,  $F_{5,48} = 7.10$ ;  $P < 0.0001$ ; pupa,  $F_{5,48} = 5.27$ ;  $P = 0.0006$ ; egg-to-adult emergence,  $F_{5,48} = 7.18$ ;  $P < 0.0001$ ). The highest survival of eggs (>96 %), larvae (75 %), and pupae (89 %) occurred at 26, 28, and 30 °C, respectively. The total survival of *T. absoluta* decreased markedly at temperatures below 22 °C and above 33 °C. This decrease was more pronounced for caterpillars and pupae (Fig. 1).

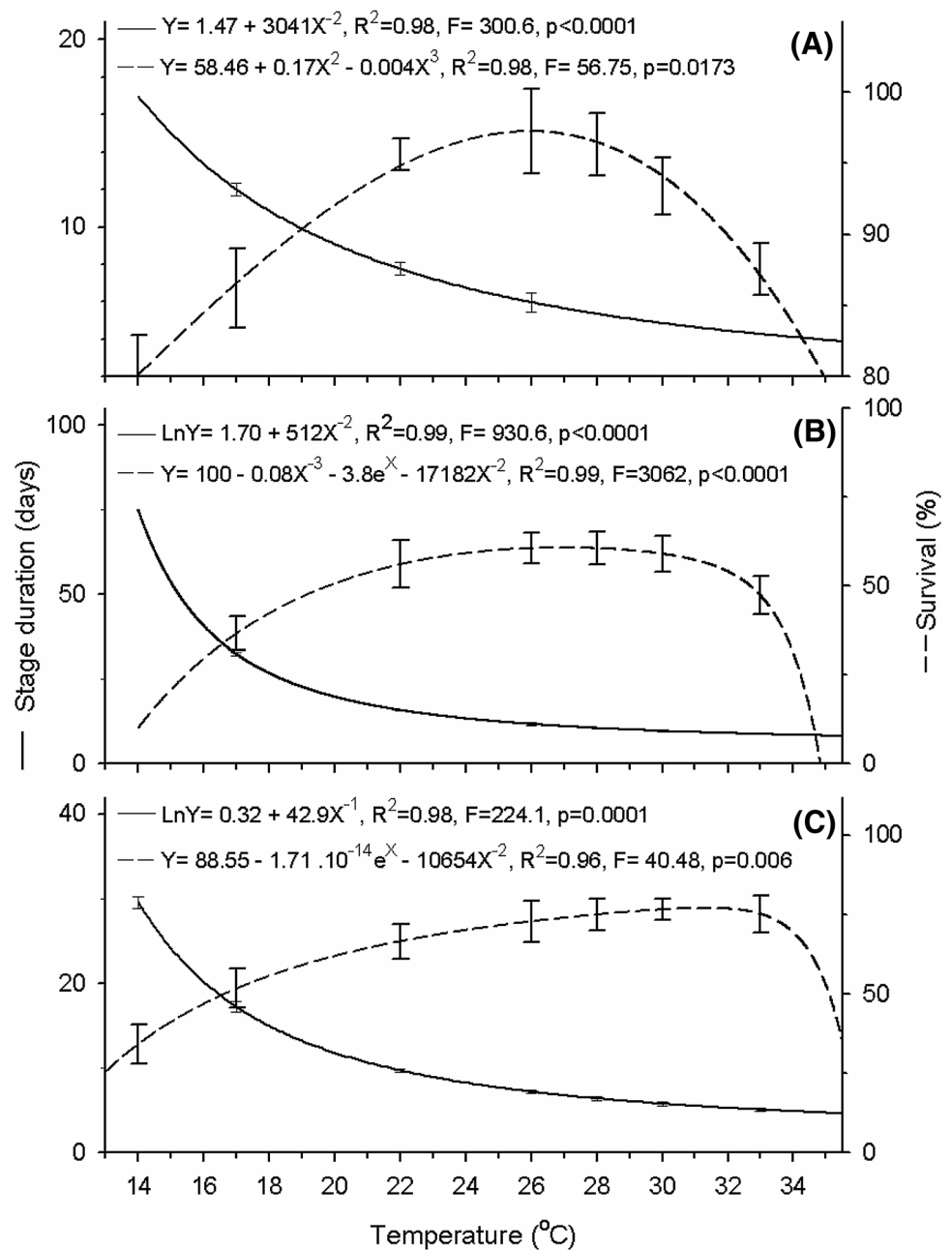
The survival curves for the total cycle of *T. absoluta* obtained by Kaplan-Meier's estimation showed significant differences according to the temperature (log-rank;  $\chi^2 = 417.83$ ; df = 5;  $P < 0.001$ ). The estimated lethal time (LT<sub>50</sub>) for *T. absoluta* decreased with an increase in the temperature (Fig. 2).

The duration of the life cycle of *T. absoluta* decreased from 75 to 26 days when the temperature ranged between 17 and 33 °C (Fig. 3). Four phases are discernible in the survival curves of *T. absoluta*. The first phase occurred during the egg stage, where insect mortality was low (<15 %). The first phase lasted until days 12, 8, 6, 5, and 4 after the beginning of the life cycle at temperatures of 17, 22, 26, 28, 30, and 33 °C, respectively (Fig. 3). The manifestation of mortality in the first stage was by observance of “no hatching.” The second phase occurred during the larval stage and lasted for 32, 15, 10, 9, 9, and 8 days at temperatures of 17, 22, 26, 28, 30, and 33 °C, respectively (Figs. 1b, 3). The third phase occurred during the pupal stage, and the manifestation of death was by observance of “no adult emergence.” The duration of the third stage lasted from 18 to 4 days at a temperature range between 17 and 33 °C (Figs. 1c, 3). The fourth phase occurred during the adult stage on days 62, 32, 23, 20, 20, and 17 after the beginning of the life cycle of *T. absoluta* at temperatures of 17, 22, 26, 28, 30, and 33 °C, respectively. The adult mortality rate was gradual until the death of the last individual (Fig. 3). The highest pre-adult mortality of *T. absoluta* occurred during the larval stage, regardless of the temperature condition.

Egg-laying by *T. absoluta* started on days 63, 31, 22, 21, 21, and 17 after the start of the life cycle at temperatures of 17, 22, 26, 28, 30, and 33 °C, respectively. The maximum egg-laying (7, 22, 17, 15, 28, and 5 eggs female<sup>-1</sup>) occurred on days 68, 36, 30, 22, 22, and 20 after the beginning of the life cycle at temperatures of 17, 22, 26, 28, 30, and 33 °C, respectively (Fig. 3).

Temperature significantly affected the generation time ( $T$ ) ( $F_{5,48} = 644.12$ ,  $P < 0.0001$ ), net reproductive rate ( $R_0$ ) ( $F_{5,48} = 3.89$ ,  $P = 0.005$ ), and intrinsic rate of natural

**Fig. 1** Developmental time (days) and survival (%) for **a** egg, **b** larval, and **c** pupal stages of *Tuta absoluta* at different temperatures



increase ( $r_m$ ) ( $F_{5,48} = 18.49$ ,  $P < 0.001$ ). However, age-specific fertility ( $m_x$ ) was not significantly affected by the temperature condition ( $F_{5,48} = 2.07$ ;  $P = 0.08$ ). The estimated generation time ( $T$ ) decreased from 144 to 21 days, while the estimated number of generations every year increased from 0 to 17 at temperatures of 14 and 33 °C, respectively (Fig. 4a, b). The age-specific fertility was found to be highest at 30 °C (7 eggs female<sup>-1</sup>days<sup>-1</sup>; Fig. 4c). The net reproductive rate ( $R_0$ ) of *T. absoluta* reached its maximum at 28 °C ( $R_0 = 25$ ) (Fig. 5a).

The intrinsic rate of increase ( $r_m$ ) reached its maximum value at 30 °C ( $r_m = 0.12$ ) (Fig. 5b). At 14 and 34.6 °C,

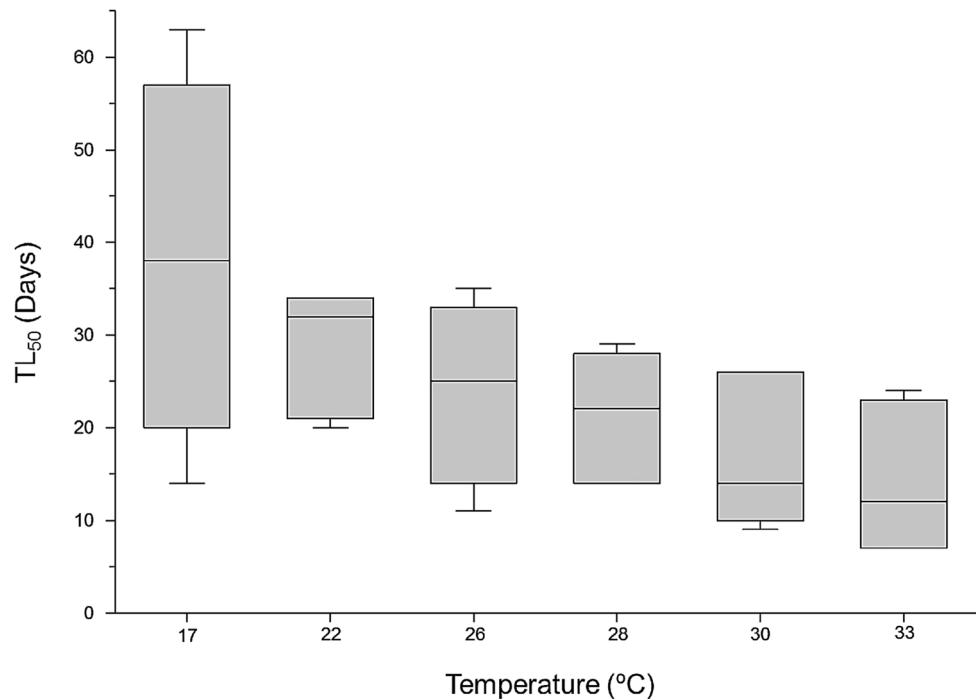
the  $r_m$  estimated values were equal to 0 (Fig. 5b). In additional experiments performed to verify whether the estimates of the upper and lower temperature thresholds were accurate, no reproduction of *T. absoluta* was observed at either 35 or 13 °C.

### Discussion

The population density of insect pests results from changes in the biotic and abiotic factors of a given system containing this organism (Price 1997). Our study provides



**Fig. 2** Lethal time ( $LT_{50}$ ) estimates from the Procedure Lifetest SAS<sup>®</sup> software for *T. absoluta* at different temperatures. The box plots indicate the median and dispersion (lower and upper quartiles) of the mean survival times ( $TL_{50}$ )

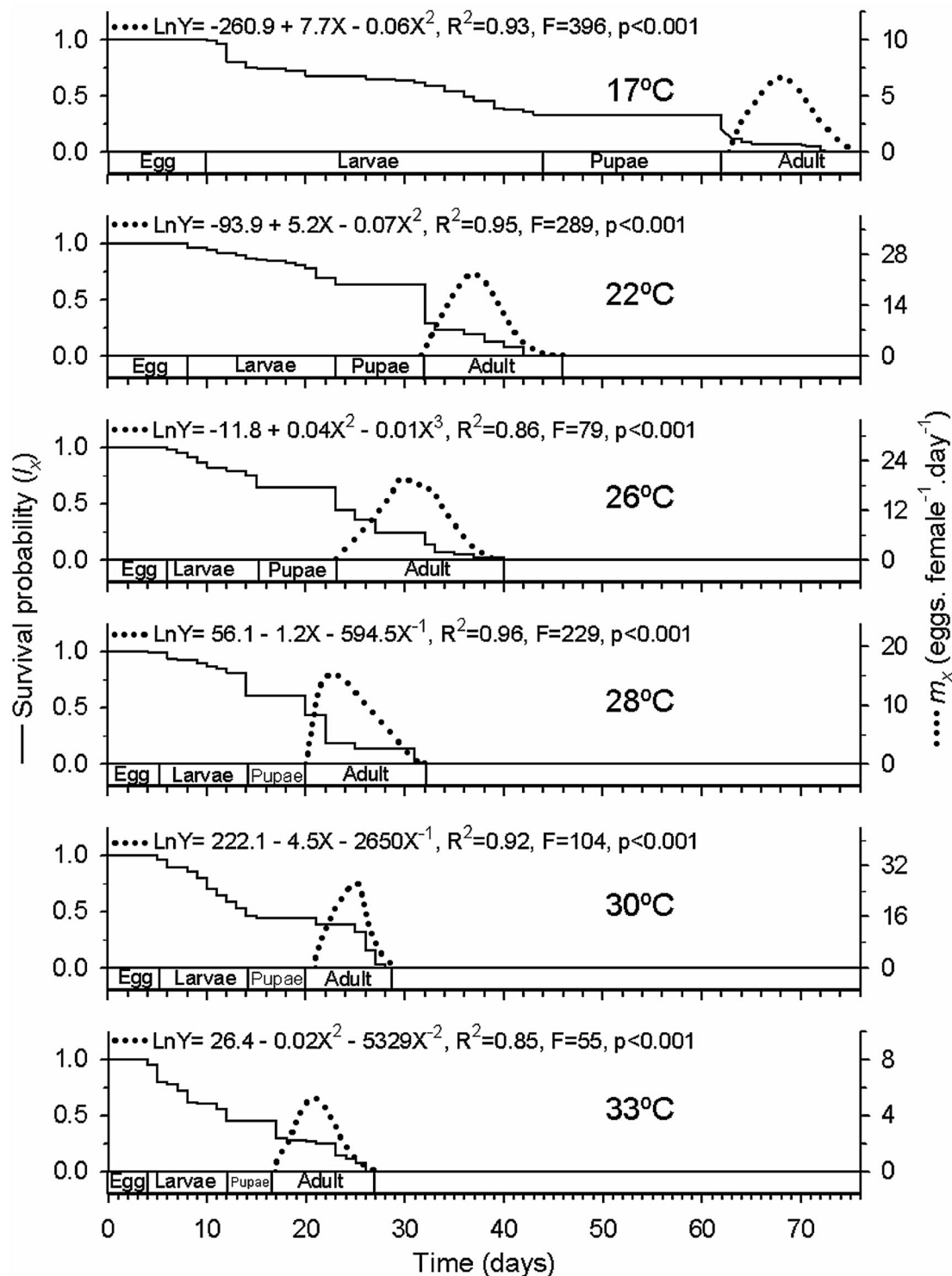


information on the effects of the abiotic factor temperature on *T. absoluta* and highlights how it affects the development, fecundity, and survival of this pest insect. The data acquired can be used to establish predictive models of occurrence of *T. absoluta* over both time (seasons) and space (different locations) and are useful in understanding the demography and population dynamics and for forecasting outbreaks of *T. absoluta* in the agroecosystem (Roy et al. 2003). In addition, our data can be used for projections of the potential geographic diffusion of *T. absoluta* because we provide information on the limiting effects of temperature extremes on several biological parameters of *T. absoluta* (i.e., developmental rate, mortality, and fecundity). These parameters are important for determining not only the geographic distribution, but also the invasiveness potential of the species (Desneux et al. 2010; Ponti et al. 2015a, b).

The developmental time and survival of *T. absoluta* were significantly affected by temperature as in other lepidopteran species (Mironidi and Savopoulou-Soultani 2008; Koda and Nakamura 2012; Park et al. 2014). The developmental time of *T. absoluta* gradually increased as the temperature decreased from 33 to 17 °C. This effect can be explained by the ectothermic nature of the insects because their metabolic, biochemical, and physiological processes are extremely dependent upon environmental temperature (Neven 2000; Bale 2002; Sgolastra et al. 2011). At lower temperatures, their metabolic processes are slower; therefore, the insects' developmental time becomes longer (Benkova and Volf 2007; Damos and Savopoulou-Soultani 2012). In addition, a

longer developmental time can also occur because of high energy consumption by insects for physiological repair injuries caused by extended cold conditions at lower temperatures (Lalouette et al. 2011). In contrast, the reduced insect survival near the threshold temperatures can be caused by heat or cold cumulative physiological damages, leading to an arrest of the occurrence of different developmental events such as egg hatch, larval molt, and adult emergence (Colinet et al. 2011).

We observed that temperature affected the overall biological performance of the tomato borer, as reflected in its population growth rate ( $r_m$ ). This parameter is important because it reflects the overall effect of temperature on the development, reproduction, and survival of the insect species (Southwood and Henderson 2000). Until now, studies have evaluated the effects of temperature on *T. absoluta* using biological characteristics such as development, survival, or reproduction (Betancourt et al. 1996; Barrientos et al. 1998; Vercher et al. 2010; Cuthbertson et al. 2013; Van Damme et al. 2015). However, none of these studies used a population parameter such as the population growth rate ( $r_m$ ), which integrates several biological characteristics, in evaluating the effect of temperature or determining the thermal requirement thresholds of *T. absoluta*. The results of the effect of temperature on isolated biological characteristics may be contradictory and incomplete because, at a particular temperature, reproduction can be high while insect development may be low and vice versa. This fact was observed in our study, which showed that at a temperature of >33 °C, the reproduction

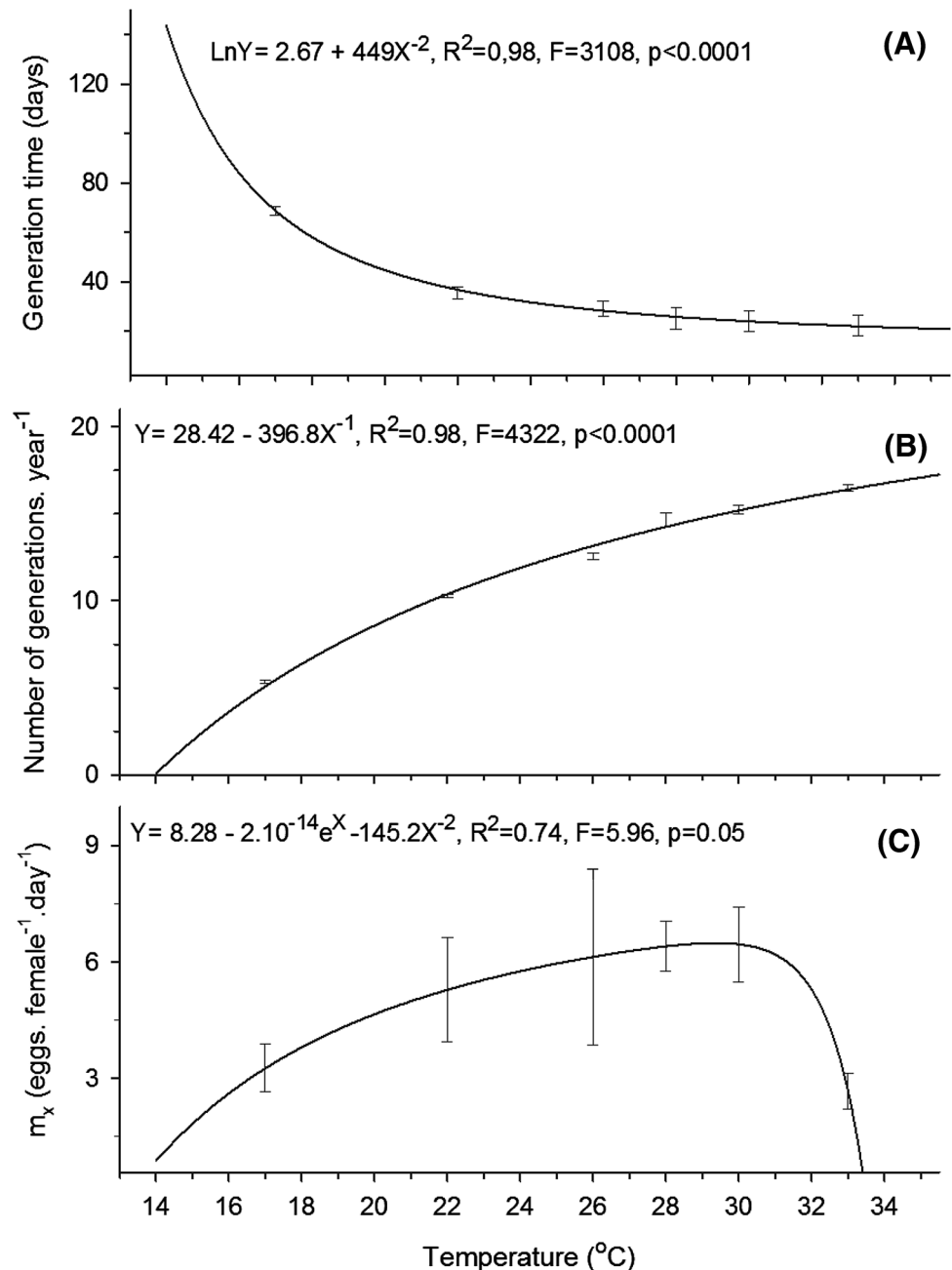


**Fig. 3** Survival (egg, larvae, pupae, and adult stages) and age-specific fertility ( $m_x$ ) of *Tuta absoluta* at different temperatures in relation to time after the beginning of the life cycle

of *T. absoluta* was low while its developmental rate was quite high. Thus, the question remains whether the temperature of 33 °C is good for the insect species. In contrast, when the effect of temperature on the population growth

rate was considered, the results were conclusive. Nevertheless, experiments that include overall biological performance parameters are laborious and time-consuming (Denlinger and Lee 2010).

**Fig. 4** **a** Generation time (days), **b** number of generations per year, and **c**  $m_x$  = age-specific fertility (eggs female<sup>-1</sup> day<sup>-1</sup>) of *Tuta absoluta*, in relation to different temperatures



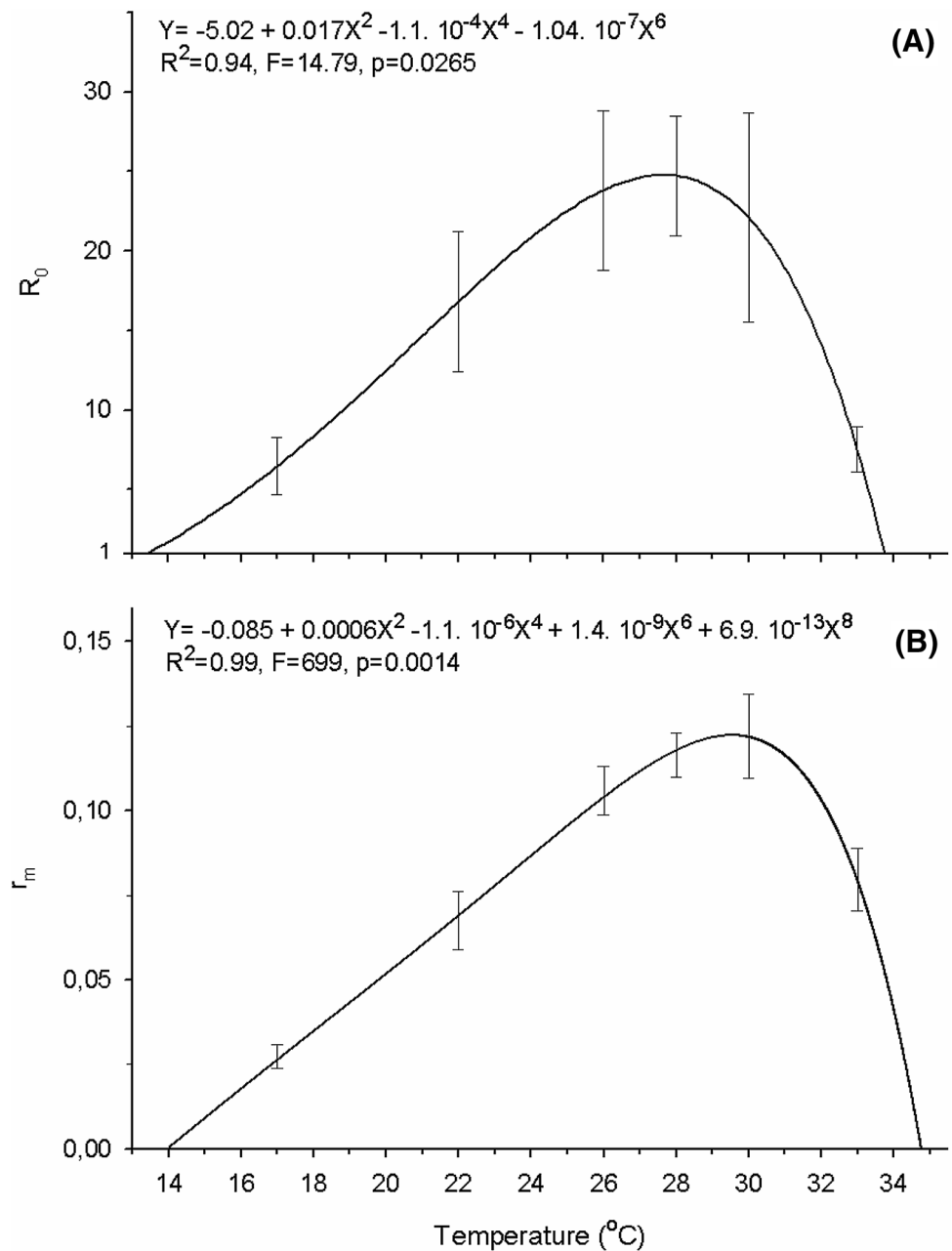
The intrinsic rate of increase ( $r_m$ ) reached its maximum at 30 °C, indicating that this temperature was optimal for *T. absoluta*. Therefore, at 30 °C the reproduction, development, and survival of the insect were high. At temperatures >30 °C, although the insect developed faster, its reproduction and survival rate decreased. The optimum temperature detected is relatively close to the upper threshold for the tomato borer (34.6 °C), as has also been reported for other lepidopteran pest species (e.g., Marchioro and Foerster 2011; Orang et al. 2014). Thus, in areas where *T. absoluta* are not limited by other factors, such as resource availability or large populations of this species, increased severity of the

damage to tomato crops will occur when this pest species is maintained at temperatures approximating 30 °C.

The fact that the population growth rate (i.e.,  $r_m$ ) was nil (i.e., = 0) at 14 °C and 34.6 °C indicates that these are the lower and upper developmental thresholds for *T. absoluta*, respectively. Although some individuals can survive at temperatures below 14 °C or above 34.6 °C, the *T. absoluta* population will not grow because when  $r_m = 0$ , the population growth remains stable (Krebs 1994). The temperature thresholds estimated by the regression models were confirmed in a supplementary experiment where no increase in the population of *T. absoluta* was observed at a temperature



**Fig. 5** **a**  $R_0$  = net reproductive rate and **b**  $r_m$  = intrinsic growth rate of *Tuta absoluta* in relation to different temperatures



<14 °C or >34.6 °C. These temperature thresholds contrast with others reported for *T. absoluta* (i.e., 42 and 8 °C, the lower and upper temperature thresholds, respectively), which were based on the insect’s developmental rate or on the assumption of this species occurrence in regions encompassing a wide range of temperatures (Barrientos et al. 1998; Desneux et al. 2010; Tonnang et al. 2015).

The thermal requirements of *T. absoluta* determined by using  $r_m$  were very different from those estimated using only the rate of insect development. In the latter context, the optimum temperature for *T. absoluta* would be 35 °C if estimated based only on the rate of insect development. However, this determination is not accurate, which was

confirmed by our supplementary experiment that detected no population growth of *T. absoluta* at 35 °C.

In studies of thermal thresholds for an insect, a minimum temperature threshold is determined below which the development of the insect ceases or decreases (Briere et al. 1999). In this sense, at lower temperatures, the immature stages of *T. absoluta* have a longer developmental period and potentially provide a wider window of opportunity for its management. Determination of the thermal thresholds also enables mass production of *T. absoluta* at its optimum temperature (30 °C). These insects can be raised and used as a food source for their natural enemies in fields and greenhouses for biological control purposes (Urbaneja

et al. 2012; Zappalà et al. 2013; Luna et al. 2015). In addition, knowledge of survival and adult longevity under different temperatures is important for understanding the biology and diapause behavior of pest insects (Cuthbertson et al. 2013; Van Damme et al. 2015). This knowledge is also important for eradication attempts of newly introduced pest species (Vargas et al. 1997), such as *T. absoluta*.

In conclusion, we elucidated the effects of different temperatures on the biological performance parameters of *T. absoluta*. We found that the optimum temperature for *T. absoluta* is 30 °C, and the upper and lower developmental thresholds for this pest species are 34.6 and 14 °C, respectively. Notably, the results of the present study provide useful data for the development of prediction models of population density and of spatial and temporal distribution of the *T. absoluta*, as well as help in designing management strategies for this pest species. Furthermore, these findings will allow the establishment of suitable sampling and monitoring programs and will also allow better timing of pesticide application and natural enemy release against the tomato borer, optimizing the management of this pest species.

### Author contribution statement

JCM, MCP, and RNCG conceived and designed the research. JCM, PASJ, and DOF conducted the experiments. JCM, MCP, and LB analyzed the data. JCM wrote the manuscript. MC made critical revisions. RNCG made critical revisions and approved the final version. All authors reviewed and approved the final manuscript.

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### Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

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