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Influence of temperature on some biological attributes and life table analysis of the tomato leaf miner, *Tuta absoluta* (Lepidoptera; Gelechiidae)

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ABSTRACT

The tomato leaf miner (TLM), Tuta absoluta (Meyrick) (Lepidoptera: Gelechiidae) is a new exotic invasive pest in Egypt and is considered one of the most economically destructive pests of tomato and other solanaceous plants worldwide. The effects of temperature on the biological attributes of TLM were studied at five constant temperatures (15, 20, 25, 30 and 35°C) combined with 60±10% R.H. Results indicated that TLM failed to survive due to the high mortality in cohort reared at 35ºC. Total developmental time was negatively correlated to the increase of temperature; being longest (67.67 days) at 15°C and shortest (14.42 days) at 35°C. Longevity of either males or females decreased as temperature increased. The daily average fecundity of females was 15.78, 18.19, 34.65 and 28.26 eggs at 15, 20, 25 and 30ºC, respectively. The mean total lifetime fecundity of TLM females was 13.92, 211, 244.17 and 177.83 eggs at 15, 20, 25 and 30°C, respectively. Adult survival rates were declined gradually to reach 0% after 11 days post emergence at 30ºC, 17 days at 25ºC, 23 days at 20ºC, and 34 days at 15ºC. Life table analysis showed that the population of TLM reared at 30°C had the highest intrinsic rate of increase (0.75), net reproductive rate (28.28), shortest population doubling time (0.93 days) and mean generation time (4.49 days), comparing to populations reared at 15, 20 and 25°C. Thereupon, the optimum temperature for population growth of T. absoluta ranged between 20 to 30°C.

Keywords: *Tuta absoluta*; Temperature; Life table; Development; Survival; Reproduction

INTRODUCTION

The ambient temperature is one of the most important environmental factors influencing the biology, physiology and behavior of insects [1-3]. The various manifestations of this influence on insect pests may be directly reflected on their distribution, phenology, activity, number of generation and, indirectly, through impact on their natural enemies. Moreover, since insects are strongly temperature-dependent, it can be expected to affect significantly the seasonal population dynamics by affecting several of their biological attributes such as adult life span, survival, fecundity, fertility and rate of population growth [4-6]. Thus, the response to local environmental conditions is a key component for the adaptation and persistence of insect pests, especially invasive alien species.

Invasive species represent a potential threat to agro-ecosystems of the invaded area [7-9]. The invasive tomato leaf miner, *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae), is one such species. It is originated from South America, and rapidly invaded various European countries and spread very quickly along the Mediterranean Basin, causing serious damages to tomato in the recently invaded areas [10-12]. In Egypt, since its initial detection at the end of 2009, TLM became a serious threat to greenhouse and open-field tomato production [13]. TLM may cause

economic losses in tomatoes of up to 80-100% if it is not managed properly [12-15]. Larvae of TLM feed on all aerial parts of tomato plants, however the main damage is usually observed as galleries or mines on the leaves and fruits, but inflorescences and stems can also be affected. *T. absoluta* is a multivoltine species, with a high reproductive potential, which rapidly develops in favorable environmental conditions, with overlapping life cycles [16]. Larvae do not enter diapause when food is available and depending on the environmental condition, up to 12 generations per year may be able to develop [14].

The life table analysis is a reliable statistical method to present and evaluate the changes in population of insect pests during different developmental stages throughout their life cycle under specified conditions [17]. The different environmental conditions could be a determinant factor on insect pest development and subsequently on its population growth parameters. Documenting the variation in construction and life table parameters among different temperature conditions is critical for understanding population dynamics and thus use the obtained information to prepare a predictive model which can be useful to use in pest management programs. In spite of the fact that insects are not subjected to constant temperatures in nature, controlled laboratory studies can provide valuable insights for understanding the development, survival, reproduction and population dynamics of insect pests [18]. In this respect, the present research may provide valuable information about the life table parameters of *T. absoluta*.

Therefore, the goal of this study was to examine the influence of different temperature regimes on the development of immature stages and adults, survivorship, reproduction and other biological attributes of TLM under laboratory conditions.

MATERIALS AND METHODS

The effect of temperature on the development and reproductive biology of TLM on tomato plants (variety GS12) was studied at five constant temperature regimes (15, 20, 25, 30 and 35±1°C), 60±10% R.H. and 16:8 L/D photoperiod in the laboratory of Public Service Center of Biological Control, Faculty of Agriculture, Suez Canal University, Ismailia, Egypt (PSCBC, SCU).

1.1. TLM culture

The initial culture of tomato leaf miner (TLM) used in this study was obtained from infested tomato plants and fruits collected from tomato fields in the Experimental Farm, Faculty of Agriculture, SCU, in April, 2011. The infested leaves or fruits, containing different immature stages, were kept at room temperature of 25±2°C and 60±10% RH in rearing cages (40 cm in width × 60 cm in length × 80 cm in height), provided with fresh tomato plants for the completion of the development of immature stages. Newly formed pupae were collected from time to time and kept in 12 cm Petri dish until emergence. Emerged adults were collected by an aspirator and confined in ovipositional cages with the same dimensions described above. Within each cage, a piece of cotton moistened with 10% honey solution was used for moth feeding, and provided with fresh batch of tomato plants (grown in plastic pots 15 cm in diameter) as an ovipositional substrate. The tomato plants (GS variety; 50-day old; 30 cm in height) harboring eggs of TLM were transferred daily to immature stages rearing cages and replaced by another fresh batch of tomato plants and so on until the death of all TLM adults. This cycle was repeated for several generations to maintain the laboratory culture. To obtain the same aged eggs of TLM, about 20 – 30 pairs of both sexes of newly emerged moths were put inside an oviposition cage. After 5-6 hours, tomato seedlings were taken and the eggs were used for the intended experiments.

2.2. Effect of temperature on the biological attributes of TLM

2.2.1. Effects on immature development

To study the effect of temperature on TLM immature stages, thirty eggs were collected from the laboratory culture (newly deposited, <6 hours) and separated individually. Each egg was placed in a clean glass tube (3×10cm) closed with piece of cotton. Upon hatching, newly hatched larvae were introduced to small tomato seedling as larval food. These seedlings were cared and watered when needed. The development of TLM was monitored and data were recorded twice a day in terms of incubation period, duration of larval stage, pupal stage as well as survival of each stage throughout the experiment.

2.2.2. Effects on adult stage

To determine the longevity, ovipositional periods, survival and fecundity, newly emerged TLM adults were paired and each couple was left for mating. Each couple was placed in a glass tube (3×10 cm) covered with piece of cotton

cloth and held in place by a rubber band and provided by small droplets of honey solution on the inner wall as food. A tomato leaf was provided for each couple as ovipositional substrate. Females of TLM laid their eggs mostly on the provided leaf. In case of laying eggs in the inner wall of the glass vial, these eggs were counted and removed smoothly by the aid of fine camel hair-brush. Adults were checked daily and the numbers of deposited eggs, alive and dead adults were recorded until the death of all tested females or males. In each temperature regime, 12 pairs of TLM adults were tested.

2.3. Construction of life table

Life table of TLM was constructed using the obtained data of survivorship and age-specific fecundity of adults along with the survivorship and development of all immature stages of TLM. The net reproductive rate (R_o), intrinsic rate of increase (r_m), mean generation time (T) and the finite rate of increase (λ) were calculated according to the description of [19], whereas doubling time (DT) was calculated according to [20] as follows:

$R_o=\sum l_x m_x$,
$T= \sum x l_x m_x / \sum l_x m_x$,
$r_m= \ln R_o/T$,
$\lambda=\exp (rm)$,
$DT= \ln 2/r_m$

Where x is the age of female (days), lx is the survivorship at the corresponding time, mx is age-specific fecundity. The parameters of the life-table were estimated on the basis of 1:1 sex ratio.

2.4. Statistical analyses

All data were examined for normality with the Shapiro-Wilk test before analysis. When a Shapiro-Wilk test indicated that data were normally distributed, data were analyzed by parametric analysis of variance (ANOVA) and then the Holm-Sidak or Student-Newman-Keuls methods were used for all pair wise multiple comparisons. When data were not normally distributed, a nonparametric Kruskal–Wallis ANOVA on ranks (H test) was used and Tukey's or Dunn's tests were used to compare treatment means at a 0.05 level of significance. Proportional data were square root transformed before analysis to improve the normality of residuals and reduce the impact of any extreme values. Data were analyzed using SigmaPlot 12.3 [21].

RESULTS

3.1. Effects on TLM immature stages

3.1.1. Effects on development

The obtained results indicated that temperature had a profound and significant effect on the development of all immature stages of TLM. As shown in Table 1, the incubation period of TLM eggs were significantly affected by temperature. As the temperature increased, there was a significant decrease in incubation period (H_4= 103.62; *P*= 0.001). While the shortest incubation period was 1.83 days at 35°C, the longest one (12.08 days) was observed at 15°C. The incubation period was intermediate in the other tested temperatures; being 8.42, 4.42 and 4.08 days at 20, 25 and 30°C, respectively.

As for total larval development, there was also a significant effect of temperature on this stage (H_4= 56.22; *P*= 0.001). The total larval period was shortest of (7.42 days) at 30°C, followed by 8.33 days at 35°C. The longest larval duration was obtained at the lowest temperature of 15°C being 37.17 days. The larval duration at 20 and 25°C was in-between being 19.67 and 11.42 days, respectively (Table 1).

Data in Table 1 also indicated that temperature had also a significant and negative correlation with pupal duration (H_4= 50.56; *P*=0.001). The pupal periods lasted 18.42, 11.67, 7.58, 4.58 and 4.25 days at 15, 20, 25, 30 and 35°C, respectively.

The total developmental period of TLM was negatively correlated to the increase of temperatures; being longest (67.67 days) at the lowest tested temperature (15°C) and shortest of (14.42 days) on the highest tested temperature (35°C) (Table 1). Statistical analysis showed that there were significant differences among the tested temperatures in terms of total developmental periods of TLM (H_4= 58.76; *P*= 0.001).

Table 1 Effect of different temperature regimes (15, 20, 25, 30 and 35°C) and 60±10% R.H. on the immature development of TLM reared on tomato plants.

Temp.	Incubation Period	Larval Period	Pupal Period	TDP*
15 °C	12.08± 1.06 a	37.17± 2.73 a	18.42± 0.68 a	67.67± 3.68 a
20 °C	8.42± 0.30 b	19.67± 0.17 b	11.67± 0.21 b	39.75± 0.53 b
25 °C	4.42± 0.15 c	11.42± 0.30 c	7.58± 0.35 c	23.42± 0.24 c
30 °C	4.08± 0.15 c	7.42± 0.52 d	4.58± 0.24 d	16.08± 0.30 d
35 °C	1.83± 0.25 d	8.33± 0.33 d	4.25± 0.21 d	14.42± 0.37 d
P	0.001	0.001	0.001	0.001

** TDP indicates Total Developmental Period*

Means within a column followed by different letters are significantly different: P<0.05; Dunn's Method.

3.1.2. Effects on survival rates

As shown in Table 2, temperature had a significant impact on the survival rate of TLM immature stages. The percentage of egg hatching was highest (100%) at 30°C, followed by (93.33%) at 25°C. The egg viability was comparable of 73.33, 70 and 70 at 15, 20 and 35°C, respectively (Table 2). Statistical analysis proved that there were significant differences in the rate of egg hatching among tested temperatures (H_4=12.31; *P*=0.015). The same trend was also observed for larval survival rate as the greatest value (85.56%) was recorded at 25°C and the lowest (15.13%) at 35°C. Apparently, there was significant differences among tested temperatures in form of larval survival rate (H_4= 20.36; *P*= 0.001).

As for pupal survival rate, the greatest percent (100%) was also observed at 35°C followed by 96.29% at 25°C and 95.83% at 20°C. Rates of pupal survival at 30 and 15°C were 93.33 and 88.89%, respectively (Table 2). The pupal periods among treatments showed insignificant differences (H_4= 3.85; *P*= 0.426).

The overall generation survival (egg-adult) was greatest (76.67%) at 25°C and lowest (10%) at 35°C. At 15, 20 and 30°C, the generation survival rates were 16.67, 46.67 and 33.33%, respectively (Table 2). Clearly, significant differences were found among tested temperatures in term of overall generation survival ($F_{4,145}$= 12.70; *P*= 0.002).

Table 2 Effect of different temperature regimes (15, 20, 25, 30 and 35°C) and 60±10% R.H. on the percentages of survival rates of TLM immature stages reared on tomato plants.

Temp.	% Hatching	% Larval survival	% Pupal survival	Generation survival
15°C	73.33± 14.53 b	30.95± 10.51 c	88.89± 11.11 a	16.67± 3.33 c
20°C	70.00± 10.00b	68.52± 17.67 ab	95.83± 4.16 a	46.67± 14.53 b
25°C	93.33± 3.33 a	85.56± 3.90 a	96.29± 3.70 a	76.67± 3.33 a
30°C	100 a	36.67± 8.82 bc	93.33± 6.67 a	33.33± 6.67 bc
35°C	70.00± 11.55 b	15.13± 2.60 c	100 a	10.00±0.00 c
P	0.015	0.001	0.426	0.002

Means within a column followed by different letters are significantly different: P<0.05; Student-Newman-Keulstest (% Hatching and Larval survival); or Holm-Sidak method (Generation survival).

3.2. Effects on TLM adult stages

As indicated in the immature survival experiment, very low number of adult moths emerged when immature stages were reared at 35°C. Therefore, the effect of temperature on adult stage of TLM was conducted at only four temperature regimes except at 35°C.

3.2.1. Effects on ovipositional periods

The effects of different constant temperatures on the ovipositional periods of TLM moth females are depicted in Figure 1. Data indicated that the tested temperatures elicited significant effect on the pre-ovipositional periods of TLM. The pre-ovipositional periods lasted 11.08, 5.96, 3.58 and 1.33 days at 15, 20, 25 and 30°C, respectively. Significant differences were found among treatments in terms of pre-ovipositional periods (H_3=43.40; *P*=0.001).

As for ovipositional period, the longest period was 11.67 days at 20°C, whereas the shortest was 3.83 days at 15°C. At 25 and 30°C, these periods were comparable at 7.38 and 6.58 days, respectively (Figure 1). Obviously, there were significant differences among ovipositional periods under the tested temperatures ($F_{3,44}$=58.56; *P*=0.001).

Regarding post-ovipositional period, this interval was very short (1 day) at 30°C, increased to 1.96, 2.92 and 13.13 days at 25, 20 and 15°C, respectively (Figure 1). Statistical analyses revealed that significant differences existed among tested thermal treatments (H_3=38.13; *P*=0.001).

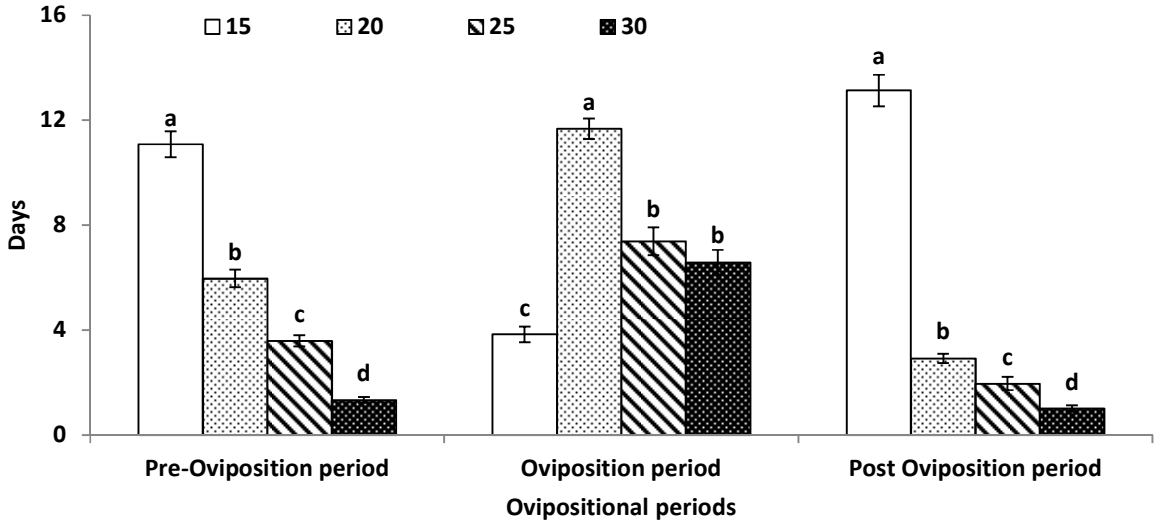

Figure 1 Effects of temperatures (15, 20, 25 and 30°C) and 60±10% R.H. on the ovipositional periods of TLM. Bars with different letters indicate significant difference(P<0.05)

3.2.2. Effects on fecundity

As shown in Figure 2, TLM females oviposited under the four tested temperatures. However, very little number of eggs (13.92 eggs) was laid per female at 15°C. Lifetime fecundity increased to 177.83, 211 and 244.17 eggs at 30, 20 and 25°C, respectively. Obviously, temperature had significant effect on the total lifetime fecundity of TLM (H_3=38.87; *P*=0.001). As for daily fecundity, the mean daily fecundity of TLM was 3.80, 18.19, 34.65 and 28.26 eggs/female at 15, 20, 25 and 30°C, respectively (Figure 2). Clearly, there was significant difference among tested temperatures in terms of daily fecundity (H_3=39.89; *P*=0.001).

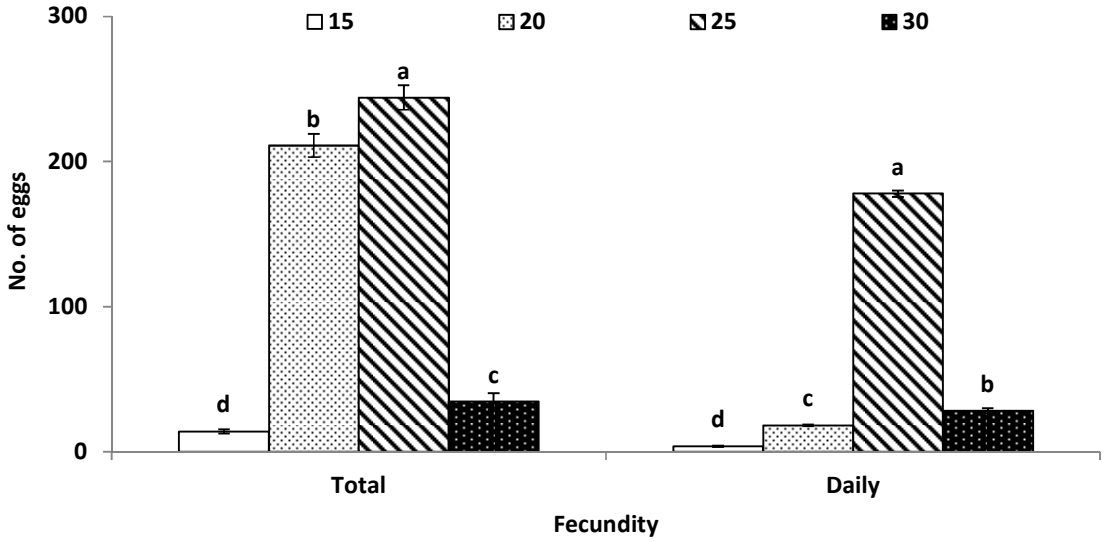

Figure 2 Mean (±SE) of daily and total lifetime fecundity of TLM at different temperatures of (15, 20, 25 and 30°C). Bars with different letters in the same treatment indicate significant difference (P<0.05)

3.2.3. Effects on adult longevity

Generally, females of TLM lived longer than males irrespective of rearing temperatures and holding conditions. Longevity of either males or females decreased as temperature increased. Longevity of TLM females lasted 27.96,

20.54, 12.92 and 8.92 days at 15, 20, 25 and 30°C, respectively (Figure 3). Apparently, there were significant differences among tested temperatures in terms of female longevity ($F_{3,44}$=168.49; *P*=0.001).

Pertaining to male, their longevities at the respective temperatures were 15.79, 7.46, 5.88 and 2.38 days (Figure 3). Indeed, significant differences were observed in male longevity among the studied temperatures (H_3=40.49; *P*=0.001).

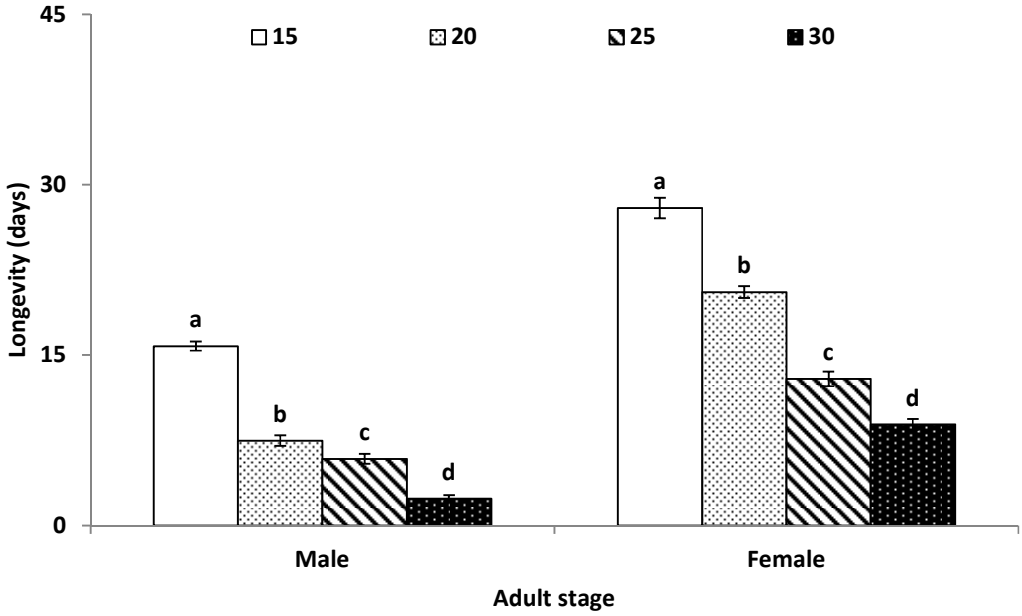

Figure 3 Mean (±SE) of male and female longevity of TLM at different tested temperatures of (15, 20, 25 and 30°C). Bars with different letters in the same treatment indicate significant difference(P<0.05)

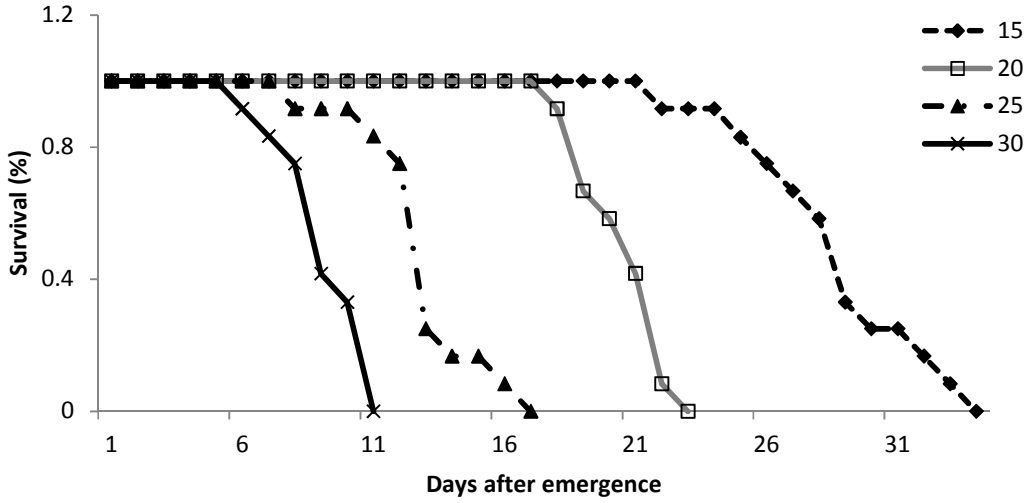

Figure 4 Survival curves of TLM females at different treated temperatures.

3.2.4. Effects on adult survival curve

Survival curves of TLM adults at different temperatures were estimated for adult cohorts used in the adult stage experiments. The obtained data are depicted in Fig. 4.

Data indicated that adult survival rate of TLM was highly influenced by temperature. At 5 days post emergence,

adult survival rates were 100% at all tested temperatures. Adult survival rates declined gradually to reach 0% after 11 days post emergence for 30°C; 17 days for 25°C; 23 days for 20°C and 34 days for 15°C (Fig. 4).

3.2.5. Effects on fecundity curve

The obtained data indicated that temperature affected the oviposition trend of TLM (Fig. 5). TLM females continued ovipositing reaching maximum oviposition on the third and fourth day at 25 and 30°C, respectively. At 15 and 20°C, the maximum number of deposited eggs was observed on the second day, and then oviposition declined until death.

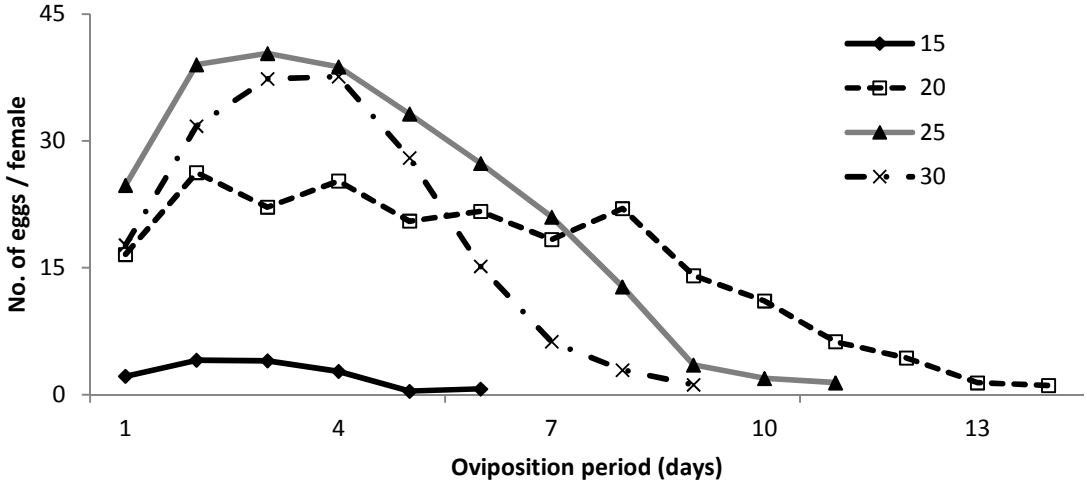

Figure 5 Oviposition curves of TLM females at different treated temperatures.

3.3. Life table parameters

The obtained data for both immature and adult stages were pooled to construct life table of TLM under different tested temperatures. Results revealed that the ambient temperature had profound impact on life table attributes for TLM. Females reared at 25°C showed the highest net reproductive rate (R_o) (86.21 females/female), followed by 48.09, 28.28 and 1.07 females/female at 20, 30 and 15°C, respectively (Table 3).

As for generation time (T), the shortest generation time was 4.49 days at 30°C, and the longest (14.58 days) at 15°C. Generation time at 20 and 25°C was in-between of 12 and 7.92 days, respectively (Table 3).

The intrinsic rate of increase (r_m) varied also among tested temperatures; being 0.004, 0.323, 0.563 and 0.748 at 15, 20, 25 and 30°C, respectively. The respective values for the finite rate of increase (λ) were 1.00, 1.38, 1.76 and 2.11. Pertaining to doubling time (DT), its values were 160.56, 2.15, 1.23 and 0.93 days for the respective tested temperatures (Table 3).

Table 3 Effect of different tested temperatures (15, 20, 25 and 30°C) on life table attributes (R_o, T, r_m, λ and DT) of TLM raised on tomato plants.

Temp.	Net reproductive rate (R_o)	Mean generation time (T) (days)	Intrinsic rate of increase (r_m)	Finite rate of increase (λ) ($days^{-1}$)	Doubling time (DT) (days)
15°C	1.07± 0.00 d	14.58± 0.69 a	0.004± 0.001d	1.00± 0.00 d	160.56± 15.50a
20°C	48.09± 2.67 b	12.00± 0.42b	0.323± 0.042c	1.38± 0.02c	2.15± 0.09 b
25°C	86.21± 2.64a	7.92± 0.18c	0.563± 0.010b	1.76± 0.02b	1.23± 0.02 b
30°C	28.28± 0.80 c	4.49± 0.23d	0.748± 0.031a	2.11± 0.07a	0.93± 0.04b
P	0.001	0.001	0.001	0.001	0.001

Means within a column followed by different letters are significantly different: P<0.05; Holm-Sidak method (Net reproductive rate, Mean generation time, Intrinsic rate of increase and Finite rate of increase); or Tukey Test (Doubling time).

Moreover, statistical analyses revealed that tested temperatures caused significant differences in net reproductive rate ($F_{3,44}$= 347.88,*P*= 0.001), generation time ($F_{3,44}$= 107.64; *P*= 0.001), intrinsic rate of increase ($F_{3,44}$= 319.82; *P*= 0.001), finite rate of increase ($F_{3,44}$= 181.97; *P*= 0.001) and doubling time (H_3= 10.39; *P*= 0.001, Table 3).

DISCUSSION

The obtained results in this study revealed that temperature has a great influence on survival and development of TLM immature stages. Temperature between 20 and 30°C was the most favorable for immature development; while the lowest and highest tested temperatures (15 and 35°C) affected significantly and negatively development and survivorship of TLM. These findings were in consistence with those reported earlier for TLM [22, 23, 24]. In this study, TLM completed its immature development in 67.67, 39.75, 23.42, 16.08 and 14.42 days at 15, 20, 25, 30 and 35°C, respectively. These findings are in harmony with those reported by [24] who reported a total duration of 58, 37 and 23 days at 13, 19 and 25°C, respectively. [23] also found that the total developmental period of TLM immature was 71.5, 32.9 and 18.5 days at 15, 21 and 30°C, respectively.

As for adult stage, adult longevity, oviposition and post-ovipositional periods, it decreased with increasing temperature. The longest female longevity was recorded at 15°C, and the shortest was observed at 30°C. Also, the longest ovipositional period was 11.67 days at 20°C, whereas the shortest was 3.83 days at 15°C. These results are close to those of [25], who found that TLM females laid eggs for more than 20 days and up to 72.30, and 90% of these eggs were deposited during the first 5 and10 days, respectively. The highest mean daily fecundity was 34.65 eggs, while the lowest mean was 15.78 eggs at 15°C. [26] reported that the most prolific oviposition period is 7 days after first mating, with a maximum lifetime fecundity of 260 eggs per female. [27] also found that the greatest oviposition were obtained at temperature between 15 and 25°C, temperature over 15°C reduced the longevity of the adults, reaching a minimum of 5.60 days at 35°C.

Temperature also influenced the fertility life table attributes. TLM kept at 30°C had the highest r_m value (r_m= 0.75) among the studied temperatures. This is mainly due to shorter generation time and higher survivorship of TLM immature stages, as well as the higher daily rate of progeny per female. Life table attributes of TLM are not only affected by temperature, but also varied on host plants used in raising TLM immature stages. For example, [28] reported that life table parameters varied when TLM reared on tomato (R_o= 48.92, T= 27.98, r_m= 0.14) as compared to TLM population reared on potato (R_o= 14.43, T= 32.35, r_m= 0.08).

CONCLUSION

The obtained results clearly demonstrated that temperature is a key factor affecting the development, survival and reproduction of TLM. Moreover the TLM has a high capacity of rapid population increase due to its higher intrinsic rate (r_m), shorter development of time and higher fecundity, which clearly observed at temperature ranged between 20 and 30°C. Although insect pests are obviously not exposed to constant temperatures in natural conditions, the results from controller laboratory studies can provide a valuable insight into the expected population dynamics of TLM and would help in setting up the proper timing for pest control under field conditions.

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