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LIFE TABLE PARAMETERS OF SOUTH AMERICAN TOMATO MOTH *TUTA ABSOLUTA* (MEYRICK) (LEPIDOPTERA: GELECHIIDAE) UNDER SIMULATED TEMPERATURES AND CO_2 ON POTATO

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ABSTRACT: Abiotic factors such as temperature and carbon dioxide (CO_2) influence the growth of crops and phytophagous insects, however, the effect of elevated temperature and CO_2 on *Tuta absoluta* is not well understood till date. *T. absoluta* have potential to cause 100% damage to the crop, if proper management practices are not followed. In the present study effect of elevated CO_2 (eCO_2) levels and temperature on *T. absoluta* revealed that temperature and eCO_2 (550 ppm) had a significant effect on the life stages. The incubation period of eggs was found significantly reduced with the increase in temperatures both in ambient (aCO_2) and elevated (eCO_2) conditions. The eCO_2 had a significant effect on the life table parameters up to 30°C. The duration of all larval stages of *T. absoluta* were decreased significantly with the increased temperatures. The pupal period decreased significantly with the increase in temperatures in both aCO_2 and eCO_2 conditions. An eCO_2 delayed the pupal period significantly compared to the aCO_2. The total pre-adult period was significantly longer in eCO_2 than the aCO_2 conditions and also, the pre-adult period decreased significantly with increase in temperatures. As eCO_2 increase the larval duration compared to aCO_2 condition, the larva will get more time to feed on foliage resulting in greater damage to the potato foliage.

KEYWORDS: Abiotic factors, generation time, intrinsic rate of increase, net reproductive rate

INTRODUCTION

Climate change involves several factors such as rising atmospheric carbon dioxide and temperature. Carbon dioxide has been predicted to increase from current 390 µmol mol^{-1} to over 550 µmol mol^{-1} by 2050 (Murray *et al.*, 2013). It is forecasted to increase average global surface temperatures by 1–4 °C before end of this century (Solomon *et al.*, 2007). Elevated CO_2 (eCO_2) and temperature may alter ecological processes in many ways, by directly affecting plant or insect herbivore species independently (Bale *et al.*, 2002; Ellsworth *et al.*, 2004; Nowak *et al.*, 2004) or indirectly biotic interactions (Tylianakis *et al.*, 2008).

South American tomato moth, *Tuta absoluta* is one of the important and devastating pests of solanaceous plants. It is rapidly spreading in the world. It invaded the Mediterranean basin (Desneux *et al.*, 2010), North-west of Iran in 2011 (Baniameri and Cheraghain, 2012), India (Sridhar *et al.*, 2014), Nepal (Bajracharya *et al.*, 2016) and recently, it has been reported from South Africa (Visser *et al.*, 2017) and sub-saharan Africa (Sylla *et al.*, 2017). The occurrence of pest was found throughout the year with varying levels of infestation (Nitin *et al.*, 2017). *T. absoluta* is an oligophagous pest (Erdogan and Babaroglu, 2014) reported on the various solanaceous plants such as tomato (*Solanum lycopersicum* L.), potato (*Solanum tuberosum* L.), eggplant (*S. melongena* L.) and tobacco (*Nicotiana tabacum* L.) (Vargas, 1970; Mallea *et al.*, 1972; Campos, 1976; Notz, 1992; Sridhar *et al.*, 2015; Bawin *et al.*, 2016). Only the

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aerial parts are susceptible to *T. absoluta* attack in the potato plant and not the tubers (Notz, 1992; Caffarini *et al.*, 1999; EPPO, 2005). The larvae damages the potato leaves by feeding on mesophyll tissues and making gallery-like transparent mines, and thereby affecting photosynthetic activity of the crop. *T. absoluta* have potential to cause 100% damage to the crop, if proper management practices are not followed (Apablaza, 1992).

Potato is the fourth largest food crop in the world's production. In 2014, world production of potatoes was 382 million tonnes. China is the largest producer with about 25% of the total world production (FAOSTAT, 2016). *T. absoluta* can spread to potato growing areas resulting in significant loss as reported from Portugal and Turkey (Desneux *et al*., 2011; Unlu, 2012). So as to develop new management strategies against this pest, it is important to be aware of population ecology of the pest. Information on the life-table parameters is more important in controlling a pest species, as the life-table gives us a complete description on the growth, survival and fecundity of the pest.

Traditional female-based age-specific life-tables did not consider contribution of males in population structure or the developmental variations at different life stages of the pest (Lotka, 1907; Lewis, 1942; Leslie, 1945; Birch, 1948). Thus, application of the traditional female-based life-table to ecological studies and biological control is limited and often causes errors (Huang and Chi, 2012). Therefore, Chi and Liu (1985) and Chi (1988) suggested the age-stage, two-sex method that takes into account both male and female sexes for the construction of the life-table and considers the variable development rates among the individuals to obtain accurate information about the life-table of any organisms. The life history of the South American tomato moth, *T. absoluta* has been studied under different temperatures with tomato as a host plant (Erdogan and Babaroglu, 2014; Gharekhani and Salek-Ebrahimi, 2014; Attwa *et al*., 2015). Till now, there is limited informations on the effect of temperature and CO_2 on the pest. So, we evaluated the effect of different temperatures and CO_2 conditions on the life table parameters of *T. absoluta* reared on the potato, *S. tuberosum*.

MATERIALS AND METHODS

Insect Rearing

Larvae of *T. absoluta* were collected from the infested potato fields and maintained in a growth chamber at ICAR-Indian Institute of Horticultural Research (IIHR), Bengaluru (13°8.12''N, 77°29.45''E, 890 m amsl). *T. absoluta* larvae were reared on the potato leaves (*cv.* Kufri Jyoti). Adults were provided with 10 % honey solution as a food source. The relative humidity (RH) of 70 ± 5 % and temperature of 27 ± 1 °C was maintained during the study period.

Open-top Chamber

Two open-top chambers (OTC's) of 3 x 3 m, were used for raising the potato plants under ambient (*a*CO_2) and elevated CO_2 (*e*CO_2) conditions. In one chamber, the elevated CO_2 concentration was maintained at 550 ppm and in another, ambient CO_2 conditions prevailed at 380 ppm. Continuous supply of CO_2 was ensured in elevated CO_2 chamber using automatic monitoring and controlling system within the OTC's. Twenty plastic pots (6 L Vol.) with seedlings of potato (*cv.* Kufri Jyoti) were placed in the OTC's (*a*CO_2 and *e*CO_2) and the regular package of practices was followed for raising the crop. Leaves from the respective OTC's were used for feeding of the *T. absoluta* larvae for further life table studies.

Developmental parameters

To obtain eggs of the same age, 35 pairs (male and female at 1:1) of *T. absoluta* (48h old) were released in a rearing container for mating, with small, potted potato plants covered with iron mesh. The potato plants in the container served as a substrate for laying eggs. Adults were observed daily, until their death. On an average, seventy five eggs were collected on daily basis on the potato leaves maintained in the OTC's. From this lot, single eggs were separated using a fine, zero brush and placed over the fresh potato leaves from the respective OTC's in petri plates (100 mm dia. and 10 mm ht.) containing cotton with wet filter paper to maintain humidity. A total of 100 petri plates containing the potato leaf and *T. absoluta* eggs were used for further observations. Petri plates were maintained at four constant temperatures (26, 28, 30, and 32 °C), RH at 75±5% and photoperiod of 14:10h (L:D) in BOD incubation chambers (Percival Scientific Pvt. Ltd., USA) under the aCO_2 (380 ppm) and eCO_2 (550 ppm) conditions.

Petri plates having *T. absoluta* eggs were observed for the egg hatching. Development at each stage in the different treatments was recorded on a daily basis. Continuous supply of potato leaves from the respective OTC chambers was ensured for the feeding *T. absoluta* larvae in the respective treatments. The incubation period, developmental period of both larvae and pupa, and their mortality were recorded. Immediately upon emergence of adults from the pupae, the moths were paired off and each pair was housed separately in a plastic container (0.5 x 0.5 m) provided with a potato seedling for egg laying and 10% honey solution as the food source. The number of eggs laid by each female was recorded and the same lot of eggs was used for repeating the experiment. Adult longevity, total lifespan, oviposition period and mortality at each stage under the different temperature levels and two CO_2 conditions were recorded and that were used for life table construction.

Life table Parameters

Life table parameters were analyzed using age-stage, two-sex life table method. The raw data were subjected to the computer programme, TWOSEX- MSChart (Chi, 2017). Age-stage specific survival rate (S_{xj}), age-stage fecundity (f_{xj}), age-specific survival rate (l_x), age-specific fecundity (m_x), population parameters *viz.*, intrinsic rate of increase (r), finite rate of increase (λ), net reproductive rate (R_0), and mean generation time (T) were calculated using the computer programme. Adult Pre-Oviposition Period (APOP) is defined as the pre-oviposition period based on female adult stage, whereas, Total Pre-Oviposition Period (TPOP) is considered as the total time from birth to initial oviposition (Jinping *et al.*, 2017). Standard error of development time, reproduction time, and population parameters were analyzed *via* a bootstrap approach, with a sample size of 100,000 (Polat *et al.*, 2015; Efron and Tibshirani, 1993; Johnson, 2001). The significant differences among treatments were analyzed using paired bootstrap test at 5% level. The graphs were plotted using SigmaPlot version 13.0 software from Systat Software, Inc., San Jose, California, USA.

RESULTS AND DISCUSSION

Effect of CO_2 and temperature on developmental rate of the *T. absoluta*

As the temperature increased from 26-32 °C, the development time of egg, larva and pupa decreased in both aCO_2 and eCO_2 conditions. The duration of development was higher in eCO_2 than the aCO_2 in the life stages of *T. absoluta* on potato leaf. eCO_2 showed a significant negative effect on the incubation period of *T. absoluta* eggs at 26, 28 and 30 °C (P<0.05) by increasing the incubation period (**Table 1**). On the first instar larval development of *T. absoluta*, significant negative effect of CO_2 was observed in all the temperatures studied (except 26 °C). At 26 °C alone, eCO_2 had a

Table 1: Developmental time (days) of different stages of *T. absoluta* on potato at four constant temperatures and two CO_2 conditions

Temperature	Incubation period		1st instar larval period		2nd instar larval period		3rd instar larval period		4th instar larval period		Pupal period		Total preadult	
°C	aCO_2	eCO_2	aCO_2	eCO_2	aCO_2	eCO_2	aCO_2	eCO_2	aCO_2	eCO_2	aCO_2	eCO_2	aCO_2	eCO_2
26	6.70±0.21a	7.35±0.13a*	3.50±0.11a	3.84±0.14a	3.30±0.13a	3.72±0.16a*	3.84±0.22a	4.20±0.17a	4.47±0.15a	5.17±0.17a*	11.93±0.34a	13.17±0.37a*	33.93±0.64a	37.17±0.56a*
28	6.30±0.24a	7.00±0.24a*	3.26±0.13a	3.79±0.12a*	2.88±0.09b	3.19±0.16b	3.38±0.50a	3.86±0.18a*	4.56±0.16a	4.85±0.19a	11.31±0.20a	13.31±0.46a*	31.94±0.27b	35.85±0.64a*
30	4.30±0.15b	4.74±0.13b*	2.40±0.17b	2.89±0.16b*	2.68±0.17b	2.56±0.16c	2.41±0.17b	2.42±0.15b	2.80±0.20b	3.17±0.17b	8.27±0.25b	8.67±0.19b	22.73±0.42c	24.00±0.43b*
32	3.65±0.21c	4.05±0.16c	2.00±0.17b	2.43±0.14c*	2.27±0.12c	2.55±0.25c	2.15±0.15b	2.64±0.28b	2.15±0.19c	2.55±0.21c	7.46±0.18c	8.30±0.26b*	19.62±0.46d	22.40±0.83b*

Note: Standard errors were analyzed using 100,000 bootstraps replicates.
Means followed by different letters in the same column are significantly different in different temperatures by the paired bootstrap test.
* indicates 5 % significance level between the two CO_2 conditions.

significant negative effect on the 2nd and 4th instar larval development. But, on the 3rd instar larva of *T. absoluta*, eCO_2 had significant negative effect at 28 °C. On the pupal period, eCO_2 had significant negative effect at 26, 28 and 32 °C with increase in the pupal duration. Overall, total pre-adult duration of *T. absoluta* reared on the potato had significant negative effect at eCO_2 in the different temperatures studied (**Table 1**).

As temperature increased, the longevity of both males and females was reduced under aCO_2 as well as eCO_2 conditions (**Table 2**). Adults of *T. absoluta* reared at aCO_2 lived longer than the eCO_2 adults. The eCO_2 had a significant negative effect on adult longevity in the different temperatures (**Table 2**). There was a significant influence of temperature on the total pre-adult duration in the different stages of *T. absoluta* (**Table 1**). As temperature increased, longevity of both males and females was reduced.

Fecundity and oviposition

Adult pre-oviposition period (APOP) increased with the temperature, *i.e.*, from 26 to 28 °C and was reduced above 30 °C. The total pre-oviposition period (TPOP) and oviposition period showed that significant negative correlation with the temperatures *i.e.*, as temperature increased, TPOP and oviposition period decreased significantly in both aCO_2 and eCO_2 conditions. APOP was higher at aCO_2, whereas TPOP was greater at eCO_2 condition. On APOP, eCO_2 had no significant effect at the temperatures studied. But, on TPOP, it had significant effect at 26 and 28 °C. Also, eCO_2 had a significant effect at 26 and 32 °C on the oviposition period, and it decreased the number of days taken. Total fecundity per female increased with a rise in temperature from 26 to 30 °C and decreased at 32 °C. The maximum fecundity per female was recorded at 30 °C both under aCO_2 and eCO_2 conditions.

Table 2: Adult *T. absoluta* longevity (days) in at four constant temperatures and two CO_2 conditions

Temperature °C	Male longevity		Female longevity	
	aCO_2	*eCO_2*	*aCO_2*	*eCO_2*
26	15.00±0.26a	12.00±0.32a*	19.44±0.29a	15.29±0.36a*
28	13.17±0.54b	8.60±0.24b*	15.00±0.61b	11.75±0.25b*
30	6.86±0.4c	4.60±0.24c*	10.62±0.42c	8.29±0.29c*
32	5.83±0.31c	3.83±0.31c*	9.14±0.26d	6.50±0.29d*

Note: Standard errors were analyzed using 100,000 bootstraps replicates.
Means followed by different letters in the same column are significantly different in different temperatures by the paired bootstrap test.
*indicates 5 % significance level between the two CO_2 conditions.

Table 3: The mean (±*SE*) of ovipostion period (days) of *T. absoluta* reared on potato.

	26 °C		28 °C		30 °C		32 °C	
	aCO_2	eCO_2	aCO_2	eCO_2	aCO_2	eCO_2	aCO_2	eCO_2
Adult Pre Oviposition Period	2.22 ± 0.46ab	1.57 ± 0.37ab	2.80 ± 0.53a	2.50 ± 0.33a	1.88 ± 0.44ab	1.29 ± 0.42b	1.57 ± 0.20b	1.25 ± 0.48b
Total Pre Oviposition Period	35.89 ± 1.01a	39.00 ± 0.58a*	35.00 ± 0.65a	39.00 ± 0.80a*	24.38 ± 0.62b	25.14 ± 0.51b	21.14 ± 0.55c	21.75 ± 1.11c
Oviposition period	13.56 ± 0.67a*	10.14 ± 0.63a	7.90 ± 0.35b	6.75 ± 0.65b	7.38 ± 0.46bc	7.00 ± 0.44b	6.29 ± 0.36c	4.00 ± 0.25c*
Total fecundity/ female	44.22 ± 2.75b	38.86 ± 1.84b	47.20 ± 2.55b	42.88 ± 3.31b	74.50 ± 3.55a	65.14 ± 4.67a	36.00 ± 1.25c	31.00 ± 2.42c

Note: Standard errors were analyzed using 100,000 bootstraps replicates.
Means followed by different letters in the same rows are significantly different between different temperatures by the paired bootstrap test.
*indicates 5 % significance level between two CO_2 conditions.

The *eCO_2* had no significant effect under any temperature studied i.e. 26-32 °C (**Table 3).**

Life Table Parameters of *T. absoluta* on potato

Life table parameters, *viz.*, net reproductive rate (R_o), intrinsic rate of increase (r) and finite rate of increase (λ) increased with rise in the temperature from 26 to 30 °C, the highest recorded at 30 °C; and all the parameters started decreasing with the further rise in temperature. *eCO_2* had no significant effect on these parameters at varied temperatures. The mean generation time (T) decreased with rise in temperature under both *aCO_2* and *eCO_2* conditions. *eCO_2* had significant effect on 'T' at 26 and 28 °C (**Table 4**).

Table 4: Variation of life table parameters of *T. absoluta* on potato at four constant temperatures and two CO_2 conditions

	26 °C		28 °C		30 °C		32 °C	
	aCO_2	eCO_2	aCO_2	eCO_2	aCO_2	*eCO_2*	*aCO_2*	*eCO_2*
R_o	19.90±5.02a	13.60±4.18ab	23.60±5.41a	17.15±4.86ab	29.80±8.28a	22.80±7.08a	12.60±3.85a	6.20±2.74b
r	0.07±0.00b	0.06±0.00b	0.08±0.00b	0.07±0.00b	0.12±0.01a	0.11±0.01a	0.11±0.01ab	0.07±0.02ab
λ	1.07±0.00b	1.06±0.00b	1.08±0.00b	1.07±0.00b	1.13±0.01ab	1.11±0.01a	1.11±0.02a	1.07±0.02ab
T	40.05±0.95a	43.29±0.67a*	39.45±0.74a	41.80±0.52a*	28.37±0.51b	29.01±0.52b	23.89±0.54c	24.10±0.81c

Note: Standard errors were analyzed using 100,000 bootstraps replicates.
Means followed by different letters in the same rows are significantly different between different temperatures by the paired bootstrap test
*indicates 5 % significance level between two CO_2 conditions.

Age-stage specific survival rate (S_{xj}) values for the insects reared at aCO_2 and eCO_2 conditions at four constant temperatures on potato foliage are shown in **Figs 1** and **3**, respectively. At 30 and 32 °C, the egg and the larval stages had lowest survival rate, while, at 26 °C, highest survival rate (S_{xj}) was recorded under both aCO_2 and eCO_2 (**Figs. 1** and **3**). **Figs. 2** and **4** showed age-specific survival rate (l_x), age-stage-specific fecundity (f_x) and age-specific fecundity (m_x) values in *T. absoluta* reared on the potato foliage at aCO_2 and eCO_2 conditions at four constant temperatures respectively. Females produced offspring in *T. absoluta.* Therefore, only one curve is seen for female age-stage-specific fecundity (f_x) under aCO_2 condition. Peak age-stage-specific fecundity (f_x) was observed at 26, 28, 30, and 32 °C, *i.e.*, at 40, 38, 29 and 22 days, respectively, with corresponding 5.64, 6.48, 13.65 and 11.73 eggs laid/female/day (**Fig. 2**). Similarly, under eCO_2 condition, peak age-stage-specific fecundity (f_x) was recorded at 26, 28, 30, and 32 °C at 44, 40, 31 and 22 days with corresponding 5.93, 8.74, 11.68 and 10.62 eggs laid/female/day respectively (**Fig. 4**).

Insects adapt to stress conditions such as extreme temperatures and elevated CO_2 conditions (Levins, 1969; Hoffmann and Parsons, 1991). The effect of temperature is species-specific in any organisms (Cornelissen, 2011). In the development of insects, temperature plays a crucial role (Bale *et al.*, 2002; Mironidis and Savopoulou-Soultani, 2008; Koda and Nakamura, 2012; Park *et al.*, 2014). The growth and development in insects increases almost linearly with increase in the temperature (Gilbert and Raworth, 1996).

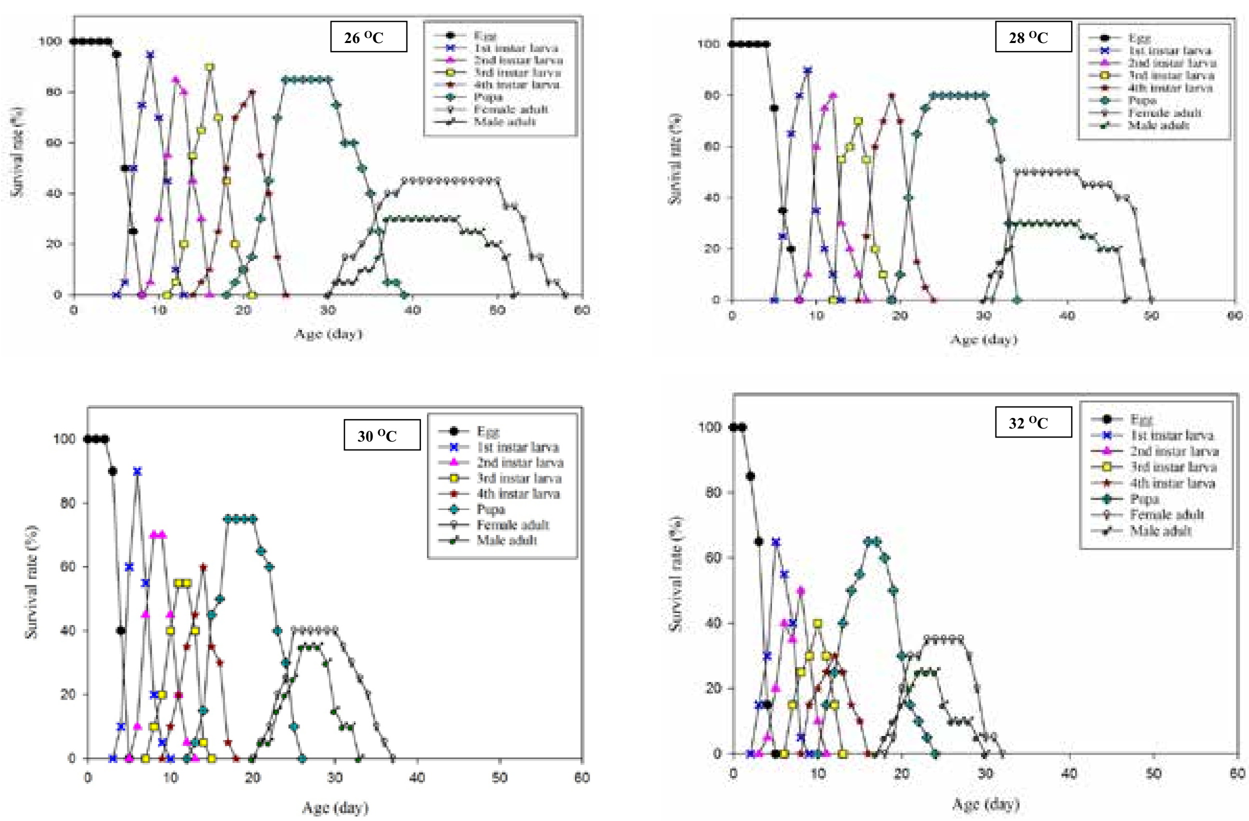

Fig. 1. Age-stage-specific survival rates (Sxj) of T. absoluta reared on potato at four different temperatures under ambient CO_2 *(380 ppm) condition.*

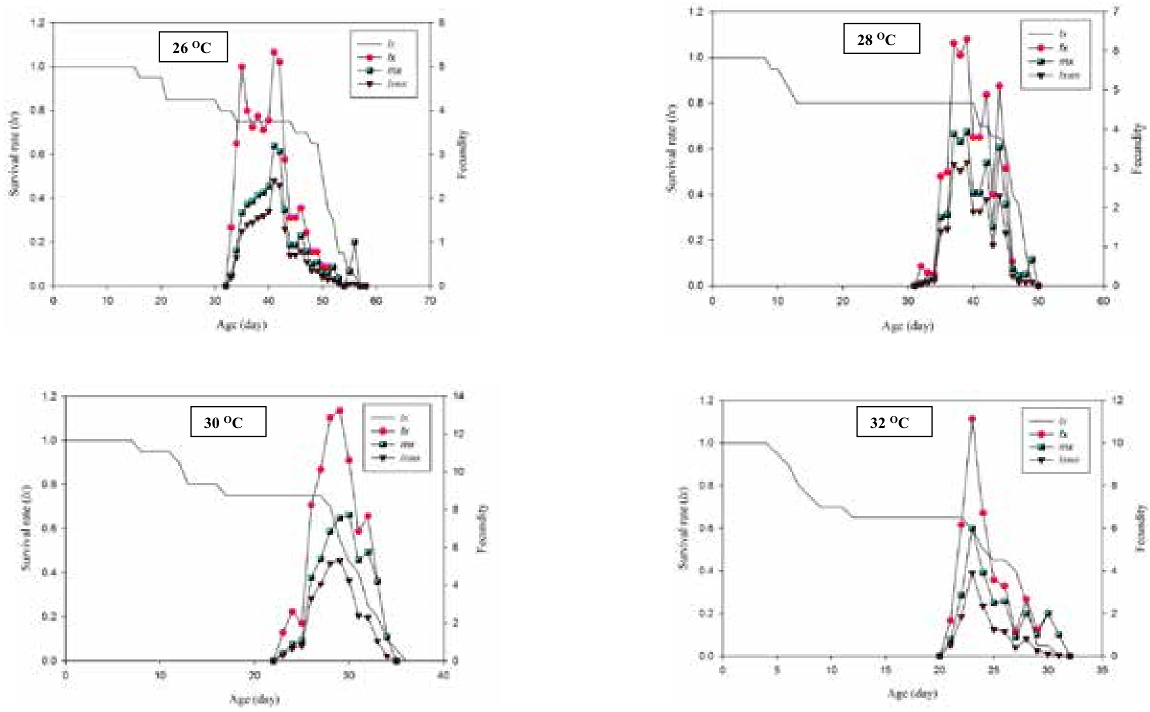

Fig. 2. Age-specific survival rate (lx), age-specific fecundity (mx), age-specific mortality (lxmx) and age-stage-specific fecundity (fx) of T. absoluta reared on potato at four different temperatures under ambient CO_2 (380 ppm) condition.

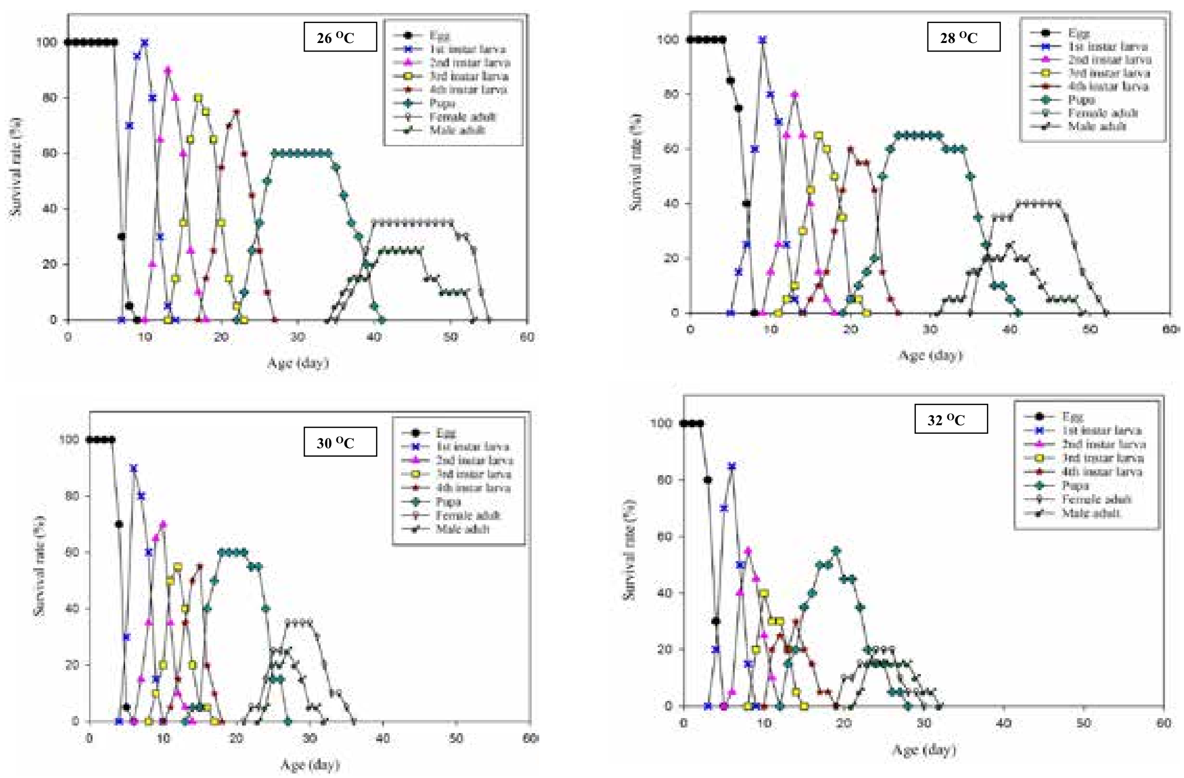

Fig. 3. Age-stage-specific survival rates (Sxj) of T. absoluta reared on potato at four different temperatures under elevated CO_2 (550 ppm) condition.

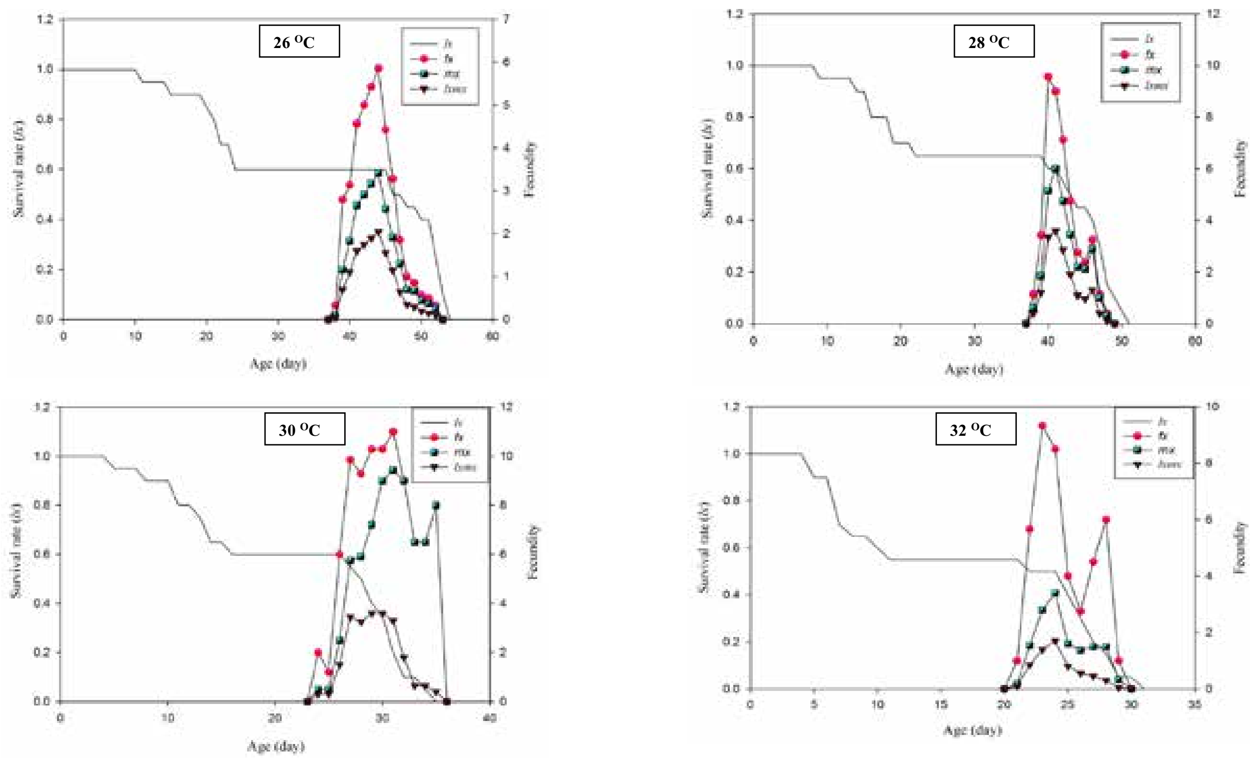

Fig. 4. Age-specific survival rate (lx), age-specific fecundity (mx), age-specific mortality (lxmx) and age-stage-specific fecundity (fx) of T. absoluta reared on potato at four different temperatures under elevated CO_2 (550 ppm) condition.

Lower temperatures reduces the metabolic rate in insects that in turn increases the development time in insects (Benkova and Volf, 2007; Damos and Savopoulou-Soultani, 2012).

Under elevated CO_2 treatments, significantly higher mean relative-growth rates were observed in Lady beetle (*Coccinella magnifica*). Larval and pupal durations in Lady beetle was significantly shorter (Fajun Chen *et al.*, 2005); which was similar to that of our results on *T. absoluta* grown on potato foliage, 1[st] instar larvae grew at significantly slower rates at 28, 30 and 32 °C at eCO_2 condition compared to that of aCO_2 condition.

Second and fourth instar larvae grew at significantly slower rate at 26 °C and third instar at 28 °C under elevated CO_2 condition. Pupa took significantly longer duration to emerge under eCO_2 at all temperatures except at 30°C compared to that of aCO_2. Such longer larval duration and longer time taken for the pupation at elevated CO_2 conditions was also observed in *T. absoluta* on tomato foliage (Nitin *et al.*, 2018) and in *Spodoptera litura* Fab. (Lepidoptera: Noctuidae) on peanut (Srinivasa Rao, 2012).

Life table parameters showed that 'R_o' ' λ ' and '*r*' values in potato grown *T. absoluta* under eCO_2 were lower than that of aCO_2 at all the temperature studied. Yin *et al*., (2010) observed the similar results at eCO_2 in '*r*' for *Helicoverpa armigera* Hub. (Lepidoptera: Noctuidae). In the present study, significant effect of eCO_2 on '*T* ' at 26 and 28 °C was recorded, which is in line with the observations of Amirijami *et al*., (2012) in aphids. Zhu *et al*., (2000) and Gedia *et al*., (2008) reported the significant variations in '*r*' for *S. litura* with various temperatures and host plants as found by us in the present study.

Decrease in development time, coupled with the increase in '*r*' up to 30 °C (under both ambient and elevated conditions) was similar to that of Sunn pest, *Eurygaster integriceps* Puton (Hemiptera: Scutelleridae) by Iranipour *et al*., (2010) and on sugarcane pest, *Elasmopalpus lignosellus* Zell. (Lepidoptera: Pyralidae) by Hardev *et al*., (2013). For a majority of insect-pest populations, '*r*' gradually increases with temperature up to a certain level and decreases sharply thereafter (Manimanjari *et al*., 2014). A similar trend was also observed in the present study under both the aCO_2 and eCO_2 conditions.

CONCLUSION

An increase in larval duration under eCO_2 conditions on the potato foliage may lead to the greater damage. This study establishes a baseline information on the effect of temperature and CO_2 based age-stage, two-sex life tables for the developmental and survival parameters of *T. absoluta* that has been reared on the potato. Information regarding the effect of temperature and CO_2 levels on the growth and development of *T. absoluta* can be used for the prediction models and further used to forecast the activity of this pest on the potato crop.

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