BIOLOGICAL FITNESS OF *SPODOPTERA LITTORALIS* ADULT FEMALES FROM EMAMECTIN BENZOATE SUSCEPTIBLE AND RESISTANT COHORTS

Sanaa A. Ibrahim
Ali M. Ali *et al.*
Minia University, Egypt

Abstract

The proportion of original cohorts that arrived to adult females (I_x) was less for emamectin benzoate resistant strain (19.12fold) than that for susceptible colony. Age specific survival rate (I_x) of adult females is mostly colony dependent and minimally temperature dependent. Gross reproductive rate (GRR = $\sum M_x$) was the lowest at 30ºC that was 705.6 for susceptible mother female compared to 565.8offspring eggs/mother female from resistant colony. The net reproductive rate ($R_0 = \sum I_x M_x$) for susceptible female ranged from 470.36 at 15ºC to 303.41offspring female/mother female at 30ºC. The corresponding values for emamectin benzoate resistant female were from 287.85 at 15ºC to 113.16 at 30ºC. The intrinsic rate of increase ($R_m = R_{max}$) for susceptible colony was 0.0669 at 15ºC and increased gradually to reach 0.2861 at 35ºC. Correspondingly, for resistant colony, the maximal intrinsic rate of natural increase elevated from 0.0538 to 0.2129female offspring/mother female/day. Similarly, the finite rate of population increase (λ) for susceptible colony was elevated from 1.0692 to 1.331female/female/day when temperature increased from 15 to 35ºC, respectively. For resistant colony this parameter increased from 1.0553 to 1.2374. Time required for duplicating the population was 1.24, 1.22, 1.37, 1.32 and 1.34-fold greater for resistant colony than that for susceptible colony at 15, 20, 25, 30 and 35ºC, respectively. In the present study with emamectin benzoate selected colony, life table parameters (I_x, GRR, R_0, R_m, F_r, except Dt and Gt), were less for resistant colony which refer to decrease the biological fitness with the evolution of resistance to this insecticide. Population duplicating time and generation time, both were higher for the resistant colony than those estimated with susceptible colony.

Introduction

Continuous use of conventional pesticides as a unique method for pest control has created many environmental problems and some of their environmental risks are summarized as follows: 1) negative impacts on beneficial arthropods; 2) negative impact on soil fauna; 3) affect soil constructions; 4) leaching properties result in the contamination of surface water and ground water; 5) volatile chemicals may contaminate air; 6) persistent and systemic pesticides may contaminate plant tissue and sometimes raise food safety concerns and 7) develop of resistance phenomena (cited from Gupta & Dikshit, 2010 and Borgio *et al.,* 2014).

Emamectin benzoate is a bacterial based insecticide with a novel site of action (GABA receptor) and could be used in pesticide rotation to reduce the development of resistance toward conventional pesticides and to minimize the impacts on environment. Also the residue profile is very favorable, leading to a very low maximum residue level and short pre-harvest interval in all edible crops (Ishtiaq & Saleem; 2011 and Ibrahim *et al.*, 2015a). Because this insecticide owns short residual activity under field conditions, there is a chance for insects to expose to sublethal doses with the possibility of developing resistance. So the question arises what are the fitness costs of the evolution of resistance toward emamectin benzoate?

A life table gives the proportion of original cohorts at birth of being alive at age x (designated as l_x). Study the effect of temperatures and other weather conditions on insect life tables is also very important to monitor the suitable weather conditions for any insect species and to predict the peaks of activity based on the dominant weather factors (Damos, 2013; Sandhu *et al.*, 2013; Diez-Rodriguez *et al.*, 2013 and Weisse *et al.*, 2013). However most of entomologists and toxicologists estimated the fitness costs of insect species when exposed to sublethal concentrations of pesticides (Ahmad *et al.*, 2013 and Yue-Qin *et al.*, (2013).

To our knowledge, there are no available publications, regarding the biological fitness of resistance to emamectin benzoate in all insect species including cotton leafworm, *Spodoptera littoralis* (Boisd.). The only available literature is with abamectin-resistant and -susceptible strains of *Plutella xylostella*, both strains exposed to sub-lethal concentration of metaflumizone (WenSu *et al.*, 2012).

For cotton leafworm, one male can fertilize a number of females and the size of the population is more dependent on the number of females present and the calculations of life table parameters are usually done using only mother females. In the current study, life table indexes were analyzed to determine the biological fitness of cotton leafworm adult females from emamectin benzoate susceptible and resistant cohorts.

Materials and Methods

Experiments were run with susceptible and emamectin benzoate resistant colonies in Heraeus ® (Model BK 500) incubators fitted with timing devises automatically adjusted to set up the required period of light (electric switch-timer) and equipped with fluorescent lamp (32 watt) providing the light. Five different temperature regimes were used to compare the life table parameters between the two colonies. Temperature regimes were adjusted from 15°C to 35°C in 5°C increments during the whole period of experiments under continuous complete darkness and 60-70 % R.H. The fluctuation of each temperature was approximately ± 0.5 °C. At each temperature regime and for each of the two tested colony, five egg masses of 0-12hr old were placed separately in petri-dishes after counting the number of eggs. Egg masses were daily observed for recording number of hatched neonates. Group of hundred neonates from each colony were placed separately in plastic vial provided with a disc of castor leaves, *Ricinus communis* as food supply and backed to the incubator. Neonate larvae were incubated at five temperature regimes (15, 20, 25, 30 and 35^{o}C) and observed daily for changing the food till pupation. Number of formed pupae was counted, then placed separately, each in clean vials and observed for adult emergence. Ten adult pairs from each colony at each temperature regime (in the first day of their emergence), each was placed separately in 1/4kg glass jar provided with small branch of Tafla, *Nerium oleainder* for egg laying and a piece of cotton soaked in 10% sugar syrup as a source of food. Jars were observed daily from the first day of emergence to death for recording surviving females and number of daily egg laying during oviposition period.

Data analysis was carried out following the single-sex method that firstly used by Birch 1948; Leslie and Park, 1949; as modified by Howe, 1953, who made an attempt to simplify the method introduced by Birch, 1948 and Leslie and Park, 1949 for use by biologists who are not mathematically inclined. Two basic parameters are important for female life table; 1) an age-specific fecundity rate (m_x) which defined as the mean number of eggs deposited by an adult female at day x and 2) an age specific survival rate (I_x) reflects that not all individuals at N_0 will reach adult female stage. Age specific survival rate (1_x) is defined as a proportion of original cohort (1_0) surviving to each stage and could by calculated by dividing number surviving at age x (N_x) by number surviving at age 0 (N_0) and may be expressed as a decimal proportion, sometimes multiply by 100 and expressed as percentage proportion of survivors at the beginning of age interval x where x is a given stage or age group within the population. In cotton leafworm, x might be expressed in days because of the short life span and also may be expressed as stages in the life cycle.

The total number of eggs laid per female during her life span is called the gross reproduction rate (GRR) = $\sum M_x$ and expressed as offspring eggs/mother female/generation. A parameter which is denoted by the letter (r) and is called the intrinsic (infinitesimal) rate of increase (I_xM_x) is calculated by methods given by Birch (1948) and by Leslie and Park (1949). Summation of M_xI_x is named r_0 or net reproductive rate = $\sum I_xM_x$. The net reproductive rate is the ratio of total female births in two successive generations, or the ratio of offspring to parents, or the number of offspring females that will be left by one mother female during her lifetime. The closer R_0 is to 1, the slower the population growth, and if R_0 is less than one, the population is declining.

Generation time is the period from a given stage to the same stage, for example from egg laying to egg laying. Life cycle means the whole period from eggs to the death of emerged adults. There is another important parameter must be calculated in life table, this parameter called the intrinsic rate of natural increased or the maximal intrinsic rate of natural increase (r_m or r_{max}) = $Log_e R_0/Gt$ = inverse of R_0 / T where $R_0 = \sum I_xM_x$ and T is the generation time and this parameter expressed as number of emerged offspring female/mother female/day.

The finite rate of population increase (F_r or lambda or λ) = e^{rm} = shift inverse of r_m and expressed as offspring females per mother female/day. Two other parameters are also important, the mean generation time (G_t) and population doubling time (D_t). The first parameter can be calculated as follow: $Gt = \log_e R_o / r_m$ and the second one can be calculated as follow: $D_t = \log_{e2}/r_m$ = inverse of 2 / r_m. Another parameter is called K-value, is just another measure of mortality, the major advantage of k-values as compared to percentages of died organisms is that k-values are additive: the k-value of a combination of independent mortality processes is equal to the sum of k-values for individual processes. Life table was constructed using some of the following column of parameters:

parameter	Definition and calculation
x	Pivotal age for the age class in units of time (days) or a given stage or age group within the population expressed in days. The pivotal age in days = generation time +1/2 of oviposition period.
I_x	The age specific survival rate (I_x) which expresses the proportion of Original cohort (N_0) at adult females in definite time (N_x). = number of surviving individual at a given age divided by the original number (Eggs) at day 0.
L_x	The number of living individuals between the ages x and x+1
d_x	The number of dying individuals during the age interval x
q_x	Per cent apparent mortality
K-value	K value = -inverse I_x. . It is just another measure of mortality, k = -ln (s or I_x)
S_x	Survival rate during a stage
T_x	Total number of age x units beyond the age x
e_x	Life expectancy for individuals of age x. The life expectancy (e_x) expressed as number of days.
M_x	Age-specific fecundity rate, the number of offspring eggs per female at each interval class
GRR	The gross fecundity rate or gross reproductive rate (GRR= ($\sum m_x$)) expressed as total number of offspring eggs/mother female/generation (during the whole period of oviposition).
F_x	Total number of daughter eggs produced during the generation = N_0 *I_x* GRR where N_0 is the number of the original cohorts (eggs).
R_o	The net reproductive rate (R_0 or $\sum I_xM$) expressed as a mean number of offspring females per mother female per generation (females per female per generation) that express the rate of increase in female population within a generation = Ratio of offspring adult females to mother females. If R_0 is less than one, the population is declining.
T_c or X	Cohort generation time (in days), $T_c = \Sigma X l_x m_x / \Sigma l_x m_x$.
r_c	Innate capacity for increase, calculated by: rc = ln Ro/Tc
R_m	The intrinsic rate of natural increase ($R_m = R_{max}$) or the maximal intrinsic is calculated by Euler's equation: $\Sigma e^{-r_m.X} l_X m_X = 1$. and also could be calculated as R_m or $r_{max} = \text{Log}_e R_0/Gt$ = inverse of R_0 / Gt
G_t in days	Corrected generation time = summation of immature stages duration + pre-oviposition period. the corrected generation time: T = ln Ro/rm
Fr (λ) or (lambda)	Finite rate of population increased (λ) = e^{rm} = shift inverse of r_m and expressed as female offspring/mother female/day.
D_t	Dt = population doubling time is the time required for duplicating the population. $D_t = \log_{e2}/r_m$ = inverse of 2 / r_m.
b	Intrinsic birth rate: $1/\Sigma e^{-r} m_x l_x$
d	Intrinsic death rate: b – r_m

Results and Discussion

1-Age specific survival rate (I_x)

Mortality of adult females was daily recorded during the whole period of its longevity. In general, the low proportion of the original cohort at the beginning of adult female stage is mostly because the death in the previous stages that was mostly occurs in egg stage particularly for resistant strain. Very small part of decline, but not significant is related to female ratio since female ratio did not significantly differ in relation to temperature regimes and tested colony; female percentages ranged from 42.75 ± 11.81 to 52.92 ± 8.24 (data are not shown).

At all temperature regimes used in this study, female specific survival rate during the first two physiological periods was greater for susceptible females than those for resistant females (Table 1). Female mortality was mostly occurred during the first day of adult emergence because some emerged females were malformed and died soon after emergence. It was hard to identify the sex of most malformed adults; so female survival rate was calculated based on healthy emerged adults that were able to lay eggs. For females from both colonies at the five temperature regimes, survival rate was constant during the oviposition period; female death was dramatically increased at postoviposition period. At each temperature regime, oviposition period did not significantly differ between susceptible and resistant females. It ranged for the two colonies from 10 day at 15°C to 3 day at 35°C.

2-Life table parameters (I_x, GRR, R_0, R_m, F_r, Gt and Dt) in relation to temperature regimes

At 15°C, as seen in Table (1), age specific survival rate at the beginning of adult female age was greater (0.38) for susceptible females than that for resistant females (0.25). This means that about 38% and 25% of eggs (N_0)

deposited by susceptible and resistant colonies developed into adult females. Generation time of susceptible colony ranged from 87.48 to 96.48 day, averaging 91.98 day (Table 2 and Figure 1). For resistant colony, this time significantly expanded, ranging from 100.74 to 109.74, averaging 105.24 day. This means that there is almost 14 day difference in the generation time of both colonies at 15ºC. During the oviposition period that was insignificantly different between the two colonies (~10 day), there was a nonsystematic fluctuation in age specific fecundity rate (M_x); ranging from 31.20 in day 10 to 163.80 in day 6 for susceptible female compared to 59.40 in day 1 to 145.4 offspring eggs/mother female in day 4 for resistant female. However the gross reproductive rate during the whole period of oviposition (GRR = ($\sum M_x$) was greater for susceptible female (1237.8 eggs/female/generation) than that for resistant female (1151.4 eggs/female/generation). At daily interval during the oviposition period, multiplying I_x by M_x resulted in age specific reproductive rate ($r = I_xM_x$) that expressed the number of offspring female/mother female at day x. As recorded in Table (2), age specific reproductive rate (I_xM_x) fluctuated from 11.86 in day 10 to 62.24 in day 6 for susceptible female compared to 14.85 on day 1 to 36.30 offspring female/ mother female on day 4 for resistant female. The net reproductive rate (R_0) is a summation of the ten values of I_xM_x ($R_0 = \sum I_xM_x$); expressing the number of offspring females produced by one mother female during her life span. This value was 470.36 and 287.85 offspring females/mother female/generation for susceptible and resistant colonies respectively. This clarifies that resistant colony had less reproductive potential than susceptible one.

At 20ºC and similarly, to what established at 15ºC, the same trend was achieved with different values, at the beginning of oviposition period, age specific survival rate (I_x) was significantly greater for susceptible colony (0.47) than that for the resistant colony (0.31 see Table 1). Also, oviposition period reduced to 7 days for susceptible female compared to 8 days for resistant female. Generation time significantly reduced to 55.73 and 61.56 day for susceptible and resistant colonies, respectively. It means that generation time of susceptible colony was almost 6 days less than that for resistant colony (Tables 1 &2 and Figure 1). Age specific fecundity rate (M_x) for susceptible colony fluctuated with no systematic change from 86.4 to 210.6 eggs. Correspondingly, this number fluctuated from 22.2 to 159.0eggs/female for resistant strain. Regardless the daily oviposition, total number of eggs laid during the whole oviposition period (GRR) was 960.0 and 802.8eggs per female/generation for susceptible and resistant female, respectively (Table 2). The net reproductive rate ($R_0 = \sum I_xM_x$) dramatically decreased at 20ºC to reach 451.20 (for susceptible population) and 248.9 daughter female/mother female/generation (for resistant population). This re-confirms that resistant colony has less reproductive capacity than susceptible colony.

At 25ºC, age specific survival rate (I_x) was 0.43and 0.23 for susceptible and resistant colony, respectively (Table 1). Almost 43 and 23% of the original population at N_0 produced adult females. Oviposition period was 6 and 7 day for susceptible and resistant female, respectively. Also, generation time averaged 32.62 and 39.27day for susceptible and resistant colony, respectively (Table 2). Gross reproductive rate ($GRR = \sum M_x$) for females from susceptible and resistant colony reached 967.2 and 870.0 eggs/female/generation, respectively. The net reproductive rate ($R_0 = \sum I_xM_x$) for females from susceptible and resistant colony was 415.90 and 200.10 female/female/generation, respectively. Net reproductive rate dramatically dropped for resistant strain mostly because the drop in survival rate that reached 0.23 for resistant female compared to 0.43 for susceptible female and also for the lower productive rate 870eggs/resistant female compared to 967.2eggs /susceptible female.

At 30ºC, age specific survival rate (I_x) was 0.43 and 0.20, respectively for susceptible and resistant females (Table 1). This means if the population in N_0 was stable for both colonies, the number of formed female in susceptible colony will be 2.15-fold greater than that of resistant colony. Both susceptible and resistant females laid eggs in a 5 day interval (Table 2). Generation time averaged 24.69 and 27.02day for susceptible and resistant strains, respectively. It is clearly evident that as temperature increased, the variation in generation time between susceptible and resistant colony decreased. Gross reproductive rate ($GRR = \sum M_x$) was 705.6 and 565.8eggs/female for susceptible and resistant female, respectively. However, the net reproductive ($R_0 = \sum I_xM_x$) was 303.41 and 113.16 offspring female/mother female/generation, respectively.

At 35ºC, age specific survival rate (I_x) was 0.41 and 0.19, respectively for susceptible and resistant colonies (Table 1). Oviposition period was 4 and 3 day for susceptible and resistant female, respectively (Table 2). The variation in generation time between the two colonies was very much reduced at 35ºC. For explanation, generation time averaged 20.22 and 22.4 day, respectively for susceptible and resistant colony. With regarding to the gross reproductive rate which expresses the total number of offspring eggs laid by one mother female during the whole oviposition period, it is obviously that, the gap between the two colonies reduced at 35^0C, but still the gross rate for susceptible female about 1.28-fold greater than that for resistant female. Egg laying averaged 793.2eggs/mother susceptible female compared to 621.0 eggs/mother resistant female. The net reproductive rate ($R_0 = \sum I_xM_x$) expressed the number of offspring females produced from one mother female.

This value reached 325.2 and 118.0 female/female for susceptible and resistant female, respectively. The net reproductive rate reflects the effect of gross reproductive rate and female specific survival rate.

3-Summary of life table parameters in relation to tested colonies

Birch (1948) was the first to assess the life table parameters for insect populations. Life table parameters were estimated in this study to predict the biological fitness of emamectin benzoate resistant cotton leafworm populations to persist under field conditions. The fourth instar larvae generated from the field collected cotton leafworm, *Spodoptera littoralis* egg masses were selected with the concentration of emamectin benzoate, corresponding to the 96hr LC_{50}'s. After seven generations of continuous selection pressure at 25ºC; resistance ratio increased to be 19.12-fold. Emamectin benzoate resistant strain was compared with laboratory strain based on the life table indexes. And obtained data could be summarized as follows:

- The K value index is just another measure of mortality and could be calculated from age specific survival rate (($k = -\ln (s \text{ or } I_x)$). Reported in this study confirms that this index was greater for resistant colony than that for susceptible colony. Moreover, the difference between the two colonies was highly significant at all temperature regimes used in the current study.

- The age specific survival rate (I_x) which expresses the decimal proportion of original cohort (N_0) at adult female stage (N_x), was found to be less for susceptible colony than resistant colony and the difference between the two colonies was highly significant at all temperature regimes used in the current study.

- Gross reproductive rate which expresses the total number of daughter eggs produced by one mother female during the whole oviposition period, this life table parameter was generally greater for susceptible colony; however the difference between the two colonies was insignificant at 15 and 25ºC, and was significant at the three other temperature regimes (20, 30 and 35ºC).

- There is another important parameter called F_x which expresses the total number of daughter eggs produced during the generation = $N_0 * I_x *$ GRR where N_0 is the number of the original cohorts (eggs). This index was less for resistant colony and the difference compared to susceptible colony was highly significant at all temperature regimes ranged from 15 to 35ºC.

- The net reproductive rate expresses the ratio of daughter females to mother females. With the exception of 35ºC, the net reproductive rate (R_0) decreased as temperature increased for each of the two tested colonies. For susceptible colony, it goes down from 470.36female/female at 15ºC to 303.41 at 30ºC. The corresponding values for resistant colony were from 287.85 at 15ºC to 113.16 at 30ºC. It was obviously and unexpected that the net reproductive rate was the lowest at 30ºC. Generally, net reproductive rate was less for resistant colony than that for susceptible colony. This parameter was 1.63, 1.81, 2.08, 2.68 and 2.76fold greater for susceptible colony than that for resistant colony at 15, 20, 25, 30 and 35ºC, respectively. Statistically, this parameter was highly significantly greater for susceptible colony at all temperature regimes used in the current study.

- In general and at all temperature regimes, generation time of resistant colony was greater than that of susceptible colony; however the difference was only significant at 15ºC.

- The maximal intrinsic rate of natural increase was positively correlated with temperature regimes. For each colony, this parameter increased as temperature increased. For susceptible colony, the rate of offspring female was 0.0669 at 15ºC and increased gradually to reach 0.2861 at 35ºC. Correspondingly, for resistant colony, this parameter elevated from 0.0538 to 0.2129offspring female/mother female/day when temperature regime increased from 15 to 35ºC.

- The intrinsic rate of female population increase was 1.24, 1.22, 1.37, 1.33 and 1.34 fold greater for susceptible colony than those for resistant colony at 15, 20, 25, 30 and 35ºC, respectively. The lower intrinsic rate of natural increase for resistant colony was surly related to the elongation of generation time and the lower fecundity compared to susceptible strain.

- Based on the statistical analysis, the maximum rate of natural increase was significantly greater for susceptible colony at 15 and 20°C; moreover, the difference with resistant colony was highly significant at 25, 30 and 35°C.

- Similarly, the finite rate of population increase (λ) was temperature dependent and increased as temperature increased for each of the two tested colony. For susceptible colony it elevated from 1.0692 to 1.331female/female/day when temperature increased from 15 to 35°C, respectively. For resistant colony this parameter increased from 1.0553 to 1.2374 when temperature increased from 15 to 35°C. At each temperature regime, it was obviously that this parameter was less for resistant colony than that for susceptible colony. It was 1.013, 1.02, 1.05, 1.06 and 1.08-fold greater for susceptible colony than that for the resistant colony at 15, 20, 25, 30 and 35°C, respectively. This index was insignificantly greater for susceptible colony than resistant colony when both reared at 15°C and 20°C. However the difference in this index was significant at 25 and 30°C and was highly significant at 35°C.

- For each of the two tested colony, population doubling time decreased as temperature increased. For susceptible colony, this parameter goes down from 10.36 to 2.42 day when temperature increased from 15 to 35°C. For female from the resistant colony, it decreased from 12.88 to 3.25 day when temperature regime increased from 15°C to 35°C. Time required for duplicating the population of adult females was greater for resistant colony; it was 1.24, 1.22, 1.37, 1.32 and 1.34-fold greater for resistant colony than that for susceptible colony at 15, 20, 25, 30 and 35°C, respectively, population doubling time was greater for resistant colony at all temperature regimes; moreover, the difference was significant at 15 and 20°C and highly significant at 25, 30 and 35°C.

- Three parameters were greater for resistant colony than susceptible. Those parameters are generation time, population doubling time and K-value. In contrast other parameters such as I_x, GRR, R_0, R_m, F_x, F_r were found to be greater in susceptible colony than emamectin benzoate resistant colony.

- It could be concluded that resistance to emamectin benzoate in cotton leafworm population is linked with the reduction in the biological fitness of this insect species. Resistance phenomenon is important for elongating insect life cycle and reduces the fecundity of adult females.

To our knowledge and based on literature searching, entomologists in the previous studies evaluated the life table parameters of insect species in relation to weather factors such as constant and fluctuating temperatures, host varieties and host species. Few researchers focused on the sublethal effects of insecticides on the life table parameters. No one focused on the comparison between insecticide resistant and susceptible colonies of cotton leafworm, *Spodoptera littoralis*.

For toxicologists they focused on the biological fitness of different insect species when exposed to the sublethal concentrations of insecticides, this help to predict what could happen if insects received sublethal concentrations under field conditions and this direction of study was undertaken in the first part of the current dissertation study (Ibrahim *et al*., 2013). Reported here is to determine the biological characteristics for susceptible and resistant colonies and also for emphasizing the fitness costs of developing resistance to emamectin benzoate in field population of cotton leafworm, *S. littoralis*.

In the current study, life table analysis revealed that emamectin benzoate resistant *S. littoralis* adult females exhibited different biological characteristics compared to susceptible colony. Females from resistant colony laid fewer eggs, and about 27% of eggs did not hatch, took longer time to complete the development from egg stage to adult stage. Also, age specific survival rate was less for resistant cohorts than that for susceptible colony. Compared to emamectin benzoate selected strain, susceptible colony exhibited about 18.63, 25.04, 27.84, 22.21 and 16.58% increase in the maximal intrinsic rate at 15, 20, 25, 30 and 35°C, respectively. Most of previous studies, with different insecticides and different insect species, confirmed what obtained in the current study. Li *et al*. (2007) compared the biological aspects of spinosad resistant and susceptible strains of diamondback moth, *Plutella xylostella* L. At the low temperature regime, the RR strain failed to produce any viable offspring. At the high temperature regime, the RR strain showed a 33% decrease in intrinsic rate of increase compared to the SS strain. The results demonstrate that fitness costs of resistance to spinosad are temperature-dependent.

In the present study great reduction in female fecundity and fertility was achieved with the resistant colony, also remarkable elongation in insect generation and life cycle was also evident with resistant colony. These data were confirmed in previous study with a field-collected population of *Heliothis virescens* (Lepidoptera: Noctuidae) conducted by Sayyed *et al.* (2008) who compared life traits between the selected (with spinosad, indoxacarb, and deltamethrin) and unselected populations and data revealed that selected populations laid a significantly lower number of eggs and that a lower percentage of eggs hatched. In present study with emamectin benzoate selected cotton leafworm, female life table parameters (GRR, R_0, R_m, F_r except Gt and Dt) were less for resistant colony. Xian-Hui *et al.* (2008) found change in the biological characteristics of the diamondback moth, *Plutella xylostella* (Lepidoptera: Yponomeutidae) when exposed to spinosad at the LC_{25} for 48hr. The mean values of the intrinsic rate of increase (r_m), finite rate of increase (lambda), gross reproductive rate (GRR) and net reproductive rate (R_0) were significantly lower in the treatment groups than in the untreated group. Xian-Hui *et al.* (2009) backed to select this insect species with spinosad for ten generations using the LC_{25}; they found that the intrinsic rate of increase (r_m), finite rate of increase (lambda) and net reproductive rate (R_0) in Sub-1 were significantly lower compared with those for the SS strain. Similar results were obtained when Dong *et al.* (2010) investigated the fitness cost of spinosad resistance in the cotton bollworm, *Helicoverpa armigera*, development periods of the resistant strain were lengthened by 4-5 days. Furthermore, pupal survival, pupal weight, the mean life span of emerged adults, eggs laid and hatched decreased greatly in the resistant strain in comparison with the susceptible strain. The author confirmed what obtained in the current study with emamectin benzoate that sex ratio did not change significantly. However, both net replacement rate (R_0) and intrinsic rate of increase (r_m) were reduced for the resistant strain.

More recent studies mostly confirm our finding, however with other insect species under chemical stress of other insecticides. Ahmad *et al.* (2012) studied the effects of a botanical based insecticide, neemarin at four different concentrations on the life table indices of *Plutella xylostella* (L.) on cauliflower in the laboratory and found that all life table parameters except generation time and population duplicating time were significantly reduced compared to those of the untreated check. Contrast to our finding that confirmed the elongation of generation time in emamectin benzoate selected cotton leafworm, Ansari *et al.* (2012) with *Spilarctia obliqua* derived from 3rd instar larvae that had ingested LC_{50} of imidacloprid (0.025%), dichlorvos (0.014%) and endosulfan (0.012%) found that mean generation time was significantly reduced after exposure to dichlorvos (37.19 days) compared to 41.34 days in the absence of insecticides. In agreement with the trend of life table parameters obtained in the current study, WenSu *et al.* (2012) evaluated the sublethal effects of metaflumizone on the experimental populations of both abamectin-resistant (AV-R) and susceptible (AV-S) strains of *Plutella xylostella*, reproduction parameters such as the intrinsic rate of increase (r_m), finite rate of increase (lambda), and the net reproductive rate (R_0) in populations treated with sublethal concentrations of metaflumizone were significantly lower than those of the control populations. Typically coincided to present data, Alizadeh *et al.* (2012) investigated the sublethal effects of pyriproxyfen (a JHA) on life-history parameters of the diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae), they found that the intrinsic rate of increase (r), finite rate of increase (lambda), gross reproduction rate (GRR) and net reproductive rate (R_0) significantly decreased while the mean generation time (T) and doubling time (DT) increased in the treated groups with pyriproxyfen compared with the control. Reda and Hatem (2012) estimated the life table parameters of tomato leaf miner, *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) under the stress of the biopesticides; *Bacillus thuringiensis* var. kurstaki and *Beauveria bassiana* (Balsamo). The female progeny (M_x) as well as survival rate (I_x) of *T. absoluta* was decreased in biopesticide treatments, especially in *B. thuringiensis* var. kurstaki treatment. The biopesticide treatments decreased the net reproductive rate (R_0), intrinsic rate of natural increase (r_m) and finite rate of increase (e^{rm}) compared with the control. On the other hand, *B. thuringiensis* var. kurstaki, followed by *B. bassiana* had increased the times of generation (T) and doubling (DT). In more recent study, Ahmad *et al.* (2013) studied the effects of feeding six instar larvae of *Helicoverpa armigera* (Hubner) on chickpea pods treated with 5, 10, 15 and 20 ppm neemazal (1% EC azadirachtin) on life table parameters. Net reproductive rate (R_0) was significantly reduced as nemzal concentration increased. The intrinsic (r_m) and finite (lambda) rate of increase were significantly decreased at 20 ppm. The mean generation time (T) was prolonged at 20 mg l^{-1}. Doubling time (DT) was significantly extended to 5.02 days with 20 ppm as compared to 3.84 days in the untreated check. In another study, YueQin *et al.* (2013); toxicological and biological effects of chlorantraniliprole (commercially named Coragen) on *Ostrinia furnacalis* (Guenee) using diet-incorporation bioassays were evaluated. The LC_{10}, LC_{40} and LC_{50} on the 3rd instar larvae were 0.038, 0.098, and 0.123PPM, respectively. Reproduction parameters, such as the net reproductive rate (R_0), intrinsic rate of increase (r_m), and finite rate of increase (lambda) in the chlorantraniliprole treated groups were significantly lower than those in the untreated group.

Study the effect of temperatures and other weather conditions on insect life tables is also very important to monitor the suitable weather conditions for any insect species and to predict the peaks of activity based on the dominant weather factors. In the current study, the authors reported that temperature ranged from 15 to 35ºC were within the zone of cotton leafworm activity since 15ºC is more than the lower threshold of development and 35 ºC is under the upper threshold of development (Ibrahim *et al*. 2015, In press). In agreement with our finding that 30ºC was the most optimum temperature, Damos (2013) found that the most suitable temperature for *Anarsia lineatella* Zeller (Lepidoptera) was 30ºC. Also, Sandhu *et al.* (2013) found that the mean fecundity, intrinsic rate of increase (r), and finite rate of increase (lambda) of *Elasmopalpus lignosellus* (Zeller) (Lepidoptera: Pyralidae) were greatest at 30ºC. The net reproductive rate (R_0) was greatest at 27ºC. The generation (T) and population doubling times (DT) were shortest at 33 and 30ºC, respectively. Weisse *et al.* (2013) investigated the life history response of *Cephalodella acidophila* toward three environmental key factors, pH, temperature and food concentration, they concluded that the growth of *C. acidophila* is severely limited in its natural habitat and low pH alone is not harmful as long as temperatures are moderate to warm and food is abundant.

Regarding the effect of host plant on the life table parameters, Satpute *et al.* (2005) studied life table of *Earias vittella* (Fabricius) on different hosts. The net reproductive rate (Ro), at the end of each generation, of *E. vittella* was 81.91 on okra, 56.70 on cotton, 53.02 on semi-synthetic diet and 36.63 on mesta (*Hibiscus cannabinus* L.). Okra seemed to be the most suitable host plant for this insect species. Golizadeh and Razmjou (2010) investigated Potato tuberworm *Phthorimaea operculella* (Zeller) (Lepidoptera: Gelechiidae) life table parameters in laboratory on six commonly grown potato cultivar tubers. The lowest r_m value indicates that Agria is a relatively insusceptible compared with the other cultivars tested and that this cultivar can be used effectively in sustainable IPM. Hu *et al.* (2010) studied the life table parameters of *Nilaparvata lugens* on two wild rice species, *Oryza officinalis* and *Oryza rufipogon* at 27ºC in the laboratory, showing that the species is resistant to *N. lugens*. This study is of great interest, this allow choosing the unsuitable varieties as an agricultural mean of pest control in the integrated weed management strategy. Different values of life table parameters of the cotton bollworm, *Helicoverpa armigera* (Hubner) on 13 soybean cultivars was achieved by Naseri *et al.* (2010). Hasan and Ansari (2011) studied the effect of different host plants including cabbage, cauliflower, mustard, radish, and broccoli on biological parameters of *Pieris brassicae* (L.) in the laboratory at 28 ºC, 65 ± 5% RH and 12L:12D photoperiod; indicating that cabbage might be the most suitable food for *P. brassicae*. Farahani *et al.* (2011) studied life table parameters of *Spodoptera exigua* (Hubner) (Lepidoptera: Noctuidae) on different host plants including corn, cotton, and many other plant crops at 26 ºC, 60% RH and a photoperiod of 16:8 (L:D); the lowest net reproductive rate (R_0) was on cotton (126.39female/female/generation). The intrinsic rate of increase (rm) was the lowest on cotton. These results indicated that *G. hirsutum* was the most unsuitable host plant as compared to other hosts tested. Xi-Hong *et al.* (2012) evaluated life table parameters of the peach fruit moth, *Carposina sasakii* Matsumura (Lepidoptera: Carposinidae) under laboratory conditions and found that the intrinsic rate of natural increase (r_m) was significantly greatest on plum (0.1294eggs per female per day), followed by jujube and apricot (0.1201 and 0.1128eggs per female per day). Jha *et al.* (2012) compared the demographic characteristics of *Helicoverpa armigera* (Hubner) reared on hybrid sweet corn (*Zea mays* L. variety saccharata) (hybrid super sweet corn KY bright jean) and on an artificial diet by using the age-stage, two-sex life table. There were significant differences in the intrinsic rate of increase and finite rate between the two treatments. The artificial diet is more suitable for the mass rearing of *H. armigera*. Abdallah *et al.* (2012) carried out life table studies for *Phthorimaea operculella* (Zeller) on four potato varieties, namely Atlas, Spunta, Simone and Nicola. Atlas proved to be the quite favorable. Dhurgude *et al.* (2012) studied the life-fecundity tables of *H. armigera* on leaves of 3 chickpea cultivars. The finite rate of increase was 1.23, 1.24 and 1.21females per female per day on leaves of Virat, G-12 and BDN-9-3, respectively. Diez-Rodriguez *et al.* (2013) indicated that *H. bipunctalis* can reproduce 57.9 times per generation. These basic data can aid in establishing strategies for the management of *H. bipunctalis* on blackberry farms. More recent study revealed significant difference between sugar beet cultivars on the life table parameters of the beet armyworm, *Spodoptera exigua* (Hubner) at 27 ºC, 60 % RH (Karimi-Malati *et al.*, 2013), the cultivar Renger was less suitable in comparison with other cultivars in the laboratory. Zare *et al.* (2013) determined the biological characteristics and life table parameters of *Apomyelois ceratoniae* on the three commercial cultivars of pomegranate including Malas daneh siah, Gabri and Shahvar and found that the highest value of the finite rate of increase (lambda) were observed in Shahvar cultivar.

Table 1. Age specific survival rates for cotton leafworm, *Spodoptera littoralis* (Boisd.) from emamectin benzoate susceptible and resistant colonies *calculated* in relation to temperature regimes and different physiological intervals of adult female longevity.

Age or stage	Physiological periods	(I_x) expressed as a decimal proportion ($I_x = N_x/N_0$)									
		15°C		20°C		25°C		30°C		35°C	
		SS	RS	SS	RS	SS	RS	SS	RS	SS	RS
Egg stage	Original cohort (N_0)	1	1	1	1	1	1	1	1	1	1
Adult female	Oviposition period	0.40	0.31	0.49	0.35	0.46	0.31	0.47	0.29	0.45	0.26
		0.38	0.25	0.47	0.31	0.43	0.29	0.43	0.20	0.41	0.19
		--	0.25	0.47	0.31	---	0.23	---	---	---	---
		0.38	0.25	0.47	0.31	0.43	0.23	0.43	0.20	0.41	0.19
		0.38	0.25	0.47	0.31	0.43	0.23	0.43	0.20	0.41	0.19
		0.38	0.25	0.47	0.31	0.43	0.23	0.43	0.20	0.41	0.19
		0.38	0.25	0.47	0.31	0.43	0.23	0.43	0.20	0.41	---
		0.38	0.25	0.47	0.31	0.43	0.23	0.43	0.20	---	---
		0.38	0.25	0.47	0.31	0.43	0.23	---	---	---	---
		0.38	0.25	0.47	0.31	---	0.23	---	---	---	---
		0.38	0.25	---	0.31	---	---	---	---	---	---
		0.38	0.25	---	---	---	---	---	---	---	---
		0.38	0.25	---	---	---	---	---	---	---	---
	Postoviposition period	0.23	0.16	0.29	0.12	0.36	0.18	0.27	0.15	0.26	0.18
		0.08	0.06	0.19	0.02	0.09	0.09	0.0	0.05	0.09	0
		0.0	0.0	0.10	0.0	0.0	0.0	---	0.0	0.0	

Table 2. Generation time in days (Gt), age specific fecundity rate (M_x) and age specific reproductive rate (I_xM_x) when the original cohort (eggs of 0-12hr old) of cotton leafworm, *S. littoralis* from the two colonies were incubated for one generation at five constant temperature regimes.

colony	15°C			20°C			25°C			30°C			35°C		
	Gt	M_x	I_xM_x	G t	M_x	I_xM_x	Gt	M_x	I_xM_x	Gt	M_x	I_xM_x	Gt	M_x	I_xM_x
	87.48	118.2	44.96	52.73	99.6	46.81	30.12	96.0	41.3	22.59	84.0	36.12	18.72	323.4	132.6
	88.48	157.8	59.96	53.73	129.0	60.63	31.12	159.0	68.4	23.59	142.8	61.40	19.72	241.8	99.14
	89.48	120.6	45.83	54.73	210.6	98.98	32.12	240.6	103.5	24.59	117.0	50.31	20.72	58.2	23.86
	90.48	160.2	60.88	55.73	174.6	82.06	33.12	193.8	83.3	25.59	202.8	87.20	21.72	169.8	69.62
SS	91.48	123.6	46.97	56.73	171.0	80.37	34.12	180.6	77.7	26.59	159.0	68.37	---	---	---
female	92.48	163.8	62.24	57.73	86.4	40.61	35.12	97.2	41.8	---	---	---	---	---	---
	93.48	140.4	53.35	---	---	---	---	---	---	---	---	---	---	---	---
	94.48	114.0	43.32	---	---	---	---	---	---	---	---	---	---	---	---
	95.48	108.0	41.04	---	---	---	---	---	---	---	---	---	---	---	---
	96.48	31.20	11.86	---	---	---	---	---	---	---	---	---	---	---	---
Mean ± SE	91.98 ± 0.96	GRR = 1237.8 ± 12.17	R_0 = 470.4 ± 4.63	55.7 ± 0.59	GRR = 960.0 ± 15.25	R_0 = 451.2 ± 7.17	32.6 ± 0.59	GRR = 967.2 ± 17.59	R_0 = 415.9 ± 7.72	Mean = 24.69 ± 0.50	GRR = 705.6 ± 14.13	R_0 = 303.4 ± 6.07	Mean = 20.22 ± 0.40	GRR = 793.2 ± 35.61	R_0 = 325.2 ± 14.60
	100.74	59.40	14.85	58.06	22.2	6.882	36.29	87.6	20.21	25.02	34.2	6.84	21.40	114.0	21.7
	101.74	91.20	22.80	59.06	70.2	21.762	37.29	231.6	53.30	26.02	158.4	31.68	22.40	237.0	45.0
	102.74	116.40	29.10	60.06	151.2	46.872	38.29	163.8	37.70	27.02	194.4	38.88	23.40	270.0	51.3
	103.74	145.20	36.30	61.06	120.0	37.20	39.29	166.8	38.40	28.02	120.0	24			
RR	104.74	113.40	28.35	62.06	159.0	49.290	40.29	115.2	26.50	29.02	58.8	11.76			
female	105.74	123.60	30.90	63.06	131.4	40.734	41.29	74.4	17.10	---	---	---			
	106.74	114.0	28.50	64.06	87.6	27.156	42.12	30.6	7.0	---	---	---			
	107.74	117.0	29.25	65.06	61.2	18.972	---	---	---	---	---	---			
	108.74	142.80	35.70	---	---	---	---	---	---	---	---	---			
	109.74	128.40	32.10	---	---	---	---	---	---	---	---	---			
Mean ± SE	105.24 ± 0.96	GRR = 1151.4 ± 7.89	R_0 = 287.9 ± 1.97	61.6 ± 0.78	GRR = 802.80 ± 15.17	R_0 = 248.9 ± 4.70	39.3 ± 0.67	GRR = 870.0 ± 21.45	R_0 = 200.10 ± 4.94	Mean = 27.02 ± 0.50	GRR = 565.8 ± 21.16	R_0 = 113.2 ± 4.23	Mean = 22.40 ± 0.32	GRR = 621.0 ± 26.02	R_0 = 118.0 ± 4.93
P (0.05, 0.01)	(0.008, 0.02)	(0.28, 0.56)	(0.001, 0.0019)	(0.33, 0.66)	(0.036, 0.071)	(0.0022, 0.014)	(0.22, 0.44)	(0.34, 0.68)	(0.009 0.013)	(0.21, 0.41)	(0.023, 0.46)	(0.003, 0.007)	(0.27, 0.53)	(0.027, 0.55)	(0.0049, 0.012)

For each column, $P_{0.05}$ value of unpaired t test expresses the difference in each biological parameter between susceptible and resistant colony.

Table 3. Summary of life table parameters in relation to tested colonies and temperature regimes.

Tested colony	Temp.	I_x	K value	GRR ($\sum m_x$)	fx	R_0 ($\sum I_x M_x$)	(x)	R_m	Fr (λ)	Dt
Susceptible population	15ºC	0.38	0.968	1237.8	47036.4	470.36	91.98	0.0669	1.06919	10.3609
	20 ºC	0.47	0.755	960.0	45120.0	451.20	55.73	0.10967	1.11591	6.320299
	25 ºC	0.43	0.844	967.2	41589.6	415.90	32.62	0.184869	1.203061	3.749397
	30 ºC	0.43	0.844	705.6	30340.8	303.41	24.59	0.232415	1.261643	2.982369
	35 ºC	0.41	0.892	793.2	32521.2	325.21	20.22	0.28608	1.331199	2.422914
Resistant population	15ºC	0.25	1.386	1151.4	28785.0	287.85	105.24	0.0538	1.055274	12.88378
	20 ºC	0.31	1.171	802.8	24886.8	248.87	61.56	0.089619	1.093757	7.734378
	25 ºC	0.23	1.469	870.0	20010.0	200.10	39.27	0.13493	1.144457	5.137087
	30 ºC	0.20	1.609	565.8	11316.0	113.16	27.02	0.175011	1.1912593	3.96059
	35 ºC	0.19	1.661	621.0	11799.0	117.99	22.40	0.212973	1.23735	3.254625
Unpaired t test ($P_{0.05}$)	15ºC	0.006	0.01098	0.28	0.005	0.001	0.008	0.019	0.0659	0.04825
	20 ºC	0.007	0.01155	0.036	o.oo4	0.0022	0.33	0.015	0.0557	0.038583
	25 ºC	0.0028	0.00253	0.34	o.oo2	0.009	0.22	9.9E-04	0.028253	0.009217
	30 ºC	2.0-E04	0.00016	0.023	2.0-E04	0.003	0.21	0.0036	0.014114	0.00611
	35 ºC	1.9-E04	0.00015	0.027	2.0-E04	0.0060	0.27	0.00105	0.0069442	0.00209

At each temperature regimes and each tested parameter, the estimated value of P at 5% level of probability reflects the statistical variation between susceptible and resistant colony in this parameter at such temperature regime.

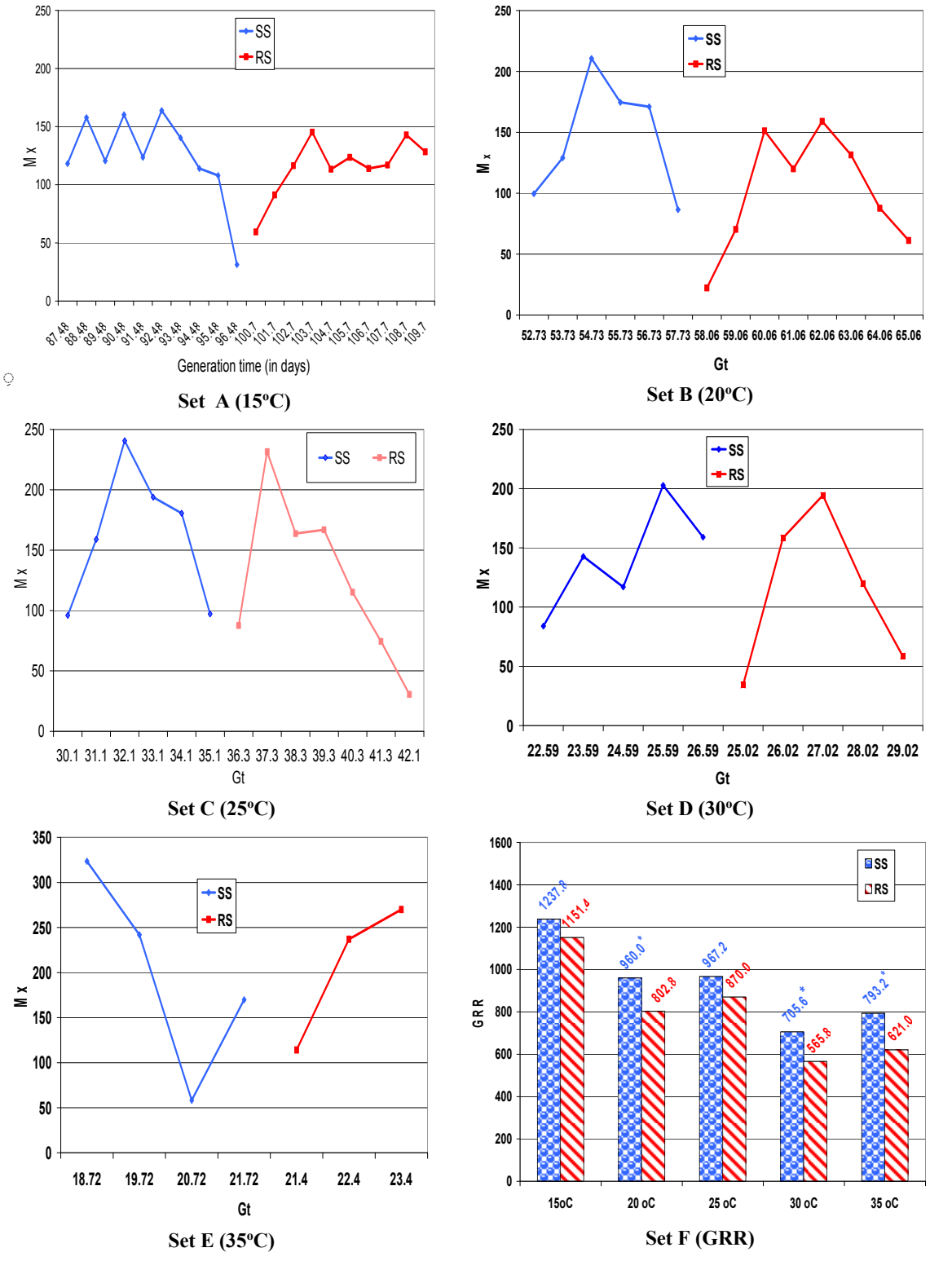

Figure 1. Age specific fecundity rate (M_x) and gross reproductive rate (GRR) of cotton leafworm adult females from susceptible and resistant colonies reared for one generation at five constant temperature regimes.

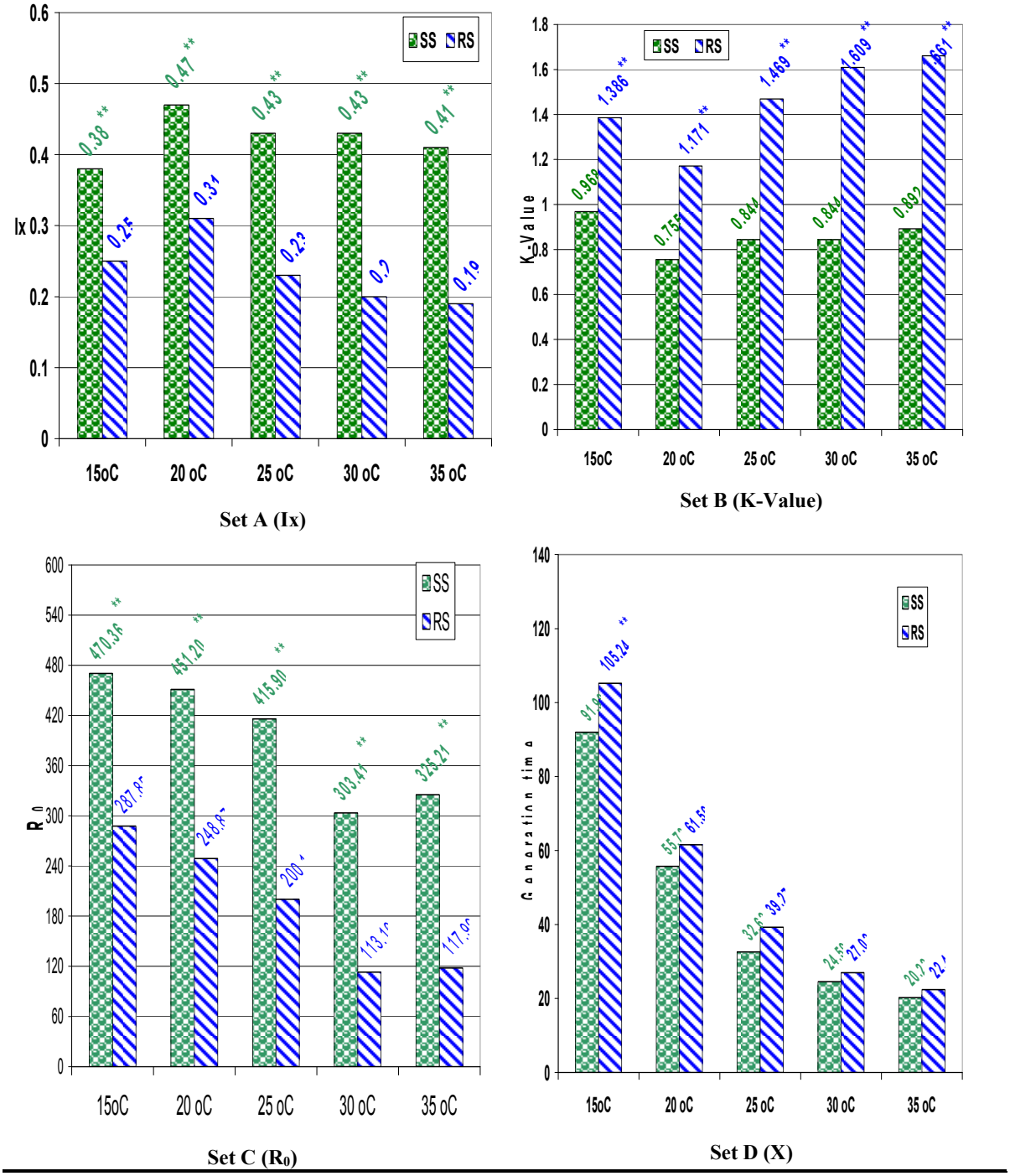

Figure 2. Age specific survival rate (l_x), K-Value, net reproductive rate (R_0) and generation time (GT or X) for emamectin benzoate susceptible and resistant colonies reared for one generation at five constant temperature regimes.

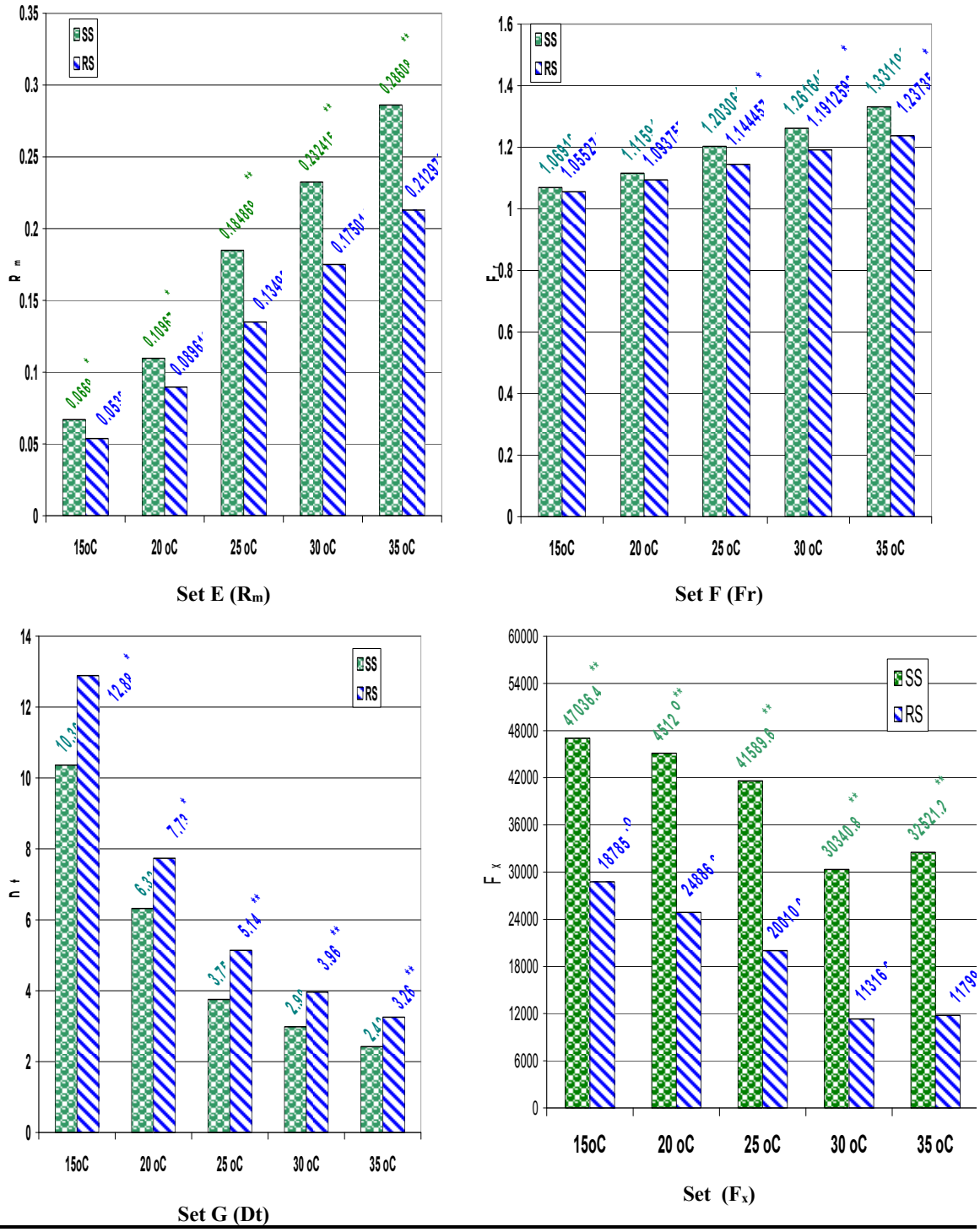

Figure 2 continuous. Maximum rate of natural increase (R_m), finite rate of increase (Fr), population doubling time and number of daughter eggs generated from the original cohorts (No = 100 eggs) for emamectin benzoate susceptible and resistant colonies reared for one generation at five constant temperature regimes.

Summary

The fourth instar larvae generated from the field collected cotton leafworm, *Spodoptera littoralis* egg masses were selected with the concentration of emamectin benzoate, corresponding to the 96hr LC_{50}'s. After seven generations of continuous selection pressure at 25ºC; resistance ratio increased to be 19.12-fold. Emamectin benzoate resistant strain was compared with laboratory strain based on the life table indexes. The proportion of original cohorts that arrived to adult females (I_x) was less for resistant colony than that for susceptible colony and this finding was confirmed at the five temperature regimes. Age specific survival rate (I_x) of adult females is mostly colony dependent and minimally temperature dependent, this means that temperature regimes ranged from 15 to 35ºC that used in the current study are within the optimum zone for adult female surviving. Gross reproductive rate (GRR = $\sum M_x$) was the lowest at 30ºC that was 705.6 for susceptible mother female compared to 565.8offspring eggs/mother female from resistant colony. The net reproductive rate ($R_0 = \sum I_x M_x$) for susceptible female ranged from 470.36 at 15ºC to 303.41offspring female/mother female at 30ºC. The corresponding values for emamectin benzoate resistant female were from 287.85 at 15ºC to 113.16 at 30ºC. The intrinsic rate of increase ($R_m = R_{max}$) for susceptible colony was 0.0669 at 15ºC and increased gradually to reach 0.2861 at 35ºC. Correspondingly, for resistant colony, the maximal intrinsic rate of natural increase elevated from 0.0538 to 0.2129female offspring/mother female/day. Similarly, the finite rate of population increase (λ) for susceptible colony was elevated from 1.0692 to 1.331female/female/day when temperature increased from 15 to 35ºC, respectively. For resistant colony this parameter increased from 1.0553 to 1.2374. Time required for duplicating the population was 1.24, 1.22, 1.37, 1.32 and 1.34-fold greater for resistant colony than that for susceptible colony at 15, 20, 25, 30 and 35ºC, respectively. In the present study with emamectin benzoate selected colony, life table parameters (I_x, GRR, R_0, R_m, F_r, except Dt and Gt), were less for resistant colony which refer to decrease the biological fitness with the evolution of resistance to this insecticide. Population duplicating time and generation time, both were higher for the resistant colony than those estimated with susceptible colony.

Acknowledgements

Financial support to participate and present this manuscript was provided in part by Minia University, Egypt. This paper is a part from the dissertation conducted by the Ph.D. student, Ali Mostafa Ali Sayed under supervision of Prof. Dr. Sanaa Abdelhameed Ibrahim *et al.*

References

Abdallah, Y. E. Y.; M. S. Abdel-Wahed and G. H. A. Youssef 2012. Life table parameters as indicator of potato varieties susceptibility to infestation with *Phthorimaea operculella* (Zeller). Egyptian Academic Journal of Biological Sciences: Entomology; 5 (1): 127-136.

Ahmad, S.; M. S. Ansari and M. A. Moraiet 2013. Demographic changes in *Helicoverpa armigera* after exposure to Neemazal (1% EC azadirachtin). Crop Protection; 50: 30-36.

Ahmad, N.; M. S. Ansari and N. Salam 2012. Effect of Neemarin on life table indices of *Plutella xylostella* (L.). Crop Protection; 38: 7-14.

Alizadeh, M.; J. Karimzadeh; G. R. Rassoulian; H. Farazmand; V. Hoseini-Naveh and H. R. Pourian 2012. Sublethal effects of pyriproxyfen, a juvenile hormone analogue, on *Plutella xylostella* (Lepidoptera: Plutellidae): life table study. Archives of Phytopathology and Plant Protection; 45 (14): 1741-1763.

Ansari, M. S.; H. Ali and S. Shafqat 2012. Insecticidal effect on a population of *Spilarctia obliqua* (Lepidoptera: Arctiidae). Entomological Research; 42 (6): 330-338.

Birch, L. C. 1948. The intrinsic rate of natural increase of an insect population. Journal of Animal Ecology 17: 15-26.

Borgio, F. J.; K. Sahayaraj and S. I. Alper (eds) 2014. Microbial Insecticides: Principles and Applications, Nova Publishers, USA. 492pp. ISBN 978-1-61209-223-2

Damos, P. 2013. Demography and randomized life table statistics for peach twig borer *Anarsia lineatella* (Lepidoptera: Gelechiidae). Journal of Economic Entomology; 106 (2): 675- 682.

Dhurgude, S. S.; S. S. Shetgar; A. G. Badgujar; D. D. Patait and S. Subhan 2012. Life fecundity tables of *Helicoverpa armigera* (Hubner) on chickpea. Indian Journal of Entomology; 72 (4): 379-382.

Diez-Rodriguez, G. I.; L. K. Hubner; L. E. C. Antunes and D. E. Nava 2013. *Herpetogramma bipunctalis* (Lepidoptera: Crambidae) biology and techniques for rearing on leaves of the blackberry (*Rubus* spp., Rosaceae). Brazilian Journal of Biology; 73 (1): 179-184.

Dong, W.; Q. XingHui; W. H.Yan; Q. Kang and W. KaiYun 2010. Reduced fitness associated with spinosad resistance in *Helicoverpa armigera*. Phytoparasitica; 38 (2): 103-110.

Farahani, S.; B. Naseri and A. A. Talebi 2011. Comparative life table parameters of the beet armyworm, *Spodoptera exigua* (Hubner) (Lepidoptera, Noctuidae) on five host plants. Journal of the Entomological Research Society; 13 (1): 91-101.

Golizadeh, A. and J. Razmjou 2010. Life table parameters of *Phthorimaea operculella* (Lepidoptera: Gelechiidae), feeding on tubers of six potato cultivars. Journal of Economic Entomology; 103 (3): 966-972.

Gupta, S. and A. K. Dikshit 2010. Biopesticides: An ecofriendly approach for pest control. Journal of Biopesticides 3 (1 Special Issue): 186 – 188.

Hasan, F. and M. S. Ansari 2011. Population growth of *Pieris brassicae* (L.) (Lepidoptera: Pieridae) on different cole crops under laboratory conditions. Journal of Pest Science; 84 (2): 179-186.

Howe, R. W. 1953. The rapid determination of the intrinsic rate of increase of an insect population. Ann. Appl. Biol.; 40: 134-151.

HU, L-X.; H. Chi; J. Zhang; Q. Zhou and R-J. Zhangi 2010. Life-Table Analysis of the Performance of *Nilaparvata lugens* (Hemiptera: Delphacidae) on Two Wild Rice Species. J. Econ. Entomol. 103 (5): 1628 – 1635.

Ibrahim, S. A.; Z. A. Zeiton; M. S. Fuad; M. A. Mohamed and A. M. Ali 2013. Effect of a macrocyclic lactone insecticide, emamectin benzoate on some biological aspects of the cotton leafworm, *Spodoptera littoralis* (Boisduval). In the Proceedings of Beltwide Cotton Conferences, Cotton Insect Research and Control Conference, San-Antonio, Texas, USA: 848-862.

Ibrahim S. A. and A. M. Ali *et al.* (2015). Lower threshold of development and thermal requirements of cotton leafworm, *Spodoptera littoralis* (Lepidoptera: Noctuidae), from emamectin benzoate-susceptible and -resistant colonies. Accepted for publication in the Proceedings of Beltwide Cotton Conferences, Cotton Insect Research and Control Conference, San-Antonio, Texas, USA, January 5-7, 2015.

Ishtiaq, M and M. A. Saleem 2011. Generating susceptible strain and resistance status of field populations of *Spodoptera exigua* (Lepidoptera: Noctuidae) against some conventional and new chemistry insecticides in Pakistan. J Econ Entomol.; 104 (4): 1343-1348.

Jha, R. K.; C. Hsin and T. LiCheng 2012. A comparison of artificial diet and hybrid sweet corn for the rearing of *Helicoverpa armigera* (Hubner) (Lepidoptera: Noctuidae) based on life table characteristics. Environmental Entomology; 41 (1): 30-39.

Karimi-Malati, A.; Y. Fathipour; A. A. Talebi and M. Bazoubandi 2013. Comparative life table parameters of beet armyworm, *Spodoptera exigua* (Lepidoptera: Noctuidae), on four commercial sugar beet cultivars. Journal of Entomological Society of Iran; 32 (1): 109-124.

Leslie, P. H. and T. Park 1949. The intrinsic rate of natural increase of *Tribolium castaneum* Herbest. Ecology, 30: 469-477.

Li, Z. M.; S. S. Liu; Y. Q. Liu and G. Y. Ye 2007. Temperature-related fitness costs of resistance to spinosad in the diamondback moth, *Plutella xylostella* (Lepidoptera: Plutelidae). Bulletin of Entomological Research; 97 (6): 627-635.

Naseri, B.; Y. Fathipour, S. Moharramipour and V. Hosseininaveh 2010. Life table parameters of the cotton bollworm, *Helicoverpa armigera* (Lepidoptera: Noctuidae) on different soybean cultivars. Journal of Entomological Society of Iran; 29 (1): 25-40.

Naseri, B.; Z. Golparvar; J. Razmjou and A. Golizadeh 2014. Age-stage, two-sex life table of *Helicoverpa armigera* (Lepidoptera: Noctuidae) on different bean cultivars. Journal of Agricultural Science and Technology; 16 (1): 19-32.

Reda, A. M. A. and A. E. Hatem 2012. Biological and eradication parameters of the tomato leafminer, *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) affected by two biopesticides. Boletin de Sanidad Vegetal, Plagas; 38 (2): 321-333.

Sandhu, H. S.; G. S. Nuessly; S. E. Webb; R. H. Cherry and R. A. Gilbert 2013. Temperature-dependent reproductive and life table parameters of *Elasmopalpus lignosellus* (Lepidoptera: Pyralidae) on sugarcane. Florida Entomologist; 96 (2): 380-390.

Satpute, N. S.; S. D. Deshmukh; N. G.V. Rao and S. A. Nimbalkar 2005. Life tables and the intrinsic rate of increase of *Earias vittella* (Lepidoptera: Noctuidae) reared on different hosts. International Journal of Tropical Insect Science. 25 (2): 73-79.

Sayyed, A. H.; M. Ahmad and N. Crickmore 2008. Fitness costs limit the development of resistance to indoxacarb and deltamethrin in *Heliothis virescens* (Lepidoptera: Noctuidae). Journal of Economic Entomology; 101 (6): 1927-1933.

Weisse, T.; N. Laufenstein and G. Weithoff 2013. Multiple environmental stressors confine the ecological niche of the rotifer, *Cephalodella acidophila*. Freshw Biol.; 58 (5): 1008 – 1015.

WenSu, H.; R. ChengCai; Y. HaiYan; Z. ShuFa; S. FuYing and G. XiWu 2012. Sublethal effects of metaflumizone on abamectin-resistant and susceptible strains of the diamondback moth, *Plutella xylostella* (Lepidoptera: Plutellidae). Acta Entomologica Sinica; 55 (6): 694-702.

Xian-Hui, Y.; W. Qing-Jun, L. Xue-Feng, Z. You-Jun and X. Bao-Yun 2008. Sublethal effects of spinosad on *Plutella xylostella* (Lepidoptera: Yponomeutidae). Crop Protection; 27 (10): 1385-1391.

Xian-Hui, Y.; W. Qing-Jun; L. Xue-Feng; Z. You-Jun; X. Bao-Yun 2009. Demographic changes in multigeneration *Plutella xylostella* (Lepidoptera: Plutellidae) after exposure to sublethal concentrations of spinosad. Journal of Economic Entomology; 102 (1): 357-365.

Xi-Hong, L.; L. Ding-Xu; L. Zheng; F. G. Zalom; G. Ling-Wang and S. Zuo-Rui 2012. Effect of host plants on developmental time and life table parameters of *Carposina sasakii* (Lepidoptera: Carposinidae) under laboratory conditions. Environmental Entomology; 41 (2): 349-354.

Yue-Qin, S.; D. Jun-Feng and S. Hui-Zhong 2013. Chlorantraniliprole at sublethal concentrations may reduce the population growth of the Asian corn borer, *Ostrinia furnacalis* (Lepidoptera: Pyralidae). Acta Entomologica Sinica; 56 (4): 446-451.

Zare, D.; J. J. Sendi; A. J. Nodoushan and R. Khosravi 2013. Life table parameters and biological characteristics of *Apomyelois ceratoniae* Zeller (Lepidoptera: Pyralidae) on three cultivars of pomegranate. Archives of Phytopathology and Plant Protection; 46 (7): 766-773.