Journal of Entomological Society of Iran
2009, 29(1), 25-40

Life table parameters of the cotton bollworm, *Helicoverpa armigera* (Lep.: Noctuidae) on different soybean cultivars

B. Naseri[1], Y. Fathipour[1&*], S. Moharramipour[1] and V. Hosseininaveh[2]
1. Department of Entomology, Faculty of Agriculture, Tarbiat Modares University, P.O. Box 14115-336, Tehran, Iran, 2. Department of Plant Protection, College of Agriculture and Natural Sciences, University of Tehran, Karaj, Iran.
*Corresponding author, E-mail: fathi@modares.ac.ir

Abstract

Influence of 13 soybean cultivars (356, M4, M7, M9, Clark, Sahar, JK, BP, Williams, L17, Zane, Gorgan3 and DPX) on the life table parameters of the cotton bollworm, *Helicoverpa armigera* (Hübner) was studied at 25 ± 1°C, relative humidity of 65 ± 5% and a photoperiod of 16: 8 (L: D) h. The survival rate (l_x) of individuals developed to adults from the initial cohort on the mentioned cultivars was estimated 0.87, 0.83, 0.96, 0.96, 0.77, 0.72, 0.81, 0.72, 0.85, 0.74, 0.85, 0.88 and 0.72, respectively. The longest and shortest life expectancy (e_x) of the pest was 44.22 and 35.98 days on Gorgan3 and BP, respectively at the beginning of life. The intrinsic rate of natural increase (r_m) on different cultivars ranged from 0.1324 to 0.1848 (day $^{-1}$), which was lowest on 356 and highest on M9. The highest net reproductive rate (R_0) was on M7 (354.92 female/female/generation) and the lowest value of this parameter was on 356 (89.35). The values of finite rate of increase (λ), mean generation time (T) and doubling time (DT) on different soybean cultivars were as follows: 1.14 to 1.20 female offspring per female per day for λ, 28.85 to 36.61 days for T and 3.75 to 5.23 days for DT. Because of the higher coefficient of determination (R^2) value in Gompertz model, data from different cultivars had a better fit to this model compared with Weibull model. The results indicated that 356, L17, Gorgan3, BP and Sahar cultivars were less suitable host plants, suggesting that they are more resistant to *H. armigera* than the other cultivars.

Key words: *Helicoverpa armigera*, intrinsic rate of natural increase, life table, soybean cultivars

چکیده

تأثیر ۱۳ رقم سویا (356، M4، M7، M9، Clark، Sahar، JK، BP، Williams، L17، Zane، Gorgan3 و DPX) روی پارامترهای جدول زندگی کرم غوزه‌ی پنبه، *Helicoverpa armigera* (Hübner)، در دمای ۱ ± ۲۵ درجه‌ی سلسیوس، رطوبت نسبی ۵ ± ٦٥ درصد و دوره‌ی نوری ١٦ ساعت روشنایی و ۸ ساعت تاریکی تعیین شد. نرخ بقاء (l_x) افراد در زمان ورود جمعیت هم‌سن اولیه به مرحله‌ی حشره‌ی کامل روی ارقام فوق به‌ترتیب ۰/۸۷، ۰/۸۳، ۰/۹٦، ۰/۹٦، ۰/۷۷، ۰/۷۲، ۰/۸۱، ۰/۷۲، ۰/۸۵، ۰/۷٤، ۰/۸۵، ۰/۸۸ و ۰/۷۲ بود. طولانی‌ترین و کوتاه‌ترین امید به زندگی (e_x) در آغاز زندگی آفت به‌ترتیب ٤٤/۲۲ و ۳۵/۹۸ روز روی ارقام Gorgan3 و BP بود. نرخ ذاتی افزایش جمعیت (r_m) روی ارقام مختلف از ۰/۱۳۲٤ تا ۰/۱۸٤۸ در نوسان بود که کم‌ترین و بیش‌ترین مقدار آن به‌ترتیب روی ارقام 356 و M9 مشاهده شد. بیشترین مقدار نرخ خالص تولید مثل (R_0) روی M7 (۳٥٤/۹۲ ماده/ماده/نسل) و کم‌ترین مقدار آن روی 356 (۸۹/۳٥) بود. مقادیر نرخ متناهی افزایش (λ)، متوسط زمان یک نسل (T) و مدت زمان دوبرابرشدن جمعیت (DT) روی ارقام مختلف سویا به‌ترتیب عبارت بودند از: ۱/۱٤ تا ۱/۲۰ ماده به ازای هر ماده در هر روز برای λ، ۲۸/۸۵ تا ۳٦/٦۱ روز برای T و ۳/۷٥ تا ٥/۲۳ روز برای DT. به دلیل بالاتربودن مقدار ضریب تبیین (R^2) در مدل Gompertz، داده‌های به‌دست‌آمده روی ارقام مختلف برازش بهتری با این مدل در مقایسه با مدل Weibull داشتند. نتایج نشان داد که ارقام 356، L17، Gorgan3، BP و Sahar به عنوان نامناسب‌ترین گیاهان میزبان آفت بوده و نسبت به سایر ارقام مقاومت بیشتری در برابر *H. armigera* داشتند.

واژگان کلیدی: *Helicoverpa armigera* ، نرخ ذاتی افزایش طبیعی، جدول زندگی، ارقام سویا

Introduction

The cotton bollworm, *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae) is a common insect pest of numerous crops in Iran (Farid, 1986), and is one of the dominant pests of soybean (Kogan & Herzog, 1980). The cotton bollworm can feed on most plant structures including stems, leaves, flower heads and fruits at different development stages (Moral Garcia, 2006). The population of *H. armigera* has been increased enormously in the soybean-producing areas especially in the Moghan region, northwest of Iran. Despite high level of natural mortality, this species needs to be controlled by synthetic pesticides (Fitt, 1994). This usage of pesticides is of environmental concern and has repeatedly led to the development of pesticide resistance in *H. armigera*, especially to the synthetic pyrethroids (Gunning *et al.*, 1984). Consequently, there is considerable interest in alternative management tactics, which might be applied in area-wide or more restricted basis (Naseri *et al.*, 2009).

Host plant resistance has been used effectively in sustainable integrated management programs for several crop pests. Plants with antibiosis machanism may reduce insect survival, size or weight, longevity, and reproduction in new generation adults, or they may have an indirect effect by increasing the exposure of the insect to its natural enemies as a result of prolonged developmental time (Dent, 2000; Sarfraz *et al.*, 2006). Host plant resistance is an important tool in terms of being both economically and environmentally acceptable (Kennedy *et al.*, 1987).

Population parameters are important in measurement of population growth capacity of species under specified conditions. These parameters are also used as indices of population growth rates responding to selected conditions and as bioclimatic indices in assessing the potential of a pest population growth in a new area (Southwood & Henderson, 2000).

Life table is an appropriate tool to study the dynamics of animal populations, especially arthropods, because this tool can provide very important demographic parameters (Maia *et al.*, 2000). Demographic studies have several applications: analyzing population stability and structure, estimating extinction probabilities, predicting life history evolution, predicting outbreak in pest species, and examining the dynamics of colonizing or invading species (Vargas *et al.*, 1997; Haghani *et al.*, 2006). Demographic information may also be useful in constructing population models (Carey, 1993) and understanding interactions with other insect pests and natural enemies (Omer *et al.*, 1996). The cohort life table gives the most comprehensive description of the survivorship, development and reproduction of a population that are fundamental factors in both theoretical and applied population ecology (Taghizadeh *et al.*, 2008).

The life table parameters, particularly the intrinsic rate of natural increase (r_m), are the most important parameters that can be used to evaluate the level of plant resistance to insects (Razmjou *et al.*, 2006). Host plants displaying lower values of r_m are relatively more resistant than the plants with higher values of r_m. In the present study, the life table parameters, especially the r_m, are used to compare the potential population growth of *H. armigera* on different soybean cultivars.

Models of population dynamics play a central role in understanding the effects of disturbance in both natural and managed ecosystems. One of the most persistent and pervasive disturbances is the widespread use of resistant plants. Of the variety of mortality models are found in the literature, the Gompertz model is the most widely used one (Preston *et al*., 2001).

Knowledge of cultivar susceptibility or resistance and the life table parameters of a pest might be fundamental components of an integrated pest management program for any crops. Such information can aid in detecting and monitoring pest infestations, cultivar selection, and crop breeding (Razmjou *et al.*, 2006).

There was little information on the life table parameters of *H. armigera* on different soybean cultivars, although most related studies have been conducted on the effects of host plants apart from soybean cultivars on life table parameters of *H. armigera* (Patal & Koshyia, 1997; Liu *et al.*, 2004; Reddy *et al.*, 2004). Therefore, the present study provides novel information on the life table parameters of *H. armigera* on different soybean cultivars. The goal of this research was to determine the life table parameters of *H. armigera* on the 13 soybean cultivars, to evaluate susceptibility or resistance of soybean cultivars. Furthermore, our findings on resistant cultivars may be applied to design a comprehensive schem for IPM program of *H. armigera*.

Materials and methods

Plant source

Seeds of the 13 soybean (*Glycine max* (L.) Merrill) cultivars including 356 (Delsoy4210), M4, M7, M9, Clark, Sahar, JK, BP, Williams, L17, Zane, Gorgan3 and DPX were obtained from Plant and Seed Modification Research Institute (Karaj, Iran) and were planted in the research field of Tarbiat Modares University in the suburbs of Tehran, Iran in

2007. For this study, the leaves and pods of different soybean cultivars were transferred to a growth chamber at 25 ± 1°C, relative humidity of 65 ± 5% and a photoperiod of 16: 8 (L: D) h. The leaves and pods were used for feeding of 1^{st} and 2^{nd} to 5^{th} larval instars, respectively.

Laboratory cultures

The specimens *H. armigera* were originally collected from cotton fields in Moghan region located in northwest of Iran in July 2007. The stock culture initiated on an artificial diet (cowpea powder 205 gr, powdered agar 14 gr, ascorbic acid 3.5 gr, sorbic acid 1.1 gr, methyl-p-hydroxybenzoate 2.2 gr, yeast 35 gr, wheat germ powder 30 gr, formaldehyde 37% 2.5 ml, vegetable oil 5 ml and distilled water 650 ml) (Naseri *et al.*, 2009). The insects tested on different soybean cultivars had already been reared for two generations on the same cultivars. The colony was supplemented, from time to time, with larvae collected from field to reduce any inbreeding effects and maintain the vigor of the colony. All experimental insects were kept inside a growth chamber at 25 ± 1°C, relative humidity of 65 ± 5% and a photoperiod of 16: 8 (L: D) h.

Experiments

Adult moths emerged from the larvae reared on different soybean cultivars were used in the experiments. In order to obtain the same aged eggs of the pest, 10-15 pairs of both sexes of the moth reared on related cultivars were kept inside oviposition container (14 cm in diameter by 19 cm in height), which were sealed at the top with a fine mesh net. After 72 h, the eggs laid were collected from the container and used for the experiments. Fifty eggs were used to start each of the cultivar treatments. Newly emerged larvae were transferred individually into plastic Petri dishes (8 cm in diameter by 2 cm in height) with a hole covered with a fine mesh net for ventilation, containing the fresh leaves of different plants tested. The petioles of detached leaves were inserted in water-soaked cotton to maintain freshness. The 2^{nd} to 5^{th} instars were reared on the pods of different soybean cultivars. A fine camel’s hair brush was used for transferring younger larvae to the Petri dishes. Fresh food material was provided as required, and observations were recorded daily for the mortality/survival of larvae in the same instar or moulting to next instar through pupation and adult emergence. Fifth instar larvae were kept in plastic containers (3 cm in diameter by 5 cm in height) for pre-pupation and pupation.

After emerging of adults, a pair of female and male moths was introduced into each transparent plastic container, as explained above. A small cotton wick soaked in 10% honey solution was placed in the oviposition containers to provide a food source of carbohydrate for the adult. When females began laying eggs, the number of eggs laid per female was recorded every day. The experiments were continued up to the death of the last female moth.

Age-specific survival rate (l_x) and life expectancy (e_x) of *H. armigera* on different soybean cultivars were calculated according to Carey (2001). The parameter entropy (*H*), days gained per averted death, was calculated using life expectancy (e_x) and frequency of deaths (d_x) and the average daily mortality ($\bar{\mu}$) of the cotton bollworm was also estimated on 13 soybean cultivars (Carey, 2001).

Life table parameters

The intrinsic rate of natural increase (r_m) for *H. armigera* on different cultivars was estimated (Birch, 1948). The net reproductive rate (R_0), finite rate of increase (λ), mean generation time (*T*) and doubling time (*DT*) were also estimated (Birch, 1948; Southwood & Henderson, 2000).

Mortality models

The Gompertz model states that above a threshold age, any important life history event, there is an exponential increase of mortality (μ_x) with age (x), expressed by the equation: $\mu_x = ae^{b(x)}$, where a is the initial mortality and b is the Gompertz parameter, which represents the slope of the mortality function (Carey, 2001). Another model utilizes the Weibull distribution (Pinder *et al*., 1978), and is called the Weibull model (Carey, 2001). In this model, mortality is a power function of age: $\mu_x = ax^b$. A plot of log(μ_x) against log(x) should give a straight line with slope b. In the Weibull model, a is the scale and b the shape parameter (Pinder *et al*., 1978; Carey, 2001).

The mortality rate (μ_x) was transformed by taking natural logarithms, and a linear fit with age was carried out for the Gompertz model, and with the natural logarithms of age for the Weibull model, both by the least squares method.

Data analysis

Life table parameters of *H. armigera* on different soybean cultivars was analyzed with one way ANOVA to determine the similarities or significant differences using the statistical softwares Minitab 14. Statistical differences among the means were evaluated using the least significant differences (LSD) test at $\alpha = 0.05$. Data were checked for normality prior to analysis.

Results

Survival rate, fecundity and life expectancy

Age-specific survival rate (l_x) and fecundity (m_x) of *H. armigera* on different soybean cultivars are shown in fig. 1. The highest and lowest survivorship of larval stages was observed on M7 and BP, respectively. The survivorship of overall immature stages was higher on M7 and lower on 356 and BP than the other examined soybean cultivars. The survival rate of individuals developed to adults from the initial cohort stage was estimated 0.87, 0.83, 0.96, 0.96, 0.77, 0.72, 0.81, 0.72, 0.85, 0.74, 0.85, 0.88 and 0.72 on 356, M4, M7, M9, Clark, Sahar, JK, BP, Williams, L17, Zane, Gorgan3 and DPX, respectively. The results of the present study indicated that the death of the last female (maximum age) on mentioned soybean cultivars occurred in the age of 56, 54, 55, 54, 53, 55, 53, 51, 48, 55, 62, 53 and 53 days, respectively (fig. 1).

The longest and shortest life expectancy of the pest was 44.22 and 35.98 days on Gorgan3 and BP, respectively at the beginning of life. Life expectancy of *H. armigera* was estimated 14.74, 16.85, 10.92, 14.51, 14.78, 12.75, 11.80, 10.50, 12.97, 10.86, 15.95, 13.00, and 13.04 days on these cultivars (the same order mentioned above), respectively at the first day of adult appearance, which revealed maximum and minimum rates of this parameter on M4 and BP, respectively.

The oviposition beginning of the first female on these cultivars (the same order mentioned above) occurred in the age of 39, 36, 34, 37, 37, 39, 40, 41, 35, 42, 35, 40 and 43 days, respectively. The highest daily fecundity (m_x) of *H. armigera* adult emerged from the larvae reared on these cultivars was 36.50, 115.65, 159.30, 99.68, 80.34, 45.03, 146.16, 103.41, 59.25, 72.00, 97.92, 73.32 and 132.30 females/female/day, respectively that occurred in the age of 48, 38, 35, 39, 37, 41, 40, 42, 46, 52, 38, 40 and 44 days, respectively. The daily fecundity of the cotton bollworm was zero on Williams in 39^{th}, 41^{st} and 42^{nd} days. This finding was also similar to the JK and Sahar in 49^{th} days (fig. 1).

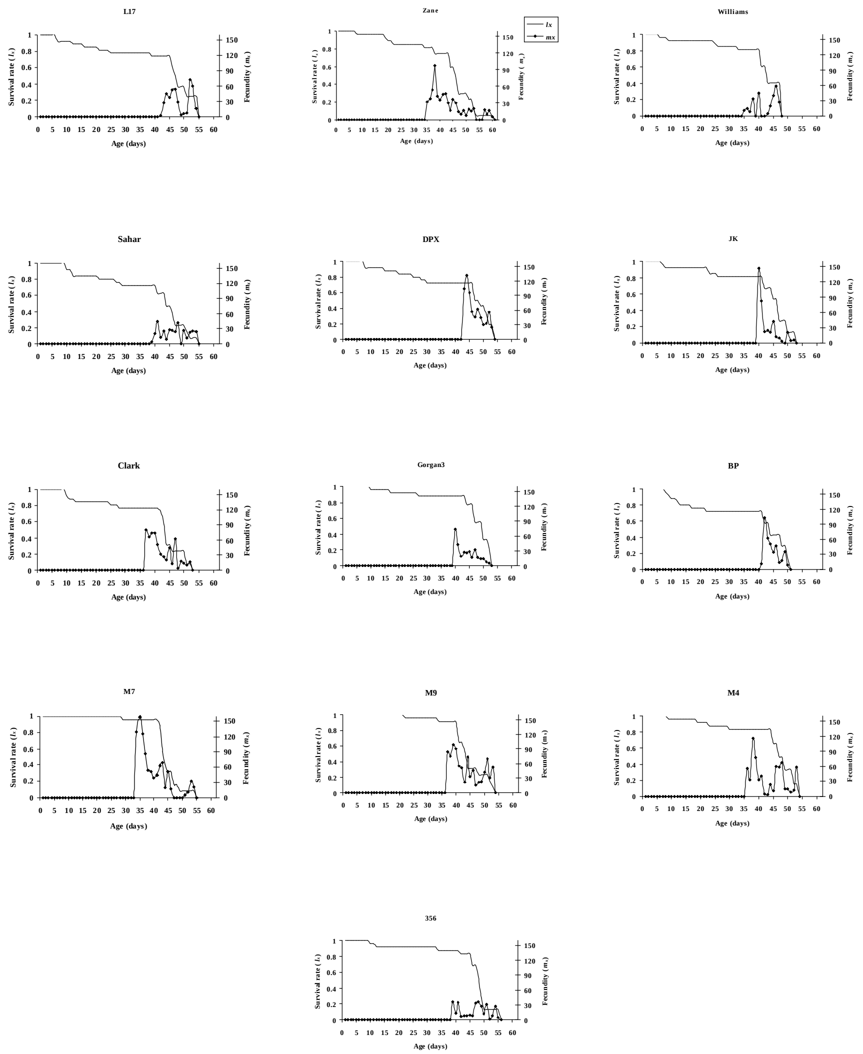

Figure 1. Age-specific survival rate (l_x) and fecundity (m_x) of *H. armigera* reared on different soybean cultivars.

Entropy and average daily mortality

The entropy (*H*) of *H. armigera* on above-mentioned soybean cultivars was 0.14, 0.16, 0.07, 0.12, 0.22, 0.26, 0.19, 0.28, 0.16, 0.24, 0.21, 0.13 and 0.23, respectively. The results suggested that the survival schedule of *H. armigera* was convex on the entire soybean cultivars (*H*

< 0.5). Daily mortality of the cotton bollworm fed on different soybean cultivars is shown in fig. 2. The results revealed that the daily mortality parameter was 0.068, 0.059, 0.092, 0.069, 0.068, 0.078, 0.085, 0.095, 0.077, 0.092, 0.063, 0.077 and 0.077 on these cultivars, respectively at the first day of adult emergence, which showed highest and lowest values of this parameter on BP and M4, respectively.

Life table parameters

The results of the life table parameters of *H. armigera* are presented in table 1. The intrinsic rate of natural increase (r_m) varied from 0.1324 to 0.1848 (day^{-1}), which was lowest on 356 and highest on M9 (P < 0.01).

The net reproductive rate (R_0) was also found to be significantly different (P < 0.01) depending on the soybean cultivars on which individuals were reared. The R_0 values of the cotton bollworm estimated on the 13 soybean cultivars ranged from 89.35 to 354.92 female/female/generation (table 1). However, the R_0 value of *H. armigera* was the highest on M7 and the lowest on 356. In addition, the mean generation time value on L17 was higher (36.61 days) than on the other cultivars. However, this parameter was lower on Zane (28.85 days) as compared to the other soybean cultivars. Furthermore, the doubling time values of the cotton bollworm showed significant differences (P < 0.01), being higher on 356, L17, Gorgan3, BP and Sahar (5.23, 5.21, 5.06, 4.94 and 4.89 days, respectively) than the other cultivars. In addition, the finite rate of increase value of this pest was lower on 356, L17, Gorgan3, BP and Sahar (1.14, 1.14, 1.14, 1.15 and 1.15 day^{-1}, respectively) as compared with the other cultivars (P < 0.01) (table 1).

Mortality models

Parameters of linear regression analysis between survival rate and age of *H. armigera* reared on different soybean cultivars, using Gompertz and Weibull models, are summarized in table 2. A significant fit was obtained between the survival rate and age of *H. armigera* reared on soybean cultivars using these models (P < 0.01). The slope of the linear regression in Weibull model was greater than Gompertz model on all examined cultivars. Because of the higher R^2 value in Gompertz model, data from different cultivars had a better fit with this model compared to Weibull model. Among different soybean cultivars, the parameters obtained for Zane was fitted better to Gompertz model (R^2 = 0.609) in comparison with the other cultivars. However, parameters for BP had a better fit to Weibull model (R^2 = 0.403) as compared with the other cultivars.

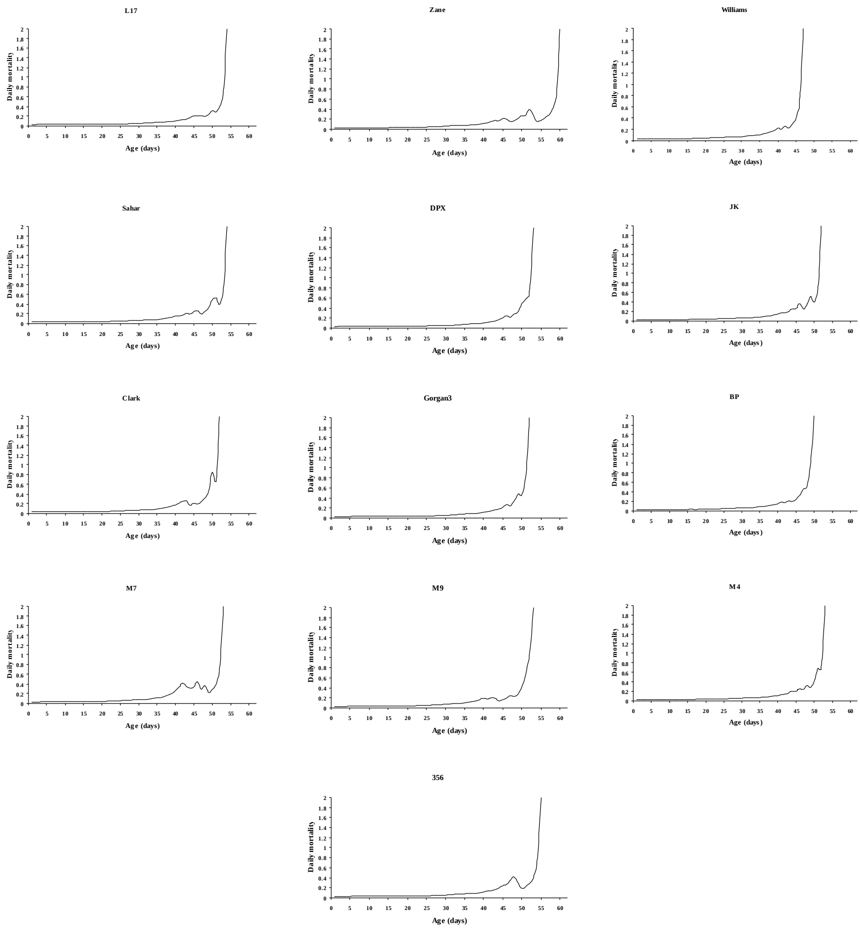

Figure 2. Daily mortality ($\bar{\mu}$) of *H. armigera* reared on different soybean cultivars.

Discussion

Plant species differ greatly in suitability as host plants for specific insects when measured in terms of survival, development and reproductive rates. Shorter developmental time and greater total reproduction of insects on a host plant indicate greater suitability of that plant (van Lenteren & Noldus, 1990). Using resistant cultivars is one of the core strategies of integrated pest management. The secondary substances of plants (allelochemicals) play a major role in plant resistance to pests (Wilson & Huffaker, 1976).

Table 1. Life table parameters of *H. armigera* on different soybean cultivars. See text for the abbreviations.

	Parameter (mean ± SE)					
Cultivar	R_0	r_m (day $^{-1}$)	λ (day $^{-1}$)	T (day)	DT (day)
M7	354.92 ± 52.34^{a}	0.1820 ± 0.0063^{a}	1.20 ± 0.007^{a}	31.92 ± 0.410^{d}	3.80 ± 0.013^{e}
JK	133.47 ± 28.85^{def}	0.1476 ± 0.0070^{cde}	1.16 ± 0.008^{cde}	33.30 ± 0.291^{c}	4.68 ± 0.211^{bc}
Clark	210.58 ± 26.57^{bc}	0.1759 ± 0.0046^{a}	1.19 ± 0.005^{a}	30.45 ± 0.192^{ef}	3.94 ± 0.104^{e}
M4	170.09 ± 20.25^{cde}	0.1577 ± 0.0051^{bc}	1.17 ± 0.006^{bc}	31.99 ± 0.381^{d}	4.39 ± 0.145^{cd}
M9	274.32 ± 31.70^{ab}	0.1848 ± 0.0050^{a}	1.20 ± 0.005^{a}	30.00 ± 0.359^{f}	3.75 ± 0.104^{e}
L17	127.76 ± 22.33^{def}	0.1329 ± 0.0050^{f}	1.14 ± 0.006^{f}	36.61 ± 0.391^{a}	5.21 ± 0.200^{a}
356	89.35 ± 18.71^{f}	0.1324 ± 0.0052^{ef}	1.14 ± 0.006^{f}	34.12 ± 0.552^{c}	5.23 ± 0.211^{a}
DPX	226.56 ± 37.22^{bc}	0.1549 ± 0.0044^{bcd}	1.17 ± 0.005^{cd}	35.09 ± 0.240^{b}	4.47 ± 0.127^{cd}
BP	142.11 ± 15.76^{cdef}	0.1402 ± 0.0024^{ef}	1.15 ± 0.003^{def}	35.40 ± 0.408^{b}	4.94 ± 0.086^{ab}
Zane	194.23 ± 29.61^{bcd}	0.1697 ± 0.0067^{ab}	1.19 ± 0.007^{ab}	28.85 ± 2.509^{de}	4.08 ± 0.165^{de}
Sahar	114.99 ± 22.87^{ef}	0.1413 ± 0.0065^{def}	1.15 ± 0.007^{def}	33.70 ± 0.369^{c}	4.89 ± 0.232^{ab}
Gorgan3	119.85 ± 18.29^{ef}	0.1367 ± 0.0047^{ef}	1.14 ± 0.004^{ef}	35.10 ± 0.380^{b}	5.06 ± 0.177^{ab}
Williams	107.48 ± 16.28^{ef}	0.1572 ± 0.0043^{bc}	1.17 ± 0.005^{bc}	29.82 ± 0.391^{f}	4.40 ± 0.113^{cd}

The means within columns followed by different letters are significantly different ($P < 0.01$, LSD).

Understanding the demographic parameters of a pest is essential to develop an integrated pest management strategy. These parameters provide population growth rate of an insect pest in the current and next generations (Frel *et al.*, 2003).

The survival rate of *H. armigera* had different trend on the 13 soybean cultivars. Since the total number of days to be lived by the average individual within a cohort from age x to the last day of possible life of the cotton bollworm was the lowest on BP at the beginning of life, the life expectancy of *H. armigera* was minimum on this cultivar in comparison with the others.

The entropy parameter provides a useful summary measure for characterizing differences in shapes of survival curves among cohorts (Carey, 2001). Because the entropy of the cotton bollworm was lower than 0.5, the survival schedule of *H. armigera* was convex on all soybean cultivars suggesting that the probability of dying was higher in late ages as compared with early ones. On the other hand, survivorship of *H. armigera* was initially high and decreased rapidly in late ages.

Table 2. Estimated parameters of linear regression between survival rate and age of *H. armigera* reared on different soybean cultivars (fitted to Gompertz and Weibull models).

		Parameter				
Model	**Cultivar**	***a*** **± SE**	***b*** **± SE**	$P_{regression}$	P_{slope}	R^2
Gompertz						
	M7	0.634 ± 0.167	-0.039 ± 0.005	< 0.0001	< 0.0001	0.498
	JK	0.305 ± 0.104	-0.024 ± 0.003	< 0.0001	< 0.0001	0.492
	Clark	0.354 ± 0.113	-0.029 ± 0.004	< 0.0001	< 0.0001	0.544
	M4	0.250 ± 0.083	-0.019 ± 0.003	< 0.0001	< 0.0001	0.486
	M9	0.460 ± 0.117	-0.029 ± 0.004	< 0.0001	< 0.0001	0.537
	L17	0.180 ± 0.064	-0.019 ± 0.002	< 0.0001	< 0.0001	0.605
	356	0.395 ± 0.129	-0.026 ± 0.004	< 0.0001	< 0.0001	0.435
	DPX	0.170 ± 0.063	-0.018 ± 0.002	< 0.0001	< 0.0001	0.589
	BP	0.133 ± 0.065	-0.019 ± 0.002	< 0.0001	< 0.0001	0.606
	Zane	0.698 ± 0.159	-0.044 ± 0.004	< 0.0001	< 0.0001	0.609
	Sahar	0.411 ± 0.121	-0.033 ± 0.004	< 0.0001	< 0.0001	0.584
	Gorgan3	0.167 ± 0.064	-0.013 ± 0.002	< 0.0001	< 0.0001	0.435
	Williams	0.139 ± 0.049	-0.015 ± 0.002	< 0.0001	< 0.0001	0.586
Weibull						
	M7	0.993 ± 0.367	-0.468 ± 0.116	< 0.0001	< 0.0001	0.224
	JK	0.568 ± 0.221	-0.302 ± 0.071	< 0.0001	< 0.0001	0.253
	Clark	0.691 ± 0.247	-0.370 ± 0.079	< 0.0001	< 0.0001	0.292
	M4	0.462 ± 0.175	-0.238 ± 0.056	< 0.0001	< 0.0001	0.251
	M9	0.740 ± 0.261	-0.356 ± 0.083	< 0.0001	< 0.0001	0.252
	L17	0.443 ± 0.145	-0.254 ± 0.046	< 0.0001	< 0.0001	0.359
	356	0.670 ± 0.272	-0.330 ± 0.085	< 0.0001	< 0.0001	0.205
	DPX	0.424 ± 0.139	-0.243 ± 0.044	< 0.0001	< 0.0001	0.360
	BP	0.417 ± 0.140	-0.264 ± 0.045	< 0.0001	< 0.0001	0.403
	Zane	1.280 ± 0.383	-0.610 ± 0.117	< 0.0001	< 0.0001	0.307
	Sahar	0.828 ± 0.273	-0.437 ± 0.086	< 0.0001	< 0.0001	0.318
	Gorgan3	0.314 ± 0.130	-0.166 ± 0.042	< 0.0001	< 0.0001	0.226
	Williams	0.290 ± 0.107	-0.172 ± 0.035	< 0.0001	< 0.0001	0.332

The present research demonstrated significant differences of the life table parameters of the cotton bollworm among the 13 soybean cultivars. The net reproductive rate is an important indicator of population dynamics (Richard, 1961). It is a key statistic that summarizes the physiological capability of an animal related to its reproductive capacity. Comparison of net reproductive rate often provides considerable insight beyond whatever that available from the independent analysis of individual life history parameters. The net reproductive rate (R_0) was the highest on M7, whereas the values for R_0 varied from 89.35 on 356 to 354.92 on M7. Liu *et al.* (2004) showed that the R_0 values of *H. armigera* differed on different host plants, which was ranged from 5.1 on hot pepper to 117.6 on cotton. According to the literature, the net reproductive rate of this pest was 143.77 on sunflower (Reddy *et al.*, 2004) and 374.01 on pearl millet (Patal & Koshyia, 1997).

The r_m value of the cotton bollworm estimated in the current study ranged from 0.1324 to 0.1848, which was minimum on 356 and maximum on M9. The higher r_m value of *H. armigera* on M9 cultivar was due to the greater fecundity and lower mortality and shorter development time of the pest fed on this cultivar. However, lower r_m value on 356 was mainly a result of the poor fecundity and survivorship as well as longer development time of the cotton bollworm on this cultivar. The intrinsic rate of natural increase for *H. armigera* was estimated 0.1135 on sunflower (Reddy *et al.*, 2004), 0.1423 on pearl millet (Patal & Koshyia, 1997) and 0.13 on an artificial diet at 25°C (Mironidis & Savopoulou-Soultani, 2008). Some possible reasons for disagreement are due to physiological differences that depend on the type of the host plant, genetic differences as a result of laboratory rearing or variation in geographic populations of the pest.

High value of r_m indicates the susceptibility of a host plant to insect feeding, while a low value indicates that the host plant species is resistant to the pest. Therefore, our data showed the tremendous growth capacity of *H. armigera* under favorable conditions. Furthermore, since some soybean cultivars such as M9, M7, Clark and Zane were susceptible hosts, the cotton bollworm had the greatest opportunity for population increase on these cultivars. However, some cultivars including L17, 356, BP, Sahar and Gorgan3 were pretty unsuitable host plants, suggesting that they are more resistant to *H. armigera* than the others.

The highest finite rate of increase was on M9, M7, Clark and Zane, which had higher intrinsic rate of natural increase. The finite rate of increase ranged from 1.14 day^{-1} on L17, 356 and Gorgan3 to 1.20 day^{-1} on M9 and M7. According to the literature, this parameter was reported for *H. armigera* as 1.12 day^{-1} on sunflower (Reddy *et al.*, 2004) and 1.15 day^{-1} on pearl millet (Patal & Koshyia, 1997).

The mean generation time of the cotton bollworm varied from 28.85 to 36.61 days, which was the shortest on Zane and longest on L17. The higher rate of this value on L17 revealed that the mean time required for a newborn female to replace herself by R_0-fold was longer on this cultivar as compared to the other cultivars. Furthermore, the lower r_m value of *H. armigera* on L17 was mainly another reason for longer mean generation time on this cultivar. Therefore, L17 was unsuitable host plant for population increase of *H. armigera*. Because of the highest intrinsic rate of natural increase of the pest on M9, M7, Clark and Zane cultivars, the shortest time period required for doubling the initial population was observed on these cultivars. Doubling time ranged from 3.75 days on M9 to 5.23 days on 356. Reddy *et al.* (2004) have noted that the doubling time of *H. armigera* was 6.11 days on sunflower. Differences of our results on doubling time of the pest from those reported by Reddy *et al.* (2004) might be either due to the host plant type and different plant parts consumed by the larvae or variation in population of the cotton bollworm examined.

The quality and quantity of nourishment ingested by an insect can directly affect its survival and reproduction. So, fitness of the plant-feeding insects depends on the nutrients in their host plants. However, the partially resistant cultivars also may enhance the effectiveness of natural enemies and insecticides. Therefore, the use of resistant cultivars can develop biological and chemical control methods as part of an IPM strategy (Du *et al*., 2004; Adebayo & Omoloyo, 2007). It can be concluded that 356, L17, Gorgan3, BP and Sahar had lower suitability as host plants for this pest in comparison with the other examined cultivars.

After laboratory studies, more attention should be devoted to semi-field and field experiments to obtain more applicable results in field conditions. Meanwhile, our results provide data for establishing suitable conditions for rearing of *H. armigera*. For instance, mass culture methods could be enhanced by selecting host plants for rapid development, maximum survival or high fecundity in order to use these individuals for mass rearing of natural enemies.

Acknowledgements

This research was partly supported by a grant from the Center of Excellence for Integrated Pests and Diseases Management of Oil Crops of Iran, which is greatly appreciated.

References

Adebayo, A. & Omoloyo, S. V. (2007) Abundance of 24-methylenecholesterol in traditional African rice as an indicator of resistance to the African rice gall midge, *Orseolia oryzivora* Harris and Gagne. *Entomological Science* 10, 249-257.

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

Carey, J. R. (1993) *Applied demography for biologists, with special emphasis on insects*. 211 pp. Oxford University Press, U.K.

Carey, J. R. (2001) Insect biodemography. *Annual Review of Entomology* 46, 79-110.

Dent, D. (2000) Host plant resistance. pp. 123-179 in Dent, D. (Ed.) *Insect pest management*. CABI Publishing, U.K.

Du, L., Ge, F., Zhu, S. & Parajulee, M. N. (2004) Effect of cotton cultivar on development and reproduction of *Aphis gossypii* (Homoptera: Aphididae) and its predator *Propylaea japonica* (Coleoptera: Coccinellidae). *Journal of Economic Entomology* 97, 1278-1283.

Farid, A. (1986) Study of bollworm *Heliothis armigera* (Hub.) on tomato in Jyroft and Kahnuj. *Applied Entomology and Phytopathology* 54, 15-24. [In Persian with English summary].

Fitt, G. P. (1994) Cotton pest management: part 3; an Australian perspective. *Annual Review of Entomology* 39, 543-562.

Frel, A. G. H., Cardona, C. & Dorn, S. (2003) Antixenosis and antibiosis of common beans to *Thrips palmi*. *Journal of Economic Entomology* 93, 1577-1584.

Gunning, R. V., Easton, C. S., Greenup, L. R. & Edge, V. E. (1984) Pyrethroid resistance in *Heliothis armigera* (Hübner) (Lepidoptera: Noctuidae) in Australia. *Journal of Economic Entomology* 77, 1283-1287.

Haghani, M., Fathipour, Y., Talebi, A. A. & Baniameri, V. (2006) Comparative demography of *Liriomyza sativae* Blanchard (Diptera, Agromyzidae) on cucumber at seven constant temperatures. *Insect Science* 13, 477-483.

Kennedy, G. G., Gould, F., Deponti, O. M. B. & Stinner, R. E. (1987) Ecological, agricultural and commercial considerations in the deployment of insect resistant King ABS (1994) *Heliothis*/*Helicoverpa* (Lepidoptera: Noctuidae). pp. 39-106 in Mathews, G. A. & Tunstall, J. P. (Eds) *Insect pests of cotton*. CAB International, U.K.

Kogan, M. & Herzog, D. C. (1980) *Sampling methods in soybean entomology*. 587 pp. Springer Verlag, New York.

Liu, Z., Li, D., Gong, P. Y. & Wu, K. J. (2004) Life table studies of the cotton bollworm, *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae), on different host plants. *Environmental Entomology* 33, 1570-1576.

Maia, A. H. N., Luiz, A. J. B. & Campanhola, C. (2000) Statistical inference on associated fertility life table parameters using jackknife technique: computational aspects. *Journal of Economic Entomology* 93, 511-518.

Mironidis, G. K. & Savopoulou-Soultani, M. (2008) Development, survivorship and reproduction of *Helicoverpa armigera* (Lepidoptera, Noctuidae) under constant and alternating temperatures. *Environmental Entomology* 37, 16-28.

Moral Garcia, F. J. (2006) Analysis of the spatio-temporal distribution of *Helicoverpa armigera* (Huber) in a tomato fields using a stochastic approach. *Biosystems Engineering* 93, 253-259.

Naseri, B., Fathipour, Y., Moharramipour, S. & Hosseininaveh, V. (2009) Comparative life history and fecundity of *Helicoverpa armigera* (Lepidoptera: Noctuidae) on different soybean varieties. *Entomological Science* 12, 51-58.

Omer, A. D., Johnson, M. W. & Tabashnik, B. E. (1996) Demography of the leafminer parasitoid *Ganaspidium utilis* Beardsley (Hymenoptera, Eucoilidae) at different temperatures. *Biological Control* 6, 29-34.

Patal, C. C. & Koshyia, D. J. (1997) Life table and innate capacity of *Helicoverpa armigera* (Hübner) on pearl millet. *Indian Journal of Entomology* 59, 389-395.

Pinder, J. E., Wiener, J. G. & Smith, M. H. (1978) The Weibull distribution: a new method of summarizing survivorship data. *Ecology* 59, 175-179.

Preston, S. H., Heuveline, P. & Guillot, M. (2001) *Demography*: *measuring and modelling population processes*. 291 pp. Blackwell Publishers, London.

Razmjou, J., Moharramipour, S., Fathipour, Y. & Mirhoseini, S. Z. (2006) Effect of cotton cultivar on performance of *Aphis gossypii* (Homoptera: Aphididae) in Iran. *Journal of Economic Entomology* 99, 1820-1825.

Reddy, K. S., Rao, G. R., Rao, P. A. & Rajasekhar, P. (2004) Life table studies of the capitulum borer, *Helicoverpa armigera* (Hübner) infesting sunflower. *Journal of Entomological Research* 28, 13-18.

Richard, O. W. (1961) The theoretical and practical study of natural insect populations. *Annual Review of Entomology* 6, 147-162.

Sarfraz, M., Dosdall, L. M. & Keddie, B. A. (2006) Diamondback moth-host plant interactions: implications for pest management. *Crop Protection* 25, 625-636.

Southwood, T. R. E. & Henderson, P. A. (2000) *Ecological methods.* 3rd ed. 592 pp. Blackwell Sciences, Oxford.

Taghizadeh, R., Fathipour, Y. & Kamali, K. (2008) Influence of temperature on life table parameters of *Stethorus gilvifrons* (Mulsant) (Coleoptera, Coccinellidae) fed on *Tetranychus urticae* Koch. *Journal of Applied Entomology* 132, 638-645.

van Lenteren, J. C. & Noldus, L. P. J. J. (1990) Whitefly-plant relationship: behavioral and biological aspects. pp. 47-89 in Gerling, D. (Ed.) *Whitefly*: *their bionomics*, *pest status and management*. Intercept, Andover, U.K.

Vargas, R. I., Walsh, W. A., Kanehisa, D. T., Jang, E. B. & Armstrong, J. W. (1997) Demography of four Hawaiian fruit flies (Diptera, Tephritidae) reared at five constant temperatures. *Annals of the Entomological Society of America* 90, 162-168.

Wilson, F. & Huffaker, C. B. (1976) The physiology, scope and importance of biological control. pp. 3-15 in Huffaker, C. H. & Messenger, P. S. (Eds) *Theory and practice of biological control*. Academic, New York, USA.

Received: 29 October 2008

Accepted: 18 February 2009