Journal of Plant Protection Research ISSN 1427-4345

ORIGINAL ARTICLE

Effect of host plant cultivar and nitrogen fertilization on life history of *Helicoverpa armigera* (Lepidoptera: Noctuidae)

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Vol. 60, No. 2: 161–175, 2020

DOI: 10.24425/jppr.2020.133310

Received: July 30, 2019
Accepted: December 9, 2019

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Abstract

The current survey was carried out to evaluate the effect of different nitrogen levels (0, 2.1, 3.0, 3.9 g · pot^{-1} nitrogen as urea 46%) on tomato fruit worm *Helicoverpa armigera* on six common tomato cultivars (e.g., Kingston, Riogrand, Earlyurbana, Redston, Superstrain-B and Primoearly) under laboratory conditions [25 ± 1°C, 60 ± 5% RH, 16 : 8 (L : D) h]. The mortality, developmental period of immature stages as well as the longevity and fecundity of adult stages were recorded. Data were analyzed based on the age-stage, two-sex life-table theory. The longest (24.21 ± 0.59 days) larval developmental period was recorded in Earlyurbana variety with zero nitrogen level and the shortest (15.44 ± 0.36 days) in Superstrain-B variety with the highest nitrogen level. Consequently, the net reproductive rate (R_0) ranged from 35.7 ± 7.06 to 62.16 ± 18.9 offspring/female/individual in Redston variety with zero nitrogen level and in Superstrain-B variety with the highest nitrogen level, respectively. The lowest and highest values of the intrinsic rate (r) and finite rate of increase (l) were estimated for Redston variety with zero level of nitrogen (0.0712 ± 0.0065 and 1.0732 ± 0.0069 day^{-1}) and Superstrain-B variety with the highest nitrogen fertilizer (0.1507 ± 0.0057 and 1.1629 ± 0.0066 day^{-1}), respectively. The results demonstrated that nitrogen fertilizer influenced nearly all the life parameters of the pest which depended on the cultivars. Finally, it could be concluded that Kingston and Superstrain-B were suitable and Earlyurbana and Redston were unsuitable host plant cultivars for *H. armigera*.

Keywords: age-stage two-sex life-table, fertilization, *Helicoverpa armigera*, nitrogen

Introduction

Tomato (*Lycopersicon esculentum* Mill.), one of the most important vegetable crops, is more susceptible to insect pests than other crops due to its tender and soft texture. Therefore, it is devastated by an array of pests. Amongst its known Setiawati pests, the greatest damage is caused by *Helicoverpa armigera* (Sajjad *et al.* 2011). *Helicoverpa armigera* is a polyphagous and key pest of various crops including cotton, chickpea, tomato, tobacco, corn, sesame, sunflower, peanut, okra, soybean and bean (Talekar *et al.* 2006; Hemati *et al.* 2012a). The larvae are able to damage almost all plant aerial parts and even cause secondary infections which result in high economic losses (Liu *et al.* 2004; Talekar *et al.* 2006).

The larvae can destroy about 40–50% of tomato fruits in the event of delayed control (1990). Furthermore, globally there is evidence of pest resistance to pesticides (Lukefahr *et al.* 1971; Downes *et al.* 2017). Thereby, integrated pest management (IPM) approaches have been developed in many countries to overcome pest outbreaks and side effects of pesticides (Mahmudunnabi *et al.* 2013). Implications of all options including, cultural, mechanical, biological and host plant resistance have led to successful manage-

ment of *H. armigera* populations in different crops, though more research is still needed to find a better integrated method especially as biological control and host plant defense mechanisms are fundamental (Peterson *et al.* 2016).

Numerous reports have verified the effect of plant cultivar and quality on pest incidence (Awmack and Leather 2002; Suzana *et al.* 2015). Undeniably, internal factors such as alkaloids, proteinase inhibitors, phenolic compounds and oxidative enzymes (Bhonwong *et al.* 2009) and nutritional quality of plants play significant roles in host plant-herbivore interactions (Chau *et al.* 2005).

The most critical macronutrient in plants, which profoundly influences the growth and fecundity of herbivorous insects, is nitrogen (Douglas 1993; Trdan *et al.* 2008). Nitrogen deposition often leads to increases in foliar nitrogen concentrations and plant biomass which consequently accelerates the growth and development rates of pest populations (Throop and Lerdau 2004; Zehnder and Huntr 2008). Briefly, N fertilization increases plant size, height and inflorescence branching as well as seed protein content. However, for ecological reasons it should be applied carefully in order to cause only optimal plant growth (Blake *et al.* 2010; Grant *et al.* 2011). Generally, insects on host plants with high N content have higher growth rates and efficiency of ingested food conversion and shorter developmental times (Chen *et al.* 2008). It is also believed that the fitness of herbivore insects depends upon the nutritious substances in the host plant (Du *et al.* 2004). Moreover, environmental conditions influence the host plant quality (Gharekhani and Salek-Ebrahimi 2014a) which in turn affect insect development, survivorship, reproduction and life-table parameters (Tsai and Wang 2001; Kim and Lee 2002). Nitrogen also may affect a plant's indirect defenses, namely the efficacy of natural enemies that kill herbivores attacking the plant (Chen *et al.* 2010). Generalist herbivores show higher sensitivity to the quality of host-plants than specialist herbivores. Therefore, it is expected that when a generalist host/prey feeds on plants with differing quality, the effects on natural enemies which follow may be more significant (Mooney *et al.* 2012).

Although numerous studies have focused on finding optimal nitrogen doses for higher yield and seed quality (Sharma and Bali 2017), little is known about the impact of fertilization on insect pests (Veromann *et al.* 2013). Therefore, application of nitrogen fertilizer should be optimized to maintain optimal plant physiology and minimize pest growth (Huang *et al.* 2002). Although various methods are available to investigate the insect herbivore-host plant interactions, an insect life-table approach has frequently been used as a reliable method in recent decades (Razmjou *et al.* 2006). The method is efficient enough for analyzing the effect of external and host plant factors on the growth, survival, reproduction and intrinsic rate of an insect population (Chi and Su 2006; Jaleel *et al.* 2017; Farrokhi *et al.* 2017). Practically, the effect of different host plants on age-specific female life-table parameters of *H. armigera* was evaluated (Jha *et al.* 2012). Similar studies have been done by Liu *et al.* (2004), Naseri *et al.* (2014), Jha *et al.* (2014), Gomes *et al.* (2017) and Liu *et al.* (2017).

A herbivore-host plant experiment using the life-table method would evaluate the pest damage on commercial cultivars. Therefore, identifying cultivars resistant to *H. armigera* would supply an effective and complementary approach in IPM to reduce losses caused by the pest (Jallow *et al.* 2004). However, the cultivation of tomato plant cultivars resistant to *H. armigera* is limited in Iran (Kouhi *et al.* 2014) as well as in the world (Muthukumaran 2016) due to the lack of information about the cultivars. Thus, the objective of this study was to evaluate the demographic characteristics of *H. armigera* reared on six common tomato cultivars at different nitrogen levels using the age-stage, two-sex life-table theory. Results may assist in the identification of resistant cultivars based on comparative pest growth and development rates in combination with N fertilization.

Materials and Methods

Tomato plants

The seeds of six tomato cultivars, Kingston (K), Riogrand (RG), Earlyurbana (E), Redston (R), Superstrain-B (SB) and Primoearly (P), were obtained from the Seed and Plant Improvement Institute (SPII), Karaj, Iran. The named cultivars are commonly cultured in Iran and have approximately the same growth period. They were planted in plastic pot trays (60 × 40 cm with 168 punctures) filled with soil in a greenhouse [27 ± 5°C, 65 ± 5% RH, photoperiod of 16 : 8 (L : D) h] in the Biological Control Research Department (BCRD), Iranian Research Institute of Plant Protection (IRIPP), Tehran, Iran. The seedlings were transferred to 30 × 15 cm pots with soil that was previously analyzed for major nutrients at the four leaf stage. They were irrigated with only 250 ml of tap water at 2 day intervals for 35 days after transplanting. Thereafter, nitrogen treatments were carried out.

Nitrogen treatments

Urea fertilizer (46%) was used as nitrogen treatments. Four levels of N: 0, 2.1, 3.0, 3.9 g · pot^{-1}, were prepared

Table 1. Composition of nitrogen regimes and cultivars used in the experiments. Treatments abbreviations were presented for the ease of application and comparisons

Nitrogen level	Code	Dose [g · pot^{-1}]	Cultivars					
			Kingston (K)	Riogrand (RG)	Earlyurbana (E)	Redston (R)	Superstrain-B (SB)	Primoearly (P)
No fertilization	n0	0	Kn0	RGn0	En0	Rn0	SBn0	Pn0
Standard – 30%	n–	2.1	Kn–	RGn–	En–	Rn–	SBn–	Pn–
Standard	ns	3.0	Kns	RGns	Ens	Rns	SBns	Pns
Standard + 30%	n+	3.9	Kn+	RGn+	En+	Rn+	SBn+	Pn+

(n0) – no fertilization; (n+) – standard fertilization plus 30%; (ns) – standard fertilization; (n–) – standard fertilization minus 30%

by dissolving the required doses in 3 l of tap water and used. Treatments included: n0 – no fertilization, n – 30% below the standard fertilization, ns – standard fertilization and n+ – standard fertilization plus 30% extra N (Table 1). The chemigation system was comprised of ordinary 500 ml plastic drink bottles containing water/N solution which was attached 1 m above the pots, while tubing with a drip chamber and a roller clamp (ATP Inc. Medical Products) led the liquid to the pots. Moreover, no pesticide or additional fertilizer was used.

Insect rearing

The first colony was established using the eggs of *H. armigera* from a stock maintained at Biological Control Research Department, Iranian Research Institute of Plant Protection. The stock colony was fed an artificial diet based on the Teakle (1991) method. Sub-colonies were made up of 24 colonies from the original colony. Each sub-colony was transferred to one treatment (six tomato cultivars with four N levels) and maintained in a growth chamber (noorsanattajhiz plus JUMO) under 25 ± 1°C, 60 ± 5% RH and 16 : 8 (L : D) h conditions. These 24 colonies were reared for three generations separately and the insects of the 4th generation were used in the experiment.

Development and survivorship of immature stages

Twenty pairs of the 4th generation pupae were selected from each of the 24 colonies. Emerged moths (female and male) were paired and kept in oviposition vessels (25 × 20 cm, made by clear plastic jars lined with baby nappies, Firooz Hygienic Group). A piece of small cotton soaked in 10% honey solution was used for the insects' feeding. Then, 100 eggs (0–24 h) were collected from each of the 24 colonies and reared on cut leaves provided daily from each treatment in ventilated plastic bowls (7 × 4 cm). Thereafter, emerged adult moths were transferred to the oviposition containers to collect eggs. Eventually, fifty eggs (0–24 h) of these moths were considered as a cohort and were individually reared on the leaves [the petioles of the leaves were inserted in vials (1.5 ml) containing agar solution (10%)] to keep them fresh and the third to sixth instar larvae were transferred to unripe and sliced green fruits of related treatments (Safuraie *et al.* 2014). The larval exuviae were used to determine the instars. The pre-pupae were kept on moist sand for pupation. All emerged adult moths were paired and kept in the above mentioned containers for oviposition. These plastic containers were checked daily for adult mortality and the number of deposited eggs.

Data analysis

Life-table analysis

Life history analysis was done on the basis of the age-stage two-sex life table (Chi and Liu 1985). The TWOSEX-MS Chart program was chosen for this purpose (Chi 2016). Then, the age-stage specific fecundity (f_{xj}), the age-specific fecundity (m_x), the age-stage specific survival rate (s_{xj}) (x refers to age, and j refers to stage), the age-specific survivorship (l_x), and the parameters of population growth: net reproductive rate (R_0), intrinsic rate of increase (r), finite rate of increase (λ), and mean generation time (T) were measured.

The intrinsic rate of increase (r) was measured using the iterative bisection method from:

$$\sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_x = 1. \quad (1)$$

Here, age can be indexed from 0 to ω (as the max. age) (Goodman 1982).

The net reproductive rate (R_0) was estimated using:

$$R_0 = \sum_{x=0}^{\infty} l_x m_x, \quad (2)$$

where: l_x = the age-specific survivorship; m_x = the age-specific fecundity.

Mean generation time T refers to the time length needed by a population to increase to R_0 – times its size as the stable increase rate and the stable age distribution are achieved (i.e., $e^{rT} = R_0$ or $\lambda^T = R_0$). Hence, the mean generation time equation can be written as follows:

$$T = \frac{\ln R_0}{r}, \quad (3)$$

where r is intrinsic rate of increase.

The life expectancy (e_{xj}) is the length of time that an individual of age x and stage j is expected to live and it is calculated according to Chi and Su (2006) as:

$$e_{xj} = \sum_{i=x}^{\infty} \sum_{v=1}^{m} s_{iy}, \quad (4)$$

where: m = the number of stages; s_{iy} = the probability that an individual of age x and stage y will survive to age i and stage j and is calculated by assuming $s_{xy} = 1$ (Chi 1988).

The reproductive value (v_{xj}) was calculated according to Tuan *et al.* (2016) as:

$$v_{xj} = \frac{e^{r(x+1)})}{s_{xj}} \sum_{i=x}^{\infty} e^{-r(i+1)} \sum_{y=j}^{m} s_{iy} f_{iy}, \quad (5)$$

where: r = the intrinsic rate of increase; s_{xj} = age-stage specific survival rate; m = the number of stages; s_{iy} = the probability that an individual of age x and stage y will survive to age i and stage j and is calculated by assuming $s_{xy} = 1$ (Chi 1988); f_{iy} = the age-stage specific fecundity ($i = x$, $y = j$).

The bootstrap method was utilized in order to estimate the means and standard errors of the parameters (Meyer *et al.* 1986; Huang and Chi 2013; Chi 2016). The paired bootstrap test was used to compare differences between the cultivars and nitrogen levels distinctly ($p \leq 0.05$) (Efron and Tibshirani 1993). The bootstrap method and paired bootstrap test are embedded in the computer program TWOSEX-MSChart. Interaction of the total nitrogen on six tomato cultivars with four nitrogen levels was investigated using a linear regression model.

Results

Developmental time

The effects of treatments on all pre-adult stages of *H. armigera* are presented in Table 2. The incubation period of both sexes was not influenced by cultivar or nitrogen levels. However, both the larval and pupal durations showed significant differences between the tomato cultivars ($p < 0.05$). The longest larval developmental period was recorded on En0 and Rn0 and the shortest on Kns and Kn+ and SBns and SBn+ for both female and male insects. Similarly, the longest pupal developmental period was recorded for insects on RGn0 and Rn–, while the shortest were observed in K, SB and P cultivars fertilized with ns and n+. The higher the level of nitrogen, the shorter the larval longevity without considering some exceptions and cultivar types (Table 3).

Adult longevity and reproductive capacity

The means for adult longevity and female fecundity of *H. armigera* on different treatments are presented in Table 3. The longest longevity of female *H. armigera* was recorded on RGns and RGn+ with all nitrogen levels except n0 and also on Rns and Rn+ and the shortest was estimated on Pn0 and Pn– treatment. The male insects were influenced almost the same in all the treatments. Furthermore, the maximum fecundity was estimated for the insects on Kn+ and SBn+ treatments.

Life-table parameters

Table 4 represents population parameters of *H. armigera* on all treatments. The net reproductive rates (R_0) ranged from 35.7 ± 7.06 to 62.16 ± 18.9 offspring/female/individual on Rn0 and SBn+, respectively (Table 4). The lowest values of the intrinsic rate of increase (r) and finite rate of increase (λ) were achieved in Rn0 and the highest rate was obtained in SBn+ (Table 4). Finally, the mean generation time (T) for different treatments lasted 32.01 ± 0.021 to 44.80 ± 0.017 days on cultivars SBn+ and Rn–, respectively (Table 4).

The l_x curve is the age-specific survivorship including all individuals of the cohort (Figs. 1–12) and, ignoring the stage differentiation, it is a simplified version of the s_{xj} curves. The probability that a newly hatched larva would survive to the adult stage was 0.39 on SBn+, which was significantly higher than that on Rn0 (0.10). The female age-stage specific fecundity (f_{xj}) shows the mean number of fertile eggs produced per day by the female (Figs. 1–12). If all individuals of age x are included, this value expresses the age-specific fecundity of the total population m_x.

The highest age-specific fecundity (m_x) also was 17.2, 14.1, 15.3, 11.8, 24.95 and 15.3 female · female^{-1} day^1 with the same treatments and occurred at the ages of 33, 36, 38, 37, 32 and 34 days, respectively (Figs. 2, 4, 6, 8, 10 and 12). The lowest and highest life expectancy (e_{xj}) of newly emerged adults of *H. armigera* was obtained in Rn0 and SBn+, respectively. The reproductive value (v_{xj}) (Eq. 5) showed that the females had the highest contribution in the next generation, on SBn+.

Table 2. Pre-adult durations (mean ± SE) of *Helicoverpa armigera* reared on six tomato cultivars with four nitrogen (N) levels

Stage	N level	Cultivars											
		Kingston (K)		Riogrand (RG)		Earlyurbana (E)		Redston (R)		Superstrain-B (SB)		Primoearly (P)	
		female	male	female	male	female	male	female	male	female	male	female	male
Egg	n0	2.93 ± 0.06 a	3.01 ± 0.02 a	2.97 ± 0.04 a	2.95 ± 0.06 a	2.95 ± 0.05 a	3.02 ± 0.06 a	3.04 ± 0.00 a	2.96 ± 0.04 a	3.00 ± 0.00 a	2.93 ± 0.04 a	3.08 ± 0.03 a	3.02 ± 0.04 a
	n–	2.94 ± 0.03 a	2.96 ± 0.05 a	2.82 ± 0.06 a	2.94 ± 0.07 a	2.93 ± 0.04 a	3.06 ± 0.05 a	3.00 ± 0.00 a	3.00 ± 0.00 a	3.00 ± 0.00 a	2.98 ± 0.06 a	3.02 ± 0.04 a	2.98 ± 0.05 a
	ns	3.10 ± 0.09 a	2.98 ± 0.06 a	2.91 ± 0.08 a	3.00 ± 0.00 a	2.87 ± 0.06 a	3.00 ± 0.00 a	3.00 ± 0.00 a	2.98 ± 0.06 a	2.90 ± 0.04 a	2.94 ± 0.04 a	3.00 ± 0.00 a	2.98 ± 0.03 a
	n+	2.91 ± 0.03 a	2.96 ± 0.07 a	3.01 ± 0.03 a	2.98 ± 0.01 a	3.00 ± 0.00 a	2.98 ± 0.07 a	2.82 ± 0.08 a	3.02 ± 0.05 a	3.00 ± 0.00 a	2.97 ± 0.05 a	2.91 ± 0.09 a	2.93 ± 0.07 a
Larvae	n0	19.59 ± 0.64 d	19.49 ± 0.37 d	21.80 ± 0.58 b	21.76 ± 0.26 b	24.21 ± 0.56 a	24.12 ± 0.35 a	23.90 ± 0.61 a	23.73 ± 0.42a	19.87 ± 0.63 d	19.72 ± 0.23 d	20.07 ± 0.67 d	20.12 ± 0.22 d
	n–	17.30 ± 0.52 f	17.11 ± 0.41 f	21.13 ± 0.33 b	21.23 ± 0.61 b	22.23 ± 0.43 ab	22.07 ± 0.31 ab	21.07 ± 0.33 b	20.97 ± 0.53b	17.83 ± 0.33 ef	17.90 ± 0.61 ef	20.05 ± 0.76 d	20.02 ± 0.45 d
	ns	17.70 ± 0.45 ef	17.62 ± 0.57 ef	21.03 ± 0.39 b	20.95 ± 0.52 bc	21.95 ± 0.55 ab	21.87 ± 0.63 ab	21.04 ± 0.39 b	20.91 ± 0.24b	16.04 ± 0.35 f	15.93 ± 0.47 f	19.00 ± 0.46 de	18.84 ± 0.31 de
	n+	17.08 ± 0.41 f	17.04 ± 0.22 f	19.30 ± 0.43 d	19.23 ± 0.38 d	20.97 ± 0.48 b	21.06 ± 0.58 b	18.97 ± 0.38 d	19.04 ± 0.66d	15.44 ± 0.36 fg	15.40 ± 0.53 fg	18.36 ± 0.57 de	18.45 ± 0.38 de
Pupa	n0	11.83 ± 0.31 c	11.80 ± 0.55 c	13.96 ± 0.35 a	13.88 ± 0.38 a	12.30 ± 0.42 b	12.16 ± 0.67 b	12.93 ± 0.32 ab	13.04 ± 0.59ab	12.05 ± 0.24 b	12.19 ± 0.47 b	11.80 ± 0.41 bc	11.77 ± 0.28 bc
	n–	11.92 ± 0.34 bc	11.97 ± 0.42 bc	12.21 ± 0.35 b	12.31 ± 0.51 b	12.14 ± 0.39 b	12.22 ± 0.51 b	13.27 ± 0.18 a	13.22 ± 0.42a	11.08 ± 0.26 ef	11.01 ± 0.36 ef	11.12 ± 0.46 e	11.15 ± 0.36 e
	ns	10.74 ± 0.30 f	10.69 ± 0.63 f	12.77 ± 0.37 b	12.51 ± 0.26 b	11.64 ± 0.91 c	11.53 ± 0.36 c	12.77 ± 0.33 b	12.63 ± 0.52b	10.51 ± 0.25 f	10.46 ± 0.55 f	11.09 ± 0.32 ef	11.06 ± 0.41 ef
	n+	10.29 ± 0.43 f	10.21 ± 0.46 f	11.93 ± 0.23 bc	11.89 ± 0.43 bc	11.56 ± 0.25 c	11.48 ± 0.33 c	12.73 ± 0.33 b	12.69 ± 0.35b	10.05 ± 0.21 f	10.13 ± 0.63 f	10.40 ± 0.34 f	10.22 ± 0.67 f
Total pre-adult	n0	34.42 ± 0.32 c	34.41 ± 0.51 c	38.47 ± 0.31 a	38.41 ± 0.55 a	39.24 ± 0.36 a	39.06 ± 0.62 a	39.15 ± 0.32 a	38.94 ± 0.42a	35.15 ± 0.24 c	35.03 ± 0.36 c	34.73 ± 0.31 cd	34.56 ± 0.44 cd
	n–	31.98 ± 0.35 ef	31.93 ± 0.44 ef	35.81 ± 0.34 c	36.02 ± 0.31 c	37.38 ± 0.37 a	37.35 ± 0.46 a	36.33 ± 0.23 b	36.14 ± 0.45b	31.77 ± 0.22 f	31.69 ± 0.37 f	34.45 ± 0.36 cd	34.29 ± 0.52 cd
	ns	31.62 ± 0.26 f	31.41 ± 0.32 f	35.93 ± 0.38 c	35.77 ± 0.35 c	36.89 ± 0.71 ab	36.77 ± 0.53 ab	35.91 ± 0.22 c	35.68 ± 0.34c	30.01 ± 0.21 f	29.91 ± 0.31 f	32.31 ± 0.26 de	32.09 ± 0.33 de
	n+	30.25 ± 0.39 f	30.11 ± 0.63 f	34.06 ± 0.23 c	33.96 ± 0.43 c	35.51 ± 0.35 c	35.43 ± 0.31 c	34.65 ± 0.35 cd	34.52 ± 0.61cd	29.13 ± 0.15 f	29.10 ± 0.45 f	32.13 ± 0.37 de	32.05 ± 0.41 de

(n0) – no fertilization; (n+) – standard fertilization plus 30%; (ns) – standard fertilization; (n–) – standard fertilization minus 30%; the means followed by different letters in rows and columns (for every stages) are significantly different (p <0.05)

Table 3. The means (±SE) of adult's longevity and fecundity of *Helicoverpa armigera* reared on six tomato cultivars with four nitrogen levels

Parameter	N level	Cultivars					
		Kingston (K)	Riogrand (RG)	Earlyurbana (E)	Redston (R)	Superstrain-B (SB)	Primoearly (P)
Female longevity	n0	10.20 ± 0.35 d	11.81 ± 0.24 b	10.08 ± 0.44 d	11.23 ± 0.32 c	10.65 ± 0.44 c	9.04 ± 0.260 d
	n–	10.42 ± 0.24 cd	12.08 ± 0.24 b	10.59 ± 0.37 c	11.83 ± 0.30 b	11.05 ± 0.33 c	9.20 ± 0.210 d
	ns	11.50 ± 0.330 b	12.33 ± 0.32 ab	10.65 ± 0.42 c	13.12 ± 0.34 a	11.22 ± 0.25 c	10.44 ± 0.19 c
	n+	11.60 ± 0.230 b	12.88 ± 0.390 a	11.25 ± 0.35 c	13.93 ± 0.35 a	11.74 ± 0.29 b	10.53 ± 0.27 c
Male longevity	n0	13.12 ± 0.26 a	12.47 ± 0.50 a	12.10 ± 0.56 b	10.13 ± 0.43 cd	12.05 ± 0.31 b	10.83 ± 0.31 c
	n–	13.27 ± 0.48 a	12.73 ± 0.50 a	12.51 ± 0.24 a	10.26 ± 0.22 cd	13.22 ± 0.33 a	11.44 ± 0.28 c
	ns	13.35 ± 0.22 a	12.61 ± 0.33 a	12.56 ± 0.26 a	10.72 ± 0.340 c	13.09 ± 0.31 a	11.95 ± 0.20 b
	n+	13.58 ± 0.28 a	13.33 ± 0.55 a	12.70 ± 0.33 a	11.33 ± 0.220 c	13.24 ± 0.41 a	12.32 ± 0.52 b
Fecundity (offspring)	n0	248.0 ± 16.6 c	240.2 ± 28.61 c	212.4 ± 17.71 d	228 ± 28.96 cd	254 ± 17.6 bc	243.1 ± 20.4 c
	n–	277.2 ± 13.7 b	263.6 ± 15.21 b	229.1 ± 16.8 cd	242.6 ± 26.81 c	272 ± 13.31 b	256 ± 13.9 bc
	ns	281.1 ± 10.3 ab	261.7 ± 22.01 b	241.4 ± 39.31 c	261.3 ± 25.33 b	286 ± 12.2 ab	269 ± 38.31 b
	n+	315.3 ± 10.4 a	268.8 ± 24.33 b	253.2 ± 26.1 bc	257.5 ± 24.4 bc	302 ± 12.31 a	288 ± 26.6 ab

The means followed by different letters in rows and columns (for every parameter) are significantly different ($p < 0.05$); (n0) – no fertilization; (n+) – standard fertilization plus 30%; (ns) – standard fertilization; (n–) – standard fertilization minus 30%

Table 4. Age-stage and life-table parameters of *Helicoverpa armigera* reared on six tomato cultivars with four nitrogen levels

Parameter	N level	Cultivars					
		Kingston (K)	Riogrand (RG)	Earlyurbana (E)	Redston (R)	Superstrain-B (SB)	Primoearly (P)
R_0 (offspring/individual)	n0	47.4 ± 11.1 Ab	45.02 ± 3.60 Ba	36.37 ± 7.09 Db	35.7 ± 7.06 Db	49.44 ± 10.2 Abc	39.91 ± 7.90 Cc
	n–	50.9 ± 13.6 Aab	47.03 ± 5.30 Ba	39.6 ± 7.04 Cb	37.0 ± 9.55 Cb	51.0 ± 31.07 Ab	47.04 ± 11.6 Bb
	ns	52.0 ± 7.21 Aa	47.01 ± 7.90 Ba	38.0 ± 7.30 Cb	40.2 ± 11.7 Ca	53.9 ± 14.050 Ab	47.9 ± 19.03 Bb
	n+	54.90 ± 7.60 Ba	49.00 ± 8.9 Ca	43.0 ± 11.30 Da	41.6 ± 14.02 Da	62.16 ± 18.91 Aa	50.1 ± 16.30 Ca
T (day)	n0	40.25 ± 0.046 Ca	43.10 ± 0.05 Ba	44.70 ± 0.030 Aa	44.83 ± 0.0171 Aa	40.30 ± 0.022 Ca	40.02 ± 0.053 Ca
	n–	35.51 ± 0.043 Dc	40.91 ± 0.03 Cb	43.80 ± 0.021 Ab	42.10 ± 0.024 Bb	35.60 ± 0.030 Db	39.8 ± 0.062 Ca
	ns	37.21 ± 0.041 Cb	40.4 ± 0.034 Bb	42.21 ± 0.05 Ac	40.90 ± 0.0211 Bc	33.2 ± 0.0301 Dce	36.00 ± 0.04 Cb
	n+	33.79 ± 0.040 Dd	39.32 ± 0.042 Bc	41.5 ± 0.035 Ad	39.70 ± 0.032 Bd	32.01 ± 0.0210 Dd	35.7 ± 0.03 Cbc
r (day^{-1})	n0	0.0959 ± 0.006 Ad	0.0961 ± 0.005 Abc	0.0727 ± 0.0063 Bb	0.0712 ± 0.006 Bb	0.0918 ± 0.006 Ad	0.0842 ± 0.0074 Bc
	n–	0.1181 ± 0.005 Ac	0.1024 ± 0.006 Bb	0.0782 ± 0.0061 Cb	0.0846 ± 0.006 Cb	0.1127 ± 0.006 Ac	0.1013 ± 0.0050 Bb
	ns	0.1255 ± 0.005 Ab	0.1105 ± 0.005 Ba	0.0889 ± 0.006 Cab	0.0949 ± 0.055 Cab	0.1293 ± 0.006 Ab	0.1191 ± 0.006A Ba
	n+	0.1372 ± 0.005 Ba	0.1147 ± 0.005 Da	0.0955 ± 0.0052 EFa	0.1058 ± 0.0065 Ea	0.1507 ± 0.0051 Aa	0.1212 ± 0.0032 Ca
λ (day^{-1})	n0	1.0990 ± 0.0063 Bd	1.1110 ± 0.0061 Ab	1.0771 ± 0.0072 Cc	1.0732 ± 0.0064 Cc	1.0962 ± 0.007 Bd	1.0822 ± 0.007 Cd
	n–	1.1211 ± 0.0052 Ac	1.1067 ± 0.0064 Ccb	1.0768 ± 0.0074 Dc	1.0812 ± 0.0070 Db	1.1137 ± 0.0061 Bc	1.1046 ± 0.0065 Cc
	ns	1.1351 ± 0.005 Ab	1.1117 ± 0.0055 Bb	1.1024 ± 0.007 Cb	1.1082 ± 0.005 Cab	1.1343 ± 0.006 Ab	1.1123 ± 0.0068 Bb
	n+	1.1442 ± 0.0065 Ba	1.1263 ± 0.0062 Ca	1.1171 ± 0.006 Da	1.1001 ± 0.007 Eab	1.1629 ± 0.0062 Aa	1.1258 ± 0.007 Ca

R_0 – net reproductive rate; T – mean generation time; r – intrinsic rate of increase; λ – finite rate of increase; the SEs were estimated using paired bootstrap test (comparison of 95% CI); for each parameter, different small letters in the columns, and different capital letters in the rows refer to the significant differences ($p < 0.05$); (n0) – no fertilization; (n+) – standard fertilization plus 30%; (ns) – standard fertilization; (n–) – standard fertilization minus 30%

Discussion

Numerous factors influence host suitability, such as the nutrient content and secondary metabolites of the host plant. Understanding the exact cause of differences between host plants that impact development and mortality of each stage, adult fecundity and survival rate remain crucial for host-plant trophic interactions and definitely deserve further examination (Liu *et al.* 2004). Smith (2005) emphasized the relevance of exploiting insect biological parameters (e.g., r) in studying herbivore-host plant interactions. On the other hand, a rapid and exact method of comparing

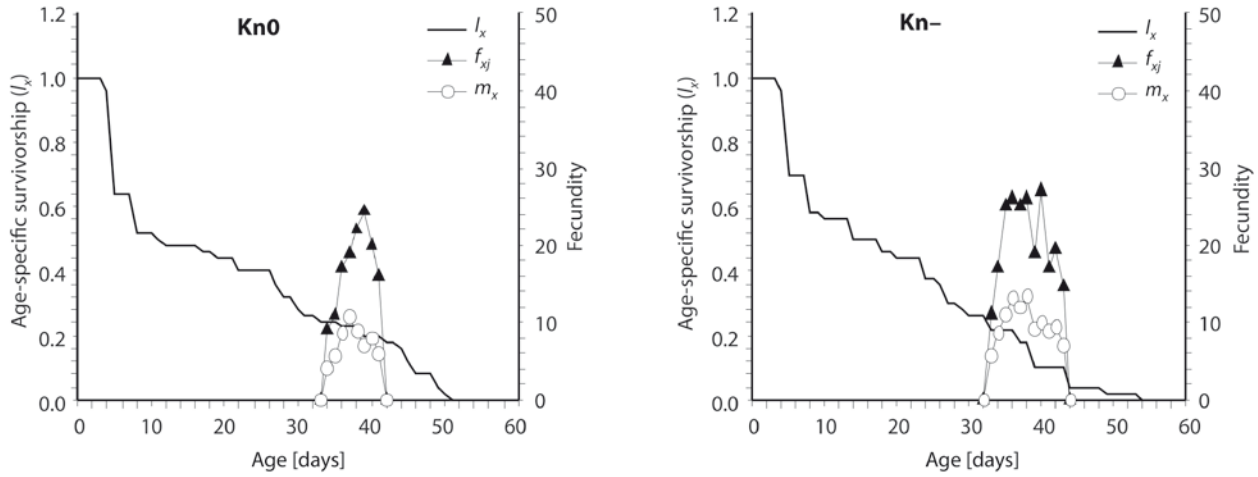

Fig. 1. Age-specific survivorship (l_x), age-stage specific fecundity (f_{xj}) and age-specific fecundity (m_x) of *Helicoverpa armigera* on Kingston cultivar (K) with zero (n0) and standard minus 30% (n–) nitrogen levels

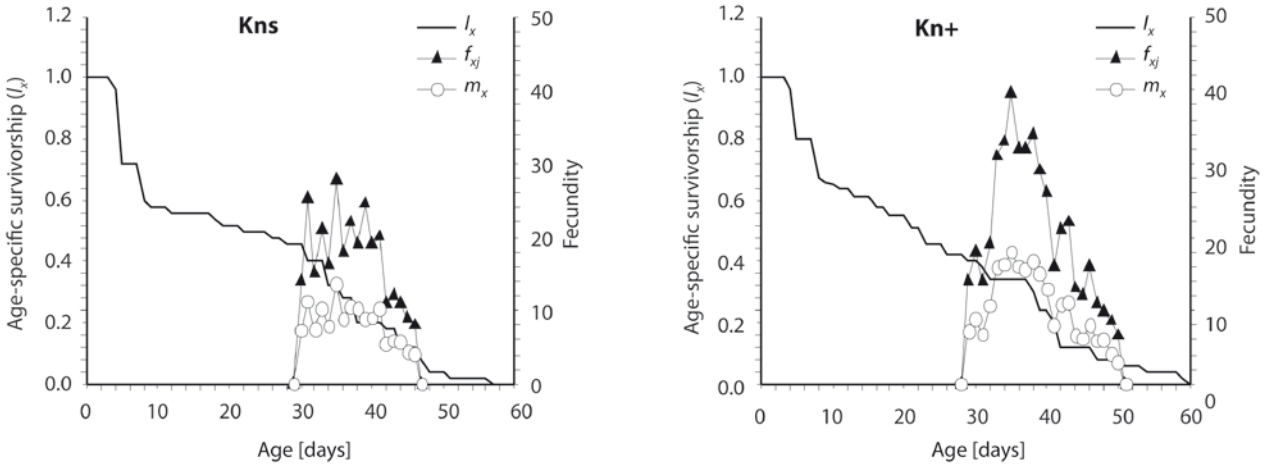

Fig. 2. Age-specific survivorship (l_x), age-stage specific fecundity (f_{xj}) and age-specific fecundity (m_x) of *Helicoverpa armigera* on Kingston cultivar (K) with standard (ns) and standard plus 30% (n+) nitrogen levels

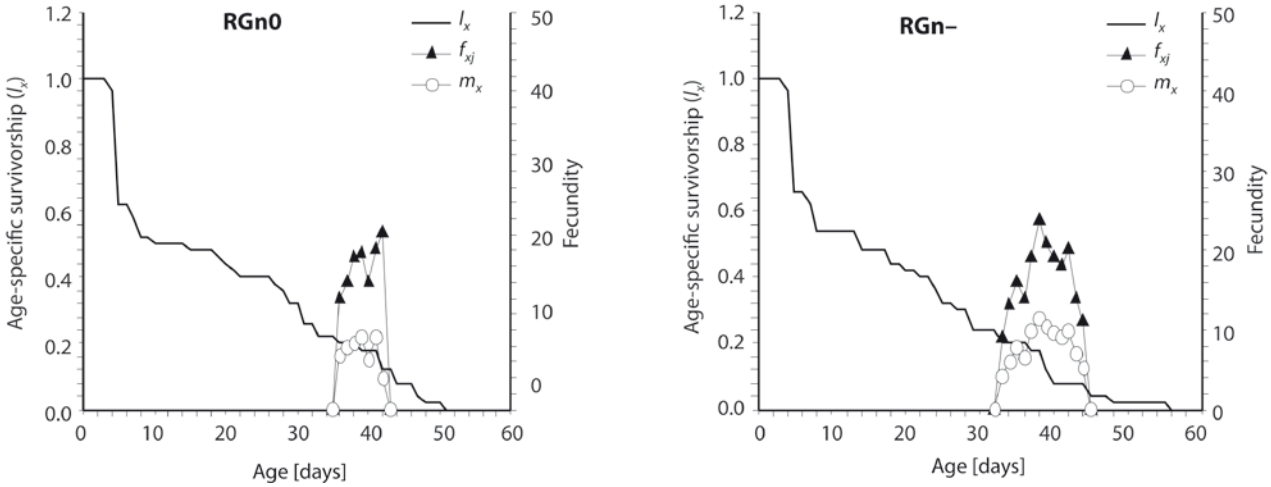

Fig. 3. Age-specific survivorship (l_x), age-stage specific fecundity (f_{xj}) and age-specific fecundity (m_x) of *Helicoverpa armigera* on Riogrand cultivar (RG) with zero (n0) and standard minus 30% (n–) nitrogen levels

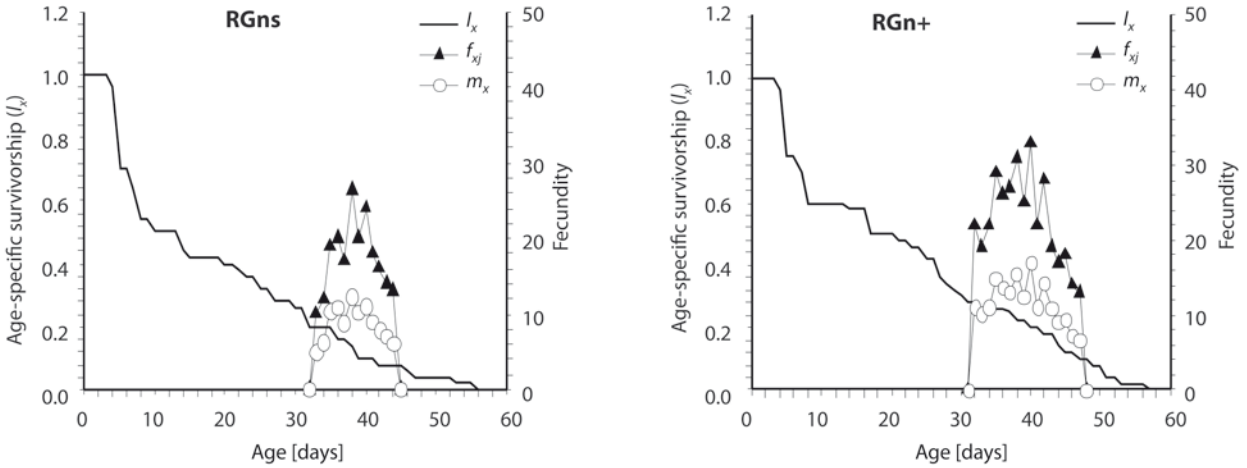

Fig. 4. Age-specific survivorship (l_x), age-stage specific fecundity (f_{xj}) and age-specific fecundity (m_x) of *Helicoverpa armigera* on Riogrand cultivar (RG) with standard (ns) and standard plus 30% (n+) nitrogen levels

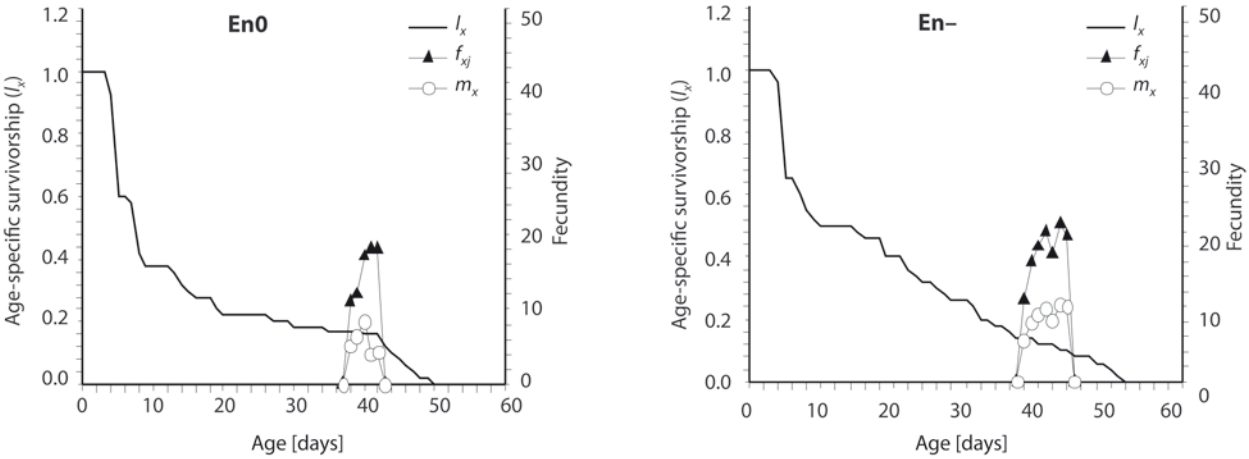

Fig. 5. Age-specific survivorship (l_x), age-stage specific fecundity (f_{xj}) and age-specific fecundity (m_x) of *Helicoverpa armigera* on Earlyurbana cultivar (E) with zero (n0) and standard minus 30% (n–) nitrogen levels

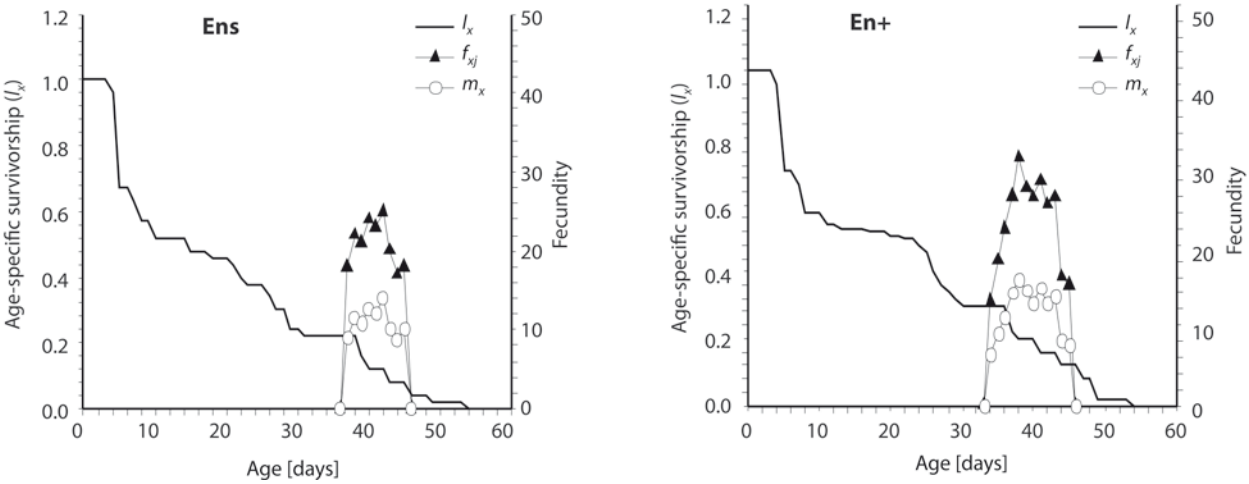

Fig. 6. Age-specific survivorship (l_x), age-stage specific fecundity (f_{xj}) and age-specific fecundity (m_x) of *Helicoverpa armigera* on Earlyurbana (E) cultivar with standard (ns) and standard plus 30% (n+) nitrogen levels

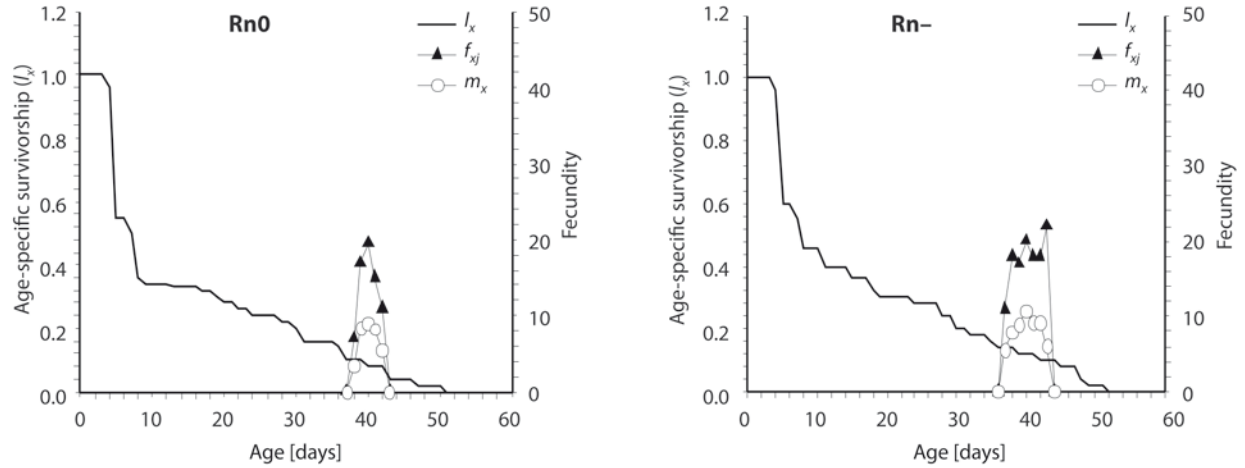

Fig. 7. Age-specific survivorship (l_x), age-stage specific fecundity (f_{xj}) and age-specific fecundity (m_x) of *Helicoverpa armigera* on Redston cultivar (R) with zero (n0) and standard minus 30% (n–) nitrogen levels

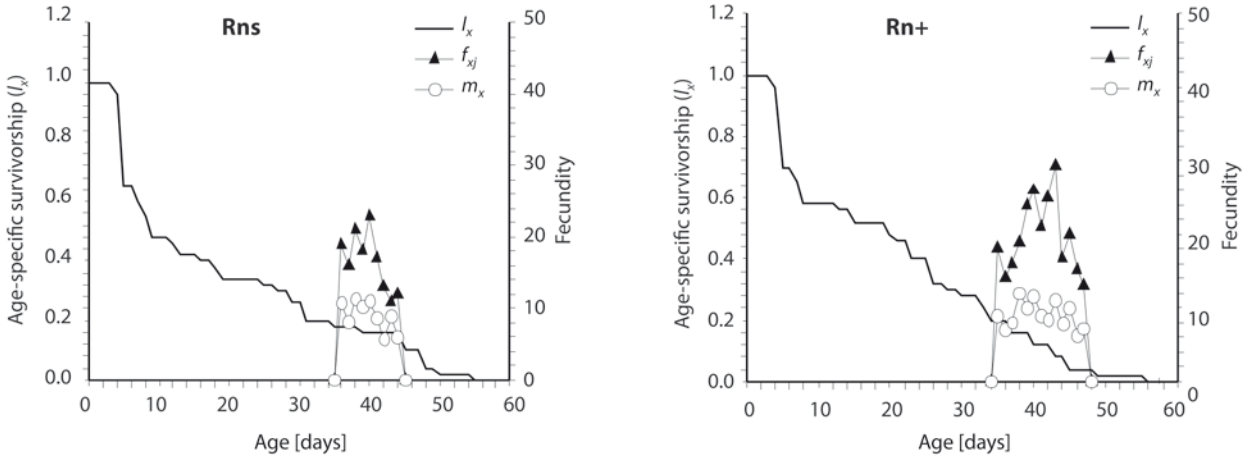

Fig. 8. Age-specific survivorship (l_x), age-stage specific fecundity (f_{xj}) and age-specific fecundity (m_x) of *Helicoverpa armigera* on Redston cultivar (R) with standard (ns) and standard plus 30% (n+) nitrogen levels

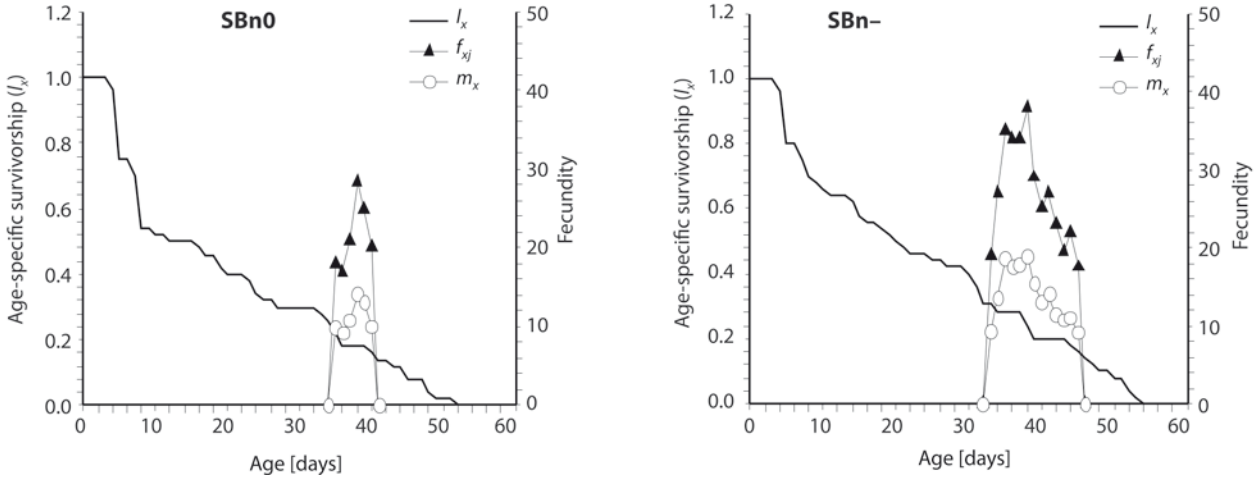

Fig. 9. Age-specific survivorship (l_x), age-stage specific fecundity (f_{xj}) and age-specific fecundity (m_x) of *Helicoverpa armigera* on Superstrain-B cultivar (SB) with zero (n0) and standard minus 30% (n–) nitrogen levels

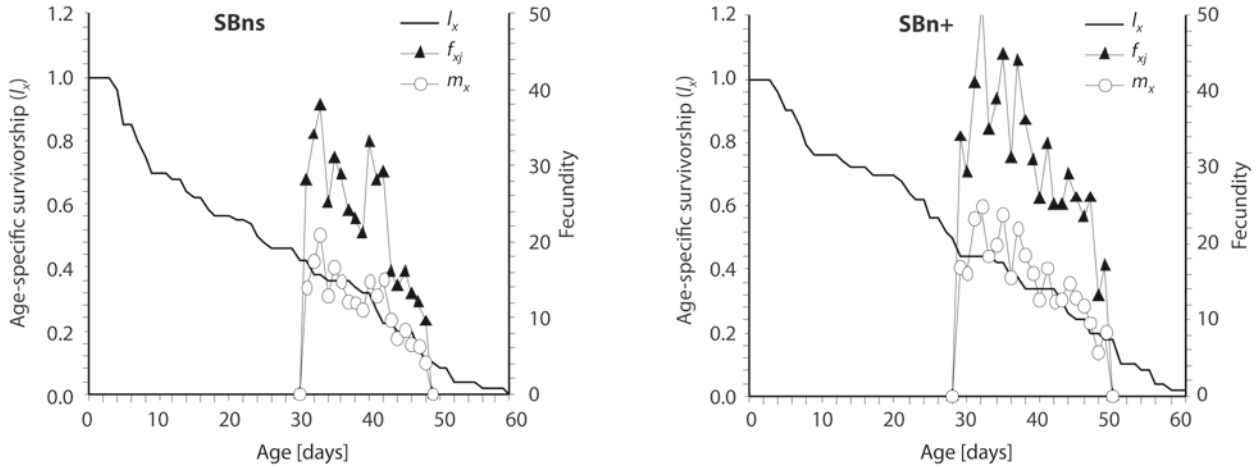

Fig. 10. Age-specific survivorship (l_x), age-stage specific fecundity (f_{xj}) and age-specific fecundity (m_x) of *Helicoverpa armigera* on Superstrain-B cultivar (SB) with standard (ns) and standard plus 30% (n+) nitrogen levels

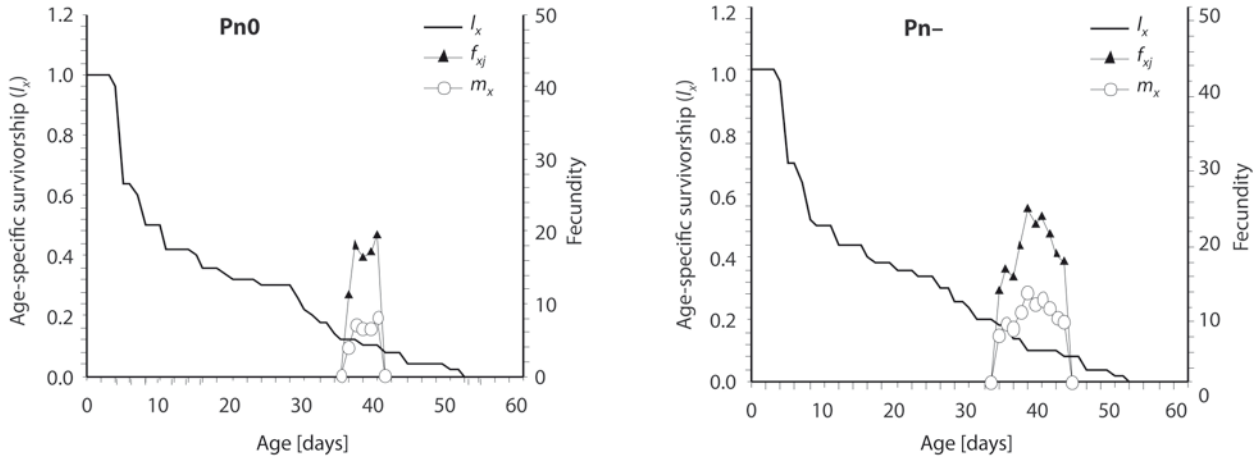

Fig. 11. Age-specific survivorship (l_x), age-stage specific fecundity (f_{xj}) and age-specific fecundity (m_x) of *Helicoverpa armigera* on Primoearly cultivar (P) with zero (n0) and standard minus 30% nitrogen levels

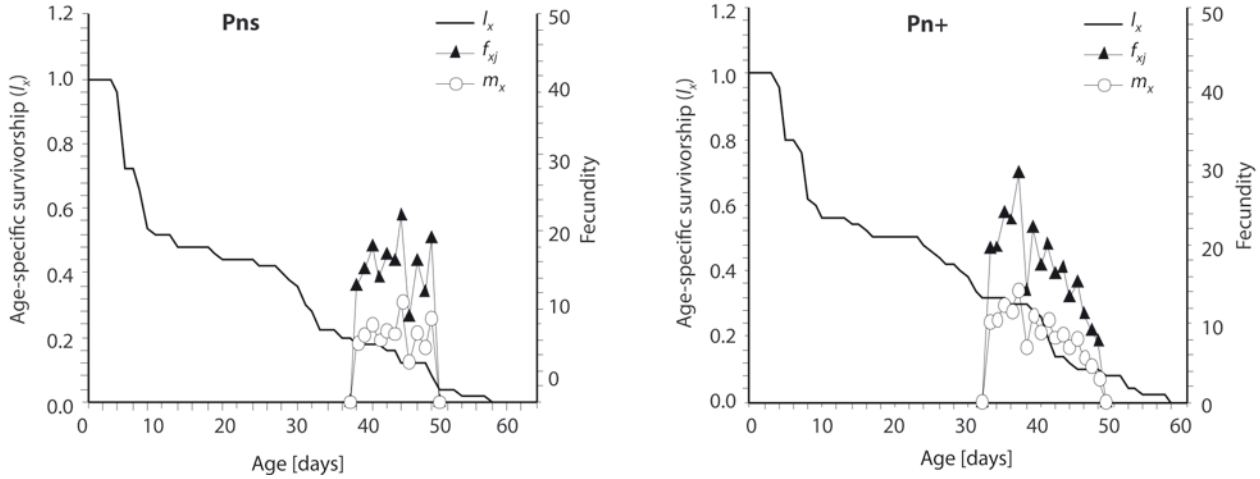

Fig. 12. Age-specific survivorship (l_x), age-stage specific fecundity (f_{xj}) and age-specific fecundity (m_x) of *Helicoverpa armigera* on Primoearly cultivar (P) with standard (ns) and standard plus 30% (n+) nitrogen levels

the effect of host plants on the life history of herbivores is a demographic approach (Chi 1988; Akköprü *et al.* 2015; Reddy and Chi 2015; Tuan *et al.* 2016; Atlihan *et al.* 2017; Wang *et al.* 2017; Liu *et al.* 2017).

Demographic parameters of *H. armigera* have previously been studied on different host plants (Liu *et al.* 2004; Jha *et al.* 2014), yet there has been limited research about the interactions between the nutritional condition of a host plant on the life history of phytophagous insects. Based on the findings of the present research, egg incubation was not affected by cultivars and nitrogen content which is in agreement with Liu *et al.* (2004). However, Gomes *et al.* (2017) reported an incubation period of 3.38 and 4.38 days on cotton and wheat, respectively. Various factors have been identified that influence the incubation period in insects such as geographic variation, photoperiod, temperature as the main factor (degree-days) (Chuche and Thiery 2012), voltinism (Gillooly *et al.* 2002) and dynamic energy budget (DEB) of an egg (Maino *et al.* 2017).

Considering the larval stage development as the most deleterious stage of the pest, Liu *et al.* (2004) reported a larval period of 25.4 ± 0.62 days for *H. armigera* on tomato cultivars which contained standard nitrogen. This is in partial agreement with the present findings in cultivars with zero nitrogen regimes (e.g., E cultivar). Also, different developmental times of *H. armigera* on various host plants were reported (Naseri *et al.* 2014; Truzi *et al.* 2017) which were similar to the results of the present study of some treatments. Compared to other research, the main advantage of this study was providing segregated information for the growth and development of immature female and male insects. Apparently, significant differences were observed between larval durations on cultivars and nitrogen concentrations, while the male and female larvae on the same cultivars showed similar longevity (Table 3). Partially, the variability in the pattern of insect growth and development has been related to the degree of herbivore response to nitrogen variation which in turn depended on specific herbivore-plant interactions (Chen *et al.* 2010). For example, the larval period of *Spodoptera exigua* reared on cotton plants fertilized with 42 ppm nitrogen concentration was significantly longer than that of 196 ppm nitrogen concentration (Chen *et al.* 2008). Similarly, cabbage cultivars, with or without nitrogen, significantly decreased and altered the larval period and growth rate of *Pieris rapae crucivora* (Yu-Tzu *et al.* 2009). Actually, the longer larval development time may increase pest susceptibility to biological control agents by increasing their exposure time and the learning ability of the predators, and thereby, increasing mortality as well as postponing potentially superior deleterious generations (Price 1980). However, slower larval development rate on low nitrogen tomatoes may be due to both increased plant defense and lower nutritive value (Coqueret *et al.* 2017). The lepidopteran larvae which fed on highly-nutritious host plants, demonstrated increased growth rates and developed faster than those which fed on low-nutrient plants (Hwang *et al.* 2008).

In this study, the immature stage or pre-adult duration of *H. armigera* on tomato cultivars with different nitrogen levels showed very clear variation (Fig. 13). Furthermore, the female and male insects on the same cultivar showed similar growth time, nevertheless, significant differences (~29 *vs* ~39 days) were observed between some treatments of different cultivars. On each cultivar the insect developmental time decreased with increasing nitrogen concentration. A similar response was also mentioned by Razmjou *et al.* (2014).

The current study reports that adult longevity of *H. armigera*, was influenced by different treatments which agrees with Liu *et al.* (2004), Kulkarni (2004), Jha *et al.* (2012), Gharekhani and Salek-Ebrahimi (2014b) and Atlihan *et al.* (2017). Furthermore, male longevity in all treatments except the R cultivar was commonly higher than that of females which was previously described by Liu *et al.* (2004) in rearing the pest on six host plants including tomato. However, Gomes *et al.* (2017) reported longer female longevity than male on four crops with an artificial diet under 25 ± 1°C, 70 ± 10% RH and 14 : 8 h (L : D) conditions.

Although nitrogen compounds are nutritious for phytophagous insects and positively influence their longevity and fertility, the energy used to keep eggs and reproduction reduces the life span of females more than males (Harwood *et al.* 2014). However, this effect was not independent of the host plant, and in Riogrand and Earlyurbun cultivars, the effect of fertilizer was weaker than the others; although male and female lifestyles were almost identical, the fecundity at different nitrogen levels was not significantly different.

Results also revealed that the total fecundity of *H. armigera* was significantly different with treatments. The fecundity values in the present study were in partial accordance with the results of Liu *et al.* (2004) and Fathipour and Naseri (2011) for this pest on tobacco and soybean cultivars with different levels of nitrogen. Nevertheless, great variations were reported between fecundity values (Jha *et al.* 2012; Fallahnejad-Mojarrad *et al.* 2017). Jallow and Matsumura (2001) counted an average of two fold of the highest fecundity which was observed in the present research.

Similar studies were performed on the effects of plants and macronutrients on fecundity of similar insects. For instance, the fecundity of *S. exigua* on nitrogen fertilized cotton plants was increased (Chen *et al.* 2008).

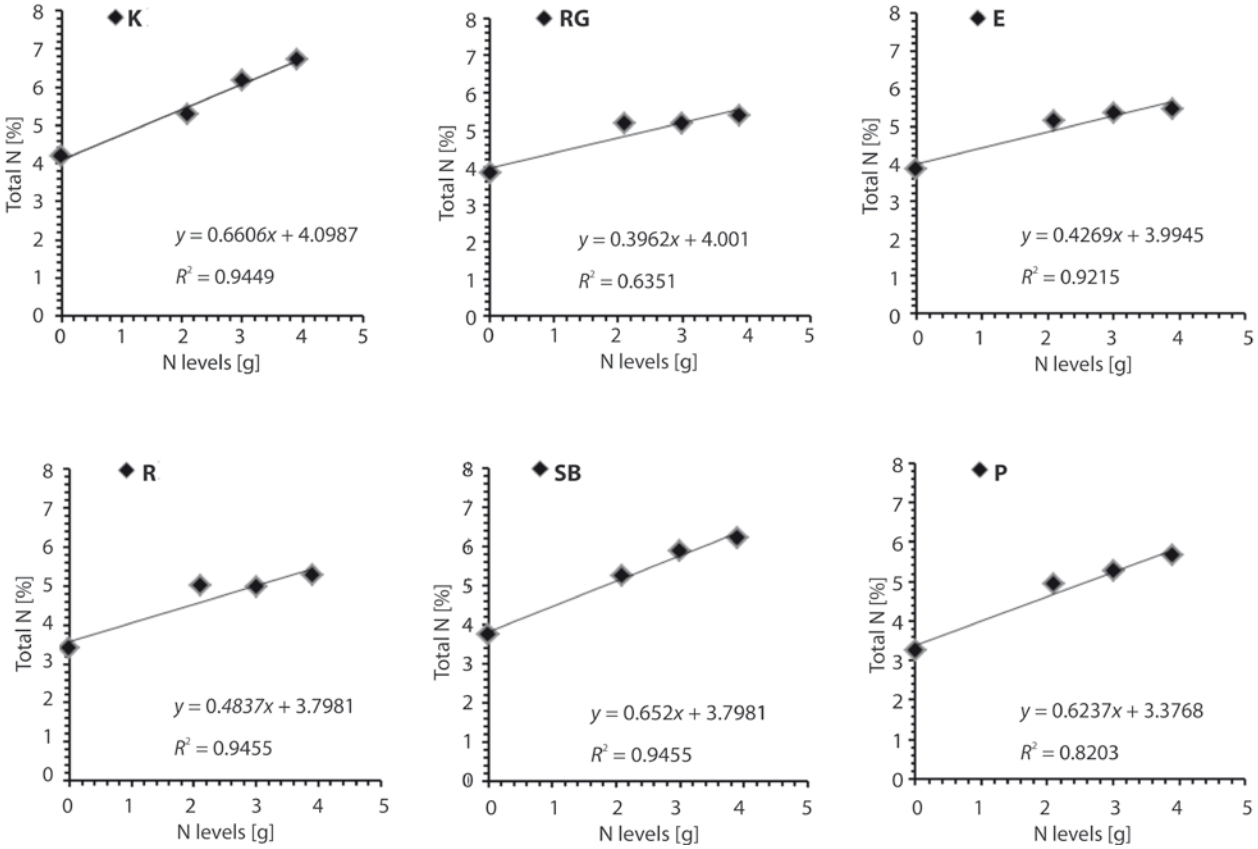

Fig. 13. Interaction of the total nitrogen (N) on six tomato cultivars with four nitrogen levels. K = Kingston, RG = Riogrand, E = Earlyurbana, R = Redston, SB = Superstrain-B, P = Primoearly

Similarly, Chu and Horng (1994) previously confirmed the effect of nitrogen fertilizer on the fecundity of *Ostrinia furnacalis*. Undoubtedly, lower nutritional quality of the host plant causes lower efficiency of food conversion and consequently lower fecundity (Awmack and Leather 2002; Chen *et al.* 2004). In the current study, the pattern of *H. armigera* fecundity on nearly all cultivars increased as nitrogen doses elevated.

Another important demographic parameter is the net reproductive rate (R_0) which varied significantly with different treatments and showed the same trend for fecundity in the present study (see Eq. 2). Nitrogen content may alter phenolic compounds which are secondary metabolites involved in a plant's innate chemical defense against pests. Low nitrogen increased the concentrations of the phenolic compounds in all organs, while higher nitrogen reduced soluble phenolics such as rutin and chlorogenic acid (Larbat *et al.* 2012), hence contributing to increased reproductive performance.

Jha *et al.* (2012) reported a higher R_0 for *H. armigera* fed an artificial diet and hybrid sweet corn than the present study. Host plant species influenced the R_0 variably, for example, R_0 ranged from 5.1 on hot pepper to 117.6 offspring on cotton (Liu *et al.* 2004) and 111.1 to 1422 offspring on tomato and chickpea, respectively (Razmjou *et al.* 2014). In addition, low R_0 values (62.9 to 255.9 offspring) were noted on sunflower genotypes (Truzi *et al.* 2017). Some possible reasons for such disagreements are physiological differences in host plants (quantity/quality of nutrients), genetic variations and differences in geographic populations of the pest and the data analyzing methods.

Regarding the relationship between the life table parameters, changing some parameters also affects other parameters. The intrinsic rate of increase (r) linearly increased by enhancement in the nitrogen concentration, but its value was not same among the treatments. Actually, lower r value is mainly due to the lower fecundity and longer total pre-oviposition period (TPOP). Also, a higher value of r demonstrates the host plant susceptibility to insect feeding. With respect to the relationship between r and finite rate of increase (λ), the same trend of the dissimilarities is expected in the insects feeding on different treatments. Similar results of the finite rate of increase were also noticed on bean cultivar (1.153 ± 0.001), which were nearly in agreement with the present results (Naseri *et al.* 2014). Furthermore, the finite rate of increase for *H. armigera* on hybrid sweet corn and artificial diet (Jha *et al.* 2012) was also similar to some results of this research. Undoubtedly, both r and λ are strongly influenced by survival and fecundity of an insect (Jha

et al. 2012). Consequently the generation time (*T*) was also influenced by the treatments and *T* values in the highest nitrogen levels of the present study were similar to the results of Razmjou *et al*. (2014) on cowpea and the results of lowest nitrogen treatments were in agreement with Jha *et al.* (2012).

Plant-defensive allelechemicals are decreased by nitrogen accumulation (Hemming and Lindroth 2003; Prudic *et al*. 2005; Goetz *et al*. 2012; Bosch *et al*. 2014; Moreira *et al*. 2018). Thereby, some elements of host plants are possible reasons for changes in plant defensive capacity. "Nitrate-responsive cis-element activation is induced by both low and high concentrations of nitrate, although high concentrations of nitrate cause much stronger responses" (Konishi and Yanagisawa 2013).

Amin *et al.* (2016) screened a number of tomato cultivars against *H. armigera* by measuring their leaf thickness, trichome density, rind thickness and nitrogen content; such morphological characteristics along with biochemical contents like starch, protein, amino acid and phenol affected mating and oviposition behavior, foraging, feeding, growth and development, as well as population dynamics of herbivore insects. Tan *et al.* (2012) hypothesized that *H. armigera* female moths broadly oviposited on tomato leaves with various fertilization histories; nevertheless, larval growth and development were different on them.

In conclusion, the present study reported that tested tomato cultivars differed significantly in their responses to female and male of *H. armigera* feeding. The changes in nitrogen content of the plant affected almost all life-table parameters of the pest which also depended on the tomato cultivar. Finally, it may be concluded that Kingstone and Superstrain-B cultivars with the highest nitrogen regime were the most susceptible hosts and Earlyurbana and Riogrand cultivars with standard and standard minus 30% were the most resistant host plants for *H. armigera*. Therefore, Earlyurbana and Riogrand could be integrated with biological control agents. More information is needed in making management decisions about this pest. Furthermore future studies are needed to evaluate the impact of genotype and nitrogen interactions on tomato and its pests.

Acknowledgements

The authors are thankful to the University of Maragheh for partial financial support and the Iranian Research Institute of Plant Protection (Tehran) for providing the facilities and equipment. Also, Mr. Kamyab Farzi, Biorun Company (Karaj) is greatly appreciated for providing *H. armigera* stock colony.

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