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Tri-trophic interactions among nitrogen-fertilized tomato cultivars, the tomato fruit worm, *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae) and the ectoparasitoid, *Habrobracon hebetor* (Say) (Hymenoptera: Braconidae)

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Abstract

Nitrogen is one of the most critical elements for plant and herbivore growth. This research aimed to investigate the bottom-up effect of varying nitrogen fertilization on the demography of the ectoparasitoid, *Habrobracon hebetor* (Say) on the tomato fruit worm, *Helicoverpa armigera* (Hübner) reared under different host-plant treatments. Six tomato plant cultivars (e.g., Kingston, Riogrand, Earlyurbana, Redston, Superstrain-B, and Primoearly) and 4 N-fertilization levels (0, 2.1, 3.0, 3.9 g/pot nitrogen as urea 46%) were tested, using 5th instar larvae of *H. armigera* parasitised by *H. hebetor* under laboratory conditions. The mortality rate and developmental time of the immature stages of the parasitoid, as well as adult longevity and fecundity, were recorded. Data were analyzed based on age-stage two-sex life-table theory. The results showed that the developmental duration of the parasitoids was affected by the increase in the levels of nitrogen. The highest value was observed at 12.83 ± 0.11 days on Earlyurbana with the lowest nitrogen level. The lowest intrinsic rates of increase (r) and finite rates of increase (λ) were 0.1058 ± 0.0147 and $1.1013 \pm 0.0157 \text{ day}^{-1}$, respectively, regarding the lowest (zero) level of added fertilizer. However, the highest rates were 0.1515 ± 0.018 and $1.1608 \pm 0.013 \text{ day}^{-1}$, respectively. The fecundity and longevity of adult wasps were positively correlated with nitrogen levels. Accordingly, differences in host-plant quality can indirectly affect the performance of parasitoids via the herbivore.

Keywords: Tri-trophic interactions, Tomato cultivars, *Helicoverpa armigera*, *Habrobracon hebetor*, Two-sex life-table, Bottom-up effect

Background

Tri-trophic interactions have been detected in many systems involving host plants, herbivores, and parasitic wasps (Havill and Raffa 2000). As predicted by the tri-trophic interaction hypothesis, compared with specialist herbivores, the generalist herbivores show higher sensitivity to the quality of host plant. Therefore, it is expected that when the generalist host/prey feeds on

plants with low quality, the following effects on natural enemies be more significant (Mooney et al. 2012).

Bottom-up cascades are one of the most frequently reported cases in different tri-trophic systems, and their importance is in specifying the structure of the community, population dynamics, and individual performance of higher trophic levels (Karimzadeh and Wright 2008; Winter and Rostas 2010). The functioning of insect herbivores and their natural enemies is greatly increased by nutritional plants (Kagata and Ohgushi 2006). Nutritional quality of plant-derived materials, reserved in the hemolymph or the herbivore's body tissues, can

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influence the interactions between herbivorous insects and their parasitoids (Gols and Harvey 2009). Studies have also demonstrated the impact of varying degrees of plant nitrogen on the growth and development of herbivores (White 1984); moreover, nitrogen inputs to the plant generally enhance parasitism success (Aqueel et al. 2015).

It is highly important to investigate the demographic characteristics of natural enemies so as to enhance their efficacy (Cobbold et al. 2009). Life tables are indispensable tools for the assessment of a parasitoid against a host in different conditions (Bastami et al. 2011). The parasitoids' life-history traits are directly dependent upon host quality and indirectly on the host-plant quality (Schadler et al. 2010). One of the main tasks for pest management is gathering life-table data for the relevant species with different trophic levels in the food chain (Gabre et al. 2005). Furthermore, important life table parameters such as mean generation time (T) and intrinsic rate of increase (r) may be indicators of the nutritional quality of the host (Wittmeyer and Coudronj 2001).

Habrobracon hebetor (Say) (Hymenoptera: Braconidae) is a global and gregarious ectoparasitoid, attacking the larval stage of various species of Lepidoptera (Chen et al. 2013). The high rate of reproduction and short generation time of *H. hebetor* are characteristics that make it a great possible biological control agent for lepidopteran pests. The life-table parameters make it possible to represent a comprehensive description of the life history, hence conducive to the prediction of population size (Southwood and Henderson 2000). Different hosts' impacts on age-specific female life-table parameters of *H. hebetor* have been investigated (Farag et al. 2015). Due to the overlapping stages, and the fact that the main piece of parasitism rate produces male offspring, the use of the female age-specific life-table method is not currently recommended (Yu et al. 2005). In contrast, the use of an age-stage two-sex life table can appropriately contain the male population as well as stage difference in analyses that are conducted for the predation rate and the life table. Several researchers have studied the demographic characteristics of *H. hebetor* on different hosts, using this approach (Amir-Maafi and Chi 2006). The (host plant nutrition-herbivore-parasitoid) experiment, using the life-table method evaluates the tri-trophic interactions. In a previous study, Salehi et al. (2017) reported the effect of host-plant variety and nitrogen fertilization on the life history of tomato fruit worm, *Helicoverpa armigera* (Hübner).

The present research reports the effect of different levels of fertilizer on the demography of parasitoid wasps in tri-trophic interactions, predicting the difference in the quality of the host plant belonging to different cultivars and soil nitrogen levels affect parasitoid

development. The objective was to determine the bottom-up effects of host-plant quality on a parasitoid's life-history parameters.

Materials and methods

Tomato plants

The seeds of six tomato cultivars including Kingston, Riogrand, Earlyurbana, Redston, superstrain-B, and Primoearly were obtained from Seed and Plant Improvement Institute (SPII), Karaj, Iran. The named cultivars are commonly cultured in Iran with 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, photoperiod of 16:8 (L:D) h) conditions 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 the soil that previously analyzed (Khak Azma Negin. co) for major nutrients at the four leaf stage (Table 1). They were only irrigated by 250 ml of tap water at 2 days interval 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 including 0, 2.1, 3.0, 3.9 g pot⁻¹ were prepared 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 2). The chemigation system comprised of ordinary 500 ml plastic drink bottles containing water/N solution, which was hooked at 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. The leaves of each treatment were sampled at the age of 55 to 60 days. An oven at a temperature of 80 °C was used for drying for 72 h, and then they were ground and sieved for analysis. The standard method of Kjeldahl analysis was used for determining leaf nitrogen concentration (LNC) (Bremner and Mulvaney 1982).

Pest rearing

The first colony was established using the eggs of *H. armigera* from a stock maintained at BCRD, IRIPP. The stock colony was reared on an artificial diet based on Teakle (1991) method and maintained in a growth chamber (noorsanattajhiz plus German JUMO) under 25 ± 1 °C, 60 ± 5% RH and 16:8 (L:D) h conditions. Subcolonies were made up of 24 colonies from the original one. Each subcolony was transferred to one treatment (6

Table 1 Soil test

N	NH3	OC ^a	Sand	Silt	Clay	K	B	Cu	Zn	Fe	P	EC ^b	pH
Test	Kjeldahl	Titration	Hydrometer	Hydrometer	Hydrometer	Flame Photometer ^f	Azomethine H ^g	Atomic	Atomic	Atomic ^d	Olsen ^e	Conductometer	pH meter
Normal	0.2<	1.5<	40–50	30–40	20–30	250	2	2	3	12	15	2>	6.5–7.5
Sample	0.04	5.4	88	6	6	108.4	1.84	1.16	12.09	7.24	20	4.83	6.85

^aOC organic carbon, ^bEC soil electrical conductivity, ^cOlsen soil P test method, ^dAtomic atomic absorption spectroscopy, ^eAzomethine H colorimetric reagent for B detection, ^fFlame Photometer determination of certain metal ions

Table 2 Composition of nitrogen regimes and cultivars used in the experiments. Treatment abbreviations were presented for the ease of pronunciation and comparisons

Nitrogen level	Code	Dose (g pot ⁻¹)	Cultivars					
			Kingston	Riogrand	Earlyurbana	Redston	Superstrain-B	Primoeearly
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+

tomato cultivars with 4 N levels) and maintained under the abovementioned conditions. The 24 colonies were reared separately on leaves of each treatment and chopped green fruits of the varieties of tomato cultivars having 4 N levels for 3 generations.

Parasitoid rearing

A stock culture of *H. hebetor* was set up based on the population originating from the parasitized larvae of *Ephestia kuehniella* Zeller in stored wheat flour, maintained at BCRD, IRIPP. Three mated wasps (2–3 days old), with 10 larvae of the 5th instar larvae of *H. armigera*, reared on each treatment, were placed in plastic cups of 7 × 5 cm. The wasps in each cup were removed after 24 h, and the parasitized larvae were maintained in a growth chamber until the emergence of complete wasps. Adult parasitoids were reared on 24 subcolonies under the abovementioned conditions for 3 generations and fed with 20% honey solution (droplets on wax paper tape).

Life table of *H. hebetor*

To investigate the parameters of the life table, 100 5th instar larvae of *H. armigera* were selected from each of the abovementioned subcolonies. Ten pairs of 0–24-h-old *H. hebetor* were released on them. The wasps were removed after 24 h, and the parasitized larvae were harvested after 24 h. On each larva, one *H. hebetor* egg was left, while other eggs were taken. Parasitized larvae were separately delivered to plastic Petri dishes (1.5 cm height, and 10 cm diameter). A growth chamber was used for keeping them, under the already described conditions. Each individual's developmental stage was recorded on a daily basis. Immediately after the emergence of the adult wasps, the male and female pairing was done in plastic dishes (with a diameter of 5 cm, and a height of 4 cm), fed with 20% honey; two 5th instar larvae were offered to the wasps daily for the purpose of oviposition. The longevity of the wasps as well as daily fecundity of the females were then recorded. The experiment was carried out until the death of the last individual.

Life-table analysis

Analysis of data on life history was done on the basis of age-stage two-sex life table (Chi and Liu 1985). Using the TWISEX-MS Chart program (Chi 2016), the age-stage specific survival rate (S_{xj}) (x refers to age, and j refers to stag), the age-specific survival rate (l_x), the age-stage specific fecundity (f_{xj}), the age-specific fecundity (m_x), and the appropriate population parameter indicators for measuring the growth and reproduction of a population: the net reproductive rate (R_0), the intrinsic rate of increase (r), the mean generation time (T), and the finite rate of increase (λ) were calculated. The age-specific survival rate was calculated as:

$$l_x = \sum_{j=1}^{\beta} S_{xj} \quad (1)$$

$$m_x = \frac{\sum_{j=1}^{\beta} S_{xj} f_{xj}}{\sum_{j=1}^{\beta} S_{xj}} \quad (2)$$

where k is the number of stages.

The intrinsic rate of increase was measured as:

$$\sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_x = 1 \quad (3)$$

Here, age can be indexed from 0 to ∞ (as the max age).

The mean generation time (T) refers to the time length needed by a population so as to increase to R_0 times of 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:

$$T = \frac{\ln R_0}{r} \quad (4)$$

The net reproductive rate (R_0) was calculated using:

$$R_0 = \sum_{x=0}^{\infty} l_x m_x \tag{5}$$

The bootstrap (Huang and Chi 2013) in TWOSEX-MS-Chart software was utilized in order to measure the standard errors and means of the parameters associated with the population (Chi 2016). The relationship between pre-adult duration of *H. armigera* and *H. hebetor* on the six tomato cultivars and the four nitrogen levels was evaluated, using a linear regression model.

Results and discussion

The effects of tomato cultivars, with different nitrogen levels on pre-adult duration of *H. hebetor*, are shown in Table 3. The egg incubation and the pupal periods were the same at the different treatments; however, the larval duration showed significant differences among different treatments ($P < 0.05$). The longest larval developmental period was recorded on En0 and the shortest on Kn + treatment (Table 3). The larval period of the parasitoid was significantly affected by N levels on different

Table 3 The mean (\pm SE) pre-adult longevity, adult longevity, pre-oviposition periods (days) and total pre-oviposition period (TPOP) of *H. hebetor* on *H. armigera* reared on six tomato cultivars with four nitrogen levels

Stage	N Level	Kingston	Riogrand	Earlyurbana	Redston	Superstrain-B	Primoeearly
Egg	n0	1.44 \pm 0.04Aa	1.40 \pm 0.03Aa	1.42 \pm 0.04Aa	1.42 \pm 0.03Aa	1.46 \pm 0.04Aa	1.44 \pm 0.04Aa
	n-	1.44 \pm 0.04Aa	1.46 \pm 0.03Aa	1.46 \pm 0.04Aa	1.40 \pm 0.03Aa	1.48 \pm 0.04Aa	1.44 \pm 0.04Aa
	ns	1.42 \pm 0.05Aa	1.44 \pm 0.03Aa	1.44 \pm 0.04Aa	1.40 \pm 0.03Aa	1.46 \pm 0.04Aa	1.42 \pm 0.03Aa
	n+	1.40 \pm 0.05Aa	1.44 \pm 0.02Aa	1.40 \pm 0.04Aa	1.40 \pm 0.03Aa	1.48 \pm 0.04Aa	1.41 \pm 0.03Aa
Larvae	n0	3.12 \pm 0.041 Ca	3.16 \pm 0.05Ca	3.77 \pm 0.04Aa	3.33 \pm 0.063Ba	3.11 \pm 0.04BCa	3.57 \pm 0.043 Aa
	n-	2.74 \pm 0.053 Db	3.08 \pm 0.06Ca	3.66 \pm 0.07Aa	3.22 \pm 0.052BCa	2.99 \pm 0.03CDab	3.46 \pm 0.073ABa
	ns	2.41 \pm 0.007Dbc	3.09 \pm 0.04Ba	3.25 \pm 0.07Ab	3.14 \pm 0.054Bab	2.71 \pm 0.054Cb	3.35 \pm 0.071Aab
	n+	2.17 \pm 0.054Dcd	3.01 \pm 0.04Ba	3.19 \pm 0.07Ab	3.03 \pm 0.051Bb	2.63 \pm 0.053Cb	3.27 \pm 0.076Aab
Pupa	n0	7.17 \pm 0.06ABa	7.21 \pm 0.08Aa	7.34 \pm 0.060Aa	7.27 \pm 0.07Aa	7.220 \pm 0.070Aa	7.31 \pm 0.07Aa
	n-	6.92 \pm 0.06ABa	7.12 \pm 0.08Aa	7.29 \pm 0.050Aa	7.21 \pm 0.06Aa	7.080 \pm 0.060Aa	7.26 \pm 0.06Aa
	ns	6.91 \pm 0.080Ba	7.06 \pm 0.06Aa	7.14 \pm 0.060Aa	7.12 \pm 0.04Aa	6.89 \pm 0.0611Ba	7.22 \pm 0.06Aa
	n+	6.73 \pm 0.050Bb	7.05 \pm 0.06Aa	7.16 \pm 0.060Aa	7.06 \pm 0.03Aa	6.92 \pm 0.054ABb	7.13 \pm 0.06Aa
Total Pre-adult	n0	11.75 \pm 0.09 Da	12.06 \pm 0.11 Ca	12.83 \pm 0.11Aa	12.10 \pm 0.12Ca	11.68 \pm 0.14 Da	12.39 \pm 0.11Ba
	n-	10.91 \pm 0.12Eb	11.44 \pm 0.13Db	12.49 \pm 0.11Ab	11.83 \pm 0.09 Cb	11.33 \pm 0.09Db	12.16 \pm 0.14Bb
	ns	10.76 \pm 0.16Eb	11.28 \pm 0.09Dbc	12.47 \pm 0.11Ab	11.72 \pm 0.08 Cb	11.22 \pm 0.11Db	12.11 \pm 0.12Bb
	n+	10.14 \pm 0.09Ec	11.21 \pm 0.08Cc	12.28 \pm 0.09Ac	11.44 \pm 0.08Bc	10.88 \pm 0.09Dc	12.26 \pm 0.12Aa
Fecundity (offspring)	n0	58.0 \pm 6.21Ac	52.0 \pm 6.87Ab	47.0 \pm 5.70Bb	48.2 \pm 6.13Bb	56.6 \pm 5.94Ac	56.02 \pm 7.33Ab
	n-	69.0 \pm 7.32Ab	63.0 \pm 6.44Aa	58.2 \pm 8.21Ba	59.7 \pm 9.11Ba	67.7 \pm 7.86Ab	65.70 \pm 6.34Aa
	ns	78.1 \pm 6.41Aa	64.0 \pm 9.38Ba	59.6 \pm 6.11Ca	66.3 \pm 7.32Ba	81.7 \pm 5.65Aa	66.9 \pm 8.330Ba
	n+	76.4 \pm 9.31Aa	66.4 \pm 7.82Ba	62.5 \pm 7.33Ba	66.0 \pm 5.51Ba	82.1 \pm 6.91Aa	66.32 \pm 6.42Ba
Longevity (♀)	n0	16.40 \pm 0.22Ab	16.22 \pm 0.24Aa	16.04 \pm 0.31Aa	16.11 \pm 0.63Aa	16.32 \pm 0.38Ab	16.03 \pm 0.32Aab
	n-	17.7 \pm 0.2ABab	16.50 \pm 0.47Ba	16.19 \pm 0.22Ba	16.61 \pm 0.57Ba	18.57 \pm 0.33Aa	17.29 \pm 0.53ABa
	ns	18.73 \pm 0.53Aa	16.60 \pm 0.43Ba	16.33 \pm 0.55Ba	16.54 \pm 0.28Ba	18.86 \pm 0.25Aa	17.28 \pm 0.46ABa
	n+	18.67 \pm 0.41Aa	16.92 \pm 0.2ABa	16.25 \pm 0.47Ba	16.73 \pm 0.42Ba	18.79 \pm 0.29Aa	17.25 \pm 0.27ABa
Longevity (♂)	n0	5.40 \pm 0.35Aa	5.10 \pm 0.36Aa	5.23 \pm 0.24Aa	5.17 \pm 0.63Aa	5.20 \pm 0.51Aa	5.16 \pm 0.26Aa
	n-	6.23 \pm 0.28Aa	6.02 \pm 0.47Aa	5.60 \pm 0.45Aa	6.18 \pm 0.61Aa	6.32 \pm 0.33Aa	6.07 \pm 0.45Aa
	ns	6.41 \pm 0.32Aa	6.21 \pm 0.52Aa	6.12 \pm 0.35Aa	6.14 \pm 0.52Aa	6.53 \pm 0.57Aa	6.13 \pm 0.52Aa
	n+	6.30 \pm 0.57Aa	6.10 \pm 0.22Aa	6.15 \pm 0.51Aa	6.22 \pm 0.47Aa	6.40 \pm 0.63Aa	6.21 \pm 0.32Aa
TPOP (day)	n0	12.34 \pm 0.14Ca	13.41 \pm 0.18Ca	13.96 \pm 0.22Aa	13.83 \pm 0.25Aa	13.21 \pm 0.25Ca	13.69 \pm 0.18Ba
	n-	12.18 \pm 0.1Cab	13.12 \pm 0.14Cb	13.88 \pm 0.18Aa	13.20 \pm 0.09Cb	12.75 \pm 0.11Db	13.48 \pm 0.22Bb
	ns	12.04 \pm 0.32Db	12.85 \pm 0.12Cc	13.81 \pm 0.22Aa	13.42 \pm 0.11Bb	12.70 \pm 0.10Cb	13.34 \pm 0.19Bb
	n+	11.76 \pm 0.16Ec	12.55 \pm 0.1CDd	13.74 \pm 0.23Aa	12.73 \pm 0.15Cc	12.35 \pm 0.08Dc	13.46 \pm 0.25Bb

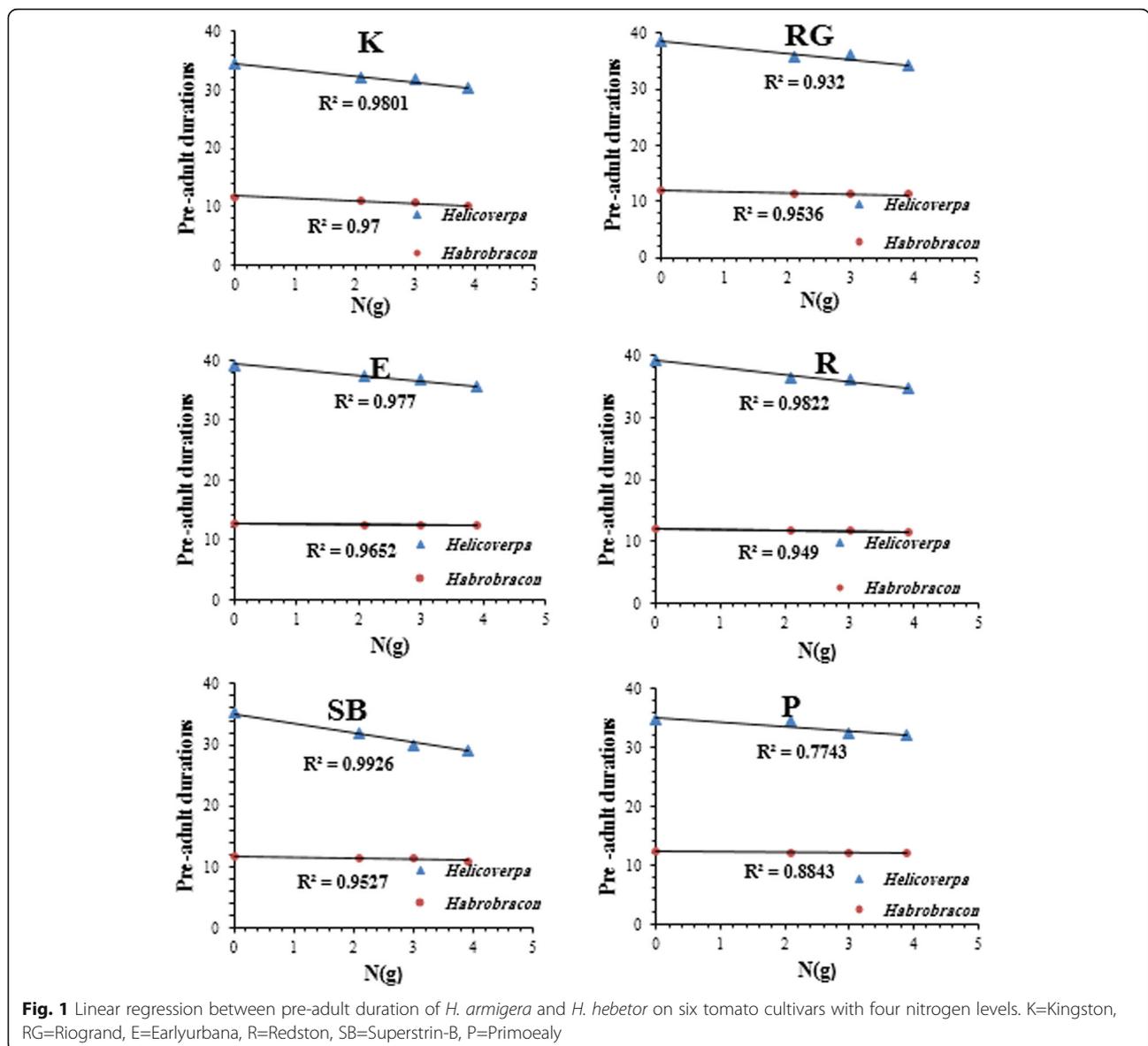
The means followed by different capital letters in the rows and small letters in the columns for every stage refer to the significant differences ($P \leq 5\%$) n0 no fertilization, n- standard fertilization minus 30%, ns standard fertilization, n+ standard fertilization plus 30%

treatments ($P < 0.05$), and the application of fertilizers improved the developmental rate of the parasitoid. These results are consistent with the findings of Chesnais et al. (2016).

The total pre-adult period ranged from 10.14 ± 0.09 to 12.83 ± 0.11 days, which was significantly different among treatments by increasing N levels, except P cultivar ($P < 0.05$). The developmental time of *H. hebetor* was extended significantly by the decrease in the quality of *Spodoptera litura* Fabricius (Kaur and Kaur 2013). Singh et al. (2016) reported that the host plant significantly influenced the development and reproduction of *H. hebetor*. Based on the previous study, the total pre-adult period of *H. armigera* was significantly decreased by increasing N levels (Fig. 1). The total pre-adult period obtained in the present

research is in line with the findings of Amir-Maafi and Chi (2006) as well as Ghimire and Phillips (2010) regarding the highest N level, and Eliopoulos and Stathas (2008) concerning the lowest N level.

Adult female longevity was decreased by increasing N levels. This duration ranged from 16.04 ± 0.31 to 18.79 ± 0.29 days. Also, the longest and shortest longevity for females were observed on SBn+, Kns and En0, Pn0, respectively. The comparison of fertilized cultivars showed that adult female longevity was lower in E, R, and RG cultivars (Table 3). With a few exceptions, female wasps derived from the eggs belonging to high nitrogen cultivars, had a long lifespan than those obtained from low nitrogen cultivars ($P > 0.05$). It has been demonstrated that an increase in adult longevity may positively



influence pest control. These findings are consistent with the findings by Farag et al. (2015). Other researchers have further approved the impact of host nutritional content and nitrogen fertilizer on adult female longevity (Aqueel et al. 2015; Singh et al. 2016).

Nevertheless, based on the parasitoid host and rearing conditions, various extents were reported for adult female longevity (Kaur and Kaur 2013; Vaez et al. 2013). Contrary to the females, the longevity of male was not affected by the increase in nitrogen fertilization on the different treatments. Natural selection, sex chromosome variation, or differences in the patterns of resource allocation between sex cells are probable reasons for the difference in adult longevity.

Fecundity (except K cultivar) was increased by the increase in nitrogen levels. The highest and lowest fecundity were on SBn+ and En0, respectively (Table 3). The amount of nitrogen in the leaf increases the nutritional quality, hence the increase in the fecundity of the second and third trophic levels (Mondy et al. 2006). In the present study, the fecundity of the parasitoids was also significantly affected. The present results further showed an increase in lower N-fertilization and stability on higher N levels (Table 3). Presumably, excessive nitrogen causes a slow decrease. These results are almost similar to the findings of Kaur and Kaur (2013) at the highest N level. Such dissimilarities may be due to the

physiological differences in the host plants' nutrients (quantity/quality), and genetic variations caused by laboratory rearing, differences in the geographic populations of pests, or analytical methods.

In this study, two host larvae were daily exposed to parasitoid, resulting in lower fertility than previous similar studies, in which more larvae were daily exposed to the parasitoid. It has been reported that several factors, such as temperature, humidity, parasitoid age, host type and size, and diet affect fecundity and sex ratio (Forouzan et al. 2009).

Larvae reared on Kn+ and En0 had the highest and lowest survival rate (l_x) during immature stages, respectively. Furthermore, the peak of the age-stage-specific fecundity ($f_{x,t}$) (the fourth stage) was observed in the wasps reared on Kn+.

The highest age-specific fecundity (m_x) also was estimated as $7.45 \text{ females}^{-1} \text{ day}^{-1}$ on Kn+ occurred at the ages of 13 days (Fig. 2). Almost all treatments showed the highest reproduction rates on the 13th and 14th days (Figs. 2 and 3).

The l_x and m_x curves showed the effect of fertilization on cultivars. Presumably, reduced nutritional quality and N-limited cultivars can result in low survival rate and reproduction (Hamilton et al. 2005). In this study, the age-specific fecundity (m_x) on the same N levels showed similar times, but significant differences (~ 3 vs ~ 7 days) were observed between fertilized and unfertilized treatments.

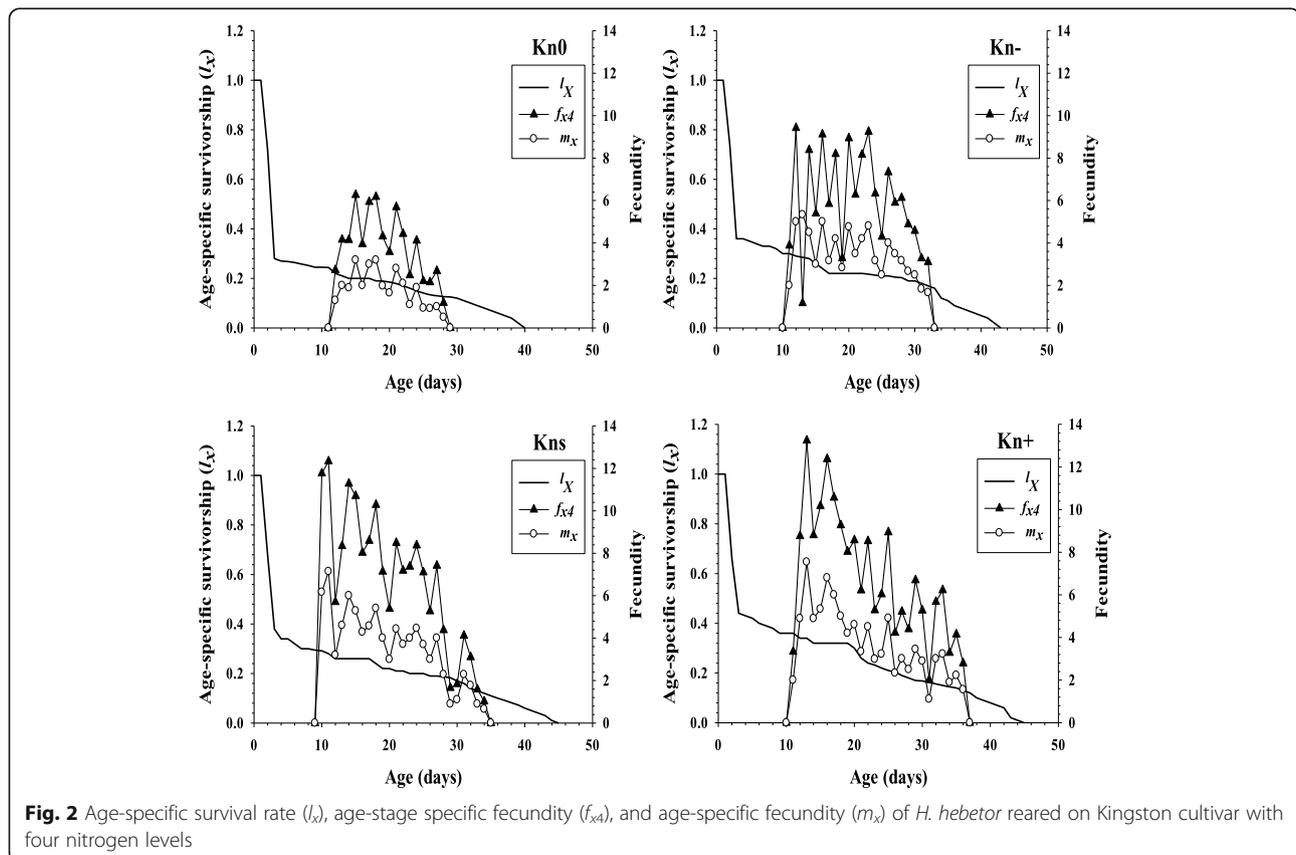


Fig. 2 Age-specific survival rate (l_x), age-stage specific fecundity ($f_{x,t}$), and age-specific fecundity (m_x) of *H. hebetor* reared on Kingston cultivar with four nitrogen levels

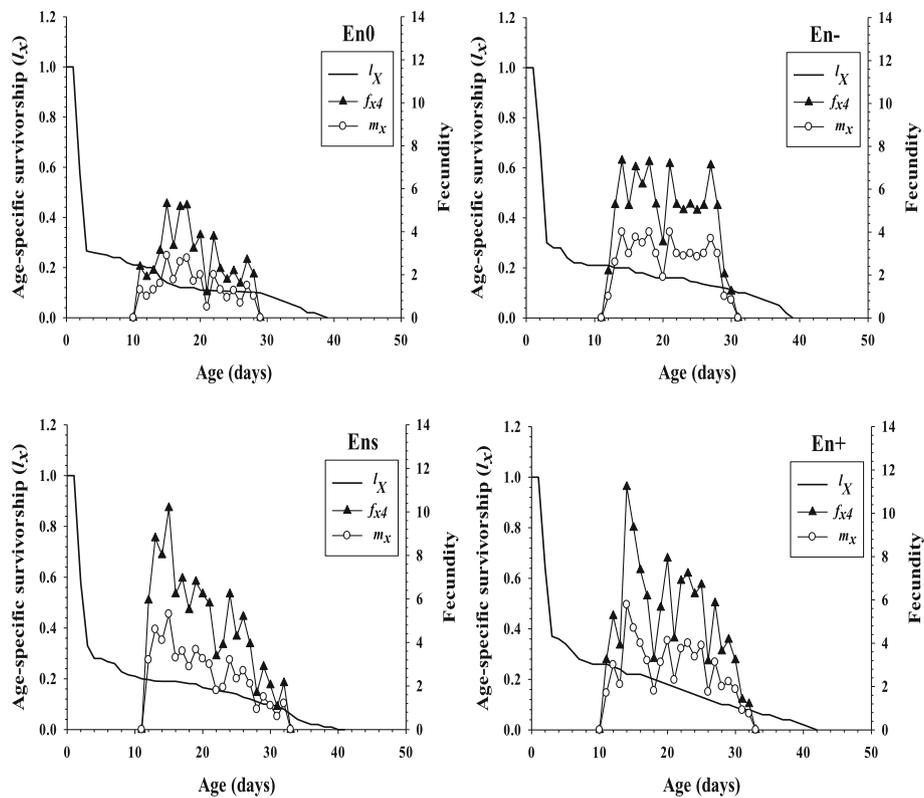


Fig. 3 Age-specific survival rate (l_x), age-stage specific fecundity (f_{xa}), and age-specific fecundity (m_x) of *H. hebetor* reared on Earlyurbana cultivar with four nitrogen levels

The mean total pre-ovipositional period (TPOP) for all *H. hebetor* females was estimated to range from 11.76 ± 0.16 to 13.96 ± 0.223 days. The longest TPOP was recorded for insects on En0, En- and Pn0, Pn- (Table 3). Total pre-ovipositional period (TPOP) was also affected by the treatments. Since TPOP influences the generation time, based on Eq. (5), the higher intrinsic rate of increase was associated with the shorter total pre-ovipositional period (Jha et al. 2012), corroborated by the present data on Kn+ (TPOP = 11.76 ± 0.16 days).

The net reproductive rate (R_0) varied from 9.5 ± 1.94 to 12.34 ± 2.81 in Pn0 and Kn+, respectively, whereas it increased by increasing the nitrogen content of cultivars, as well as the intrinsic rate of increase (r). Although the net reproductive rate (R_0) showed a negative interaction with nitrogen levels, the nutrition resulted in insignificant differences in the total number of eggs. The same ranges of *H. hebetor* net reproductive rate were reported by Amir-Maafi and Chi (2006) and Forouzan et al. (2009). Although the optimal levels of N fertilized tomato plants positively affect the efficiency of natural enemy (Han et al. 2014), poor and excessive nitrogen treatments may trigger negative bottom-up effects on the second and third levels of the food chain Sarfraz et al. 2009, probably due to the more defensive compounds (Larbat et al. 2012).

The highest and lowest r were observed on Kn+ and Sbn+ and En0, Pn0, and Rn0, respectively (Table 4), with the same trend; the finite rate of increase (λ) in all treatments (except for E cultivars) was significantly different between the fertilized and non-fertilized cultivars. The lowest values of the finite rate of increase (λ) belonged to En0 and the highest were observed for Kn+ (Table 4). In the present study, the intrinsic rate of increase (r) and the finite rate of increase (λ) are in agreement with the results obtained by Amir-Maafi and Chi (2006) and Eliopoulos and Stathas (2008), but in contrast to those of Sedratian et al. (2011) and Singh et al. (2016).

A small change in (r) and (λ) significantly impacts the population size of an insect (Goundoudaki et al. 2003). In traditional age-specific life tables, only females were considered in the calculation of life-table parameters, hence the fact that most calculated parameters were higher than the actual values. However, in two-sex life tables, both males and females were involved in the calculation; therefore, parameters were more precisely and accurately calculated (Yu et al. 2005).

The mean generation time (T) of *H. hebetor* at different N levels ranged from 16.41 ± 0.117 to 18.8 ± 0.259 days on the cultivars. Moreover, the mean generation time (T) was longest at En0 and shortest

Table 4 Age-stage, two-sex life table parameters of *H. hebetor* on *H. armigera* reared on six tomato cultivars with four nitrogen levels

N level		Kingston	Riogrand	Earlyurbana	Redston	Superstrain-B	Primoeearly
R_0 offspring/female/individual	n0	11.04 ± 1.28Aa	10.14 ± 1.24Aa	9.960 ± 1.93Aa	9.721 ± 1.13Aa	10.36 ± 0.96Aa	9.500 ± 1.94Aa
	n-	11.61 ± 1.56Aa	10.92 ± 1.61Aa	10.06 ± 1.92Aa	10.09 ± 1.46Aa	11.01 ± 1.44Aa	10.48 ± 1.48Aa
	ns	12.14 ± 2.55Aa	11.78 ± 1.90Aa	10.32 ± 1.31Aa	10.12 ± 1.55Aa	11.16 ± 1.76Aa	10.68 ± 1.53Aa
	n+	12.34 ± 2.83Aa	12.16 ± 1.73Aa	10.30 ± 1.41Aa	10.21 ± 1.81Aa	12.21 ± 1.83Aa	11.80 ± 1.63Aa
$r_{(\text{day}^{-1})}$	n0	0.1134 ± 0.01Ab	0.1093 ± 0.01Ab	0.1058 ± 0.014Aa	0.1112 ± 0.065Aa	0.1103 ± 0.006Ab	0.1110 ± 0.014Ab
	n-	0.1438 ± 0.01Aa	0.1366 ± 0.012Aa	0.1186 ± 0.138Aa	0.1263 ± 0.013Aa	0.1390 ± 0.016Aa	0.1331 ± 0.012Aa
	ns	0.1491 ± 0.01Aa	0.1390 ± 0.011Aa	0.1273 ± 0.012Aa	0.1318 ± 0.128Aa	0.1466 ± 0.013Aa	0.1357 ± 0.012Aa
	n+	0.1515 ± 0.01Aa	0.1450 ± 0.010Aa	0.1352 ± 0.122Aa	0.1374 ± 0.018Aa	0.1487 ± 0.114Aa	0.1411 ± 0.009Aa
T (day)	n0	17.62 ± 0.20Aa	17.86 ± 0.18Aa	18.80 ± 0.25 Aa	17.52 ± 0.01Aa	17.38 ± 0.25 Aa	17.84 ± 0.17Aa
	n-	17.10 ± 0.19Aa	17.42 ± 0.17Aa	18.24 ± 0.15 Aa	17.41 ± 0.20Aa	17.07 ± 0.16 Aa	17.33 ± 0.32Aa
	ns	16.88 ± 0.4Aab	17.51 ± 0.14Aa	17.98 ± 0.18Aab	17.61 ± 0.28Aa	16.75 ± 0.15Aab	17.32 ± 0.28Aa
	n+	16.47 ± 0.25Ab	17.11 ± 0.18Aa	17.86 ± 0.21 Ab	17.56 ± 0.15Aa	16.41 ± 0.11 Ab	17.02 ± 0.28Aa
$\lambda_{(\text{day}^{-1})}$	n0	1.1102 ± 0.01Ab	1.1086 ± 0.017Ab	1.1013 ± 0.015Aa	1.1055 ± 0.017Ab	1.1096 ± 0.015Ab	1.1078 ± 0.016Ab
	n-	1.1378 ± 0.01Aa	1.1322 ± 0.013Aa	1.1195 ± 0.015Aa	1.1222 ± 0.013Aa	1.1410 ± 0.018Aa	1.1265 ± 0.018Aa
	ns	1.1481 ± 0.02Aa	1.1381 ± 0.012Aa	1.1310 ± 0.014Aa	1.1326 ± 0.014Aa	1.1586 ± 0.015Aa	1.1336 ± 0.011Aa
	n+	1.1603 ± 0.02Aa	1.1582 ± 0.011Aa	1.1344 ± 0.013Aa	1.1415 ± 0.012Aa	1.1608 ± 0.013Aa	1.1543 ± 0.011Aa

The SEs were estimated using 100,000 bootstraps resampling and compared by paired bootstrap test (comparison of 95% CI). Different capital letters in the rows and small letters in the columns refer to the significant differences ($P \leq 5\%$) R_0 net reproductive rate, r intrinsic rate of increase, T mean generation time, λ : finite rate of increase

at Kn+. The results of the present study indicated that host-plant nutrition influenced the parasitoids indirectly and among the 24 tested treatments, the longest larval, and pre-adult durations as well as the lowest, R_0 , T , λ , and r values belonged to E and R, indicating that this cultivar is partially unsuitable or tolerant; however, K and SB seemed to be favorable for development of herbivores and wasps. In fact, the lower (r) and (λ) values observed in the present study can mainly be attributed to the longer pre-adult developmental time, lower fecundity, lower survival rates, and delayed peaks in reproduction (Atlihan et al. 2017). Efficiency of wasps declined when herbivores fed on poor nitrogen host plant (Winter and Rostas 2010) and application of fertilizers enhanced the development rate of the parasitoid (Garratt et al. 2010).

Conclusion

The results support the findings of different researchers on the tri-trophic interactions among herbivores, plants, and their natural enemies. Excessive delivery of N induces plant suitability, positively affecting herbivore parameters. Such positive effects entail either no outcomes or positive results regarding parasitoid parameters, while having negative effects on the environment and the economy. Accordingly, it is anticipated that the findings of the present study may provide basic information for extended experiments under field or greenhouse conditions.

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Competing interests

The authors declare that they have no competing interests.

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