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Soybean Cultivars Affecting Performance of *Helicoverpa armigera* (Lepidoptera: Noctuidae)

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1. Introduction

Helicoverpa armigera (Hübner) is one of the major devastating and highly polyphagous insect pests in many parts of the world (Liu et al., 2004; Naseri et al., 2009 a, b; Naseri et al., 2011). This species has a high potential for population increase and outbreak on different host plants including soybean (*Glycine max* (L.) Merrill) throughout the world. *Helicoverpa armigera* is a major pest of more than 60 cultivated and uncultivated plant species, distributed in 47 families (Zalucki et al., 1994).

To determine the potential of different soybean cultivars to help manage *H. armigera* populations, data on the effects of various cultivars on the pest's digestive enzymes, survival, development time, reproduction, population growth and nutritional indices are necessary. Such experiments essentially measure the potential for antibiosis resistance. Host plant resistance has been used effectively in sustainable integrated management programs for several crop pests. Plants with antibiosis machanism may reduce directly insect survival, size or weight, longevity, and fecundity in new generation adults, or they may have an indirect effect by increasing the exposure of the insect to its natural enemies due to prolonged developmental time (Sarfraz et al., 2006).

In terms of production and trade, soybean is the most important leguminous crop in the world due to its high protein (35-40 %) and oil content (15-22 %). In recent years (especially after 1950), soybean production has been seriously affected by *H. armigera*. In spite of high level of natural mortality, *H. armigera* needs to be controlled by synthetic pesticides (Fitt, 1994). Despite extensive use of synthetic insecticides to control *H. armigera*, it has developed/evolved resistance to these insecticides, extremely reducing the number of effective approaches to its control (Armes et al., 1992). Consequently, there is considerable interest in alternative management tactics, which might be applied in area-wide or more restricted basis. Environmentally safe techniques are not widely used in rural areas, probably because these products are too expensive or their effectiveness is highly variable (Sharma, 2001). Therefore, the study of potential resistance of soybean cultivars by comparing the performance of *H. armigera* on these cultivars can play an important role in identifying the anti-digestive or anti-feedant compounds and their further use in the pest management programs.

In this chapter we would like to emphasize the strong effect of the selected soybean cultivars (as representatives of the gene pool of soybean) on life table, nutritional indices and physiology of digestive enzymes of *H. armigera* and discover the crucial importance of the cultivar selection and breeding in control program of the pest.

2. Soybean cultivars pods affecting the life table parameters of *H. armigera*

It is known that the quality and quantity of food ingested by an insect can influence directly its survival, development and reproduction (Razmjou et al., 2006). So, the fitness of plant-feeding insects depends upon the nutritious substances in the host plant (Du et al., 2004). To study the dynamics of animal populations, especially arthropods, life table parameters are appropriate tools because these tools provide very important demographic parameters (Maia et al., 2000). Demographic information may also be useful in constructing population models (Carey, 1993). The life table gives the most extensive description of the survivorship, development and reproduction of a population which are basic factors in both theoretical and applied population ecology (Taghizadeh et al., 2008). Effects of various host plants, apart from soybean cultivars, were studied on life table parameters of *H. armigera* (Patal & Koshyia, 1997; Liu et al., 2004; Reddy et al., 2004).

2.1 Case study

2.1.1 Experimental conditions

Helicoverpa armigera tested on different soybean cultivars (356 (Delsoy4210), M4, M7, M9, Clark, Sahar, JK, BP, Williams, L17, Zane, Gorgan3 and DPX), had already been reared for two generations on the same cultivars. 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 (Naseri et al., 2009 a, b). In order to study the life table parameters of *H. armigera* on different soybean cultivars, the adult moths emerged from the larvae reared on different soybean cultivars were used in the experiments. Life table parameters of *H. armigera* were studied using the same aged eggs laid within 24 h by females reared as larvae on the related cultivars. Each cohort of eggs (fifty eggs) was used to start experiment on each cultivar. Upon egg hatching, the 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. These Petri dishes contained the fresh detached leaves of different test plants for feeding of the 1st instar larvae. The petioles of the detached leaves were inserted in water-soaked cotton to maintain their freshness. The 2nd to 5th instars were fed on the pods of different soybean cultivars until pre-pupation. The larva in each Petri dish was observed daily for the mortality or ecdysis. The fifth instar larvae were kept in plastic containers (3 cm in diameter by 5 cm in height) for pre-pupation and pupation (Naseri et al., 2009 a, b). Duration of pre-pupal and pupal stages and their mortality were recorded daily.

A pair of female and male adults emerged from the pupae were introduced into each plastic oviposition container (14 cm in diameter by 19 cm in height), which was closed at the top with a fine mesh net for ventilation. To provide a source of carbohydrate for the adult feeding, a small cotton wick soaked in 10% honey solution was placed in the oviposition containers. Daily number of eggs laid per female, the longevity and gender of each adult were recorded.

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). The life table parameters of *H. armigera* on different soybean cultivars were analyzed using one-way ANOVA. The means associated with soybean cultivars for each parameter were separated using least significant differences (LSD) test when significantly different values were obtained.

2.1.2 Results

According to the results of the study conducted (Naseri et al., 2009 a), among different life history parameters of *H. armigera* reared on different soybean cultivars during the larval stage, development time of the immature stages, life span and fecundity are affected by the pods of soybean cultivars. Both the larval period and entire development time were longest on L17 and shortest on M7 (Table 1). Taking longer time required to complete immature stages of *H. armigera* on L17 may enhance the effectiveness of its management techniques by using natural enemies and insecticides, so the use of cultivar L17 can be a part of an IPM strategy (Du et al., 2004). It is also indicated that because of shortest larval period and development time of *H. armigera* on the cultivar M7, it may be more suitable host plant, perhaps because of higher nutritional quality compared with the other cultivars tested. Variations in the development time of *H. armigera* on different soybean cultivars can be attributed to either differences in nutrients or primary and secondary compounds among the soybean cultivars pods, or physiological differences depending on the host plant.

As can be seen in Table 2, the lowest development index (the ratio between the percentage of individuals completing development and the average period required to do) of the immature stages of *H. armigera* is observed on L17 and BP. It may be due to the presence of some phytochemicals in these cultivars as antibiotic agent, or the absence of some primary nutritious substances essential for development of *H. armigera*, leading to higher percentage of mortality on these cultivars. Since the lowest level of mortality of immature stages is recorded on M7, the development index of *H. armigera* is higher on this cultivar. Differences in mortality and the development index of the pest on different soybean cultivars might be the result of antibiotic effects, poor nutritional quality of the food ingested, and/or secondary phytochemicals (Naseri et al., 2009 a).

This study shows that the fecundity (daily and total number of oviposited eggs per female) of *H. armigera* is affected by different soybean cultivars consumed by the larvae (Table 3). The females reared as larvae on DPX produced the highest total number of eggs (582.70 eggs) whereas the lowest total number of eggs was observed on 356 (177.10 eggs), suggesting that the quantity and/or the quality of nutrients in cultivar 356 are less suitable for larval feeding compared with other soybean cultivars (Naseri et al., 2009 a).

We have demonstrated the significant difference of life table parameters of *H. armigera* on different soybean cultivars (Naseri et al., 2009 b). The net reproductive rate (R_0) is a key parameter, summarizing the physiological ability of an animal related to its reproductive capacity. Comparison of the net reproductive rate often provides important perception beyond that available from the independent analysis of individual life cycle parameters. The net reproductive rate of *H. armigera* was the highest on M7, whereas the values of R_0 varied from 89.35 on 356 to 354.92 females/female on M7 (Table 4). Liu et al. (2004) showed that the R_0 values of *H. armigera* differed depending on host plant, which ranged from 5.1 on hot pepper to 117.6 females/female on cotton. According to the literature, the net reproductive rate of *H. armigera* was 143.77 on sunflower (Reddy et al., 2004) and 374.01 females/female on pearl millet (Patal & Koshyia, 1997).

						Longevity (days)		Whole life span (days)	
Cultivar	Incubation period (days)	Larval period (days)	Pre-pupal period (days)	Pupal period (days)	Development time (days)	Male	Female	Male	Female
M7	3.00 a (0.00)	17.30 f (0.60)	2.23 a (0.15)	11.63 a (0.17)	34.21 f (0.77)	12.71 a (0.94)	9.69 a (0.36)	46.57 de (1.49)	44.00 d (1.12)
JK	3.00 a (0.00)	20.86 cd (0.66)	2.62 a (0.18)	12.05 a (0.34)	38.42 bcde (0.89)	9.25 a (0.81)	9.33 a (0.62)	48.08 cde (0.88)	44.92 cd (0.94)
Clark	3.00 a (0.00)	18.50 f (1.22)	2.79 a (0.22)	12.41 a (0.36)	36.82 def (1.49)	8.89 a (0.35)	10.14 a (0.52)	45.11 e (0.45)	46.00 bcd (1.22)
M4	3.00 a (0.00)	20.21 cde (0.96)	2.68 a (0.15)	12.44 a (0.23)	38.39 bcde (0.92)	9.69 a (0.65)	9.70 a (0.86)	47.54 cde (1.04)	48.30 ab (0.82)
M9	3.00 a (0.00)	18.17 ef (0.64)	2.48 a (0.21)	12.12 a (0.33)	36.06 ef (1.03)	10.75 a (1.12)	9.92 a (0.47)	48.00 cde (1.48)	44.77 cd (1.32)
L17	3.00 a (0.00)	26.20 a (1.62)	2.39 a (0.18)	1.06 a (0.27)	42.71 a (1.41)	9.40 a (1.06)	9.08 a (0.67)	53.40 a (1.70)	49.82 a (0.95)
356	3.00 a (0.00)	18.80 def (0.48)	2.65 a (0.20)	11.86 a (0.31)	36.71 cde (0.69)	11.25 a (0.97)	10.63 a (0.99)	47.00 de (0.53)	47.00 abcd (0.99)
DPX	3.00 a (0.00)	21.28 bc (0.74)	2.55 a (0.23)	12.00 a (0.39)	38.59 bcd (0.95)	12.37 a (0.86)	10.92 a (0.53)	50.37 abc (1.13)	47.92 abc (0.90)
BP	3.00 a (0.00)	23.33 ab (1.01)	2.59 a (0.17)	12.29 a (0.32)	40.29 ab (1.28)	10.12 a (1.49)	9.50 a (0.80)	51.86 ab (1.07)	46.54 bcd (1.55)
Zane	3.00 a (0.00)	21.77 bc (1.05)	2.73 a (0.17)	11.35 a (0.39)	37.95 bcde (0.91)	10.89 a (0.90)	10.85 a (1.02)	49.22 bcd (1.07)	48.31 ab (1.52)
Sahar	3.00 a (0.00)	21.56 bc (0.74)	2.65 a (0.28)	11.60 a (0.21)	39.20 abc (0.75)	9.44 a (1.09)	9.54 a (0.68)	48.14 cde (1.53)	48.00 abc (1.14)
Gorgan3	3.00 a (0.00)	22.09 bc (0.79)	2.30 a (0.17)	11.44 a (0.21)	38.28 bcde (0.64)	9.44 a (0.72)	9.31 a (0.62)	47.00 de (0.97)	48.00 abc (0.77)
Williams	3.00 a (0.00)	18.41 ef (0.73)	3.00 a (0.23)	12.30 a (0.17)	36.60 def (0.76)	9.69 a (0.67)	8.42 a (0.55)	48.08 cde (1.18)	43.82 d (0.73)

*The means followed by different letters in the same columns are significantly different ($P<0.01$, LSD)

Table 1. Mean development time and longevity of *Helicoverpa armigera* on different soybean cultivars

	Larvae		Pre-pupae		Pupae		Overall immature	
Cultivar	Mortality (%)	D.I.	Mortality (%)	D.I.	Mortality (%)	D.I.	Mortality (%)	D.I.
M7	0.00 (46)*	5.78	4.35 (46)	42.89	13.64 (44)	7.42	17.39 (46)	2.41
JK	15.38 (52)	4.06	4.45 (44)	36.43	9.52 (42)	7.51	26.92 (52)	1.90
Clark	23.08 (52)	4.16	5.26 (40)	33.96	10.53 (38)	7.21	34.61 (52)	1.77
M4	24.00 (50)	3.76	0.00 (38)	37.31	5.26 (38)	7.61	28.00 (50)	1.87
M9	8.00 (50)	5.06	0.00 (46)	40.32	26.09 (46)	6.10	32.00 (50)	1.88
L17	29.63 (54)	2.68	20.00 (40)	33.47	5.55 (36)	7.83	40.74 (54)	1.39
356	20.00 (50)	4.25	0.00 (40)	37.73	30.00 (40)	5.90	44.00 (50)	1.52
DPX	28.00 (50)	3.38	0.00 (36)	39.21	5.55 (36)	7.87	32.00 (50)	1.76
BP	28.00 (50)	3.09	0.00 (36)	38.61	22.22 (36)	6.33	44.00 (50)	1.39
Zane	18.52 (54)	3.74	0.00 (44)	36.63	9.09 (44)	8.01	25.92 (54)	1.95
Sahar	28.00 (50)	3.34	5.55 (36)	35.64	11.76 (34)	7.61	40.00 (50)	1.53
Gorgan3	8.33 (48)	4.15	4.76 (42)	41.41	10.00 (40)	7.87	20.83 (48)	2.07
Williams	15.38 (52)	4.60	9.09 (44)	30.30	0.00 (40)	8.13	23.08 (52)	2.10

*Numerals in parentheses are the number of samples tested

Table 2. Percentage of mortality and development index (D.I.) of *Helicoverpa armigera* on different soybean cultivars

The life table parameters, particularly, the intrinsic rate of natural increase (r_m), are the most important parameters that can be used to assess plant resistance level to insects (Razmjou et al., 2006). The r_m value of *H. armigera* ranged from 0.1324 to 0.1848 female/female/day, which was minimum on 356 and maximum on M9 (Table 4). The higher r_m value of *H. armigera* on M9 is due to the greater fecundity, lower mortality and shorter development time of the pest fed on this cultivar. Therefore, *H. armigera* fed on M9 has greater potential to population increase and outbreaks in the next generation. However, lower r_m value on 356 was mainly as a result of the poor fecundity and survivorship as well as longer development time of *H. armigera* on this cultivar (Naseri et al., 2009 b). The intrinsic rate of natural increase for *H. armigera* was estimated 0.1135 on sunflower (Reddy et al., 2004) and 0.1423 on pearl millet (Patal & Koshyia, 1997). Some possible reasons for disagreement are due to physiological differences of the host plant tested, genetic differences as a result of laboratory rearing or variation in geographic populations of the pest.

The higher value of r_m indicates the susceptibility of a host plant to insect feeding, while the lower value indicates that the host plant species is resistant to the pest. Therefore, these data show the considerable population growth capacity of *H. armigera* under desirable conditions. Furthermore, since some soybean cultivars such as M9, M7, Clark and Zane were susceptible hosts, *H. armigera* had the greatest opportunity to increase its population on these cultivars. However, some cultivars including L17, 356, BP, Sahar and Gorgan3 were pretty unsuitable host plants, suggesting that they are partially resistant to *H. armigera* compared with others.

Cultivar	Pre-oviposition period (days)	Oviposition period (days)	Post-oviposition period (days)	Daily fecundity	Total fecundity
M7	3.58 abcde* (0.25)	4.33 a (0.44)	1.83 bc (0.23)	118.40 a (14.54)	569.30 a (104.76)
JK	3.73 abcd (0.27)	4.64 a (0.50)	1.45 cd (0.20)	55.39 efg (13.25)	280.6 cde (62.41)
Clark	3.00 de (0.27)	5.54 a (0.52)	1.61 bcd (0.21)	98.45 ab (11.76)	518.00 ab (92.19)
M4	3.20 bcde (0.19)	4.90 a (0.72)	1.60 bcd (0.30)	83.35 h (13.77)	419.30 abcd (113.49)
M9	3.00 de (0.27)	5.50 a (0.54)	1.42 cd (0.43)	85.90 abc (10.99)	511.70 ab (78.73)
L17	3.44 abcde (0.29)	5.00 a (0.47)	1.22 cd (0.22)	81.03 bcde (10.42)	450.50 abc (85.70)
356	2.90 e (0.17)	5.10 a (0.74)	3.00 a (0.78)	37.88 g (5.09)	177.10 e (41.48)
DPX	3.90 ab (0.37)	4.40 a (0.59)	2.40 ab (0.33)	118.92 a (14.61)	582.70 a (95.72)
BP	3.40 abcde (0.26)	4.70 a (0.74)	1.40 cd (0.21)	76.48 bcd (10.40)	393.90 abcd (40.20)
Zane	4.00 a (0.32)	6.50 a (0.94)	0.75 d (0.21)	63.06 defg (8.32)	423.70 abcd (89.98)
Sahar	3.54 abcde (0.15)	5.18 a (0.51)	1.36 cd (0.24)	63.86 defg (12.38)	302.30 bcde (58.51)
Gorgan3	3.83 abc (0.23)	4.25 a (0.47)	1.25 cd (0.12)	47.81 fg (7.60)	262.00 cde (39.98)
Williams	3.11 cde (0.20)	3.67 a (0.40)	1.33 cd (0.28)	66.45 cdef (14.52)	225.50 de (35.45)

The means followed by different letters in the same columns are significantly different (P<0.01 and P<0.05*, LSD)

Table 3. The mean (SE) pre- and post-oviposition and oviposition periods and fecundity of *Helicoverpa armigera* emerging from larvae reared on different soybean cultivars

3. Soybean cultivars pods affecting the nutritional indices of *H. armigera*

Food consumption and utilization link plant attributes with insect performance (Slansky, 1990). For polyphagous insects, the accessibility of various host plants plays an important function triggering population increase and outbreaks (Singh & Parihar, 1988). Growth, development and reproduction of insects are strongly dependent upon the quality and quantity of ingested nourishment (Scriber & Slansky, 1981). The factors determining nutrient availability for growth and maintenance over a given time of development are the quantity and type of food consumed and the efficiency with which is utilized (Barton Browne & Raubenheimer, 2003). Feeding and foraging behaviour of *H. armigera* on mung bean, *Vigna radiata* (L.) R. Wilczek were determined by Johnson & Zalucki (2007). The effect of morpho-physical factors on consumption and coefficient of utilization of *H. armigera* has been already demonstrated (Ashfaq et al., 2003).

3.1 Case study

3.1.1 Experimental conditions

The neonate larvae, collected from the stock culture which reared on cowpea-based artificial diet, were divided into four replicates (10 larvae in each) and transferred into plastic

container (diameter 16.5 cm, depth 7.5 cm). The first instar larvae were reared in groups until developing to the third instar, then they were separated and transferred to plastic tubes (diameter 3 cm, depth 5 cm) individualy to prevent cannibalism. The fifth instar larvae were kept in the above-described tubes for pre-pupation and pupation.

			Parameter (mean±SE)		
Cultivar	Net reproductive rate (R_0)	Intrinsic rate of natural increase (r_m) (day^{-1})	Finite rate of increase (λ) (day^{-1})	Mean generation time (T) (day)	Doubling time (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)

Table 4. Life table parameters of *Helicoverpa armigera* on different soybean cultivars

To determine the nutritional indices of *H. armigera*, the consumption of the fourth instar, fifth instar and second to fifth instar larvae on the soybean cultivars were measured by using the gravimetric technique (Waldbauer, 1968). The nutritional indices were measured based on dry weight for weight gain, food consumption and feces produced by *H. armigera* larvae. After measuring the weight of the second instar larvae, they were introduced onto the pods of different soybean cultivars and the weight of the larvae were recorded daily before and after feeding until they reached the pre-pupal stage. The pre-pupa, pupa and adults from the larvae reared on each cultivar were weighed as well. The initial fresh pods and the pods and feces remaining at the end of each experiment were weighed daily. The quantity of food ingested was determined by subtracting the diet remaining at the end of each experiment from the total weight of diet provided. The weight of feces produced by the larvae fed on each soybean cultivar was recorded daily. All of the calculations to determine the nutritional parameters were based on dry-weight determinations made after the extra

specimens including the pods, feces and larval to adult stages (20 specimens for each) had been oven dried (48 hours at 60°C) to a constant weight (Naseri et al., 2010 a).
The following formulae can be used to calculate *CI* (consumption index), *AD* (approximate digestibility), *ECI* (efficiency of conversion of ingested food) and *ECD* (efficiency of conversion of digested food) (Waldbauer, 1968):

$$CI = E/A$$

$$AD = E\text{-}F/E$$

$$ECI = P/E$$

$$ECD = P/E\text{-}F$$

where, *A* = mean dry weight of insect over unit time, *E* = dry weight of food consumed, *F* = dry weight of feces produced and *P* = dry weight gain of insect.

3.1.2 Results

According to the results (Naseri et al., 2010 a) a significant difference was found within the nutritional indices especially *ECI* and *ECD* values of whole larval instars (second to fifth instars) of *H. armigera* reared on different soybean cultivars (Table 4), suggesting that the host plants can change their nutritional values. *ECI* is an overall variable of an insect's ability to utilize the food that it ingests for growth and *ECD* is a variable of the efficiency of conversion of digested food into growth (Nathan et al., 2005).
The nutritional indices of the fourth instar larvae of *H. armigera* were significantly different depending on the type of soybean cultivar (Table 5). However, no significant difference was observed on the nutritional indices of the fifth instar on soybean cultivars except for the larval weight and *ECI*. Therefore, the data obtained for the fourth and fifth instars are not coherent with each other. This may be due to this fact that the nutritional requirements of an insect change during development and such changes are typically reflected in changes of food consumption and feeding behavior (Barton Browne & Raubenheimer, 2003). In a larva, the nutritional requirements over different developmental periods are positively correlated with growth over the period, since growth is directly funded by nutrients.
According to Barton Browne & Raubenheimer (2003), total consumption in the fifth instar of *H. armigera* fed on a navy bean-based diet was about 3.5 times greater than in the fourth, mainly due to the greater rate of ingestion. Another possible reason for this variation could be due to the larval age in a particular stadium at the time of weighing. For instance, the weights of either fourth or fifth stadia are expected to be lower when the larvae are near to enter the next stadium (where the larva stops feeding while entering to next stadium) or recently entered to next stadia (where it losses some water and exuviae) as compared to the larvae growing in the middle age of any stadia. Additionally, differences in physiological changes during penultimate and ultimate instar larvae are probably responsible for the differences in data generated for these two larval instars on soybean cultivars.
Physiological changes in the nervous system of ultimate instar (fifth instar) cessation of feeding, cause wandering behavior, and metabolic changes happen in the fat body. Because of such physiological and behavioral changes, feeding period of the larvae fed on soybean cultivars was shorter in fifth instar than fourth instar, and subsequently nutritional responses of these two larval instars were different (Naseri et al., 2010 a).

The highest *ECI* value of *H. armigera* was on the cultivars Zane and M7, indicating that they were more efficient at the conversion of ingested food to biomass. As can be seen in Table 3, the larvae fed on the cultivar Sahar had the lowest value of *ECD*, which suggests that these larvae were apparently not as efficient in turning digested food into biomass. It is well known that the degree of food utilization depends upon the digestibility of food and the efficiency, which digested food is converted into biomass (Batista Pereira et al., 2002). The reduction in dietary utilization suggests that reduction in nutritional values may be resulted from both behavioral and physiological effects (Nathan et al., 2005).

Cultivar				Parameter (mean±SE)			
	FC (mg)	*FP* (mg)	*DW* (mg)	*CI*	*AD*	*ECI*	*ECD*
M7	78.89 ± 3.06b	26.67 ± 6.11a	30.725 ± 3.453a	7.351 ± 0.958a*	0.610 ± 0.042c	0.524 ± 0.040a	0.820 ± 0.046a
JK	119.15 ± 17.43a	17.55 ± 4.44a	21.580 ± 3.549a	6.906 ± 1.197ab	0.848 ± 0.070ab	0.287 ± 0.075b	0.357 ± 0.123c
Clark	84.60 ± 3.98b	21.44 ± 1.89a	16.037 ± 4.606a	4.457 ± 0.352c	0.699 ± 0.041bc	0.495 ± 0.022a	0.625 ± 0.056ab
M4	120.80 ± 18.33a	18.44 ± 3.79a	16.310 ± 4.306a	4.693 ± 1.566bc	0.857 ± 0.069a	0.281 ± 0.073b	0.357 ± 0.123c
M9	95.54 ± 9.46ab	23.89 ± 6.50a	16.037 ± 4.606a	6.939 ± 1.214ab	0.858 ± 0.064a	0.489 ± 0.052a	0.581 ± 0.077abc
L17	81.66 ± 4.59b	23.96 ± 0.66a	15.497 ± 0.911a	5.302 ± 0.331abc	0.704 ± 0.016abc	0.482 ± 0.017a	0.687 ± 0.039ab
356	88.17 ± 0.735c	23.66 ± 4.13a	24.788 ± 4.548a	4.022 ± 0.870c	0.733 ± 0.044abc	0.495 ± 0.054a	0.693 ± 0.108ab
DPX	84.60 ± 3.99b	31.67 ± 2.80a	19.034 ± 2.624a	4.236 ± 0.313c	0.841 ± 0.090ab	0.502 ± 0.041a	0.705 ± 0.117ab
BP	79.76 ± 3.07b	28.67 ± 2.74a	23.197 ± 1.494a	3.462 ± 0.152c	0.643 ± 0.020c	0.502 ± 0.033a	0.786 ± 0.065a
Zane	81.05 ± 2.81b	21.15 ± 2.01a	26.809 ± 3.221a	5.488 ± 0.922abc	0.597 ± 0.039c	0.499 ± 0.035a	0.787 ± 0.071a
Sahar	118.28 ± 15.12a	28.91 ± 2.73a	23.197 ± 1.494a	5.302 ± 0.331abc	0.843 ± 0.067ab	0.279 ± 0.068b	0.353 ± 0.119c
Gorgan3	98.77 ± 5.95ab	17.55 ± 4.26a	18.244 ± 3.975a	3.594 ± 0.222c	0.852 ± 0.060ab	0.467 ± 0.058a	0.505 ± 0.058bc
Williams	84.60 ± 3.99b	22.40 ± 1.94a	19.579 ± 2.583a	4.457 ± 0.352c	0.736 ± 0.019abc	0.456 ± 0.036a	0.621 ± 0.054ab

The means followed by different letters in the same columns are significantly different ($P < 0.01$, $P < 0.05^*$, LSD)

FC = dry weight of food consumed, *FP* = dry weight of feces produced, *DW* = mean dry weight of larvae, *CI* = consumption index, *AD* = approximate digestibility, *ECI* = efficiency of conversion of ingested food and *ECD* = efficiency of conversion of digested food

Table 4. Nutritional indices of whole larval instars (second to fifth instars) of *Helicoverpa armigera* on different soybean cultivars

Cultivar				Parameter (mean±SE)			
	FC (mg)	*FP* (mg)	*DW* (mg)	*CI*	*AD*	*ECI*	*ECD*
M7	80.62 ± 5.73a*	25.95 ± 3.60ab*	18.102 ± 2.563a	5.309 ± 0.466a	0.779 ± 0.043abc	0.149 ± 0.016a	0.244 ± 0.044abc
JK	69.73 ± 5.12abc	23.35 ± 5.26ab	18.891 ± 2.109a	3.357 ± 0.415cdef	0.610 ± 0.055def	0.147 ± 0.020a	0.147 ± 0.028e
Clark	76.43 ± 5.19ab	19.95 ± 3.99abc	20.767 ± 2.565a	3.496 ± 0.405cde	0.699 ± 0.047bcde	0.125 ± 0.021a	0.251 ± 0.043ab
M4	55.37 ± 4.56c	11.28 ± 0.15c	16.330 ± 1.570a	3.390 ± 0.279cdef	0.783 ± 0.022abc	0.126 ± 0.012a	0.147 ± 0.006e
M9	75.85 ± 8.78ab	17.66 ± 4.13bc	17.860 ± 2.066a	4.247 ± 0.492bc	0.754 ± 0.050abc	0.133 ± 0.017a	0.191 ± 0.032bcde
L17	62.12 ± 4.93bc	26.55 ± 7.05ab	17.653 ± 2.357a	3.377 ± 0.313cdef	0.603 ± 0.083def	0.138 ± 0.036a	0.211 ± 0.038abcde
356	53.82 ± 4.83c	11.46 ± 2.36c	20.150 ± 1.714a	2.671 ± 0.239ef	0.807 ± 0.029ab	0.098 ± 0.015a	0.133 ± 0.023e
DPX	64.02 ± 8.63abc	21.42 ± 3.85abc	17.824 ± 2.240a	3.724 ± 0.459bcd	0.532 ± 0.071f	0.124 ± 0.013a	0.155 ± 0.024de
BP	81.72 ± 7.62a	22.55 ± 3.92ab	17.335 ± 1.973a	4.716 ± 0.440ab	0.722 ± 0.039bcd	0.106 ± 0.011a	0.164 ± 0.023bcde
Zane	69.75 ± 7.17abc	27.04 ± 4.52ab	19.342 ± 2.240a	2.431 ± 0.216f	0.867 ± 0.019a	0.150 ± 0.019a	0.299 ± 0.049a
Sahar	69.40 ± 6.20abc	22.68 ± 3.24ab	19.012 ± 2.359a	4.609 ± 0.477ab	0.659 ± 0.061cdef	0.113 ± 0.016a	0.158 ± 0.022cde
Gorgan3	64.49 ± 8.20abc	17.98 ± 4.37bc	22.869 ± 2.894a	3.039 ± 0.303def	0.713 ± 0.045bcde	0.127 ± 0.017a	0.211 ± 0.029abcde
Williams	64.87 ± 4.83abc	30.38 ± 4.44a	16.958 ± 2.229a	3.825 ± 0.284bcd	0.585 ± 0.062ef	0.152 ± 0.021a	0.241 ± 0.042abcd

The means followed by different letters in the same columns are significantly different ($P < 0.01$, $P < 0.05^*$, LSD) *FC* = dry weight of food consumed, *FP* = dry weight of feces produced, *DW* = mean dry weight of larvae, *CI* = consumption index, *AD* = approximate digestibility, *ECI* = efficiency of conversion of ingested food and *ECD* = efficiency of conversion of digested food

Table 5. Nutritional indices of fourth instar larvae of *Helicoverpa armigera* on different soybean cultivars

The body weight is an important indicator of fitness of an insect, which can be measured easily (Liu et al., 2004). The pupae produced by the larvae reared on Sahar and M4 were lighter than those produced by the larvae reared on the other cultivars (Table 7). This reinforces the suggestion that Sahar and M4 are more unsuitable host plants for *H. armigera* larvae in comparison with the others. Liu et al. (2004) showed that the pupal weight of *H. armigera* was affected by different host plants, which was ranged from 167.1 ± 3.9 mg on tomato to 285.2 ± 4.2 mg on corn. Furthermore, the heaviest pupal weight of *H. armigera* was on cultivar Clark.

Despite significant difference between the pupal weight of *H. armigera* on 13 soybean cultivars, no significant differenc was observed for adult weight on these cultivars. Pupal and adult phenotypic characteristics may be affected by the quality of larval food. Apparent influences of larval diets are body distortions in the pupa and wing malformations in the adult (Rosenthal & Dahlman, 1975). The fecundity (number of eggs laid per female),

longevity and fore-wing area of lepidopteran adults are the most commonly used parameters to determine the larval diet effect on adult stage. Probably, because of no significant effect of the soybean cultivar as larval food on the adult size (fore-wing area) of the pest, this effect has disappeared in the adult. In addition, ability of an insect to store energy (e.g., pupal weight and lipids and glycogen levels) is varied depending on host plant of its larvae (Liu et al., 2007). The results of this study suggest that M7 and Zane are more nutritive and M4, Sahar and JK are less nutritive for *H. armigera* larvae compared to the others.

Cultivar				Parameter (mean±SE)			
	FC (mg)	*FP* (mg)	*DW* (mg)	*CI*	*AD*	*ECI*	*ECD*
M7	124.69 ± 9.57a	93.27 ± 9.53a	48.55 ± 3.19bcd	2.119 ± 0.167a	0.393 ± 0.054a	0.198 ± 0.018abc	0.675 ± 0.132a
JK	137.79 ± 7.99a	90.08 ± 11.35a	58.08 ± 5.31abcd	2.139 ± 0.218a	0.420 ± 0.051a	0.222 ± 0.021a	0.500 ± 0.041a
Clark	118.04 ± 8.33a	75.38 ± 10.29a	59.83 ± 3.83ab	2.051 ± 0.104a	0.401 ± 0.053a	0.163 ± 0.019bc	0.437 ± 0.070a
M4	111.68 ± 8.24a	63.09 ± 10.93a	48.32 ± 4.18cd	2.311 ± 0.170a	0.460 ± 0.075a	0.156 ± 0.017c	0.379 ± 0.056a
M9	123.54 ± 8.95a	91.36 ± 10.64a	56.98 ± 4.79abcd	2.168 ± 0.157a	0.262 ± 0.052a	0.187 ± 0.027abc	0.483 ± 0.080a
L17	107.62 ± 7.25a	73.99 ± 10.04a	52.34 ± 3.92bcd	2.056 ± 0.138a	0.429 ± 0.050a	0.193 ± 0.010abc	0.476 ± 0.060a
356	114.43 ± 6.47a	65.67 ± 8.68a	59.25 ± 3.65abc	1.931 ± 0.109a	0.458 ± 0.050a	0.231 ± 0.014a	0.513 ± 0.064a
DPX	138.60 ± 8.38a	77.33 ± 10.16a	48.19 ± 4.32cd	2.147 ± 0.192a	0.424 ± 0.062a	0.225 ± 0.018a	0.618 ± 0.116a
BP	116.33 ± 9.38a	84.62 ± 11.07a	57.65 ± 4.18abcd	2.018 ± 0.163a	0.387 ± 0.051a	0.212 ± 0.015ab	0.544 ± 0.067a
Zane	136.48 ± 9.10a	63.72 ± 7.10a	51.79 ± 5.47bcd	1.788 ± 0.220a	0.378 ± 0.047a	0.235 ± 0.018a	0.437 ± 0.070a
Sahar	115.32 ± 6.24a	60.95 ± 10.50a	47.42 ± 4.18d	2.146 ± 0.124a	0.445 ± 0.052a	0.203 ± 0.027abc	0.463 ± 0.049a
Gorgan3	120.04 ± 8.78a	51.38 ± 6.32a	54.52 ± 4.46bcd	1.788 ± 0.220a	0.461 ± 0.038a	0.203 ± 0.019abc	0.431 ± 0.053a
Williams	119.19 ± 5.85a	80.71 ± 9.31a	66.79 ± 2.97a	1.940 ± 0.095a	0.400 ± 0.050a	0.168 ± 0.017bc	0.498 ± 0.054a

The means followed by different letters in the same columns are significantly different ($P < 0.05$, LSD)
FC = dry weight of food consumed, *FP* = dry weight of feces produced, *DW* = mean dry weight of larvae, *CI* = consumption index, *AD* = approximate digestibility, *ECI* = efficiency of conversion of ingested food and *ECD* = efficiency of conversion of digested food

Table 6. Nutritional indices of fifth instar larvae of *Helicoverpa armigera* on different soybean cultivars

Cultivar	Pre-pupal weight (mg)		Pupal weight (mg)		Adult weight (mg)		Fore-wing area (cm^2)
	Wet	Dry	Wet	Dry	Wet	Dry	
M7	278.88 ± 14.57bcde	71.67 ± 3.75bcde	242.61 ± 8.99bc	84.91 ± 3.15bc	163.00 ± 7.13a	63.57 ± 2.78a	1.124 ± 0.030a
JK	299.86 ± 18.08abcd	77.06 ± 4.65abcd	245.47 ± 9.30abc	85.91 ± 3.26abc	156.80 ± 9.12a	61.00 ± 3.55a	1.081 ± 0.045a
Clark	317.73 ± 13.07a	81.66 ± 3.36a	269.50 ± 9.35a	94.33 ± 3.27a	155.50 ± 6.24a	60.65 ± 0.65a	1.144 ± 0.043a
M4	254.00 ± 9.62e	65.28 ± 2.47e	203.75 ± 7.87e	71.31 ± 2.75e	143.58 ± 6.78a	56 ± 2.64a	1.154 ± 0.041a
M9	264.00 ± 23.01de	67.85 ± 5.92de	241.79 ± 6.56bc	84.63 ± 2.30bc	163.36 ± 7.81a	63.71 ± 3.05a	1.234 ± 0.057a
L17	271.73 ± 15.24cde	69.83 ± 3.92cde	237.62 ± 5.97bcd	83.17 ± 2.09bcd	153.55 ± 6.95a	59.88 ± 2.71a	1.106 ± 0.048a
356	316.82 ± 12.18a	81.42 ± 3.13a	268.61 ± 10.35a	94.01 ± 2.62a	159.82 ± 12.65a	62.01 ± 4.91a	1.173 ± 0.055a
DPX	286.73 ± 13.34abcde	73.69 ± 3.43abcde	237.89 ± 8.24bcd	83.26 ± 2.88bcd	159.00 ± 7.71a	61.53 ± 2.98a	1.125 ± 0.033a
BP	298.18 ± 10.96abcd	76.63 ± 2.82abcd	261.89 ± 8.93ab	91.66 ± 3.13ab	160.29 ± 6.28a	62.35 ± 2.44a	1.170 ± 0.032a
Zane	313.07 ± 10.59ab	80.46 ± 2.72ab	256.87 ± 12.38ab	89.90 ± 4.33ab	157.31 ± 8.68a	61.35 ± 3.38a	1.132 ± 0.036a
Sahar	249.00 ± 9.21e	63.99 ± 2.37e	216.68 ± 8.81de	75.84 ± 3.08de	155.09 ± 8.35a	60.49 ± 3.25a	1.181 ± 0.031a
Gorgan3	307.65 ± 13.03abc	79.07 ± 3.35abc	228.72 ± 8.31cd	80.05 ± 2.91cd	148.00 ± 7.08a	57.42 ± 2.75a	1.176 ± 0.044a
Williams	293.19 ± 13.42abcd	75.35 ± 3.45abcd	255.68 ± 6.40ab	89.49 ± 2.24ab	148.77 ± 6.41a	57.87 ± 2.52a	1.100 ± 0.062a

Table 7. The mean (±SE) body weights of pre-pupa, pupa and adult stages and fore-wing area of *Helicoverpa armigera* on different soybean cultivars. The means followed by different letters in the same columns are significantly different ($P < 0.01$, LSD)

4. Soybean cultivars seeds affecting the life table parameters of *H. armigera*

Determining the effect of different diets on the life table parameters of insects is of particular importance in understanding host suitability of plant infesting species and determining magnitude of injury to the crops attacked by them (Greenberg et al., 2001). 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).

4.1 Case study

4.1.1 Experimental conditions

To study the effect of soybean cultivars seeds on the life table parameters of *H. armigera*, the artificial diet based on the seeds of various soybean cultivars including Clark, Gorgan3, L17, M7, M4, M9, Sahar, Sari, Tellar and Zane was used. The artificial diet contained: soybean

seed powder (250 g), wheat germ (30 g), yeast (35 g), sorbic acid (1.1 g), ascorbic acid (3.5 g), sunflower oil (5 ml), agar (14 g), methyl-p-hydroxy benzoate (2.2 g), formaldehyde 37% (2.5 ml) and distilled water (650 ml) (Teakle, 1991). The prepared artificial diets were kept refrigerated for no longer than two weeks before use (Soleimannejad et al., 2010). The experimental conditions to determine the life table parameters of *H. armigera* were the same as the previously described conditions on the pods of soybean cultivars (see the section 2.2).

4.1.2 Results

According to the results (Soleimannejad et al., 2010), there was strong effect of the seeds of different soybean cultivars on development time of *H. armigera* when incorporated into artificial diet (Table 8). The larvae reared on Clark and Sari had comparatively shorter development time of immature stages which was more than the value (29.7 days on cotton) previously reported on different hosts by Liu et al. (2004). However, the development time of the immature stages was lower on our artificial diets than published by Shanower et al. (1997) for *Cajanus scarabaeoides* (53 days). Slower development time on a particular host means a longer life cycle, usually a lower reproductive ability and slower population growth (Singh & Parihar, 1988). In this study the larvae which had eaten an artificial diet based on Sahar, L17, Gorgan3 and M4 completed their larval period in five instars, as reported already by Saour & Causse (1996) and Naseri et al. (2009 a). On the other examined cultivars (Clark, M7, M9, Sari, Tellar, Zane) the larvae completed development in six instars. Six instars of *H. armigera* have been reported by Goyal & Rathore (1988) and Borah & Dutta (2002).

Using Sahar, L17 and Gorgan3 diets resulted in very poor survival. Survival rate on soybean was low (12 %) in comparision with chickpea and maize as artificial diets for *H. armigera* (Singh & Rembold, 1992). The pupae produced by the larvae reared on Sahar and L17 were much lighter than others Table 8). These findings support the suggestion that Sahar and L17 are less suitable host plants for *H. armigera* larvae than other cultivars.

Adult life span was significantly different depending upon the soybean seed which the larvae had been feeding on. The adults reared as larvae on some soybean cultivars have lower longevity (Table 8) compared with values reported by Borah & Dutta (2002) (6.38: 8.66 days, male: female on pigeon pea) and Liu et al. (2004) (12.1: 14 days male: female on hot pepper). Such effects might be due to the presence of some secondary allelochemicals in seeds of these cultivars. It seems that the life span of *H. armigera* tended to be sensitive to different artificial diets.

Fecundity in heliothines is influenced by temperature, humidity, and larval and adult nutrition (Adjei-Maafo & Wilson, 1983, Liu et al., 2004). Females laid the highest number of eggs when reared on Sari compared with the other diets, and females reared on Sahar oviposited least number of eggs during their oviposition period (Table 9).

As can be seen in Table 10, the lower value of r_m is on Sahar and L17, which might be attributed to considerably lower fecundity and survivorship. Similarly a close association was found between the effects of pods and seeds of soybean cultivars on life table parameters as minimum r_m was 0.132 on L17 (Naseri et al., 2009 b). A skewed female-biased sex ratio was not observed in *H. armigera* reared on pods of soybean (Naseri et al., 2009 b) nor has this phenomenon been reported on other host plants. The main reasons for male-killing agents are less clear but clues have been provided by the timing of male death (Hurst & Majerus, 1992).

Table 8. The mean (± SE) duration of different development stages, survivorship and pupal weight of *Helicoverpa armigera* on different soybean cultivars

Cultivar	Egg period	Larval stages						Pre pupal period	Pupal period
		First	Second	Third	Fourth	Fifth	Sixth		
Clark	2.50 ± 0.12 f	4.3 ± 0.02 e	2.4 0 ± 0.24 e	2.50 ± 0.66 cd	2.10 ± 0.28 d	3.03 ± 0.05 h	2.00 ± 0.24 e	3.50 ± 0.02 c	10.81 ± 0.28 f
Gorgan3	4.50 ± 0.57 c	5.6 ± 0.12 ab	4.60 ± 0.24 bc	3.50 ± 0.24 a	3.00 ± 0.25 ac	5.70 ± 0.03 c	-	5.00 ± 0.00 b	16.39 ± 0.28 b
L17	6.00 ± 0.47 a	5.5 ± 0.33 bc	7.27 ± 0.30 a	3.40 ± 0.25 ac	3.54 ± 0.15 a	7.62 ± 0.02 a	-	4.55 ± 0.28 b	18.76 ± 0.22 a
M4	4.75 ± 0.24 bc	5.5 ± 0.09 ab	5.33 ± 0.66 b	3.50 ± 0.24 a	3.25 ± 0.20 ab	6.75 ± 0.037 b	-	4.69 ± 0.20 b	16.50 ± 0.06 b
M7	4.25 ± 0.24 cd	4.7 ± 0.06 d	3.65 ± 0.28 de	2.60 ± 0.28 cd	2.80 ±0.25 bd	4.77 ± 0.06 e	4.20 ± 0.24 b	3.50 ± 0.28 c	13.50 ± 0.07 d
M9	4.25 ± 0.24 cd	4.0 ± 0.03 e	4.00 ± 0.00 cd	2.40 ± 0.28 d	2.80 ± 0.28 bd	5.36 ± 0.06 d	4.50 ± 0.14 a	2.50 ± 0.28 d	14.50 ± 0.28 c
Sahar	5.60 ± 0.25 ab	5.8 ± 0.040 a	5.50 ± 0.28 b	3.81 ± 0.22 a	3.40 ± 0.24 ab	7.49 ± 0.04 a	-	5.80 ± 0.15 a	16.79 ± 0.20 b
Sari	3.18 ± 0.44 ef	4.7 ± 0.05 e	3.00 ± 0.40 de	3.06 ± 0.28 acd	2.50 ± 0.03cd	3.68 ± 0.05 g	2.50 ± 0.28 d	3.63 ± 0.06 c	12.42 ± 0.02 e
Tellar	4.00 ± 0.28 cde	4.2 ± 0.52 e	3.25 ± 0.25 de	2.50 ± 0.24 cd	2.75 ± 0.00bd	4.60 ± 0.03 f	3.60 ± 0.37 bc	3.40 ± 0.24 c	13.50 ± 0.28 d
Zane	3.49 ± 0.28 def	5.4 ± 0.28 c	3.00 ± 0.00 de	3.25 ± 0.28 acd	2.50 ± 0.10 cd	4.59 ± 0.07 f	3.27 ± 0.02 c	3.75 ± 0.25 c	13.20 ± 0.04 d

Values followed by the same letter in each column are not significantly different (P <0.01 ,Duncan)

Values followed by the same letter in each column are not significantly different (P <0.01; Duncan).

Table 9. The mean (± SE) adult longevity, life span, fecundity, pre- and post- oviposition and adult weight of *Helicoverpa armigera* on different soybean cultivars

Cultivar	Longevity		Whole life span		Fecundity		Pre-oviposition period	O
	Female	Male	Female	Male	Total	Daily		
Clark	17.30 ± 0.18 j	7.30 ± 0.10 j	50.92 ± 0.08 i	39.65 ± 0.18 h	1779.78 ± 51.91b	102.66 ± 2.73 b	1.10 ± 0.03 e	9.7
Gorgan3	22.30 ± 0.14 d	15.36 ± 0.18 d	70.75 ± 0.14 c	64.51 ± 0.57 d	741.21 ± 32.19 ef	33.68 ± 2.29 ef	10.22 ± 0.08b	6.3
L17	26.10 ± 0.089 a	20.60 ± 0.17 a	81.68 ± 0.29 a	76.91 ± 0.23 a	916.61 ± 66.47 e	35.23 ± 3.52 e	10.74 ± 0.06b	3.9
M4	23.57 ± 0.12 c	16.30 ± 0.15 c	74.06 ± 0.25 b	67.16 ± 0.16 c	1157.61 ± 15.16 d	48.20 ± 1.01 d	7.75 ± 0.03 c	5.2
M7	21.25 ± 0.13 e	12.22 ± 0.13 f	65.75 ± 0.32 d	56.16 ± 0.18 e	1253.89 ± 59.26 d	59.71± 2.61 d	6.81 ± 0.06 d	6.8
M9	18.65 ± 0.04 g	14.43 ± 0.23 e	63.25 ± 0.32 f	59.87 ± 0.17g	1451.29 ± 65.6 c	76.36 ± 2.83 c	3.28 ± 0.06 f	8.3
Sahar	25.37 ± 0.12 b	18.30 ± 0.10 b	79.25 ± 0.16 ab	72.77 ± 0.18 b	589.67 ± 43.58 f	23.30 ± 6.81 f	10.96 ± 0.08 a	3.3
Sari	17.30 ± 0.05 i	9.42 ± 0.11 i	54.92 ± 0.14 h	47.47 ± 0.18 i	2558.40 ± 86.83 a	149.87± 4.82 a	1.10 ± 0.05 g	10.
Tellar	19.56 ± 0.04 f	11.20 ± 0.10 g	61.75 ± 0.32 e	52.36 ± 0.32 f	1679.19 ± 25.91 b	83.10 ± 1.29 c	4.58 ± 0.05 e	7.7
Zane	17.30 ± 0.05 h	10.45 ± 0.15 h	59.70 ± 0.66 g	52.75 ± 0.02 h	1432.74 ± 58.05c	84.29 ± 3.22 c	1.75 ± 0.04 g	8.1

Cultivar	R_0	r_m	λ	T	DT
Clark	270 ± 4.2 a	0.113 ± 0.003 ab	1.121 ± 0.004 a	40.32 ± 0.61 bc	6.08 ± 0.18 e
Gorgan3	34 ± 1.1 f	0.093 ± 0.001 bc	1.078 ± 0.002 e	42.98 ± 0.57 ab	7.43 ± 0.05 ab
L17	16 ± 1.56 g	0.090 ± 0.008 c	1.086 ± 0.003 de	42.21 ± 0.95 abc	8.10 ± 0.29 a
M4	20 ± 0.90g	0.092 ± 0.005 bc	1.097 ± 0.006 cd	42.46±1.18 abc	7.69 ± 0.18 a
M7	17 ± 0.87 g	0.099 ± 0.001 abc	1.105 ± 0.001 de	45.28 ± 0.75 a	7.98 ± 0.11 a
M9	94 ± 1.01 cc	0.100 ± 0.004 abc	1.100 ± 0.003 cd	36.72 ± 1.30 d	7.34 ± 0.14 abc
Sahar	17.43 ± 0.87 cg	0.084 ± 0.001 c	1.087 ± 0.001 de	45.28 ± 0.75 a	7.98 ± 0.10 a
Sari	162.27 ± 2.49 cb	0.114 ± 0.005 a	1.116 ± 0.005 ab	40.68 ± 0.56 bc	6.18 ± 0.22 cde
Tellar	83.91 ± 0.13 d	0.100 ± 0.001 abc	1.111± 0.004 abc	39.54 ± 0.32 cd	6.70 ± 0.08 ab
Zane	153.78 ± 0.48 b	0.110 ± 0.007 ab	1.107 ± 0.007 abc	41.48 ± 0.73 bc	6.65 ± 0.35 cde

Values followed by the same letter in each column are not significantly different (P <0.01; Duncan).

Table 10. Life table parameters of *Helicoverpa armigera* on different soybean cultivars

5. Soybean cultivars seeds affecting the nutritional indices of *H. armigera*

5.1 Case study

5.1.1 Experimental conditions

A total of 50 larvae of 3rd and 4th instars in five replicates (10 larvae in each) were weighed to an accuracy of 0.001 g and provisioned on adequate and weighed amount of the rearing food. In each daily observation, all the larvae, food remains and feces were weighed and a fresh weighed amount of food provided for each larva. In the old larvae (5th instars to end of larval stage), each larva and provided food were weighted individually. Pre-pupae, pupae and adults were weighted and compared in each cohort. The nutritional indices as described by Waldbauer (1968) were calculated. All indices were calculated using dry weights. To estimate initial dry weights, three fresh larvae and three blocks of the diet were measured separately. The larvae and food were each oven-dried at 60°C for 72 h and then weighed to determine dry weights. The measured nutritional indices were relative growth rate (*RGR*), relative consumption rate (RCR), efficiency of conversion of ingested food (*ECI*), efficiency of conversion of digested food (*ECD*), approximate digestibility (*AD*) and consumption index (*CI*) and calculated as follows:

$$RGR = B/Tb$$

$$RCR = F/Tb$$

$$ECI = RGR/RCR\ (\%)$$

$$ECD = [B/\ (F\text{-}M_F)] \times 100$$

$$AD = (F\text{-}M_F)/F \times 100$$

$$CI = F/b\ (mg/mg/d)$$

where B= weight gained in feeding period (weight of live insects on the last day - weight of insects at first day (mg)), b = mean dry weight of larva during the feeding period (mg), T= feeding period (day), F= weight of food ingested (mg), M_F = weight of feces (mg). The weights (mg) of pupae and adults were recorded on the second day after pupation and adult emergence.

Effects of the main factor (host plant) on the life table parameters and nutritional indices of *H. armigera* were analyzed using ANOVA multiple comparisons by Duncan test. A t-test was used to compare nutritional index values between young and old larvae.

5.1.2 Results

Different soybean seed diets had significant effects on nutritional indices of *H. armigera*. The lowest *AD* on Clark (48.1%) and the highest ECD on Sari (38.3%) indicated that these seeds had a large effect on the physiology of *H. armigera.* The highest value of *AD* in young larvae was noticed on Sahar (9.57 %), however the lowest *AD* in old larvae (48.09% on Clark) was five times higher, and this significant difference may be related to better feeding ability of *H. armigera* in these stages than diet effects.

Significant differences of *ECD* and *ECI* were observed in both young and old larvae reared on seeds of various soybean cultivars (Table 11). The lowest value of *AD* in old larvae was 48.1% higher than that reported by Wang et al. (2006) on wheat based artificial diet. This could be in related to higher performance of soybean compared with wheat as an artificial diet.

Among soybean cultivars, Sahar has presented as the most resistant cultivar to *Tetranychus*

Cultivar	*RGR* (mg/mg/d)	*RCR* (mg/mg/d)	*ECI* %	*ECD* %	*CI* (mg/mg/d)	*AD* %
Young Larvae (3th and 4th instars)						
Clark	0.08 ± 0.002 a	2.62 ± 0.59 a	3.11 ± 0.19 a	3.17 ± 0.12 a	2.44 ± 1.02 a	9.15 ± 0.67 b
Gorgan3	0.01 ± 0.003 e	1.64 ± 0.27 cd	0.91 ± 0.27 de	0.90 ± 0.079 c	1.53 ± 2.66 c	9.47 ± 0.65 a
L17	0.01 ± 0.003 e	1.60± 0.76 d	0.84 ± 0.06 e	0.88 ± 0.06 c	1.40 ± 2.73 c	9.50 ± 0.55 a
M4	0.02 ± 0.002 d	1.82 ± 0.83 cd	0.98 ± 0.12 de	1.32 ± 0.18 bc	1.61 ± 1.44 bc	9.47 ± 0.68 a
M7	0.03 ± 0.011 c	1.92 ± 0.25 cd	1.49 ± 0.15 cd	1.74 ± 0.24 b	1.88 ± 1.15 bc	9.40 ± 1.45 ab
M9	0.02 ± 0.003 c	1.83 ± 0.87 cd	1.28 ± 0.09 cde	1.56 ± 0.16 b	1.74 ± 4.76 bc	9.45 ± 0.71 ab
Sahar	0.01 ± 0.000 e	1.47 ± 0.88 d	0.79 ± 0.14 e	0.85 ± 0.17 c	1.26 ± 0.99 c	9.57 ± 0.57 a
Sari	0.05 ± 0.003 b	2.20 ± 0.35 ab	2.51±0.76 b	2.71 ± 0.87 a	2.22 ± 3.22 a	9.16 ± 0.42 b
Tellar	0.04 ± 0.002 bc	2.05 ± 0.16 bc	1.83 ± 0.22 c	1.91 ± 0.23 b	2.08 ± 2.90 a	9.37 ± 1.35 ab
Zane	0.04 ± 0.002 bc	1.94 ± 0.39 cd	1.65 ± 0.10 c	1.80 ± 0.11 b	2.02 ± 2.62 a	9.35±1.34 ab
Old Larvae (5th instars to end of larval stage)						
Clark	0.59 ± 0.01 a	3.36 ± 0.28 a	17.24 ± 0.77 a	36.40 ± 2.46 a	3.02 ± 0.10 a	48.09 ± 2.42 c
Gorgan3	0.32 ± 0.02 de	2.62 ± 0.07 bcd	10.12 ± 1.03 d	15.01 ± 2.73 c	1.14 ± 0.11 cd	63.52 ± 2.34 a
L17	0.23 ± 0.01 d	2.33 ± 0.11 cd	12.28 ± 0.99 bcd	21.43 ± 1.98 bc	1.08 ± 0.16 d	64.62 ± 2.184 a
M4	0.27 ± 0.01 de	2.57 ± 0.12 bcd	10.54 ± 1.40 cd	18.39 ± 1.41 bc	1.21 ± 0.10 cd	61.99 ± 3.65 a
M7	0.36 ± 0.01 c	2.65 ± 0.10 bc	13.80 ± 1.39 b	24.98 ± 1.60 b	1.58 ± 0.12 bcd	61.08 ± 3.22 ab
M9	0.35 ± 0.01 c	2.64 ± 0.16 bc	13.24 ± 0.41 bc	22.20 ± 1.73 b	1.38 ± 0.15 bcd	61.28 ± 5.112 ab
Sahar	0.20 ± 0.03 e	2.13 ± 0.12 d	9.81 ± 0.63 d	14.81 ± 1.38 c	0.94 ± 0.28 d	66.97 ± 2.48 a
Sari	0.45 ± 0.01 b	3.02 ± 0.23 ab	15.23 ± 1.04 ab	38.30 ± 2.94 a	1.93 ± 0.31 b	50.58 ± 3.04 c
Tellar	0.39 ± 0.01 bc	2.68 ± 0.15 bc	14.76 ± 0.83 ab	33.37 ± 2.34 a	1.60 ± 0.07 bcd	53.05 ± 2.91 bc
Zane	0.40 ± 0.02 bc	2.71 ± 0.21 bc	15.05 ± 0.64 ab	32.53 ± 2.50 a	1.78 ± 0.21 bc	50.91 ± 2.66 c

Values followed by the same letter in each column of larvae stages groups are not significantly different (Duncan).

*values of each nutritional index on each cultivar between larval stage groups (young and old larvae) are significantly different, ($P < 0.01$, t- test).

Table 11. Nutritional indices of Young (3th and 4th instars) and old larvae (5th instars to end of larval stage) of *Helicoverpa armigera* on different soybean cultivars

*urtica*e (Koch) and L17 was classified as susceptible (Sedaratian et al., 2009), however L17 was resistant cultivar for *H. armigera*. Overall we suggest that Sahar could serve as a key tool in integrated pest management in soybean fields due to its resistance to *H. armigera* and *T. urtica*e. Our observations provided evidence that seeds from different soybean cultivars as a diet for immatures affected life history and nutrition of *H. armigera*.

6. Soybean cultivars pods affecting digestive proteolytic and amylolytic activities of *H. armigera*

Insect digestive proteases catalyze the release of peptides and amino acids from dietary proteins in the insect digestive system to meet its nutritional requirements (Terra & Ferreira, 1994). The larval midgut in Lepidoptera harbors complex digestive proteolytic activities including trypsins, chymotrypsins, elastases, cathepsin-B like proteases, aminopeptidases and carboxypeptidases. Works on the protease digestive enzymes of lepidopteran insects showed that they prevalently (95% of total digestive activity) depending on serine proteases for protein digestion (Bown et al., 1997). In addition to complexity of multiple protease specificities, there usually exists a set of diverse protease isoforms. The gut of *H. armigera* has been known to contain around 20 different types of active serine protease isoforms at any given moment (Purcell et al., 1992). The α-amylases (α-1, 4-glucan-4-glucanohydrolases; EC 3.2.1.1) are hydrolytic enzymes that are found in microorganisms, plants and animals, which catalyze the hydrolysis of α-D-(1, 4)-glucan linkage in starch and related carbohydrates (Stroble et al., 1998). In insects, the activity of digestive enzymes such as proteases and α-amylases depends upon the nature of food sources or chemical substances consumed (Slansky, 1982). Protease and α-amylase activities in crude extracts of larval guts of *H. armigera* have been described by some researchers (e.g. Patankar et al., 2001; Chougule et al., 2005; Kotkar et al., 2009).

6.1 Case study

6.1.1 Experimental conditions

In order to preparation of crude midgut enzyme extracts of *H. armigera* larvae, fifth-instar larvae reared on either cowpea-based artificial diet or different soybean cultivars for 24 h are cold-immobilized, rapidly dissected under a stereomicroscope. The haemolymph is washed away with precooled distilled water, and the midguts are then cleaned by removal of extraneous tissues. The midguts, including contents, are collected into a known volume of distilled water, homogenized with a hand-held glass grinder on ice and the homogenates centrifuged at 16,000 × g for 10 min at 4°C. The resulting supernatant is collected, frozen in aliquots and stored at -20°C until required for protease and amylase assays (Naseri et al., 2010 b).

General proteolytic activity present in the midgut of *H. armigera* larvae fed either on artificial diet or different soybean cultivars can be determined using azocasein as a substrate at the pH optimum. The universal buffer system (50 mM sodium phosphate-borate) is used to determine the pH optimum of proteolytic activity over a pH range of 7 to 12. To determine the azocaseinolytic activity, the reaction mixture containing 80 µl of 1.5% azocasein solution in 50 mM universal buffer pH 12 and 50 µl of crude enzyme is incubated at 37°C for 50 min. Proteolysis is stopped by the addition of 100 µl of 30% trichloroacetic acid (TCA), followed by cooling at 4°C for 30 min and centrifugation at 16,000 × g for 10 min. An equal volume of 2 M NaOH is added to the supernatant and the absorbance is measured at 440 nm.

Appropriate blanks in which TCA had been added prior to the substrate are prepared for each assay. Unit activity is expressed as an increase in optical density per milligram protein of the tissue min^{-1} due to ***azocasein*** proteolysis (Naseri et al., 2010 b)

Digestive trypsin-, chymotrypsin- and elastase-like activities of the larvae fed either on artificial diet or soybean cultivars using final concentrations of 1 mM BAρNA, 1 mM SAAPFρNA and 1 mM SAAAρNA as substrates, respectively were estimated. A reaction mixture consisted of 20 µl enzyme extract for trypsin- and elastase-like activities and 10 µl enzyme extract for chymotrpsin-like activity, 75 µl universal buffer at the appropriate pH optimum (pH 10.5 for trypsin- and chymotrpsin-like enzymes and pH 11 for elastase-like enzyme), and 5 µl of the above-mentioned substrate. Absorbance was then measured at 405 nm for 40 min (at 2, 1 and 4 min time intervals, respectively). All assays were carried out in triplicate against appropriate blanks (Naseri et al., 2010 b).

The dinitrosalicylic acid (DNSA) method (Bernfeld, 1955), with 1% soluble starch as the substrate can be used to assay digestive amylolytic activity of *H. armigera* larvae fed either on artificial diet or the different soybean cultivars. According to this method, fifty microliters of the enzyme are incubated with 250 µl universal buffer pH 10 and 20 µl soluble starch for 30 min at 37°C. The reaction is stopped by addition of 50 µl DNSA and heating in boiling water for 10 min. The absorbance is then read at 540 nm after cooling on ice. One unit of amylase activity is defined as the amount of enzyme required to produce 1 mg maltose in 30 min at 37°C under the given assay conditions. All assays are performed in triplicate (Highley, 1997; Naseri et al., 2010 b).

We determined the effect of different protease inhibitors on proteolytic activities of midgut extract of *H. armigera* larvae. Chemical and plant inhibitors are used at final concentrations of: 1 mM PMSF (serine protease inhibitor), 0.5 mM TLCK (trypsin inhibitor) and 0.05 mM chymostatin (chymotrypsin inhibitor), 0.002 mM SKTI (trypsin inhibitor), 0.002 mM STI (trypsin inhibitor) and 0.002 mM SBBI (trypsin-chymotrypsin inhibitor). All inhibition assays are conducted as described in the enzyme assay section except that the enzyme extract and inhibitor are pre-incubated in the buffer (pH optimum) at room temperature for 15 min prior to addition of the substrate (Naseri et al., 2010 b).

To determine the effect of different combinations of protease inhibitors on endogenous proteolytic activity of *H. armigera*, fifth instar larvae (20 larvae) are fed for 24 hours on artificial diet containing either 0.5% (w/v) SKTI, STI or SBBI or control diet (without any inhibitor). The larvae are placed in 250 ml plastic container with holes pierced in the lid, and lined with tissue paper to take out moisture. After larval feeding for 24 hours, the midguts are dissected and the midgut enzymes are prepared as above. Relative contributions of different proteolytic activities are assessed using combinations of inhibitors in assays of general and specific proteolytic activities using appropriate substrates. The percentage inhibition of general and specific proteolytic activities by individual inhibitors, or mixture of inhibitors, is measured (Naseri et al., 2010 b).

The visualization of protease activity present in homogenates of larval midguts fed on different soybean cultivars is carried out after non-denaturing SDS-polyacrylamide gel electrophoresis (PAGE) using the procedure of Garcia-Carreno et al. (1993) with minor modification (Naseri et al., 2010 b). Electrophoresis is performed in a 7.5% (w/v) separating gel and a 4% stacking gel. The sample buffer contained 25% glycerol, Tris-Hcl 0.2 M (pH 6.8), 5% SDS and 2.5% bromophenol blue, but no mercaptoethanol, and was not boiled. Electrophoresis is conducted at room temperature at a constant voltage of 110 V until the blue dye reached the bottom of the slab gel. For visualization of protease activity, gels are

washed by shaking gently in 0.1 M phosphate buffer (pH 7.5) containing 2.5% triton X-100 thrice for 10 min, followed by 0.1 M borate buffer (pH 8) for 30 min. Gels are then incubated in 0.5% casein for 120 min, and gel strips stained with commassie blue to detect protease activity bands as clear zones against a dark blue background.
Protein concentrations were determined by the method of Bradford (1976) using bovine serum albumin as a standard (2, 1.5, 1, 0.5, 0.25, 0.125 and 0.063 mg ml^{-1}).

6.1.2 Results

Helicoverpa armigera larvae show complicated and diverse forms of proteolytic digestion that is influenced by the host plant on which they are feeding (Patankar et al., 2001; Chougule et al., 2005). We investigated how diet affected gut proteolytic activity and subsequent sensitivity to inhibition by plant-derived or chemical protease inhibitors (PIs) (Naseri et al., 2010 b). The highest level of general proteolytic activity was in the artificial diet-fed larvae (Figure 1), suggesting its nutritionally balanced composition. Artificial diets are usually complete nourishments formed for high insect performance and commonly considered to be better than natural diets (Hari et al., 2007). According to Kotkar et al. (2009) *H. armigera* fed on artificial diet completed its life cycle somewhat early compared with natural diets. Among different soybean cultivars, the highest general proteolytic activity was in the larvae reared on L17, M4 and Sahar, indicating the presence of some PIs on these cultivars, leading to hyperproduction of proteases by midgut cells of *H. armigera* in response to protease inhibition by PIs. The larvae of *H. armigera* fed on chickpea show more than 2.5 to 3- fold protease activity compared with those reared on the other host plants (Patankar et al., 2001). Higher protease activities in the chickpea or artificial diet-fed larvae may be due to either high protein content of the diet or response of the insect to the dietary PIs which partly inhibit the activity of midgut proteases (Patankar et al., 2001). Furthermore, hyperproduction of proteases in response to consumed PIs leads to an additional load on the insect for energy and essential amino acids resulting in postponement of the insect growth and development (Broadway & Duffy, 1986).

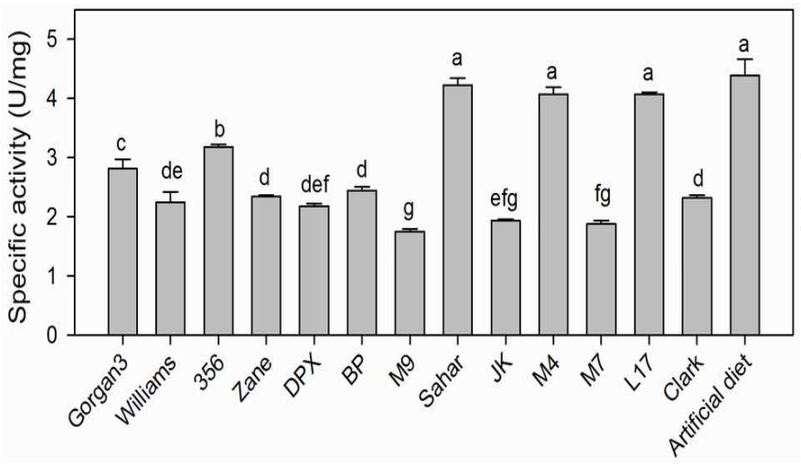

Fig. 1. General proteolytic activity of midgut extracts from *Helicoverpa armigera* larvae reared on either artificial diet or different soybean cultivars using azocasein as substrate, pH 12. Bars represent means of three independent estimations associated with standard error (P = 0).

The highest trypsin- and elastase-like activities were also in artificial diet-fed larvae compared with the soybean cultivars (Figure 2). Among soybean cultivars, the activity of trypsin-like enzymes in the midgut extract of larvae reared on L17 and Sahar was the lowest. It could be suggested that the inhibition of tryptic activity by PIs present in these two cultivars happened probably to decrease activity of trypsin-like enzymes in midgut extracts of the larvae fed on these cultivars. However, the larvae reared on L17 and Sahar had the highest chymotryptic activity compared with the other cultivars may be because of overexpression of chymotrypsin-like enzymes in response to the trypsin inhibitors on these cultivars.

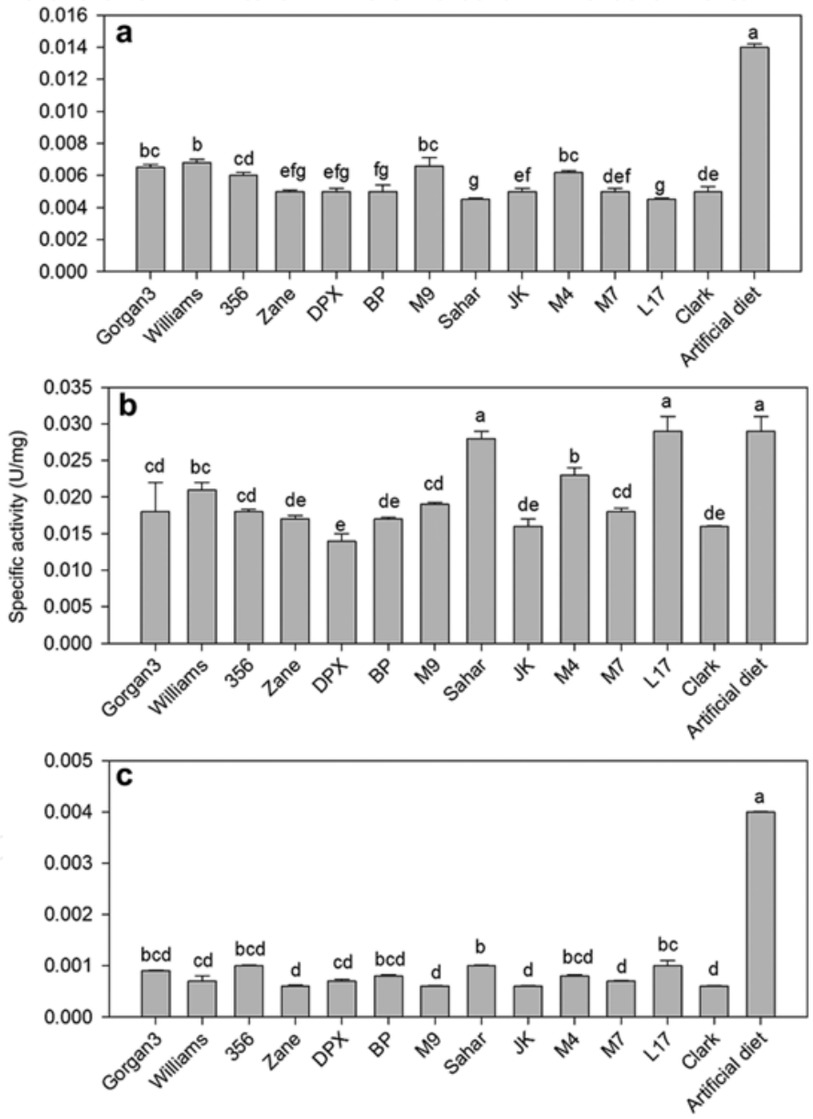

Fig. 2. Trypsin- (a), chymotrypsin- (b) and elastase-like (c) activities of midgut extracts from *Helicoverpa armigera* larvae reared on either artificial diet or different soybean cultivars using BAρNA, pH 10.5; SAAPFρNA, pH 10.5 and SAAAρNA, pH 11 as substrates, respectively. Bars represent means of three independent estimations associated with standard error (P = 0).

The same result on elastase-like activity was detected in Sahar fed larvae in response to the presence of trypsin inhibitors of this cultivar. Previous studies pointed out that *H. armigera* fed on L17 and Sahar had a weakly potential to population increase and these cultivars were less suitable host plants for the growth and development of *H. armigera* than the other cultivars tested (Naseri et al., 2009 a,b). By composing the results of our earlier studies on demographic parameters of *H. armigera* on L17 and Sahar and results of proteolytic activity of the larvae fed on these two cultivars, it would be deduced that, perhaps, the presence of some PIs in these cultivars, which acting as antibiosis agents were responsible for a weakly performance of *H. armigera* reared on these cultivars. Generalized overexpression of some trypsin-like and chymotrypsin-like proteases was reported in *H. armigera* fed on various non-host plant protease inhibitors (Chougule et al., 2005).

Digestive amylolytic activity of *H. armigera* is affected by either artificial diet or different soybean cultivars (Naseri et al., 2010 b). Artificial diet-fed larvae of *H. armigera* showed nearly two times higher midgut amylase activity than those fed on soybean cultivars (Figure 3). Such inconsistency in enzyme activities of the artificial and natural diet-fed insects has been reported by Chougule et al. (2005). Artificial diet-fed larvae of *H. armigera* are healthier and they can complete their life history earlier compared with natural diet, indicating that the artificial diet does not exert pressure for a metabolic adjustment. There were little significant differences in amylolytic activity of midgut extracts from *H. armigera* larvae reared on the most soybean cultivars. It could be suggested that since the total carbohydrate substance in soybean cultivars was probably equal with each other, thus any high significant differences in amylase activity of the larvae fed on different soybean cultivars were not detected. However, the amylolytic activity was the highest on M4 and lowest on Williams and DPX. Kotkar et al. (2009) have indicated that natural diet-fed *H. armigera* had three times lower gut amylase activities compared with those fed on artificial diet. It was also reported by above-mentioned researchers that the larvae reared on legume and vegetable crops showed double gut amylolytic activity than those fed on ornamental and cereal crops.

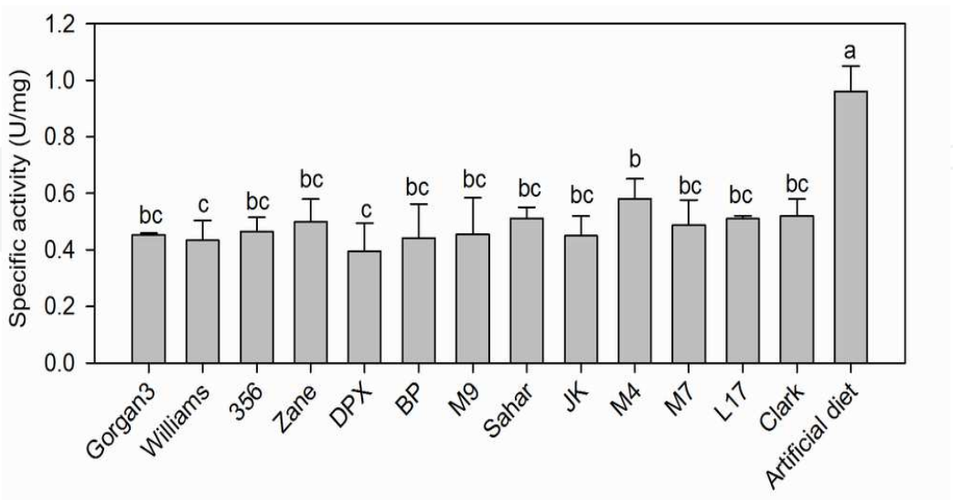

Fig. 3. Amylolytic activity of midgut extracts from *Helicoverpa armigera* larvae reared on either artificial diet or different soybean cultivars using 1% starch as substrate, pH 10. Bars represent means of three independent estimations associated with standard error (P = 0).

According to Figure 4, since the azocaseinolytic activity of STI-fed larvae was lower than SBBI- or SKTI-fed larvae, it could be suggested that the recompense of proteolytic inhibition by means of hyperproduction of enzymes in response to STI had no effect on general proteolytic activity.

The percentage inhibition of serine proteases by PMSF in artificial diet and artificial diet containing protease inhibitors indicates that higher inhibition of enzyme in SBBI- and SKTI-fed larvae by PMSF may be due to the induction of hyperproduction of serine proteases by these two plant protease inhibitors (Figure 5a). According to Bown et al. (1997), PMSF could inhibit 28% of the proteolytic activity of *H. armigera* larvae fed on an artificial diet.

The percentage inhibition of tryptic activity by STI in inhibitor-free diet was more than that of STI-fed larvae, may be attributed to the overexpression of trypsin-like enzymes to compensate for inhibitory effect of STI. Inhibitory activity of STI in inhibitor-free diet was more 2-fold than that of TLCK. The comparison of inhibitory effect of *in vitro* use of STI in STI-fed larvae with the inhibitory effect of *in vitro* use of SBBI and SKTI in the larvae reared on SBBI and SKTI indicates that the STI diet-fed insects compensate the enzyme inhibition by hyperproduction of proteolytic enzymes (Figure 5b) (Naseri et al., 2010 b).

Although the inhibitory effect of STI *in vivo* and *in vitro* was more than SBBI and SKTI, it could not completely inhibit tryptic activity, probably because of the high sensitivity to STI, leading to the overexpression of trypsin-like proteases to compensate enzyme inhibition (Naseri et al., 2010 b). Assays with *Spodoptera exigua* (Hübner) larvae fed on PIs-containing diets have showed increases (Broadway and Duffy, 1986) or reductions (Lara et al., 2000) of tryptic activity. Johnston et al. (1993) have reported that STI was more effective on the inhibition of *H. armigera* larval growth and larval midgut protease activities than SBBI.

According to the reports of Broadway and Duffy (1986) the potato protease trypsin inhibitor (PPTI) and soybean trypsin inhibitor (STI) had no effects on the *in vivo* digestion of protein, and the trypsin activity was significantly elevated. Thus, they concluded that the mode of action of protease inhibitors was to cause the hyperproduction of trypsin. For *H. armigera*, Johnston et al. (1993) reported that SKTI caused continued stoppage in the *in vivo* trypsin-like enzyme activity.

Chymotryptic activity of the larvae fed on artificial diet and artificial diet containing plant protease inhibitors was powerfully inhibited by chymostatin, indicating the presence of high levels of chymotrypsin-like enzyme in these larvae. STI-fed larvae did not show the inhibition of chymotrypsin, suggesting the lack of inhibitory effect by STI on chymotrypsin-like activity (Figure 5c) (Naseri et al., 2010 b).

SBBI inhibited trypsin-like activity more than chymotrypsin-like, in contrast to *Heliothis virescens* (Fabricius) and *lacanobia oleracea* L. larval gut proteases, where it inhibited chymotrypsin-like activity more than trypsin-like (Johnston et al., 1995; Gatehouse et al., 1999). Chougule et al. (2005) noted that SBBI inhibited chymotrypsin-like and trypsin-like activity of *Mamestra brassicae* L. gut proteases almost equally.

High inhibitory effect of chymostatin in PIs-fed larvae demonstrated that the insect's chymotrypsin-like enzymes had not any sensitivity to the diets including STI and SBBI. Jongsma et al. (1996) have reported that the chymostatin inhibited 88% of proteolytic activity of *S. exigua* larvae. The gut protease activity of *H. armigera* larvae reared on cotton, okra and pigeonpea was inhibited 39, 45 and 78%, respectively by chymostatin (Patankar et al., 2001).

Visualization of the protease activity of midgut extracts from *H. armigera* larvae reared on different soybean cultivars using substrate SDS-PAGE electrophoresis revealed the presence of at least seven bands (Naseri et al., 2010 b). Although the majority showed similar profiles,

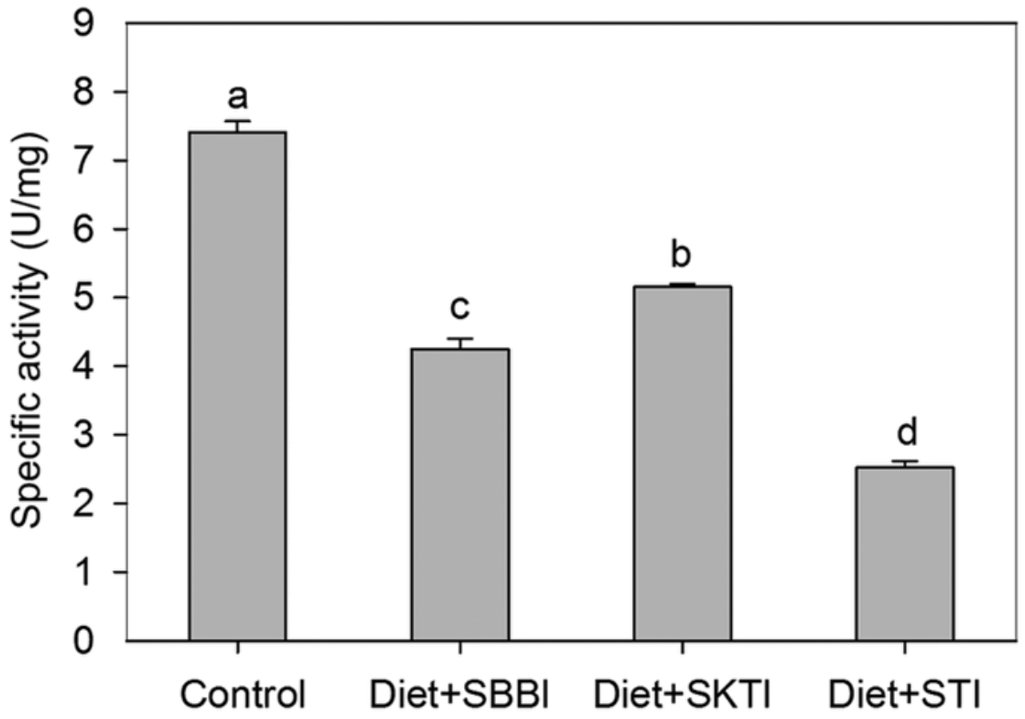

Fig. 4. The effects of three protease inhibitors, when incorporated into artificial diet at a single concentration (0.5% W/V) on general proteolytic activity of *Helicoverpa armigera* larvae using azocasein as substrate, pH 12. Bars represent means of three independent estimations associated with standard error (P = 0). STI: soybean trypsin inhibitor; SKTI: soybean Kunitz trypsin inhibitor; SBBI: soybean Bowman-Birk inhibitor.

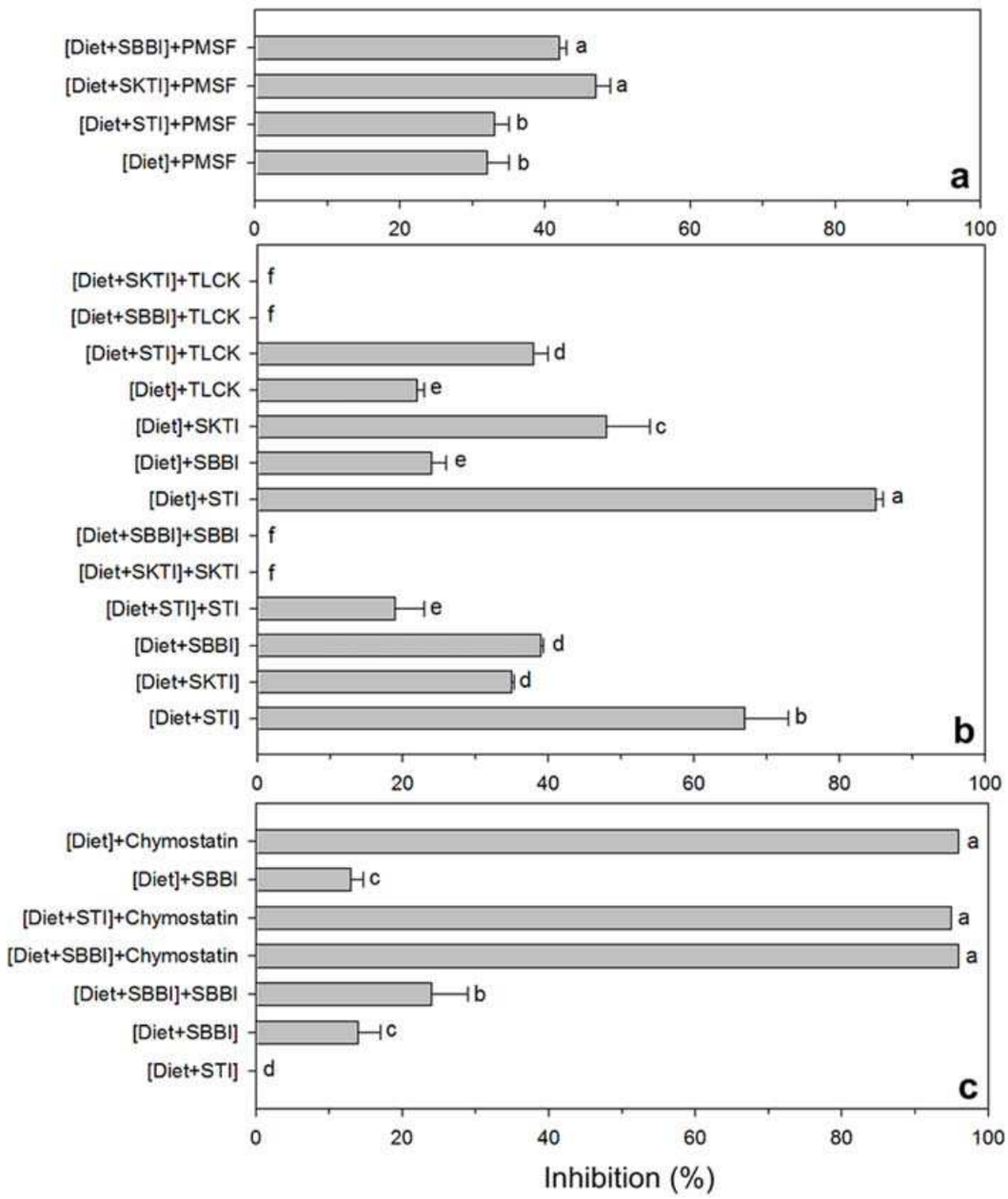

Fig. 5. Effect of different combinations of protease inhibitors *in vitro* and *in vivo* on enzyme inhibition (%) of gut protease activity (a), trypsin inhibition (%) (b) and chymotrypsin inhibition (%) (c) of gut enzyme extracts from *Helicoverpa armigera* larvae using azocasein, pH 12; BAρNA, pH 10.5 and SAAPFρNA, pH 10.5 as substrates, respectively. Bars represent means of three independent estimations associated with standard error (P = 0). The assay treatments were presented as "[*in vivo*] + *in vitro*". STI: soybean trypsin inhibitor; SKTI: soybean Kunitz trypsin inhibitor; SBBI: soybean Bowman-Birk inhibitor; TLCK: Nα-ρ-tosyl-$_L$-lysine chloromethyl ketone; PMSF: phenylmethylsulfonyl fluoride.

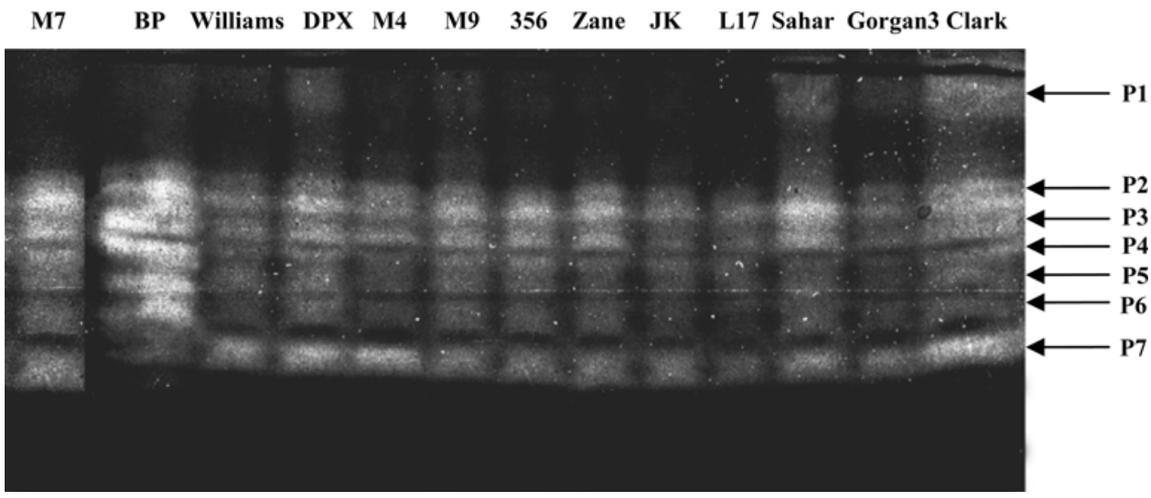

Fig. 6. Zymogram analysis of casein hydrolytic activity of midgut extracts from *Helicoverpa armigera* larvae reared on different soybean cultivars. Protease activity bands are indicated by arrows (P1-P7).

both qualitatively and quantitatively, four appeared to exhibit lower levels of activity (Williams, JK, L17 and Gorgan3). Three cultivars (Clark, Sahar and BP) appeared to exhibit different expression patterns especially due to high molecular weight proteases. However, perhaps of greater importance was the fact that M7, and in particular BP and Clark, exhibited different expression patterns (Figure 6). Visualized general proteolytic patterns in zymogram did not match completely with this issue except for the cultivar Sahar. This may be related to inactivation of the over-expressed proteases during gel electrophoresis**.**

7. Conclusion

All of the case studies substantiated in this chapter are to prove this fact that host plant cultivars (e.g. soybean cultivars) can significantly affect the life table parameters, nutritional indices and digestive enzymes activity of *H. armigera*, and can be used as a tool to control this devastating pest in integrated pest management programs. In this chapter, to demonstrate such influence of different crop cultivars on the performance of *H. armigera*, we reconsidered the works conducted on crop cultivars (including soybean cultivars and other host crops) effect on the life table parameters and nutritional indices of *H. armigera*. A complementary case study was also considered on digestive proteolytic and amylolytic activities of the larvae fed on different soybean cultivars, and response of the larvae to feeding on some soybean-based protease inhibitors. We have also emphasized on the influence of the seeds of different soybean cultivars on the life table parameters and nutritional indices of *H. armigera* when incorporated into artificial diets. It would be concluded that the leaves and green pods of the different soybean cultivars and the seeds of the examined soybean cultivars differed greatly in suitability as diets for *H. armigera* when measured in terms of the life table parameters (e.g., life history, fecundity and population growth parameters) and nutritional indices. By combining the data resulted from the studies on digestive enzymes activity, the life table parameters and nutritional indices of *H. armigera* reared on the leaves and pods of different soybean cultivars and findings of the life table parameters and nutritional indices of this pest on different soybean cultivars seeds, it could be concluded that *H. armigera* did not perform well on some

cultivars such as Sahar and L17, and therefore these cultivars were partially resistant to *H. armigera*. Among soybean cultivars, Sahar was the most resistant cultivar to *Tetranychus urtica*e (Koch) and L17 was reported as susceptible (Sedaratian et al., 2009). Our study, however, indicated that L17 was resistant cultivar to *H. armigera*. In general we conclude that Sahar could serve as a key tool in integrated pest management in soybean fields because of its resistance to *H. armigera* and *T. urtica*e.

The information obtained from these researches will be important in the management of *H. armigera* by providing a better understanding of its life history and its ability to survive on different host plants. Such information and further field and laboratory experiments are needed in developing integrated pest management (IPM) program of this pest and other economically important pests like spider mites (e.g. Sedaratian et al., 2009; Sedaratian et al., 2010).

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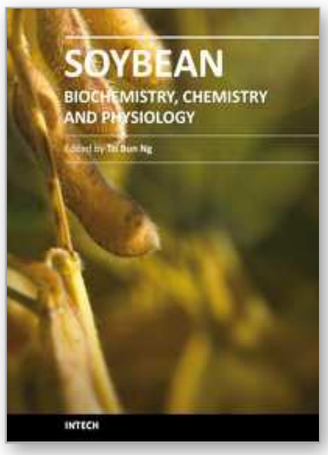

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