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Effect of different sunflower cultivars on nutritional and physiological responses of *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae)

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Abstract. *Helicoverpa armigera* (Hübner) is one of the invasive pests of crops worldwide, and several studies have focused to compare the growth, consumption, and digestion of *H. armigera* larvae on different plants. However, studies evaluating the insect's food consumption and digestive physiological response using biochemical profile of sunflower cultivars are scarce. In this research, the impacts of various sunflower cultivars (Golsa, Ghasem, Shams, and Zarrin) based on artificial diet were evaluated on enzymes activity and nutritional responses of *H. armigera*. Among the different sunflower cultivars, the relative growth rate (RGR), efficiency of conversion of ingested food (ECI), and efficiency of conversion of digested food (ECD) were highest on Ghasem. Likewise, the heaviest weight of larvae and pupae was obtained on Ghasem, while the lightest was found on Zarrin. The highest proteolytic activity was detected on Zarrin, whereas the highest amylolytic activities were found on Ghasem and Shams. In addition, ECD and RGR values of *H. armigera* larvae were negatively correlated with secondary metabolites content (phenol). The cluster analysis revealed that Ghasem was a nutritionally appropriate cultivar for *H. armigera*, while Zarrin illustrated the greatest level of tolerance against this polyphagous pest. These results could be useful in selection of sunflower cultivars for cultivation and breeding programs that entail *H. armigera* control.

Keywords: Body mass, Digestive enzymes, Host plant resistance, Phytochemicals, Nutritional response

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Introduction

Sunflower (*Helianthus annuus* L.) is one of the main oil seed crops (Skoric *et al.*, 2007; Hussain *et al.*, 2014; Sarvari *et al.*, 2017). It is an annual allogamous plant belonging to the Asteraceae family (Hosni *et al.*, 2022), which contains 39 to 49 percent oil in the seed and ranked third in production after soybean and rapeseed throughout the world (USDA, 2021).

Helicoverpa armigera (Hübner) (Lepidoptera: Noctuidae) is a polyphagous and key pest of various crops including cotton, chickpea, tomato, tobacco, corn, sesame, peanut, okra, soybean, bean, and sunflower (Wilson, 1976; Hemati *et al.*, 2012; Sigsgaard *et al.*, 2002; Bonvari *et al.*, 2024). The larvae start infesting leaves in early growth stages. At later stage, the fruits are infested, reducing their market value and making them unfit for human consumption (Hussain & Bilal, 2007). The larvae are extremely damaging because they prefer to feed and develop on the reproductive structures of crops, which are rich in nitrogen and are often harvested (Fitt, 1989; Singh *et al.*, 2019). The larvae have a polyphagous habit because their development depends on the plant species on which they feed (Suzana *et al.*, 2015; Jafari *et al.*, 2023).

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According to the reports, *H. armigera* is one of the chief biotic constraints to the global output of sunflower and it alone causes up to 50 percent yield loss by directly inflicting damage to flower buds, ovaries, and developing seeds (Lewin *et al.*, 1973; Basavaraj *et al.*, 2018). Loss due to *H. armigera* is more if the star bud and bloom stage of the crop coincides with peak activity of the pest. The pest directly inflicts damage to sunflower by depriving the plant's ovaries and developing seeds, and even one *H. armigera* larva per capitulum could cause economic damage (Horvath *et al.*, 2004; Jayewar & Sonkamble, 2015).

Modern agricultural pest management typically relies on synthetic insecticides, but developing insect-resistant cultivars can decrease reliance on these compounds (Shishehbor & Hemmati, 2022). Host plant resistance is compatible with other approaches of insect control, exercises a constant and cumulative effect on insect populations over time and space, has no adverse effect on environment, reduces the need to pesticides, and involves no extra cost to the farmers (Sharma *et al.*, 2003; Zamani Fard *et al.*, 2022). Resistance lets plants tolerate, avoid, or recover from the harmful effects of herbivores (Scriber & Slansky, 1981; Golizadeh & Abedi, 2016). Consequently, host plant resistance could be regarded as the most important sustainable approach to reduce insect pests' losses (Sarwar, 2013). Antixenosis and antibiosis are the mechanisms that confer resistance in plants. Antibiosis may cause reduction in insect size, weight, survival, longevity, reproduction, and resulting in longer development time (Devi *et al.*, 2017; Hemmati *et al.*, 2022).

The performance of herbivores in response to nutrients obtained from their host plants are assesed by feeding indices (Lazarevic & Peric-Mataruga, 2003). Physiological responses of herbivores are affected via nutritional and biochemical characteristics of host plants (Hemmati *et al.*, 2022). Therefore, the relationship between digestive enzyme function and the biochemical characteristics of those host plants can further elucidate tolerance traits (Zamani Fard *et al.*, 2022). Given that biochemical traits of host plants play an important role in determining their suitability to insect pests, comparative investigation of herbivore digestive physiology on various cultivars can help identify sources of resistance that may be useful in integrated pest management (IPM) programs (Babamir-Satehi *et al.*, 2022).

Although insecticides are the key control tool used against *H. armigera*, most of them have substantial toxic residual impacts on the fruits. Moreover, the pest is quickly evolving resistance against some insecticides used for its management (Shishehbor & Hemmati, 2022). This situation urges developing alternative control options against this destructive pest. In this study, we evaluated repercussions feeding diet constituted different sunflower cultivars to characterize the feeding behavior and enzymes' activities in *H. armigera* larvae. In parallel, we investigated interactions between metabolite compounds and susceptibility or resistance of sunflower cultivars to this pest. Consequently, selection of tolerant cultivars has been suggested as a sustainable, environment-friendly tool with negligible side effects. Our findings could be a basis for selection of available sunflower cultivars to cultivation and breeding efforts that entail *H. armigera* control.

Materials and methods

Experimental host plants

The seed of four sunflower cultivars (Golsa, Ghasem, Shams and Zarrin) were obtained from the Seed and Plant Research Improvement Institute (Karaj, Iran). These cultivars are widely grown in Iran and mainly used for obtaining commercial oil. The artificial diets consisted of seed powder of each sunflower cultivar were prepared based on the method described by Shorey and Hale (1965).

Experimental insects

The initial population of *H. armigera* was originally collected from corn fields in the Behbahan region, Khuzestan province, Iran, in October 2022. It was reared on each sunflower cultivar for two generations to adapt with the new host plant. Adults that emerged were nourished with honey solution (10%). The colony was kept in a growth chamber at 25± 1°C, 65 ± 5% RH, and 16:8 h (L:D)

Determination of feeding performance in *H. armigera* larvae

The nutritional responses of *H. armigera* from the third to fifth instar were evaluated on sunflower cultivars (25 replicates for each cultivar) according to Waldbauer (1968) formulae:

Consumption index (CI) = [(E/A)]; Approximate digestibility (AD) = [(E-F)/E]; Efficiency of conversion of ingested food (ECI) = [(P/E)×100]; Efficiency of conversion of digestion food (ECD)= [(P/E-F)×100]; Relative consumption rate (RCR)=[(E/W0×T)] and Relative growth rate (RGR)= [P/ W0×T].

Where A= average of larval dry weight over time (mg), E= dry weight of the food consumed (mg), F= dry weight of feces produced, P = dry weight gain of larvae (mg), T= the feeding duration (day), and W0= primary weight of larvae (mg).

Moreover, the pupal weight of *H. armigera* was measured after 24 h of pupation on each cultivar. The standardized insect-growth index (SII) was determined by Itoyama *et al.* (1999) formula:

SII = [Pupal weight (Pw)/Larval period (T)]

Furthermore, index of plant quality (IPQ) was determined using Koricheva and Haukioja (1992) formula:

IPQ = [Pupal weight (Pw)/Frass dry weight (Fw)]

Newly emerged larvae from the eggs laid by females, which had already been reared for two generations on sunflower cultivars, were reared together in plastic dishes (25 ×15 cm) until the desired age. To prevent cannibalism, the larvae were individually kept in Petri dishes (9 cm in diameter). The observations including larvae and pupae weight, the amount of eaten food, and the produced frass were daily recorded until the pre-pupal phase. The foods were daily substituted with new ones. To estimate the dry weight percentage of larvae and offered food, 15 specimens of them for each tested sunflower cultivar were weighed. Then, the specimens were oven-dried at 60 °C for 48 h, and weighed once more.

Preparation of enzyme source

The activities of enzymes (protease and amylase) were determined in the crude midgut homogenates. After 24 h of rearing on each tested sunflower cultivar, *H. armigera* larvae (fifth instar) were decomposed in pre-cooled distilled water under a stereomicroscope. The hemolymph was washed away with precooled distilled water, and the midguts were then cleaned by deletion of irrelevant tissues (Hemmati *et al.*, 2022). The homogenates were obtained following homogenization in ice-cold and centrifugation (14,000g for 10 min) at 4˚C. Next, the supernatants were used for the determination of enzyme activities. All assays were carried out in three replicates.

Proteolytic and amylolytic activities in *H. armigera* larvae

The proteolytic activity was determined according to Elpidina *et al.* (2001) using 2 % azocasein as a substrate in universal buffer (50 mM sodium phosphate-borate) at pH 12 (Hemati *et al.*, 2012). Fifty µl of midgut extract mixtures were combined with 80 µl of the substrate, which was then incubated at 37 °C for 50 min. Thereafter, 100 µl of 30% trichloroacetic acid was added to the mixture, which was then centrifuged for 10 minutes at 14,000 *g* after being chilled for 30 minutes at 4°C. The supernatant was mixed with an equal volume of 2M NaOH, and finally the absorption was measured at 440 nm. Furthermore, protein concentrations were determined using the Bradford (1976) protein assay, and known amounts of bovine serum albumin (BSA) (2, 1.5, 1, 0.5, 0.25, 0.125, and 0.063 mg ml^{-1}) were used to generate a standard curve.

The amylolytic activity of midgut extracts from *H. armigera* larvae on the examined sunflower cultivars was assayed by the dinitrosalicylic acid (DNSA) procedure (Bernfeld, 1955), with starch (1%) as a substrate in universal buffer (10 mM succinate-glycine-2, morpholinoethan sulfunic acid) at pH 9 (Hemati *et al.*, 2012). Midgut extract mixtures with 1% starch were incubated at 37 °C for 30 min. The enzymatic reaction was stopped by adding 50 µl of DNSA reagent and heated for 15 minutes in boiling water. After cooling on ice, the mixture's adsorption was measured at 540 nm (Bernfeld, 1955). The amount of maltose released during the α-amylase assays was calculated using the standard curve created by using known amounts of maltose.

Phytochemical metabolites of sunflower cultivars

Phytochemical properties of the tested treatment (protein, starch, flavonoids, phenols, and anthocyanin) were assessed to find possible correlation between these traits and feeding or enzymatic performance of *H. armigera*. Three replicates for each sunflower cultivar were used.

The Bradford method was used to estimate protein content of the sunflower seeds using bovine serum albumin as a standard (Bradford, 1976). Firstly, the seeds of each cultivar were pulverized in a mortar using liquid N2 (Malik & Bradford, 2005). This procedure can also minimize proteolysis and other modes of protein degradation occurring during seeds pulverizing. Afterwards, 200 mg from the powdered seeds of each cultivar was homogenized in 4 ml of 0.5 M phosphate potassium buffer (pH= 7), and the homogenates were centrifuged (10 min at 14,000 *g*). Then, 100 µl of the homogenate was mixed with 3 ml of Bradford reagent, and finally the absorbance was read at 595 nm.

Starch content in the sunflower seeds was measured by the method of Bernfeld (1955) using starch of seed as the standard. Two hundred milligrams of the powdered seed of each sunflower cultivar were homogenized in 35 ml of distilled water and heated to boiling point. Next, 100 µl of each sample was mixed with 2.5 ml of iodine reagent (0.02% I_2 and 0.2% KI). The absorbance was determined at 580 nm.

The phenolic content of the plant extracts was assayed using the Folin-Ciocalteu reagent (Slinkard & Singleton, 1997). Briefly, a quantity of 2 g of powdered sunflower seeds was homogenized in methanol and later centrifuged at 13,000 ×g for 12 min. The supernatants were transferred to 1.5 mL Folin–Ciocalteu reagent 10%. Then, sodium carbonate solution 7% was combined with the mixture. The absorbance was determined at 765 nm using gallic acid as a standard.

The number of flavonoids in various sunflower cultivars was evaluated according to Jia *et al.* (1999) method utilizing catechin as a standard. In a nutshell, 2 g of each sample was homogenized in acidified ethanol (1 acid acetic:100 ethanol), and then centrifuged (13,000 ×g for 12 min). Following cooling the filtrates, the absorbance was recorded at 520 nm.

The anthocyanin content of the treatments was estimated based on the method of Kim *et al.* (2003). In summary, a quantity of 2 g of each milled sunflower seed was homogenized in acidified ethanol. The extract was filtered and boiled. Finally, after cooling samples, the absorbance was measured at 520 nm using cyanidin as a standard.

Data analysis

One-way multivariate analysis of variance (MANOVA) was used to analyze the sunflower biochemical traits, digestive enzyme activities, and feeding performance of *H. armigera* larvae. The Shapiro-Wilk test was used to validate the data (SPSS Inc, 2007). The mean differences were compared using Tukey HSD test (P< 1%). Pearson correlation coefficients were used to analyze the probable interactions between biochemical features of the tested sunflower cultivars with feeding indices, pupal weight, and digestive enzyme activiy of *H. armigera*. Moreover, a dendrogram of sunflower cultivars based on feeding and digestive functions of *H. armigera* on examined treatments was constructed by Ward's method using SPSS.

Results

Influence of biochemical compositions of various cultivars of sunflower on larval feeding-related response

The mean feeding indices of third to fifth instar larvae of *H. armigera* are presented in Table 1. Nutritional indices of larvae were significantly affected by various sunflower cultivars. Regarding these indices, the larvae fed on Zarrin (2.46) and Shams (2.41) exibited a higher consumption index (CI) compared to those on other treatments ($F_{3,96}$ = 11.52; P < 0.01). The highest value of approximate digestibility (AD) ($F_{3,96}$ = 8.99; P < 0.01) of *H. armigera* larvae was obtained on Zarrin (56.44 %). The larvae fed on Ghasem had the highest efficiency of conversion of ingested food (ECI) (16.96 %) ($F_{3,96}$ = 45.76; P < 0.01) and efficiency of conversion of digested food (ECD) (46.36 %) ($F_{3,96}$ = 23.73; P < 0.01). In addition, our results indicated that the highest values of relative consumption rate (RCR) ($F_{3,96}$ = 14.67; P < 0.01) and relative growth rate (RGR) ($F_{3,96}$ = 54.30; P < 0.01) were on Shams and Ghasem, respectively. The RCR (0.62 mg/mg/day) and RGR (0.07 mg/mg/day) values were lowest on Zarrin (Table 1).

Larval weight (41.56 mg/larva) ($F_{3,96}$ = 75.80; P < 0.01) and food consumed (84.77 mg/larva) ($F_{3,96}$ = 23.22; P < 0.01) were lowest on Zarrin compared with other cultivars (Fig. 1). The *H. armigera* larvae fed on Ghasem (75.67 mg/larva) and Shams (72.97 mg/larva) had the maximum value of frass produced weight, while the lowest one was on Zarrin (56.31 mg/larva) ($F_{3,96}$ = 4.87; P< 0.01). The larval weight gain was highest on Ghasem (20.25 mg/larva), whereas the lowest one was obtained on Zarrin (7.28 mg/larva) ($F_{3,96}$ = 82.96; P < 0.01) (Fig. 1).

Table 1. Nutritional indices (mean ± SE) of third to fifth instar larvae of *Helicoverpa armigera* reared on various sunflower cultivars contained artificial diet.

Cultivar	CI*	AD (%)	ECI (%)	ECD (%)	RCR (mg/mg/day)	RGR (mg/mg/day)
Golsa	2.020 ± 0.074b	42.354 ± 1.585b	12.985 ± 0.481b	36.315 ± 2.389b	0.683 ± 0.025bc	0.088 ± 0.003c
Ghasem	2.000 ± 0.046b	42.893 ± 2.063b	16.962 ± 0.373a	46.362 ± 2.897a	0.73 ± 0.017b	0.123 ± 0.003a
Shams	2.411 ± 0.099a	47.545 ± 1.387b	12.031 ± 0.376bc	26.822 ± 1.164c	0.837 ± 0.032a	0.101 ± 0.003b
Zarrin	2.469 ± 0.064a	56.44 ± 3.193a	10.545 ± 0.384c	23.455 ± 1.562c	0.626 ± 0.016c	0.07 ± 0.003d

Means followed by different letters in the same column are significantly different (Tukey, $P < 0.01$). Experiments were performed in 25 replications for each cultivar.

*CI, consumption index; AD, approximate digestibility; ECI, efficiency of conversion of ingested food; ECD, efficiency of conversion of digested food; RCR, relative consumption rate; RGR, relative growth rate.

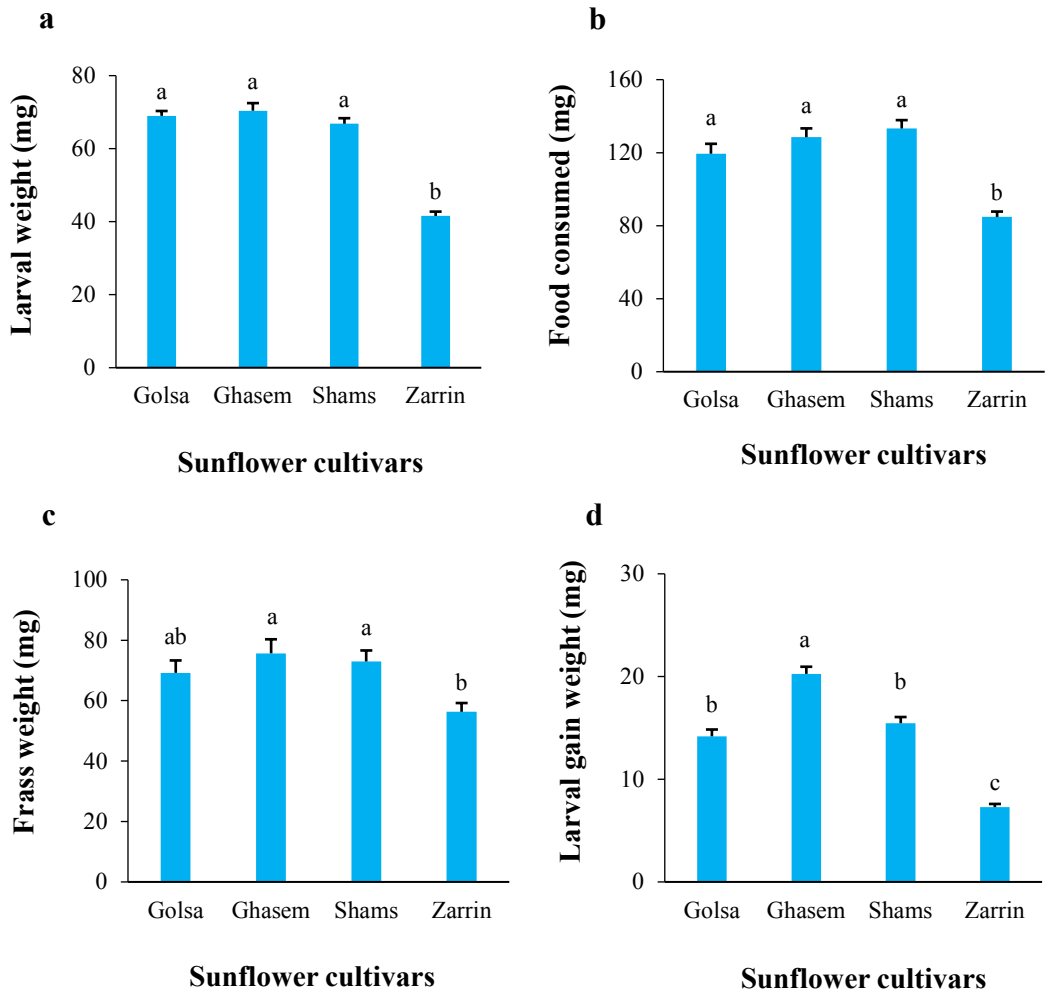

Fig. 1. (a) Mean larval weight, (b) food consumed, (c) frass produced, and (d) larval weight gain of *Helicoverpa armigera* third to fifth instar reared on various sunflower cultivars contained artificial diet. Experiments were performed in 25 replications for each cultivar.

The weights of pre-pupa ($F_{3,96} = 8.36$; $P < 0.01$) and pupa ($F_{3,96} = 5.25$; $P < 0.01$) were the highest (88.56 and 46.42 mg/individual, respectively) on Ghasem. However, the lowest pre-pupal (74.48 mg/pre-pupa) and pupal (38.62 mg/pupa) weights were obtained on Zarrin (Fig. 2).

The value of standardized insect-growth index (SII) was highest for larvae reared on Ghasem (1.97) and lowest for those fed on Zarrin (1.65) ($F_{3,96} = 3.53$; $P < 0.01$). Moreover, the value of index of plant quality (IPQ) was maximum on Ghasem (0.68) and Shams (0.62) ($F_{3,96} = 19.03$; $P < 0.01$) (Fig. 3).

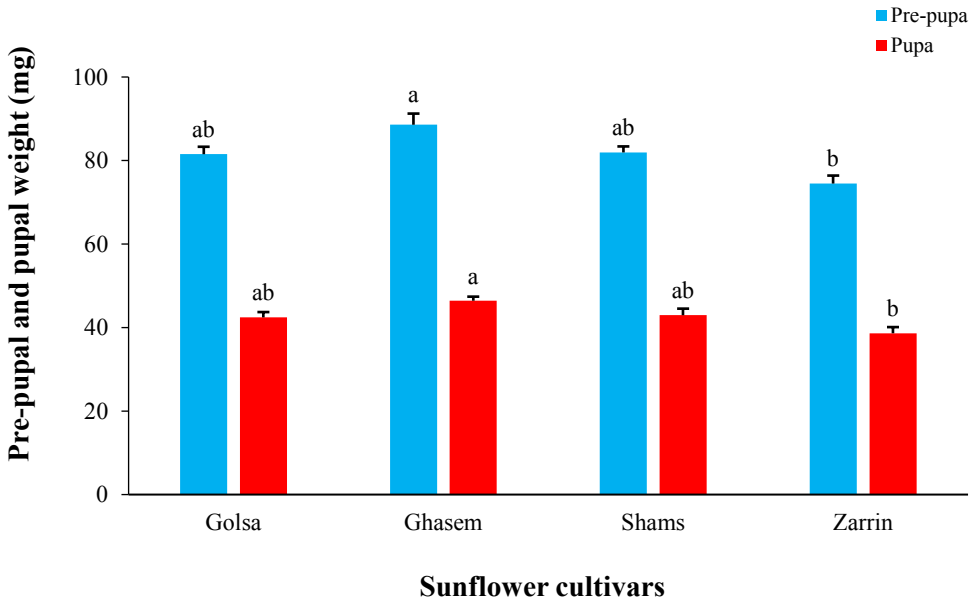

Fig. 2. Pre-pupal and pupal weight (mg/individual) of *Helicoverpa armigera* reared on various sunflower cultivars contained artificial diet. Experiments were performed in 25 replications for each cultivar.

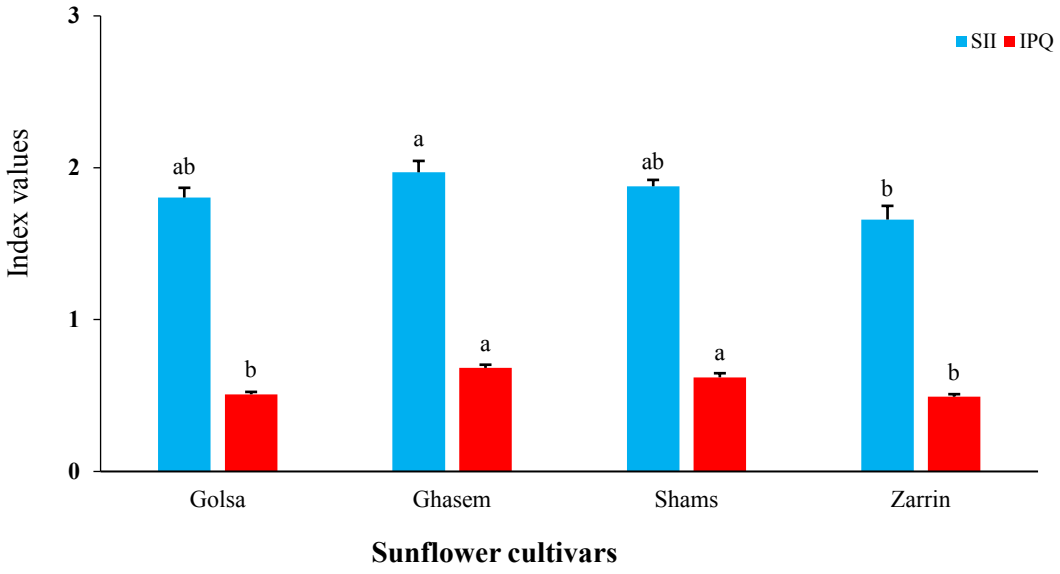

Fig. 3. Standardized insect-growth index (SII) of *Helicoverpa armigera* and index of plant quality (IPQ) on various sunflower cultivars contained artificial diet. Experiments were performed in 25 replications for each cultivar.

Influence of biochemical compositions of various cultivars of sunflower on larval digestive enzyme activity-related response

Data revealed the significant increase in proteolytic activity within the midgut of larvae reared on Zarrin (1.03 U/mg), but its lowest activity was observed on Golsa (0.406 U/mg) and Ghasem (0.502 U/mg) ($F_{3,8}$ = 152.53; P < 0.01) (Fig. 4). Moreover, maximum level of amylolytic activity in midgut was observed on Shams (1.25 U/mg) and Ghasem (1.24 U/mg), whereas the minimum activity was found on Zarrin (1.02 U/mg) and Golsa (0.86 U/mg) ($F_{3,8}$ = 16.88; P < 0.01).

Hierarchical classification of sunflower cultivars

Cluster analysis of sunflower cultivars was grouped based on feeding indices and enzymes' activities of *H. armigera* on different sunflower cultivars (Fig. 5). The findings revealed two chief clusters of A (comprising of A_1 and A_2 subclusters) and B, indicating a considerable difference among the studied cultivars. The dendrogram demonstrates cultivars of group A based on their similarities in suitability as acceptable food resources of *H. armigera*, which Ghasem was the most suitable. Cultivar in cluster B (Zarrin) was unsuitable host for *H. armigera* feeding.

Measurement of phytochemical contents in various sunflower cultivars

Our results indicated that among sunflower cultivars, the highest starch content was detected in Ghasem (1.14 mg/g), while lowest level was observed in Zarrin (0.68 mg/g) ($F_{3,8}$ = 26.67; P < 0.01) (Table 2). Protein level in Shams (3.47 mg/g) was statistically higher than other tested cultivars, and Zarrin (0.46 mg/g) exhibited the lowest protein content ($F_{3,8}$ = 16.35; P < 0.01). The amount of phenolic in Zarrin (137.55 µg/g) and Shams (47.675 µg/g) were significantly maximum and minimum compared to other cultivars, respectively ($F_{3,8}$ = 41.26; P < 0.01). The highest value of total flavonoids was obtained for Shams (2.70 µg/g), and its lowest value was observed in Ghasem (1.22 µg/g) ($F_{3,8}$ = 10.99; P < 0.01). Furthermore, the anthocyanin content was insignificantly affected by different sunflower cultivars (P > 0.05).

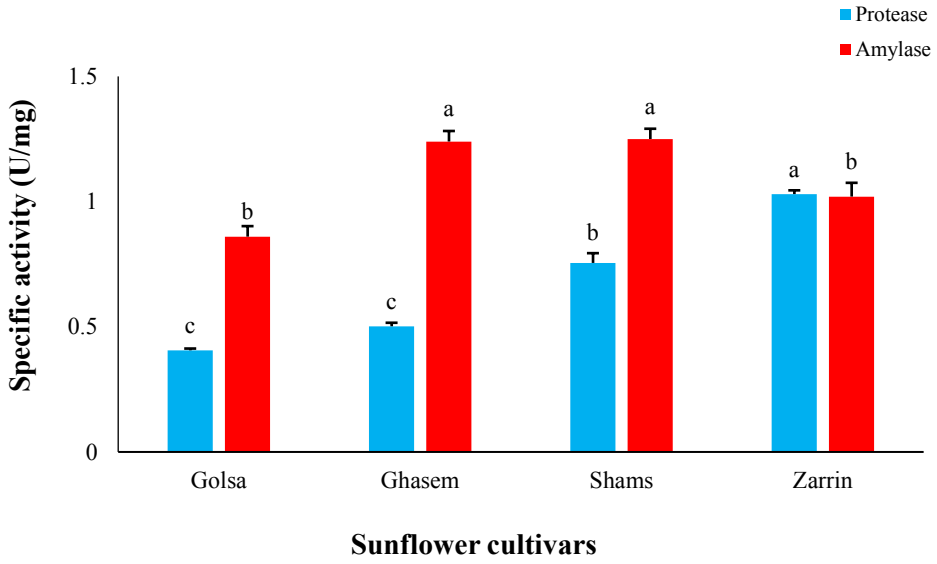

Fig. 4. General proteolytic and amylolytic activity in midgut extracts from fifth instar larvae of *Helicoverpa armigera* reared on various sunflower cultivars contained artificial diet. Assays were carried out in three replications for each cultivar.

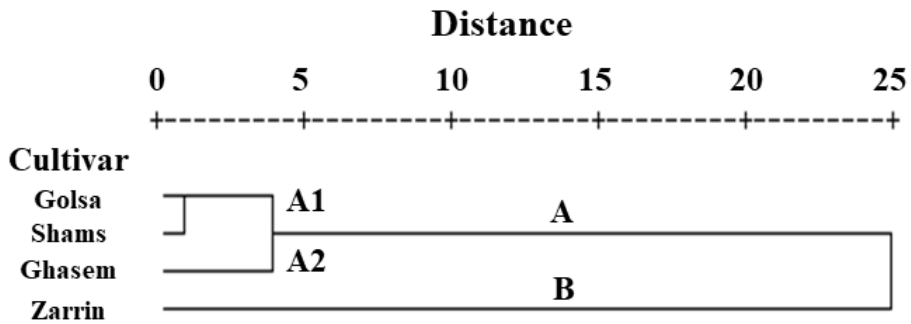

Fig. 5. Dendrogram of various sunflower cultivars based on nutritional indices and enzymatic activities of *Helicoverpa armigera* reared on sunflower cultivars contained artificial diet.

Correlation analysis

The relationships between the digestive enzymatic activities and nutritional indices of *H. armigera* with phytochemical metabolites of sunflower cultivars were studied using Pearson's correlations (Table 3). The results revealed that ECD (r = -0.737; $P < 0.01$) and RGR (r = -0.722; $P < 0.01$) of *H. armigera* had significant negative correlation with the phenolic content of sunflower cultivars. Nevertheless, it was found that there were no significant correlations between RCR, pupal weight, amylolytic and proteolytic activities of the pest, and the total phenolic content in sunflower cultivars ($P > 0.05$). Additionally, a significant positive correlation was found between RCR and flavonoid content of the tested cultivars (r = 0.622; $P < 0.05$). However, ECD, RGR, and pupae weight along with enzyme activities of *H. armigera* were insignificantly correlated with the content of flavonoid ($P > 0.05$). In addition, starch, protein, and anthocyanin contents tested in various sunflower cultivars were not correlated with any of the nutritional indices, and the enzymatic activities of *H. armigera* ($P > 0.05$).

Conclusion

In the current study, the nutritional performances of *H. armigera* larvae reared on different sunflower cultivars were significantly different, suggesting that the cultivars had unlike nutritional values. Similar to our results, other researchers reported that feeding indices of *H. armigera* larvae were differently affected by various host plants or cultivars (Baghery *et al.*, 2013; Razmjou *et al.*, 2014; Kouhi *et al.*, 2014; Jafari *et al.*, 2023; Bonvari *et al.*, 2024). According to the results of the present study, *H. armigera* larvae on Ghasem had the highest ECI and ECD values. The same trend was observed for the value of RGR. The ECI, ECD, and RGR are important indices, which reflect the nutritional responses of insects (Golizadeh & Abedi, 2016). The elevated amounts of ECI and ECD on Ghasem indicate that the larvae became more adept at converting their eaten and digested food into body mass. The highest RGR of *H. armigera* larvae on Ghasem shows that this cultivar experienced the fastest rate of larval growth. As a result, the highest pre-adult and pupae weight were detected on Ghasem. The variation in RGR of *H. armigera* larvae on the tested treatments may be attributed to differences in primary and secondary metabolites of sunflower cultivars. Evaluating the biochemical characteristics of sunflower cultivars showed that Ghasem had the highest amount of starch (primary metabolites) and lowest content of flavonoids (secondary metabolites), indicating that it was nutritionally suitable than other tested sunflower cultivars for larval feeding and growth. So, more growth and performance and undoubtedly more damage of the larvae would potentially be expected on this cultivar.

Table 2. Biochemical characteristics (mean ± SE) of various sunflower cultivars.

Cultivar	Starch content mg/g	Protein content mg/g	Total phenolic content µg/g	Flavonoid content µg/g	Anthocyanin content µg/g
Golsa	0.834 ± 0.017c	1.225 ± 0.028c	90.625 ± 4.950b	1.568 ± 1.028b	0.180 ± 0.018a
Ghasem	1.145 ± 0.005a	1.658 ± 0.068b	65.987 ± 2.223bc	1.228 ± 0.090c	0.268 ± 0.025a
Shams	1.018 ± 0.016b	3.476 ± 0.072a	47.675 ± 2.254c	2.705 ± 0.068a	0.276 ± 0.040a
Zarrin	0.686 ± 0.010d	0.462 ± 0.051d	137.550 ± 10.601a	1.785 ± 0.046ab	0.286 ± 0.024a

Means followed by different letters in the same column are significantly different (Tukey, $P < 0.01$). Assays were carried out in three replications for each cultivar.

Table 3. Pearson's correlation coefficients (r) between nutritional and physiological characteristics of *Helicoverpa armigera* with biochemical traits of various sunflower cultivars.

Parameter	Starch content	Protein content	Total phenolic content	Flavonoid content	Anthocyanin content
ECD*	-0.308 (0.330)	0.378 (0.225)	**-0.737 (0.006)**	0.053 (0.869)	-0.381 (0.222)
RGR	-0.156 (0.629)	0.380 (0.223)	**-0.722 (0.008)**	0.367 (0.241)	-0.321 (0.308)
RCR	0.292 (0.356)	0.213 (0.506)	-0.272 (0.982)	**0.622 (0.031)**	0.831 (0.080)
Pupal weight	0.597 (0.611)	0.279 (0.380)	0.448 (0.144)	0.280 (0.078)	-0.831 (0.069)
Proteolytic activity	0.252 (0.430)	-0.187 (0.561)	-0.469 (0.124)	0.112 (0.728)	0.497 (0.100)
Amylolytic activity	-0.220 (0.592)	0.369 (0.238)	0.253 (0.428)	0.220 (0.193)	0.379 (0.224)

Correlations were evaluated based on Pearson's correlation test ($P < 0.05$).

Numbers in parenthesis represent P values. Significant correlations are shown in bold.

* ECD, efficiency of conversion of digested food; RGR, relative growth rate; RCR, relative consumption rate.

According to Zamani Fard *et al.* (2022) and Hemmati (2024), the suitable host plant cultivar in their study had the lowest amount of flavonoid and highest amount of starch, respectively, which confirm the findings of our study.

In this study, when *H. armigera* larvae were reared on Zarrin, the value of ECI was significantly decreased compared to other cultivars, indicating that the larvae were less effective in changing the consumed food into body matter. Furthermore, the lowest RGR value on this cultivar may be attributed to diminished consumption of food and/or ECI. The ECI and RGR values of *H. armigera* larvae fed on Zarrin were nearly similar to those reported by Kouhi *et al.* (2014) for whole larval instars of *H. armigera* reared on tomato (*cv.* Rio grande UG) (11.535 ± 0.225 %) and by Fallahnejad-Mojarrad *et al.* (2015) for the third instar larvae of the pest fed on chickpea (*cv.* Hashem) (0.074 ± 0.006 mg/mg/d), respectively. Based on the results, the AD value was highest on Zarrin, which was probably due to the limited access to essential nutrients for the growth of insect, and the pest was forced to compensate the nutrient deficiency. The lowest ECD values were also quantified for *H. armigera* feeding on Shams and Zarrin, indicating a greater metabolic cost that impacts the catabolism of larvae. Possibly, a great AD amount could not make up for a less ECD value on Zarrin, which finally led to a decreased growth rate. This result is consistent with the findings of other researchers (Singh & Parihar, 1988; Lazarevic & Peric-Mataruga, 2003). In the current study, the value of ECD on Zarrin was less than the value reported by Fathipour *et al.* (2018) for whole larval instars of *H. armigera* on canola (*cv.* Talaye) (52.937 %), indicating that the larvae fed on sunflower were not so much efficient in turning digested food into biomass compared with those nourishing on canola.

The differences between the results of ECD values in both studies may be related to dissimilarities of host plants, plant parts, and larval stages of *H. armigera* used for the experiments. In general, the pest's larvae reared on Zarrin had the least capability of converting the ingested food into biomass, as indicated by the ECI, ECD, RCR, and RGR values. So, this cultivar was a poor host for *H. armigera* feeding and growth. The low quality of Zarrin as a food source for the larvae was also apparent in low consumption of food, gained weight of larvae and pupae, and SII. The lowest value of SII can be attributed to the decreased plant quality, as determined by the index of IPQ. Similarly, Rahimi Namin *et al.* (2014) reported the lowest values of SII and pupal weight of *H. armigera* on a resistant red kidney bean cultivar (Sayyadof). The unsuitability of Zarrin was clearly supported by results obtained from the biochemical analysis of the tested sunflower cultivars. According to the obtained results, Zarrin was significantly poor in protein and starch concentrations and rich in total phenolic content compared to other sunflower cultivars.

Furthermore, negative correlation between ECD and RGR values of *H. armigera* and the total phenolic content of sunflower cultivars highlight the role of phenols in decreasing the quality of Zarrin. Protein and starch are important primary metabolites, which are directly required for plant growth (Erb & Kliebenstein, 2020). However, plants synthesize secondary metabolites, which play a defensive role against herbivores (Erb & Kliebenstein, 2020). Among the secondary metabolites, phenolic compounds can cause unfavorable effects on insects' fitness and physiology, such as significant reduction in larval weights and even mortality (Dixit *et al.*, 2017). The current study supported prior studies in that reduced host quality decreases *H. armigera* growth and feed (Naseri *et al.*, 2010; Fathipour *et al.*, 2018; Jafari *et al.*, 2023; Bonvari *et al.*, 2024).

Based on the results, the RCR values of *H. armigera* larvae were highest on Shams, suggesting that this cultivar was highly nutritive for the larvae. This result might be due to the high protein content and low total phenolic content of Shams. Surprisingly, the highest amount of flavonoid was also detected in this cultivar. Correlation analysis revealed that there was a positive correlation between the RCR value of *H. armigera* and the flavonoid content of the sunflower cultivars. Flavonoids are small molecular secondary metabolites synthesized by plants and have been reported to negatively influence the reproductive and feeding behavior of insect pests (Mierziak *et al.*, 2014). However, they may act as feeding/growth stimulants for certain insect species (Mierziak *et al.*, 2014). For example, flavonoids like quercetin-3-O-rutinoside act as a deterrent to *Pieris rapae* L., but as a stimulant to *Danaus plexippus* L. (Tabashnik, 1987; War *et al.*, 2012). It is probable that the consumption of *H. armigera* larvae on Shams may have been stimulated by the flavonoid. To verify this hypothesis, supplementary biochemical studies are needed to determine how RCR of *H. armigera* may have been affected positively by this secondary metabolite.

The results of this study indicated that different sunflower cultivars significantly affected amylolytic and proteolytic activities of *H. armigera* larvae. Among the examined treatments, the highest digestive proteolytic

activity was detected in larvae fed on Zarrin, while the cultivar's protein content was relatively low. A possible explanation for this finding might be related to the hyperproduction of protease to overcome the inhibitory effects of protease inhibitors in this cultivar (Hemmati *et al.*, 2021; Zamani Fard *et al.*, 2022). Moreover, the highest amylolytic activities of *H. armigera* larvae were on Shams and Ghasem, while the lowest activities were on Zarrin and Golsa. The low amylase activity of *H. armigera* larvae, especially on Zarrin, might be associated with the low quantity of starch and/or increased activities of α-amylase inhibitors in this cultivar. Similar to our results, other researchers reported that α-amylase inhibitors in resistant host plants interfere with gut amylolytic activity of insect pests (Bouayad *et al.*, 2008; Ebadollahi & Borzoui, 2019).

According to dendrogram results, the sunflower cultivars could be grouped into three different clusters. The cluster A_1 included Golsa and Shams, which appeared to be an intermediate group for growth and nutrition of *H. armigera*. Ghasem was grouped in cluster A_2, which was the most favorable cultivar for *H. armigera* because of the highest feeding indices (ECI, ECD, and RGR), amylase activity, and pre-adult weight of the pest. Cluster B consisted of Zarrin, which the poor physiological performance (lowest ECI, ECD, RCR, RGR, and pre-adult weight) of *H. armigera* on this cultivar made it least suitable host for the pest. The low primary (starch and protein) and high secondary (total phenolic content) metabolites in Zarrin had important role in negatively affecting the above-mentioned parameters. Thus, Zarrin could be recommended for sowing in regions where the population of *H. armigera* is high to reduce sunflower damage. This cultivar needs to be further evaluated, especially for other secondary metabolites, and can constitute a useful genetic resource for sunflower breeding programs aimed at developing resistant cultivars against *H. armigera*.

Author's Contributions

Nima Goudarzi Mohammadi: Data curation (equal); investigation (equal); methodology (equal); software (equal). **Seyed Ali Hemmati**: Conceptualization (lead); data curation (lead); formal analysis (lead); funding acquisition (lead); investigation (lead); methodology (lead); project administration (lead); resources (lead); software (lead); supervision (lead); validation (lead); visualization (lead); writing – original draft (lead); writing – review and editing (lead). **Parviz Shishehbor**: Data curation (supporting); investigation (supporting); methodology (supporting); validation (supporting); visualization (supporting); writing – review and editing (supporting).

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Data Availability Statement

The datasets generated in this study are available from the corresponding author upon reasonable request.

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Ethics approval

Insects and plant were used in this study. All applicable international, national, and institutional guidelines for the care and use of animals were followed. This article does not contain any studies with human participants performed by any of the authors.

Conflict of interest

The authors declare that they have no conflict of interest.

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اثر ارقام مختلف آفتابگردان بر واکنش‌های تغذیه‌ای و فیزیولوژیکی *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae)

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چکیده

شب‌پره *Helicoverpa armigera* (Hübner) یکی ازآفات خسارت‌زای محصولات زراعی مختلف در سراسر جهان است و مطالعات متعددی به مقایسه رشد، مصرف غذا و گوارش لاروهای *H. armigera* روی گیاهان مختلف پرداخته‌اند. با این وجود، مطالعه‌ای که تغذیه حشره و واکنش‌های فیزیولوژیکی گوارش آن را با استفاده از ویژگی‌های بیوشیمیایی ارقام آفتابگردان ارزیابی نماید، محدود می‌باشد. در این پژوهش، تاثیر ارقام مختلف آفتابگردان (گلسا، قاسم، شمس و زرین) در قالب رژیم غذایی مصنوعی بر فعالیت آنزیم‌های گوارشی و واکنش‌های تغذیه‌ای *H. armigera* ارزیابی گردید. در بین ارقام مختلف آفتابگردان، نرخ رشد نسبی (RGR)، کارایی تبدیل غذای خورده شده (ECI) و کارایی تبدیل غذای هضم شده (ECD) در لاروهای تغذیه شده با رقم قاسم بیش‌ترین بود. هم‌چنین، بیش‌ترین وزن لارو و شفیره نیز روی رقم قاسم به دست آمد، در حالی که کم‌ترین وزن این شاخص‌ها روی رقم زرین ثبت شدند. بیش‌ترین فعالیت آنزیم گوارشی پروتئولیتیک کل در لاروهای پرورش یافته روی رقم زرین اندازه‌گیری شد، در حالی که بیش‌ترین فعالیت آنزیم گوارشی آمیلولیتیک در لاروهای تغذیه شده با ارقام قاسم و شمس بدست آمد. علاوه‌بر این، مقادیر شاخص‌های ECD و RGR لاروهای *H. armigera* همبستگی منفی با محتوی ترکیبات شیمیایی ثانویه (فنل) داشت. یافته‌های تجزیه کلاستر ثابت کرد که از نظر تغذیه‌ای، قاسم رقم مناسبی برای *H. armigera* بود، در حالی که زرین تحمل بیشتری به این آفت چندین‌خوار نشان داد. این نتایج می‌تواند در انتخاب ارقام آفتابگردان برای کاشت و استفاده در برنامه‌های به‌نژادی جهت کنترل *H. armigera* مفید واقع شوند.

کلمات کلیدی: توده بدنی، آنزیم‌های گوارشی، مقاومت گیاه میزبان، ترکیبات شیمیایی گیاهی، واکنش تغذیه‌ای.

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