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Research Article

OVIPOSITIONAL PREFERENCES OF FALL ARMYWORM, *SPODOPTERA FRUGIPERDA*, ON DIFFERENT HOST PLANTS UNDER LABORATORY CONDITIONS

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ABSTRACT

The interaction between insects and their host plants is essential for understanding successful oviposition, particularly for polyphagous insects. The fall armyworm (FAW), *Spodoptera frugiperda*, is a significant pest affecting over 300 host plant species. In light of its impact, an experiment was conducted to examine FAW oviposition on *Brassica rapa* L., *B. oleracea* var. *capitata*, and *Zea mays* L. Results from this study revealed a notable influence of host plant species on FAW oviposition preferences. The highest egg count (675 ± 32.4 eggs) was recorded on maize, specifically on the maize strain of FAW. In choice experiments, the FAW maize strain showed a strong preference for ovipositing on maize. Interestingly, neither the mustard strain (139 ± 37.3 eggs) nor the cabbage strain (37.0 ± 4.6 eggs) laid the highest number of eggs on their respective host plants. Among reproductive parameters, the primary difference observed was in the oviposition period. For adult diets, the highest fecundity, with 1188 ± 64.84 eggs, was achieved with a honey + protein solution diet. These findings suggest that adult diet has a substantial impact on oviposition period and can be beneficial for mass-rearing FAW in laboratory settings. In conclusion, the results indicate that FAW in Pakistan still shows a strong preference for maize and has not adapted to other host plants as primary options. This preference for maize warrants focused pest management strategies to keep FAW populations below threshold levels and minimize crop damage.

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INTRODUCTION

Maize (*Zea mays* L.) is the third most important crop globally after rice and wheat, serving as a staple food in many countries. Approximately 1,147.7 million tons of maize kernels are produced annually worldwide, cultivated on 193.7 million hectares with an average yield of 5.75 tons per hectare (FAO, 2020). Beyond its role as a cereal, maize is widely used in industries for fuel, food, animal feed, beverages, and chemicals (Naz et al., 2019; Gamage et al., 2022) and serves as a raw material in the synthesis of numerous products (Kaul et al., 2019). Its demand is steadily rising due to these diverse applications

(Jaliya et al., 2008; Andorf et al., 2019).

Despite maize being highly susceptible to a range of pest species, a few are particularly damaging, affecting the crop from field to storage (Nabeel et al., 2018; Seerat et al., 2022). The recent invasion of *Spodoptera frugiperda* (Noctuidae: Lepidoptera), commonly known as the fall armyworm (FAW), has emerged as a major pest for various field crops and vegetables, including cotton, millets, sugarcane, rice, sorghum, maize, groundnut, cabbage, beet, onion, pasture grasses, and tomato (Bueno et al., 2010; Kenis et al., 2022). Among these, maize is especially vulnerable due to its high preference by this pest (Cock et al., 2017; FAO, 2018). FAW is a highly migratory, polyphagous pest with voracious feeding habits, high fecundity, and no diapause.

Originally native to the tropical and subtropical Americas, FAW spread rapidly to various regions of Western and sub-Saharan Africa (Bueno et al., 2010; Goergen et al., 2016; Brévault et al., 2018; Nagoshi et al., 2018). It was first reported in India around 2018-2019, quickly dispersing across Asia-Pacific countries such as Korea, China, Japan, Malaysia, and Thailand, causing significant maize damage (Pogue, 2002; Prasanna et al., 2018; FAO, 2019a, b). In Pakistan, the presence of FAW was confirmed in Sindh in 2019 (Bhatti et al., 2021).

Farmers predominantly manage FAW through synthetic insecticides. However, the extensive use of various insecticide classes has led to resistance in FAW populations and has also negatively impacted beneficial insects, wildlife, and human health globally (Goergen et al., 2016; Kumar et al., 2021). Due to behavioral and physiological traits of FAW, resistance to pesticides develops rapidly (Gutiérrez-Moreno et al., 2019), underscoring the need for an Integrated Pest Management (IPM) approach (Javed et al., 2017; Muhammad et al., 2021a, b). Effective IPM strategies require detailed knowledge of FAW behavior, especially in terms of foraging and reproductive performance. Given the economic impact of FAW, numerous studies are underway, with a critical focus on host plant interactions, particularly related to oviposition, which remains a marginally explored area.

FAW has not been reported to enter diapause, and its host plant preferences vary across ecological zones, with climatic changes significantly influencing its behavior. Understanding biology of FAW and its host plant choices for feeding and oviposition is essential for effective pest management. Oviposition is a critical aspect of insect behavior and plays a crucial role in host plant interactions, especially when herbivorous insects have the option to select among various host plants. Finding a suitable site for egg-laying is one of the most important biological functions of an insect. Herbivorous insects base their oviposition choices on the nutritional quality of plants for their offspring while also considering protection from natural enemies (Singer et al., 2004; Videla et al., 2012; Garvey et al., 2020).

Plant investment in defensive chemicals often negatively impacts herbivore performance (Schoonhoven et al., 2005). An ideal oviposition habitat should allow newly hatched insects easy, quick, and ample opportunities to locate suitable food before they risk starvation (Claridge and Wilson, 1978). This strategy is commonly seen among many phytophagous insects, which often lay eggs on or near suitable host plants (Jadeja and Tenhumberg, 2017). For polyphagous insect pests, however, this behavior involves assessing the relative importance and potential of various host plant species (McClay and Hughes, 2007).

Insects extensively examine plants using various body parts, including the tarsi, proboscis (Städler and Reifenrath, 2009), antennae (Yamamoto et al., 1969), and ovipositor (Seada et al., 2016), all of which are equipped with sophisticated mechanical and chemical sensors (Koutroumpa et al., 2021). These investigative behaviors offer valuable insights into the quality of host plants.

If a plant is suitable for egg-laying, moths memorize its odor, aiding in the future recognition or search for plants of similar quality. Studies on the ovipositional behavior of various species have been conducted, including *Spodoptera exigua* (Azidah and Sofian-Azirun, 2006), diamondback moths (*Plutella xylostella* L.) (Saeed et al., 2010), and the tobacco cutworm (*S. litura* Fabricius) (Tuan et al., 2014). However, there is a lack of published literature on the oviposition behavior of the fall armyworm in this context. Oviposition learning could be a critical strategy to overcome limitations in host plant selection accuracy (Carrasco et al., 2015). In light of this, our study aimed to assess the ovipositional preferences and reproductive period of *S. frugiperda* on various non-Poaceae host plants, with the goal of identifying potential future threats, as this invasive pest may impact locally cultivated crops, particularly maize, under regional environmental conditions.

MATERIALS AND METHODS

Insect culturing for experimentation

The experiment was conducted in the Beneficial and Productive Insects Laboratory at the Department of Entomology, Sindh Agriculture University (SAU), Tando Jam. The FAW larvae were collected from multiple maize fields surrounding the SAU experimental area in Tando Jam (25.42260 N; 68.53700 E) during the spring and autumn seasons of 2021-22. These larvae were initially reared on maize leaves at a room temperature of 27 ± 2°C, with a relative humidity of 60-70% and a photoperiod of 11:13 to establish a culture stock.

The FAW larvae were first kept in small plastic containers with fresh maize leaves. After reaching the third instar stage, each larva was transferred to an individual jelly cup to prevent cannibalism. The trials were then conducted on second-generation moths to assess oviposition responses.

To evaluate the polyphagous behavior of FAW, two different FAW cohorts/strains were reared on mustard (*Brassica rapa* L.) and cabbage (*Brassica oleracea* var. *capitata*) in addition to maize, under the same laboratory conditions. Third-generation FAW strains reared on maize, mustard, and cabbage were used to assess oviposition responses on seedlings of various host plants.

Seedlings were grown in imported plastic trays filled with culture media and maintained under greenhouse conditions. The trays were watered daily, and fertilizer (N:P:K = 12:18:12) was applied as needed, depending on the growth stage of the plants.

Oviposition response bioassays for FAW females (choice and no-choice experiments)

No-choice test for oviposition

This experiment began after eclosion, when naïve mated females from three different FAW strains were each transferred to small insect cages (1.5 × 2.0 × 0.5 m). Each cage contained a single host plant, either *Z. mays*, *B. rapa*, or *B. oleracea* var. *capitata*, for the no-choice setup. The cages were constructed with PVC pipe frames, with all sides covered in mesh netting, and the bottom lined with moist paper. A fluorescent lamp (100W) was positioned 40 cm above each cage to provide nighttime illumination. Females were given a 3:7 (w/v) sucrose solution as a food source. The experimental design was completely randomized with three treatments and four replicates, resulting in 12 experimental units. Four females from each strain were introduced to the host plant on which they had been reared during the larval stage.

Oviposition choice test

In the choice experiment, each FAW strain (maize, mustard, and cabbage) was provided with three host plants in a single arena setup. Four seedlings of each host plant were offered to twelve FAW females. Eggs were removed from the plants and counted daily until the death female. The rest of the experimental setup was kept consistent with the no-choice test (Figure 1).

In addition to observing oviposition responses of FAW on different host plants, data on pre-oviposition period, oviposition period, post-oviposition period, and female longevity were also recorded. To assess the impact of adult diet on oviposition, maize strain FAW moths were fed a variety of artificial diets and introduced to maize plants (four mated females per pot or replicate). The four diets included: a honey solution (3:7 w/v), a yeast solution (6:4 w/v), a honey + yeast solution (3:3:5), a protein solution (1:9), and a honey + protein solution (1:2:7). All parameters mentioned above were then recorded again.

Statistical analysis

All experiments were conducted under uniform conditions, and a completely randomized design (CRD) was used. Differences in the number of eggs (fecundity) for oviposition responses, as well as pre-oviposition, oviposition, and post-oviposition periods and female longevity, were analyzed using one-way analysis of variance (ANOVA). Treatment means were compared using the Least Significant Difference (LSD) test as a post-hoc analysis, with significance set at $P < 0.05$. All data analyses were performed using the Statistix 8.1 software package.

RESULTS

The results of the study clearly demonstrated the oviposition preference of *S. frugiperda* for specific host plants. Significant differences in oviposition responses were observed ($P<0.05$) in a no-choice experiment. The highest egg count, with an average of 675 ± 32.4 eggs and the largest clusters of 16.75 ± 0.62 eggs, was recorded on maize (Figure 2). Although different numbers of eggs were laid on mustard (553.25 ± 28.9) and cabbage (300 ± 11.3), there was no significant difference in egg cluster size between these two plants (Figure 3). This indicates that a higher number of egg clusters does not necessarily correlate with greater overall fecundity.

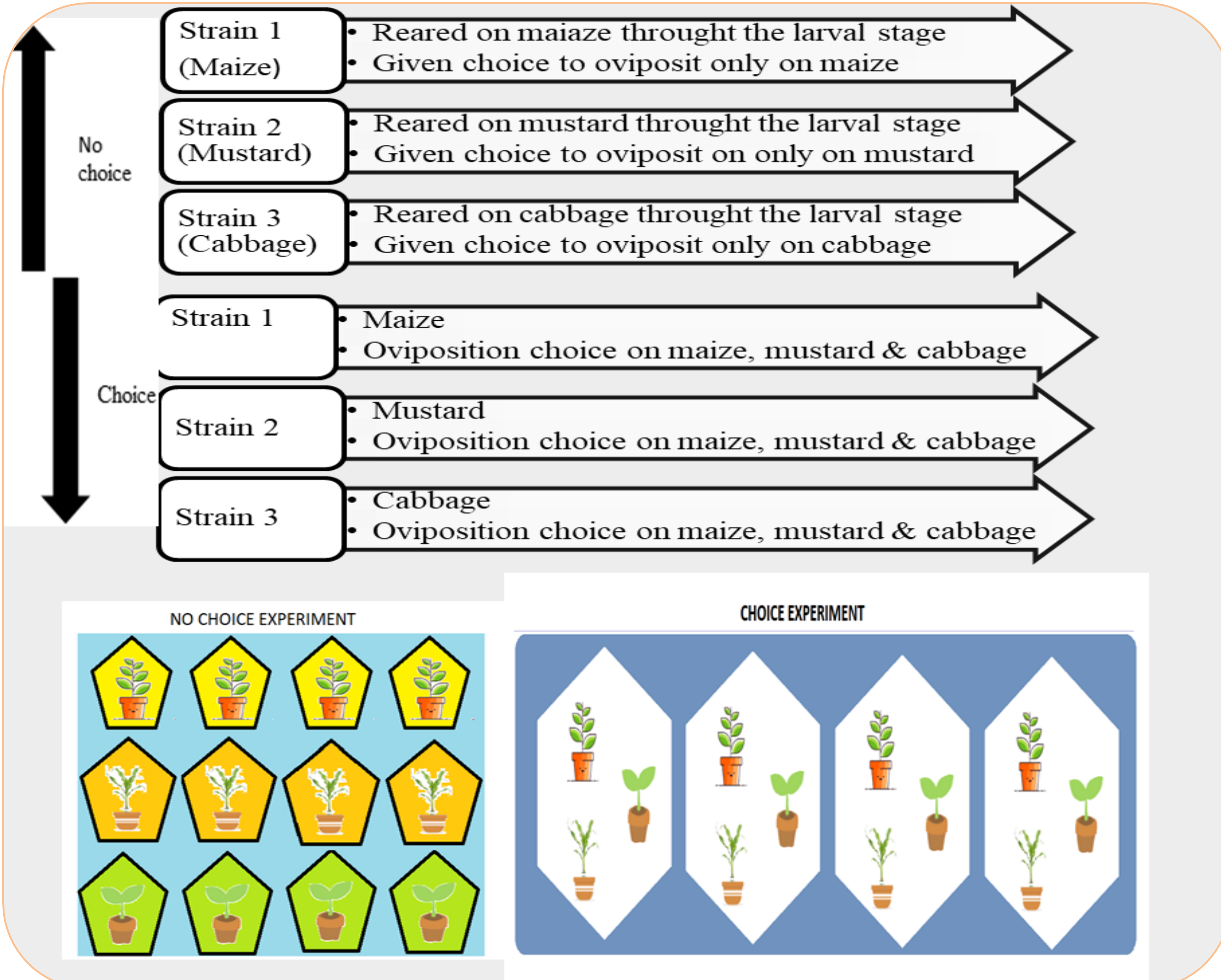


Figure 1. Experimental setup showing choice and no choice conditions.

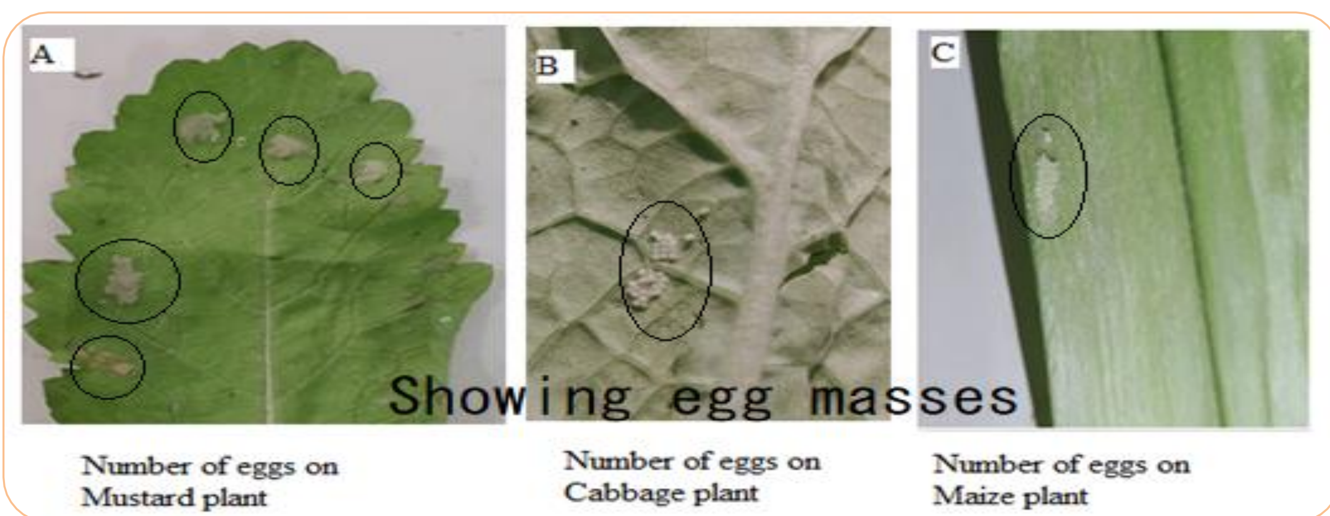


Figure 2. Egg clusters laid by *S. frugiperda* on various host plants: (a) mustard, (b) cabbage, and (c) maize.

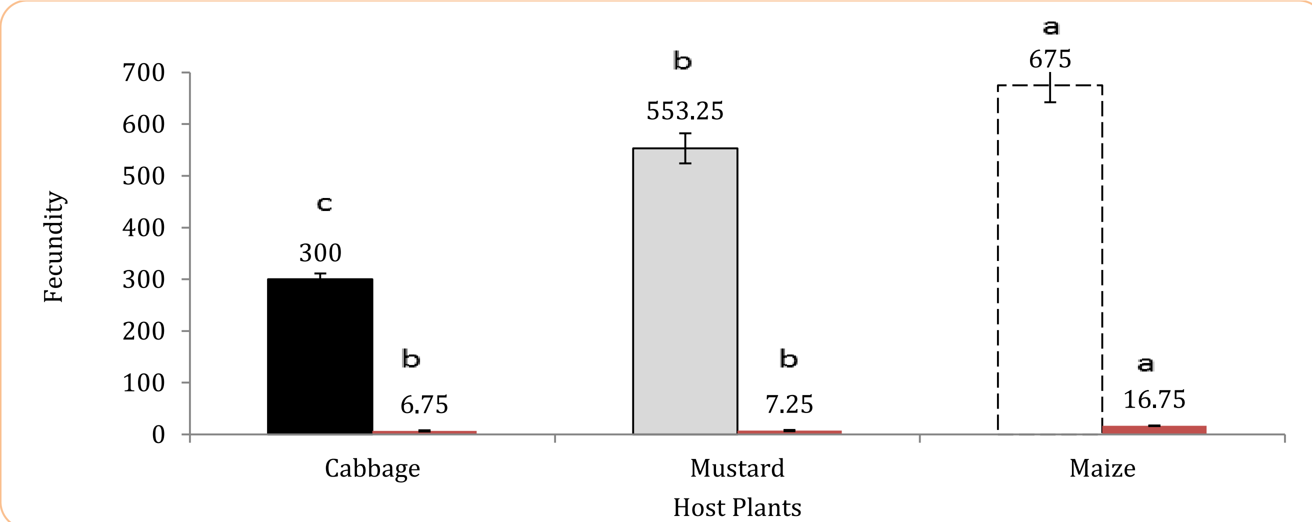
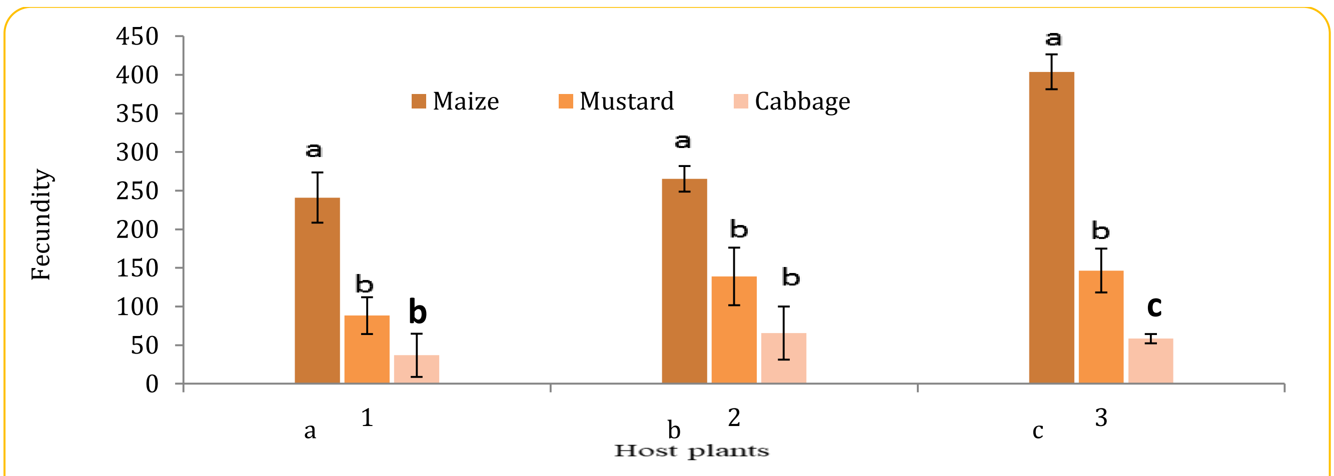


Figure 3. Mean number (± S.E.) of eggs and egg clusters laid by *S. frugiperda* moths on various host plants following larval feeding on maize.

To confirm the combined effect of larval feeding and host plant preference for oviposition, a choice experiment was conducted. A significant difference in oviposition response was observed under these conditions (P<0.05). FAW cohorts reared on maize were dominant, with their moths laying the highest number of eggs. Not only did these cohorts produce the maximum number of eggs overall, but their moths also showed a marked preference for maize plants as an oviposition site, with a significant difference (403.75 ± 22.6 eggs; P<0.05) compared to other host plants (Figure 4). Interestingly, neither the FAW cohort reared on mustard (139 ± 37.3 eggs) nor the one reared on cabbage (37.0 ± 4.6 eggs) laid the most eggs on their respective host plants. Instead, both cohorts demonstrated a strong preference for oviposition on maize (265.25 ± 16.5 and 241.00 ± 32.4 eggs) respectively. This suggests that, despite being reared on different host plants, FAW moths consistently preferred maize for oviposition.



a. FAW cabbage cohort b. FAW mustard cohort c. FAW maize cohort

Figure 4. Egg-laying behavior of *S. frugiperda* moths on host plants under choice conditions.

There was no significant difference (P > 0.05) in the pre-oviposition, post-oviposition periods, or adult longevity of FAW moths (Table 1), indicating that larval diet did not notably affect these parameters. However, a significant variation (P < 0.05) was observed in the oviposition period, with the FAW moth spending the longest time laying eggs when larvae were pre-fed on maize compared to other host plants. The maximum oviposition period of 7.5 ± 1.2 days was recorded on maize. No statistical difference in the oviposition period was found when larvae were reared on mustard or cabbage.

Table 1. Effect of larval food on reproductive parameters of FAW *S. frugiperda*.

Treatments	Pre-oviposition period (days)	Oviposition period (days)	Post-oviposition period (days)	Adult longevity
Maize	3.25 ±0.48 [a]	7.5 ± 1.2 [a]	1.75 ± 0.48 [a]	12.5 ± 0.96 [a]
Mustard	3.5 ± 0.5 [a]	3.75 ± 0.75 [b]	1.5 ± 1.2 [a]	8.75 ± 1.31[a]
Cabbage	4.75 ± 0.75 [a]	5.0 ± 0.70 [ab]	1.25 ± 0.25 [a]	11.0 ± 1.22 [a]

To assess the effect of moth diet on oviposition, we used only a maize cohort. The results revealed a significant difference (P < 0.05) in overall fecundity, with the highest number of eggs (1188 ± 64.84) recorded on the honey + protein solution, and the lowest (443.5 ± 48.08) on the yeast solution (Figure 5). Table 2 shows statistically significant differences (P < 0.05) in both the pre-oviposition and oviposition periods of the FAW moth when fed different diets. The longest oviposition period (7.50 ± 0.64 days) occurred on the honey + protein solution, followed by the protein solution (6.75 ± 0.25 days), while the shortest oviposition period (3.50 ± 0.28 days) was recorded on the yeast solution. However, no significant differences (P > 0.05) were observed in the post-oviposition period or adult longevity across the different diets. Overall, these findings indicate that the adult diet significantly impacts the oviposition period, with the honey + protein solution supporting the highest fecundity compared to the other diets (Figure 5).

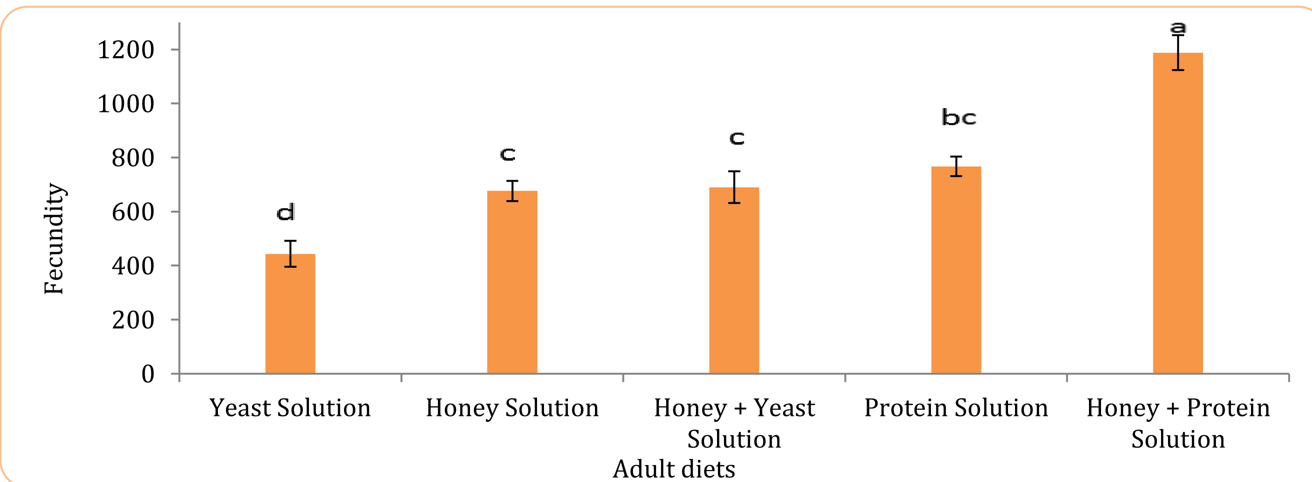


Figure 5. Oviposition of *S. frugiperda* moths reared on maize and adults fed on a variety of foods.

Table 2. Effect of adult (moths) diets on reproductive parameters of *S. frugiperda*.

Adult (moth) diets	Pre-oviposition Period	Oviposition Period	Post-oviposition Period	Adult longevity
Honey solution	3.00 ± 0[bc]	6.00 ± 0.40[a]	2.25 ± 0.47[a]	11.25 ± 1.47[a]
Yeast solution	4.25 ± 0.25[a]	3.50 ± 0.2 [c]	2.50 ± 0.28[a]	10.25 ± 1.28[a]
Honey+ Yeast solution	3.50 ± 0.28[b]	5.25 ± 0.25[b]	2.25 ± 0.47[a]	11 ± 1.12[a]
Protein solution	2.50 ± 0.28[cd]	6.50 ± 0.25[a]	2.75 ± 0.25[a]	11.75 ± 1.67[a]
Honey + protein solution	2.25 ± 0.25[d]	7.50 ± 0.64[a]	3.25 ± 0.25[a]	13 ± 1.98[a]

DISCUSSION

To date, the foraging behavior of insects has been extensively explored, while studies on insect oviposition remain limited. *S. exigua* H. a well-identified species from the order Lepidoptera (Noctuoidea), has been thoroughly studied for its distinct behaviors, including oviposition (Azidah and Sofian-Azirun, 2006). However, there is limited information available about *S. frugiperda* due to its recent invasion into agro-ecosystems. Given the potential damage and spread of the invasive FAW in

Asia, it has become essential to understand its developmental biology on different crops in new geographical regions. Previous reviews of the fall armyworm highlight its attributes as a polyphagous insect pest. The primary host plants recorded are from the Poaceae (Gramineae) family, including maize, wheat, sorghum, rice, oats, and pasture grasses (Montezano et al., 2018; Nagoshi et al., 2018; Sisay et al., 2023). Meanwhile, secondary host plants (apart from gramineous crops) include species from the Brassicaceae family (mustard, cabbage, and broccoli), Asteraceae family (sunflower, lettuce, pyrethrum, and marigold), and Fabaceae family (soybean, peanut, and chickpea) (Montezano et al., 2018; Nagoshi et al., 2018; Sisay et al., 2023).

Considering the importance of host plants for FAW, this study was conducted using multiple host plants, primarily maize, and secondarily cabbage and mustard. These plants were first offered for feeding and later for oviposition. We observed a significant effect of host plants on oviposition by *S. frugiperda*, regardless of their larval feeding on different host plants. The highest number of eggs was recorded on maize, followed by mustard. The variation in oviposition responses could be due to chemical cues received from the host plants and the larval fitness of those reared on their respective plants. According to Thompson (1988), insect oviposition can be influenced by host plant nutrients, varietal characteristics, and the size, shape, and stage of the host plants. He et al. (2021) also conducted laboratory trials on FAW oviposition on different host plants and found that oviposition on Bt-maize and conventional maize (with no statistical variation) was significantly higher compared to millet, peanut, wheat, sorghum, and soybean. *S. frugiperda* has been reported in Pakistan for the last four to five years (Bhatti et al., 2021), with maize being its primary host. However, this lab experiment clearly showed its survival and biological development on other plants, posing a potential threat to the main cash crops of Sindh (Pakistan) under field conditions. This is particularly concerning given the similar feeding behavior of *S. litura*, which is known for its wide host range.

The FAW cohorts produced the highest total number of eggs overall and demonstrated a strong preference for oviposition on maize plants over other host plants. Interestingly, neither the FAW mustard nor the FAW cabbage cohorts laid their maximum number of eggs on their respective host plants; instead, both preferred maize for oviposition. This suggests that, although FAW larvae were reared on various host plants, adults still showed a preference for maize as an oviposition site. This attraction may be due to specific plant allelochemicals that serve as olfactory cues. These cues, often complex blends, play a fundamental role in guiding moths to appropriate mates, food sources, and oviposition sites (Dahanukar et al., 2005). Olfactory cues differ in intensity between host and non-host plants, which may complicate host plant recognition.

Oviposition preference suggests that females select oviposition sites based on perceived nutritional benefits for their offspring, supporting faster larval development, greater biomass, and enhanced reproductive potential. Occasionally, a conflict arises between the preferences of offspring and adult females; while larvae may have a broader range of suitable host plants for feeding, adults might choose different plants for oviposition. In this study, no significant effect of host plant on reproductive parameters, such as pre- and post-oviposition periods and adult longevity, was observed in FAW moths. These results differ from the findings of Zhu et al. (2005) in China and Ahmad et al. (2007) in Pakistan, who reported host plant influences on various biological parameters, including pre- and post-oviposition periods. However, consistent with our findings, they also observed that FAW moths spent the longest time ovipositing on maize compared to other host plants. Additionally, they noted that host plants affected parameters like larval and pupal weight, oviposition rates, and survival in various insect species.

In another experiment, a significant effect of adult diets on oviposition was observed when adults, following the larval stage, were also provided with various artificial nectars. The results clearly demonstrated the influence of adult diets on fecundity, though host plant preference for oviposition was unaffected. The highest egg count was recorded on maize plants by adults fed with a honey and protein solution. Honey, as a rich sugar source mimicking flower nectar, provides essential energy, while protein supports biochemical processes critical for egg development in the ovaries of the moth.

Similarly, Simmons and Lynch (1990) studied the survival and egg production of three lepidopteran moth species, including *S. frugiperda*, *Helicoverpa zea* (Boddie), and *Elasmopalpus lignosellus* (Zeller), across eight artificial diets. They found optimal moth performance on honey or sucrose diets, with the highest survival rate (8.4 days) and maximum egg production (2,375 eggs per female for *S. frugiperda*) observed with the low-cost honey diet. Our findings on FAW add valuable insights to existing literature by advancing understanding of its ecology and reproductive fitness in relation to host plants across varied ecological conditions.

CONCLUSIONS

It was concluded that the host range of fall armyworm is largely influenced by female moths, as they show a strong preference for laying eggs on maize plants rather than on other hosts. This preference is not necessarily related to the ability of the larvae to feed and survive on different host plants. Egg production was also affected by the presence or absence of maize plants, with diets such as honey and protein solutions significantly boosting egg output. Therefore, effective management of this pest on maize requires close monitoring of other host plants within similar plant families, enabling timely pest control measures.

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AUTHORS' CONTRIBUTIONS

AMG collected data and performed this research during his master's degree; AMA and WAP planned and designed all the experiments; FNK and MIK provided technical facilities with equipment for performing these experiments; AZAQA revised this whole manuscript after review for necessary correction and incorporation.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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