Maize Journal (October 2026) 15(2): 101-106

RESEARCH PAPER

Influence of host-plant alteration on the oviposition performance of fall armyworm, *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae)

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Abstract: The study evaluated the influence of larval host-plant nutrition and subsequent host-plant alteration during oviposition on the reproductive performance of fall armyworm, *Spodoptera frugiperda*. Larvae were reared on six host plants viz., maize, teosinte, sorghum, cowpea, pearl millet, and Napier bajra hybrid and adult females were either allowed to oviposit on their larval host or transferred to an alternative host. Fecundity and egg hatching varied significantly among various host-plant. In case of same larval and oviposition host plants, highest number of eggs per plant (496.00 ± 25.01) were laid on maize, followed by those on teosinte (311.50 ± 13.75). Egg hatching was highest on maize (70.96 ± 6.28%) followed by sorghum (67.99 ± 4.00%) and teosinte (66.95 ± 6.10%). When maize-reared females were offered alternative hosts for oviposition, teosinte supported the highest fecundity (200.60 ± 15.39 eggs) and egg hatching (69.20 ± 7.91%). Conversely, when females reared on alternative hosts were offered maize for oviposition, the highest egg production occurred in females reared on teosinte (198.60 ± 5.12 eggs) that was followed by sorghum (116.40 ± 13.58 eggs). These results indicate that maize was the most suitable host among the various plants tested, irrespective of the host plants on which the larvae were fed. However, teosinte and sorghum also supported oviposition and egg development. Thus, these hosts may contribute to the persistence of *S. frugiperda* populations when preferred hosts are less available especially in more suitable habitat of sub tropics offering this polyphagous pest a varied agricultural landscape.

Keywords: Egg hatching • Fecundity • Host-plant alteration • Larval nutrition • Oviposition • *Spodoptera frugiperda*

Introduction

India is widely recognized for its intensive cultivation of both food and fodder crops, with farmers in some regions adopting multiple cropping systems. However, this continuous land use with consecutive crops throughout the year can lead to the survival of pests even in the absence of their preferred hosts, resulting in frequent outbreaks in various agro-ecosystems (Kennedy and Storer, 2000; Saeed *et al.,* 2017). Therefore, it is essential to understand the factors responsible for the quicker adaptation of polyphagous insects to different agro-ecosystems (Bortolotto *et al.,* 2014). Effective management of migratory and polyphagous pests requires a holistic approach that considers not only the major seasonal crop but also the diverse cropping systems in a wide area (Herde, 2009). The fall armyworm, *Spodoptera frugiperda* (J.E. Smith) is a highly destructive and invasive pest that feeds on a wide range of crops with over 353 plant species from 76 families recorded as its host plants (Montezano *et al.,* 2018). The pest was originally native to the Americas but was first reported in Africa in 2016 (Goergen *et al.,* 2016). Later, it was reported from 16 Asian countries including India (Sharanabasappa *et al.,* 2018) In India, annual maize yield was recorded to be reduced from 14.3 to 22.7% with control measures and from 21 to 53 per cent without them (Suby *et al.,* 2020).

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Received: 29 September 2026/ Accepted: 13 October 2026
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Maize is grown throughout the year in India and in Punjab region with respect to host plants of fall armyworm, maize and sorghum are mainly grown from spring to summer during which this moth invades by migration and continues in rainy season. The continuity and abundance of preferred host plants suggested that pest can survive and reproduce several generations in a single crop season which may led to the pest endemic (Ganiger *et al.,* 2018; Keerthi *et al.,* 2021). Based on polyphagous nature of *S. frugiperda*, this study was aimed to understand the female oviposition behaviour when feeding on alternative plant resources. Basically, oviposition was a crucial process because it regulates the survival and development of insect pest and their progeny (Renwick, 1989). In Lepidopterans, the host-plant recognition and selection process is primarily a function done by the gravid females because neonate larvae are restricted in their dispersal abilities (Konstantopoulou *et al.,* 2002). According to the preference-performance hypothesis (Poykko, 2006; Refsnider and Janzen, 2010), females will prefer to oviposit in hosts that provide the best nutrition for their offspring. As a result, the chosen host would enable the offspring to develop more quickly, produce more biomass, and have higher reproductive potential. However, earlier studies also suggest that there may be a conflict between parents and offspring and females potentially maximizing fecundity at the expense of larval performance on suboptimal hosts (Gamberale-Stille *et al.,* 2014). Therefore, the present study investigated whether larval feeding on different host plants influences the reproductive performance of adult *S. frugiperda*. Fecundity and egg-hatching performance were assessed to determine whether larval host history affects subsequent reproduction and to clarify the potential contribution of alternative hosts to fall armyworm persistence in diversified agricultural landscapes.

Materials and methods

Study area

The present studies were carried at the Maize Research Farm and the Maize Entomology Laboratory, Department of Plant Breeding and Genetics, Punjab Agricultural University (PAU), Ludhiana-141004. The university is located at 30° 45' N, 75° 40' E with an altitude of 246 meters above sea level.

Maintenance of S. frugiperda colony and host plants

The fall armyworm larvae (F_o) were collected from PAU maize fields and maintained under controlled conditions (25±2°C and 70% RH and a photoperiod of 16:8 h light: dark) on natural food (six host plants) for a generation. The next generation insects (F_1) were used in the present studies. Six host plants viz., Maize (*Zea mays*) (hybrid PMH 1), Napier bajra hybrid (*Pennisetum purpureum x Pennisetum glaucum*) (hybrid PBN 233), Sorghum (*Sorghum bicolor*) (var. PSC 4), Pearl millet (*Pennisetum glaucum*) (hybrid FBC 16), Teosinte (*Zea mays* ssp. *parviglumis*) (var. TL 16) and Cowpea (*Vigna unguiculata*) (var. CL 367) tested in this study were obtained from Principal Maize Breeder and Principal Forage Breeder in the Department of Plant Breeding and Genetics, PAU, Ludhiana.

Influence of larval nutrition on oviposition performance of S. frugiperda

The oviposition studies were conducted on potted plants of different hosts in the month of August. The pot used, were size of 27 x 25 cm. The potted plants were maintained in an insect-proof screen house (18-20 mesh size) situated at Maize Research Farm of University. The mean maximum and minimum temperature were 33.66°C (with 81.6% RH) and 27.04°C (with 67.6% RH), respectively. The experiment was replicated 5 times and there were 3 plants of each host in one replication with one plant as an experimental unit. The fall armyworm larvae were reared on each of different six host plants. "Larval host" refers to the plant on which larvae were reared, whereas "oviposition host" refers to the plant on which adult females were allowed to lay eggs. To determine fecundity parameter on larvae reared host i.e. same larval and oviposition host, single pair of moths was allowed to oviposit on 20-day old potted plants of same host plants where larvae were fed. The napier bajra hybrid plants were trimmed to leave only a single tiller of similar size to that of maize plants (Van den Berg, 2006). For fecundity parameter on different oviposition host plants for the larvae reared on maize, the larvae reared on maize plants and single pair of moth emerged was allowed to oviposit on 20-day old potted plants of other five host plants. Fecundity parameter on maize as oviposition host for the larvae reared on different host

plants was studied by rearing larvae on different host plants and then allowed to oviposit on 20-day old potted maize plants. The eggs were collected and counted at 24 h interval till female mortality from each set. After that, eggs were placed under controlled conditions (25±2°C and 70% RH and a photoperiod of 16:8 h light: dark) and egg hatching pattern was observed every day. The observations on hatching of eggs (%) were also recorded.

Statistical analysis

The mean differences in egg laying on different host plats and after switching the host plants for feeding and oviposition were analysed by using one way analysis of variance (ANOVA) through statistical software SPSS v 16.0. Statistical analysis was done using complete randomized design (CRD for 6 treatments and five replications). The different treatment means and standard errors were calculated by least significant differences test (LSD) at p=0.05 (Gomez and Gomez, 1984).

Results

Fecundity parameter of S. frugiperda on larvae reared host

The adult fecundity was significantly higher when larvae were reared on maize (496.00±25.01 eggs) as compared to napier bajra hybrid (36.30±8.19 eggs), pearl millet (42.10±10.73 eggs), and cowpea (44.70±5.78 eggs) ($F_{5, 24}$ = 165.93, P ≤ 0.0001). Significantly higher number of eggs were also laid on teosinte (311.50±13.75 eggs) ($F_{5, 24}$ = 165.93, P ≤ 0.0001) after maize host. The hatching (%) of eggs was also significantly more on maize (70.96±6.28 %), sorghum (67.99±4.00 %) and teosinte (66.95±6.10%) as compared to napier bajra hybrid (39.87±8.94 %) followed by pearl millet (43.57±8.06%) ($F_{5, 24}$ = 3.73, P ≤ 0.006) (Table 1).

Keerthi *et al.* (2021) also reported that adult fecundity was more in larvae when reared on maize (1083.6 ± 188.13 eggs) and sorghum (1029.4 ± 133.31 eggs) as compared to artificial diet (815 ± 102.57 eggs). The present study showed that fecundity and hatching percentage of eggs were higher when larvae were reared on maize and teosinte. Therefore, it is important to find the best host plant that favours the growth and development of fall armyworm. This will help in formulating an effective strategy to control this destructive pest. This may be due to food ingested and accumulated during the larval period greatly influenced the adult fecundity (Wheeler, 1996).

Table 1. Adult fecundity and hatching of eggs of fall armyworm, *S. frugiperda* with same larval and oviposition hosts

Host	Number of eggs per plant	Hatching of eggs (%)
	Mean ± SE	Mean ± SE
Maize	496.00±25.01	70.96±6.28
Teosinte	311.50±13.75	66.95±6.10
Sorghum	155.80±15.55	67.99±4.00
Cowpea	44.70±5.78	52.14±7.50
Pearl millet	42.10±10.73	43.57±8.06
Napier bajra hybrid	36.30±8.19	39.87±8.94
CD (p= 0.05)	41.31	19.85

Values are the mean ± S.E. of five replicates

Fecundity parameter of S. frugiperda reared on maize and egg laying on different host plants

When larvae were reared on maize and allowed to oviposit on other host plants, significantly higher number of eggs were recorded on teosinte (200.6±15.39 eggs) as compared to napier bajra hybrid (39.60±3.02 eggs) followed by pearl millet (44.20±4.12 eggs) and cowpea (69.80±21.28 eggs) ($F_{4, 20}$=29.69, P ≤ 0.0001). The sorghum (122.60±6.89 eggs) had recorded significantly more number of eggs after teosinte host plant ($F_{4, 20}$= 29.69, P ≤ 0.0001). The hatching percentage of eggs laid by females on teosinte (69.20±7.91%) and sorghum (58.20±13.89%) were significantly higher than that were laid on pearl millet (21.60±2.6%) and napier bajra hybrid (22.00±3.28%) ($F_{4, 20}$=4.30, P ≤ 0.011) (Table 2). This

Table 2. Adult fecundity and hatching of eggs of fall armyworm, *S. frugiperda* with maize as larval host and other plants as oviposition hosts

Host	Number of eggs per plant	Hatching of eggs (%)
	Mean ± SE	Mean ± SE
Teosinte	200.6±15.39	69.20±7.91
Sorghum	122.60±6.89	58.20±13.89
Cowpea	69.80±21.28	45.20±15.92
Pearl millet	44.20±4.12	21.60±2.63
Napier bajra hybrid	39.60±3.02	22.00±3.28
CD (p= 0.05)	36.51	30.32

Values are the mean ± S.E. of five replicates

may be because the quality of the host plant highly affects the host preference for oviposition. In general, gravid females prefer to lay eggs on suitable host plants for better performance and survival of the larvae (Signoretti *et al.,* 2012). Similar to present studies, Heo *et al.* (2022) reported that when larvae were reared on maize for two generations and then shifted to sudan grass and proso millet in F_3 generation, the total fecundity was reduced to half than that on maize (942.3 ± 326.96 eggs) in sudan grass (447.8 ± 135.39 eggs) and proso millet (422.8 ± 155.33 eggs). However, the egg hatch (%) was on par among maize (64.9 ± 10.48), sudan grass (61.5 ± 8.74) and proso millet (60.5 ± 15.37). However, in present studies, the number of eggs and hatching were reduced when larvae were fed on maize and adults derived from them were allowed to oviposit on other host plants. However, it shows a possibility that *S. frugiperda,* in spite of reduced fecundity, could establish its population with altering host plants in the absence of preferred host plant.

Fecundity parameter on maize for the larvae reared on different host plants

In alternate studies of larval feeding on other host plants and maize as host for oviposition, a significantly higher number of eggs were laid on maize by females whose larvae were reared on teosinte (198.60±5.12 eggs) and sorghum (116.40±13.58 eggs) as compared to pearl millet (24.60±10.96 eggs) followed by napier bajra hybrid (33.20±7.74 eggs) and cowpea (39.00±14.61 eggs) ($F_{4, 20}$= 45.99, P ≤ 0.0001). The larvae reared on teosinte (63.60±11.81%) had recorded significantly higher egg hatching in comparison to pearl millet (13.40±5.10%), napier bajra hybrid (19.20±7.63%) and cowpea (22.00±9.42 %) while it was intermediate in sorghum (50.40±12.65 %) ($F_{4, 20}$= 4.98, P ≤ 0.006) (Table 3). Similar to the above findings, Heo *et al.* (2022) reared the larvae of *S. frugiperda* on maize for two generations (F_1-F_2) previously and then shifted to other host plants. The larvae fed on other host plants for another two generations (F_3-F_4) and some of larvae shifted on maize in F_4 generation. At F_5 generation of fall armyworm, significant differences in adult fecundity were observed on maize (973.0 ± 131.33 eggs) in comparison to proso millet (408.9 ± 84.87) and sudan grass (522.7 ± 145.07 eggs). However, the non- significant results were observed in egg hatching (%) on maize (51.9 ± 4.15), sudan grass (47.5 ± 6.50) and proso millet (54.8 ± 3.90). In contrast, fecundity was reduced in the absence of suitable maize host plant in present studies.

Table 3. Adult fecundity and hatching of eggs of fall armyworm, *S. frugiperda,* when larvae fed on teosinte, sorghum, cowpea, pearl millet and napier bajra hybrid and oviposited on maize

Host	Number of eggs per plant	Hatching of eggs (%)
	Mean ± SE	Mean ± SE
Teosinte	198.60±5.12	63.60±11.81
Sorghum	116.40±13.58	50.40±12.65
Cowpea	39.00±14.61	22.00±9.42
Pearl millet	24.60±10.96	13.40±5.10
Napier bajra hybrid	33.20±7.74	19.20±7.63
CD (p= 0.05)	32.48	29.02

Values are the mean ± S.E. of five replicates

In present study, various fecundity parameters were designed to determine the effect of host plant alterations on the reproductive performance of fall armyworm. Most of fecundity parameters showed variations in egg count according to alternation of host plants. Adult fecundity was significantly higher on maize, followed by teosinte, when larvae were reared and adults were allowed to oviposit on the same host plant. Host alternation influenced the fecundity of *S. frugiperda*. Larvae reared on maize and adults allowed to oviposit on other hosts, particularly teosinte followed by sorghum, exhibited the highest fecundity. Conversely, larvae reared on teosinte produced more eggs when adults were allowed to oviposit on maize. Oviposition declined more markedly when larvae were reared on cowpea, pearl millet, and Napier–bajra hybrid and subsequently allowed to oviposit on maize than when larvae were reared on maize and allowed to oviposit on these hosts. Thus, larval nutrition appears to have a carry-over effect on adult reproductive performance and influences oviposition patterns. The varied nutritional values of host plants were reported to significantly affect the growth, development and survival of insect (Montezano *et al.,* 2018; Moreau *et al.,* 2006). Maize in comparison to other host plants might have more nutritional balance of carbohydrates, amino acid, vitamins than other host plants (Behmer, 2009). Several other mechanisms that are believed to be involved during host selection for egg laying, such as colour and presence of trichomes on the leaves, not considered in this study,

however, they might have contributed towards selection of oviposition site (Nogueira *et al.,* 2018). Traore *et al.* (1989) also reported that limited larval feeding, poor growth and development of fall armyworm on pearl millet genotypes were due to higher trichome density as compared to maize and sorghum. Within the limits of our study, it is challenging to fully discuss how various responses (such as variation in number of eggs and per cent egg hatching on offered plants) of *S. frugiperda* shown above can be explained physiologically or genetically. The key finding is that *S. frugiperda* can continuously feed and reproduce on a range of potential host plants. This might be due to its adaptation ability to new host plant, despite the fact that it is usually found on maize. The fall armyworm has wide host range and availability of one or more host in diversified habitat of tropics may be helpful in survival and complete several generations over a large time period.

Conclusion

The results demonstrate that larval host-plant as well as the host available for oviposition, both influence the reproductive performance of fall armyworm, *S. frugiperda*. Maize supported the highest fecundity and high egg hatching, whereas teosinte and sorghum also supported substantial reproduction. Host alteration reduced egg production in several combinations but did not prevent oviposition or egg hatching. Thus, the alternative hosts may contribute to the persistence of *S. frugiperda* populations when preferred hosts are temporarily unavailable. These findings highlight the importance of considering host-plant continuity and crop diversity when assessing the seasonal carryover of *S. frugiperda*.

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