Host Plant Feeding and Ovipositional Preferences of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) under Laboratory Conditions[1]

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Abstract In India, the invasive fall armyworm, *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae), has emerged as the most devastating pest of maize, *Zea mays* L., and is expanding its host range. In this study, we assessed its preference for feeding and oviposition in both choice and nonchoice bioassays including maize, sorghum, castor, cowpea, cotton, banana, and marigold as hosts. At 24 h after release in choice tests, the number of larvae was greatest on maize ears and lowest on cotton (*Gossypium hirsutum L.*) leaves among the host plants tested. In nonchoice tests, third-instar larvae that fed on maize leaves and ears had the shortest growth periods (2.05 and 2.2 d, respectively) and the longest on marigold (*Tagetes erecta L.*) flowers (5.2 d). In oviposition preference tests, maize was the most preferred host, with the greatest number of egg masses deposited in choice and nonchoice tests compared with other hosts. Thus, maize was the most preferred host for fall armyworm in our tests, but fall armyworm may also survive on plants other than maize during the nongrowing season, posing a risk to other economically important crops in its expanded range in India.

Key Words invasive, India, maize, host range, choice, nonchoice

The fall armyworm, *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae), is a major pest of maize, *Zea mays* L., in its native and expanded range. It is native to tropical and subtropical areas of Latin and North America, but it historically migrated from its overwintered sites northward into the mid-Atlantic region of the United States (Luginbill 1928, Sparks 1979). Being a polyphagous pest, it feeds on 353 host plants belonging to 76 plant families (Montezano et al. 2018), but it prefers members of the family Poaceae (Casmuz et al. 2010).

The morphologically identical C-strain (corn strain) and R-strain (rice strain) mostly prefer graminaceous host plants; however, maize is the most preferred host by C-strain and rice (*Oryza sativa* L.), millets, and other grains are preferred by the R-strain (Nagoshi et al. 2022, Wu et al. 2019). It also causes economic damage to cotton (*Gossypium*) and soybean (*Glycine max* (L.) Merrill) (Pitre and Hogg 1983).

Goergen et al. (2016) first reported fall armyworm from maize-growing countries in Western and Central Africa. Food security and subsistence farming in sub-Saharan

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Table 1. Host plants and their components evaluated for *S. frugiperda* feeding and oviposition preferences.

Crop (Component Tested)	Scientific Name	Variety	Host Age (months)
Maize (ears)	*Zea mays* L.	Pioneer P3304	2
Maize (leaves)	*Zea mays* L.	Pioneer P3304	1
Sorghum (leaves)	*Sorghum bicolor* (L.) Moench	M 35-1	1
Cowpea (leaves)	*Vigna unguiculata* L.	UAHS 28	1
Castor (leaves)	*Ricinus communis* L.	HCH-6	3
Banana (leaves)	*Musa paradisiaca* L.	G9	4
Marigold (flower petals)	*Tagetes erecta* L.	Local variety	2
Cotton (leaves)	*Gossypium hirsutum* L.	DCH-32	2

Africa have been challenged by the fall armyworm invasion and spread (Kasoma et al. 2021). In Asia, the pest was first reported in Karnataka (Sharanabasappa et al. 2018) and has continued to expand its range to several Indian states (Suby et al. 2020). Conventional insecticides are widely used in fall armyworm management (Deshmukh et al. 2021). It is now reported from Bangladesh, China, Thailand, Myanmar, Sri Lanka, Vietnam, and Australia (Food and Agriculture Organization 2021).

Host preference varies with larval instar, and larval survival varies with host plant type (Rojas et al. 2018). Similarly, the biology of fall armyworm is influenced by climatic conditions and host plants, making it crucial to understand its developmental cycle, growth attributes, and host preferences in its expanded range for implementation of effective management programs for this invasive pest. Hence, we studied the feeding and oviposition preference among seven host plants to predict and avoid its incidence on commercial crops. These host plants were chosen because the fall armyworm may pose a threat to these major crops in the future.

Materials and Methods

Insects. The fall armyworm larval colony used in this study was initially collected from the maize fields in and around the College of Agriculture, Shivamogga, Karnataka. Larvae were fed on maize leaves collected from the field. Adults were fed with 10% (v/v) honey. The colony was maintained at 26 $\pm$ 2°C, 75–80% relative humidity (RH), and a photoperiod of 16:8 (L:D) h.

Feeding preference. The feeding preference tests were conducted as choice and nonchoice tests in the laboratory at the previously described conditions in a completely randomized design. The treatments and host components are listed in Table 1. The treatments were replicated five times.

The assay arenas in the choice tests were 25-cm-diameter circular plastic containers with the bottoms lined with moistened filter paper. Plastic lids with a small hole for aeration were used to cover the top of each container to prevent larval escape.

Foliage, flowers, or ears of the host plants were placed in a circular arrangement equidistant from each other in each arena. A 5-cm-diameter Petri dish containing neonates ($n = 25$) from the F_1 generation of the laboratory colony was placed in the center of each arena. Orientation of the neonates toward the host plants was observed for 1 h, and the numbers of larvae on each plant were counted at 1, 6, and 24 h after release. The attraction of the neonates to a plant structure within 1 h of release was considered as feeding preference, whereas host plants remaining relatively uneaten or unoccupied up to 24 h after larval release were defined as not preferred (e.g., nonpreference) (Campos et al. 2012).

In nonchoice tests, preweighed third-instar larvae of the F_1 generation of the laboratory colony were released into arenas containing a preweighed plant part of a single host. The plant structure was replaced with fresh material at each larval molt, and frass was collected and weighed daily. Data included plant material consumption, larval weight gain, feeding duration, and frass weight.

Oviposition preference. Oviposition preferences were evaluated in choice and nonchoice tests in a polyhouse maintained at 26 ± 2°C, 75–80% RH, and a photoperiod of 12:12 (L:D) h in a completely random design with eight treatments and three replications. Adult moths that emerged from the F_1 larval generation in the laboratory colony were used for these tests.

Test arenas for the choice tests were 4 × 4 × 3 m cages covered with 30-mesh nylon screen. Individual host plants (Table 1) grown in 2-L pots (17 × 17 cm) were placed in the test arena cage in a circular pattern. Six male and female moths that had been allowed to cohabitat and mate for 2 d were released into each cage. Cotton balls soaked with 10% (v/v) honey were provided as food. The moths were confined in the cage until death. The numbers of egg masses on each plant and on the cage inner surface were recorded daily and were removed on alternate days.

Small cages (45 × 45 × 60 m) covered with a 30-mesh nylon screen were used as test arenas for the nonchoice tests. Host plants were grown in a 2-L pot (17 × 17 cm) with one plant per pot representing a treatment. For each treatment, six male and female moths were released into the cages and 10% honey solution was supplied to the adults. For the treatment of maize ear, the plant with ear was transported to the laboratory and 50 cm of the plant portion was cut ensuring that the plant had leaves and the ear. Observations on plant height, number of egg masses on each host plant and on the cage inner surface, and number of eggs per mass were recorded.

Statistical analyses. The Statistical Packages for the Social Sciences, version 21.0 (IBM SPSS, Armonk, NY) was used for analysis. The parametric data were analyzed using one-way analysis of variance, and treatment means were separated using Tukey's honestly significant difference test at $P = 0.05$.

Results

Feeding preference. In the choice test, *S. frugiperda* larvae were found on all host plants 1 h after the release of the neonates. The mean number of larvae in the arena, but not on any of the host plants, was significantly higher than the numbers found on the individual plants ($F = 25.38$; df = 8, 36; $P < 0.05$). The host plant with the greatest number of larvae 1 h after release was the maize ear and foliage, with a mean ± SEM of 3.8 ± 0.2 larvae per ear or leaf, followed by the caster leaf (2.8 ±

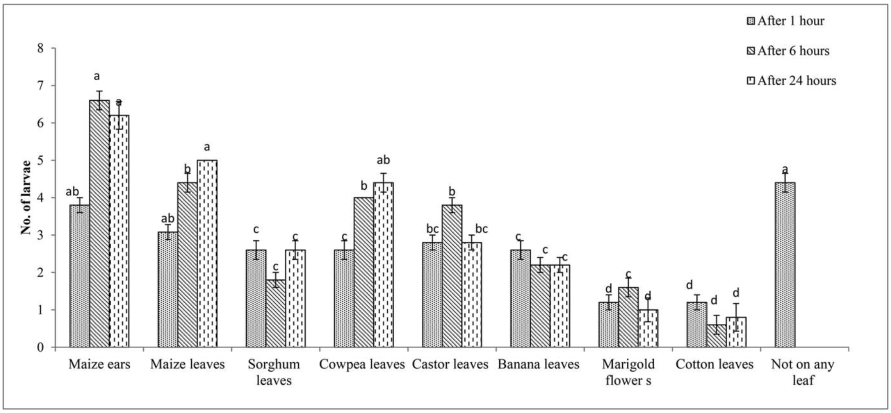

Fig. 1. Mean (±SE) number of *S. frugiperda* larvae ($n = 25$) found on different host plants at various time intervals after larval release in choice tests. Means followed by the same letter on the error bars do not differ significantly (Tukey's honestly significant difference test, $P = 0.05$).

0.2 per leaf), whereas the lowest numbers were found on the cotton leaf and the marigold flower with 1.2 larvae per host (Fig. 1).

At 6 h after release, the number of larvae was the highest on the maize ear 6.60 ± 0.25 larvae per ear slice) followed by maize foliage (4.40 ± 0.25 larvae per leaf) and cowpea foliage (4.0 ± 0.0 larvae per leaf) ($F = 55.53$; df = 7, 32; $P < 0.05$). The lowest larval count was on cotton foliage (0.60 ± 0.25 larvae per leaf) and marigold flower (1.60 ± 0.25 larvae per flower portion) (Fig. 1).

Similar results were seen at 24 h after release ($F = 33.16$; df = 7, 32; $P < 0.05$) when the greatest number of larvae was on the maize ear (6.20 ± 0.37 larvae per ear slice) followed by maize foliage (5.0 ± 0.0 larvae per leaf) and cowpea leaves (4.40 ± 0.25 larvae per leaf). The least numbers of larvae were found on cotton leaf (0.80 ± 0.37 larvae per leaf) and marigold flower (1.00 ± 0.32 larvae per flower portion) (Fig. 1).

In the nonchoice feeding test, the quantity of food intake by the third-instar larvae was highest on marigold flower (630.33 ± 17.30 mg) followed by banana leaf (524.67 ± 13.60 mg), whereas it was lowest on cowpea (346.67 ± 24.17 mg) ($P = 0.05$). The amount of food intake did not vary significantly among sorghum leaf (473.33 ± 20.86 mg), maize ear (460.67 ± 21.08 mg), and maize leaf (450.33 ± 14.72 mg). The duration of the third instar was shortest on maize leaf (2.05 ± 0.05 d) followed by maize ear (2.20 ± 0.09 d) and sorghum leaf (2.30 ± 0.11 d), whereas there was a longer larval feeding duration on marigold (5.20 ± 0.17 d) followed by banana leaves (3.80 ± 0.14 d) ($F = 18.99$; df = 6, 14; $P < 0.05$). The mean frass weight was highest for the larvae fed on banana (119.60 ± 2.06 mg) and lowest on castor leaves (30.43 ± 1.94 mg). The larval weight gain was higher on castor leaf (69.65 ± 1.68 g) and did not vary significantly among maize ear, maize foliage, sorghum leaves, cowpea leaves, and banana leaves. Larvae fed on cotton foliage did not reach the next instar (Table 2).

Table 2. Feeding preferences of third-instar larvae of *S. frugiperda* under nonchoice condition.*

Serial No.	Crop	Weight of Food Intake (mean ±SEM, mg)	Weight of Excreta (mean ±SEM, mg)	Larval Weight Gain (mean ±SEM, mg)	Time (mean ±SEM, d)
1	Maize ear	460.67 ± 21.08 b	59.97 ± 1.88 b	62.52 ± 0.31 b	2.20 ± 0.09 ab
2	Maize leaf	450.33 ± 14.72 bc	110.25 ± 5.64 a	61.06 ± 0.19 b	2.05 ± 0.05 a
3	Sorghum leaf	473.33 ± 20.86 b	71.82 ± 1.86 b	59.24 ± 0.91 b	2.30 ± 0.11 ab
4	Cowpea leaf	346.67 ± 24.17c	40.17 ± 2.06 c	61.24 ± 3.12 b	2.65 ± 0.11 b
5	Castor leaf	426.33 ± 13.42 bc	30.43 ± 1.94 c	69.65 ± 1.68 a	3.20 ± 0.09 c
6	Banana leaf	524.67 ± 13.60 ab	119.60 ± 2.06 a	59.22 ± 0.52 b	3.80 ± 0.14 d
7	Marigold flower	630.33 ± 17.30 a	70.12 ± 3.07 b	51.36 ± 0.67 c	5.20 ± 0.17 e

* Values within columns followed by the same letter do not differ significantly (Tukey's honestly significant difference test, $P = 0.05$).

Oviposition preference. In the choice test, the oviposition preference of *S. frugiperda* varied significantly among the different host plants ($F = 70.16$; df = 8, 18; $P < 0.05$). The number of egg masses on maize foliage (8.67 egg masses per host) was highest when compared with that of other host plants, followed by sorghum (3.6 egg masses per host) and castor (2.0 egg masses per host). The number of egg masses on banana, cotton, and cowpea did not differ significantly among those hosts. No oviposition occurred on maize ear and marigold (Table 3).

In the nonchoice test, the number of egg masses on maize foliage was higher than on the other plants, with 11.6 egg masses ($F = 6.57$; df = 7, 16; $P < 0.05$). No significant differences in the number of egg masses oviposited on cowpea, castor, and banana foliage were observed. The lowest number of egg masses was on marigold (0.6 egg masses per host) followed by cotton (2.6 egg masses per host). No egg masses were recorded on maize ear. The number of egg masses observed on the cage was highest in the cage containing the maize ear with 10.0 ± 1.0 egg masses per cage ($F = 15.17$; df = 7, 16; $P < 0.05$), whereas the lowest number of egg masses on the cage was with the maize leaf (0.6 ± 0.6) egg masses per cage (Table 3).

Discussion

Of the eight plants or plant structures tested herein, F_1 generation *S. frugiperda* larvae from a laboratory colony established from larvae collected from field-grown maize at Shivamogga, Karnataka, India, preferred feeding on maize ears, maize leaves, and castor leaves (Fig. 1). Wijerathna et al. (2021) and Nandhini et al. (2023) also reported the highest larval survival (80%) on maize compared with other plants in their study with *S. frugiperda* preference. We also noted that numbers of larvae on the plants in the choice test increased over time on maize ears, maize leaves, and cowpea leaves. Similarly, Praveen and Mallapur (2019) reported more larvae feeding on maize and sorghum compared with other hosts.

In the nonchoice test, the weight gain was more or less similar on maize ear and foliage of maize, sorghum, cowpea, and banana. The larvae reared on marigold flowers had higher food intake and longer larval feeding duration. Extended larval duration becomes a compensatory strategy when food is inappropriate for growth and development (Hwang et al. 2008) and likely accounted for the greater intake of food.

Neonate larvae have limited mobility and rely on host plants chosen by ovipositing females (Garcia-Robledo et al. 2010). Although oviposition preference not necessarily predicts offspring performance in the fall armyworm (Sotelo?Cardona et al. 2021), in the present study, the females oviposited more egg masses on maize and sorghum plants, aligning with the preference-performance hypothesis (Garcia-Robledo and Horvitz 2012).

As with other insects, the fall armyworm selects its host by a process regulated by factors such as behavioral plasticity, larval mobility, plant suitability, competitors, and natural enemies (Carrasco et al. 2015). In the absence of the preferred host plants, adult females may choose less favorable hosts, such as cotton and marigold plants, as their sites for oviposition. Ali et al. (1989) and Guo et al. (2021) reported that the fall armyworm would oviposit on readily available host plants or cage surfaces under restricted situations. If an adult female oviposits on nonpreferred host plant, subsequently yielding offspring that survive, that plant could be

Table 3. Oviposition preferences of *S. frugiperda* females among different host plants in choice and nonchoice tests.*

		Choice Test		Nonchoice Test			
Plant	Plant height (m)	No. of Egg Masses/Plant (mean ± SEM)	No. of Eggs/Mass (mean ± SEM)	No. of Egg Masses/Plant (mean ± SEM)	No. of Eggs/Mass (mean ± SEM)	No. of Egg Masses on Cage (mean ± SEM)	No. of Eggs/Mass (mean ± SEM)
Maize plant with ear	0.50	0.0 d	0.0 e	0.0 d	0.0 c	10.0 ± 1.0 a	249.6 ± 33.5 ab
Maize	0.30	6.6 ± 0.3 a	394.0 ± 37.6 a	11.6 ± 0.8 a	458.6 ± 63.7 a	0.6 ± 0.3 f	45.6 ± 11.3 d
Sorghum	0.45	2.6 ± 0.3 b	274.0 ± 10.0 b	7.0 ± 0.5 b	271.3 ± 95.1 ab	1.3 ± 0.3 ef	67.3 ± 5.8 cd
Cowpea	0.45	1.0 ± 0.0 c	174.6 ± 14.1 c	5.0 ± 0.5 bc	239.6 ± 64.1 abc	2.6 ± 0.3 cde	153.6 ± 16.1 bc
Castor	0.75	1.0 ± 0.0 c	172.6 ± 11.8 c	4.0 ± 0.5 bc	284.3 ± 45.1 ab	4.0 ± 0.5 bcd	148.3 ± 18.8 c
Banana	0.50	1.3 ± 0.3 c	174.6 ± 3.1 c	4.6± 0.3 bc	175.6 ± 37.8 bc	2.3 ± 0.3 def	114.67 ± 10.3 cd
Marigold	0.60	0.0 d	0.0 e	0.6 ± 0.6 d	285.6 ± 36.3 ab	6.3 ± 0.6 ab	135.6 ± 6.9 cd
Cotton	0.60	1.3 ± 0.3 c	113.3 ± 13.3 cd	2.6 ± 0.3 c	126.3 ± 4.1 bc	5.3 ± 0.8 bc	264.3 ± 33.3 a
On cage	—†	0.6 ± 0.3 cd	49.3 ± 9.2 de	0.0 d	—	—	—

* Values within columns followed by the same letter do not differ significantly (Tukey's honestly significant difference test, $P = 0.05$).
† Dashes indicate not applicable.

defined as a host (Coapio et al. 2018). In this event, if the females oviposit on cotton and marigold plants followed by offspring survivability, there could be a potential chance for the establishment and colonization of fall armyworm populations on cotton, marigold crops, and other commercially cultivated crops.

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