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ORIGINAL RESEARCH ARTICLE

Influence of age, diurnal cycle, and plant and non-plant surfaces on oviposition by *Spodoptera litura* (Fabricius)(Lepidoptera: Noctuidae)

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Abstract
Spodoptera litura is a highly polyphagous pest which causes significant yield losses to wide range of economically important agricultural and horticultural crops. Laboratory studies were conducted to determine the effects of age, diurnal cycle, and plant and non-plant surfaces on the ovipositional responses of tobacco caterpillar, *Spodoptera litura*. Females laid eggs beginning from the first day of emergence, and the number of eggs laid was highest on day 4. Thereafter, egg laying decreased successively, and was stopped on day 13. A profound effect of the day-night cycle on oviposition was observed: oviposition was lowest and highest in the beginning of light and dark phase respectively of the 24-hour cycle. However, the egg laying increased slowly as day progressed and decreased gradually as the night progressed, but on the whole, egg laying was significantly high in dark phase as compared to light phase. Further, both plant and non-plant surfaces affect egg delivery response. Females preferred the plant surface for egg laying, compared to non-plant surfaces. The eggs laid on castor, radish and cotton leaves were similar in the no-choice test. In two-choice test, however, the number of eggs laid on castor leaves was significantly higher than those laid on radish and cotton leaves, but were not significantly different from those on pigeon pea. Among the non-plant surfaces, females laid higher number of eggs on rough surface like glass nylon, filter paper, muslin cloth, as compared those on a smooth glass plate surface. The implications of findings in integrated management of this pest has been discussed.

Keywords *Spodoptera litura* · Age · Diurnal cycle · Oviposition substrates

Introduction

Spodoptera litura (Fabricius) is a serious pest, which was reported to infest 87 plant species from 40 plant families, including economically important crops like, groundnut, soybean, cotton, tobacco, legumes, in India and its neighboring countries (Chari and Patel 1983). Recent survey report of European Food Safety Authority listed 128 plant species as the host range, including 67 major hosts plants (Rondoni and Graziosi 2022). This insect has been mostly reported from south and east Asia, and Oceania (EPPO 2022), and occasionally reported from the United States, central America and Africa (EPPO 2022). Although it is known to be highly polyphagous (Brown and Dewhurst 1975; Hill 1993; Qin et al. 2004, 2006; Ahmad et al. 2013; Abdullah et al. 2019; Datta et al. 2019), however, certain legume species like pigeon pea, do not support growth and development of larvae and are thus non-hosts for the insect (Singh 1986; Rondoni and Graziosi 2022). Differences in the infestation of different host and non-host plants by an insect, under otherwise identical and favourable conditions, may be determined by its behavioral responses, particularly its orientation, oviposition and feeding behaviors (Saxena 1969, 1985, 1990). Orientational responses are pre-alighting behavior of an insect, elicited by volatile chemical stimuli from plant that determine its arrival on a plant or its avoidance. This is followed by post-alighting behavior, elicited by contact chemical and physical stimuli from plant surface. Post alighting behavior

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in larvae elicits feeding that determines food consumption, whereas in adults determines egg laying propensity on plant. Higher the level of these behavioral responses of an insect to a plant greater will be its suitability for colonization, provided other conditions are favourable.

As in most lepidopterans (Thompson and Pellmyr 1991; Renwick and Chew 1994), the adult female of *Spodoptera* species actively selects the plant surface for its oviposition (Islam 1970; Nasr and Nassif 1970; Combs and Valerio 1980; Pitre et al. 1983; Berdegue et al. 1998; Kathuria and Kaushik 2004; Sambaraju and Philips 2008; Meaghre et al. 2011). Extensive studies notwithstanding (Xue et al. 2010; Narvekar et al. 2018; Iqbal et al. 2023), there are still many unanswered questions about the ovipositional responses of *Spodoptera litura.* Adequate information is also lacking on the quantitative difference in oviposition of *S. litura* with regard to the plant selection, and factors governing oviposition. It is also not well understood that to what extent insect discriminates between plant and non-plant substrates for laying eggs. Importantly, the understanding of oviposition behavior of *Spodoptera litura* could be useful for developing pest management strategies for effective pest suppression in agricultural fields. We, therefore, thought to study the ovipositional responses of females in relation to the age and diurnal cycle, and their ovipositional preferences for certain plant and non-plant surfaces.

Materials and methods

Insects

Culture of *Spodoptera litura* was maintained in the insectary at a temperature 27° ± 1° C, relative humidity 60-65 % and light regime of 12 h light: 12 h dark cycle (light on at 08:00 a.m.). Larvae were reared in round glass jars (7 x 7 cm) on freshly excised castor leaves, obtained from the field plots of Department of Zoology, University of Delhi. Around 100-200 larvae were kept in each jar during earlier instars but their number were reduced in succeeding instars, 10-15 larvae/jar in last instar. These larvae were transferred to another round glass jar (10 x 10 cm) in pre-pupal stage that was half filled with sterilized soil for pupation. The adults emerging from the pupae were transferred to a mating cum oviposition cage (20 x 20 x 20 cm) provisioned with 10% honey solution soaked on cotton wool swabs as food and freshly excised castor leaves for egg laying. The eggs laid by the females were harvested with the help of wet camel hair brush, sterilized by rinsing in 0.2% sodium hypochlorite solution and kept for emergence. However, for conducting oviposition bioassays, male and female pupae were separated and kept individually in plastic jars (7 x 7 cm) for emergence. The emerging adults were maintained individually in plastic jar and fed 10% honey solution soaked on cotton. These moths were used for the bioassays as per the requirement of a test.

Bioassays

Ovipositional responses of the insect were monitored in two types of clear plexiglass chambers. One of these chambers was cube-shaped (20 x 20 x 20 cm) having its two sidewalls of the glass nylon net (40 mesh/cm) and a window (10 x 10 cm) on its front side covered with a removable nylon net (10 mesh/cm) to facilitate handling of moths. The second type of chamber was a rectangular box (60 x 20 x 20 cm), with its two ends covered by the glass nylon net, and the front wall with a window covered with removable net as in the first type of chamber. The side of the presentation of stimuli in the test chamber was changed randomly each time so as to eliminate positional bias. Each bioassay was replicated five times, each replicate having responses of fresh five pairs of males and females from different batches of culture. The test plants were grown in the field plots of the Department of Zoology, University of Delhi, under pesticide free condition following standard farm practices. The numbers of adult males and females, their age, the methods of presentation of test materials and other conditions varied according to the experiments as described below.

Effect of age

For examining age related differences in ovipositional responses, a pair of male and female insect was released in each test chamber (20 x 20 x 20 cm) on the day of their emergence. A freshly excised castor leaf, trimmed to a rectangular shape (10 x 4 cm) having its petiole dipped in water contained in a glass vial (7 cm ht x 2 cm dia) was kept in the center of the chamber. The chamber was then placed in an incubator under 12L: 12D photoperiod, as before, maintaining 27° ± 1° C and 50-60% relative humidity. After 24 h, the pair was transferred to another identical chamber. The numbers of eggs laid over 24 hours on the leaf rectangle and elsewhere in the chamber were recorded separately till the time the egg laying was stopped or the insect died. The daily egg laying in 24 h was expressed as a percent of its lifetime reproductive output. Eggs laid by five females on different days constituted one replicate, and experiment was replicated five times with different batches of males and females.

Effect of diurnal cycle

To determine the relationship of the time of the day with oviposition, newly emerged male and female were kept separately in a plastic jar (7 x 7 cm) and provided with 10% honey solution to serve as food. On the third night post emergence, five pairs of male and female were released into a cage (20 x 20 x 20 cm) for mating. The mated males and females were selected next day for the bioassay when they have been

observed to lay the highest number of eggs. These insects were transferred to identical test chamber in the morning at 08.00 h, having a vial containing a freshly excised, watered, castor leaf rectangle (10 x 4 cm) and 10% honey solution on a cotton wool swab. The chamber was then placed in an incubator maintaining conditions, as mentioned above. The insects were transferred at 4 h intervals to a new chamber having identical provisions. Egg counts in each chamber at successive 4 h intervals, provided oviposition rates during the observation period, which were expressed as a percentage of the total 24-hour egg production.

Responses to plant surfaces

Castor (*Ricinus communis*) (Euphorbiaceae), cotton (*Gossypium hirsutum* and *Gossypium barbadense*) (Malvaceae), radish (*Raphanus sativus*) (Cruciferae) and pigeon pea (*Cajanus cajan*) (Leguminosae) were tested. The ovipositional responses to the leaves of these plants were compared in a no-choice and dual-choice tests. Each test was conducted in a rectangular chamber (60 x 20 x 20 cm), as described earlier. The test chamber was provisioned with bouquets of freshly excised leaves of the test plants, each having its petiole immersed in water in a glass vial (7 x 2 cm) to prevent wilting during the experiment. The top open end of vial was plugged with cotton and the leaf lamina positioned vertically above it. The test chamber was also provided 10% honey solution on cotton wool swab as food. Five pairs of 4-day old mated males and females were released in test chamber at the end of light phase and allowed to oviposit during scotophase. The moths were removed next morning and eggs laid on different surfaces were counted. The number of leaves in a bouquet varied according to their size. For testing the castor plant, one medium sized leaf having laminar area of about 150 sq cm, was taken. However, for tests with cotton and radish two or more leaves were used. Likewise, for testing pigeon pea, 10 - 12 cm long twigs bearing leaflets were used. The number of twigs was such that the leaflets together would approximate the average size of a single castor leaf tested. A bouquet of leaves was placed at centre of a test chamber on its floor in the no choice test.

In dual-choice tests, a bouquet of castor leaves was placed in the rectangular chamber, about 1 cm distance from one end wall at its middle. Another test plant leaf bouquet, with laminar area approximately the same as that of castor, was placed near the opposite end-wall of the chamber. Castor leaves were chosen as the standard reference for comparison. The numbers of eggs laid on the leaf bouquets kept near the opposite end walls in the test chamber were separately recorded. On the basis of total numbers of eggs laid on the surfaces of test leaves, the differences being tested for statistical significance.

Responses to non-plant surfaces

The oviposition by *S. litura* on the non-plant surface was tested using glass nylon (40 mesh/cm), glass plate, muslin cloth and filter paper (Whatman No.1). The tests were conducted in rectangular plexiglass chamber, as described above. One end of the test chamber was fitted with glass nylon and the other end with muslin or glass plate or filter paper. The test substrates were spread along the inner side of the end wall of cage. Five pairs of 4-day old mated females were released in the cage just before the onset of scotophase. Next morning at the beginning of photophase, the moths were removed from the cage and the numbers of eggs laid on different surfaces were counted. On the basis of the total number of eggs laid by the females on test surfaces during the observation periods, the percentage of eggs laid on each surface was calculated, and the difference being tested for statistical significance.

Data analysis

The percentage of eggs laid in relation of age and day-night cycle were statistically analysed after arcsin transformation. The eggs laid by females under more than two conditions were compared by using analysis of variance (ANOVA), followed by Duncan's multiple range tests (Duncan 1955). Means of dependent samples were compared using chi-square test. All statistical analyses were performed using Sigma Stat 2.0, Jandel Scientific Software, 1995.

Results

Effect of age on oviposition

Egg laying by females was highly variable on different days ($F_{11, 48} = 17.844$; $p < 0.001$) (Fig. 1). The oviposition was very low (2.8% of the total) on the first day of their emergence, but increased on subsequent days and reached its maximum on the fourth day. The egg delivery was maintained for next few days till day 9, but a progressive decline was found from day 6 onwards. The last batch of eggs (0.09% of the total) was laid on the 12th day. Thereafter, the females stopped laying eggs or they died.

Diurnal differences in the oviposition

Moths did not lay eggs during 1st time sector of light phase. However, oviposition was recorded in subsequent time sector of day, although it remained very low during entire photophase. The egg laying was high during the dark phase, accounting for about 96% of total output. Within the dark period, the oviposition was maximum (38.5 %) during the

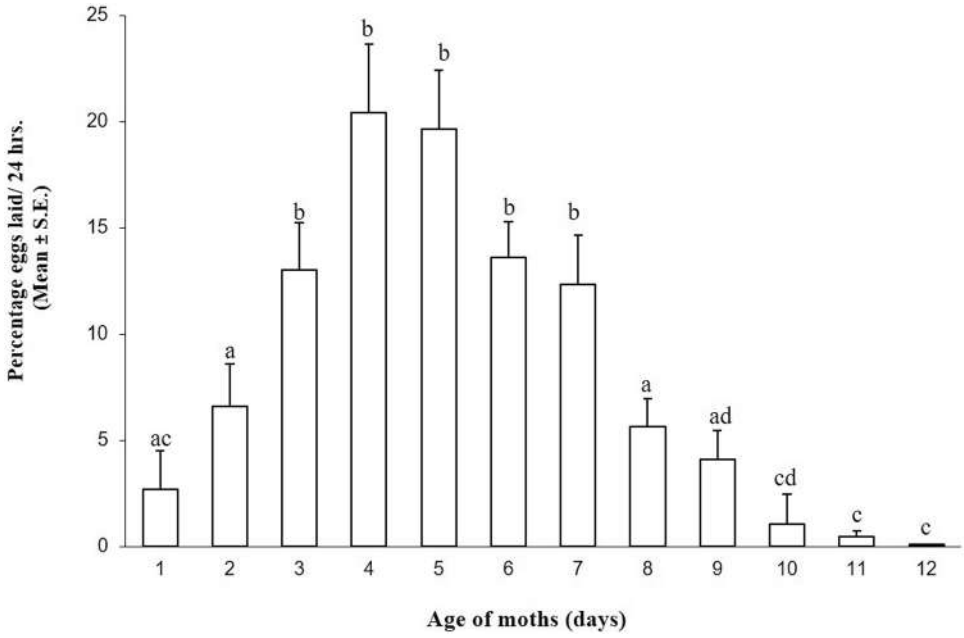

Fig. 1 Percentages of eggs laid by the *Spodoptera litura* on successive days after emergence. Columns bearing same letters are not significantly different (ANOVA; DMRT; $p<0.05$). Percentages were subjected to statistical analysis after arcsin transformation; untransformed value presented in figure

initial time sector. The egg laying later declined progressively to 31.16 % from midnight and reached 24.4 % in the last 4 hours of night. The difference in egg laying during different 4 h time sectors of night was statistically significant ($F_{5, 24} = 8.221$; $p < 0.001$) (Fig. 2).

Ovipositional response to plants

In the tests presenting leaves of a single plant in the test chamber at one site, the percentage of eggs laid was highest on castor leaves (75 %) as compared to the chamber

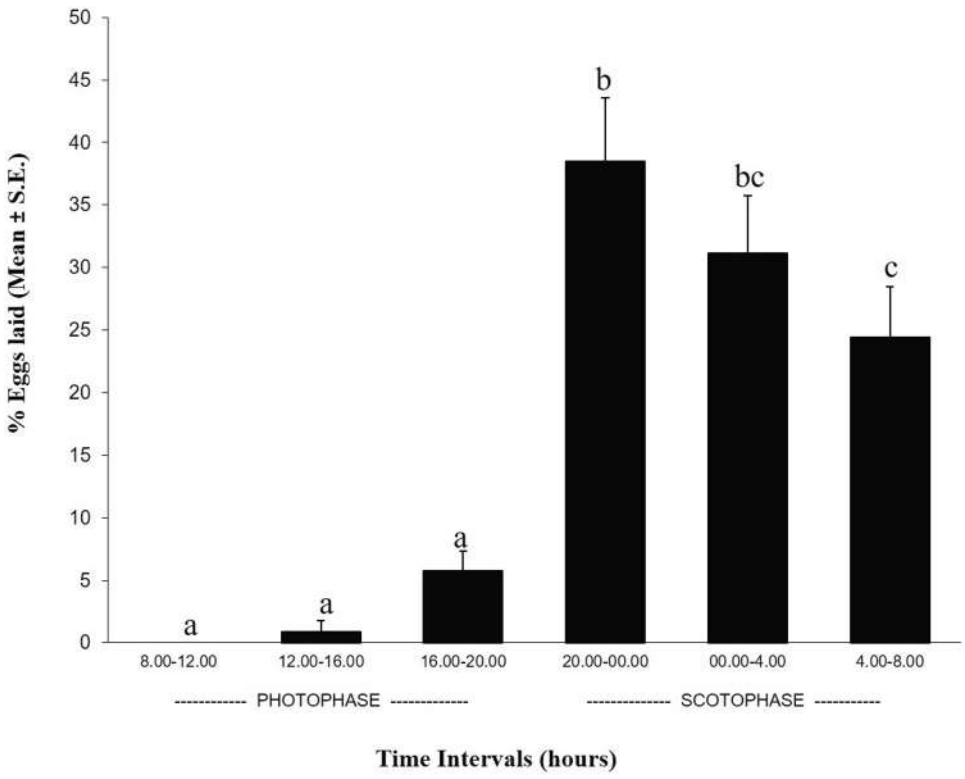

Fig. 2 Egg laying by *Spodoptera litura* in relation to diurnal cycle. Means (± S.E.) followed by a different letter differ significantly (ANOVA; DMRT; P<0.05). Percentages were subjected to statistical analysis after arcsin transformation; untransformed value presented in figure

walls (Table 1). The percentage of eggs laid on four test plants ranged from 59 % to 63 % but this was not significantly different from that on the castor leaves (chi square test; $p<0.05$), irrespective of the test plants. However, the percentage of eggs laid was significantly higher on a leaf surface than on the chamber wall ($p<0.05$).

In a dual-choice test, the test leaves were compared with castor leaves for the ovipositional preference. The eggs laid by the females on castor leaves were significantly higher in number than on either the cotton or radish leaves (chi-square test of independence, $p<0.05$), but statistically not different from that on the pigeon pea leaves (Table 2).

Ovipositional response to non-plant surfaces

In these tests, the glass nylon was used as the standard reference with which other test substrates were compared. The results (Table 3) show that the percentages of eggs laid on muslin and filter paper were not significantly different from those laid on the standard, glass nylon wall. However, the egg-laying on a glass plate was significantly lower than that on the glass nylon (LSD; $p<0.01$).

Discussion

Oviposition activity in *Spodoptera litura* clearly indicates diel periodicity with highest egg delivery in the beginning of dark phase alternating with lowest delivery in the light phase. This is consistent with earlier reports in this species (Chu and Yang 1991; Li et al. 2012). Circadian control of oviposition rhythm has also been reported in other lepidopteram moths like *Plodia interpunctella* (Lum and Flaherty 1970), *Chilo partellus* (Kumar and Saxena 1985), *Helicoverpa armigera* (Singh and Rembold 1989), *Cyptophlebia illepida* (Shearer et al. 1995), *Mamestra brassicae* (Rojas 2001), and *Earias fabia* (Krishna et al. 1977). Our results suggest that light initially inhibits the oviposition by *S. litura*. However, when this inhibition is removed oviposition is resumed at a higher intensity, which is comparable to oviposition rebound. It appears that there is a limited window of darkness for oviposition activity in *Spodoptera litura*, which is inhibited by light signal. This indicates the involvement of endogenous mechanism that controls the physiological and behavioral rhythms in lepidopteran insects (reviewed by Brady et al. 2021) for feeding (Adler 1987; Coombs 1992; Niepoth et al. 2018; Zhang et al. 2021), diapause (Spieth and Sauer 1991), eclosion (Chandrashekaran 1967), calling (Delilse and McNeil 1987; Groot et al. 2014) and release of pheromones (Kamimura and Tatsuki 1993). We speculate that oviposition in *S. litura* is under photoperiodic control. The pattern of egg-laying during night phase is probably an evolutionary adaptation for survival and reproduction of moth, searching a suitable surface for oviposition.

Table 1 Egg laying by *Spodoptera litura* presented leaves of a test plant inside a rectangular oviposition chamber at one station

Test Plant[a]	Number of eggs laid (mean ± S.D.)	
	Plan leaves	Chamber Walls
Castor	936 ± 87.0 **	311 ± 68.7
Cotton (GH)	672 ± 64.5 **	456 ± 76.9
Cotton (GB)	631 ± 57.25*	405 ± 73.1
Radish	812 ± 63.0*	503 ± 63.0
Pigeonpea	612 ± 53.4 **	361 ± 81.7

χ^2 - test of independence performed, *GH Gossypium hirsutum*, *GB Gossypium barbadense*

*; ** indicate significance at 0.05 % and 0.01 % levels respectively

[a]Leaf bouquet of a test plant was presented inside the chamber at one site

Table 2 Egg laying by *Spodoptera litura* presented castor leaves as a choice against the leaves of another test plant in a rectangular chamber at its two opposite ends

Test Plants[a]		Number of eggs laid (mean ± S.D.)	
'A'	'B'	'A'	'B'
Castor	Cotton (GH)	541.0** ± 49.0	255.0 ± 33.16
Castor	Cotton (GB)	575.0** ± 64.7	247.4 ± 40.45
Castor	Radish	524.4** ± 46.2	328.6 ± 42.04
Castor	Pigeonpea	386.0 ns ± 53.8	430.0 ± 82.31
Castor	Blank[b]	674.0** ± 75.0	45.23 ± 13.02

GH Gossypium hirsutum, *GB Gossypium barbadense*

** indicate significance at 0.05 % levels, ns indicate not significant χ^2 - test performed ($p = 0.05$)

[a]Bouquets of freshly excised leaves of each test plant were presented inside test chamber at opposite end walls

[b]Number of eggs laid on opposite end wall

Table 3 Ovipositional response by *Spodoptera litura* on non-plant surfaces, each presented as a choice against glass nylon

Oviposition substrate		% Eggs laid[a] (mean ± S.D.)		LSD [b]
'A'	'B'	'A'	'B'	(P=0.05)
Glass nylon	Muslin	37.9 ± 24.04 ns	62.1 ± 24.0	35.12
Glass nylon	Filter paper	48.33 ± 8.72 ns	51.67 ± 8.72	12.74
Glass nylon	Glass plate	91.21 ± 12.2 **	8.79 ± 12.2	17.88

** indicate highly significant; ns: not significant

[a]Percentage calculated based on total number of eggs laid on the two substrates

[b]Significance ($p = 0.01$) between means was determined by least significant difference (LSD)

We recorded profound effect of age of female on the oviposition rate of *Spodoptera litura* females. Oviposition depends on the rate of egg production and maturation time of eggs in the ovary of females. Moreover, host-plant quality is key determinant for fecundity in phytophagous insects. The females start laying eggs from very first day of emergence, which gradually increases on successive days, reaching at its peak on 4th day of emergence. Such peak in egg delivery response was also recorded in *Helicoverpa armigera* on 6th day (Singh and Rembold 1989), *Ectomyelois ceratoniae* third to sixth day (Vetter et al. 1997), *Mamestra brassicae* fifth day (Rojas 1999), *Spodoptera eridania* fourth day (Favetti et al. 2015) *Copitarsia uncilata* third day (Altamar-Varon et al. 2020) of emergence. The egg laying by females starts declining from 6th day onwards and ends on 12th day of emergence.

Physical characteristics of a non-plant surface were also observed to be important in determining the oviposition in *S. litura*. The fact that the females laid more eggs on glass nylon than on glass plate suggests that plain smooth surface is less suitable for the oviposition compared to the rough surface. This may be because the rough surface allows perching of a female for egg laying, which is not at a level on the smooth surface. The female *Spodoptera frugiperda* were also reported to lay significantly more eggs on the rough substrate like pitted or grooved surfaces of a paper (Rojas et al. 2003) and nylon window cage screen (Meaghre et al. 2011). The oviposition preference for a rough surface has also been observed in *Heliothis armigera* (Saxena and Rembold 1983). Kathuria and Kaushik (2004) reported difference in ovipositional preference by *Helicoverpa armigera* females in descending order: cotton wool, tissue paper and muslin cloth. Sambaraju and Philips (2008) showed that a dish surface with spherical glass beads significantly enhanced egg laying by female *Plodia interpunctella,* as compared to the surfaces of the cheese cloth, filter paper or sand paper. Recently, Akhtar et al. (2022) reported black muslin cloth as the most suitable oviposition substrate for *Pectinophora gossypiella.* On the other hand, a smooth surface is preferred for the oviposition by *Diatraea grandiosella* (Poston et al. 1979), *Chilo partellus* (Kumar and Saxena 1985), *Epiphyas postvittana* (Foster et al. 1997), *Lobesia botrana* (Maher and Thiery 2004; Markheiser et al. 2018), *Spodoptera frugiperda* (Azidah and Sofia-Azirun 2006; Greenberg et al. 2002; Sotelo-Cardona et al. 2021) and *Busseola fusca* (Calatayud et al. 2008)

The present study showed that all the test plants elicited high ovipositional response from *Spodoptera litura* females. This was true even for a non-host plant like the pigeon pea, which elicited as much ovipositional response as the cotton plant did. Oviposition by an insect on a plant surface depends on distance perceivable stimuli and contact stimuli. Distance perceivable stimuli are generally plant volatile chemicals, which determines arrival of insect on plant surface whereas contact stimuli may be chemical or physical or both. Combined effect of these two stimuli determines egg laying on a surface. Our results suggest the existence of positive oviposition stimuli in the leaf to which the female responded positively. This is consistent with earlier reports in other insects namely *Trichoplusia ni* (Shorey 1964), *Manduca Sexta* (Sparks 1973), *Papilio protenor demetrius* (Ichinose and Honda 1978), *Agrius convolvuli* (Shimoda and Kiuchi 1998), *Diaphania indica* (Gharaei et al. 2019). Difference in perception of these stimuli from flowering stage of different plants has been reported to cause difference in egg laying by *Helicoverpa armigera* females (Rajapakse and Walter 2007).

This has been observed that *Spodoptera litura* larvae failed to complete development on pigeon pea (Singh 1986), like non-host plant surface. Moreover, we were neither able to find any published report about pigeon pea being host plant of *S. litura* nor this has been catalogued in "Pest Survey Card on *Spodoptera litura*" (Rondoni and Graziosi 2022). Pigeon pea has not been included in host list of *Spodoptera litura* as it does not fulfill two basic criteria to qualify for it, i.e. a gravid female must be able to locate and oviposit, and the larvae must be able to feed and develop as adults on its surface (Volp et al. 2022). Present study indicated that both pigeon pea and cotton elicit high oviposition responses from *Spodoptera litura* female. A practical implication of the present finding and earlier report (Singh 1986) may be useful for management of *S. litura* by growing pigeon pea as trap crop adjacent to cotton. Pigeon pea will elicit ovipositional response from *S litura*, but neonate larvae emerging on its surface will not be able complete development. This will ultimately suppress its population growth in the field. Similar success by push-pull strategy to increase maize production in Africa was observed by using Napier grass (*Pennisetum purpureum*) as trap crop for management of *Chilo partellus* (Khan et al. 2006), and Desmodium for *Spodoptera frugiperda* (Midega et al. 2018). Furthermore, pigeon pea will enhance soil fertility by fixing atmospheric nitrogen.

Conclusion

Spodoptera litura females show diel periodicity in oviposition, laying maximum number of eggs on 4th night of emergence. Moreover, females exhibit oviposition preference for rough surfaces. Leaves from a host plant like cotton as well as the non-host plant like pigeon pea attracted equally females for egg laying. Since pigeon pea does not support development of larvae, this can be grown as trap crop in the field. Overall, present results may be helpful in developing ecofriendly management strategy of this insect pest in agricultural field.

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Data availability The data that support the findings of present research article are available from the corresponding author, upon reasonable request.

Declarations

Conflict of interest The corresponding author states that there is no conflict of interest.

Competing interest The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this manuscript.

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