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Research Article

Oviposition site preferences of fall armyworm moth, *Spodoptera frugiperda* J. E. smith (Lepidoptera: Noctuidae) on selected crops

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Abstract: The fall armyworm (*Spodoptera frugiperda*) is a destructive invasive pest threatening food security across Sub-Saharan Africa, especially maize-based systems. This study assessed the oviposition preferences of female fall armyworm moths on maize, cowpea, and okra (crops commonly intercropped by Nigerian smallholder farmers) under no-choice laboratory tests. Two-week-old seedlings of each crop were individually exposed to mated female moths in sleeve cages for 72 hours, and egg masses were examined for quantity, position on plant, and distribution across leaf surfaces and regions (distal-, mid- and proximal- portions of the leaf). Results showed that maize and cowpea were significantly more preferred than okra, with maize receiving the highest number of egg masses and eggs. Cowpea had the highest number of eggs per mass, suggesting its potential as a viable secondary host. Okra received the fewest eggs and was associated with a high proportion of off-plant oviposition. Across all crop types, females consistently preferred to lay eggs on the abaxial and distal portions of leaves rather than on stems or adaxial leaf surfaces. These findings highlight that, while female fall armyworm moths may not strictly follow the preference–performance hypothesis at the plant species level, they exhibit marked discrimination at the microhabitat scale.

Keywords: *Spodoptera frugiperda*, insect ecology, egg-laying behaviour, host-plant interaction, no choice test

1. Introduction

Achieving the global target of zero hunger by 2030, as outlined in Sustainable Development Goal 2, depends on sustained improvements in food production and the strengthening of food systems against various risk factors, including climate change and invasive pests (Sundström et al., 2014; Kansiime et al., 2023).

The fall armyworm, *Spodoptera frugiperda* J.E. Smith (Lepidoptera: Noctuidae), is a highly destructive, transboundary, and invasive moth species native to North and South America. It was first detected in Africa in 2016 (Goergen et al., 2016) and has since become a persistent and significant threat to food security across the region (Huesing et al., 2018). Infestation begins when female moths lay eggs on host plants and the emerging larvae feed on plant tissues, with feeding intensity increasing as they grow and develop (Capinera, 2000; CABI, 2020).

In Africa, the fall armyworm primarily targets maize, causing varying degrees of damage to the leaves, stem, whorl, tassel, and kernels (Midega et al., 2018; Prasanna et al., 2018; CABI, 2020). The livelihoods of millions of smallholder farmers across Sub-Saharan Africa are at risk due to the persistent threat of fall armyworm infestation. Yield losses ranging from 11% to 58% have been reported, with estimated annual revenue losses reaching approximately 9 billion USD across the continent (Harrison et al., 2019; Kansiime et al., 2019; Chimweta et al., 2019; Eschen et al., 2021).

In addition to maize, the fall armyworm is known to attack a wide variety of other crops and non-crop plant species. Several reports highlight its impact on both cereal and non-cereal crops. In the Americas, Montezano

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et al. (2018) documented that the pest has a broad host range, feeding on over 353 plant species across 76 plant families. In African countries such as Ghana and Zambia, crops including sorghum, millet, tomato, and Napier grass have been reported as hosts (Rwomushana et al., 2018; Overton et al., 2021). Furthermore, across other parts of the continent, the fall armyworm has been reported to infest additional important crops, including cassava, groundnut, okra, onion, soybean, sunflower, sweet pepper, sweet potato, and yam. However, confirmed cases of significant damage to many of these crops remain limited (Rwomushana et al., 2018).

In Nigeria, there is a lack of comprehensive information on the suitability or non-suitability of other crop and non-crop plant species as hosts for fall armyworm. Specifically, it is unclear which species the pest can infest, damage, or utilize as alternative hosts in the absence of maize. Understanding the moth's oviposition and larval feeding preferences or aversions is crucial for developing effective and sustainable pest management strategies tailored to local agroecological conditions (Can et al., 2024). For example, crops that are unsuitable for oviposition can serve as "push" crops in either climate-smart or conventional push-pull systems to deter fall armyworm moths (Midega et al., 2018; Hailu et al., 2018). Conversely, crops that are found to be suitable for oviposition or larval feeding would benefit from more targeted and holistic management strategies.

In this study, we examined the host status of cowpea and okra varieties that are commonly intercropped with maize by smallholder farmers in Nigeria. Specifically, the oviposition preferences of mated fall armyworm moths for the selected crop varieties under no-choice conditions was assessed. The study also investigated the specific parts of the crops the moths preferred for egg-laying. Findings from the study would inform more precise insecticide applications and other targeted crop protection strategies.

2. Materials and methods

2.1. Study location

The study was conducted at the Department of Crop Protection, Faculty of Agriculture, University of Ilorin, Nigeria (8°30′ N, 4°40.8′ E). Maize seedlings were raised in a 12 m × 8 m screenhouse with netted sides and translucent roofing, under natural conditions (27 ± 2 °C, 70–85% RH, 12L:12D photoperiod). Experiments were performed in the departmental laboratory under ambient conditions (29.4 ± 0.9 °C, 74.0 ± 3.8% RH, 12L:12D photoperiod).

2.2. Seeds and seedling

Maize seeds, Zea mays L. – variety DMR-SR-Yellow, and cowpea seeds, Vigna unguiculata L. – variety Ife Brown, were obtained from the Institute of Agricultural Research and Training (IAR&T), Ibadan, Nigeria. Okra seeds, Abelmoschus esculentus L. (Moench.) – variety NHAe21, were purchased from a local vegetable seed shop in Ilorin, Nigeria. These crop varieties were selected for their widespread cultivation and ready availability in the study's agroecological zone. Also, maize was included in the study as a control given its status as the preferred host for fall armyworm in Nigeria and Africa (Goergen et al., 2016; Prasanna et al., 2018). For each crop type, two seeds were sown in 50 cL ornamental poly pots filled with sterilized loamy soil. The seeds were watered daily, and after one week, seedlings were thinned to one plant per pot. Watering and weeding continued until two weeks after sowing, at which point the seedlings were used for the oviposition preference experiment. To ensure an adequate number of two-week-old seedlings for the experiment, 20 single potted plants were established every other day for each crop type.

2.3. Fall armyworm culture

Fall armyworm larvae were collected from an infested maize plot at the University of Ilorin Teaching and Research Farm. Each larva was individually reared in a 200 mL disposable cup covered with muslin cloth secured with a rubber band. The larvae were fed daily with fresh maize leaf pieces until pupation. After pupation, any remaining substrate and frass were removed from each cup. The pupae were then returned to their respective cups and monitored daily for moth emergence. Fall armyworm larvae were reared under the laboratory conditions of 29.4 ± 0.9 °C, 74.0 ± 3.8% RH, and 12-hour photoperiod; with moths emerging approximately seven days after pupation.

2.4. Moth oviposition preference under a no-choice condition

A completely randomized design was used, with one crop type assigned per cage and the three cages randomly positioned on the laboratory bench. Each cage contained six poly pots, each holding a single healthy two-week-old seedling of the assigned crop, arranged equidistantly. Three pairs of newly emerged moths (0 – 1 day old) were introduced into each cage and provided with a 10% sugar solution (Marri et al., 2023) on a cotton pad in a Petri dish. The moths were allowed to mate and oviposit freely for 72 hours. Every 24 hours, all six seedlings in each cage were replaced with fresh ones, and sugar solution replenished. The removed seedlings were examined for egg masses. Moths were however not removed. Due to the availability of only three cages at a time, temporal replication was used instead of simultaneous replications, with one replication conducted each week for three consecutive weeks.

For each egg mass, data were collected on its location on the plant (i.e., whether on the leaves or stem). Egg masses laid off the plant, such as on the cage netting and other parts of the cage, were also recorded. For egg masses found on leaves, further observations were made regarding their placement on either the abaxial or adaxial surface. Additionally, each leaf was divided into three regions to record the precise location of egg masses: the distal portion (the outer one-third near the tip), the mid portion (the middle one-third), and the proximal portion (the one-third closest to the stem). Eggs within each egg mass were gently separated using a moistened camel hairbrush onto brown paper and then counted using a tally counter.

2.5. Data analysis

Data was initially analysed as a randomized complete block design with 'week' as blocking factor. But because the block effect was not significant and the estimated variance component was negligible, data across weeks were pooled and analysed as a simple completely randomized design.

Data on the number of egg masses, total egg count, and eggs per mass for each crop were analyzed using a one-way Analysis of Variance (ANOVA). Also, the number of egg masses deposited off plant, on different plant parts namely leaves versus stems; abaxial versus adaxial leaf surfaces; and distal, mid, or proximal leaf regions, were expressed as a percentage of the total egg masses. Subsequently, data on egg distribution were analyzed using a two-way ANOVA, with crop type and egg location (in the cage, on the plant, or on specific leaf surfaces) as factors. Where applicable, pairwise comparisons were performed using Tukey's Honestly Significant Difference (HSD) test at a 5% significance level. ANOVA was performed using the aov () function, and Tukey's HSD test using the HSD.test () function from the agricolae package. Graphs were created using ggplot () from ggplot2 and arranged with ggarrange () from the ggpubr package. All statistical analyses were done in R software (version 4.4.3).

3. Results

While no egg mass was found within 24 hours post setup, deposition of egg masses by female moths was observed to increase steadily on maize and cowpea plants from the second to the third day of observation (Table 1). On the third day when oviposition was generally highest, the mean number of egg masses on maize plants (4.67) was comparable with the numbers on cowpea plants (2.67) but significantly higher ($F2,6 = 8.45$; $p = 0.018$) than on okra plants (0.33). A similar trend was observed with the mean number of eggs laid on each crop with a significantly higher number observed on maize plants (311.67) compared to cowpea (177.00) and okra (11.67) (Table 2). Nevertheless, there were no significant differences ($F2,6 = 3.61$; $p = 0.094$) in the mean number of eggs laid on all three crop types by the third day after setup (Table 2). Conversely, the highest mean number of eggs per egg mass at 2DAS (32.00) and at 3 DAS (70.00) were recorded on cowpea plants and not on the control maize plants (Table 3). However, while there were no significant differences ($p >0.05$) in the number of eggs per egg mass on cowpea and maize, both had significantly more ($F2,6 = 7.81$; $p = 0.0214$) eggs per egg mass than okra plants at 3 DAS (Table 3).

Table 1: Mean number of egg mass laid on host crops by fall armyworm moths in a no-choice oviposition preference bioassay

Host Crop	1 DAS	2 DAS	**3 DAS**
Cowpea	0.00a	1.00a	2.67ab
Maize	0.00a	1.33a	4.67a
Okra	0.00a	0.00a	0.33b
	$F_{2,6} = 0.00$	$F_{2,6} = 1.30$	$F_{2,6} = 8.45$
	$p = 1.00$	$p = 0.340$	$p = 0.018$

Mean value followed by the same letter(s) are not significantly different at 5% level of significance according to Tukey's HSD test
DAS: Day After Setup

Table 2: Mean number of eggs laid on host crops by fall armyworm moths in a no-choice oviposition preference bioassay

Host Crop	1 DAS	2 DAS	3 DAS
Cowpea	0.00a	44.67a	177.00a
Maize	0.00a	51.33a	311.67a
Okra	0.00a	0.00a	11.67a
	$F_{2,6} = 0.00$	$F_{2,6} = 1.16$	$F_{2,6} = 3.61$
	$p = 1.00$	$p = 0.376$	$p = 0.094$

Mean value followed by the same letter(s) are not significantly different at 5% level of significance according to Tukey's HSD test
DAS: Day After Setup

Table 3: Mean number of eggs per egg mass laid on host crops by fall armyworm moths in a no-choice oviposition preference bioassay

Host Crop	1 DAS	2 DAS	3 DAS
Cowpea	0.00a	32.00a	70.00a
Maize	0.00a	27.67a	68.67a
Okra	0.00a	0.00a	11.67b
	$F_{2,6} = 0.00$	$F_{2,6} = 1.814$	$F_{2,6} = 7.81$
	$p = 1.00$	$p = 0.242$	$p = 0.0214$

Mean value followed by the same letter(s) are not significantly different at 5% level of significance according to Tukey's HSD test
DAS: Day After Setup

When presented with okra plants alone, moths laid most of their eggs (62.77%) off-plants. This mean percentage of eggs laid was significantly higher (F2,12 = 4.62; p = 0.0325) than the 3.90% and 0.00% of eggs laid off-plant when presented with maize and cowpea plants, respectively (Figure 1A). However, there was no significant difference (F1,12 = 1.191; p = 0.297) in the mean percentage of eggs laid off plants (23.25%) and on plants (43.42%) by female fall armyworm moths. With regards to eggs laid on plants, egg laying on stems was observed only on cowpea plants (Figure 2A). Generally, plant leaves regardless of the crop type offered was significantly (F1,12 = 6.898; p = 0.0221) preferred by female moths for oviposition than stems (Figure 2B). Similarly, while only cowpea leaves had some percentage (12.33%) of eggs laid adaxially (Figure 1C), significantly higher (F1,12 = 6.250; p = 0.0279) mean percentage number of eggs were laid on the abaxial surface of leaves of cowpea, maize and okra plants (Figure 2C). Furthermore, on maize leaves, moths laid eggs on the distal, mid and proximal portions of maize leaves. Similarly, they laid eggs on the distal and mid portions of cowpea leaves. However, eggs were only recorded on the distal portion of okra leaves (Figure 1D). Regardless of the type of crop or side of leaf selected for oviposition, moth generally laid significantly higher (F1,18 = 4.355; p = 0.0287) mean percentage number of eggs on the distal portions (42.63%) than on the mid (9.19%) or proximal (3.73%) portions of leaves.

4. Discussion

Several interrelated factors have been identified as influencing host plant selection for oviposition by female insects. These include the nutritional quality and quantity of the plant (Chen et al., 2008), which are often shaped by plant age, tissue type, genotype, and environmental conditions. Other factors include the presence of induced plant defenses triggered by prior or ongoing herbivory by conspecifics or allospecifics; and the presence of eggs and other cues indicating the likelihood of future herbivory (Dicke & Baldwin, 2010; Hrabar & DuToit, 2014; Hilker & Fatouros, 2015).

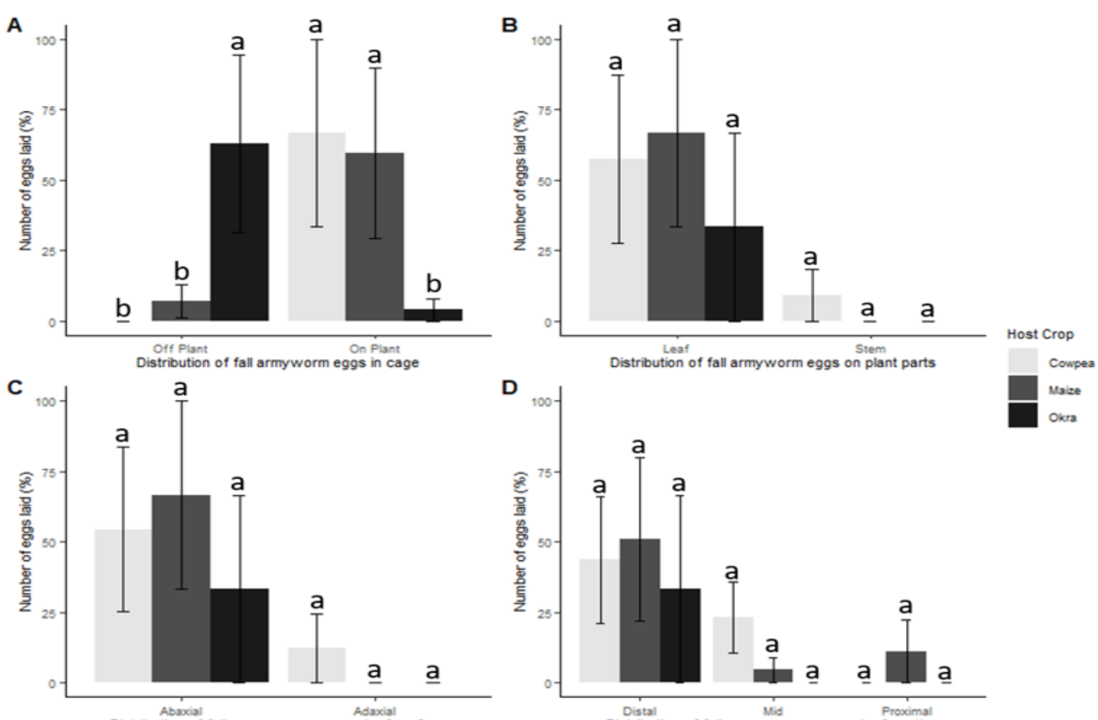

Fig. 1: Effect of host crop and location on the number of eggs laid by fall armyworm moths (A) in cage (B) on plant part (C) on leaf surface (D) on leaf section

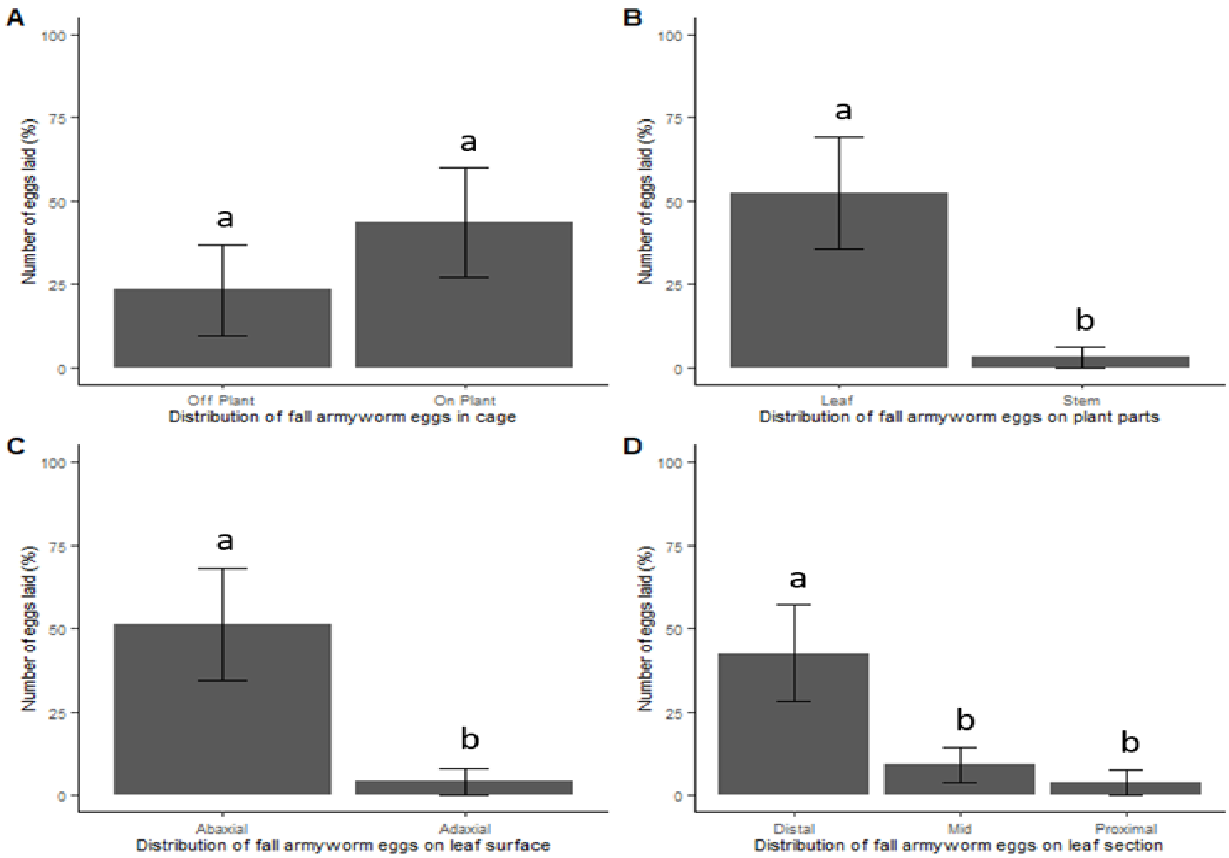

Fig. 2: Overall distribution of fall armyworm eggs on (A) in cage (B) on plant part (C) on leaf surface (D) on leaf section

Additionally, female insects consider the perceived risk of parasitism or egg mortality (Bellota et al., 2018; Rojas et al., 2018), as well as the presence of constitutive plant defenses (Karban, 2011; Garcia et al., 2021), when selecting oviposition sites. In general, ovipositing female insects are thought to adhere to the preference-performance or 'mother-knows-best' hypothesis, which posits that females preferentially select host plants that enhance the survival and performance of their offspring (Gripenberg et al., 2010; Rojas et al., 2018).

However, in the present study, female fall armyworm moths (*Spodoptera frugiperda*) laid comparable numbers of eggs on cage nettings as they did on actual plants. In other words, the females selected non-plant oviposition sites (cage nettings) that offered no nutritional value or other apparent benefits to their larvae, thereby deviating from the preference-performance hypothesis. This behaviour aligns with findings from several other studies, which have also reported that female fall armyworm moths do not discriminate between host and non-host plants when making oviposition choices (Bernal et al., 2015; Rojas et al., 2018; Gripenberg, 2010; Can et al., 2024). Rather, they exhibit the capacity to lay eggs on any plant species or even non-plant objects, with little regard for how they enhance the survival of their eggs and larvae (Rojas et al., 2018). One plausible explanation for this behaviour is the ability of neonate larvae to disperse from the oviposition site, often by ballooning, to locate and colonize more suitable host plants (Rojas et al., 2018).

This seemingly haphazard egg-laying behaviour may explain why all crops assayed in the present study were selected as oviposition sites. Nevertheless, the study showed that the moths had significantly lower mean number of eggs per egg mass in okra, indicating their low preference for okra plants compared to maize or cowpea plants. Female moths in this study generally preferred to lay their eggs on the cage netting rather than on the okra plants. The observation contradicts Wijerathna et al. (2021) who reported that the mean number of eggs per egg mass laid by female fall armyworm moths on plants of okra (Hibiscus esculentus – variety MI5) was comparable with that of maize (Zea mays – variety Pacific) and beans (Phaseolus vulgaris – variety Gannoruwa green) in Sri Lanka. Variations in biophysical and biochemical traits among different varieties of the same crop species often result in differing levels of resistance to insect pest attack. Morphological characteristics such as silica content, trichome density, and leaf toughness, along with primary and secondary metabolites like free amino acids, total sugars, terpenes, tannins, and phenols, play critical roles in enhancing a plant's resistance to insect pests (Deguine & Hau, 2001; Abang et al., 2014; Ali & Wright, 2021). The relatively low preference of female fall armyworm moths for okra observed in this study may be due to the physico-chemical characteristics of the okra variety used.

In the present study, both maize and cowpea were equally preferred by female fall armyworm moths for oviposition. Since its invasion of Africa in 2016, the fall armyworm has shown a strong preference for maize, which remains the most heavily infested and damaged crop across the continent (CABI, 2020; Eschen et al., 2021). However, its host range includes over 350 plant species, among which is cowpea (Montezano et al., 2018; CABI, 2020). Despite this broad host range, reports of significant field damage or yield loss to cowpea remain limited in Africa. Interestingly, Bhagat et al. (2022) reported that maize intercropped with cowpea experienced significantly less fall armyworm damage than sole maize in Punjab, India. In contrast, Baudron et al. (2019) found no reduction in infestation levels when maize was intercropped with cowpea, groundnut, or common beans in Eastern Zimbabwe. The high oviposition preference for cowpea observed in this study suggests that cowpea could potentially experience feeding damage from fall armyworm larvae comparable to that observed in maize. However, to validate this hypothesis, further assessments are required to evaluate larval survival, growth, and development on cowpea plants following egg hatch.

In the present study, female fall armyworm moths consistently chose leaves over stems as oviposition sites across all tested plants. Stems are typically smoother, harder, and more lignified than leaves, which could make it more difficult for the moths to secure their egg masses. Although egg-laying behaviour by female fall armyworm moths might initially appear indiscriminate, these findings suggest that moth oviposition is guided by specific considerations. Rojas et al. (2018) reported that although female moths did not seem to prioritize the nutritional value of oviposition sites for their larvae, they consistently preferred plants with prior oviposition and those experiencing or likely to experience herbivory. Similarly, female moths in the present study appeared to prioritize factors such as the ease of egg adhesion to oviposition sites over the nutritional benefits those sites might offer to their larvae.

On the leaves, female moths strongly favoured the abaxial surface over the adaxial surface, and the distal portions of the leaves over the mid or proximal regions, across all crop types under no-choice conditions. Female fall armyworm moths typically lay their eggs on the undersides of leaves, particularly during periods of low population density (Sparks, 1979; Capinera, 1999; Prasanna et al., 2018). This preference for the abaxial rather than the adaxial leaf surface is probably related to the need to shield the eggs from direct sunlight and reduce the risk of desiccation. Similarly, the stronger preference for the distal portions of selected leaves, as opposed to the proximal parts, may reflect strategies aimed at enhancing the survival and dispersal of neonate larvae after hatching. Leaf tips or distal regions of many crop plants often contain younger, more tender tissues that are easier for newly hatched larvae to feed on. In addition, egg masses placed near the leaf tip position the larvae to take advantage of wind currents, facilitating ballooning and spread to other suitable host plants. However, further investigation is needed to fully understand the factors driving the fall armyworm's preference for the abaxial surface and distal sections of leaves on certain crops.

If these oviposition preferences are indeed driven by factors that enhance larval survival, as suggested, it may indicate that the preference–performance hypothesis holds true for fall armyworm when selecting specific parts or portions of a host plant, but not necessarily when choosing between host plant species. As noted by Jones (2022), the preference–performance hypothesis does not always apply to all insect oviposition choices, since insects may rely on one set of cues to recognize host species and another to differentiate between individual plants of the same species. For example, European butterflies such as *Polygonia c-album* and *Vanessa cardui* have been shown to lay more eggs on plant species suitable for their offspring (Nylin & Janz, 1993; Janz, 2005), yet they failed to distinguish between high- and low-quality individual plants within those species (Janz & Nylin, 1997). The reverse may be true for the female fall armyworm moth, which appears indifferent to offspring performance when selecting between host and non-host plants, yet exhibits greater discrimination when choosing specific parts or portions of the selected host plant.

5. Conclusion and recommendations

Findings in the present study suggest that while female fall armyworm moths may not strictly follow the preference - performance hypothesis at the plant species level, they exhibit marked discrimination at the microhabitat scale. This behaviour has significant implications for pest management strategies, especially in intercrop systems. Future studies should investigate the survival, growth, and reproductive success of fall armyworm larvae on cowpea, and evaluate the potential of maize–okra intercropping to enhance sustainable control of the pest in smallholder farming systems within the study area.

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