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RESEARCH

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Acceptability and suitability of some Poaceae plants for fall armyworm feeding and oviposition

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Abstract

Background: The fall armyworm (FAW), *Spodoptera frugiperda* (Lepidoptera: Noctuidae), has invaded new geographical regions, now spanning Africa, Asia, Oceania and Europe, from its native distribution in the last decade. Little is known about FAW host plants in recently invaded habitats; although more than 300 hosts have been reported in the Americas, its native habitat. In our study, we evaluated the acceptability and suitability of 12 cultivated varieties of plants from Africa, in the family Poaceae, for FAW herbivory and oviposition. Methods: Experiments investigating larval development, no-choice oviposition, and no-choice larval arrestment-feeding were conducted to evaluate the insect´s ability to utilize these plants for survival. Results: We found that *Pennisetum* ex. Sengerema, *Brachiaria brizantha*, *Brachiaria* ex. Mwanza, *Panicum maximum* ex. Machakos, *Melinis minutiflora* and *S. bicolor* cv. Ochuti were unsuitable plants for FAW larvae. In contrast, *Zea mays* HB WH505, *Panicum glaucum* Nutrifeed, *S. bicolor* cv. Serena and *P. purpureum* were suitable plants and *S. bicolor* cv. Ochuti was well accepted for egg-laying. However, *M. minutiflora* was not accepted for egg-laying but retained early instar larvae. *S. bicolor* cv. Andiwo was not well accepted for egg-laying and *S. bicolor* cv. Gadam yielded lighter pupae. Conclusions: Our findings provide insights into the performance of FAW larvae on different Poaceae plants and how well they are accepted by FAW female moths for oviposition. We recommend to study further selected plants (*M. minutiflora*, *S. bicolor* cv. Andiwo and *S. bicolor* cv. Ochuti), as potential trap or repellent plants for different FAW life stages, in choice tests. This knowledge will help to design ecologically based management strategies for FAW in its new habitats in Kenya and beyond.

Keywords: fall armyworm, host plants, Poaceae, larval feeding, larval development, oviposition

Introduction

The fall armyworm (FAW), *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae), is one of the most important noctuid pests in the Americas (Montezano *et al*., 2018; Kenis *et al*., 2023), but now has worldwide relevance due to its spread to Africa, the Near and Middle East, South-east and East Asia, and Oceania. It now occurs in Japan, Australia and New Zealand and is also reported in the Canary Islands, with a few occurrences in Cyprus, Greece, Portugal and Turkey (FAO, 2023, 2024; EPPO, 2025). The bionomics of *S. frugiperda* make this insect a plague of several important cultivated crop plant species around the globe, due to its polyphagy, voracious appetite and invasive potential (Goergen *et al*., 2016; Early *et al*., 2018). The FAW has become the greatest threat to maize in sub-Saharan Africa (Day *et al*., 2017), Asia and Australia (Overton *et al*., 2021). It has also been observed in grasses and green amaranth in India (Maruthadurai and Ramesh, 2020), and in pulses in Australia (GRDC, 2023). Overall, the greatest FAW damage has been recorded in monocot crops such as maize (Siloto, 2002) and sorghum (Cortez and Waquil, 1997), and dicots such as cotton (Hardke *et al*., 2015) and soybean (Pitre and Hogg, 1983). On the other hand, literature reports several grass species (family Poaceae) as hosts of FAW;

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examples include: *Brachiaria mutica* (Forssk) Stapf, *Megathyrsus maximus* (Jacq.), *Sorghum halepense* (L.) Pers, *Eleusine indica* (L.) Guertno, *Setaria parviflora* (Lam.) Beauv., *S. viridis* Beauv., *Digitaria sanguinalis* (L.) Scop. and *D. pseudodiagonalis* Chiov (Andrews, 1988). Unknown species of the genus *Digitaria* and *E. indica* are remarkably mentioned as infestation sources, for larvae that move towards maize crops in Honduras (van Huis, 1981; Andrews, 1988). Moreover, turf grasses and rice are reported as hosts of FAW (Nagoshi and Meagher, 2004; Murúa *et al*., 2015; Valdez *et al*., 2023). Several studies have demonstrated genetic differences between two FAW strains and that one strain is common in rice while the other in maize (Pashley and Martin, 1987; Murúa *et al*., 2015); although overlapping populations have also been found in certain geographical regions (Herlinda *et al*., 2022). Indeed, more than 300 monocot and dicot plant species have been reported as FAW hosts in its native range (Andrews, 1980; Montezano *et al*., 2018). Furthermore, genetic variations between different FAW strains suggest that these populations may exhibit preferences specific to a particular host plant (Pashley and Martin, 1987; Murúa *et al*., 2015).

FAW host plants are well studied and identified in their native habitats (i.e. the Americas), and recently some studies have been carried out on FAW host plants in Africa (Caniço *et al*., 2021; Ahissou *et al*., 2022; Winsou *et al*., 2022; Mubayihua *et al*., 2023). However, it is important to study which plants are accepted by FAW neonates for feeding and females for oviposition in the absence of primary hosts; and how suitable these plants are for FAW larvae development. Therefore, identifying potential host plants of the FAW, including grasses and volunteer plants in agroecosystems and neighboring areas of newly invaded regions, is urgently required to support the development of efficient and adaptable FAW control strategies (Feldmann *et al*., 2019; Sisay *et al*., 2023; Peter *et al*., 2024).

Secondary host plants can offer alternate food sources and/or oviposition sites to support part of the FAW life cycle (Ribeiro *et al*., 2020). Moreover, FAW can complete its entire life cycle and survive in a reservoir in the absence of primary hosts (Pencoe and Martin, 1982; Pitre *et al*., 1983; Ali *et al*., 1989; Meagher *et al*., 2004; Prasifka *et al*., 2009; Firake and Behere, 2020). In addition, investigating alternative host plants enhances our understanding of how various food sources influence FAW life history traits (Pencoe and Martin, 1982). For crop breeding, this research can also identify alternative hosts that provide tolerance or antibiosis mechanisms against FAW (Chiriboga Morales *et al*., 2021).

Larval arrestment behavior (i.e. reduced movement), larval feeding and development are key parameters that can be used as a proxy for plant herbivore acceptability (Bueno *et al*., 2010; Chiriboga Morales *et al*., 2021). Moreover, egg deposition can be used as a measure of acceptability of a plant for insect oviposition (Khan *et al*., 1997a, b; Sobhy *et al*., 2022). We hypothesized that different grass and cereal cultivars have varying suitability for the larvae of FAW, influencing larval development as well as adult oviposition behavior. To test this hypothesis, we carried out no-choice experiments to investigate the suitability of selected plants for insects.

Methods

PLANTS

Potted plants of six grass species (Family Poaceae): *Melinis minutiflora* (P. Beauv.), *Pennisetum purpureum* Schumach., *Panicum maximum* Jacq. ex. Machakos, *Brachiaria* sp. ex. Mwanza, *Brachiaria brizantha* (Hochst.), *Pennisetum sp.* ex. Sengerema; and six cereal species (Family Poaceae): maize *Zea mays* L. HB WH505 (Western Seed Company), *Sorghum bicolor* (L.) Moench. cv. Andiwo (local farmers), *Sorghum bicolor* (L.) Moench cv. Ochuti (local farmers), *Sorghum bicolor* (L.) Moench HB Serena (Kenya Seed Company), *Sorghum bicolor* (L.) Moench HB Gadam (Easeed Kephis) and pearl millet *Pennisetum glaucum* (L.) R. Br. Nutrifeed (Advanta) were used for the experiments. Plants of grasses were grown vegetatively from rhizomes obtained from plants of the grass collection garden maintained at *icipe*-Thomas Odhiambo Campus (iTOC), Mbita Point (Homa Bay County, Kenya). Cereal plants were grown from seeds sown in plots filled with agricultural soil from the Mbita farm in an insect proof screen house at iTOC under controlled conditions (27 ± 3°C, 65 ± 5% RH, 12L:12D). After seed germination or stems sprouting (in the case of grasses), 3.5 g of fertilizer (Diammonium Phosphate-DAP, Elgon Kenya) was applied to each plant. Plants used in experiments were 2–3 weeks old, but *M. minutiflora*, *P. purpureum*, *P. maximum*, *Brachiaria sp.* ex. Mwanza and *Pennisetum sp.* ex. Sengerema were 3–4 months old, since they grow slower.

INSECTS

FAW neonate larvae (1-day old) were used for the experiments 1, 2 and 3, and obtained from a FAW colony reared at the ITOC insectary (25 ± 3°C, 75 ± 5% RH) with an artificial diet (Southland Products Inc., Arkansas, United States). The FAW colony was initiated from larvae collected from FAW infested maize fields in Western Kenya. To avoid cannibalism, FAW larvae were reared individually in glass tubes (2.8 × 7.3 cm) with the diet until pupation; and pupae were kept in Petri dishes on a moist filter paper and placed within an insect cage until adult emergence (Mihm, 1983).

EXPERIMENTAL PROCEDURE

Experiment 1: Larval arrestment/dispersal and leaf consumption

Arrestment experiments were carried out to evaluate the acceptance of cereals and grass leaf cuts, by FAW neonate larvae, in a no-choice set up. A leaf cut of 6 cm length and 2 cm width was placed in a Petri dish (9 cm) lined with a moistened filter paper as described in Chiriboga Morales *et al.* (2021). Thereafter, ten neonate larvae were placed on the leaf cut and the Petri dishes were sealed with Parafilm (Pechiney Plastic Packaging, Wisconsin, United States) to maintain humidity and avoid escape of larvae. The sealed Petri dishes were kept in the dark under controlled laboratory conditions to prevent light effects on the larvae (25 ± 3°C, 75 ± 5% RH). The number of neonates remaining on the leaf cut was counted after 4 and 24 h (Chiriboga Morales *et al*., 2021). Five replicates were performed per plant species. Using the same setup, we assessed larval feeding by capturing a photo of the leaf cut with a smartphone after 4 and 24 h. The consumed leaf area was then measured automatically using the App Leafbyte (©Zoe Getman-Pickering).

Experiment 2: Larval performance on plants

Experiments were conducted using potted plants, within insect cages, in outdoor conditions (26 ± 3°C, 65 ± 5% RH, 12L:12D). Three potted plants of each species were placed in an insect mesh cloth-wooden frame cage (50 cm × 50 cm × 70 cm). Each plant was infested with ten FAW neonate larvae, introduced individually, using a camel hair paintbrush. Plants were covered with plastic bottles cut at the bottom and at the top and covered with a mesh cloth on top, secured with a rubber band (Erb *et al*., 2011). Pots had a hole in the bottom for plants to absorb water as needed. The experiment was checked for 15 days until the larvae developed to the last larval instar or pupae (Chiriboga Morales *et al*., 2021), after which the insect final weight, percentage mortality and percentage pupation were recorded.

Experiment 3: Larval development and survival in glass vials

The larval stage did not progress beyond the first instar stages when fed on all the grass plants; thus, we conducted the larval development and survival trials in glass vials using only cereals. We evaluated the weight gain of larvae fed on leaf cuts of cereals under laboratory conditions (25 ± 3°C, 75 ± 5% RH, 12L:12D). FAW neonates were placed individually in glass vials (2.8 × 7.3 cm) with leaf cuts of test plant species. Leaf cuts were obtained from plants grown in screen-house conditions and ten replicates were used per plant species. The live larvae were counted and weighed every 3 days, and fresh leaf cuts were provided (every 3 days) for 15 days, then the numbers of dead larvae were also recorded. Pupal weight was recorded at day 15.

Experiment 4: Female oviposition

To assess FAW oviposition behavior on different species of cereals and grasses, no-choice oviposition experiments were performed using adult moths. Six plants were placed individually in an insect-proof mesh cloth-wooden frame cage (50 cm × 50 cm × 70 cm) and newly emerged FAW moths (three male and five females) were released in each cage at dusk (Sobhy *et al*., 2022), ensuring that only newly mated females of similar age were selected for the experiment. The experiments were carried out in cages outdoors (25 ± 3°C, 65 ± 5% RH, 12L:12D). Moths were left for 15 h overnight for egg-laying and then the number of eggs per plant was estimated by weighing the eggs on a Mettler Toledo PM 460 scale (Mettler Instruments; Greiffensee, Switzerland). To estimate the number of eggs on plants, a calibration between the weight of the eggs and the number of eggs was calculated beforehand (Cheruiyot *et al*., 2021).

Statistical analysis

All data were tested for normality with the Shapiro–Wilk test before the statistical analysis was performed using SigmaStat 15.4.0 software. Data from larval arrestment and larval performance were root square transformed before analysis with one-way ANOVA. Consumed leaf areas were compared with one-way ANOVA. Data on larval development in glass vials were root square transformed and analyzed with two-way ANOVA, the study factors were the varieties of cereals and the time after the experiment started (day); thereafter the means were separated by Tukey test. Data on pupal weight was analyzed using One-way ANOVA. Significant means were separated using Tukey's Studentized Range Test (HSD).

Results

EXPERIMENT 1: LARVAL ARRESTMENT AND LEAF CONSUMPTION

After 4 h, significant differences ($F_{5,29}$ = 8.34; $p < 0.001$) were found in arrestment behavior of FAW neonate larvae on leaf cuts of different grass species. Larval arrestment was significantly higher on *B. brizantha*, *Brachiaria* ex. Mwanza, *P. maximum* ex. Machakos, *P. purpureum* and *M. minutiflora* compared to *Pennisetum* ex. Sengerema (Fig. 1a). In contrast, no significant differences for larval arrestment were found between cereals ($F_{5,29}$ = 0.81; $p = 0.55$) (Fig. 1b).

When assessing larval feeding, no significant differences between grasses ($F_{5,29}$ = 0.28; $p > 0.05$) were found in consumed leaf area (Fig. 2a). However, significant differences ($F_{5,29}$ = 7.07; $p < 0.05$) were found between cereals (Fig. 2b). Consumed leaf area after 4 h was significantly higher in *Z. mays* HB WH505 and *P. glaucum* Nutrifeed, with more than twice as much eaten, compared to *S. bicolor* cv. Gadam and *S. bicolor* cv. Serena; meanwhile, consumed leaf area was not different between *S. bicolor* Ochuti and *S. bicolor* Andiwo.

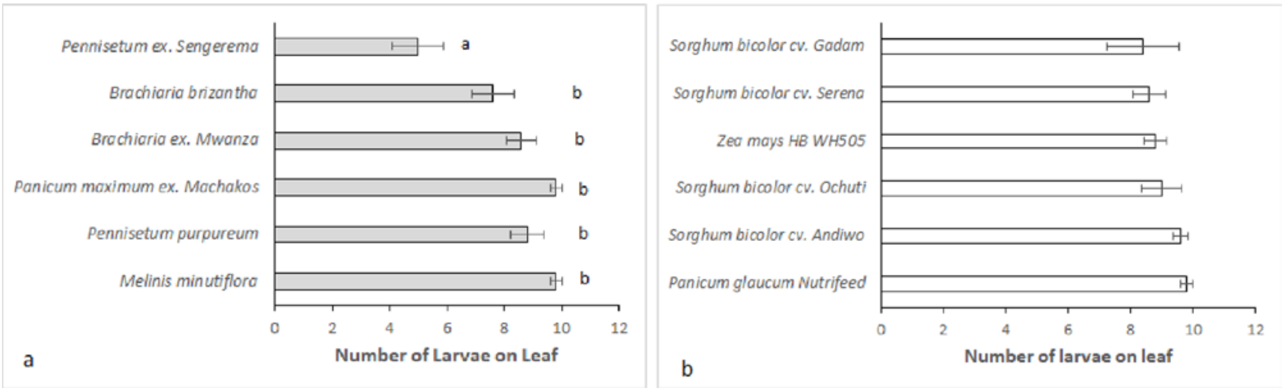

Fig. 1. Arrestment of FAW larvae (mean ± SE; n = 5) on leaf cuts of different varieties of: (a) grasses (gray bars) and (b) cereals (white bars) in a no-choice experiment after 4 h. Different letters represent significant differences ($p < 0.001$) and no letters represent no significant differences ($p = 0.55$) based on Tukey test.

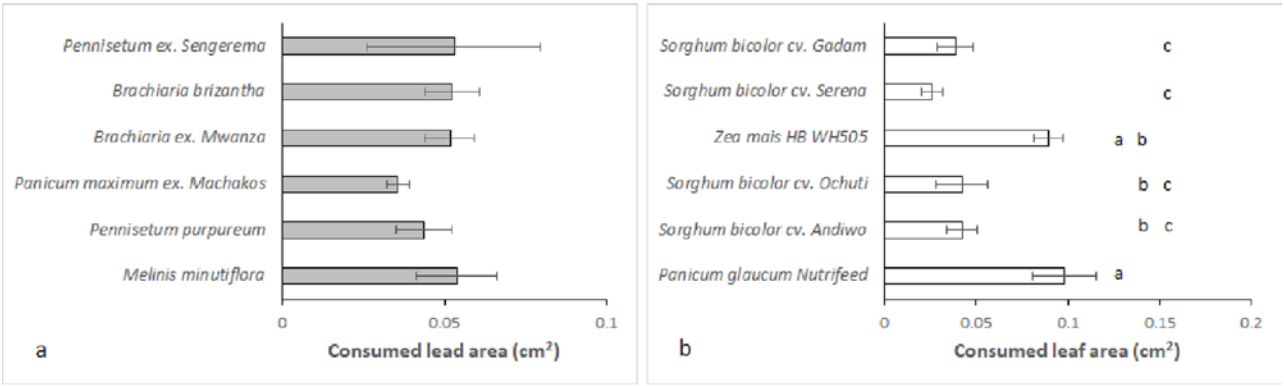

Fig. 2. Consumed leaf area (cm^2; mean ± SM; n = 5) by FAW larvae of different varieties of: (a) grasses (gray bars) and (b) cereals (white bars) in a no-choice experiment after 4 h. Different letters represent significant differences ($p < 0.05$) and no letters represent no significant differences ($p > 0.05$) based on Tukey test.

After 24 h, significant differences in FAW larval arrestment on leaf cuts were found between grasses ($F_{5,29} = 7.22$; $p < 0.001$) and between cereals ($F_{5,29} = 3.16$; $p < 0.05$). For grasses, larval arrestment was significantly higher in *B. brizantha*, *P. maximum* ex. Machakos, *P. purpureum* and *M. minutiflora* compared to *Brachiaria* ex. Mwanza and *Pennisetum* ex. Sengerema (Fig. 3a). For cereals, larval arrestment was significantly higher in *S. bicolor* cv. Gadam, *S. bicolor* cv. Serena, *Z. mays* HB WH505, *S. bicolor* cv. Ochuti and *P. glaucum* Nutrifeed compared to *S. bicolor* cv. Andiwo (Fig. 3b).

When measuring consumed leaf area, we found significant differences between grasses ($F_{5,29} = 8.47$; $p < 0.05$) and cereals ($F_{5,29} = 3.47$; $p < 0.05$). Consumed leaf area was significantly higher in *B. brizantha*, *M. minutiflora*, *P. purpureum*, *P. maximum* ex. Machakos and *Brachiaria* ex. Mwanza compared to *Pennisetum* ex-Sengerema (Fig. 4a). When evaluating feeding on cereals, consumed leaf area was significantly higher only when comparing *S. bicolor* cv. Serena with *S. bicolor* cv. Ochuti, *S. bicolor* cv. Gadam, *Z. mays* HB WH505 and *P. glaugum* Nutrifeed compared with *S. bicolor* cv. Andiwo (Fig. 4b).

EXPERIMENT 2: LARVAL PERFORMANCE ON PLANTS

Significant differences in larval development were found after 15 days of feeding on grasses ($F_{3,37} = 4.35$; $p < 0.05$) and cereals ($F_{5,111} = 7.28$; $p < 0.001$). Larvae gained significantly more weight when fed on *P. purpureum* and *P. maximum* ex. Machakos compared to *B. brizantha* and *Brachiaria* ex. Mwanza (Fig. 5a). Larvae reached a significantly higher weight when fed on *Panicum*

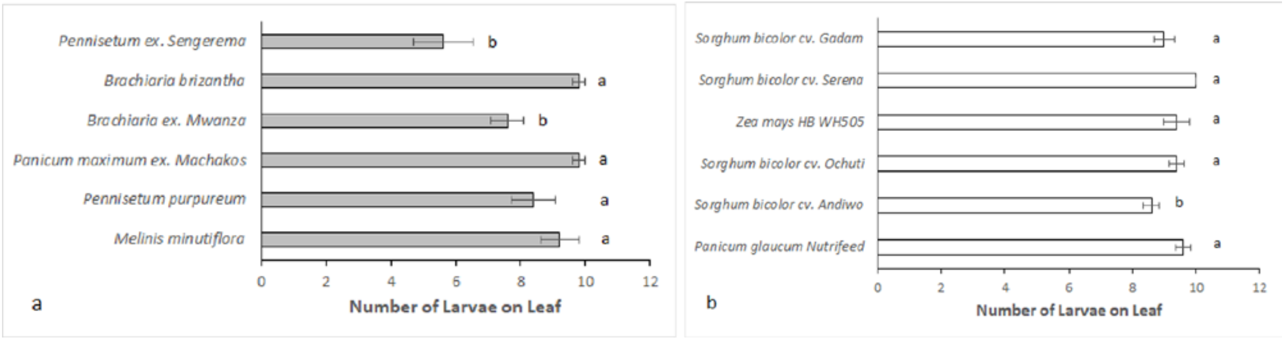

Fig. 3. Arrestment of FAW larvae (mean ± SE; n = 5) on leaf cuts of different varieties of: (a) grasses (gray bars) and (b) cereals (white bars) in a no-choice experiment after 24 h. Different letters represent significant differences between grasses ($p < 0.001$) and between cereals ($p < 0.05$) based on Tukey test.

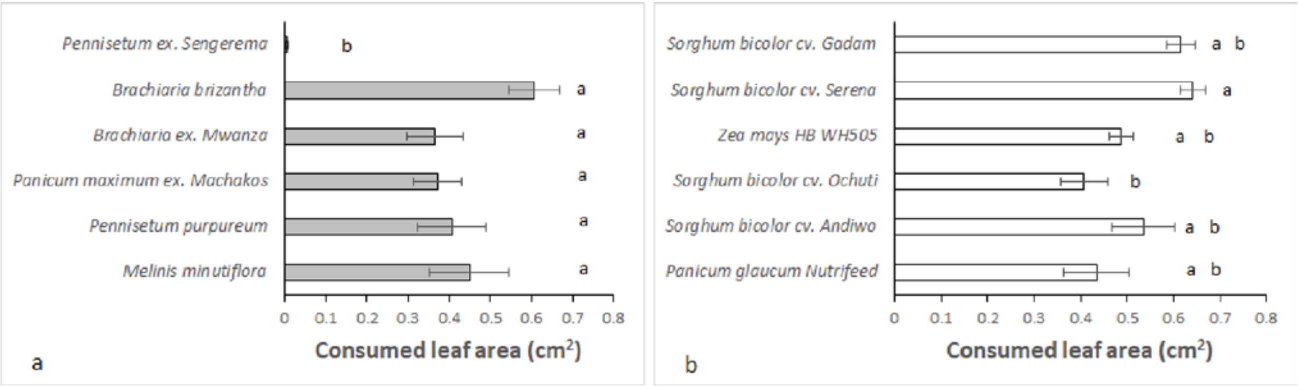

Fig. 4. Consumed leaf area (cm^2; mean ± SE; n = 5) by FAW larvae on different varieties: (a) grasses (gray bars) and (b) cereals (white bars) in a no-choice experiment after 24 h. Different letters represent significant differences ($p < 0.05$) between grasses and between cereals based on Tukey test.

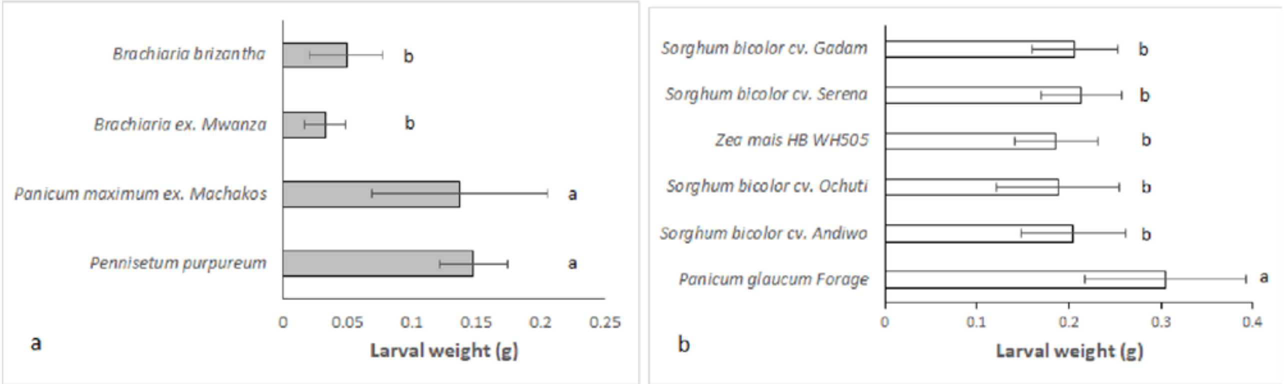

Fig. 5. Larval weight (g; mean ± SEM; grasses n = 41; cereals n = 117) of FAW developed on different varieties of: (a) grass plants (grey bars) and (b) cereal plants (white bars) after 15 days. Different letters represent significant differences ($p < 0.05$) between grasses and between cereals ($p < 0.001$) based on Tukey test. *Pennisetum* ex. Sengerema and *Melinis minutiflora* were excluded from the analysis because only one larva remained at the end of the experiment in each treatment.

glaucum Nutrifeed compared to *S. bicolor* cv. Gadam, *S. bicolor* cv. Seredo, *Z. mays* HB WH505, *S. bicolor* cv. Ochuti and *S. bicolor* cv. Andiwo (Fig. 5b).

EXPERIMENT 3: LARVAL DEVELOPMENT IN VIALS

Plant species/varieties had no significant effects ($F_{5,95}$ = 1.29; *p* > 0.1) on larval development, whereas the time of development was significantly affected ($F_{1,95}$ = 26.51; *p* < 0.001). We also found a significant ($F_{5,95}$ = 24.66; *p* < 0.0001) effect of their interactions. On day 9, the weight of neonates was similar when neonates fed on *S. bicolor* cv. Gadam, *S. bicolor* cv. Serena, *S. bicolor* cv. Ochuti and *S. bicolor* cv. Andiwo. However, the larval weight was significantly higher when fed on these plants compared to *Z. mays* and *P. glaucum* Nutrifeed. At day 12, larval weight of those larvae fed on *Z. mays* HB WH505 and *P. glaucum* Nutrifeed was significantly higher than those fed on *S. bicolor* cv. Gadam. We found a significantly higher larval weight at day 12 compared to day 9 in both *Z. mays* HB WH505 and *P. glaucum* Nutrifeed fed larvae (Fig. 6).

Observations of percentage mortality and pupation represent the proportions of insects that died and those that pupated out of all the insects used in experiments. Thus, we show the accumulated mortality at the end of the experiment of larvae development in vials. The lowest mortality rate was recorded when larvae fed on *P. glaucum* Nutrifeed and *S. bicolor* cv. Ochuti, moderate rates of mortality were observed on *S. bicolor* cv. Serena, *S. bicolor* cv. Andiwo and *Z. mays* HB WH505, and the highest rate of mortality was recorded on *S. bicolor* cv. Gadam. Correspondingly, the highest percentage of pupation occurred when larvae fed on *P. glaucum* Nutrifeed and *S. bicolor* cv. Ochuti. An intermediate percentage of pupation occurred when larvae fed on *S. bicolor* cv. Serena, *S. bicolor* cv. Andiwo, and *Z. mays* HB WH505, whereas the lowest percentage of pupation occurred in *S. bicolor* cv. Gadam (Table 1).

In the larval development experiment on plants, the lowest mortality rates were recorded when larvae fed on *P. purpureum*, *S. bicolor* cv. Gadam, *S. bicolor* cv. Serena, *Z. mays* HB WH505 and *P. glaucum* Nutrifeed. However, intermediate rates of mortality were recorded on *S. bicolor* cv. Ochuti, *S. bicolor* cv. Andiwo, and the highest rates of mortality were recorded on *B. brizantha*, *Brachiaria* ex. Mwanza, *P. purpureum* ex. Sengerema, *P. maximum* ex. Machakos and *M. minutiflora*. No pupation was recorded on either grasses or *P. glaucum* Nutrifeed at the end of the experiment (day 15). Furthermore, a minimal percentage of pupation occurred when larvae fed on *S. bicolor* cv. Gadam, in *S. bicolor* cv. Serena, *S. bicolor* cv. Andiwo and *Z. mays* HB WH505. Higher percentages of pupation were recorded in *S. bicolor* cv. Ochuti and *S. bicolor* cv. Andiwo (Table 1).

We found significant differences in the pupal weight between cereal cultivars (*p* < 0.001) (Fig. 7). Pupal weight for those larvae fed on *S. bicolor* cv. Ochuti was significantly higher compared to larvae fed on *S. bicolor* cv. Gadam, as well as *Zea mays* HB WH505 and *P. glaucum* Nutrifeed. Moreover, the pupal weight of insects fed on *S. bicolor* cv. Andiwo was significantly higher than insects fed on *Zea mays* HB WH505, *S. bicolor* cv. Gadam and *P. glaucum* Nutrifeed.

EXPERIMENT 4: FEMALE OVIPOSITION

No significant differences were found between grasses ($F_{5,30}$ = 2.26; p > 0.05) (Fig. 8a), or between cereals ($F_{5,30}$ = 1.13; P > 0.05) (Fig. 8b) in the number of eggs laid by FAW moths. Although there was considerable variation in the number of eggs laid per plant between the different plant cultivars, the variation in egg laying within genotypes was too large for the differences to be detected statistically.

Discussion

Our results showed significant differences in FAW larvae performance on the different plants tested, and no differences in acceptability of plants for oviposition under no-choice conditions.

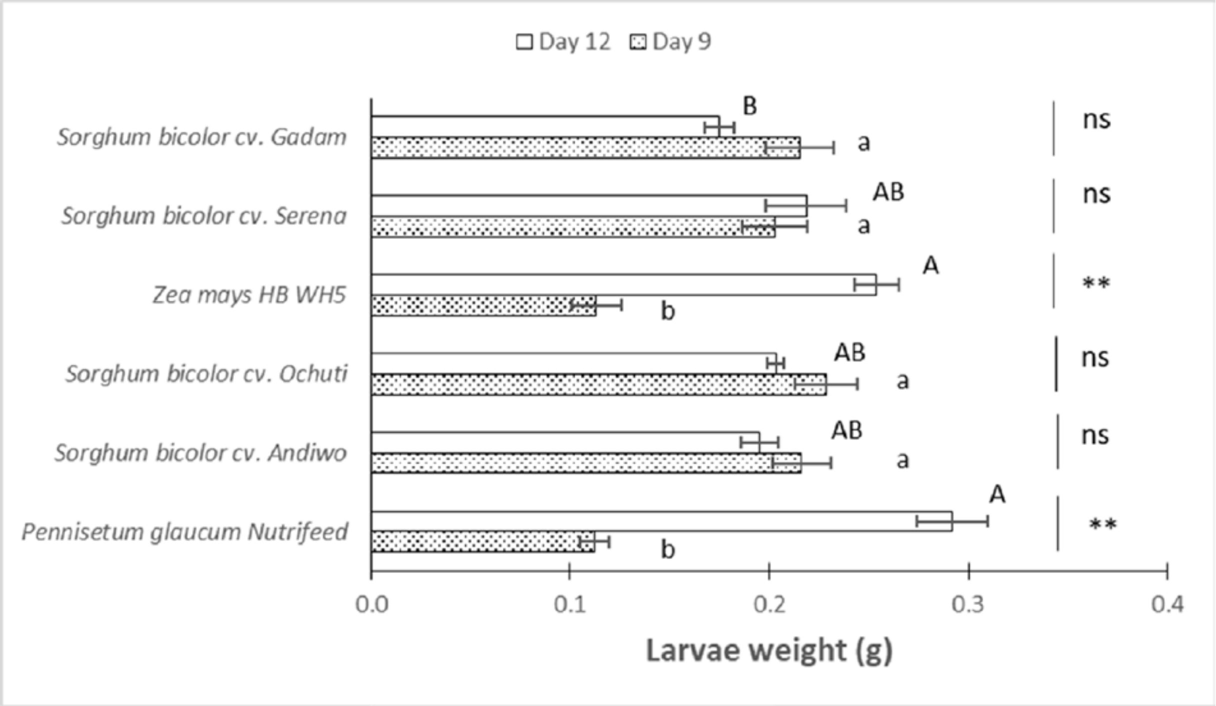

Fig. 6. Larval weight (mean ± SE; n = 10) of FAW fed on different varieties of cereals at day 9 and day 12. Different lowercase and uppercase letters represent significant differences between varieties within Day 9 and day 12, respectively, based on Tukey test (Two-way ANOVA). (ns) represents no significant differences in larval weight between day 9 and day 12 whereas (**) represents significant differences (*p* < 0.0001).

The grass species tested were poor hosts compared with the cereals tested. Larval arrestment and feeding rate on leaf cuts, under no-choice conditions, are likely indicators of the plant acceptability (Bueno *et al*., 2010; Chiriboga Morales *et al*., 2021). Arrestment measurements reflected the amount of leaf consumed in grasses. For instance, the lowest number of FAW larvae was arrested on *Pennisetum* ex. Sengerema, which corresponded with the minimal leaf area consumed on this grass after 24 h. Since hardly any leaf area was consumed on *Pennisetum* ex. Sengerema, it is possible that this grass species has an antifeedant chemical. In tests with cereal species, one of the least consumed leaf cuts was *S. bicolor* cv. Ochuti. It is noteworthy that the lowest weight of FAW larvae on plants was found in *Pennisetum* ex. Sengerema and *S. bicolor* cv. Ochuti. This suggests that *Pennisetum* ex. Sengerema and *S. bicolor* cv. Ochuti are not well accepted by FAW neonate larvae for early feeding. Furthermore, the low weight and high mortality of FAW larvae on *Pennisetum* ex. Sengerema indicate that the grass is not a suitable host for their development. While FAW larvae were able to develop on *S. bicolor* cv. Ochuti, their mortality rate remained high. These results suggest that both plant species have poor nutritional quality for FAW larvae development (Schoonhoven *et al*., 2007).

Table 1. Percentage mortality and pupation of FAW larvae when fed on different varieties of cereal in and grass species in glass vials[1] and in plants[2].

Plant species/ varieties	Leaf cuts		Whole plants	
	%Mortality[1]	%Pupation[1]	%Mortality[2]	%Pupation[2]
Grasses				
P. purpureum ex. Sengerema	nd*	nd	98.3	0
B. brizantha	nd	nd	95	0
Brachiaria ex. Mwanza	nd	nd	93.3	0
P. maximum ex. Machakos	nd	nd	93.3	0
P. purpureum	nd	nd	50	0
M. minutiflora	nd	nd	98.3	0
Cereals				
S. bicolor cv. Gadam	40	60	68.3	3.33
S. bicolor cv. Serena	30	70	60	5
Z. mays HB WH505	30	70	73.33	3.33
S. bicolor cv. Ochuti	20	80	86.66	11.66
S. bicolor cv. Andiwo	30	70	78.33	10
Panicum glaucum Nutrifeed	10	90	40	0

*nd means "no data".

Among grasses, FAW larvae were mostly arrested on *B. brizantha*, *P. maximum* ex. Machakos, *P. purpureum* and *M. minutiflora* after 24 h. Regarding *M. minutiflora*, Cheruiyot *et al*. (2021) showed that this grass species retains more FAW larvae compared with other evaluated grasses after 48 h, suggesting a potential role as a trap plant for early instar FAW larvae. Our results also show that FAW larvae did not develop on *M. minutiflora*. Thus, further studies are needed to investigate potential mechanisms of antibiosis that negatively impact FAW larvae survival on *M. minutiflora*. In contrast, *P. purpureum* leaf cuts exhibited one of the highest consumption rates after 24 h. Notably, the heaviest larvae were found developing on this grass species, indicating its high nutritional quality for FAW larvae growth (Schoonhoven *et al*., 2007).

Although the experiment was not extended beyond day 15, the relatively low mortality rate of FAW larvae on *P. purpureum*, compared with other grasses, suggests that this plant could serve as an alternate host for FAW larvae in the absence of their primary host. This could support the pest's establishment, development, and spread, as highlighted by Chen *et al*. (2023). Furthermore, we recorded the lowest FAW larvae weights on *Brachiaria* ex. Mwanza and *B. brizantha*, with high percentage of mortality, indicating the unsuitability of these plants for FAW larval growth. Similar results were reported by other authors when evaluating alternative hosts

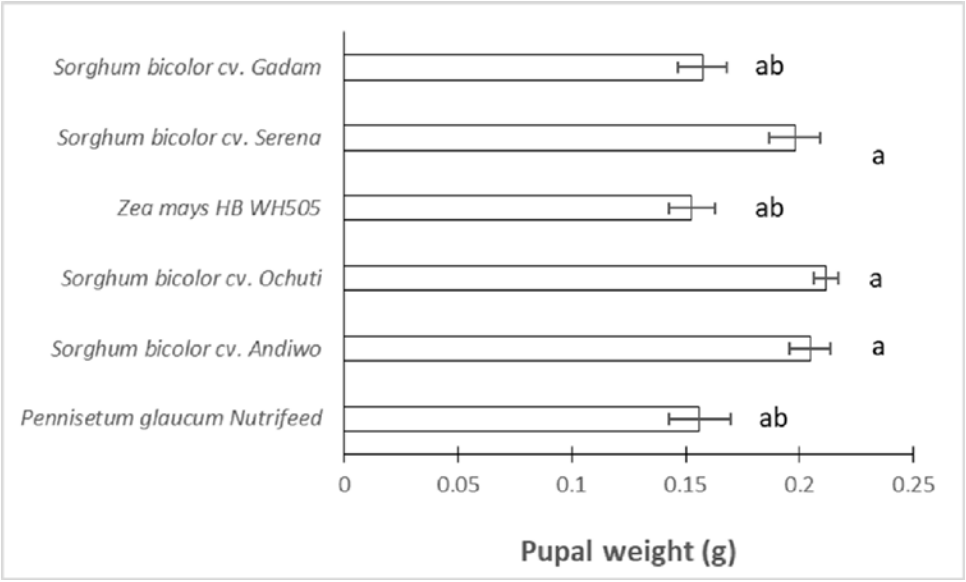

Fig. 7. Pupal weight (g; mean ± SE; n = 10) of FAW larvae fed on leaf cuts of different species/varieties of cereals in glass vials at day 15. Different letters represent significant differences ($p < 0.001$) based on Tukey test.

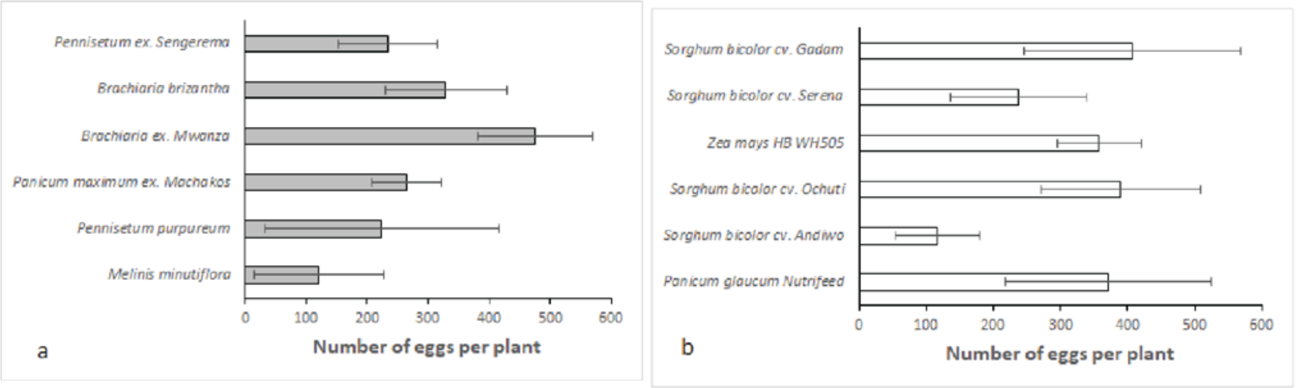

Fig. 8. FAW laid eggs (mean ± SE; n = 6) on different varieties of grasses and cereals. Gray and white bars represent (a) grasses and (b) cereals, respectively.

of FAW under similar conditions (Sá *et al*., 2009; Cheruiyot *et al*., 2021). In contrast, FAW larvae have been reported to gain substantial weight when fed on certain cultivars of *B*. *brizantha* such as Marandú (dos Santos *et al*., 2022), suggesting high variability between *B*. *brizantha* cultivars regarding their nutritional value and suitability for FAW. Although the FAW larvae showed weight gain on *P*. *maximum* ex. Machakos plants, the high mortality rate indicates that this plant is not suitable for their development. Similar results were obtained by dos Santos *et al*. (2022) with FAW larvae when fed on *P*. *maximum* cv. Massai and *P*. *maximum* cv. Tamani.

Five of the grasses tested in this study resulted in high mortality rates for FAW larvae and should be regarded only as temporary or supplementary food sources. However, *P*. *purpureum* requires further investigation beyond 15 days to assess its potential as an alternative host plant for FAW larvae development. The leaf cuts of *Z*. *mays* HB WH505 and *P*. *glaucum* Nutrifeed were consumed most after 4 h, and FAW larvae performed best on *Z*. *mays* HB WH505 plants. This is in line with a study with a different maize hybrid, in which it retained FAW larvae for longer and supported higher survival, compared to a Mexican variety (de la Rosa-Cancino *et al*., 2016). Similarly, in our larval development experiment in vials, we observed higher weight gain when larvae developed on *Z*. *mays* HB WH505 and *P*. *glaucum* Nutrifeed compared to *S*. *bicolor* cultivars. Indeed, *P*. *glaucum* Nutrifeed is a pearl millet hybrid with no prussic acid, a cyanide compound that may impede FAW larvae development (Moran, 2005). This fact might explain good performance and high survival of FAW larvae on this plant. There is increasing evidence that crop domestication has consistently reduced plant chemical resistance against herbivorous insects, making plants prone to herbivory and reducing natural enemy performance on crop plants (Tamiru *et al*., 2011; Chen *et al*., 2015). The low pupation rate (3.33%) on whole maize plants can be attributed to cannibalism between larvae, which was not the case in the vial experiments where each larva was isolated individually preventing cannibalism. The fact that 0% pupation was recorded in *P*. *glaucum* Nutrifeed by day 15 does not mean that pupation could not have occurred later, if we had continued the experiment beyond day 15. The relatively low FAW mortality rates on *P*. *glaucum* Nutrifeed indicate that this plant is able to support FAW development. However, this plant requires further investigation beyond 15 days to assess its potential as an alternative host plant for FAW larvae development. Other plants that sustained FAW survival were *Z*. *mays* HB WH505, *P*. *purpureum*, *S*. *bicolor* cv. Gadam and *S*. *bicolor* cv. Serena. Interestingly, these sorghum cultivars were also the most consumed after 24 h. In contrast, *S*. *bicolor* cv. Ochuti caused high mortality (>85%) of FAW larvae. We recommend further investigation to unravel the antibiosis mechanisms of *S*. *bicolor* cv. Ochuti to FAW larvae. Indeed, several studies have showed different responses in the biology of FAW to distinct cultivars of certain plant species (dos Santos *et al*., 2022; Chen *et al*., 2023).

For the developmental time of FAW larvae, we did not find differences between the varieties of cereals evaluated. However, we found differences in pupal weight of FAW fed with different cultivars of *S*. *bicolor*, which is in line with other studies (Castro *et al*., 1988; Barcelos *et al*., 2019). Previous research has indicated that some varieties of *S*. *bicolor* produce lighter FAW pupae than others (Castro *et al*., 1988), suggesting possible antibiosis effects of the plant on the insect. In our study, *S*. *bicolor* cv. Gadam, *Z*. *mays* HB WH505 and *P*. *glaucum* Nutrifeed yielded lighter pupae compared with *S*. *bicolor* Ochuti and *S*. *bicolor* Andiwo. Another study has shown that the geographic origin of larvae affects both their development time and pupal weight (van Antwerpen, 2019). However, this does not apply to our research, as all the larvae used originated from the same location. Thus, it is essential to conduct further research to explore the factors influencing the negative impact of Gadam sorghum cultivars on the pupal weight of FAW.

Our oviposition experiment data indicate no significant differences in egg-laying behavior of FAW females between the grasses and cereals tested in no-choice tests. These observations are similar to findings in previous studies that assessed moth oviposition on different plant species (Rojas *et al*., 2003, 2018; Sisay *et al*., 2023). Despite the unrealistic conditions of the no-choice experiments, our results suggest that FAW females use different plant species or varieties for oviposition in distinct ways, especially in the absence of preferred hosts. Our results show that certain cereals such as *Z*. *mays* HB WH505, *P*. *glaucum* Nutrifeed, *S*. *bicolor* cv. Gadam and *S*. *bicolor* cv. Ochuti tended to receive more eggs on their leaves compared to other plants such as *M*. *minutiflora* and *S*. *bicolor* cv. Andiwo that received fewer eggs. These findings represent gravid FAW moth behavior when no other plants are available. In previous studies, we showed that FAW females preferred to lay eggs on the side of the cage rather than on *Desmodium* plant species (Sobhy *et al*., 2022), indicating avoidance even under no choice conditions.

Previous work by López *et al*. (1996) observed significant variation in egg-laying among different sorghum varieties. Castro *et al*. (1988) found that female insects raised on maize laid more eggs than those raised on sorghum. In our research, we can eliminate the influence of diet on egg-laying behavior, as all insects used in our experiments were fed the same diet. Importantly, *M*. *minutiflora* has been recognized previously as a repellent plant for female stemborers (Khan *et al*., 1997b) and hence it could also be the case for FAW, since they are both noctuid lepidopterans. Indeed, two-choice experiments showed that *M*. *minutiflora* is not a preferred oviposition site for FAW female moths when compared with maize (data not shown). It has been previously suggested that while some plants are more attractive for egg laying of noctuid insects (Renwick, 1989; Khan *et al*., 1997a; Sisay *et al*., 2023), other are rather repellent to female moths of these insects (Khan *et al*., 1997b); and the behavioral events leading to oviposition are, in part, mediated by plant volatiles (Renwick, 1989). Although, Ramaswamy (1988) proposed that generalist moths do not rely on plant volatiles to find a host, other studies have demonstrated the opposite (e.g. Bruce and Cork, 2001). Moreover, Rojas *et al*. (2018) reported that FAW females may not necessarily choose the best or worst host plants for their eggs. Meanwhile, the larvae may further search for better hosts not randomly, with third instar larvae apparently relying on visual cues. Thus, there are several other plant factors such as chemical, visual, and tactile cues that should be further evaluated to better understand the acceptance of a plant for oviposition by female FAW moths.

In conclusion, out of the grass cultivars tested in the current study, only *P. purpureum* supported FAW larvae development, which may serve as a temporary host for FAW. The cereal cultivars tested were found to be more suitable than the grass genotypes. The hybrid cereals *Z. mays* HB WH505, *P. glaucum* Nutrifeed and the landrace *S. bicolor* cv. Serena were the best host plants. *Pennisetum* ex. Sengerema performed as one of the poorest food plants for FAW larvae, as well *P. maximum* ex. Machakos, *B. brizantha* and *Brachiaria* ex. Mwanza. Although, *S. bicolor* cv. Ochuti and *S. bicolor* cv. Andiwo are suitable hosts for FAW larvae development, they caused high mortality. We suggest that *S. bicolor* cv. Ochuti could be tested as a trap plant for FAW eggs, since this sorghum cultivar received as much egg deposition as hybrid *Z. mays* and *P. glaucum*, but there was a high level of larval mortality. The species *M. minutiflora* and *S. bicolor* cv. Andiwo tended to receive fewer eggs than the other plants tested. These plants deserve to be studied as potential repellent species for FAW female moths. As mentioned above, *M. minutiflora* is also a potential trap plant for young larvae. Our results support further study of potential antibiosis effects of the sorghum cultivars Gadam, Ochuti and Andiwo, and the grass *M. minutiflora* against FAW.

Our results provide insights into how grasses and cereals cultivated in Kenyan agroecosystems can impact FAW development and populations. Nevertheless, additional research in choice-tests is necessary to explore how specific grasses (e.g., *M. minutiflora*) and cereals (e.g., *S. bicolor* cv. Andiwo and *S. bicolor* cv. Ochuti) can be integrated into managed biodiverse farming systems. They could serve as companion crops alongside maize or other crops, potentially acting as repellent or trap plants for FAW in its new African habitat.

CONFLICT OF INTEREST

The authors have no competing interests to declare that are relevant to the content of this article.

ETHICS STATEMENT

The authors confirm that the research meets any required ethical guidelines, including adherence to the legal requirements of the study country.

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AUTHOR CONTRIBUTIONS

XCM, ISS, DC, AT, TJAB, CAOM and ZK contributed in conception and design of the experiments; XCM and ISS contributed in acquisition, analysis and interpretation of data; XCM drafted the manuscript; ISS, DC, AT, TJAB, CAOM and ZK contributed in revising the manuscript.

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DATA AVAILABILITY

The data are available from the corresponding author upon reasonable request.

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