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Eco-friendly management of fall armyworm: can host-plant intercropping drive to a sustainable IPM?

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ABSTRACT

Although over 350 species of plants have been documented to host the fall armyworm (FAW), *Spodoptera frugiperda* (Lepidoptera: Noctuidae), its invasion in West Africa has been mainly on maize. This study investigated the factors that limit the host utilization and tested the effects of intercropping of Poaceae (maize, sorghum, rice and Proso millet), Solanaceae (tomato and sweet pepper), and Fabaceae (cowpea and soybean) plants on FAW severity. The laboratory larvae fed with those crops showed higher pupation rates for maize (33.6%) than sorghum (20%), rice (24.2%), Proso millet (17.6%), tomato (fruit = 5.3% and leaf = 6 .4%), sweet pepper (fruit $= 1.3\%$ and leaf $= 1.6\%$). Only larvae fed with Poaceae plants reached the adult stage. Female ovipositional potentiality was higher with maize compared to other Poaceae plants. In the field experiments, FAW severities were recorded only on Poaceae plants. However, the severity of FAW was significantly reduced on the intercropped maize with other crops compared to monocultures of maize. Therefore, intercropping can be considered as an eco-friendly FAW-IPM program in West Africa.

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KEYWORDS *Spodoptera frugiperda*; reproduction; survival; developmental stage; severity; control

1. Introduction

The polyphagous insect fall armyworm (FAW), *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae), is a pest of many crops of economic importance in its native Americas. Unfortunately, it has been spread to different regions of the globe from Western Africa to Asia and Oceania (Cock et al. [2017;](#page-8-0) Nagoshi et al. [2017,](#page-9-0) [2018,](#page-9-1) [2019,](#page-9-2) [2020;](#page-9-3) Ganiger et al. [2018;](#page-8-1) Sharanabasappa et al. [2018;](#page-9-4) Industries DoP [2020;](#page-8-2) Sun et al. [2021](#page-9-5)). Its diverse host plants coupled with the high dispersal ability of its adults has been increasing risks for global agricultural production as well as food and nutritional security.

The FAW host range covers over 350 species of plants (Montezano et al. [2018](#page-9-6)). This large host range may result from the genetic and physiological differentiations between the two FAW host strains corn (C) and rice (R), which interbreed into rice (female) corn (male) (RC) and rarely corn-rice (CR) hybrid offspring (Pashley [1986](#page-9-7); Pashley et al. [1987](#page-9-8); Nagoshi and Meagher [2022](#page-9-9)). However, C-strain is mainly associated to maize, sorghum, and other tall grasses,

and the R-strain is associated to rice, pasture grasses and other small grasses (Pashley [1988;](#page-9-10) Meagher and Nagoshi [2004](#page-8-3); Nagoshi and Meagher [2004;](#page-9-11) Nagoshi et al. [2007;](#page-9-12) Juárez et al. [2012;](#page-8-4) Murúa et al. [2015](#page-9-13)). Generally, FAW is attracted to plants that are considered as global economic and nutritional value crops and need to be under seasonal monitoring programs. Unfortunately, the unexpected invasion of FAW occurred in West Africa, followed by rapid spread across the continent and into Asia and Oceania (Tay et al. [2023](#page-10-0)).

To establish a list for crops at risk, tests for FAW host strains were conducted on samples from different newly invaded regions (Nagoshi et al. [2017](#page-9-0), [2018](#page-9-1), [2020](#page-9-14), [2022\)](#page-9-15). Primarily C-strain has been detected to date (Nagoshi et al. [2017](#page-9-0), [2021](#page-9-16); Koffi et al. [2021](#page-8-5)), despite a possible new introduction of FAW into West Africa discovered in 2018 (Nagoshi et al. [2022](#page-9-17)). Considering the host range for the C-strain and the high infestation level recorded during the first invasion years (Koffi et al. [2020a](#page-8-6), [2020b](#page-8-7), [2022](#page-8-8)), many crops may be at risk. However, only maize is generally damaged by FAW larvae although adults were trapped in the agroecosystems of maize, sorghum,

© 2024 Informa UK Limited, trading as Taylor & Francis Group **CONTACT** Djima Koffi **&** kdeskos@gmail.com **@** West African Center for Applied Research and Innovation, Lomé, Togo rice, and pasture grass in the West African countries of Togo and Ghana (Koffi et al. [2020a,](#page-8-6) [2020b,](#page-8-7) [2021](#page-8-9)). This may be due by chance of long flights from maize habitats (Mitchell et al. [1991;](#page-9-18) Nagoshi and Meagher [2008](#page-9-19); Nagoshi et al. [2012,](#page-9-20) [2014](#page-9-21)).

However, the polyphagous status of FAW combined to the captures of adults in all agroecosystems could be considered as an opportunity for infesting many suspected plants. This absence of infestations in some traditionally host plants, can be used as a management strategy to limit damage to important crops. That may be the baseline for the different push–pull technology (PPT) strategies, and intercropping systems to manage insect pests (Hailu et al. [2018](#page-8-10)). Since its invasion in Uganda, maize intercropping with leguminous crops was recommended to reduce the incidence of FAW on maize (Hailu et al. [2018](#page-8-11)). However, the role of leguminous crops is not yet investigated although the efficacy of intercrops can have both bottom–up and top–down effects. Therefore, this study investigated the interactions effects between FAW and plant species from Poaceae, Solanaceae, and Fabaceae families, and explored the impact of intercropping on the incidence and severity of FAW on maize.

2. Materials and methods

2.1. Plants and study sites

The study was conducted using plants from Poaceae (maize, *Zea mays* L., sorghum, *Sorghum bicolor* (Moench), rice, *Oryza sativa* L., and Proso millet, *Panicum miliaceum* L.), Solanaceae (tomato, *Solanum lycopersicum* L. and sweet pepper, *Capsicum annuum* L.), and Fabaceae (cowpea, *Vigna unguiculata* (L.) Walp. and soybean, *Glycine max* (L.) Merr.). The no-choice feeding bioassays were conducted in the laboratory at Ecole Supérieure d'Agronomie, Université de Lomé, Lomé, Togo, to assess FAW survival capacities and reproductive performances of adults on different crops. Artificial infestation of plants was conducted in the semi-field trials in screen houses (plots of $1.5 \text{ m} \times 2 \text{ m}$ covered by net that contained L1 FAW larvae). Finally, the on-station field experiments of monocropping and intercropping were conducted during three consecutive seasons: September–December 2021 (Period 1), January–April 2022 (Period 2), and May–August 2022 (Period 3). Both the semi-field and field experiments were conducted at the Station d'Expérimentations Agronomiques de Lomé (SEAL). SEAL is a portion of land within the Université de Lomé located in the Agro-Ecological Zone five (AEZ 5), which is characterized by small, wooded forest mixed with coastal savannah of southern Togo (Koffi et al. [2020a](#page-8-6)).

2.2. Performance of FAW fed with plant species

Newly hatched larvae $(\leq 24h$ -old) of the second generation from our laboratory mass-rearing were fed leaves of the eight crops (maize, sorghum, rice, Proso millet, tomato, sweet pepper, cowpea, and soybean) and fruits of tomato and sweet pepper until pupation or death of the larva. This second generation was obtained from the mass-rearing of eggs collected from maize at SEAL, where larvae were previously fed maize leaves and adults provided 10% diluted honey. The survival tests were conducted using seven larvae for each crop with five replications for three generations. For the plants where no adults were produced during the F1, the same F1 tests were repeated three times instead of three consecutive generations. The numbers of surviving larvae were recorded daily, then the numbers of pupae and emerged adults were counted. The survival rates were calculated after 24, 48, and 72h feeding of larvae, and then for pupation and emerged adult rates. The reproductive capacities of emerged females were determined by counting the number of eggs laid per female.

2.3. Survival and reproduction of FAW under controlled field

Nine shaded screen houses of $4m^2$ each, were designed to host a monocrop of the eight crops mentioned above and a mixture of the eight crops (containing five plants each species). The screen houses were designed to transplant or germinate plants using natural soil. The screen house nets used is a 100D, 24 holes per cm² of 100% polyester (L4.0 \times W4.0 \times H2.5 m) (Vestergaard Group SA, Vietnam), and locally manufactured for this study (Koffi et al. [2022](#page-8-12)). A week after plants were transplanted or germinated, two male and three female moths between 24 and 48h old were released into each screen house. The new plants were transplanted or seeded every three weeks to conserve fresh leaf tissue for larval feeding. After 5 weeks, plants were cut down and kept in their screen houses to avoid possible losses of small larvae. Data were collected weekly for egg masses and larvae per plant, and adults in screen houses for three FAW generations, including the screen house which hosted the mixture of the eight crops.

2.4. Population densities and severity in monoand intercropping systems

The field experiments were conducted in two different parcels that held each monocropping and inter-cropping plots [\(Figure 1](#page-3-0)). Plots were $3m \times 3m$ (9m2) designed with plants separated within and between rows by 0.5m. A randomized complete

[Figure 1.](#page-2-0) On-station design of mono-cropping and intercropping parcels with plots of 9m² separated by 2m within and between blocks. The green dots represent the growing plants while the yellow dots represent the intercropping of maize with other crops.

block design (RCBD) with five blocks was used during three consecutive seasons. Although maize was intercropped with other crops, it served as a monocrop as control in the intercropping parcels. Proso millet, tomato, and sweet pepper were transplanted on the same dates, whereas other crops were seeded according to their germination time to provide fresh plant leaves at the same time point. Ten days after plants were transplanted or seeded, 10 plants of each crop within each plot were randomly selected and permanently marked. The marked plants were then each artificially infested with one 3rd instar larva obtained from the laboratory cultures. Data were collected weekly from the 10 artificially infested plants, and at the same time, 10 other plants of each crop were selected for sampling of natural infestations. The collected data included numbers of egg masses and larvae per plant, number of damaged leaves and plants, and damage scores caused by FAW.

2.5. Calculations and data analysis

After the numbers of egg masses, larvae, damaged plants, damaged leaves, alive larvae, pupae, and emerged adults were recorded, indexes were calculated in Excel according to:

$$
d = \frac{t}{T} \tag{1}
$$

or

$$
p = \frac{n}{N} * 100,\tag{2}
$$

where $d =$ number of egg masses or larvae per plant, *t* = number of egg masses or larvae counted and *T* = total number of selected plants. For percent damaged plants or leaves (p) , $n =$ number of damaged plants or leaves and *N* = total number of selected plants or leaves on plants. For percent alive larvae (p) , $n =$ number of alive larvae and $N =$ total number of larvae used to start the bioassay. For pupation rate (p) , $n =$ number of pupae and $N =$ total number of larvae used to start the bioassay. For emerge rate of adults (p) , $n =$ number of emerged adults and $N =$ total number of larvae used to start the bioassay.

The damage scores, numbers of eggs per female and measured variables were grouped per host plant. The percentage data were arcsine square root transformed prior to statistical analysis. All data were placed in Microsoft Excel edition 2013 before being submitted to a Shapiro test for normality in GenStat Twelfth Edition, GenStat Procedure Library Release PL20.1. Normal data were submitted to one-way analysis of variance, and the non-normal data to a non-parametric test (Kruskal–Wallis). Multiple means were compared and separated with the Tukey test, whereas the *t*-test was applied for two means at 95% confidence in GenStat Twelfth Edition GenStat Procedure Library Release PL20.1.

[Figure 2.](#page-4-1) Larval surviving rates after 24, 48, and 72; percentage of population that pupated and emerged as adults for FAW fed with leaves of maize, sorghum, rice, Proso millet (panicum), tomato and sweet pepper (fruit and leaf), cowpea (bean), and soybean. Means within each crop, stage, and generation with the same letter are not significantly different (*p*>.05).

3. Results

3.1. Performance of FAW fed with different plant species

No-choice feeding from the first instar larvae on different crops provided significant differences for the larval survival rates after 24, 48, and 72h, pupae and emerged adults during three consecutive generations of laboratory rearing ([Figure 2\)](#page-4-0). The highest survival rates were recorded with larvae that fed on maize leaves. Larval survival rates were similar for sorghum, rice and Proso millet during the first generation (F1), and were higher than fruits and leaves of Solanaceae plants (tomato and sweet pepper) and Fabaceae plants (cowpea and soybean). Very few larvae fed Solanaceae and Fabaceae plants developed to the pupal stage, but no adults emerged from these pupae F1 [\(Figure 2](#page-4-0)). During the second generation (F2) trials, larvae used for the Poaceae plants were from adults fed during the F1, whereas larvae used for the Solanaceae and Fabaceae plants were from the laboratory cultures. Survival rates of larvae fed with small Poaceae plants (rice and Proso millet) were significantly decreased and were similar to rates for larvae fed Solanaceae and Fabaceae plants. Larvae fed maize recorded the highest survival rate followed by sorghum, and only FAW fed on maize, sorghum, and Proso millet reached the adult stage ([Figure 2](#page-4-0)). For the F3 trials, larvae fed maize and sorghum were descendants of the F1 generation through the F2 generation, larvae fed Proso millet were from the F2 generation, and L1 larvae had to be introduced from the laboratory cultures to feed rice, Solanaceae and Fabaceae plants. Surprisingly, the survival rates of FAW fed Proso millet statistically increased to the level of sorghum, but both were still lower than the rates in maize. From the newly hatched larvae to adults the survival rates were observed only on Poaceae plants that recorded 26.3 to 28.7% for maize, 12.3 to 14.4% for sorghum, up to 10.2% for rice, and 4.6 to 9.6% for Proso millet. Larvae fed on Solanaceae and Fabaceae plants didn't reach adult stage in any generation [\(Fig 2](#page-4-0)). The mean number of eggs per female for the three generations were highest on maize (326.7 ± 17.3) , followed by sorghum (109.6±12.8), Proso millet (72.8 ± 8.3) , and rice (43.5 ± 7.4) (df = 3.119; $F=8,35$; *p=*.017).

3.2. Population increases on plants under controlled field conditions

When the experiments were extended to the field-controlled screen houses, plants were infested with FAW adults. In monocropping systems, only females on maize and sorghum plants oviposited, produced larvae and plant damage, and had emerged adults during the three generations (F1, F2, and F3). Although the other crops were initially infested at the beginning of each generation, FAW populations did not increase. The screen house containing maize recorded the highest FAW densities (numbers of egg masses and larvae per plant), damages (damage scores), and emerged adults ([Figure 3](#page-5-0)).

When FAW was in a screen house containing all eight plants, egg masses, larvae, and emerged adults were recorded. The number of emerged adults in the combined-plant plots was lower than the number of emerged adults in the monocropped maize plots $(7.1 \pm 0.1 \text{ vs. } 14 \pm 0.3; \text{ df} = 29; \ p = .017)$. However, the number of emerged adults in the combined-plant plots was higher than the number recorded on sorghum (3.3±0.1) (df = 29; *p*=.036). In the combined-plant plots, egg masses were only observed on maize plants during the three generations [\(Table](#page-6-0) [1](#page-6-0)); however, very low numbers of larvae and plant

[Figure 3.](#page-4-2) The number of egg masses per plant (A) and larvae per plant (B), damage scores (C), and emerged adults (D) from the screen houses hosting maize, sorghum, rice, Proso millet (panicum), sweet pepper, tomato, cowpea (bean), and soybean plants during three FAW generations. Means within the same crop, life stage, and period that are the same are not significantly different $(p > .05)$.

damage were recorded on sorghum [\(Table 2](#page-7-0)). Finally, no egg masses, larvae, or damage were found on Proso millet, rice, tomato, sweet pepper, cowpea, or soybean in the combined-plant plots ([Table 2](#page-7-0)).

3.3. FAW populations and severity in mono- and intercropping systems

The monocropping field experiments exposed to natural infestations had egg masses only on maize, sorghum, and Proso millet, with the highest egg masses per plant on maize. Although egg masses were observed on these three Poaceae, larvae and feeding damage were observed only on maize and sorghum. However, the density of larvae, percent damaging plants and leaves, and damage scores were higher on maize than on sorghum [\(Table 2\(A\)](#page-7-0)). In the artificially infested plants by L3 larvae (1 larva per plant), only maize and sorghum recorded live larvae, and these means were less than 0.2 larva per plant each. Although larvae were not found in the artificially infested rice and Proso millet, plant damage was observed but was numerically lower than damage on sorghum ([Table 2\(A\)](#page-7-0)).

In the intercropping systems, egg masses were observed mainly on maize, with only one egg mass found on Proso millet. The control parcel (monocropped maize) recorded the highest number of egg masses per plant, while maize mixed with other crops had similar numbers of egg masses. Sorghum plants contained few larvae per plant even though no egg masses were found, compared to Proso millet which had no larvae even though an egg mass was found. The number of larvae per plant was higher in the monocropped maize plots than on maize in the intercropped plots. Damaged plants were only observed in plots that contained maize or sorghum; however, damage in the sorghum-only plots were very low.

| sweet pepper, cowpea, and soypean. | | | | | | | | | |
|------------------------------------|----------------------|-----------------|------------------|-------------------|-------------------|-------------------|-------------------|-------------------|--------------------|
| Crop | Egg masses per plant | | | Larvae per plant | | | Damage scores | | |
| | F1 | F ₂ | F3 | F1 | F ₂ | F ₃ | F1 | F ₂ | F ₃ |
| Maize | $0.72 \pm 0.12b$ | 0.56 ± 0.05 | $1.13 \pm 0.32b$ | 1.06 ± 0.12 b | 2.14 ± 0.23 b | 2.17 ± 0.52 b | 3.21 ± 0.68 b | 2.18 ± 0.42 b | 4.65 ± 1.05 b |
| Sorghum | 0.00a | 0.00a | 0.00a | $0.01 \pm 0.02a$ | $0.05 \pm 0.03a$ | $0.02 \pm 0.03a$ | $0.03 \pm 0.02a$ | $0.15 \pm 0.03a$ | 0.09 ± 0.03 ab |
| Proso millet | 0.00a | 0.00a | 0.00a | 0.00a | 0.00a | 0.00a | 0.00a | 0.00a | 0.00a |
| Rice | 0.00a | 0.00a | 0.00a | 0.00a | 0.00a | 0.00a | 0.00a | 0.00a | 0.00a |
| Tomato | 0.00a | 0.00a | 0.00a | 0.00a | 0.00a | 0.00a | 0.00a | 0.00a | 0.00a |
| Sweet pepper | 0.00a | 0.00a | 0.00a | 0.00a | 0.00a | 0.00a | 0.00a | 0.00a | 0.00a |
| Cowpea | 0.00a | 0.00a | 0.00a | 0.00a | 0.00a | 0.00a | 0.00a | 0.00a | 0.00a |
| Soybean | 0.00a | 0.00a | 0.00a | 0.00a | 0.00a | 0.00a | 0.00a | 0.00a | 0.00a |
| Df (treatment, total) | 7.39 | 7, 39 | 7, 39 | 7, 39 | 7, 39 | 7, 39 | 7, 39 | 7, 39 | 7, 39 |
| F | 9.12 | 7.23 | 12.39 | 4.62 | 8.38 | 9.51 | 13.09 | 11.25 | 15.38 |
| Р | < 0001 | < .0001 | < .0001 | .003 | .001 | < .0001 | < .0001 | < .0001 | < .0001 |

[Table 1.](#page-4-3) Number of egg masses, larvae and damage scores per plant, and emerged adults in the screen houses infested with three females and two males of FAW, and containing five plants of each crop of corn, sorghum, Proso millet, rice, tomato, sweet pepper, cowpea, and soybean.

Means in the same column with the same letter are not significantly different $(p > .05)$

Plant damage was highest in maize-only plots, followed numerically by maize-rice, maize-sorghum, and maize-Proso millet plots [\(Table 2\(B\)\)](#page-7-0).

4. Discussion

Insect pests have been managed based on their communications, responses, and behaviors to their environments. The recent dissemination of FAW into new regions of the globe has been surprisingly limited to the C-strain (Nagoshi et al. [2017](#page-9-22), [2018](#page-9-23), [2021](#page-9-24)). Correspondingly, since its invasion in West Africa, infestations have been limited mainly to maize, and sporadically on sorghum (Goergen et al. [2016;](#page-8-13) Cock et al. [2017;](#page-8-14) Koffi et al. [2020a,](#page-8-15) [2020b](#page-8-7)). But factors that limit host plant utilization in West Africa for the C-strain which has preference for high grasses is still unknown. Therefore, this study investigated and highlighted the reproductive, survival, behavior and damage capacities of the current West African FAW population on crops from the families of Poaceae, Solanaceae and Fabaceae. Moreover, it tested an eco-friendly management strategy by intercropping maize plants with Poaceae (sorghum, rice and Proso millet), Solanaceae (tomato and sweet pepper), and Fabaceae (cowpea and soybean) crops.

Experiments from this study highlight FAW preference for maize and suggest sorghum as an alternative host in the absence of maize in the field as found in previous studies from Florida, US (Meagher et al. [2004\)](#page-8-16). However, our study showed that infestations on sorghum can produce high larval mortality for the first generation and limit FAW population increase or severe outbreaks. But, if only sorghum is continuously planted, adaptation of FAW to this plant as a main host can occur (Anderson and Cherry [1983;](#page-8-17) Chamberlin and All [1991;](#page-8-18) Portillo et al. [1991\)](#page-9-25). Proso millet and rice can also be considered as candidate alternative crops in the absence of maize and sorghum, as these plants can maintain low FAW population levels. However, Poaceae plants can serve as low level hosts in between maize seasons, producing populations that will later infest the maize crop. Therefore, farmers, in regions of overlapping maize seasons or short times between seasons, should consider intercropping with Solanaceae (tomato and sweet pepper) or Fabaceae (cowpea and soybean) crops. These intercrops appear to have low risk of infestation by the current population of FAW that is in West Africa. Solanaceae and Fabaceae crops had also been reported to not be threatened by FAW in Florida, US (Meagher et al. [2004,](#page-8-16) [2022](#page-8-19)).

Unsuccessful development of FAW on Solanaceae and Fabaceae plants justify its limitation for the host plants utilizations in West Africa. However, the mechanism of female moths not recognizing these plants as hosts was not studied. Herbivorous insects interact with plants for shelter, food, and reproduction (Bruce et al. [2005](#page-8-20)) and acceptance of the host plant by the insect is crucial and can vary under different environmental, nutritional or secondary metabolite conditions (Ton et al. [2007](#page-10-1); Bruce and Pickett [2011;](#page-8-21) Jinwon et al. [2011](#page-8-22); Martin et al. [2011](#page-8-23)). The choice of the perfect host can be determined by the physical appearance of the plant or volatiles released (Riffell et al. [2009;](#page-9-26) Webster et al. [2010](#page-10-2)). Although insects' nervous system and capacity to learn affect their interactions with plants (Cunningham et al. [2004](#page-8-24); Bruce and Pickett [2011](#page-8-25); Webster et al. [2013](#page-10-3)), cues from some plants (especially the Fabaceae and Solanaceae) used during this study may not be perceived as hosts by local FAW populations. Therefore, intercropping these plants with maize can be suitable for an eco-friendly management of this herbivorous insect. This concept of using intercrops or push-pull systems has had some success in both in the Western Hemisphere (van Huis [1981](#page-10-4)) and in Africa (Njuguna et al. [2021](#page-9-27); Scheidegger et al. [2021](#page-9-28)). Fortunately, the intercropping of maize with the other seven plants reduced

Table 2. Population densities and damage levels of FAW in artificial infested and natural exposed plants in mono-cropping and intercropping systems. **[Table 2.](#page-5-1)** Population densities and damage levels of FAW in artificial infested and natural exposed plants in mono-cropping and intercropping systems.

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FAW severity on maize. However, the level of reduction varies according to the plant intercropped. For example, plant damage in maize–soybean and maize–cowpea plots were numerically the lowest, which demonstrates a promising management strategy by intercropping maize with Fabaceae plants. Although this intercropping technology did not compare the level of damage reductions with the economic threshold, leguminous were also recommended to being intercropped with maize to manage FAW (Tanyi et al. [2020;](#page-10-5) Wu et al. [2022](#page-10-6)). Therefore, it can be considered as one of the key elements for FAW-IPM.

Disclosure statement

No potential conflict of interest was reported by the author(s).

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