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# Influence of agricultural practices on *Spodoptera frugiperda* (JE Smith) infestation, natural enemies and biocontrol in maize

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**Abstract.** Maize (*Zea mays* L.) production in Africa is threatened by the recent invasion of the fall armyworm (FAW), *Spodoptera frugiperda* (JE Smith). The management of this pest is laborious and requires effective, sustainable and environmentally friendly control approaches. The present study investigated the natural enemies associated with *S. frugiperda* in maize fields through three climatic zones in Benin. Besides, the impact of different agricultural practices on its infestation and the performance of biocontrol agents were assessed. Larvae were collected from 67 maize fields and transferred to the laboratory, incubated and monitored for parasitoid emergence. The complex of natural enemies recorded in this study consisted of: entomopathogenic fungus *Metarhizium* sp., nematode *Hexameris* sp. and parasitoids *Chelonus bifoveolatus*, *Coccygidium luteum*, *Charops* sp. and *Drino quadrizonula*. The results revealed that maize fields sown after soybean or cotton crops and those in which insecticides and herbicides were applied were associated with higher FAW infection rates by *Metarhizium* sp. The use of agricultural inputs led to lower FAW parasitism by *Hexameris* sp. Regarding FAW infestation, the probability of high damage scores was higher in maize fields cultivated after fallow or cotton crops and in fields with mixed crops or those in which herbicides or relatively high fertilizer rates were applied. These findings provide several insights on the interaction between agricultural practices and FAW natural enemies that can be used for the implementation of an effective integrated management system for this pest in Benin or Africa.

**Keywords:** Fall armyworm, maize, infestation, agricultural practices, entomopathogenic fungi, nematodes, endoparasitoids, Benin.

## INTRODUCTION

Maize, *Zea mays* L., (Poaceae) is an important staple food and cash crop in Sub-Saharan Africa (SSA). Unfortunately, its production is threatened by the invasion of fall armyworm (FAW), *Spodoptera frugiperda* (Lepidoptera: Noctuidae) since 2016 (Day *et al.*, 2017; Goergen *et al.*, 2016). FAW is an exotic pest native to tropical and subtropical regions of the Americas (Andrews, 1980). Its invasion pathway in Africa is still unknown but molecular characterization results suggest that the ecotype present in Africa originated from Florida and the Caribbean (Huesing *et al.*, 2018). FAW larvae attack all the aerial parts of maize plants (Kasoma *et al.*, 2020). The defoliation caused by larval feeding affects plant yield and its effect is most detrimental at the early stage of maize plants (Hruska, 2019). In Africa, yield losses in maize caused by FAW during the 2016-2017 agricultural campaign were estimated at 13.5 million tons (or 17% of total production) representing approximately US\$ 3 billion (Abrahams *et al.*, 2017). In Benin, findings by (Houngbo *et al.*, 2020) that estimated these yield losses at 797 kg/ha, representing ~49% of the average farmer's production.

Currently, chemical pesticides are the main control strategy for this serious pest in several African countries (Kumela *et al.*, 2018). In this context, surveys of maize farmers in several SSA countries revealed that farmers rely on many synthetic pesticides to control FAW attacks (Houngbo *et al.*, 2020; Kumela *et al.*, 2018; Togola *et al.*, 2018). Although the efficacy of some chemical insecticides in FAW management has been shown, their indiscriminate use by farmers has led to poor results (Baudron *et al.*, 2019). Oftentimes, the presence of larvae deep inside the maize whorl prevents their contact with the pesticide and reduces its efficacy (Cook *et al.*, 2004). Besides, several studies showed the resistance of this pest to a wide range of conventional pesticides as well as transgenic crops (Bernardi *et al.*, 2017; Carvalho *et al.*, 2013; Giraudo *et al.*, 2014; Miraldo *et al.*, 2016).

The effective control of this pest in Africa should be based on methods and techniques that can be compatible with integrated pest management programs and are sustainable (Aniwanou *et al.*, 2021). Most farmers have limited resources so cultural control methods are promising and are deemed to have relatively low risks for human health and the environment. Several agricultural practices that can help control pest populations such as (alteration of planting and harvesting dates, crop rotation, use of resistant cultivars, etc.) exist among smallholders in Africa (Baudron *et al.*, 2019; Kumela *et al.*, 2018), but empirical research addressing their efficacy against FAW is limited (Patient *et al.*, 2019; Tanyi *et al.*, 2020). Agro-ecological systems favor the use of environmental resources instead of chemical pesticides in pest control through natural enemies, biodiversity, natural plant resistance, etc. (Harrison *et al.*, 2019). Although FAW invasion is recent in African agricultural landscapes,

several native parasitoid species have been isolated from different developmental stages of the pest. These include *Trichogramma* spp., *Telonomus remus* Nixon and *Chelonus* spp., parasitizing FAW eggs and *Cotesia* spp., *Coccygidium luteum* (Brullé), *Charops* spp., *Drino quadrizonula* (Thomson) attacking the larvae (Agboyi *et al.*, 2020; Caniço *et al.*, 2021; Kenis *et al.*, 2019; Ogunfunmilayo *et al.*, 2021; Sisay *et al.*, 2018; Youssef, 2021). In addition, FAW is attacked by entomopathogenic fungi and nematodes; causing significant larval mortality rates (Ngangambe and Mwatawala, 2020; Tendeng *et al.*, 2019).

Agricultural practices can be used for crop protection directly or indirectly through conservation biological control. Therefore, some agricultural practices (e.g. crop rotation and intercrop) are carried out to reduce pests' incidence in crop production (Harrison *et al.*, 2019). In addition, many agricultural practices such as soil tillage, maintaining within-field diversity, nitrogen fertilization, etc. sometimes induce important changes to the environment (Mesmin *et al.*, 2020; Rusch *et al.*, 2017). In the field, these practices can variably influence the presence and abundance of natural enemies (Rusch *et al.*, 2017; Wood *et al.*, 2015), which are key elements for the success of cultural control strategies. The harmonious management of interactions between these practices and natural resources may determine the efficiency and balance of agroecosystems. Therefore, the present study was designed to investigate the effect of some agricultural practices on *S. frugiperda* infestation, its natural enemies and biocontrol.

## MATERIALS AND METHODS

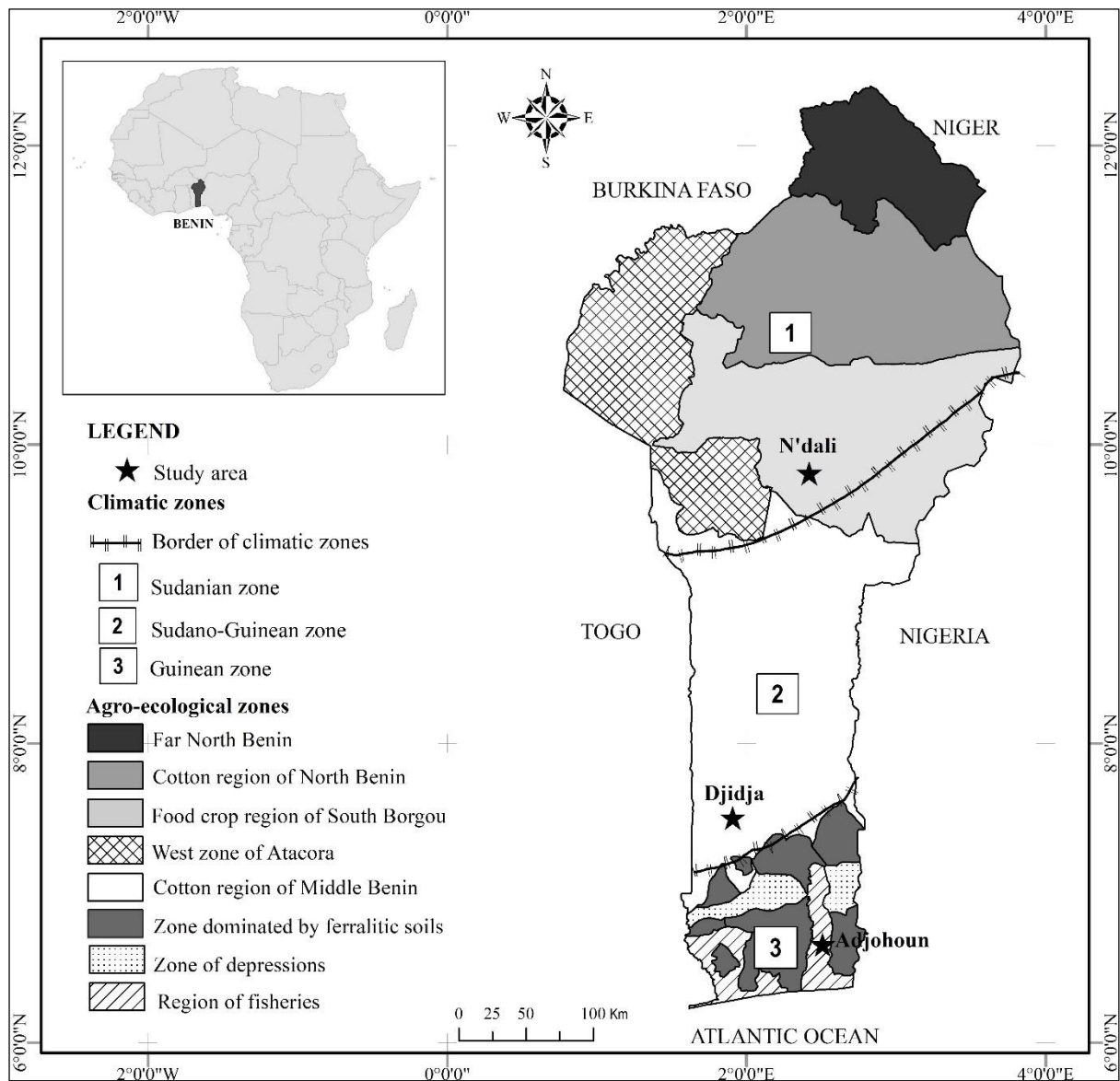
### Study area

This study was conducted from May to December 2019 in the districts of N'dali, Djidja and Adjohoun which are located in different agroecological zones spread through the three climatic zones of Benin (Figure 1).

N'dali has a continental climate of Sudanian type characterized by one rainy season and one dry season; Adjohoun has a Guinean climate with two rainy seasons and two dry seasons, while Djidja is a transitional area that has a Sudano-Guinean climate with two rainy and two dry seasons and tends towards the Sudanian type in the northern parts, where the two rainy seasons become almost one (Mensah *et al.*, 2014). The climatic characteristics of these three areas during 2019 are presented in (Figure 2).

### Field investigations

Field investigations were carried out during the rainy season from August to September in N'dali; from May to



**Figure 1.** Map of Benin showing the study area.

July and September to October in Djidja; and from mid-October to mid-November in Adjohoun (2019). Rainfall during the survey was 158.7 mm in Adjohoun and ranged from 120.5 to 206.2 mm in N'dali and 86.4 to 203.8 mm in Djidja (Figure 2). A total of 67 maize fields, randomly chosen, were sampled during the study: 22 in N'dali, 34 in Djidja, and 11 in Adjohoun. The selected field areas were  $\geq 0.25$  ha and their geographic coordinates were recorded by GPS (GPS<sub>MAP</sub> 78s, GARMIN, Lenexa, KS, USA). Data were collected in each maize field at the whorl stage, before panicle formation (V5-V10, 1.5 to 2 months after sowing) (Jepson *et al.*, 2018).

The level of FAW damage severity in maize fields was assessed using scores from a rating scale (4-score scale) adapted from Davis *et al.* (1992) (Table 1).

Observations were performed on 40 maize plants randomly selected along the diagonals of the fields. All plants were stripped to collect FAW larvae at different stages except stage 6 and the larvae were transferred to the laboratory. A total of 3810 larvae were collected, with 1323 larvae from N'dali, 1870 larvae from Djidja and 617 larvae from Adjohoun. The larvae were placed separately in plastic containers (3.8 cm diameter  $\times$  3.4 cm height) with perforated lids to avoid cannibalism and were provided with a few portions (2 to 4 g) of fresh maize leaves (Mutamiswa *et al.*, 2017; Sisay *et al.*, 2018).

In addition, a complete enumeration survey was carried out among all farmers of the selected maize fields to identify the agricultural practices adopted using questionnaires and interview guides. Data collected were

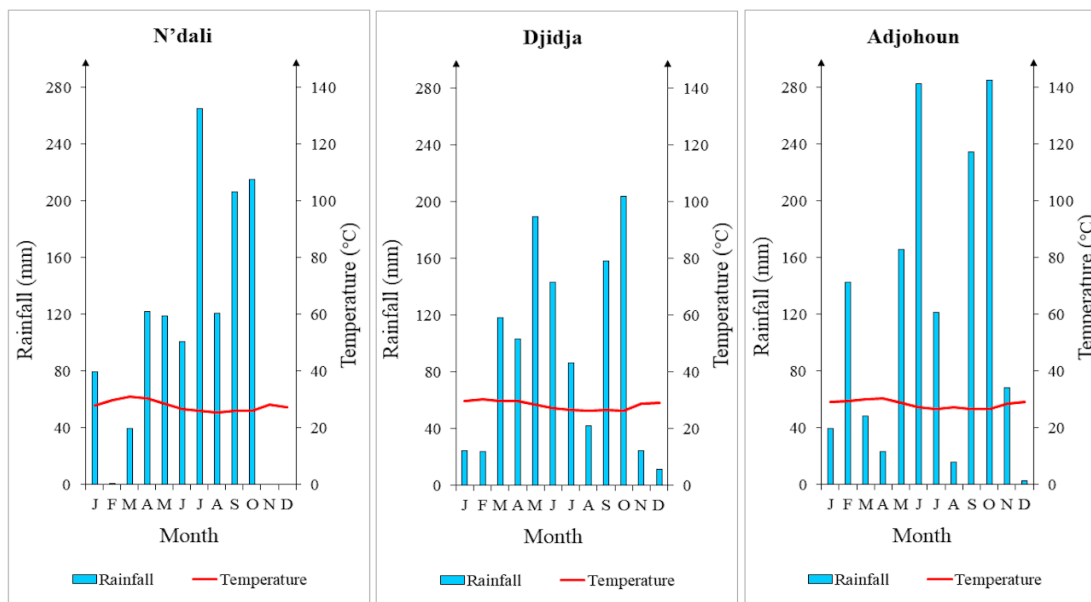


Figure 2. Umbro-thermal diagram 2019 of study area (from METEO BENIN)

Table 1. FAW damage rating scale for maize.

Score	Description
0	No visible leaf-feeding damage
1	Small superficial perforations on a few leaves
2	Several small and elongated perforations of up to 2.5 cm in length on several leaves (including rolled-up whorled leaves)
3	Several holes of all sizes (large, small and elongated) are present on several leaves (including rolled-up whorled leaves)
4	Rolled up whorled leaves and almost destroyed growing points which can lead to plant death due to considerable leaf damage

These scores were adapted from Davis *et al.* (1992).

related to the socio-demographic characteristics of the respondents, cropping systems and crop sequences, soil-tillage, sowing operations, weeding, and input supply practices (fertilizer and insecticide).

### Evaluation of FAW natural enemies' performance

To assess the performance of natural enemies, larvae collected from the field were reared separately in the laboratory ( $28 \pm 2^\circ\text{C}$ ,  $60 \pm 10\%$  relative humidity and a photoperiod of 12L:12D) to allow potential parasites to complete their development and emerge. They were fed daily with maize shoots. The emerging parasitoids were systematically preserved in 70% ethyl alcohol solution (Sisay *et al.*, 2018).

On the other hand, FAW larvae completed their development without being parasitized or infected with pathogens and were reared until pupation and moths' emergence. No natural enemies emerged from FAW pupae during the study.

The parasitism/infection rate (P) of FAW larvae was determined as follows (Caniço *et al.*, 2020):

$$P = \frac{np}{N}$$

Where  $np$  = The number of larvae killed by a natural enemy species;  $N$  = The total number of larvae collected - Number of dead larvae. Dead larvae due to transportation or other unknown reasons were not included in the calculations (Riggin *et al.*, 1992).

In addition, the frequency of occurrence (F.O.%) of FAW natural enemies was evaluated using the following formula (Dajoz, 1971):

$$\text{F.O.}\% = \frac{pi \times 100}{P}$$

$pi$  = The number of sites where the natural enemy was observed and  $P$  = The total number of sites.

The identification of the parasitoids was carried out at the Insect Museum of the International Institute of Tropical

Agriculture (IITA) in Benin. The nematode and the entomopathogenic fungus (EPF) were identified down to genus level (Firake and Behere, 2020; Hominick *et al.*, 1982; Mongkolsamrit *et al.*, 2020; Reboredo and Camino, 2019; Tendeng *et al.*, 2019; Visalakshi *et al.*, 2020).

### Data analyses

Statistical analyses were performed using the R statistical software, version 4.1.1 (R Core Team, 2021). In order to assess the similarity between the composition of natural enemies (entomopathogenic fungus, nematode and parasitoids) of *S. frugiperda* in the three climatic zones, a non-metric multidimensional scaling (NMDS) using Bray and Curtis (1957) distance was performed on the abundance matrix of FAW larvae parasitized or infected by the different natural enemies inventoried after standardizing the samples by bootstrap. This analysis was performed using the *metaMDS* function of the *vegan* library (Oksanen *et al.*, 2019). An analysis of similarities (ANOSIM) test was performed to check if a statistical difference exists between communities of FAW natural enemies in these climatic zones.

For the effect of agricultural practices on FAW natural enemies, mixed-effects binary logistic regressions were used. In these regression models, the response variable was “infected/parasitized or not by a natural enemy species”, the explicative variables were the agricultural practices, and the random factor was the climatic zone. Tukey’s pairwise comparison test was performed to separate the different means. Ordinal logistic regressions with mixed effects were performed using the *ordinal* library (Christensen, 2019) to assess the effect of agricultural practices on the severity of FAW damage. The response variable was damage severity, while the explicative variables and the random factor in these regression models were the same as in the binary logistic regressions. The values of the response variable predicted by the models were generated to construct histograms describing the probabilities of the different severity levels according to the modalities of the factors. To evaluate the relationships between FAW biocontrol and its field infestation, a linear Spearman correlation was performed.

## RESULTS

### Plot characteristics and agricultural variables in three climatic zones

The maize fields in the present study were large in the Sudanian zone (4.81 ha on average), of medium size in the Sudanese-Guinean zone (1.03 ha on average) and small in the Guinean zone (0.50 ha on average) (Table 2). Maize was grown in the previous season in 9 to 26% of

cases; the main crop rotation with maize was soybean in the Sudanian zone and cowpea in the other climatic zones. Tillage was carried out in most of the surveyed fields (95%). Moreover, mechanized tillage was dominant in the Sudanian zone, while traditional tillage was more present in the other climatic zones. Intercropping was marginal (11%) and it was often practiced with millet, cowpea, groundnut and squash crops. In the Guinean zone, intercropping was more common (36%) than in the other climatic zones (5 and 9%). All farmers applied mineral fertilizers (NPK and/or urea) at an average rate of 214 kg/ha in the Sudanian zone; the majority (71%) applied them in the Sudano-Guinean zone but at a lower average rate (167.39 kg/ha) while only 45% applied fertilizers in the Guinean zone at an even lower average rate of 150 kg/ha). Staggered seeding was not used in any field in the Sudanian zone, but in the two other climatic zones, it was present on half of the fields. Regarding pesticides (herbicides and insecticides), several active ingredients from different chemical families were applied in the fields. Herbicides were applied in most fields (95%) in the Sudanian zone and a few fields in the other two climatic zones (9 and 26%). The majority of the fields (88%) in the three climatic zones did not receive an insecticide dose.

### FAW natural enemies in the studied climatic zones

Four parasitoid species (ichneumonid *Charops* sp., braconids *Chelonus bifoveolatus* Szépligeti and *Coccygidium luteum* (Brullé) and tachinid *Drino quadrizonula* (Thomson)), one EPF (*Metarhizium* sp.; *Clavicipitaceae*) and one mermithid nematode species (*Hexameris* sp.) were identified during this study. *Charops* sp. and *C. bifoveolatus* were recorded in all three climatic zones (4.5 to 27.3% and 9.1 to 47% of the fields, respectively), while *C. luteum* and *D. quadrizonula* were observed only in the Sudanian and Sudano-Guinean zones (2.9 to 54.5% and 4.5 to 8.8% of the fields, respectively). On the other hand, *Metarhizium* sp. was observed exclusively in the Sudanian zone (95.5% of the fields), while *Hexameris* sp. was in the Sudanian and Sudano-Guinean zones (47 and 36.4% of the fields, respectively; Figure 3).

The NMDS stress value was less than 0.2, confirming the effectiveness of the ordination analysis (Thomas *et al.*, 2013). The analysis of similarity ANOSIM revealed a significant dissimilarity between species communities of FAW natural enemies in the three climatic zones ( $R = 0.99$ ;  $P < 0.001$ ) (Figure 4).

### Effect of agricultural practices on FAW natural enemies

The results (Table 3) exhibited that maize fields sown after cotton or soybean crops were associated with significantly

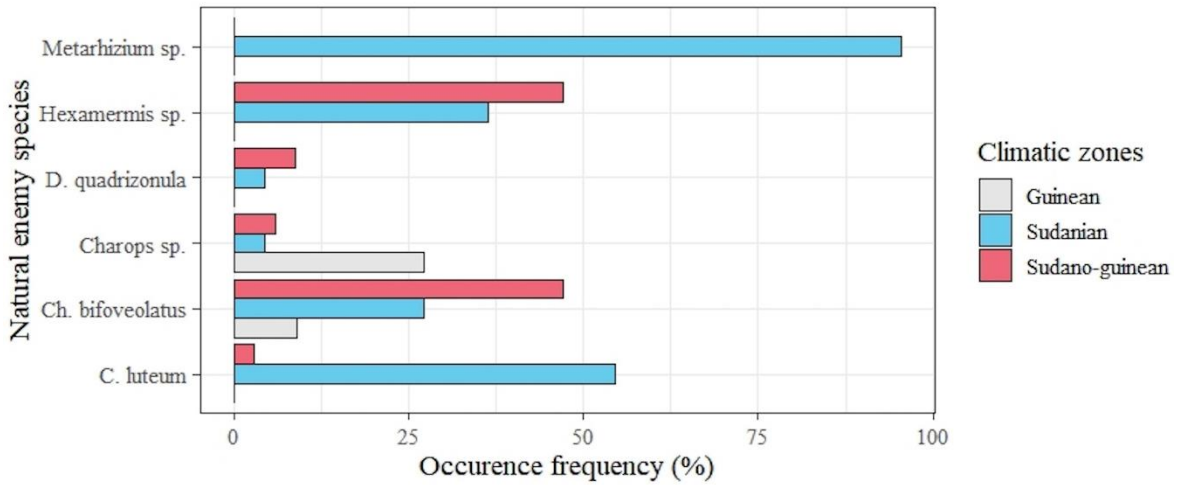
**Table 2.** Plot characteristics and agricultural variables in three climatic zones in Benin.

Plot characteristics	Sudanian zone	Sudano-Guinean zone	Guinean zone	Total	More information
Plot size (ha)	4.81 ± 1.05	1.03 ± 0.09	0.50 ± 0.12	2.18 ± 0.41	
Previous crop (%)					
Cotton	18.18	17.65	0.00	14.93	
Cowpea	0.00	32.35	36.36	22.39	
Fallow	9.09	17.65	36.36	17.91	
Groundnut	4.55	2.94	0.00	2.99	
Maize	18.18	26.47	9.09	20.90	
Soybean	45.45	2.94	0.00	16.42	
Squash	4.55	0.00	18.18	4.48	
Soil-tillage (%)					
Mechanized	59.09	0.00	0.00	19.40	
Traditional	40.91	100.00	100.00	76.12	
Cropping system (%)					
Intercrop	4.55	8.82	36.36	11.94	<i>Crops often associated with maize: millet, sorghum, cowpea, squash</i>
Monoculture	95.45	91.18	63.64	88.06	
Fertilization (%)					<i>Fertilizers used : NPK, Urea</i>
Done	100.00	70.59	45.45	74.63	
Not done	0.00	29.41	54.55	25.37	
Fertilizer rate (kg.ha <sup>-1</sup> )	214.3 ± 11.4	167.39 ± 8.67	150.0 ± 22.4	185.71 ± 7.54	
Sowing mode (%)					
Staggered	0.00	47.06	54.55	32.84	Staggered sowing over 7 to 30 days
Not staggered	100.00	52.94	45.45	67.16	
Weed control (%)					
Herbicide	95.45	26.47	9.09	46.27	<i>Herbicides used (active ingredients) : Nicosulfuron; Paraquat dichloride; Glyphosate salt; Fluometuron + prometryne + Glyphosate; Atrazine</i>
Manual	4.55	73.53	90.91	53.73	
Insecticide application (%)					
Done	18.18	8.82	9.09	11.94	<i>Insecticides used (active ingredients) : Emamectin benzoate; Emamectin benzoate + acetamiprid ; Acetamiprid + lambda-cyhalothrin; Chlorpyrifos ethyl + Cypermethrin</i>
Not done	81.82	91.18	90.91	88.06	

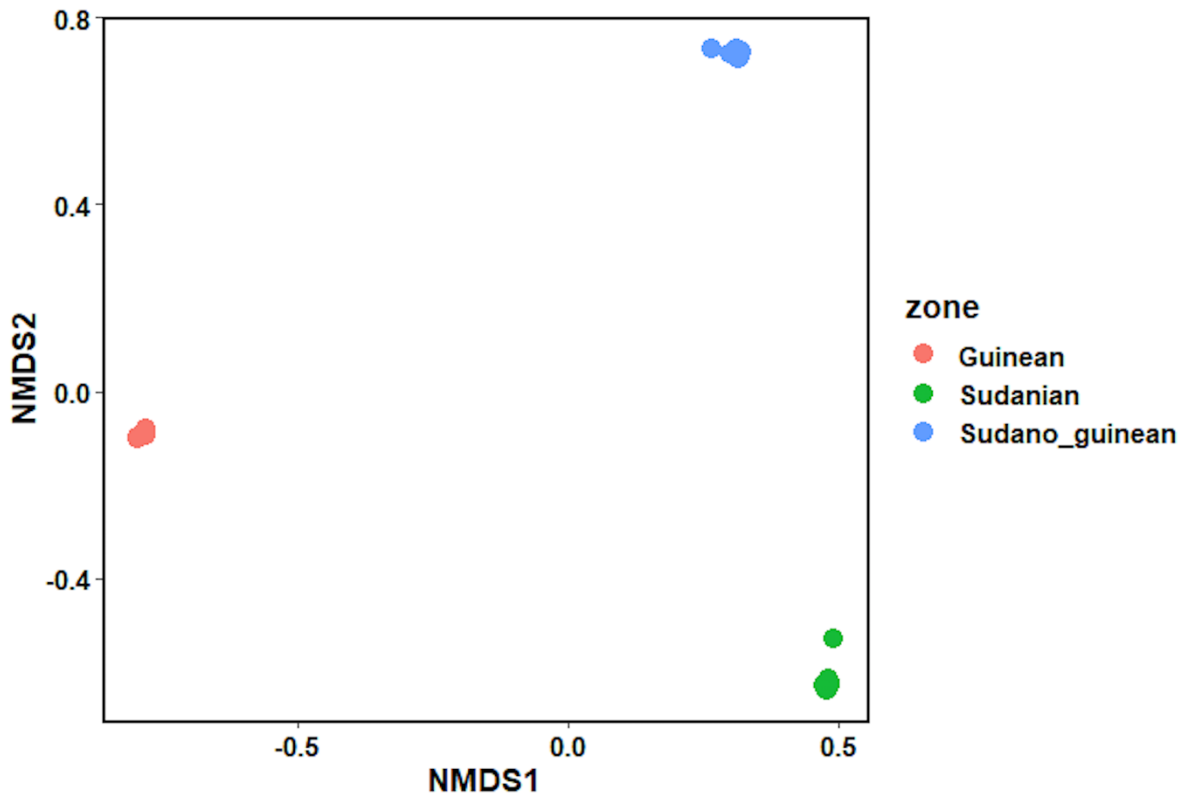
higher FAW biocontrol by *Metarhizium* sp. ( $\chi^2 = 53.24$ , df = 6, N = 67,  $P < 0.001$ ). FAW parasitism by *Hexameris* sp. was also significantly higher in fields that had maize or cowpea as a previous crop ( $\chi^2 = 34.01$ , df = 6, N = 67,  $P < 0.001$ ). Regarding parasitoids, except for *C. luteum*, which caused higher parasitism in fields after groundnut cultivation ( $\chi^2 = 23.71$ , df = 6, N = 67,  $P = 0.001$ ), no effect

of the previous crop was observed on parasitoids ( $p > 0.05$ ).

Mechanized tillage significantly contributed to lower FAW parasitism by *Hexameris* sp. ( $\chi^2 = 8.04$ , df = 1, N = 67,  $P = 0.018$ ) and *Charops* sp. ( $\chi^2 = 8.72$ , df = 1, N = 67,  $P = 0.013$ ), while significantly higher parasitism related to *C. luteum* was observed with this practice ( $\chi^2 = 14.04$ , df = 1,



**Figure 3.** Occurrence frequency (%) of natural enemies isolated from FAW larvae collected from 67 maize fields and distributed across the three climatic zones in Benin.



**Figure 4.** NMDS analysis plot of *S. frugiperda* natural enemy communities across Benin climatic zones.

N = 67,  $P = 0.001$ ). FAW parasitism by the Mermithid nematode was significantly higher in intercropping systems ( $\chi^2 = 37.02$ ,  $df = 1$ ,  $N = 67$ ,  $p < 0.001$ ) and relatively low with field fertilization ( $\chi^2 = 25.81$ ,  $df = 1$ ,  $N = 67$ ,  $p < 0.001$ ) (Table 3).

The effect of pesticide uses on FAW natural enemies is shown in Table 4 and Figures 5 and 6. The maize fields where farmers applied herbicides and insecticides had significantly higher rates of FAW biocontrol by *Metarhizium* ( $16.4 \pm 2.8\%$  and  $16.9 \pm 7.0\%$ , respectively) and

**Table 3.** Performance of *S. frugiperda* natural enemies according to different agricultural practices.

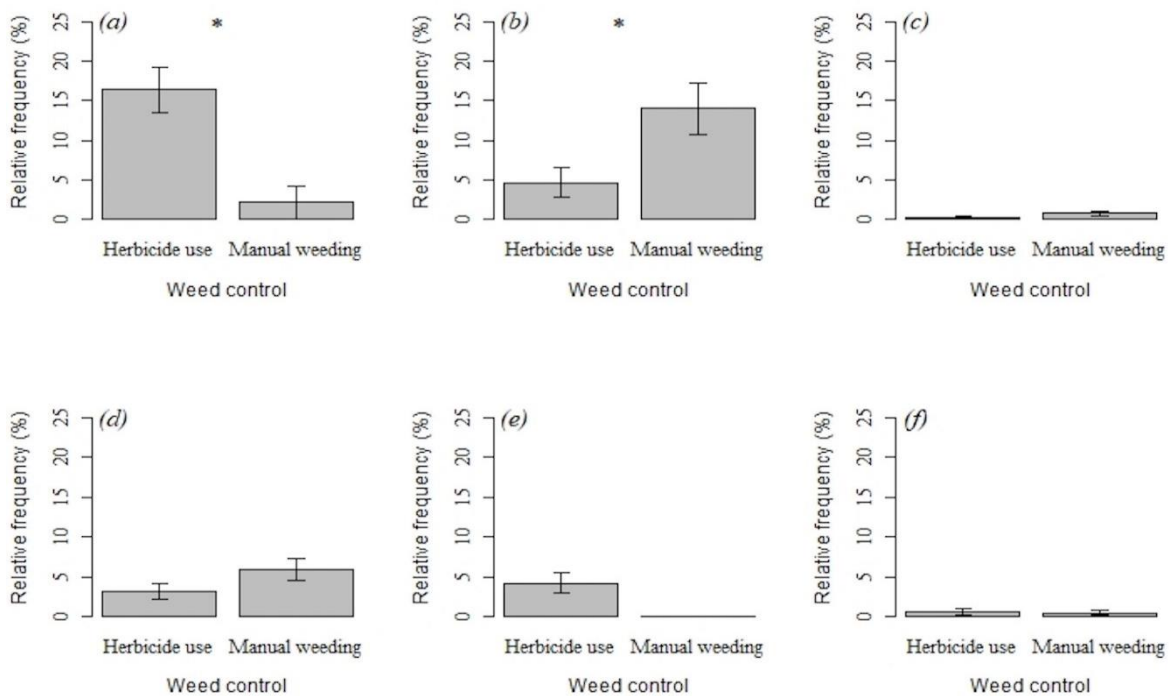
Agricultural practices	Natural enemies of <i>S. frugiperda</i> (mean $\pm$ SE)					
	<i>Metharhizium</i> sp.	<i>Hexameris</i> sp.	<i>Charops</i> sp.	<i>Ch. bifoveolatus</i>	<i>C. luteum</i>	<i>D. quadrizonula</i>
<b>Previous crop</b>						
Fallow	0.040 $\pm$ 0.020 <sup>bc</sup>	0.100 $\pm$ 0.020 <sup>ab</sup>	0.000 $\pm$ 0.000 <sup>a</sup>	0.051 $\pm$ 0.017 <sup>a</sup>	0.006 $\pm$ 0.006 <sup>ab</sup>	0.000 $\pm$ 0.000 <sup>a</sup>
Maize	0.060 $\pm$ 0.020 <sup>b</sup>	0.150 $\pm$ 0.020 <sup>a</sup>	0.040 $\pm$ 0.003 <sup>a</sup>	0.040 $\pm$ 0.012 <sup>a</sup>	0.040 $\pm$ 0.012 <sup>ab</sup>	0.000 $\pm$ 0.000 <sup>a</sup>
Cotton	0.220 $\pm$ 0.030 <sup>a</sup>	0.030 $\pm$ 0.010 <sup>b</sup>	0.010 $\pm$ 0.005 <sup>a</sup>	0.062 $\pm$ 0.017 <sup>a</sup>	0.010 $\pm$ 0.007 <sup>ab</sup>	0.026 $\pm$ 0.011 <sup>a</sup>
Cowpea	0.004 $\pm$ 0.004 <sup>c</sup>	0.140 $\pm$ 0.020 <sup>a</sup>	0.009 $\pm$ 0.006 <sup>a</sup>	0.055 $\pm$ 0.015 <sup>a</sup>	0.004 $\pm$ 0.005 <sup>b</sup>	0.000 $\pm$ 0.000 <sup>a</sup>
Soybean	0.190 $\pm$ 0.020 <sup>a</sup>	0.050 $\pm$ 0.010 <sup>b</sup>	0.000 $\pm$ 0.000 <sup>a</sup>	0.016 $\pm$ 0.007 <sup>a</sup>	0.042 $\pm$ 0.011 <sup>ab</sup>	0.003 $\pm$ 0.003 <sup>a</sup>
Groundnut	0.010 $\pm$ 0.040 <sup>ab</sup>	0.100 $\pm$ 0.040 <sup>ab</sup>	0.000 $\pm$ 0.000 <sup>a</sup>	0.058 $\pm$ 0.032 <sup>a</sup>	0.096 $\pm$ 0.041 <sup>a</sup>	0.000 $\pm$ 0.000 <sup>a</sup>
Squash	0.070 $\pm$ 0.030 <sup>abc</sup>	0.000 $\pm$ 0.000 <sup>c</sup>	0.030 $\pm$ 0.020 <sup>a</sup>	0.017 $\pm$ 0.017 <sup>a</sup>	0.017 $\pm$ 0.017 <sup>ab</sup>	0.000 $\pm$ 0.000 <sup>a</sup>
Probability	<0.001*	<0.001*	0.222	0.217	0.001*	0.795
<b>Soil-tillage</b>						
Mechanized	0.225 $\pm$ 0.040 <sup>a</sup>	0.050 $\pm$ 0.010 <sup>b</sup>	0.000 $\pm$ 0.000 <sup>b</sup>	0.022 $\pm$ 0.012 <sup>a</sup>	0.032 $\pm$ 0.012 <sup>a</sup>	0.006 $\pm$ 0.006 <sup>a</sup>
Traditional	0.055 $\pm$ 0.019 <sup>a</sup>	0.100 $\pm$ 0.010 <sup>a</sup>	0.007 $\pm$ 0.003 <sup>a</sup>	0.051 $\pm$ 0.011 <sup>a</sup>	0.020 $\pm$ 0.009 <sup>b</sup>	0.005 $\pm$ 0.003 <sup>a</sup>
Probability	0.929	0.018*	0.013*	0.810	0.001*	0.773
<b>Sowing mode</b>						
Staggered	0.002 $\pm$ 0.002 <sup>a</sup>	0.110 $\pm$ 0.016 <sup>a</sup>	0.010 $\pm$ 0.005 <sup>a</sup>	0.062 $\pm$ 0.012 <sup>a</sup>	0.022 $\pm$ 0.008 <sup>a</sup>	0.007 $\pm$ 0.004 <sup>a</sup>
Not staggered	0.130 $\pm$ 0.010 <sup>a</sup>	0.078 $\pm$ 0.009 <sup>a</sup>	0.002 $\pm$ 0.002 <sup>a</sup>	0.031 $\pm$ 0.006 <sup>a</sup>	0.034 $\pm$ 0.011 <sup>a</sup>	0.004 $\pm$ 0.002 <sup>a</sup>
Probability	0.998	0.470	0.629	0.448	0.721	0.138
<b>Cropping system</b>						
Intercrop	0.050 $\pm$ 0.020 <sup>a</sup>	0.160 $\pm$ 0.030 <sup>a</sup>	0.015 $\pm$ 0.011 <sup>a</sup>	0.015 $\pm$ 0.011 <sup>a</sup>	0.000 $\pm$ 0.000 <sup>a</sup>	0.000 $\pm$ 0.000 <sup>a</sup>
Monoculture	0.120 $\pm$ 0.010 <sup>a</sup>	0.070 $\pm$ 0.010 <sup>b</sup>	0.004 $\pm$ 0.002 <sup>a</sup>	0.046 $\pm$ 0.006 <sup>a</sup>	0.031 $\pm$ 0.005 <sup>a</sup>	0.006 $\pm$ 0.002 <sup>a</sup>
Probability	0.687	<0.001*	0.999	0.728	0.998	0.999
<b>Fertilization</b>						
Done	0.115 $\pm$ 0.023 <sup>a</sup>	0.066 $\pm$ 0.015 <sup>b</sup>	0.006 $\pm$ 0.002 <sup>a</sup>	0.040 $\pm$ 0.010 <sup>a</sup>	0.028 $\pm$ 0.008 <sup>a</sup>	0.006 $\pm$ 0.003 <sup>a</sup>
Not done	0.024 $\pm$ 0.024 <sup>a</sup>	0.202 $\pm$ 0.080 <sup>a</sup>	0.000 $\pm$ 0.000 <sup>a</sup>	0.062 $\pm$ 0.019 <sup>a</sup>	0.000 $\pm$ 0.000 <sup>a</sup>	0.000 $\pm$ 0.000 <sup>a</sup>
Probability	0.686	<0.001*	0.162	0.959	0.998	0.195

Note: Means within columns followed by different letters are significantly different; \* denotes a significant difference between groups at  $\alpha = 0.05$ .

**Table 4.** Effect of pesticide application for weed (herbicide) and pest control (insecticide) on FAW natural enemies.

Natural enemy species	N <sup>a</sup>	df <sup>b</sup>	Herbicide application		Insecticide application	
			$\chi^{2c}$	P-value	$\chi^{2c}$	P-value
<i>Metarhizium</i> sp.	67	1	17.385	< 0.001*	8.940	0.003*
<i>Hexamermis</i> sp.	67	1	14.708	< 0.001*	11.217	0.001*
<i>Charops</i> sp.	67	1	1.951	0.162	1.034	0.309
<i>Ch. bifoveolatus</i>	67	1	0.003	0.959	0.084	0.772
<i>C. luteum</i>	67	1	0.002	0.998	7.402	0.007*
<i>D. quadrizonula</i>	67	1	1.677	0.195	8.797	0.003*

Note: <sup>a</sup> number of sampled fields; <sup>b</sup> degrees of freedom; <sup>c</sup> chi-square statistic value; \* denotes significant difference at  $\alpha = 0.05$ .



**Figure 5.** Relative frequencies of natural enemies isolated from *S. frugiperda* larvae collected from maize fields in Benin according to the type of weed control: (a) *Metarhizium* sp., (b) *Hexamermis* sp., (c) *Charops* sp., (d) *Ch. bifoveolatus*, (e) *C. luteum*, and (f) *D. quadrizonula*. \* denotes significant difference between groups at  $\alpha = 0.05$ .

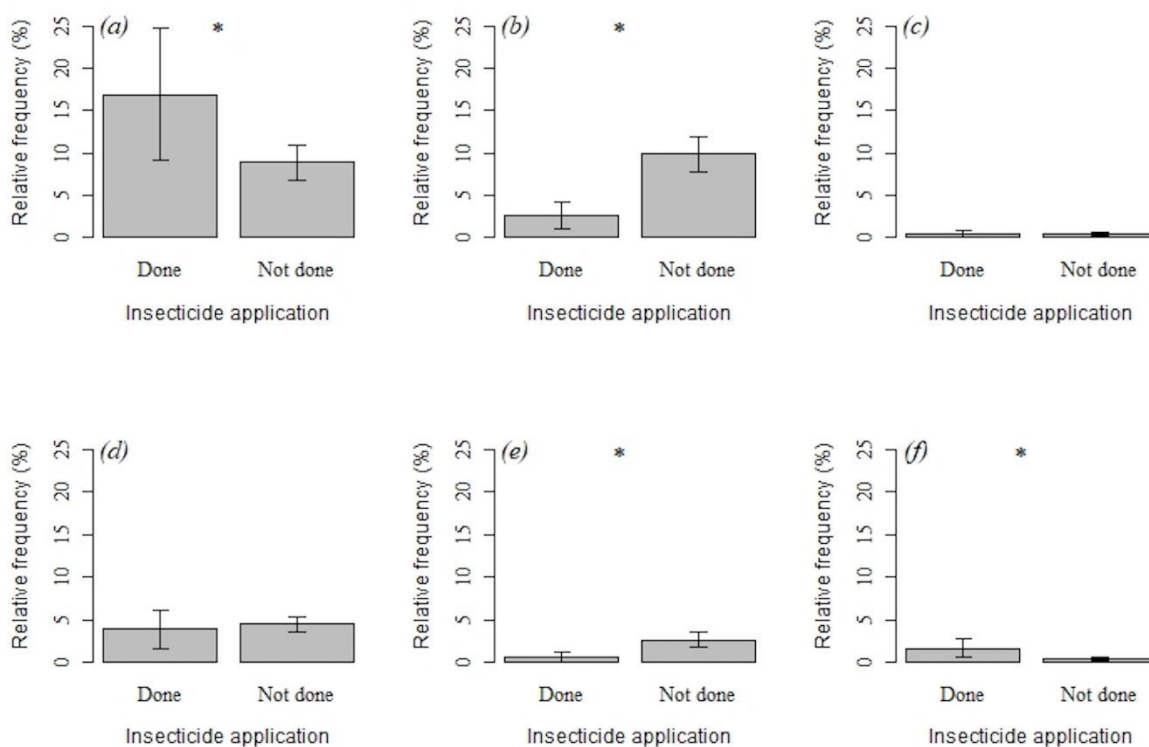
significantly lower rates of FAW biocontrol by *Hexamermis* ( $4.6 \pm 1.8\%$  and  $2.7 \pm 1.6\%$ , respectively). Insecticide application was also associated with low parasitism by *C. luteum* and *D. quadrizonula* ( $0.6 \pm 0.6\%$  and  $1.6 \pm 1.1\%$ , respectively).

#### Effect of agricultural practices and biocontrol on FAW infestation

Ordinal logistic regression models indicated that damage severity was significantly different ( $P < 0.05$ ) for agricultural practices such as previous crop, cropping

system, weed control, insecticide application and fertilizer rate. In contrast, soil-tillage, sowing mode and fertilizer application did not induce a significant effect on the damage severity (Table 5).

Regarding the previous crop, high FAW score damage (scores 2 and 3) had a higher probability in fields planted after fallow or cotton, while it had a lower probability in fields with groundnut as a previous crop (Figure 7a). High score damage was also more likely to be observed in fields with cultural associations compared to those with maize monoculture (Figure 7d), and in untreated fields compared to those treated with insecticides (Figure 7f). Although no significant differences ( $P > 0.05$ ) were noted between the



**Figure 6.** Relative frequencies of natural enemies isolated from *S. frugiperda* larvae collected from infested maize fields in Benin according to insecticide use: (a) *Metarhizium* sp., (b) *Hexameris* sp., (c) *Charops* sp., (d) *Ch. bifoveolatus*, (e) *C. luteum*, and (f) *D. quadrizonula*. \* denotes significant difference between groups at  $\alpha = 0.05$ .

**Table 5.** Effect of different agricultural practices on FAW damage severity.

Agricultural practices	N <sup>a</sup>	Df <sup>b</sup>	$\chi^2$ <sup>c</sup>	P- value
Previous crop	67	6	80.866	<0.001*
Soil-tillage	67	1	2.700	0.100
Sowing mode	67	1	0.650	0.420
Cropping system	67	1	14.977	<0.001*
Weed control	67	1	4.028	0.045*
Insecticide application	67	1	22.523	<0.001*
Fertilizer application	67	1	1.028	0.311
Fertilizer rate	67	1	7.553	0.006*

Note: <sup>a</sup> number of sampled fields; <sup>b</sup> degrees of freedom; <sup>c</sup> chi-square statistic value; \* denotes significant difference at  $\alpha = 0.05$ .

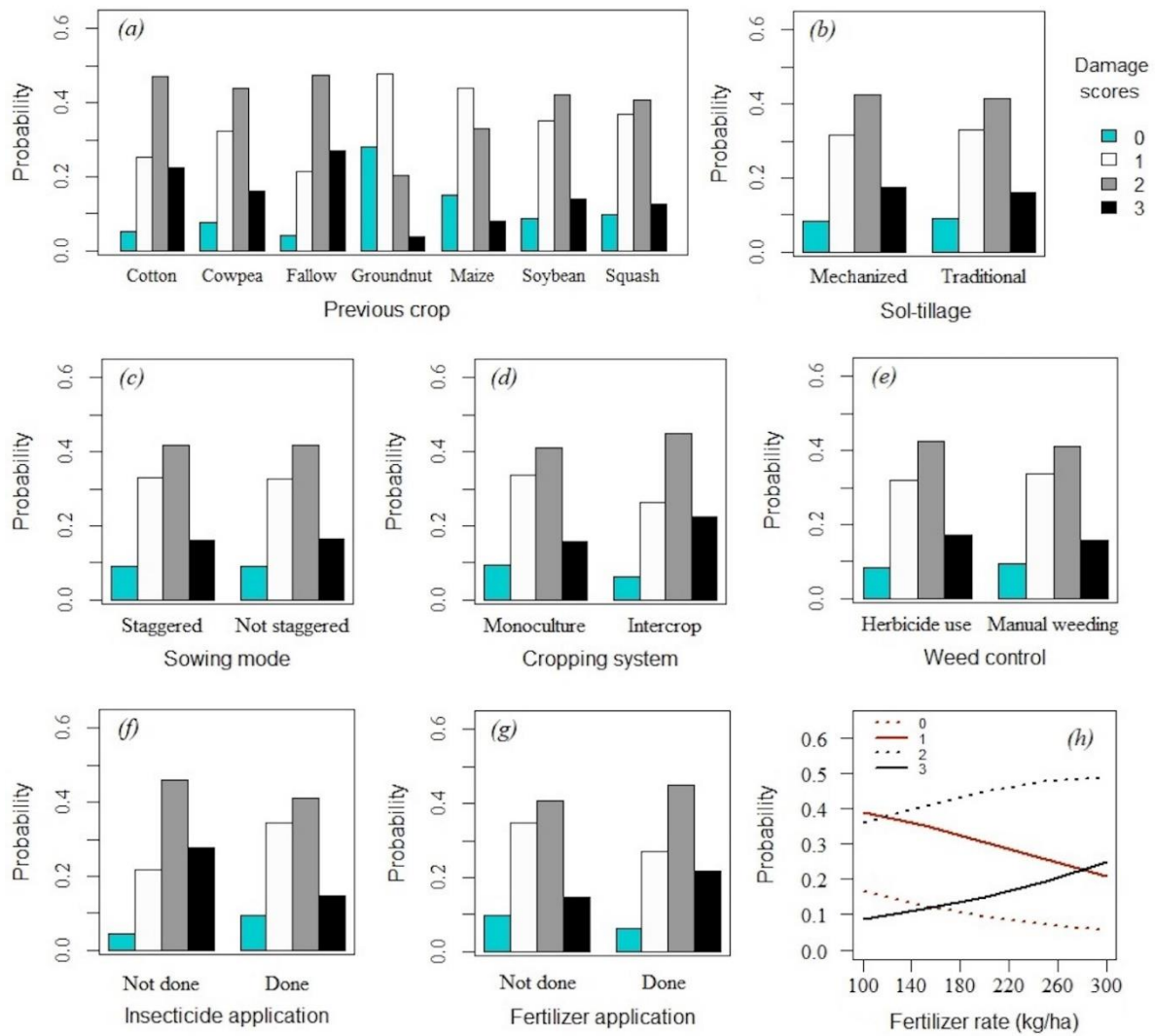
FAW damage of fertilized and unfertilized fields, the probability of a high damage score in fields where fertilization was used tended to increase as the rate of fertilizer applied increased.

The results of Spearman's linear correlation tests showed a non-significant correlation ( $r = 0.12$ ;  $P = 0.336$ ) between overall biocontrol and infestation of FAW.

## DISCUSSION

For a long time, different agronomic or cultural interventions

have been used to modify the weathering agents to minimize their impact on agricultural production. Therefore, this study evaluated the impact of some agricultural practices frequently adopted by farmers on *S. frugiperda* infestation and its natural enemies in different climatic zones of Benin to facilitate effective management of this invasive pest. These practices are previous crop, tillage, sowing method, cropping system, weed control, fertilization and crop protection. The previous crop is dependent on crop rotation (Crotty *et al.*, 2016; Mazzilli *et al.*, 2016). Intercropping systems, tillage, and crop rotation are traditional methods used by farmers for weed management



**Figure 7.** Probability of plant damage severity by *S. frugiperda* according to: (a) previous crop, (b) tillage, (c) seeding method, (d) cropping system, (e) weed control, (f) insecticide application, (g) fertilizer application, and (h) fertilizer rate.

and soil fertility improvement (Reddy, 2017). However, these methods applied by farmers or not can directly or indirectly (through environmental modification) affect arthropods. The same is true for weed control whether chemical or manual whose ultimate goal is to reduce the weed population (Harker and O'Donovan, 2013). Mineral fertilization was the only method practiced by the surveyed, providing plants with easily and rapidly assimilated fertilizers. However, some other farmers in Benin use other methods of soil fertility management such as animal penning, mulching of fields with cereal residues and the use of cover crops (mucuna) (Djenontin *et al.*, 2002). Regarding maize protection; weeds, soil fertility and drought are the major constraints of maize production and therefore most farmers did not practice plant protection before the FAW invasion (Baco *et al.*, 2011). Some

farmers (11.94%) currently protect their crops from FAW, but the products used are often chemical insecticides such as Emamectin benzoate. Other methods of protection used by a few farmers are botanical insecticides (e.g. leaves or seeds of *Azadirachta indica*, pepper of *Capsicum annum*), application of wood ash to leaf whorls and handpicking of larvae (Houngbo *et al.*, 2020).

### Impact of agricultural practices on FAW natural enemies

Several studies have been carried out worldwide on different natural enemies emerging from FAW (Firake and Behere, 2020; Ginting *et al.*, 2020; López *et al.*, 2018; Meagher *et al.*, 2016; Sisay *et al.*, 2018; Sun *et al.*, 2020).

In the present study, the impact of some agricultural practices on the biocontrol agents associated with FAW was assessed in Benin. Our findings indicated dissimilarity in the natural enemy communities across the three climatic zones which present distinctive characteristics (Mensah *et al.*, 2014). These results are consistent with those reported previously by Durocher-Granger *et al.* (2021) who indicated the effect of location on FAW natural enemies' occurrence despite the relatively short distances between sites. These observations suggest that apart from climate, other factors including vegetation and agroecological landscape can disturb the dynamic of FAW natural enemies' populations (Mama Sambo *et al.*, 2019). In addition, the average size of the fields varied highly from one area to another and thus agricultural practices are not carried out in the same way by farmers in different regions. All this can impact the occurrence and distribution of natural enemies from one zone to another.

The present study was conducted in three different climatic zones during the plant's vegetative stages (V5 to V10) with FAW larval stages (1 to 5) which are known to be favorable periods for abundance and diversity in FAW natural enemy species as observed by Abang *et al.* (2021). However, in the Adjohoun district which is located in the Guinean zone, the composition and performance of FAW's natural enemies were particularly poor. This can be explained by the fact that FAW samples were collected during a relatively short period. As a result of the short rainy season and other economic reasons, most farmers in this region plant short-cycle maize varieties with rapid panicle initiation which limited the sampling duration. In addition, the misuse of pesticides in this region may also explain the low diversity and occurrence of natural enemies (Agossou *et al.*, 2019).

The complex of larval and egg-larval parasitoids of FAW obtained in this study is less rich than that identified by Agboyi *et al.* (2020) in 9 out of the 12 departments of Benin. The parasitoids *Cotesia icipe* and *Pristomerus pallidus* were found exclusively in the coastal regions of the country by Agboyi *et al.* (2020), but were not recorded in our study. Species of *Charops* and *Chelonus* were reported on other lepidopterans in Benin before the FAW invasion (Agboton *et al.*, 2014; Bordat and Goudegnon, 1991). Besides, these parasitoid species have a wide geographical distribution and they have been reported on FAW in several studies conducted in Africa (Agboyi *et al.*, 2020; Koffi *et al.*, 2020); Senegal (Tendeng *et al.*, 2019); Burkina Faso (Ahissou *et al.*, 2021); Cameroon (Abang *et al.*, 2021); Mozambique (Caniço *et al.*, 2020); Zambia (Durocher-Granger *et al.*, 2021); Uganda (Otim *et al.*, 2021); and Tanzania, Kenya and Ethiopia (Sisay *et al.*, 2018). The parasitoids, *Drino (Palexorista)* sp. and *Coccygidium luteum* were also observed in the African agroecosystem before FAW invaded Africa (Madl and Van Achterberg, 2014; Robertson, 1973). Most of the parasitoids recorded in our study probably attack other

*Spodoptera* species or species in closely related genera and are successful at parasitizing this new host. Therefore, these parasitoids could facilitate the implementation of biological control programs for this invasive pest in Africa.

This is the first report of an entomopathogenic fungus (*Metarhizium* sp.) and a Mermithid nematode, *Hexameris* sp. emerging from FAW in Benin. An undetermined species of the genus *Hexameris* was isolated from FAW in Senegal (Tendeng *et al.*, 2019) and a related Mermithid was also recorded recently in Burkina Faso by Ahissou *et al.* (2021). *Hexameris* is the most frequently reported genus of the Mermithidae family in FAW and induces high levels of parasitism with up to 50% in Nicaragua (Van Huis, 1981); 23% in Mexico and Honduras (Ruiz-Nájera *et al.*, 2013; Wheeler *et al.*, 1989); 14% in Senegal (Tendeng *et al.*, 2019); and 8% in India (Firake and Behere, 2020). Besides, the occurrence of high infection rates by the EPF in our study may be due to the abundance of rain during insect collection, as humidity can favor the development of fungi (Acheampong *et al.*, 2020; Ríos-Velasco *et al.*, 2010). The existence of the EPF, *Metarhizium flavoviride* in other insects such as grasshoppers and locusts, was previously reported in northern Benin (Shah *et al.*, 1994).

Regarding the influence of agricultural practices on FAW natural enemies, the results clearly showed the sensitivity of the EPF and the mermithid nematode species to several agricultural practices, and a low to no impact on the parasitoids. This may be partly attributed to the fact that parasitoids are highly mobile, and can escape quickly from adverse conditions in their environment and recolonize later. In contrast, fungi and nematodes are less mobile and cannot escape from any sudden changes in their environment (Purvis and Faddl, 1996).

The effectiveness of FAW biocontrol by *Metarhizium* sp. after cotton and soybean may be due to the presence of lepidopterans of the same family as *S. frugiperda* such as *Helicoverpa armigera*, in which a natural fungal infection by *Metarhizium rileyi* has been reported in Brazil (Costa *et al.*, 2015), and whose dead bodies may constitute a source of inoculum which may spread the pathogen during the next production season. A similar result could be expected when maize is the previous crop, but the more developed cotton or soybean foliage could create a favorable microclimate for the fungus development and persistence. The overall occurrence of *Metarhizium* sp. in the Sudanian zone could be influenced by cotton and soybean cultivation, which are mainly carried out in northern Benin which covers this climatic zone. Our results also showed a higher FAW infection rate by the entomopathogenic fungus in fields treated with insecticides and herbicides than in untreated and weeded fields. Insecticides and herbicides have been reported to be compatible with *Metarhizium* spp. as mentioned previously by Mochi *et al.* (2005), Silva *et al.* (2013) and Yousef *et al.* (2015). Indeed, several insecticides have a synergistic effect with fungi of the *Metarhizium* genus to control crop pests (Schumacher

and Poehling, 2012; Sivakumar *et al.*, 2020). Combinations of low doses of insecticides with EPFs can improve integrated pest management (IPM) programmes against FAW (Rivero-Borja *et al.*, 2018). This synergistic effect was also observed with herbicides by Smith *et al.* (2021) who showed that glyphosate had the potential to inhibit melanin, impair immunity and perturb the microbiota composition of insects, making them more susceptible to microbial pathogens. The *Metarhizium* species found in this study has an indisputable potential as an entomopathogenic agent for biological control. Due to the natural occurrence of this fungal species in the Sudanian zone, which is the most arid zone and also its tolerance to most agricultural practices applied in the conventional production systems, it is a potential biological agent that can be used in all climatic zones of Benin regardless of the abiotic or agronomic factors. In this context, further research is urgently needed to identify the EPF to the species/strain level to characterise its status in pest control.

The high parasitism rate of FAW by *Hexameris* sp. in cropping systems may be due to the fact that these systems have a higher spatial cover which would protect a large area of the soil from solar radiation, and thus provide a humid microclimate for the nematodes (Grant and Villani, 2003; Lacey and Unruh, 1998). In contrast, our results showed that agricultural inputs (mineral fertilizer, herbicides and insecticides) reduced FAW biocontrol by *Hexameris* sp. Several studies have highlighted the deleterious effect of mineral fertilization on the performance of entomophagous nematodes (Kolombar *et al.*, 2020; Sharmila *et al.*, 2018). On the other hand, the use of organic fertilization can lead to an increase in nematode population density (Bednarek and Gaugler, 1997). Regarding the effect of insecticides and herbicides, Sharmila *et al.* (2018) showed that pesticides used in vegetable production are harmful to nematodes. Similarly, Togola *et al.* (2018) revealed that most pesticides used in maize production by farmers in Nigeria for FAW management leave residues in the soil, which can directly affect nematodes.

Apart from agricultural inputs, mechanized tillage (intensive tillage) was associated with low FAW parasitism by nematode at the expense of traditional tillage (light tillage). The sensitivity of nematodes to tillage is variable (Campos-Herrera *et al.*, 2015; Millar and Barbercheck, 2002; Okada and Harada, 2007). According to Millar and Barbercheck (2002), this can be explained by the environmental tolerance of the nematodes and also their ability to disperse deeper into the soil profile. Studies related to the tillage effect on *Hexameris* species are non-existent. But, it is admitted that intensive tillage, by fragmenting the soil, promotes water infiltration into the soil and then water evaporation at the surface, exposing the soil surface to desiccation; and thus can affect nematodes' survival and activity (Cruz-Martínez *et al.*, 2017). The

scarcity of field studies on factors affecting mermithid nematodes, particularly the genus *Hexameris* is a gap filled by this study. In production systems without agricultural inputs, the parasitism rate of *Hexameris* sp. reached more than 50% in some fields in our study, which makes it a potential biological control agent for FAW management, particularly in organic production systems.

### **Impact of agricultural practices on FAW infestation and biocontrol**

Our findings are in line with those of Baudron *et al.* (2019) who demonstrated that FAW attacks were high in maize fields when established after fallow. According to the authors, the spontaneous vegetation predominated by *Poaceae* may have hosted the pest. However, this vegetation also sheltered several natural enemies that could regulate the FAW population (Harrison *et al.*, 2019; Hay-Roe *et al.*, 2016). Moreover, FAW did not diapause and pupation only lasted approximately a week, so it is not evident that individuals from previous crops would attack a new crop established more than a month after the previous one. This could also explain the non-significant effect of tillage, which is an agricultural practice performed early in a new season, on FAW damage severity.

Moreover, the present study observed that insecticide application by farmers reduced FAW damage, but did not provide effective protection against this pest. The same trend was also reported previously by Baudron *et al.* (2019) and Dassou *et al.* (2021) in Zimbabwe and Benin, respectively. This observation may be due to the fact that farmers sprayed the insecticides only when the FAW infestation level increased in the fields. In addition, the low efficacy of insecticides may be due to their incorrect use by farmers such as the wrong pesticides being applied and/or not following the recommended dose, etc (Kumela *et al.*, 2018). Besides, several studies highlighted the development of resistance of this pest to a wide range of chemical insecticides (Bernardi *et al.*, 2017; Carvalho *et al.*, 2013; Giraudo *et al.*, 2014). Furthermore, the presence of FAW larvae feeding inside the maize whorls does not favor sufficient insecticide contact with the insects, and thus reduces the effectiveness of such a control method (Cook *et al.*, 2004). Regarding the effect of weed control techniques, the trend of higher damage in herbicide-treated fields compared to manually weeded fields may be due to the indirect effect of herbicides on the natural regulation of FAW. While herbicides have low direct toxicity on arthropods (Volkmar *et al.*, 2003), such as *S. frugiperda*, they can have strong indirect effects by removing the floricultural resources required by auxiliaries (Heard *et al.*, 2006; Landis *et al.*, 2000) and the vegetation that shelters them (Harrison *et al.*, 2019; Hay-Roe *et al.*, 2016). Furthermore, herbicides based on glyphosate widely used by farmers leave residues in the soil which

have the potential to alter the biosynthesis of plant defense compounds and plant interactions with herbivores and mutualistic organisms (Fuchs *et al.*, 2021).

Several studies demonstrated the beneficial effect of intercropping systems in reducing *S. frugiperda* attacks (Harrison *et al.*, 2019; Hruska, 2019; Midega *et al.*, 2018; Tanyi *et al.*, 2020; Udayakumar *et al.*, 2020). On the contrary, the present study revealed that maize monoculture is less attacked than that with intercropping. These contrasting results were also observed by Baudron *et al.* (2019) and Wale *et al.* (2007) in maize association with sweet potato or pumpkin. Studies showing the effect of intercropping on the reduction *S. frugiperda* attacks, associated maize with legumes such as desmodium, cowpea, common bean and groundnut. Therefore, the companion plant species likely determines the effectiveness of the association (Baudron *et al.*, 2019). In addition, the time and area of experimentation may also influence the efficacy of this agricultural practice in controlling the pest (Patient *et al.*, 2019).

FAW damage severity was not significantly different between fertilized and unfertilized fields but tended to increase as the fertilizer rate increased. The attractiveness of plants provided with a high dose of fertilizers to phytophagous species is well documented (Bala *et al.*, 2018; Baudron *et al.*, 2019; Mochiah *et al.*, 2011). If fertilization makes the plant more appealing to the pest, it provides the plants with sufficient nutrients; making them more vigorous, and less vulnerable to depredation (Bala *et al.*, 2018; Rowen and Tooker, 2020), and allows them to quickly recover from pest attacks (Hruska, 2019).

Our findings revealed the absence of a correlation between the biocontrol rate of natural enemies and FAW infestation. This result needs to be further investigated as we did not assess the biocontrol of all FAW stages in this study. Some of the natural enemies observed in this study have the potential to control other Lepidopteran species (Fite *et al.*, 2020; Kfir, 1997; Robertson, 1973). In addition, some studies showed that the high performance of *Metarhizium* sp., *Hexameris* sp. and many parasitoid species correlated with high host populations (Acharjee *et al.*, 2020; Durocher-Granger *et al.*, 2021; Fronza *et al.*, 2017), meaning that they tend to achieve higher biocontrol when host populations are important. Ultimately, the obtained results revealed that agricultural practices modulate the performance of natural enemies and FAW damage; suggesting that variations in agricultural practices in maize fields can also differently affect FAW populations and its natural enemies. In view of the above findings, several factors can affect the natural enemies' activity.

## CONCLUSION

This study investigated the diversity of natural enemies associated with FAW in maize fields in three climatic zones

in Benin and the impact of different agricultural practices on the damage of this pest and on the performance of its natural enemies. The study indicated that several types of natural enemies (entomopathogenic fungus, mermithid nematode and parasitoids) are present in the field and associated with *S. frugiperda* in Benin. Furthermore, the study shows that some agricultural practices performed in these agroecological zones, particularly, the previous crop and the use of agricultural inputs (fertilizers, herbicides and insecticides) during cultivation, have a variable influence on FAW attacks or the natural regulation induced by its different natural enemy species.

Although the results of this study are preliminary, they provide essential information that should be taken into consideration for developing and improving biological control and IPM programs for FAW in Africa.

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