



Fall Armyworm *Spodoptera frugiperda* (Lepidoptera: Noctuidae) in South Kivu, DR Congo: Understanding How Season and Environmental Conditions Influence Field Scale Infestations

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Abstract

The fall armyworm (FAW) *Spodoptera frugiperda* (J. E. Smith) has become a global devastating pest because of its broad dispersal capacity and the high crop damages. At present, research on FAW infestations of crops in the DR Congo remains undocumented. Here, FAW infestations in two agro-ecological zones (Kabare and Ruzizi Plain) were compared in South-Kivu Province. Surveys were carried out during the early 2018 and late 2019 crop seasons to assess the impact of FAW on maize crops. In each agro-ecological zone, 50 fields were selected for investigation. A total of hundred (100) fields were assessed in the 2018 crop season. During the 2019 crop season, the same fields were investigated. The two zones had very different bioclimatic characteristics. FAW attacks were more pronounced under conditions of relatively high temperatures with high evapotranspiration, which occurred in the Ruzizi Plain and late 2019 season. In comparison, Kabare territory and the early 2018 season were characterized by heavy rainfall. The incidence, level of leaf damage, and density of FAW larvae varied significantly with season and agro-ecological zone. The Ruzizi Plain had the highest incidence ($60 \pm 30\%$), level of leaf damage and larval density (28.5 ± 19.3). The late 2019 season had the highest incidence ($70 \pm 20\%$) as well as the larval density (27.8 ± 19.2). Total annual number of FAW generations was 5.64 and 3.36 in the Ruzizi Plain and Kabare territory, respectively. In conclusion, FAW infestation represents a major problem for agricultural production due to the climatic conditions in the study region.

Keywords *Spodoptera frugiperda* · infestations · season · agro-ecological zone · degree day

Introduction

The fall armyworm (FAW) *Spodoptera frugiperda* (J. E. Smith) is one of the most important pests in the world due to its polyphagous behavior and high damages on major crops (e.g., maize, rice, sorghum) (CABI 2020) and also to its extreme potential of expansion (Early et al. 2018). A recent study conducted by Montezano et al. (2018) reported 353 plant species attacked by FAW, which are distributed in 76 families whose the main plant families are Poaceae, Asteraceae, and Fabaceae.

The FAW was first reported in the Americas as its place of origin (Luginbill 1928; Ayala et al. 2013; Early et al. 2018). At the present day, FAW has become one of the most important pests at the global stage (Zacarias 2020) since it first invaded Africa in 2016 (Goergen et al. 2016), and also infested Asia in 2018 (Sharanabasappa et al. 2018; Shylesha et al. 2018). FAW exists in two morphologically

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indistinguishable strains, the corn strain (CS) and the rice strain (RS) (Pashley 1986; Vélez-Arango et al. 2008; Nagoshi et al. 2015; Cano-Calle et al. 2015).

Maize is grown across diverse agro-ecological zones in Sub-Saharan Africa, where over 208 million people depend on this crop to meet their nutritional needs (Day et al. 2017). While maize is the most important staple cereal crop grown by smallholder farmers in Sub-Saharan Africa (Macauley 2015; Ekpa et al. 2018), the susceptibility of this crop to FAW infestation is high due to physiological differences between strains, which affect the ability of FAW to consume maize efficiently (Veenstra et al. 1995). FAW often infests maize at the whorl stage, causing leaf damage (Capinera 2000). This direct foliar damage is alarming to many farmers, who have never experienced this type of damage before (Hruska 2019). FAW also infests the ears, especially during large infestation causing the direct loss of grain (Buntin 2008). Estimates provided by Day et al. (2017) indicate that FAW impacts between 8.3 and 20.6 million tons maize yield per year out of the total expected production of 39 million tons per year in Africa. Yield losses of 15–73% were predicted by Hruska and Gould (1997) when 55–100% of corn plants were infested with FAW.

It is important to understand how pests, hosts, and the environment interact, with environment being primarily represented by weather conditions (López et al. 2019). Climatic conditions appear to be the most cited factor driving the presence of FAW, including temperature, length of exposure, and precipitation during the warm/wet season (Du Plessis et al. 2018; Early et al. 2018). Recent studies (Nboyine et al. 2020; Koffi et al. 2020) reported that maize infestation of FAW in Africa varied over time within seasons and agro-ecological zones (AEZ). The degree day (DD) is also an important parameter for forecasting pest phenology and voltinism (Tu et al. 2014), as well as identifying key biological events for the FAW, such as egg hatching adult dispersal and to determine when to respond by setting traps, assessing damage, and collecting samples (Labatte 1994; Westbrook et al. 2016; Du Plessis et al. 2020).

Since its invasion of the African continent, several countries (e.g., Benin, Ghana, Togo, Cameroun, Kenya...) have carried out infestation assessment studies (Goergen et al. 2016; Fotso Kuate et al. 2019; Baudron et al. 2019; Nboyine et al. 2020; Koffi et al. 2020). However, studies and data on FAW infestation in DR Congo remain limited and poorly documented. This study aimed to evaluate FAW infestations with regard to season and the agro-ecological zones (AEZ) of selected maize-growing areas in the eastern DR Congo. Within this framework, accumulated degree days (DD) by FAW were evaluated from a starting date in each season and agro-ecological zone. The results are expected to provide baseline information to update FAW pest status and develop effective strategies to manage it in the Eastern DR Congo.

Materials and methods

Study area description

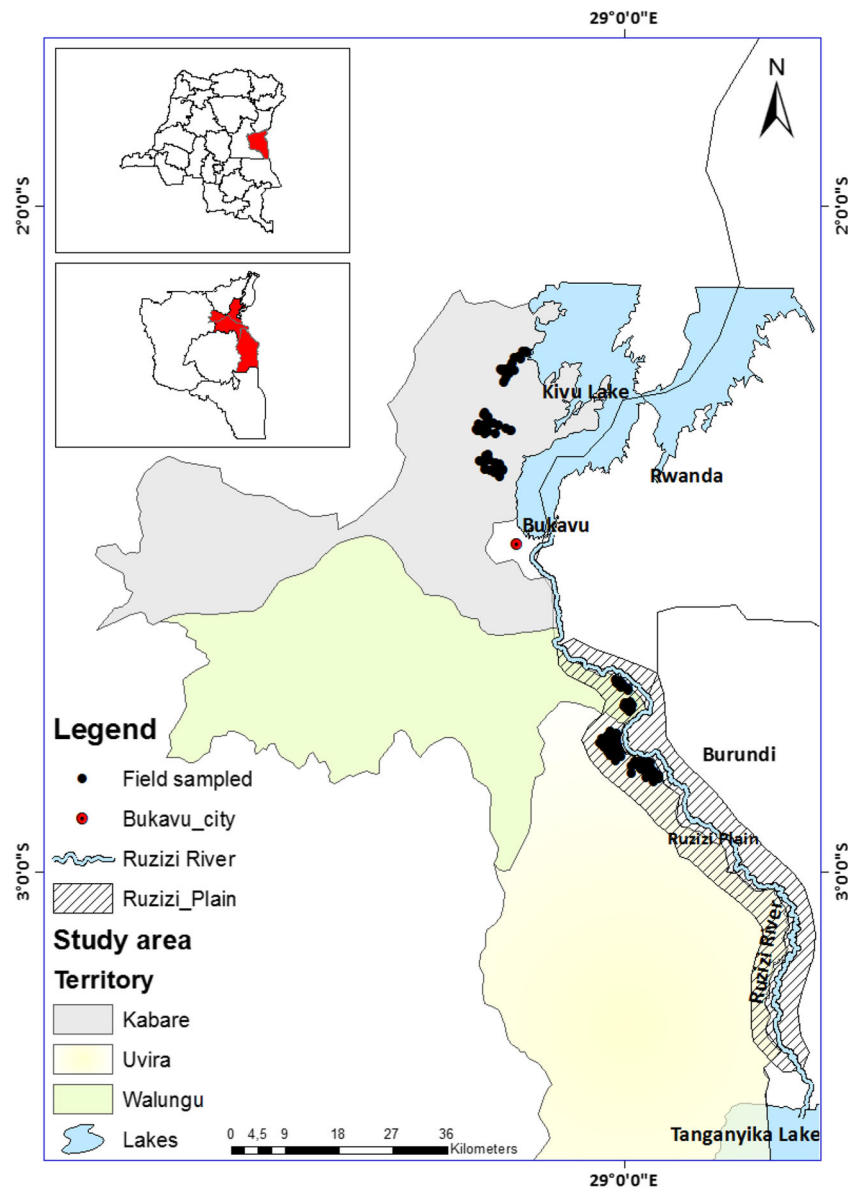
To assess FAW infestations, a survey was conducted in South-Kivu Province, DR Congo. Investigations were set up in two agro-ecological zones (Fig. 1): Kabare (2°27'26.94"S, 28°49'12.75"E, 1563 m), and Ruzizi Plain (2°47'14.54"S, 28°59'54.1"E, 899 m). Kabare is located in the extreme East of DR Congo (mid-altitude zone), on the western shores of Lake Kivu. It has a humid tropical type climate. This territory has two seasons: a dry season that lasts 3 months (June to August) and a rainy season that lasts 9 months (September to May). The rainy season is divided into two crop seasons: September to January (season A) and February to June (season B). The Ruzizi Plain is divided between three countries; namely DR Congo, Rwanda, and Burundi. The name Ruzizi Plain derives from its relief, which is a large plain (lowland area) located along the Ruzizi River. Ruzizi Plain has a semi-arid climate with a bimodal rainfall regime: from October to January and from February to May (Vancoppenolle et al. 1984).

Evaluation of the seasonal infestation of FAW

Incidence surveys of damaged plants by FAW were conducted at Kabare in November 2018 and at Ruzizi Plain in December 2018, when maize was at the 8-leaf stage. The same surveys were conducted at Kabare in March 2019 and Ruzizi Plain in April 2019, when all maize crops were at the 8-leaf stage. The assessment consisted of analyzing the incidence and severity of infestation on maize leaves. A transect method was used on maize farms in each agro-ecological zone. Fifty (50) fields were selected for the investigation in each agro-ecological zone. A total of hundred (100) fields were assessed in the 2018 crop season. During the 2019 crop season, the same fields were investigated using a tracking system. The tracking system, GPSMAP (GARMIN GPS devices) allowed the same geographical coordinates to be evaluated in 2019 as in 2018. This approach allowed us to determine seasonal variability in FAW infestation. Seven quadrats, each 20 m² in size, were randomly formed in each field using the W sampling method proposed by McGrath et al. (2018). Maize plants were considered infested when larvae, fresh sawdust-like frass, or fresh larval feeding plant injury were found (Koffi et al. 2020).

To assess incidence, several parameters were considered in each quadrat. These parameters included the number of infested plants (NIP), total number of plants (TNP), number of larvae per plant (NLP), and number of larvae per defined area (20 m²) (NLDA). The number of damaged leaves per plant (NIL) and the number of lesions per leaf (NLL) were

Fig. 1 Map of the study area. Fields sampled are indicated.



determined by considering the whorled and furled leaves. These variables were determined on 10 plants randomly selected from the quadrat. In each quadrat, the number of larvae per plant (NLP) was assessed by counting the larvae on each infested plant. The detection of larvae was carried out by opening the whorled leaves on each infested plant (Koffi et al. 2020). Next, the number of larvae per quadrat (NLDA) was assessed by summing the NLP for all plants infested in the quadrat. To ascertain that the damages observed were indeed those of FAW, samples of FAW larvae in each agro-ecological zone were taken for subsequent morphological identification in the laboratory. Severity was determined based on the number and size of lesions for each leaf based on the scale of the evaluation proposed by Davis et al. (1992). The percentage of infested plants per field was also determined.

Climatic data collection and calculation of FAW degree days

The climatic data including environmental and bioclimatic parameters were measured during the 2018 and 2019 seasons. Particularly, the information on the bioclimatic characteristics of the study areas was obtained from images of bioclimatic variables that were downloaded from the Africlim site (<https://www.york.ac.uk/environment/research/kite/resources/>) over long periods of time (1950–2000) using the geographical coordinates of the investigated maize fields. The bioclimatic variables of the study areas are presented in Table 1. These variables were then used as additional variables in the principal component analysis that provided a better understanding of the variation in FAW infestation and the factors that are likely to influence them.

Table 1 Environmental and bioclimatic parameters.

Environmental and bioclimatic parameters	Code	Units
Mean annual temperature (* 10)	BIO1	°C
Mean daytime temperature range (monthly average) (* 10)	BIO2	°C
Isothermality (bio1/bio7) * 100	BIO3	-
Temperature seasonality (Standard deviation * 100)	BIO4	°C
Maximum temperature of the hottest month (* 10)	BIO5	°C
Minimum temperature of the coolest month (* 10)	BIO6	°C
Annual temperature range (bio5-bio6) (* 10)	BIO7	°C
Mean temperature of the warmest quarter (* 10)	BIO10	°C
Mean temperature of the coldest quarter (* 10)	BIO11	°C
Annual rainfall	BIO12	mm
Rainfall during the wettest month	BIO13	mm
Rainfall during the driest month	BIO14	mm
Rainfall seasonality	BIO15	mm
Rainfall in the wettest quarter	BIO16	mm
Rainfall in the driest quarter	BIO17	mm
Longest dry season duration	LLDS	-
Annual moisture index	MI	-
Moisture index of the dry quarter	MIAQ	-
Moisture index of the wet quarter	MIMQ	-
Potential evapotranspiration	PET	mm
Elevation	DEM	m

To determine the number of FAW generations (NOG) in each season and agro-ecological zone, degree days (DD) were estimated. This measure was used because each species requires a defined number of DD to complete its development (Zalom et al. 1983). According to Day and Karayiannis (1998), DD may be calculated using four main methods. In our case, mean daily temperature (from daily maxima and minima) was used. DD was calculated using the following formula (Snyder 1985; Michaud and Moreau 2011):

$$DD = [(T_{\min} + T_{\max})/2] - T_{HR}$$

where T_{\min} and T_{\max} represent the minimum and maximum air temperatures reached per day and T_{HR} is the minimum threshold temperature. For estimated T_{HR} , we accounted for the variation reported in published literature (Hogg et al. 1982; Ali et al. 1990; Valdez-Torres et al. 2012; Early et al. 2018; López et al. 2019). We considered a T_{HR} of 12°C based on Du Plessis et al. (2018), which reflected the tropical distribution of FAW. The number of FAW generations (NOG) was calculated as follow:

$$NOG = \frac{\sum_{n=1}^{\infty} DD}{PDD}$$

where NOG is the number of FAW generations, PDD is the minimum degree day sum needed to complete a

generation (600 degree days) according to Du Plessis et al. (2018), and DD is the mean daily degree day.

Data analysis

R version 3.5.1 was used for statistical analysis (R development Core Team 2018). Wilcoxon rank test was applied at the 5% significance level ($P < 0.05$) to compare FAW infestation parameters (incidence, NIP, TNP, NIL, NLL, NLP, and NLDA) from season and AEZ. The multivariate statistical analyses allow to summarize principal data structure or to reveal particular correlations between original variables. We used principal component analysis (PCA) to describe our dataset using package FactoMineR (Lê et al. 2008). Eight variables were used to characterize FAW infestation: NIP, TNP, NIL, NLP, NLL, NLDA, Severity, and incidence. Bioclimatic variables, season and AEZ, were considered additional variables in the PCA. The PCA produced eight main axes, of which four were used to interpret the relationships between the variables characterizing FAW infestation. The Kaiser criterion was used to select the main components for factor analysis, the eigenvalues of which were above unity, since they generated components with relevant amounts of the original information.

Results

Bioclimatic characterization of maize fields in Kabare territory and Ruzizi Plain

The fields investigated here were located at different altitudes, and so had very different bioclimatic characteristics (Table 2). For instance, in Kabare, the environment was characterized by low values for almost all characteristic variables related to temperature, but exhibited high values for all rainfall variables. The opposite trend in bioclimatic characteristics was obtained for Ruzizi Plain. The Ruzizi Plain was characterized by high temperatures and low rainfall, whereas Kabare was characterized by high rainfall and low temperatures.

Characterization of FAW seasonal infestation in the maize fields of Kabare and Ruzizi Plain

Table 3 shows the differences in FAW infestation in Kabare and the Ruzizi Plain. FAW infestation appeared to be more severe in Ruzizi Plain compared to Kabare. Ruzizi Plain had the highest values for NIP, TNP, NLP, NLL, NLDA, Severity, and incidence. However, the range of variation in the observed infestation parameters noticeably differed. Data from Ruzizi Plain showed high statistically differences, highlighting some

Table 2 Description (mean \pm SD) of bioclimatic characteristics of sampled field locations in Kabare and Ruzizi Plain.

Variables	Kabare	Ruzizi Plain	Total
BIO1	186.2 \pm 5.3	231.3 \pm 3.8	209 \pm 23.1
BIO2	106.7 \pm 2	122.8 \pm 1.3	114.8 \pm 8.2
BIO3	839.9 \pm 9.1	800.1 \pm 4.6	819.8 \pm 21.2
BIO4	3 \pm 0	3.5 \pm 0.5	3.3 \pm 0.4
BIO5	250.4 \pm 5.7	310.2 \pm 3.7	280.6 \pm 30.4
BIO6	123.5 \pm 5.8	156.8 \pm 4.4	140.3 \pm 17.5
BIO7	126.9 \pm 2.8	153.3 \pm 2	140.2 \pm 13.5
BIO10	189.5 \pm 5.5	236.6 \pm 3.7	213.3 \pm 24
BIO11	183 \pm 5.9	227.7 \pm 3.9	205.6 \pm 23
BIO12	1579.4 \pm 41.3	1063.7 \pm 30.4	1318.9 \pm 261
BIO13	184.6 \pm 5	142.8 \pm 4.9	163.5 \pm 21.5
BIO14	22.2 \pm 1.4	7.7 \pm 0.6	14.9 \pm 7.4
BIO15	54.4 \pm 2.1	46 \pm 1	50.2 \pm 4.5
BIO16	508 \pm 14.6	389.4 \pm 8.4	448.1 \pm 60.6
BIO17	118.7 \pm 4.8	50 \pm 4.1	84 \pm 34.8
DEM	1609.2 \pm 87.5	917.3 \pm 45.1	1259.6 \pm 353.7
LLDS	3 \pm 0	4.4 \pm 0.5	3.7 \pm 0.8
MI	107.1 \pm 3.9	59.8 \pm 2	83.2 \pm 23.9
MIAQ	33.4 \pm 1.8	12 \pm 0.9	22.5 \pm 10.8
MIMQ	138.6 \pm 4.9	91.1 \pm 2.4	114.6 \pm 24.1
PET	1474 \pm 16.9	1775.6 \pm 14.5	1626.4 \pm 152

Table 3 Effect of season and agro-ecological zone (AEZ) on the parameters of fall armyworm infestations.

Variables	Agro-ecological zones (AEZ)		Season	
	Kabare	Ruzizi Plain	A2018	B2019
NIP	13.1 \pm 8 a	20.6 \pm 10.1 b	14.2 \pm 7.9 a	19.5 \pm 10.8 b
TNP	31.4 \pm 11.1 a	35.4 \pm 9.3 b	38.7 \pm 10.4 b	28.2 \pm 7.3 a
NIL	5.1 \pm 1.9 a	5.4 \pm 1.8 a	4.6 \pm 1.6 a	5.9 \pm 1.8 b
NLP	1.5 \pm 0.5 a	1.7 \pm 0.6 b	1.5 \pm 0.6 a	1.6 \pm 0.6 a
NLL	13.3 \pm 6.2 a	16.6 \pm 7.8 b	14.1 \pm 6.4 a	15.8 \pm 7.9 a
NLDA	16.1 \pm 11.9 a	28.5 \pm 19.3 b	16.9 \pm 12.9 a	27.8 \pm 19.2 b
Severity	5.4 \pm 1.2 a	6.2 \pm 1.5 b	5.8 \pm 1.3 a	5.8 \pm 1.5 a
Incidence	0.4 \pm 0.2 a	0.6 \pm 0.3 b	0.4 \pm 0.2 a	0.7 \pm 0.2 b

Means \pm SD followed by the same lowercase letter within rows are not significantly different according Wilcoxon rank test at 5% significance level ($P < 0.05$). *NIP*, number of infested plants; *TNP*, total number of plants; *NIL*, number of infested leaves per plant; *NLP*, number of larvae per plant; *NLL*, number of lesions per leaf; *NLDA*, number of larvae per defined area (20 m²).

variability in FAW infestation. In comparison, in Kabare, the ranges of variation seemed to be smaller, reflecting lower heterogeneity in infestation compared to Ruzizi Plain. Thus, FAW infestation was more pronounced in the warmer environment with lower rainfall, and was less pronounced in environments with higher rainfall and cooler temperatures. Seasonal infestations of FAW (Table 3) were more pronounced in the B2019 season compared to the A2018 season. Season B2019 had the highest NIP, NIL, NLDA, and incidence. The severity of infestation was similar for both seasons.

Principal component analysis of FAW infestations in Kabare and Ruzizi Plain

The principal component analysis of the two study areas is presented in Table 4 and Fig. 2. Four (4) principal components with eigenvalues greater than 1 were retained for interpretation. All bioclimatic variables, Season, and Area of study were used as supplementary variables, and did not contribute to the principal components. The four principal components represented more than 78% of total variance of the entire data set, with the first two components representing more than 52% of total inertia.

The first axis (Dim.1) captured more than 35% of total variance. It was highly correlated with NLDA, Severity, and incidence. This axis made it possible to characterize FAW infestation better. It provided information on the relationship between the incidence and severity of FAW infestation at the two study areas as a function of season and bioclimatic factors. FAW infestation was more pronounced under relatively higher temperatures (BIO1, BIO2, BIO5, BIO6, BIO7,

Table 4 Principal component analysis of fall armyworm infestation.

	Configuration	Dim.1	Dim.2	Dim.3	Dim.4
Eigen value		2.8495	1.3440	1.0748	1.0120
Percentage of variance		35.6187	16.8000	13.4348	12.6497
Cumulative percentage of variance		35.6187	52.4188	65.8536	78.5033
NIP	Active variable	<i>0.4586</i> (7.3812)	<i>0.3297</i> (8.0870)	<i>0.7498</i> (52.3029)	0.0484 (0.2319)
TNP	Active variable	-0.0443 (0.0688)	<i>-0.6481</i> (31.2526)	<i>0.3865</i> (13.8967)	<i>0.5177</i> (26.4793)
NIL	Active variable	0.0527 (0.0976)	<i>0.8131</i> (49.1864)	-0.0445 (0.1841)	<i>0.3478</i> (11.9499)
NLP	Active variable	<i>0.5434</i> (10.3618)	-0.0150 (0.0166)	<i>-0.5913</i> (32.5277)	<i>0.4236</i> (17.7288)
NLL	Active variable	<i>0.3246</i> (3.6971)	0.1117 (0.9280)	0.0762 (0.5399)	<i>0.5503</i> (29.9241)
NLDA	Active variable	<i>0.8989</i> (28.3541)	-0.1184 (1.0430)	-0.0529 (0.2606)	-0.0533 (0.2804)
SEVERITY	Active variable	<i>0.8512</i> (25.4278)	<i>-0.3219</i> (7.7075)	-0.0255 (0.0604)	-0.0944 (0.8813)
INCIDENCE	Active variable	<i>0.8374</i> (24.6115)	<i>0.1546</i> (1.7789)	0.0495 (0.2276)	<i>-0.3560</i> (12.5243)
A2018	Supplementary category	<i>-0.5628</i>	<i>-0.6568</i>	0.0429	<i>0.2126</i>
B2019	Supplementary category	<i>0.5510</i>	<i>0.6432</i>	-0.0420	<i>-0.2082</i>
KABARE	Supplementary category	<i>-0.7012</i>	0.0131	<i>-0.2227</i>	<i>-0.2128</i>
RUZIZI PLAIN	Supplementary category	<i>0.6865</i>	-0.0129	<i>0.2180</i>	<i>0.2084</i>
BIO1	Supplementary variable	<i>0.4204</i>	-0.0261	<i>0.2207</i>	<i>0.2051</i>
BIO2	Supplementary variable	<i>0.4115</i>	-0.0053	<i>0.2219</i>	<i>0.1990</i>
BIO3	Supplementary variable	<i>-0.4114</i>	0.0149	<i>-0.2394</i>	<i>-0.1705</i>
BIO4	Supplementary variable	<i>0.3178</i>	0.0223	<i>0.1539</i>	0.0439
BIO5	Supplementary variable	<i>0.4215</i>	-0.0225	<i>0.2269</i>	<i>0.2056</i>
BIO6	Supplementary variable	<i>0.4087</i>	-0.0347	<i>0.2150</i>	<i>0.2081</i>
BIO7	Supplementary variable	<i>0.4181</i>	-0.0060	<i>0.2287</i>	<i>0.1926</i>
BIO10	Supplementary variable	<i>0.4191</i>	-0.0242	<i>0.2243</i>	<i>0.2055</i>
BIO11	Supplementary variable	<i>0.4154</i>	-0.0278	<i>0.2221</i>	<i>0.2081</i>
BIO12	Supplementary variable	<i>-0.4140</i>	0.0210	<i>-0.2225</i>	<i>-0.2147</i>
BIO13	Supplementary variable	<i>-0.4052</i>	0.0262	<i>-0.2191</i>	<i>-0.2189</i>
BIO14	Supplementary variable	<i>-0.4091</i>	0.0247	<i>-0.2198</i>	<i>-0.2130</i>
BIO15	Supplementary variable	<i>-0.3769</i>	0.0157	<i>-0.2138</i>	<i>-0.2192</i>
BIO16	Supplementary variable	<i>-0.4079</i>	0.0207	<i>-0.2223</i>	<i>-0.2189</i>
BIO17	Supplementary variable	<i>-0.4151</i>	0.0208	<i>-0.2151</i>	<i>-0.2132</i>
DEM	Supplementary variable	<i>-0.4177</i>	0.0163	<i>-0.2209</i>	<i>-0.2014</i>
LLDS	Supplementary variable	<i>0.3965</i>	-0.0200	<i>0.1912</i>	<i>0.1985</i>
MI	Supplementary variable	<i>-0.4156</i>	0.0206	<i>-0.2251</i>	<i>-0.2126</i>
MIAQ	Supplementary variable	<i>-0.4126</i>	0.0224	<i>-0.2223</i>	<i>-0.2116</i>
MIMQ	Supplementary variable	<i>-0.4116</i>	0.0216	<i>-0.2276</i>	<i>-0.2128</i>
PET	Supplementary variable	<i>0.4221</i>	-0.0171	<i>0.2257</i>	<i>0.2030</i>

Values in italic are significantly different from 0 at $\alpha = 0.05$ (p value < 0.05). NIP, number of infested plants; TNP, total number of plants; NIL, number of infested leaves per plant; NLP, number of larvae per plant; NLL, number of lesions per leaf; NLDA, number of larvae per defined area (20 m²).

BIO10, and BIO11) with high evapotranspiration (PET) over relatively long periods (LLDS). These conditions were characteristic of the Ruzizi Plain and/or B2019 season. In comparison, FAW infestation was less pronounced in conditions with heavy rainfall (BIO12, BIO13, BIO14, BIO15, BIO16, and BIO17). These characteristics were encountered at Kabare and/or A2018 season.

The second axis (Dim.2) described the relationships between the number of infested leaves (NIL), total number of

plants (TNP), and seasonal FAW infestation. It described the distribution of FAW in fields with respect to field characteristics. Fields with high numbers of plants (TNP) tended to have low numbers of infested leaves per plant (NIL). During the A2018 season, NIL was lower in maize. FAW infestation was less pronounced during the A2018 season, and was mostly characterized by heavy rains and low temperatures. These conditions represent unfavorable periods (low temperatures) for FAW, which, while present, caused less damage, with

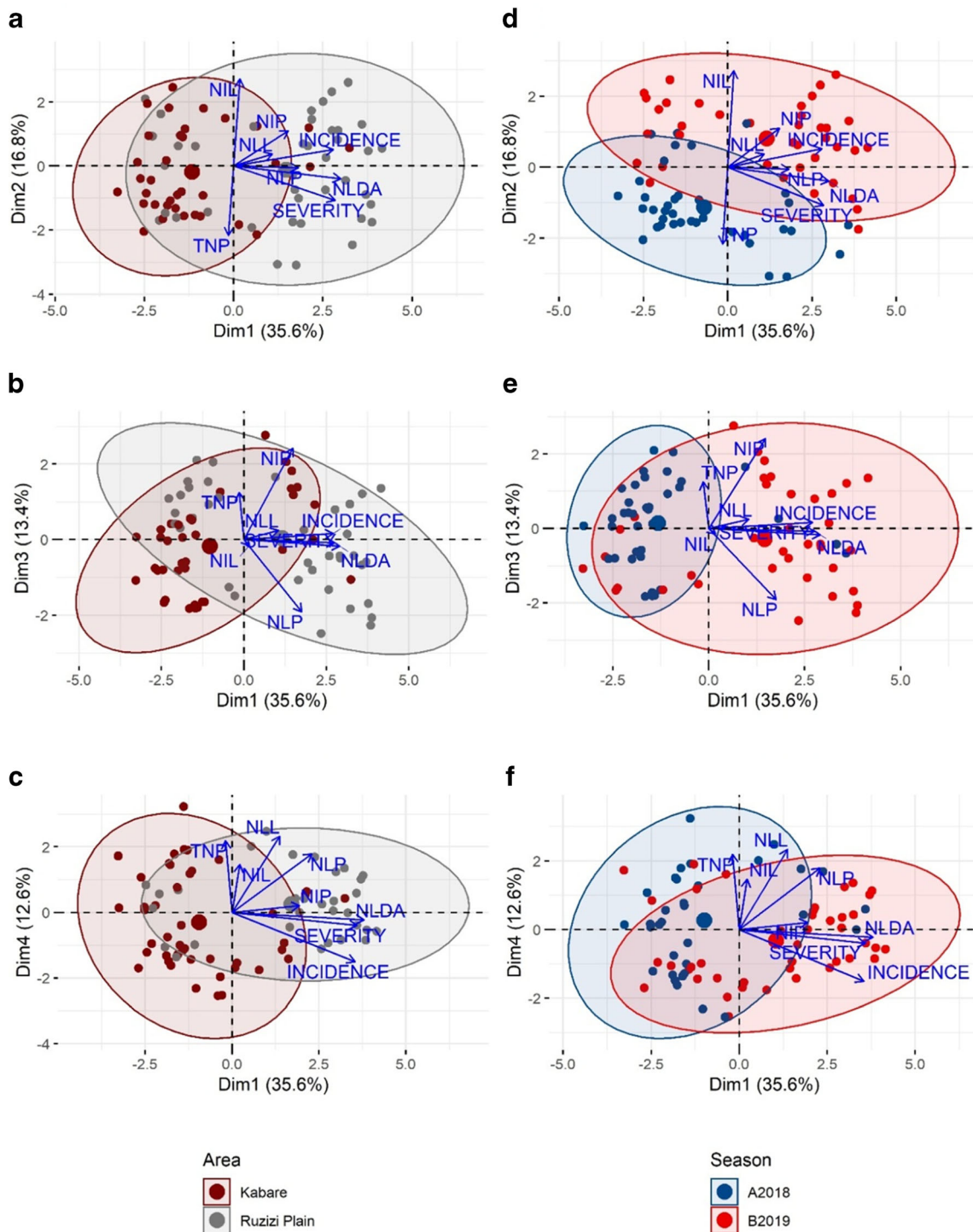


Fig. 2 Output of the principal component analysis: characterization of fall armyworm infestation in the study areas (A–C) and seasons (D–F) in the planes Dim.1-Dim.2, Dim.1-Dim.3, and Dim.1-Dim.4.

almost no incidence. In other words, larvae were present, but were not yet at the stage where they would cause damage to plants, with almost nil incidence in the A2018 season.

The third axis (Dim.3) provided information on the relationships between the number of infested plants (NIP), number of larvae per plant (NLP), and total number of plants in the

field (TNP). FAW tended to infest all plants in a field, with the highest numbers of infested plants being observed in fields with the highest numbers of maize plants. However, when infestation was spread across a larger number of maize plants, larval numbers per plant were low. Unexpectedly, the fourth axis (Dim.4) showed that cases existed where the incidence

was low, because maize fields contain large numbers of plants (TNP). Consequently, plants containing large numbers of larvae (NLP) infected a large number of leaves (NIL), causing a large number of lesions on leaves (NLL); however, the degree of damage was very low.

Variation of degree day, precipitation, and number of FAW generations across seasons and agro-ecological zones

Table 5 shows the difference in terms of infestation between the two seasons and the two agro-ecological zones. The Ruzizi Plain was more favorable to FAW based on the sum of accumulated degree days. Mean NOG was 1.68 (~2) and 2.82 (~3) in Kabare territory and Ruzizi Plain, respectively. Across the two seasons, about two and three generations were observed in Kabare territory and the Ruzizi Plain, respectively. The total annual number of generations was 5.64 (~6) and 3.36 (~3) in the Ruzizi Plain and Kabare territory, respectively. Precipitations were higher in the A2018 season in Kabare territory compared to Ruzizi Plain (Table 5). Of note, higher rainfall was recorded during the B2019 season compared to the A2018 season in the Ruzizi Plain compared to Kabare territory.

Discussion

FAW infestations on maize have been observed since 2016 in South-Kivu Province (personal observations), the year it was first introduced to the African continent. However, preliminary research has been limited, due to the negligible extent of damage observed during this time. Over the last 3 years, this pest has started to devastate maize crops in the region. Koffi et al. (2020) reported that infestation levels of FAW vary from

one agro-ecological zone to another. López et al. (2019) and Koffi et al. (2020) reported that damage to crops (such as corn) by FAW varies across years. The incidence, level of leaf damage, and larval density of FAW varied significantly depending on the season and agro-ecological zone. The incidence of FAW was higher in the Ruzizi Plain and B2019 season (Table 3). Baudron et al. (2019) showed that the incidence of plants with FAW damage symptoms varied depending on the estimate used for determining the parameter. Around 48.3% of plants were estimated to have leaf damage, while 31.6% of plants had frass in the whorl (Baudron et al. 2019). FAW infestation varied considerably among farms in three countries surveyed by Sisay et al. (2019), with mean percent FAW infestation ranging from 5.3 to 100%. When 100% of the irrigated maize plants were infested by FAW under experimental conditions, yield declines by 45% (Hruska and Gladstone 1988). Under natural rainfall, where 100% of infestation occurs, yield declines by 15–30% (Van Huis 1981) and up to 73% (Hruska and Gould 1997). The Davis damage score was intermediate for each season and each agro-ecological zone of the current study, dominated by score 5 (Table 3). In comparison, low to moderate leaf damage scores were reported by Sisay et al. (2019). A lower Davis damage score of 3.78 was recorded by Baudron et al. (2019). Baudron et al. (2019) suggested that FAW damage does not necessarily significantly impact crop yield.

Beserra et al. (2002) showed that the distribution of FAW larvae and eggs varied with the phenological stage of corn. At the 8-leaf stage (V6), the larval density of FAW per plant varied with respect to agro-ecological zone in our study, with 1.7 larvae per plant being recorded in the Ruzizi Plain and 1.5 in Kabare (Table 3). Only one larva was recovered per plant in a study by Murúa et al. (2006), and Fotso Kuate et al. (2019). This decrease in NLP was due to cannibalism, dispersal, and predation (Peireira and Hellman 1993, Chapman et al. 1999,

Table 5 Sum of degree day (DD) and number of FAW generations (NOG), and precipitations (P^{mm}) during the seasons in the agro-ecological zones.

Season	Month	DD		P^{mm} (mm)		NOG	
		Ruzizi Plain	Kabare	Ruzizi Plain	Kabare	Ruzizi Plain	Kabare
A2018	September	357	215.8	50	129.7	2.89	1.72
	October	359.9	210.2	83.3	167.3		
	November	331.5	195.2	103	178.1		
	December	343	202.8	121.5	169.6		
	January	344.9	209.8	120.2	148.2		
	Σ	1736.6	1034.1	478.2	793.1		
B2019	February	312.5	188.5	109.8	147.3	2.75	1.64
	March	345.5	210.1	136.3	178.8		
	April	333.3	200.7	141.6	180.2		
	May	343.6	206.3	96.8	124.7		
	June	319.3	183.7	24.3	44.1		
	Σ	1654.4	989.3	509	675.4		

Capinera 2000), because larval density per plant is higher at the start of infestation. Marengo et al. (1992) documented that a mean density of 0.2 to 0.8 larvae per plant during the late whorl stage could reduce yield by 5 to 20%.

Differences recorded in the parameters of FAW infestations during this study were directly related to climatic conditions. Indeed, Hruska and Gladstone (1988) stated that damage caused by FAW is strongly associated to environmental conditions. The study areas had totally different bioclimatic characteristics (Table 2). Nboiyine et al. (2020) reported that the abundance of FAW in maize is influenced by the growth stage of the crop, rainfall, and relative humidity. Murúa et al. (2006) suggested that temperature and rainfall are the climatologic factors that significantly impact FAW density. FAW infestation was pronounced at relatively higher temperatures with high evapotranspiration, which were conditions characteristic of the Ruzizi Plain and B2019 season. In comparison, Kabare territory and A2018 season were characterized by heavy rainfall conditions (Table 5). One factor that might have contributed to the high severity and incidence of FAW infestation during the B2019 season was a short period of drought between the end of the A2018 season and the beginning of the B2019 season. However, Fotso Kuate et al. (2019) observed that areas with bimodal rainfall have a higher accumulation of FAW populations during the first planting season. Indeed, rainfall enhances larval mortality state of FAW (Early et al. 2018; Cokola 2019) with the first season (A2018) characterized by huge amounts of rain (Table 5).

Barfield and Ashley (1987) reported that the developmental times of FAW are temperature-dependent, being modified by the stage of maize consumed. Hogg et al. (1982), Barfield and Ashley (1987), and Busato et al. (2005) reported that the development time of eggs, larvae, and pupae decreases with temperature up to 35°C. Accumulated DD by FAW was important in the Ruzizi Plain compared to Kabare (Table 5), because the Ruzizi Plain is dominated by a semi-arid climate. Fatoretto et al. (2017) documented that FAW is highly reproductively efficient in tropical areas. In warmer temperature conditions (such as the Ruzizi Plain), there may be several generations per year versus two or less generations in temperate areas. The development of FAW and other insects is favored by warm temperatures, which increase the number of generations in a given region (Westbrook and Sparks 1986).

Up to three generations of FAW were reported in this study during the B2019 season in the Ruzizi Plain and Kabare territory and two during A2018 in both areas. The total annual number of generations is about six in the Ruzizi Plain and three in Kabare territory. Busato et al. (2005) reported up to eight generations per year in the maize fields of tropical areas. Du Plessis et al. (2018) reported that the NOG of FAW occurring in an area varies with the appearance of the dispersing adults. However, outside the growing season, FAW populations can be maintained by infesting other crops

(Montezano et al. 2018). During the dry season, the annual NOG of FAW likely increases, because FAW infest crops other than maize and sorghum in the study area (personal communication). Vegetable crops, such as onion, have been reported as alternate hosts during the dry season. Rapid generation turnover in FAW is facilitated by the presence of intercropping, where different crops grow at the same time and successively throughout the year, maintaining a high density of FAW (Fatoretto et al. 2017).

FAW is an important pest in the Eastern DR Congo, with infestation varying with the cropping seasons and agro-ecological zone. The late season (B2019) and the Ruzizi Plain were the most favorable for FAW development. Rainfall seemed to be a factor limiting FAW infestation in the region, whereas warm temperatures accelerated development and increased the number of generations per year. Because of its polyphagous feeding behavior, FAW threaten agriculture in Eastern DR Congo. In the context of monitoring and developing effective control strategies against FAW, it is necessary to be vigilant for dry season populations by identifying alternative host plants.

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Author Contribution Statement F Francis and EB Bisimwa planned and supervised the project. MC Cokola, Y Mugumaarhama, N Grégoire, LK Muzee, JZ Mugisho, VM Aganze, and AK Lubobo performed the experiments, analyzed the data, and contributed reagents/materials/analysis tools. All authors contributed to the writing and revision of the final manuscript. All authors read and corrected the manuscripts.

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