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ORIGINAL RESEARCH ARTICLE

# Could fall armyworm, *Spodoptera frugiperda* (J. E. Smith) invasion in Africa contribute to the displacement of cereal stemborers in maize and sorghum cropping systems

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**Abstract**
The fall armyworm (FAW), *Spodoptera frugiperda* (J.E. Smith), which has recently invaded the African continent, has become a new threat to cereal production. Being an invasive pest with certain competitive advantages, the impact of FAW on other lepidopteran pests is unclear. This study assessed the infestation of FAW and cereal stemborers on maize and sorghum under mono-cropped systems that are adjacently placed in five districts in Uganda. Data on maize and sorghum infestation cereal stemborers and FAW was collected at 6, 9 and 16 weeks after planting (WAP), to determine intensity and severity. Cereal stemborer infestations on maize at 6, 9 and 16 WAP were only 36.7%, 48.2% and 24.0%, respectively, which was significantly lower than the infestations on sorghum, at 55.5%, 53.2%, 64.0%, respectively. On the contrary, the infestations of FAW on maize at 6, 9 and 16 WAP were 89.5%, 84.7% and 86.0%, respectively, while on sorghum they were 51.0%, 56.5% and 47.0, respectively. The severity of stemborers on sorghum was statistically higher than on maize, whereas the damage severity of FAW was generally higher on maize than on sorghum. Intensity of damage and cavity length due to stemborer on sorghum was higher than on maize. Historical records showed that in maize stemborer infestation could reach 60%. This infestation started significantly declining in 2016, suggesting an early arrival of FAW in Uganda. The present study indicates a possible displacement of stemborer from maize onto sorghum. Any Integrated Pest Management (IPM) package should consider managing FAW and stemborer together in both maize and other cereal hosts.

**Keywords** Invasiveness · Displacement · Pest · Competition · Stem borer · Fall armywom

## Introduction

Cereal crops (maize and sorghum) are a dietary staple for more than 200 million people in sub-Saharan Africa, and their value chain involves millions of farmers and private sector companies including seed and grain producers, millers and others (Macauley and Ramadjita 2015). In Uganda, cereals such as maize, sorghum, millet and rice occupy 24.8% of the total cultivated area planted (UBOS 2018). However, cereal production is vulnerable to drought, diseases and pests such as lepidopteran species. The two most injurious lepidopteran pests are *Busseola fusca* (Füller) (Noctuidae), a native stemborer and the invasive *Chilo partellus* (Swinhoe) (Crambidae). Cereal stemborers predominantly *B. fusca* and *C. partellus* damage can cause over 80% grain yield loss (Kfir et al., 2002). Various studies have shown that stemborer species can use the same ecological niches (Calatayud et al. 2014b; Kfir et al. 2002; Reddy 1983; Sokame et al. 2019). However, the composition of these stemborer communities varies with the crop, locality, altitude, and season (Ntiri et al. 2019). In 2016, the FAW *Spodoptera frugiperda* J.E. Smith, a noctuid native to tropical and subtropical regions of America (Sparks 1979), invaded Africa (Day et al. 2017; Goergen et al. 2016). FAW is a polyphagous pest feeding on more than 300 plants, but with a preference for grasses and cereal crops such as

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maize and sorghum (Montezano et al. 2018). FAW has become a significant economic pest in the region, causing substantial losses on maize and *sorghum Sorghum bicolor* (L.) Moench and has the potential to damage other crops such as rice, *Oryza sativa* L.; cotton, *Gossypium hirsutum* L.; groundnut, and forage and turf grasses (Day et al. 2017; Rwomushana et al. 2018). Fall armyworm is now present in 44 African countries (Rwomushana et al. 2018). In Uganda, the pest was first observed in May 2016, in three districts, Kayunga (Central Uganda), Kasese and Bukedea located in the Eastern part of the country (Abrahams et al. 2017; Otim et al. 2018). It subsequently spread rapidly to the rest of the country.

The arrival of the FAW in Africa also raises several questions relating to the previous status quo of cereal lepidopteran pests. It is generally hypothesized that the presence of an invasive species with some competitive advantages creates interspecific competition with the indigenous pest species which might lead to the displacement of the local pests. Some cases reported in the literature relate to the displacement of *B. fusca* by the invasive species *C. partellus* (Kfir 1997; Mutamiswa et al. 2017) and *Chilo orichalcocilillus* (Overholt 2008a); *Ceratitis cosyra* (Walker) (Diptera: Tephritidae) by *Bactrocera dorsalis* (Hendel) (Diptera: Tephritidae) (Ekesi et al. 2009); and the whitefly *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) species by *Bemisia tabaci* species B (Luan et al. 2012). In European greenhouses, *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae) has replaced *Thrips tabaci* Lindeman (Thysanoptera: Thripidae) as the major thrips pest (Paini et al. 2008; van Rijn et al. 1995). In the case of FAW, which is highly competitive (cannibalistic and non-diapausing), the displacement of the local cereal stemborers (*B. fusca* and *C. partellus*) from their major hosts (maize) to alternative host plants might occur. While Integrated Pest Management (IPM) strategies are being promoted to curtail FAW invasion, it is critical to investigate the dynamics of the cereal stemborers and FAW on maize and sorghum in this context of competition. The objective of this study was therefore, to determine if the cereal stemborers infestation of maize and sorghum is affected due to the invasion of FAW.

## Materials and methods

### Study area

The study was conducted in five districts of eastern Uganda, namely Iganga, Pallisa, Bukedea, Bugiri and Tororo (Fig. 1). The soils in the study area were once favorable for agricultural production, but are now mostly depleted, and consist mostly of sandy clay (Minai 2015). Maize and sorghum are the most important cereal crops in the study area. The area has a bimodal precipitation pattern with the annual rainfall varying from 500 to 2800 mm, with an average of 1180 mm (NEMA 2007; Ssentongo et al. 2018) and with two cropping seasons namely the long rains (February to July) and short rains (August to November). The field study was conducted during the short rainy season (August to December) in 2017.

### Long-term maize stemborer survey

Cereal stemborers infestation data was collected from Bugiri, Bukedea, Iganga, Tororo, and Pallisa districts in eastern Uganda. In each district, 30 maize farms were randomly selected, and in each farm, four quadrants measuring 9 sq. meter were selected. Each quadrant contains four rows and about 10 plants per row. The location of the quadrants and scoring were fairly representative of the farm. Data on the number of plants infested were collected to estimate percent infestation.

### The plot layout and crop management

On-farm experiments comprising of two treatments were replicated in five districts. The treatments consisted of (1) Mono-cropped maize and (2) Mono-cropped sorghum. Each treatment had a plot size of 12 × 17 m where maize was grown at a spacing of 75 cm between rows and 30 cm within the row, while sorghum was grown at a spacing of 75 cm between rows and 15 cm within the row.

The crop varieties used included “Longe 4 maize” and “milk-white sorghum”. Planting was done between 25th August and 16th September 2017 due to variation in rainfall pattern across the districts. Weeding was done twice, at three and nine weeks after planting (WAP). At planting, about 8 g/hill DAP was applied using a water bottle lid. No additional intervention, such as herbicide or insecticide applications, was done.

### Sampling procedure and data collection

Data were collected from four cell quadrants demarcated within a plot, each measuring 3 × 4 m (Fig. 2), where 20 plants were randomly selected per quadrant and examined for signs and symptoms of infestation by FAW and cereal stemborers. Signs and symptoms were used to distinguish infestation by FAW and cereal stemborers. FAW infestation was distinguished by the presence of larvae and whitish excrement as well as leaf feeding pattern. Infestation due to cereal stemborer was the characteristic circular holes on the leaves and absence of whitish sawdust like excrements. Infestation by cereal stemborers and FAW was recorded as presence (1) and absence (0) without destructive sampling. Infestation scoring was conducted at 6, 9, and 16 WAP by examining each of the 20 marked plants per quadrant for signs of injury during each of the three inspections. The plant was examined for new


**Fig. 1** The five study sites in the five districts

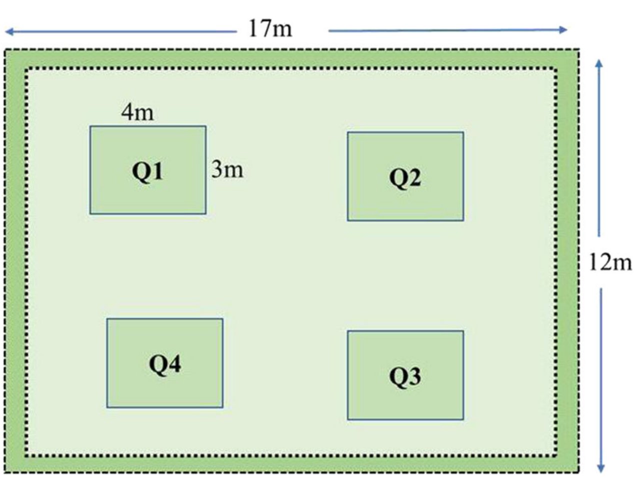


**Fig. 2** Scoring stations Q1, Q2, Q3, Q4 (four quadrants per plot size of 17 m × 12 m)

signs of infestation by one of the two insect types (stemborers and FAW).

Furthermore, the extent of damage caused by FAW and stemborers was assessed on a 1 to 5 scale where 1 = No sign of infestation, 2 = foliage infestation visible on some part of the leaves, 3 = About 50% of the younger leaves are showing infestation symptoms, 4 = About 75% of the plants showing infestation symptom where leaves are heavily fed by the larvae with visible frass accumulated on the plants, 5 = total plant infested often with dead heart showing complete damage of the plant due to FAW. At harvest maize stalks in the sampling quadrants were assessed for exit holes and tunnels to make corrections of the visual scoring. From those infested by stemborers, plants were randomly selected from each cell quadrant and each sample was divided into two segments (1 m from the base assigned for the first generation and above

1 m for second generation infestation) to assess first and second generation. Data collected include number of exit hole, and cavity length.

### Statistical analysis

The binary data on presence (1) and absence (0) of infestation of FAW and stemborer were analyzed using a generalized linear mixed model (GLMM) with random intercept assuming a binomial distribution error to evaluate the effect of crop (maize and sorghum) on presence/absence of infestation of maize stemborers (MSB) and FAW, respectively. The GLMM was fitted using the lme4 package (Bates et al. 2015). To estimate the variance components of the severity of stemborers and FAW, the number of exit holes, and cavity length of stemborers, we used a linear mixed model with the district, the sampling date and the crop as fixed factors, and quadrant and plant as random factors. The significance of the fixed factors was determined using the Satterthwaite approximation implemented in the R library lmerTest (Kuznetsova et al. 2017). Where significant difference was obtained, pairwise comparison was made using the least squares means and adjusted Tukey multiple comparison procedure ($\alpha = 0.05$) in lsmeans and multicompview packages, respectively (Mangiafico 2016; Russell 2016). All statistical analyses were carried out in R statistical software, version 3.5.2 (R core Team 2019).

## Results

### Long-term stemborer infestation history

Cereal stemborer infestation was recorded from five districts (Bugiri, Bukedea, Pallisa, Iganga and Tororo) of eastern Uganda. Averaged over the districts, the infestation of maize ranged between 31% and 52%, irrespective of the long and short rainy seasons (Table 1). However, there was a distinct reduction of stemborer infestation during the 2016 scoring in Bugiri and Bukedea districts (17% and 6%) which could probably be, related to FAW invasion.

**Table 1** Percent infestation of maize by maize stemborer scored from different districts of eastern Uganda (2013–2016)

| Year | Infestation rate (%) |
|---|---|
| 2013 | 52.4 ± 2.9d |
| 2014 | 43.1 ± 1.8b |
| 2015 | 47.3 ± 2.1c |
| 2016 | 31.34 ± 2.1a |

Means followed by different letters in the column were significantly different using the least squares means (LSMEANS) and adjusted Tukey multiple comparison procedure ($\alpha = 0.05$)

The comparison made between the long-term average before the arrival of FAW indicates that there is a significant decline of stemborer infestation on maize in Bugiri, Bukedea, and Tororo districts in 2016 with the exception in Tororo (Fig. 3). The infestation of maize due to stemborer continued to further decline in 2017. For example, the long-term average stemborer infestation in Bugiri, Bukedea, and Pallisa were 38%, 28%, and 65% respectively, whereas in 2017, the infestation declined to 15%, 19%, and 24% where the differences were significant. The data collected from Tororo however did not show a significant difference.

### Stemborers and FAW infestation on maize and sorghum

Overall, there was a statistically significant effect of the location (district), the sampling date and the crop on stemborer infestation (Location: LR $\chi^2 = 37.61$, df = 4, $P < 0.001$; Sampling date: LR $\chi^2 = 7.22$, df = 2, $P = 0.027$; Crop: LR $\chi^2 = 100$, df = 1, P < 0.001). Similarly, the interaction between the sampling date and the crop significantly affected the stemborer infestation (LR $\chi^2 = 53.67$, df = 2, P < 0.001) (Table 2).

There was a statistically significant effect of the location (district), the crop and the interaction between the sampling date and the crop on the FAW infestation (Location: LR $\chi^2 = 115.91$, df = 4, P < 0.001; Crop: LR $\chi^2 = 317.82$, df = 1, P < 0.001; Interaction sampling date x Crop: LR $\chi^2 = 7.57$, df = 2, $P = 0.023$). However, the sampling date had no effect on the FAW infestation (LR $\chi^2 = 4.56$, df = 2, $P = 0.102$).

Stemborer incidence varied significantly across the districts regardless of the crop and sampling date. Iganga recorded a significantly higher stemborer infestation compared with Bukedea, Tororo, and Bugiri. The lowest stemborer infestation occurred in Bugiri. Similarly, irrespective of the crop and sampling date, FAW infestation resulted in highly significant differences among districts. FAW infestation was higher at Iganga than it was in the other districts whereas, Bugiri recorded the lowest infestation (Table 2).

Stemborer infestation was statistically higher on sorghum (57.58 ± 1.43%) than on maize (36.33 ± 14.27%), irrespective of the district and the sampling date. Contrary to stemborers, FAW infestation was statistically higher on maize (86.75 ± 0.98%) than on sorghum (51.50 ± 1.44%).

At each sampling date, the infestation of stemborer was consistently higher on sorghum than on maize (Table 3). The highest infestation was recorded at 16 WAP on sorghum, while on maize, it was at 9 WAP (Table 3). The infestation of

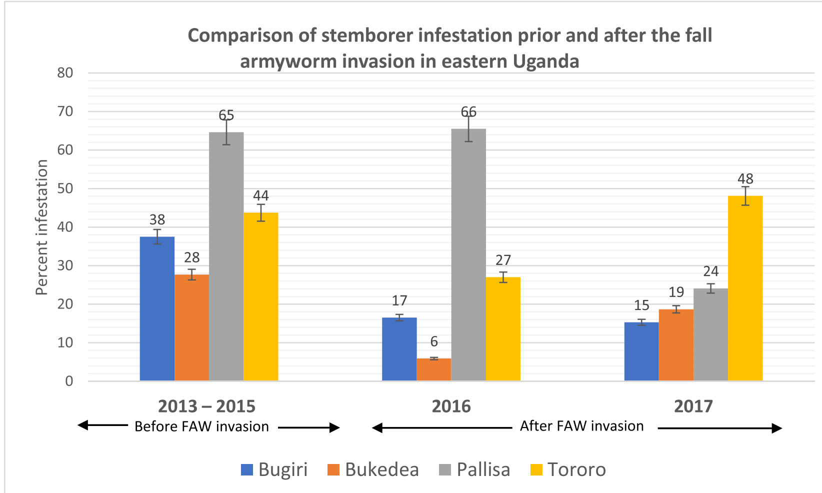


**Fig. 3** Comparison of stemborer infestation prior and after the fall armyworm invasion in eastern Uganda

FAW was consistently higher on maize at all sampling dates (Table 3).

## Stemborers and FAW damage severity on maize and sorghum

There was a highly significant effect of the district (F = 12.05, Num. df = 4, Den. df = 2387, $P < 0.001$), the crop (F = 24.58, Num. df = 1, Den. df = 2387, P < 0.001) and, the interaction between the sampling date and the crop (F = 12.50, Num. df = 2, Den. df = 2387, P < 0.001) on stemborer damage severity. The sampling date, however, was not significant (F = 0.47, Num. df = 2, Den. df = 2387, $P = 0.627$).

There was a highly significant effect of the district (F = 69.46, Num. df = 4, Den. df = 2390, P < 0.001), the sampling date (F = 72.68, Num. df = 2, Den. df = 2390, P < 0.001), and the crop (F = 459.80, Num. df = 1, Den. df = 2390, P < 0.001) as well as the interaction between the sampling date and the crop (F = 5.48, Num. df = 2, Den. df = 2390, $P = 0.004$), on FAW damage severity.

Iganga district recorded a significantly higher stemborer severity compared with the other districts, while in Bukedea, the severity recorded was the lowest (Table 4). Iganga and Tororo districts recorded the highest damage severity of FAW. The lowest damage severity was registered from Bugiri district (Table 4).

The severity of stemborers on sorghum (1.80 ± 0.03) was statistically higher than on maize (1.62 ± 0.02); in contrary, the damage severity of FAW was generally higher on maize (2.58 ± 0.03) than on sorghum (1.74 ± 0.03) irrespective of the location and the sampling date.

Among maize and sorghum, the highest severity of stemborers infestation occurred on sorghum and the lowest on maize both at 6 and 16 weeks after planting (Table 5). Maize recorded a significantly higher FAW damage severity at six weeks after planting. The lowest was noted on sorghum at 16 weeks after planting (Table 5).

## Exit holes, cavity length due to stemborer larvae in maize and sorghum

The destructive sampling conducted on maize and sorghum at harvest confirmed that the intensity of damage on sorghum was higher than on maize. The effect of the first generation cereal stemborer infestation was measured by the number of exit holes on the lower part (about a meter long from the base) of the stalk. The district (F = 1.99, Num. df = 4, Den. df = 163.96, $P = 0.097$) and the crop (F = 3.52, Num. df = 1, Den. df = 164.86, $P = 0.062$) had no significant effect. However, the interaction between the district and crop significantly affects the number of exit holes (F = 3, Num. df = 4, Den. df = 164.18, $P = 0.02$). The assessment done on the upper part of maize and sorghum stalks (second generation infestation) showed a significant effect of the district (F = 6.78, Num. df = 4, Den. df = 198, $P < 0.001$), the crop (F = 42, Num. df = 1, Den. df = 198, P < 0.001) and, the interaction between the district and the crop (F = 3.4, Num. df = 1, Den. df = 198, $P = 0.019$) on the number of exit holes. An exception was

**Table 2** Percentage infestation of stemborer and fall armyworm recorded in different locations regardless of the crop and date of sampling

| District | Stemborer infestation (%) | Fall armyworm infestation (%) |
|---|---|---|
| Iganga | $57.50 \pm 2.26^{c}$ | $81.67 \pm 1.77^{c}$ |
| Pallisa | $49.58 \pm 2.28^{bc}$ | $61.87 \pm 2.22^{ab}$ |
| Bukedea | $44.58 \pm 2.27^{ab}$ | $78.33 \pm 1.88^{c}$ |
| Tororo | $42.50 \pm 2.26^{ab}$ | $67.29 \pm 2.14^{b}$ |
| Bugiri | $40.62 \pm 2.24^{a}$ | $56.46 \pm 2.26^{a}$ |

Means followed by different letters in the same column were significantly different using the least squares means (LSMEANS) and adjusted Tukey multiple comparison procedure ($\alpha = 0.05$)

**Table 3** Interaction effect of crop and the sampling date on the percentage infestation of stemborer and fall armyworm

| Sampling date | Crop | Stemborer infestation (%) | Fall armyworm infestation (%) |
|---|---|---|---|
| 6 WAP | Maize | 36.75 ± 2.41$^{b}$ | 89.50 ± 1.53$^{b}$ |
| | Sorghum | 55.50 ± 2.49$^{cd}$ | 51.00 ± 2.50$^{a}$ |
| 9 WAP | Maize | 48.25 ± 2.50$^{c}$ | 84.75 ± 1.78$^{b}$ |
| | Sorghum | 53.25 ± 2.50$^{c}$ | 56.50 ± 2.48$^{a}$ |
| 16 WAP | Maize | 24.00 ± 2.14$^{a}$ | 86.00 ± 1.74$^{b}$ |
| | Sorghum | 64.00 ± 4.81$^{d}$ | 47.00 ± 2.50$^{a}$ |

Means followed by different letters in the same column were significantly different using the least squares means (LSMEANS) and adjusted Tukey multiple comparison procedure (α = 0.05). WAP: Week after planting

noted at Iganga, where the number of exit holes was consistently higher on sorghum than on maize (Table 6).

The assessment of cavity length attributable to the feeding of stemborer larvae showed the prevalence and intensity of the damage with varying degrees. Thus, on the lower part of the stalk, the district (F = 0.99, Num. df = 4, Den. df = 164.22, $P = 0.413$) and crop (F = 1.42, Num. df = 1, Den. df = 167.81, $p = 0.235$) had no significant effect, whereas the interaction between the district and the crop (F = 2.12, Num. df = 4, Den. df = 163.81, $P = 0.031$) had a significant effect. The second-generation stemborer effect was significant at district (F = 3.81, Num. df = 4, Den. df = 190, $P = 0.005$), crop (F = 27.9, Num. df = 1, Den. df = 190, P < 0.001), and the interaction between district and crop (F = 4.98, Num. df = 3, Den. df = 190, $P = 0.002$) levels. As for the exit holes, cavity length was higher on sorghum than on maize (Table 7).

## Discussion

FAW and cereal stemborer infestations on maize and sorghum varied significantly across the districts. This could be attributable to the differences in rainfall patterns and agro-ecological characteristics (Pair et al. 1986) such as temperature and the availability of wild host plants, which might or might not favor the buildup of the FAW population. Many studies have shown a difference in insect species composition, distribution and importance, according to agro-ecological zones (Overholt 2008a; Sétamou et al. 2000). The cumulative infestation over the sampling period (growth stages), averaged over five districts, suggests that maize is more affected by FAW attack than sorghum. This might explain the greater public attention on maize as compared with other cereals such as sorghum.

The long-term infestation scored from over 150 farms across five districts show that stemborer infestation was highly prevalent in the area. The stemborer infestation scored after the arrival of FAW steadily declined in most of the surveyed districts indicating the competitiveness of FAW and the potential displacement of stemborer. Recent studies in the laboratory has highlighted that factors such as temperature (Sokame et al. 2020) and larval dispersal behaviour (Sokame et al. 2020) could influence the interaction between FAW and cereal stemborers in Africa. Ballooning among FAW was much higher than stemborers (Sokame et al. 2020). Further studies at field level need to ascertain this assertion of displacement.

Contrary to FAW incidence on maize, there was a high level of infestation by stemborer on sorghum. Although both FAW and cereal stemborers prefer maize as a host, the high

**Table 4** District effect on stemborer and fall armyworm damage severity

| District | Stemborer severity | Fall armyworm damage severity |
|---|---|---|
| Iganga | 1.94 ± 0.04$^{b}$ | 2.58 ± 0.06$^{c}$ |
| Bugiri | 1.73 ± 0.05$^{a}$ | 1.9 ± 0.05$^{a}$ |
| Pallisa | 1.68 ± 0.04$^{a}$ | 1.74 ± 0.03$^{a}$ |
| Tororo | 1.61 ± 0.01$^{a}$ | 2.48 ± 0.06$^{c}$ |
| Bukedea | 1.59 ± 0.04$^{a}$ | 2.09 ± 0.04$^{b}$ |

Means followed by different letters in the same column were significantly different using the least squares means (LSMEANS) and adjusted Tukey multiple comparison procedure (α = 0.05)

**Table 5** Interaction of sampling date and crop effect on the severity of stemborers and fall armyworm

| Sampling date | Crop | Stemborer severity | Fall armyworm severity |
|---|---|---|---|
| 6 WAP | Maize | 1.55 ± 0.04$^{a}$ | 2.96 ± 0.06$^{d}$ |
| | Sorghum | 1.82 ± 0.05$^{bc}$ | 2.01 ± 0.06$^{b}$ |
| 9 WAP | Maize | 1.76 ± 0.05$^{bc}$ | 2.33 ± 0.05$^{c}$ |
| | Sorghum | 1.69 ± 0.05$^{ab}$ | 1.68 ± 0.03$^{a}$ |
| 16 WAP | Maize | 1.54 ± 0.04$^{a}$ | 2.43 ± 0.05$^{c}$ |
| | Sorghum | 1.90 ± 0.044$^{c}$ | 1.53 ± 0.03$^{a}$ |

Means followed by different letters in the same column were significantly different using the least squares means (LSMEANS) and adjusted Tukey multiple comparison procedure (α = 0.05)

**Table 6** Interaction of district and crop effect on the number of stemborer exit holes at the lower and upper parts of the stalk

| Districts | Crops | Mean number of exit holes at the lower part | Mean number of exit holes at the Upper part |
|---|---|---|---|
| Bugiri | Maize | $1.75 \pm 0.43^{a}$ | $2.08 \pm 0.49^{ab}$ |
| | Sorghum | $1.80 \pm 0.47^{a}$ | $3.33 \pm 0.41^{abc}$ |
| Bukedea | Maize | $1.71 \pm 0.36^{a}$ | $1.83 \pm 0.41^{a}$ |
| | Sorghum | $2.11 \pm 0.25^{a}$ | $2.74 \pm 0.28^{ab}$ |
| Iganga | Maize | $2.00 \pm 1.5^{ab}$ | – |
| | Sorghum | $1.67 \pm 0.87^{ab}$ | $1.65 \pm 0.43^{a}$ |
| Pallisa | Maize | $1.64 \pm 0.26^{a}$ | $1.79 \pm 0.30^{a}$ |
| | Sorghum | $2.87 \pm 0.30^{ab}$ | $4.64 \pm 0.31^{c}$ |
| Tororo | Maize | $1.55 \pm 0.45^{a}$ | $1.4 \pm 0.55^{a}$ |
| | Sorghum | $3.90 \pm 0.27^{b}$ | $3.57 \pm 0.33^{bc}$ |

- Missing data

Means followed by different letters in the same column were significantly different using the least squares means (LSMEANS) and adjusted Tukey multiple comparison procedure ($\alpha = 0.05$)

infestation of FAW in maize could be explained by its competitive advantage of a shorter life cycle and not entering into diapauses, as compared with cereal stemborers (Hardke et al. 2015; Sparks 1979). Although FAW is known to feed on diverse plants, its highly prefers maize (Sparks, 1979) which could explain why it was predominantly on maize and not on sorghum. Rebe et al. (2004) has reported the preference of *B. fusca* for maize over sorghum, even when the plants are of similar height due to the physical property of the leaf sheath and stem that attracts the moth to lay its eggs. Moreover, before the FAW invasion, several studies reported that there was greater oviposition by stemborers on maize than sorghum with the more signs of stemborer infestation were recorded (Haile 2015; Haile and Hofsvang 2002; Calatayud et al. 2014a). Furthermore, the level of stemborer infestation reported on maize in studies conducted before the invasion of FAW was higher than what is recorded in the current study. Kalule et al. (1997) has reported that *B. fusca* infestation varied from 12.1 to 60.5% on maize according to the season and the phenology of the plant. Moreover, historical data collected in Uganda in the same locations as the current studies from 2013 to 2016 showed a higher level of infestation of stemborers on maize prior to the detection of FAW in 2016 (Hailu et al., unpublished data). This study, therefore, has confirmed that the invasion of FAW seems to have changed this "*status quo*".

In general, displacement effects caused by invasive species are not a new phenomenon. For example, Kfir (1997) observed an expulsion of the sub-Saharan Africa endemic *B. fusca* by the invasive *C. partellus*. This was accounted for by the competitive advantage of *C. partellus*, which ends diapauses earlier than *B. fusca* does (Ingram 1958). A study by Overholt (2008b) also indicated the displacement of an indigenous stemboer (*Chilo orichalcociliellus*) due to the invasive *C. partellus*. Nevertheless, the indigenous stemborer found two native alternative grasses which is not hosting *C. partellus*.

**Table 7** Interaction of district and crop effects on the mean cavity length at the lower and upper parts of maize and sorghum stalks

| District | Crop | Mean cavity length at the lower part | Mean cavity length at the Upper part |
|---|---|---|---|
| Bugiri | Maize | $6.94 \pm 1.82^{ab}$ | $12.31 \pm 2.67^{abcd}$ |
| | Sorghum | $8.69 \pm 1.90^{ab}$ | $16.59 \pm 2.30^{bcd}$ |
| Bukedea | Maize | $9.18 \pm 1.49^{ab}$ | $8.67 \pm 2.23^{ab}$ |
| | Sorghum | $8.56 \pm 1.05^{b}$ | $17.51 \pm 1.55^{cd}$ |
| Iganga | Maize | $6.02 \pm 5.99^{ab}$ | – |
| | Sorghum | $5.75 \pm 3.47^{ab}$ | $10.94 \pm 2.26^{abc}$ |
| Pallisa | Maize | $3.75 \pm 1.08^{a}$ | $3.97 \pm 1.62^{a}$ |
| | Sorghum | $9.65 \pm 1.18^{b}$ | $21.33 \pm 1.82^{d}$ |
| Tororo | Maize | $5.89 \pm 1.74^{ab}$ | $4.57 \pm 3.63^{ab}$ |
| | Sorghum | $8.56 \pm 1.14^{b}$ | $7.86 \pm 1.78^{ab}$ |

- Missing data

Means followed by different letters in the same column were significantly different using the least squares means (LSMEANS) and adjusted Tukey multiple comparison procedure ($\alpha = 0.05$)

Eight general mechanisms of interspecific competition that have contributed to the cases of displacement have been identified: differential resource acquisition, differential female fecundity, differential searching ability, resource preemption, resource degradation, agonistic interference competition, reproductive interference, and intraguild predation (Reitz and Trumble 2002). In this study, FAW outcompeted stemborers on maize as it does not enter into diapause (~ 1 month to complete a full cycle). It also interacts /competes actively with lepidopteran stemborer communities, particularly during the early instars when stemborers are also leaf feeders and then occupy the same niche.

Both pests prefer maize, and this is because maize plants usually grow faster, and bigger plants offer more space to lay eggs (Calatayud et al. 2014a; Pitre et al. 1983). Moreover, neonates can abseil down from taller plants to neighboring plants in what is referred to as a 'ballooning' tactic (Berger 1989; Rojas et al. 2018). The higher the areas from which they abseil, the larger the radius of neighboring plants they can reach. Recently Sokame et al. (2020) reported a significantly higher dispersal behaviour of FAW compared to other stemborers. The aggressive nature and short lifecycle of FAW could explain the difference in infestation on maize compared with sorghum. The FAW invasion has likely aggravated the infestation of sorghum by cereal stemborers. Thus, sorghum crops are at a higher risk of heavy stemborer infestations, and also FAW invasion. The high infestation of sorghum by stemborers could also be explained by the preference of stemborer moths for plants that are not already infested by FAW. Since there was less infestation of FAW on sorghum than on maize, they might have avoided the maize plants infested by FAW and relocated to alternative sorghum plants. The displacement of stemborers to sorghum can also be explained by their sensitivity to herbivore-induced plant volatiles (HIPVs) (Birkett et al. 2006). FAW moths suppress the release of herbivore-induced plant volatiles (HIPVs), thus preventing plants from defending themselves against aggressors (Penaflor et al. 2011) and in the process send signals that encourage other FAW moths to lay eggs on the same plant which probably is the reason for the high level of infestation.

Current FAW management interventions are focused on maize, and minimal mention is made of sorghum. However, our study suggests that sorghum is vulnerable directly or indirectly with the arrival of FAW, with stemborer attacks to become more severe on sorghum. The results of the infestation rate according to the sampling date showed that stemborer infestations gradually built up on sorghum, where they have more space left by FAW. On maize, stemborer infestations significantly decreased at the last sampling date most likely because of the competition between the FAW and the few stemborers which managed to infest the plant. The destructive sampling conducted on maize and sorghum provided clear evidence on increased stemborer infestation on sorghum compared with maize.

## Conclusions

Our study has provided evidence that the arrival of FAW might lead to the displacement of stemborers from maize, its preferred host to sorghum. This is the result of aggressive feeding behavior of FAW in occupying the entire plant/farm. This situation puts maize crops at higher risk, but also indirectly places risk on sorghum for high stemborer attacks. Therefore, IPM designs should take into consideration the major pests and vulnerable crops such as maize and sorghum. Agroecological management options, such as the push-pull technology which has been proved to control FAW and stemborer on maize and sorghum can play an essential role in the pest management strategy.

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## Compliance with ethical standards

**Conflict of interest** The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, or in the decision to publish the results.

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