Understanding the factors influencing fall armyworm (Spodoptera frugiperda J.E. Smith) damage in African smallholder maize fields and quantifying its impact on yield. A case study in Eastern Zimbabwe

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ARTICLE INFO

Keywords:
Lepidopteran pests
Integrated pest management
Biocontrol
Agronomic management
Cultural control

ABSTRACT

Fall armyworm (FAW, Spodoptera frugiperda J.E. Smith) is an invasive lepidopteran pest established in most of sub-Saharan Africa since 2016. Although the immediate reaction of governments has been to invest in chemical pesticides, control methods based on agronomic management would be more affordable to resource-constrained smallholders and minimize risks for health and the environment. However, little is known about the most effective agronomic practices that could control FAW under typical African smallholder conditions. In addition, the impact of FAW damage on yield in Africa has been reported as very large, but these estimates are mainly based on farmers’ perceptions, and not on rigorous field scouting methods. Thus, the objectives of this study were to understand the factors influencing FAW damage in African smallholder maize fields and quantify its impact on yield, using two districts of Eastern Zimbabwe as cases. A total of 791 smallholder maize plots were scouted for FAW damage and the head of the corresponding farming household interviewed. Grain yield was later determined in about 20% of these fields. FAW damage was found to be significantly reduced by frequent weeding operations and by minimum- and zero-tillage. Conversely, pumpkin intercropping was found to significantly increase FAW damage. FAW damage was also found to be higher for some maize varieties, although these varieties may not be the lowest yielding. If the incidence of plants with FAW damage symptoms recorded in this research (32–48%, depending on the estimate used) is commensurate with what other studies conducted on the continent found, our best estimate of the impact of FAW damage on yield (11.57%) is much lower than what these studies reported. Although our study presents limitations, losses due to FAW damage in Africa could have been over-estimated. The threat that FAW represents for African smallholders, although very real, should not divert attention away from other pressing challenges they face.

1. Introduction

Fall armyworm (FAW, Spodoptera frugiperda J.E. Smith) is a lepidopteran pest native to tropical and subtropical America that attacks over 80 different crop species, but with a preference for graminaceous crops, and maize in particular (Sparks, 1979). In early 2016, the presence of the pest was reported in Central and Western Africa (Goergen and Tam, 2016), and later in most of sub-Saharan Africa (Day et al., 2017). It is unclear how this invasion occurred, but evidence suggests that the haplotype present in Africa originated from Florida and the Caribbean (Huesing et al., 2018). The prolificacy of FAW (egg batches often contain several hundreds of eggs; Sparks, 1979) associated with its ability to migrate long distances (several hundreds of kilometers; Rose et al., 1975) are two of the species traits that could explain the speed at which it invaded the continent. The prevalence of maize – and other crops on which this highly polyphagous pest feeds – associated with agroecological conditions suitable for FAW in much of the region makes it a serious (and most certainly perennial) threat to food security in sub-Saharan Africa (Day et al., 2017).

Since the invasion of the continent by FAW, the immediate reaction of...
the value of maize
selected as the drier, intermediate and wetter wards, respectively. In-
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selected following a strati-
and Makoni Districts, respectively. In each district, households were
were used addressing the characteristics of the main maize
notation, maize variety, crop species being intercropped if any), tillage
(more and dates), fertilization (type and quantity of fertilizer, manure,
and compost) and crop protection (date and number of weeding opera-
tions, herbicide applications, and pesticide applications). Each maize plot
was then scouted using the method described by McGrath et al. (2018):
five sampling points of 10 plants located on the same row were selected
using a ‘W’ scouting pattern and the number of plants displaying leaf
damages caused by FAW larvae and with FAW frass in the whorl were
recorded at each sampling point. The Davis scale, which rates the extent
of leaf damage from 1 to 9 (Davis and Williams, 1992), was also used to
give a score for each cluster of 10 plants in each sampling point.

2.3. Yield assessment

From the 791 fields assessed during the growing season, a total of 167
fields (54 in Chipinge District and 113 in Makoni District) were selected
for yield assessment. These fields were purposefully selected to span the
whole range of damage levels observed during the growing season (a
stratified sampling scheme based on the tertiles of FAW damage was
used). Grain yield from these fields was then estimated using the ear
digital imaging method (Makanza et al., 2018). For each plot, five
quadrats of 2 m by 1 m were laid out following a ‘W’ sampling frame (as
for the damage scouting). The number of plants and the number of cobs
were counted in each quadrant. Cobs were then harvested and pooled for
each field. After husks were removed, cobs were laid on a black plastic
sheet side by side and a picture was taken using an 8-inch Samsung’s
Galaxy Tab S2 camera with a resolution of 8-megapixels equipped with
an f/1.9 lens (Fig. 1a and b). To enable the conversion of pixel scale
measurements to centimeters, a ruler was placed near the cobs before
taking each picture (Fig. 1b). The pictures were later processed using a
script that runs on ImageJ, an open source software (https://imagej.nih.
.gov/ij/features.html). The script estimates grain weight based on two
models (i) the total kernel number derived from the number of kernels
visible on the image and (ii) the average grain weight generated from
average grain size (Fig. 1c and d; Makanza et al., 2018).

2.4. Calculations and statistical analysis

2.4.1. Data manipulation and calculations

Soil types were grouped in five texture categories: ‘Sandy’, ‘Sandy
loam’, ‘Loamy’, ‘Loamy clay’, and ‘Clayey’. Intercrops were grouped in
varieties were grouped in 10 categories: ‘SC500’, ‘SC400’, ‘SC600’,
‘PAN413’, ‘PANS3’, ‘PHB30G19’, ‘ZAP61’, ‘Recycled’ (i.e., seeds har-
nested from a previous hybrid maize crop, often of unspecified variety),
‘OPV’ (i.e., open-pollinated varieties), and ‘Other’. Manure application,
compost application, herbicide application, and pesticide application
were converted into binary variables (‘Yes’, ‘No’). The number of
weeding operations was converted into ‘Infrequent’ (one or less) or
‘Frequent’ (two or more). The quantities of fertilizer applied were
converted into quantities of nitrogen (N) and quantities of phosphorus
pentoxide (P₂O₅) using specific fertilizer compositions and were
expressed on a per hectare basis. For each sampling point, the proportion
of plants with leaf damage and with frass in the whorl was calculated. For
each plot, the grain weight in the five quadrats (as estimated through
image analysis) was summed and converted into grain yield in kg ha⁻¹.
To be able to relate grain yield with damage estimates – which are
assessed on a per plant basis – and as the variability in plant density was
high between the different plots assessed, grain yield was also calculated
in kg plant⁻¹ by dividing grain yield (in kg ha⁻¹) by plant population (in
plants ha⁻¹).

2.4.2. Statistical analyses

The variability of the proportion of plants with leaf damage symp-
toms, of the proportion of plants with frass in the whorl and of the Davis
damage score in each sampling point (N = 3955) was analyzed using

2.2. Farm survey

A total of 394 and 397 farming households were surveyed in Chipinge
and Makoni Districts, respectively. In each district, households were
selected following a stratified sampling scheme, with roughly a third of
them each selected randomly from a relatively wetter ward, a relatively
drier ward and a ward of intermediate climate. In Chipinge District,
Wards 16, 18 and 20 were selected as the drier, intermediate and wetter
wards, respectively. In Makoni District, Wards 26, 28 and 34 were
selected as the drier, intermediate and wetter wards, respectively.
Information related to the main maize field of the selected households was
then collected through interview of the head of these households before
scouting that field. Interviews were conducted between 2 and 7 February
2018 in Chipinge District and between 22 and 28 March 2018 in Makoni
District, each time by a team of 12 trained enumerators. A standardized
questionnaire was used addressing the characteristics of the main maize
plot (area, soil type, presence or absence of a hedgerow, previous crop),
the characteristics of the crop (maize growth stage estimated using the

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10 years average; UNDP, 2016). Sandy soils,
black and red clays are the major soil types. The main crops are maize,
cotton, and sorghum. The main livestock species are cattle, goats, pigs
and chicken. The population density is about 33 inhabitants km⁻² (PCO,
2012).

Makoni is located in northeastern Zimbabwe at an average altitude of
1372 m above sea level, and is characterized by a mean annual rainfall of
750–1000 mm per year (4 years average) and a mean annual temperature
of 27 °C (10 years average; UNDP, 2016). Sandy soils to sandy loams are
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generalized linear models (GLM). A logit distribution was used for proportion data, and a Poisson distribution for the Davis damage score (count data). Response variables included plot size (ha), soil type, District, Ward (as a factor nested in District), hedgerow presence/absence, previous crop, maize variety, intercrop species, tillage intensity, rate of mineral N applied (kg ha\(^{-1}\)), rate of mineral P\(_2\)O\(_5\) applied (kg ha\(^{-1}\)), application or not of manure; application or not of herbicide, application or not of pesticide, and the V stage. Plot size, rate of mineral P\(_2\)O\(_5\) applied, rate of mineral P\(_2\)O\(_5\) applied, and V stage were continuous variables, whilst all other variables were factors. A probability of 0.05 was used to test the significance of each factor.

To quantify yield losses due to FAW damage whilst accounting for the fact that variables influencing FAW damage may also influence yield directly, structural equation models were used (R package ‘lavaan’). A construct model was developed linking District, Ward, plot area, variety, hedgerow presence or absence, soil type, previous crop, intercrop, tillage intensity, N applied, manure application or not, compost application or not, frequency of weeding, pesticide application or not and V stage to FAW damage, and all these variables as well as plant population and FAW damage to grain yield per plant (see Fig. 2 with the Davis damage score used as example of the estimate of FAW damage). Three models were used, each using a different estimate of FAW damage (proportion of plants with leaf damage symptoms, proportion of plants with frass in the whorl, and Davis damage score). As this approach does not support the use of nominal endogenous variables, the variable ‘Ward’ was recoded for each District as an ordered variable based on agroecological conditions (relatively dry, intermediate, relatively wet). Similarly, the variable ‘variety’ was recoded as an ordered variable based on the effect of each variety on FAW damage (from output of the GLMs above, with ‘1’ for varieties having a statistically negative effect in at least one of the GLMs, ‘2’ for varieties having no effect in any of the GLMs, and ‘3’ for varieties having a statistically positive effect in at least one of the GLMs). Finally, the variable ‘soil type’ was coded as an ordered variable based on texture (‘1’ for sandy soils, ‘2’ for sandy loam soils, ‘3’ for loamy soils, ‘4’ for loamy clay soils, and ‘5’ for clayey soils). To determine models’ fit, we used the Chi-square test (X\(^2\)) and the probability level (P) associated with the model. The goodness of fit index (GFI), comparative fit index (CFI), Tucker-Lewis index (TLI), root mean squared error of approximation (RMSEA), and Akaike Information Criterion (AIC) were also considered. In the Chi-square test, a good model fit is evidenced if the null hypothesis is not rejected (P > 0.05). Values of the indexes GFI > 0.95, CFI > 0.90, TLI next to 1, and RMSEA ≤ 0.10 suggest an appropriate model fit. Finally, AIC index lower values when comparing models are indicative of better fits.

3. Results

3.1. General characteristics of plots

Maize plots included in the study were much larger in Chipinge (1.268 ha on average) than in Makoni District (0.362 ha on average; Table 1). Fertilizer rates used in Chipinge were, however much lower (3.798 kg N ha\(^{-1}\) and 2.391 kg P\(_2\)O\(_5\) ha\(^{-1}\)) than those applied in Makoni (64.094 kg N ha\(^{-1}\) and 55.337 kg P\(_2\)O\(_5\) ha\(^{-1}\)) on average). Maize in both Chipinge and Makoni was scouted for FAW damage when, on average, most plants were at V4 to V5 stages. The main soil type was sandy loam in both districts, followed by loamy soils in Chipinge and sandy soils in Makoni. Only a minority of the fields surveyed were surrounded by a hedgerow (9% of the total sample). The previous crop was mainly maize (for about \(\frac{2}{3}\) of the fields sampled) illustrating the rarity of crop rotation for maize. When maize was rotated, it was mainly after sorghum in Chipinge, and after a fallow or a pulse crop in Makoni. Most maize was grown as sole crop (i.e., no intercrop) in both districts, but a significant proportion of the fields were intercropped with pumpkins and/or pulses, particularly in Makoni. The main maize varieties planted were Seedco hybrids from the 500 series. The majority of the crop assessed was established following minimum-tillage (i.e., a single tillage operation) in both districts. Zero-tillage was also common in Chipinge.

![Fig. 1. (a,b) Photo acquisition procedure using a tablet, and (c,d) key image processing procedure (from Makanza et al., 2018).](image-url)
3.2. Fall armyworm damage

The incidence of plants with FAW damage symptoms varied depending on the estimate used for determining the parameter: the proportion of plants with leaf damage was estimated at 48.3 ± 28.3% and the proportion of plants with frass in the whorl at 31.6 ± 16.8% (Fig. 3). The Davis damage score for the entire data set was found to be 3.78 ± 2.09 (Fig. 3). FAW damage was found to be higher in Makoni than in Chipinge, regardless of the estimate used, although differences were only significant for the proportion of plants with leaf damage (P < 0.0005) and for the proportion of plants with frass in the whorl (P < 0.005), but not for the Davis damage score (Fig. 4). The proportion of plants with leaf damage was 41.5 ± 28.0% in Chipinge and 54.9 ± 26.3% in Makoni while the proportion of plants with frass in the whorl was 26.4 ± 24.8% in Chipinge and 36.8 ± 26.7% in Makoni. Finally, the Davis damage score was 3.74 ± 2.21 in Chipinge and 3.83 ± 1.96 in Makoni (Fig. 4).

From the outputs of the GLMs, a number of factors were found to explain the variability in FAW damage symptoms (Table 2). The location – District and Ward – appeared to have a strong influence in all three models. FAW damage was statistically higher for crops following a fallow, or following a land use other than maize, sorghum, pulse or fallow, regardless of the estimate used. Conversely, FAW damage was found to be statistically lower with zero tillage and with frequent weeding, in the three models used. FAW damage was also found to be higher for PAN413, SC600 series and ‘Other’ varieties compared to SC500 series (used as reference variable) in two out of three models. Finally, the use of minimum-tillage, the application of manure and the application of compost were found to lower FAW damage in two out of three models.

3.3. Yield and yield losses due to fall armyworm damage

The mean grain yields were 2966.3 ± 1649.9 kg ha⁻¹ for the total sample, 2032.9 ± 1644.1 kg ha⁻¹ for Chipinge, and 3416.3 ± 1547.5 kg ha⁻¹ for Makoni (Fig. 5).

All three structural equation models were characterized by a P-value < 0.05, a GFI > 0.95, a CFI > 0.90, a TLI next to 1, and a RMSEA ≤ 0.10, and thus considered to be good fits of the measured data (Table 3). However, the third model – which included the Davis damage score as an estimate of FAW damage – had a lower AIC than the two other models, indicating a better fit. Details of the regression coefficient estimates, their standard error, Z-value and P-value are given in Appendix A. In the first and the second models, the regression between FAW damage (the proportion of plants with leaf damage and the proportion of plants with frass in the whorl, respectively) and grain yield per plant was not significant. Fig. 6 illustrates regressions that were statistically significant (P < 0.05) in the third model, which used the Davis damage score as estimate of FAW damage and was also the model with the lowest AIC. The outputs of this model suggest District, variety, plant population, Davis damage score, and nitrogen rate as having a significant influence on grain yield per plant (Fig. 6, Appendix A). It further indicates that 1.752 g plant⁻¹ of grain yield were lost for an increase of one point in the Davis damage score. Using this estimate, we calculated an estimated percentage of yield loss for each of the 167 fields included in the yield assessment. The distribution of these estimated losses (our best estimates) is given in Fig. 7A, showing a mean value of 11.57% and a median value of 8.14% for the total sample. Losses tended to be higher in Chipinge District (mean of 16.39% and median of 10.64%) than in Makoni District (mean of 9.24% and median of 7.38%).

Maize grain yield, as well as its 95th percentile – ‘boundary line’ representing the maximum attainable yield in farmers’ conditions – appeared to be correlated to plant population (Fig. 7B). In contrast, grain yield and its 95th percentile appeared uncorrelated to the Davis damage score (Fig. 7C).

4. Discussion

4.1. What factors influence fall armyworm damage?

The levels of FAW damage reported in this study – 26.4–41.5% in Chipinge, and 36.8–54.9% in Makoni, depending on the estimate of FAW damage used (Fig. 3), appear to be in the same range as previous studies and reports that estimated FAW damage in sub-Saharan Africa over the past two years (e.g., Kamla et al., 2015). The higher incidence with leaf damage compared to frass in the whorl could be due in part to failure to distinguish between leaf damage caused by FAW and leaf damage caused by other species (e.g., Busseola fusca or Chilo partellus).

Plants receiving pesticides were characterized by a higher FAW damage, regardless of the estimate used (Table 2), probably an illustration of farmers attempting to contain FAW infestation through chemical control for crops displaying high FAW damage. However, the fact that the coefficients for pesticide were positive in all three models and of high absolute values compared to other coefficients may suggest a poor efficacy
Similarly, Kumela et al. (2018) reported little efficacy of pesticides against FAW in Kenya. This may be due, among other factors, to the wrong pesticides being applied, or pesticides being applied at the wrong dose, with not enough volume of water or at the wrong height.

Frequent weeding tended to decrease FAW damage in all three models. This may be explained by the fact that the weed flora in the study areas tends to be dominated by graminaceous species which may be FAW hosts. Similarly, the fact that FAW damage tended to be higher for maize crops following a fallow – in all three models – may be due to the dominance of graminaceous species in short-term fallows. However, we should be cautious with this finding as native grasses and weeds may also host natural enemies of FAW (e.g., Hay-Roe et al., 2016). Conversely, they may also host other crop pests like stem borers (B. fusca and C. partellus) with which FAW shares the same habitat (Le Rü et al., 2006; Moolman et al., 2014; Van den Berg, 2017). If research confirms that graminaceous weeds attract FAW, it could be recommended to avoid having graminaceous plants mixed with maize within the field, but graminaceous plants could be planted around the field as a trap crop. This is one of the key principles of the push-pull technology, originally developed to control lepidopterous stem borers (Khan et al., 1997). Midega et al. (2018) recently demonstrated the effectiveness of the push-pull technology in controlling FAW as well. In addition to a trap crop, the push-pull technology is based on the use of a repellent crop – generally Desmodium spp. or another legume – intercropped with maize (Khan et al., 1997). In the present study, however, legume intercropping did not appear to reduce FAW damage (Table 2). This may be because the main legume species intercropped with maize were cowpea, groundnut,
Table 2
Summary of the results of the GLM models (see text) for explaining the variability in the proportion of plants with leaf damage, in the proportion of plants with frass in the whorl, and in the Davis damage score. Chipinge District, sandy soil, absence of hedgerow, maize as a previous crop, SC500 series as maize variety, no intercrop, conventional tillage, no manure, no compost, infrequent weedng, no herbicide and no pesticide were reference variables.

<table>
<thead>
<tr>
<th>Term</th>
<th>Incidence of plants with leaf damage</th>
<th>Incidence of plants with frass in the whorl</th>
<th>Damage score from the Davis scale</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Estimate</td>
<td>Standard error</td>
<td>Z value</td>
</tr>
<tr>
<td>Intercept</td>
<td>−1.519</td>
<td>0.210</td>
<td>−7.245</td>
</tr>
<tr>
<td>Maloni</td>
<td>0.998</td>
<td>0.172</td>
<td>5.794</td>
</tr>
<tr>
<td>Chipinge/Ward16</td>
<td>0.917</td>
<td>0.156</td>
<td>5.859</td>
</tr>
<tr>
<td>Chipinge/Ward18</td>
<td>2.253</td>
<td>0.172</td>
<td>13.107</td>
</tr>
<tr>
<td>Maloni/Ward26</td>
<td>0.920</td>
<td>0.166</td>
<td>5.552</td>
</tr>
<tr>
<td>Maloni/Ward28</td>
<td>0.230</td>
<td>0.153</td>
<td>1.505</td>
</tr>
<tr>
<td>Plot size</td>
<td>−0.071</td>
<td>0.038</td>
<td>−1.855</td>
</tr>
<tr>
<td>Sandy loam soil</td>
<td>0.183</td>
<td>0.111</td>
<td>1.655</td>
</tr>
<tr>
<td>Loamy soil</td>
<td>0.252</td>
<td>0.141</td>
<td>1.793</td>
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<tr>
<td>Loamy clay soil</td>
<td>0.324</td>
<td>0.155</td>
<td>0.915</td>
</tr>
<tr>
<td>Clayey soil</td>
<td>−0.352</td>
<td>0.216</td>
<td>−1.632</td>
</tr>
<tr>
<td>Hedgerow</td>
<td>0.229</td>
<td>0.133</td>
<td>1.713</td>
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<td>Previous sorghum</td>
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<td>0.131</td>
<td>1.011</td>
</tr>
<tr>
<td>Previous pulse</td>
<td>0.043</td>
<td>0.160</td>
<td>0.270</td>
</tr>
<tr>
<td>Previous fallow</td>
<td>0.392</td>
<td>0.191</td>
<td>2.650</td>
</tr>
<tr>
<td>Previous other</td>
<td>0.530</td>
<td>0.168</td>
<td>3.147</td>
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<tr>
<td>Open pollinated variety</td>
<td>−0.006</td>
<td>0.215</td>
<td>−0.026</td>
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</table>

and common bean but not Desmodium spp. However, and although this was not demonstrated for FAW, Kebede et al. (2018) found common bean to be as effective as Desmodium spp. in repelling B. fusca. Thus, although the potential to control FAW through push-pull appears high in sub-Saharan Africa, further research is needed to determine which companion crops (trap crops and repellent crops) would be the most efficient in controlling FAW and the most acceptable to smallholders.

We found the presence of a pumpkin intercrop to significantly increase FAW damage, regardless of the estimate used. Pumpkins (Curcurbita spp.) are known to be FAW host plants (https://www.cabi.org/isc/datasheet/29810) but in our study, only maize plants were scouted. Pumpkins may provide better shelter habitat than maize for FAW moths during the day. The closed canopy leaves of pumpkins may also offer ‘bridges’ to larvae which fall short of their ‘landing zones’ when ballooning from the maize plants where they hatched (Zalucki et al., 2002). This contrasts with many studies that have shown reduced FAW infestation when maize is intercropped with non-host plant. For example, Altieri et al. (1978) reported reduced FAW incidence as cutworm or whorl feeder in maize by 14 and 23%, respectively, when maize was intercropped with beans in Colombia. However, some studies have also found intercropping (with non-legume crops) to increase infestation by lepidopteran pests. For example, in Eastern Amhara region (Ethiopia), Wale et al. (2007) found intercropping maize with sweet potato to increase C. partellus damage to maize, although pest densities were not affected. FAW damage was found to be lower for maize crops established through zero-tillage compared to maize crops established through conventional tillage in all three models. Minimum-tillage was also found to decrease FAW damage in two models. Similar results were reported in Florida and Mexico, with lower FAW damage hypothesized to be due to higher densities of general predators (e.g., carabid beetles, rove beetles, spiders, ants) in minimum-tillage plots (Clark et al., 1993; Rivers et al., 2016). The higher density of general predators in zero- and minimum-tillage plots may be attributed to an increase of alternative prey due to the organic mulch left on the soil surface when tillage is reduced or foregone (Landis et al., 2000). The lower FAW damage found in two of the three models when manure or compost were applied may be explained by similar mechanisms i.e., organic material on the soil surface leading to higher densities of alternative prey for general predators (Landis et al., 2000; Thomson and Hoffmann, 2007). On the other hand, Kumar and Mihm (2002) have found that zero-tillage combined with mulching tended to significantly increase damage by FAW on maize hybrids. It has been suggested that this might be due to the retention of moisture in the mulch, which provides optimum conditions for larval feeding. In addition, moisture retained in the mulch was reported to attract ovipositing moths for some other lepidopteran species (Kumar,
We also found evidence of higher FAW damage for some maize varieties (e.g., PAN413 and SC600 series compared to SC500 series in two models out of three; Table 2). Maize breeding for insect resistance has traditionally focused on both genetic engineering and genetic improvement from available natural resistance sources. Several authors reported the feasibility of using resistant genotypes to control FAW infestation (Lara et al., 1984; Wiseman and Widstrom, 1992). However, limited progress has been made on developing maize lines showing resistance to FAW. Transgenic maize hybrids expressing Bt toxins can reduce damage by FAW (Burtet et al., 2017; Siebert et al., 2008; Williams et al., 1998, 1997). These include hybrids expressing Cry1A, Cry2A, Cry1F, and/or Vip3Aa20 protein. The main problem with the transgenic option for controlling FAW is the durability of the insecticidal toxins, especially for single-toxin Bt, as widespread resistance to Cry1F has been reported (Farias et al., 2014; Huang et al., 2014; Storer et al., 2010). Conventional breeding has identified several potential mechanisms of resistance to FAW, including the rapid accumulation of proteins or phytochemicals such as maysin in the silks, chlorogenic acid, aspartic acid, cell wall/cellulose buildup that enable plants to poison or starve pests or other herbivores that feed on them (Constabel and Kurz, 1999; Snook et al., 1993; Hedin et al., 1990). In addition to this induced direct defense mechanism, the indirect defense possibility is through attraction of natural enemies (Chuang et al., 2014). Host selection by FAW moths and larvae was reported to be affected by plant volatiles emissions which can be used in developing or improving push-pull strategies against FAW (Rojas et al., 2018). Plant characteristics, like density of leaf hairs or density of cuticular wax layer were also reported to lessen foliar damage (Williams et al., 2000).

Finally, it is important to highlight that lower damage does not necessarily translate into higher yield. Using maize hybrids with resistance to FAW, Kumar (2002) reported that some hybrids, even though presenting less FAW damage, had significantly lower yield than those having higher damage. This indicates that, in some genotypes, FAW damage does not lead to serious injury to the crop to the extent that yield is highly impacted. Therefore, yield loss assessment using FAW damage as primary criteria may lead to overestimation of the associated losses. Breeding strategies to develop varieties with resistance against FAW will have to deploy genes controlling both FAW resistance and suitable agronomic traits.

In the present study, we found no effect of planting dates on FAW damage. Many studies, however, have found this to be an important parameter on the incidence of lepidopteran pests. For example, depending on the interaction between seasonal moth flight patterns and their interactions with the phenological stage of maize (Van Rensburg et al., 1987), B. fusca infestation levels may be decreased or increased by early planting (Chinwada et al., 2001; Snook et al., 1993; Hedin et al., 1990). In addition to this induced direct defense mechanism, the indirect defense possibility is through attraction of natural enemies (Chuang et al., 2014). Host selection by FAW moths and larvae was reported to be affected by plant volatiles emissions which can be used in developing or improving push-pull strategies against FAW (Rojas et al., 2018). Plant characteristics, like density of leaf hairs or density of cuticular wax layer were also reported to lessen foliar damage (Williams et al., 2000).

**4.2. What is the impact of fall armyworm damage on yield losses?**

Although it was not developed as a predictor of damage-yield relationship, but rather to identify small differences in resistance to FAW damage, we found evidence of higher FAW damage for some maize varieties (e.g., PAN413 and SC600 series compared to SC500 series in two models out of three; Table 2). Maize breeding for insect resistance has traditionally focused on both genetic engineering and genetic improvement from available natural resistance sources. Several authors reported the feasibility of using resistant genotypes to control FAW infestation (Lara et al., 1984; Wiseman and Widstrom, 1992). However, limited progress has been made on developing maize lines showing resistance to FAW. Transgenic maize hybrids expressing Bt toxins can reduce damage by FAW (Burtet et al., 2017; Siebert et al., 2008; Williams et al., 1998, 1997). These include hybrids expressing Cry1A, Cry2A, Cry1F, and/or Vip3Aa20 protein. The main problem with the transgenic option for controlling FAW is the durability of the insecticidal toxins, especially for single-toxin Bt, as widespread resistance to Cry1F has been reported (Farias et al., 2014; Huang et al., 2014; Storer et al., 2010). Conventional breeding has identified several potential mechanisms of resistance to FAW, including the rapid accumulation of proteins or phytochemicals such as maysin in the silks, chlorogenic acid, aspartic acid, cell wall/cellulose buildup that enable plants to poison or starve pests or other herbivores that feed on them (Constabel and Kurz, 1999; Snook et al., 1993; Hedin et al., 1990). In addition to this induced direct defense mechanism, the indirect defense possibility is through attraction of natural enemies (Chuang et al., 2014). Host selection by FAW moths and larvae was reported to be affected by plant volatiles emissions which can be used in developing or improving push-pull strategies against FAW (Rojas et al., 2018). Plant characteristics, like density of leaf hairs or density of cuticular wax layer were also reported to lessen foliar damage (Williams et al., 2000).

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**Table 3**

Fit indexes for comparing structural models with different estimates of fall armyworm damage. LFD: proportion of plants with leaf damage, FWL: proportion of plants with frass in the whorl, SCR: Davis damage score, X²: Chi-square test statistic, df: degree of freedom, P: probability level associated with the model, GFI: goodness of fit index, CFI: comparative fit index, TLI: Tucker-Lewis index, RMSEA: root mean squared error of approximation, and AIC: Akaike Information Criterion.

<table>
<thead>
<tr>
<th>Model</th>
<th>X²</th>
<th>df</th>
<th>P</th>
<th>GFI</th>
<th>CFI</th>
<th>TLI</th>
<th>RMSEA</th>
<th>AIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Model 1 (with LFD)</td>
<td>0.252</td>
<td>1</td>
<td>0.615</td>
<td>1</td>
<td>1</td>
<td>1.002</td>
<td>0.000</td>
<td>2755</td>
</tr>
<tr>
<td>Model 2 (with FWL)</td>
<td>1.826</td>
<td>1</td>
<td>0.177</td>
<td>0.999</td>
<td>1</td>
<td>0.998</td>
<td>0.071</td>
<td>2756</td>
</tr>
<tr>
<td>Model 3 (with SCR)</td>
<td>0.167</td>
<td>1</td>
<td>0.683</td>
<td>1</td>
<td>1</td>
<td>1.002</td>
<td>0.000</td>
<td>2173</td>
</tr>
</tbody>
</table>

**Fig. 5.** Density plots of maize grain yield (A) for the total sample, (B) for Chipinge District, and (C) for Makoni District.

**Fig. 6.** Structural equation model using the Davis damage score as estimate of fall armyworm damage and displaying only regressions – and their coefficients – that are statistically significant (P < 0.05). GYD: grain yield per plant, SCR: Davis damage score, DST: District, VAR: variety, PVC: previous crop, NIT: nitrogen applied, NBW: frequency of weeding, VSG: V stage, and PPO: plant population. See text for details.
larval feeding between breeding lines (Davis and Williams, 1992), the Davis damage score was the only of the three estimates of FAW damage to correlate with grain yield: models including the other estimates had a lower fit (see AIC values in Table 3) and the regressions between FAW damage (estimated by the proportion of plants with leaf damage or the proportion of plants with frass in the whorl) were non-significant in these models (Appendix A).

The levels of incidence of plants with FAW damage symptoms recorded in this research are commensurate with levels found by other studies conducted on the continent (Abrahams et al., 2017; Rwomushana et al., 2018). However, our best estimate of the impact of FAW damage on yield – 11.57% (Fig. 7C) – is much lower than what these studies reported. For example, using data from socio-economic surveys, Day et al. (2017) reported yield losses ranging from 22 to 67% in Ghana and Zambia, Rwomushana et al. (2018) from 26 to 35% for the same countries but a year later, and Kumela et al. (2018) from 32 to 47% in Ethiopia and Kenya. In our study, other factors than FAW damage were much more important in explaining grain yield, including plant population (Fig. 6; Fig. 7B vs. 7A) which is a key driver for yield and can buffer FAW damage due to the spread of the pest population over a large number of plants as reported for sorghum by Trabanino et al. (1990), although plant populations are usually much greater for sorghum than for maize. We argue that our study produced more accurate estimates of damage (rigorous field scouting) and yield (harvesting of quadrats) than studies based on socio-economic surveys focusing on farmers’ perceptions. However, our study presents limitations as well. Damage was estimated only once during the season, and probably too early to correlate with significant yield losses (the mean V stage of crops during scouting was 4.6). Farmers could have also applied pesticide between the time of scouting and the time of yield assessment, although this is unlikely as chemical control is recommended after early detection of the pest, as small larvae are easier to control and are more exposed to insecticides than larger larvae (McGrath et al., 2018) and only few farmers (8.4%, Table 1) had sprayed pesticide at the time of scouting.

However, it could well be that losses due to FAW damage in sub-Saharan Africa have been over-estimated since the arrival of the pest on the continent. Maize plants are usually able to compensate for foliar injuries incurred over a short period of time. In fact, maize growth stages vary in their susceptibility to FAW attack (Gross et al., 1982). During mid-vegetative growth stages, larvae are, most often, found defoliating leaves within the whorl. The hybrids within the CML-AG lines, in spite of suffering high leaf feeding damage by FAW, produced the highest yield (Kumar, 2002). Severe losses usually occur when the whorl is destroyed, reducing photosynthetic area and compromising the grain yield (Lima et al., 2010). It may be that the high yield losses reported in previous studies in Africa were due to other factors than FAW damage, including damage by other pests, dry spells, or poor weeding.

It should also be mentioned that the season under observation was characterized by an early dry spell, affecting emergence and ultimately plant population. This may explain the strong effect of plant population on maize yield (Figs. 6 and 7A). Therefore, the threat that FAW represents –which is very real – should not divert the attention of research and development away from the need for development and adoption of good agronomic practices, including the use of seeds adapted to the local circumstances, timely planting, adequate fertilization, and proper crop protection. Finally, for effective implementation of appropriate management strategies, loss estimations and/or sampling methods, behavioral and spatial distributions of populations should be carefully considered. The incidence of larvae in maize can show different distribution patterns: ‘binomial-negative’ or ‘aggregated’ when larvae are small (Baez et al., 1980; Melo et al., 2006), random, which is the most frequently reported (Clavijo, 1978; Hernandez-Mendoza, 1989; Melo et al., 2006), and uniform (Baez et al., 1980; Melo et al., 2006). Multiple factors can also influence distribution patterns, such as cannibalism among larvae (Barbosa and Perecin, 1982; Fernandes et al., 2003).

5. Conclusions

Although the results of this study should been seen as preliminary, as the data analyzed were generated from two District of Zimbabwe and from one season only, several factors were found to influence FAW damage in smallholder maize fields. FAW damage was found to be significantly reduced by frequent weeding operations, as graminaceous weeds, which are dominant in the agroecologies considered, are likely to host FAW. Similarly, FAW damage was significantly lower in maize plots established through minimum- and zero-tille, probably because of higher densities of natural enemies. Conversely, pumpkin intercropping was found to significantly increase FAW damage, hypothetically because it provided a day shelter for moths and/or facilitated maize-to-maize migration of larvae. Finally, FAW damage was higher for some maize varieties, although these varieties may not be the lowest yielding. The Davis damage score was the only estimate of FAW damage that was found...
to be significantly associated with yield. Although the levels of damage recorded in this research are commensurate with levels found by other studies conducted on the continent, our best estimate of the impact of this damage on yield (11.57%) is much lower than what these studies found. This may be due in part to limitations in our study (e.g., scouting conducted only once in the season, and probably too early for the recorded damage to have a significant impact on yield). It may also be that losses due to FAW damage in sub-Saharan Africa have been over-estimated. In the present study, plant population – which can be affected by e.g., early dry spell – was much more important than FAW damage in explaining yield. The threat that FAW represents for African smallholders, although very real, should not divert attention away from other pressing challenges they face.

Acknowledgements

This work was implemented by the International Maize and Wheat Improvement Center (CIMMYT, www.cimmyt.org), GOAL (www.goallglobal.org), and the University of Zimbabwe and was made possible by the generous support of Irish Aid (www.irishaid.ie), Bakker Brothers (www.bakkerbrothers.nl) and CRP MAIZE (www.maize.org).

Any opinions, findings, conclusions, or recommendations expressed in this publication are those of the authors and do not necessarily reflect the view of Irish Aid, Bakker Brothers and CRP MAIZE. We thank three anonymous reviewers for their critical and constructive comments.

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.cropro.2019.01.028.

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