

Breeding of maize for fall armyworm resistance in southern Africa

By

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Summary

In 2016 sub-Saharan Africa (SSA) was invaded by the transboundary maize-eating pest, fall armyworm [*Spodoptera frugiperda* (J.E. Smith); FAW]. The pest has threatened food security and livelihoods of the majority of smallholder farmers in the region. The main aim of this study was to investigate the potential of breeding maize with resistance to FAW in southern Africa. The first study aimed to assess the breeding potential of introduced exotic FAW resistant trait donor maize lines with southern Africa germplasm. Thirteen mid-altitude adapted inbred lines were crossed with seven FAW-resistant exotic donor lines, in a line x tester mating scheme that produced 84 F₁s which were evaluated together with checks at four locations under natural FAW infestation. The best exotic donor lines with low and negative general combining ability (GCA) effects for foliar FAW damage (FFAWD) resistance scores and good grain yield (GYD) *per se* performance were CML139, CML67, CML121 and CML345. Local lines that showed similar good attributes were CimExp1, CimExp4, CimExp5, CimExp8 and CimExp10. The best crosses were CimExp1/CML331, CimExp1/CML345, CimExp10/CML331 CimExp5/CML331 and CimExp5/CML345. In the second study, two sets of germplasm (hybrids/OPVs and inbred lines) were evaluated for FAW resistance under managed and natural FAW infestation. The objective was to evaluate commercial and experimental maize hybrids and parental lines cultivated in southern Africa for resistance to FAW. Commercial cultivars were significantly more affected by FAW infestation than experimental hybrids. The introduced FAW-resistant donor lines (CML338, CML67, CML121 and CML334) showed better resistance to FAW damage, individually and in hybrid combinations. Local inbreds, SV1P, CML491 and CML539, also showed good FAW resistance. Husk cover, ear rot, anthesis date and plant height were correlated with FAW resistance. The third study aimed to investigate the stability of grain yield performance and resistance to FAW of resistant maize lines, cultivars and experimental hybrids under natural FAW infestation. The hybrids Mutsa-MN521 and CimExp55/CML334 were the most preferred, combining FAW

resistance, adaptation and stability across FAW infested environments. Other acceptable hybrids were 113WH330, Manjanja-MN421, CML338/CML334 and PAN53. The local inbred lines SV1P and CML491 combined adaptability and stable FFAWD resistance across environments. The best exotic donor lines exhibiting stable FAW resistance were CML67, CML346, CML121 and CML338. Harare and Gwebi were identified as the most discriminating sites for GYD performance in hybrids, while Kadoma and Rattray-Arnold Research Stations were the most discriminating environments for FFAWD among inbred lines. The fourth study explored the opportunity of using mutation breeding in maize crop improvement with the intention to enhance genetic diversity and trait performance to combat emerging threats such as FAW. The study determined optimum gamma irradiation doses to use in maize mutation breeding. Doses in the range of 160 gy - 250 gy were recommended for maize inbred lines while 200 - 275 gy were recommended for OPVs. Overall, the study concluded that effective FAW resistance can be attained in southern Africa using local and exotic genetic resources. The study recommends the use of gamma irradiation to broaden genetic diversity for effective selection. Furthermore, doubled haploid technology and the development and validation of markers will hasten genetic gains, increase selection accuracy and reduce linkage drag in breeding for FAW resistance in southern Africa.

Key words: Exotic lines, Fall armyworm, Gamma irradiation, Local lines, Resistance, Stability

Declaration

I declare that the thesis hereby submitted by me for the degree of Philosophiae Doctor in Plant Breeding at the University of the Free State (UFS) is my own independent work and has not previously been submitted by me at another university/faculty.

I further cede copyright of the thesis in favour of the UFS.

Prince M. Matova

A handwritten signature in blue ink, appearing to read 'Prince M. Matova', is positioned above a horizontal line.

July 2021

Dedication

To the people who have inspired me, and will always continue to. These include: my late father and uncle (Muneyi Matova Snr and Manyowa Matova), my mother Rosemary Tsitsi Matova, my wife Joyce and the kids (Prince Jnr, Quniton Muneyi Jnr and Miss Talia Mufaro), Dr Cosmos Magorokosho and Prof Hussein Shimelis.

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Abbreviations and symbols

Gy	Gray
ABNE	African Biosafety Network of Expertise
ACAPS	Assessment Capacities Project
AD	Anthesis date
AGD-R	Analysis of genetic designs in R
AMMI	Additive main effect and multiplicative interaction
ANOVA	Analysis of variance
AN	Ammonium nitrate
ASI	Anthesis silking interval
ASV	AMMI stability value
AV	Additive variance
Avg-FFAWD	Average foliar fall armyworm damage
BC	Backcross
<i>Bt</i>	<i>Bacillus thuringiensis</i>
BLUP	Best linear unbiased prediction
CBI	Crop Breeding Institute
CML	CIMMYT maize line
CimExp	CIMMYT Experimental
CIMMYT	International Maize and Wheat Improvement Center
Coeff Reg	Coefficient of regression
CRI	Cotton Research Institute
Cs	Cultivar superiority
CV	Covariance
CV (%)	Covariance percentage
CZL	CIMMYT Zimbabwe line
DF	Degrees of freedom
DH	Doubled haploid
DLB	Demand led breeding
DNA	Deoxyribonucleic acid
DR&SS	Department of Research and Specialist Services
DS	Days to silking
DSE	Days to seedling emergence
DT	Drought tolerance
DV	Dominance variance
E	Environment
EC	Emulsifiable concentrate
EFAWD	Ear fall armyworm damage
EIL	Economic injury level
EMBRAPA	Brazilian Agricultural Research Cooperation
Env	Environment
ER	Ear rot
ETL	Economic threshold level
ESA	East and Southern Africa
F ₁	First filial generation
FAO	Food and Agriculture Organisation
FAW	Fall armyworm

FFAWD	Foliar fall armyworm damage
FB	Forward breeding
g	gram
G	Genotype
GC	Grain colour
GCA	General combining ability
GE	Genotype-by-environment
GEI	Genotype-by-environment interaction
GGE	Genotype main effect plus genotype-by-environment interaction
GI	Gamma irradiation
GM	Genetically modified
GP	Genomic prediction
GS	Genomic selection
GYD	Grain yield
GWAS	Genome wide association study
h^2	Narrow sense heritability
H^2	Broad sense heritability
HC	Husk cover
HRS	Harare Research Station
HTP	High throughput phenotyping
<i>i</i>	Selection intensity
IAEA	International Atomic Energy Agency
ICIPE	International Centre of Insect Physiology and Ecology
IITA	International Institute of Tropical Agriculture
IPCA	Interactive principal component axes
IPM	Integrated pest management
IRM	Insect resistance management
ISAAA	International Service for the Acquisition of Agri-biotech Applications
KRS	Kadoma Research Station
LxT	Line by Tester
LD ₅₀	Lethal dose 50
LSD	Least significant difference
m	meter
mm	millimetre
M ₀	Mutant generation zero
MABC	Marker assisted backcross
masl	Meter above sea level
MARS	Marker assisted recurrent selection
MAS	Marker assisted selection
META-R	Multi-environmental Trials Analysis in R
MLN	Maize lethal necrosis
MVDB	Mutant variety database
MW	Maize weevil
NA	Not available
NES	Number of emerged seedlings
NAbs	Number of abnormal seedlings
NAS	Number of albino seedlings
NPK	Nitrogen, Phosphorous, Potassium

OPV	Open pollinated varieties
PC	Principal component
PH	Plant height
PP	Product profiling
PPT	Push-Pull Technology
QTL	Quantitative trait loci
QTN	Quantitative trait nucleotides
<i>r</i>	Selection accuracy
<i>R</i>	Response to selection
RARS	Ratray-Arnold Research Station
RCBD	Randomised complete block design
RGA	Rapid generation advance
Rep	Replication
RS	Radio-sensitivity
S	Selection differential
SB	Speed breeding
SCA	Specific combining ability
SH	Seedling height
SL	Stem lodging
<i>Spp</i>	Species
SSA	sub-Saharan Africa
<i>t</i>	Time
TEX	Texture
UFS	University of the Free State
US	United States
USA	United States of America
USD	United States Dollar
USDA-ARS	United States Department of Agriculture - Agricultural Research Services
UN	United Nations
UZ	University of Zimbabwe
VIB	Vlaams Instituut voor Biotechnologie
VTC	Variety Testing Center
<i>We</i>	Wricke's ecovalence
WEMA	Water use Efficient Maize for Africa
wks	Weeks
WHO	World Health Organisation
WP	Wettable powder
<i>YSI</i>	Yield stability index

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Chapter 1

Introduction

Maize (*Zea mays* L.), which is believed to be entirely tropical and American in origin, has effectively conquered the world (Edmeades et al., 2017; Wu et al., 2019). In sub Saharan Africa (SSA) maize is life. It is food and a source of livelihood for approximately 300 million smallholder farmers (CIMMYT, 2019; IITA, 2019). However, its production continues to be threatened by emerging challenges such as new diseases and insect pests (Nyaga et al., 2020). In 2016, SSA was invaded by the migratory and polyphagous fall armyworm [*Spodoptera frugiperda* (J.E. Smith); FAW] (Goergen et al., 2016; Nagoshi et al., 2018; Prasanna et al., 2018; Wightman, 2018). The pest has caused significant crop yield losses across SSA since its arrival on the continent (Abrahams et al., 2017; Baudron et al., 2019; Harrison et al., 2019; Kansime et al., 2019; Kumela et al., 2019). Breeding for FAW resistance has the potential to improve food security in SSA and potentially improve livelihoods through surplus production and sales from the booming global maize market.

Breeding a desirable variety of any crop requires: (i) selection of a suitable pool of donor parents carrying the desired traits, (ii) crossing of donor parents to lines targeted for improvement, (iii) selection and advancement of generations of the desired progenies, and (iv) evaluation for adaptation, agronomic performance and farmer preference. For self-pollinating crops, the process ends with testing of inbred lines while for maize and other cross-pollinating crops, another cycle of hybrid constitution and evaluation for combining ability, adaptability, agronomic performance and farmer and consumer acceptance is needed for the developed hybrids. In the absence of recent breeding techniques, the process can take more than 10 years to develop a hybrid with the desired trait; in this case, FAW resistance. This implies that an integrated breeding strategy is needed for speedy breeding of FAW resistance and similar stresses that may affect crop production in the future.

This study aimed to explore the possibility of breeding adapted and farmer preferred FAW resistant maize genotypes in southern Africa. Development of FAW resistant maize is desirable, as it targets the protection of smallholder farmers' maize crops from the devastating effects of the pest on their food security and livelihoods. Africa's invasion by FAW was sudden and abrupt, and in much of SSA significant food and economic losses were realised (Abrahams

et al., 2017). Finding varietal solutions to such crop production challenges requires fast and efficient breeding strategies that can bring solutions in the shortest time. However, the use of donor genetic resources in the breeding process may bring undesirable traits and reduce preferences by farmers, industry and consumers. Further to that, there is always a need to explore innovative ways of solving emerging problems such as diseases and insect pest epidemics.

Genetic variation is the backbone for selection response in plant breeding and it is the first component that is required for effective breeding. FAW resistance variation exists in various genetic materials, including elite programme lines, segregating materials, populations, pools, exotic lines, landraces and wild relatives of maize (Kumar, 2002; Womack et al., 2018; Kasoma et al., 2020). Some of these materials can be too diverse and non-adapted and have to go through a pre-breeding process to make them ‘manageable’ genetic materials (Xu et al., 2017). Several institutions including the International Maize and Wheat Improvement Center (CIMMYT), United States Department of Agriculture - Agricultural Research Service (USDA-ARS), the Brazilian Agricultural Research Corporation (EMBRAPA), and several US universities identified and developed several improved temperate, tropical and subtropical maize materials with at least partial resistance to FAW (Mihm, 1997; Kumar, 2002; Ni et al., 2008).

Donor parental lines bring in the needed traits, but further to that they should have good *per se* performance and *inter se* performance when crossed with local lines in hybrid formulations or breeding crosses. Elite performance in the source population is key to enhancing the probability for successful desired improvement (Moose & Mumm, 2008). In this study exotic FAW resistant donor lines were sourced from CIMMYT, Mexico, for introgression of FAW resistant genes into locally adapted SSA maize lines. These exotic lines need to be evaluated for their suitability for use in FAW resistance breeding with local lines, hence they will be tested through combining ability trials.

Screening of local materials, including elite programme lines, old lines and populations could identify resistant materials for potential breeding. Very few locally adapted genetic resources have been tested and only a few have been identified that have acceptable levels of FAW resistance for use in further breeding for FAW resistance (Kasoma et al., 2020; Matova et al., 2020). Effective FAW resistance selection can be best achieved under artificial infestation,

however, most national and private breeding companies do not have FAW rearing and screening facilities (Matova et al., 2020; Prasanna et al., 2018). CIMMYT and its partners have developed and documented screening protocols that can be effectively used for FAW resistance screening under natural FAW infestation (Prasanna et al., 2018), and encouraging results have been reported (Kasoma et al., 2020; Matova et al., 2020). Rapid genetic gains in FAW breeding can only be realised with the use of modern techniques that foster faster development of inbred lines and efficient screening. These include the use of doubled haploid (DH) and marker assisted selection (MAS) technologies. Most national programmes and growing seed companies cannot afford the cost of DH induction. Womack et al. (2018) suggested that use of MAS can help achieve accelerated genetic gains in FAW resistance breeding, however markers have not been developed as yet. Furthermore, Badji et al. (2020) reported that quantitative trait loci analysis on FAW resistance has not been done on African germplasm and this hinders rapid selection of breeding populations for FAW resistance.

However, there is potential for FAW resistance breeding in SSA. FAW resistant donor lines have been introduced through the International Institute of Tropical Agriculture (IITA), CIMMYT and other partners and several breeding programmes have been reported to have started FAW resistance breeding, mainly under natural infestation. CIMMYT evaluated different pools of maize genetic resources and reported that there is enough genetic diversity to support conventional breeding for FAW resistance in SSA (Prasanna et al., 2018). Mutation induction, gene editing and gene tilling poses an opportunity for faster development of FAW resistant genotypes using exotic donors or locally adapted materials. However, mutation breeding can be effectively used when the technique is optimised (Shu, 2009). For the maize crop, there is need to determine optimal doses for effective gamma irradiation on target candidates. DH induction can be used to speed up the development of pure lines that can be screened for FAW resistance and identified lines can then be used in hybrid formulations for hybrid development.

Rationale of the study

More than 300 million families living in SSA depend on maize for food and livelihood. Invasion of the region by FAW is a threat to food security and livelihoods of the multitudes of smallholder farmers in SSA (Abrahams et al., 2017). The situation is exacerbated by the fact that there are no known resistant or tolerant non-genetically modified (GM) cultivars to recommend to farmers. There have not been any documented studies that report on the

resistance or tolerance levels of cultivars grown in the region (Prasanna et al., 2018; Matova et al., 2020). Countries in SSA, with the exception of South Africa have policy restrictions on the use of GM crop varieties (ISAAA, 2017). The region relies mainly on conventionally bred cultivars and farmers' varieties in producing the maize crop. Most of these cultivars have succumbed to the pest and significant losses have been reported (Baudron et al., 2019; Kansiime et al., 2019).

The current study addressed the need to evaluate some of the cultivars and inbred lines utilised in the southern Africa region for FAW resistance. A significant number of varieties grown in Zimbabwe are also grown in eastern and southern Africa or at least share the same parental lines. Further to that, it was also imperative to investigate the possibility of developing FAW resistant varieties that are adapted to the SSA region. A number of lines with excellent FAW resistance were developed several decades ago in the Americas and these are potential trait donors for locally adapted materials. Some of these materials have some temperate background, hence it is important to evaluate their performance under the tropical and sub-tropical environments of SSA. There is a need to assess their breeding potential in combination with locally adapted lines. Mutation breeding is also envisaged as a potential strategy to enhance FAW resistance in introgression crosses with exotic donor lines as well as to create/enhance FAW resistance in local materials. The technique also poses a chance to improve the agronomic performance of the local lines, making them more adapted to SSA. In order to utilize mutation breeding effectively there is a need to optimise the technique through radio-sensitivity tests. In view of the above, a study on maize genetic improvement for resistance to FAW was deemed necessary.

Overall objective

The study aimed to investigate the possibility of breeding for FAW resistance in maize in southern Africa.

Specific objectives

- i. To assess the breeding potential of introduced exotic FAW resistant trait donor maize lines with southern Africa germplasm
- ii. To evaluate commercial maize hybrids and parental lines cultivated in southern Africa for resistance to FAW

- iii. To assess the stability of grain yield performance and resistance to FAW of resistant maize lines, cultivars and experimental hybrids under natural FAW infestation environments
- iv. To determine the optimum gamma irradiation doses to use in maize mutation breeding using inbred lines and OPVs for use in FAW resistance breeding

Hypotheses

- i. The introduced FAW tolerant donor lines have good combining ability and breeding potential for FAW resistance with locally adapted SSA germplasm.
- ii. Commercial maize cultivars, experimental hybrids and their parental lines, cultivated in southern Africa, have varying levels of resistance to FAW infestation.
- iii. Stable lines, cultivars and experimental hybrids can be identified under natural FAW infestation environments.
- iv. Gamma irradiation doses can be optimised for trait improvement in maize inbred lines and OPVs for effective mutation breeding.

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Chapter 2

Literature review

Fall armyworm invasion, control practices and prospects of breeding fall armyworm resistant maize in Sub-Saharan Africa: A review

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Abstract

Fall armyworm [*Spodoptera frugiperda* (J.E. Smith); FAW] invasion has exacerbated maize (*Zea mays* L.) crop yield losses in sub-Saharan Africa (SSA), already threatened by other stresses, especially those that are climate-change induced. FAW is difficult to control, manage or eradicate, because it is polyphagous and transboundary, multiplies fast, has a short life cycle and migrates easily, and lacks the diapause growth phase. In this study, FAW and its impact in Africa was reviewed, as well as past and present control strategies for this pest. Pesticides, cultural practices, natural enemies, host-plant resistance, integrated pest management (IPM) and plant breeding approaches were examined as possible control strategies. It was concluded that an IPM control strategy, guided by cultural approaches already being used by farmers, and what can be adopted from the Americas, coupled with an insect resistance management strategy, is the best option to manage this pest in Africa. These strategies will be strengthened by breeding for multi-trait host-plant resistance through stacking of genes for different modes of control of the pest.

2.1 Introduction

The sub-Saharan Africa (SSA) region is dominated by smallholder farming systems characterized by intense cereal crop production, maize (*Zea mays* L.) being the most important staple crop for humans and feed crop for livestock (Smale et al., 2011; ACAPS, 2017; Tambo et al., 2019). More than 300 million farming families depend on maize for food security and livelihoods in Africa (Cock et al., 2017; VIB, 2017; Kumela et al., 2019). Maize production in SSA is dominated by smallholder farmers (Edmeades et al., 2017; Sisay et al., 2018; CIMMYT,

2019), growing the crop under diverse climatic and socio-economic conditions (Cairns et al., 2013). Climate-induced maize production constraints include heat and drought stress (Cairns et al., 2013), and emerging invasive insect pests and diseases (CIMMYT, 2019; IITA, 2019). The socio-economic factors affecting productivity of maize include small pieces of land, unaffordable input costs, limited labor, and lack of machinery to ease farming operations (VIB, 2017). As a result of the above constraints, maize yields in Africa are generally low, averaging around 2.0 t ha⁻¹ or below (Cairns et al., 2013; Edmeades et al., 2017; VIB, 2017).

Fall armyworm [*Spodoptera frugiperda* (J.E. Smith); FAW] is currently the most damaging crop pest affecting maize in SSA, where it has spread very widely (ACAPS, 2017; Kumela et al., 2019). It is a polyphagous (can feed on several hosts) and migratory (can spread to other countries) pest that survives on at least 80 plant species, including maize, wheat (*Triticum aestivum* L.), sorghum (*Sorghum bicolor* (L.) Moench) and rice (*Oryza sativa* L.) (Sibanda, 2017; Prasanna et al., 2018; Harrison et al., 2019). In the past, the pest was only found in North and South America where it is the most important pest of maize (Pannuti et al., 2016; Fatoretto et al., 2017; Hruska, 2019), but recently, its two strains, the rice strain (R-strain) and the corn strain (C-strain), invaded new territories in the tropical and sub-tropical African regions (Cock et al., 2017; FAO, 2019a). The two strains are morphologically identical but different in physiological features and host-plant preferences (Nagoshi et al., 2018; Nagoshi & Meagher, 2018). The R-strain prefers smaller grass species (especially millet) and pasture habitats, whereas the C-strain prefers larger grasses, such as maize and sorghum (Nagoshi & Meagher, 2018). FAW was first reported in Africa in 2016 (Goergen et al., 2016; Cock et al., 2017); and since then, it has spread throughout SSA and Asia, causing significant crop damage resulting in economic losses (Abrahams et al., 2017; Rwomushana et al., 2018; Tambo et al., 2019). Evidence suggests that the races introduced in Africa originated from south Florida (USA) and the Caribbean (Nagoshi et al., 2018). The consequences of FAW invasions on food and nutrition security in SSA have been made worse by lack of resistant/tolerant cultivars, poor capacity to control and manage the pest (Abrahams et al., 2017; Harrison et al., 2019), and the suitability of the climatic conditions for the rapid multiplication and perpetuation of this pest (Prasanna et al., 2018). FAW, riding on migratory winds, has the potential to travel for long distances, and can prolifically breed in suitable environmental conditions typical of SSA (Abrahams et al., 2017; Baudron et al., 2019; Kumela et al., 2019).

Currently, researchers are working on immediate and long-term solutions to the problem. Breeders are developing cultivars that can offer native resistance to the pest, while chemical companies, entomologists and other researchers are developing insecticides, bio-controls and cultural-methods, respectively, to minimize crop damage that can result after infestation (Wightman, 2018). Most farmers are relying on chemical and mechanical control methods, indigenous and farmer-to-farmer advice and recommendations from extension services (Baudron et al., 2019; Kumela et al., 2019). Chemical control constitute the use of pesticides while mechanical control methods are those cumbersome approaches that include hand crushing of the larvae, moths and eggs, placing sand and ashes in leaf whorls, and other cultural practices. Baudron et al. (2019) viewed such practices as labor intensive, exhaustive, time-consuming and not practical, especially for women, who are usually the dominant labor force in smallholder agricultural systems. Research and extension are advising farmers to use IPM to manage the pest. This is targeted at minimizing chemical damage to people and the environment, while targeting effective pest control (Abrahams et al., 2017). In this review, the aim is to provide: (i) a summary of the current and the potential negative effects of FAW invasion on the livelihoods of smallholder communal farmers in SSA, (ii) a synthesis of past and present approaches targeted at managing this pest, and (iii) the prospects for developing FAW-resistant maize genotypes for SSA. The research questions guiding the review included: (i) the current and anticipated FAW impact in SSA, (ii) the management of the pest by smallholder farmers, and (iii) possible FAW management practices and strategies suited for SSA.

2.2 The pest, its migration into Africa and its impact

2.2.1 Morphology and biology of fall armyworm

FAW larvae resembles some other noctuids including the African army worm [*Mythimna unipuncta* (Haworth)], and corn earworm [*Helicoverpa zea* (Boddie)]. However, FAW larvae has some distinct features that can help separate it from its close relatives (Prasanna et al., 2018). These include: (i) a white-colored inverted "Y" mark on the front of the dark head and (ii) a brown head with dark honey-combed markings (Figure 2.1A) and, (iii) four dark spots displayed in a square on top of the eighth abdominal segment (Rwomushana et al., 2018; Prasanna et al., 2018), as shown in Figure 2.1B.

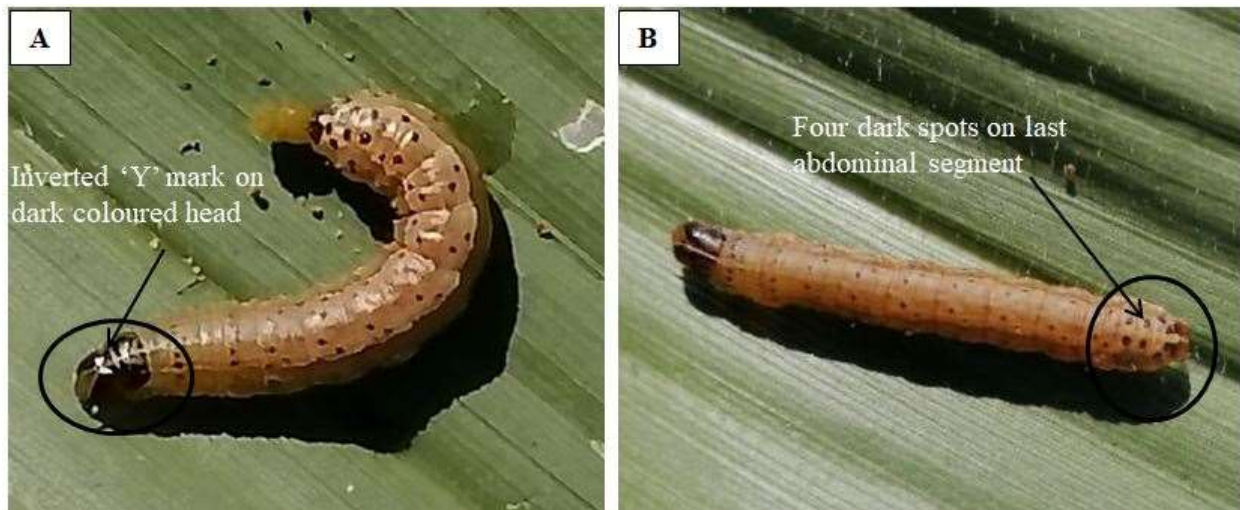


Figure 2.1 Physical appearances of the fall armyworm (FAW) larvae highlighting the most distinguishing features of the larva (photograph produced by Stanley Gokoma, edited by Prince M. Matova)

Typical early FAW infestation signs and symptoms include small ‘pin holes’ and ‘window panes’ (Figure 2.2A), resulting from feeding of the small larvae on leaves (Figure 2.2B). Damage of maize plants caused by FAW attack is severe during the early and late pre-tassel stage (Figure 2.2C). Bigger larvae consume large amounts of tissue and do much more damage compared to small larvae, resulting in a ragged appearance of the leaves (Figure 2.2D; Prasanna et al., 2018). It is also important to appreciate that foliar damage on maize may look serious but may not necessarily translate into high grain yield losses (Wightman, 2018; Hruska, 2019). Hruska (2019) reported a study carried out by the United States Department of Agriculture - Agricultural Research Service (USDA-ARS), in which they noted that FAW defoliation as high as 70% at 12-leaf stage could cause just about 15% grain yield loss. FAW defoliation on maize rarely goes above 50% (Hruska, 2019).

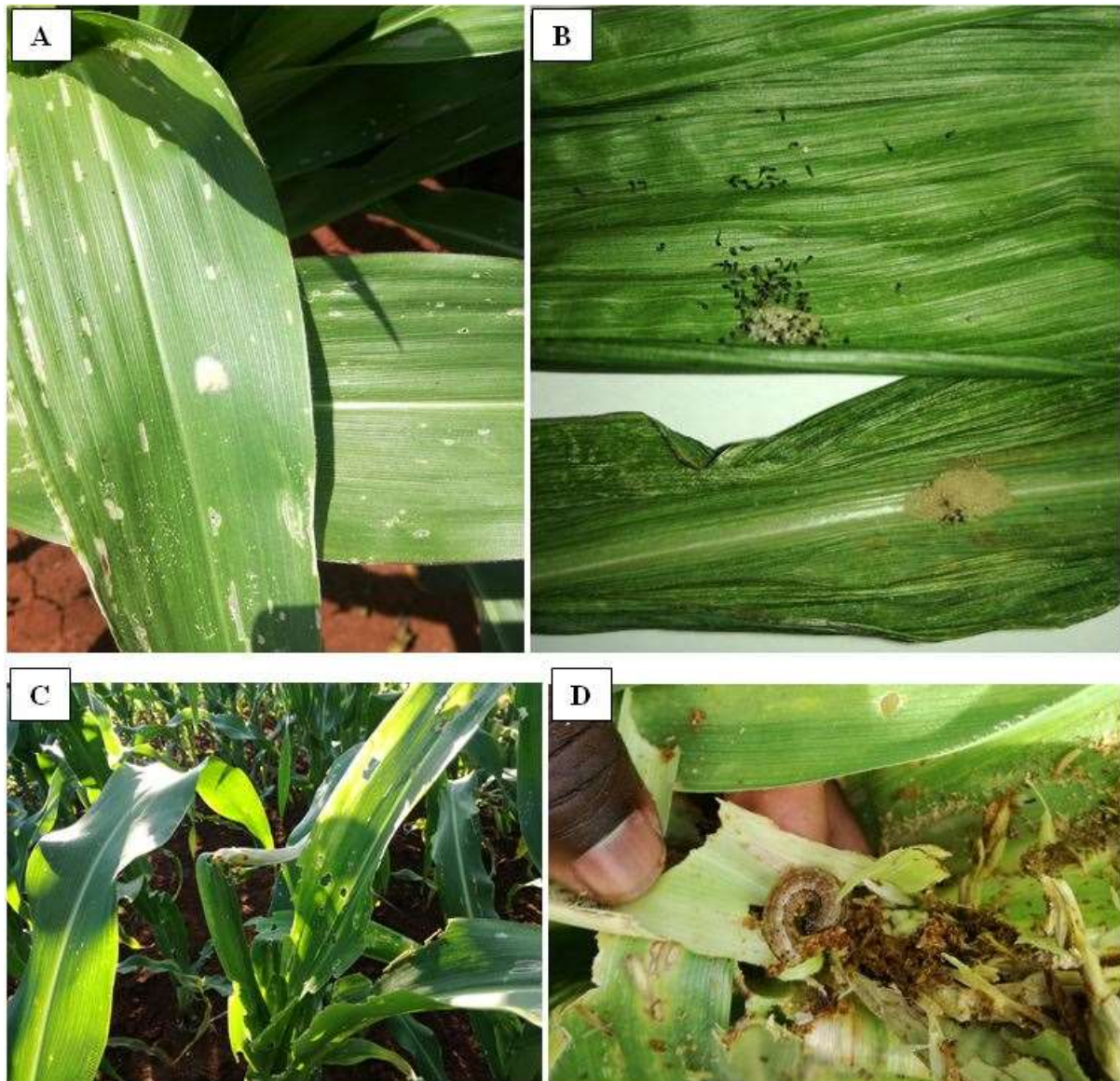


Figure 2.2 Fall armyworm egg masses and damage on maize plants (A) Fall armyworm (FAW) egg masses and first signs of FAW infestation on leaves, (B) Young FAW larvae (black heads) emerging from egg masses on window pane damaged leaves, (C) Advanced FAW damage, showing dead heart on the growing point, (D) Large FAW larvae protected by ‘frass plug’ while feeding in the whorl during tasseling stage (photographs produced by Prince M. Matova)

The FAW’s rate of reproduction and multiplication is rapid. For instance, one adult female moth is capable of laying between 1000-2000 eggs during its lifetime (Hruska, 2019). Eggs are laid in egg masses of between 100-200 eggs (Figure 2.2A and 2.2B). In warmer climates, the duration of the egg stage is only 2-3 days (Hruska, 2019). The larval stage lasts between 14 and 30 days in warmer summer and cooler winter months, respectively (Pitre et al., 1983; Kumela et al., 2019), whereas the lifespan of an adult moth is approximately 10 days. The pest

is able to complete its life cycle in 30 days at an average daily temperature of 28°C (ACAPS, 2017; Prasanna et al., 2018). This implies that in warm climates, such as those experienced in SSA, FAW can have multiple generations in one season (Nboyine et al., 2020). Coupled with the fact that FAW does not have a diapause (the biological resting period), it can establish as an endemic pest (Harrison et al., 2019; Hruska, 2019).

2.2.2 Introduction and spread of FAW in sub-Saharan Africa and beyond

FAW is native to the western hemisphere (particularly North and South America) (Pannuti et al., 2016; Sisay et al., 2018), where the insect has been a problem pest in crops for several decades (FAO, 2017; Faretto et al., 2017; Hruska, 2019). Several reports confirmed that FAW was initially established in São Tomé and Príncipe, Benin, Nigeria and Togo in 2016 (Goergen et al., 2016; Nagoshi et al., 2018; Nagoshi & Meagher, 2018; Prasanna et al., 2018). FAW is thought to have come into Africa through stowaways on commercial aircrafts, in cargo or airplanes (Abrahams et al., 2017). As of December 2018, the trans-boundary pest was reported to be present in almost all SSA countries (FAO, 2019a). The pest was detected in Yemen and India in August 2018 (FAO, 2019a; Tambo et al., 2019). As was predicted by modeling (Day et al., 2017), FAW has spread to all of the SSA countries, parts of the Middle East and Asia (Wightman, 2018; Hruska, 2019; Tambo et al., 2019), and there are chances that the pest will spread to Europe. The spread is suspected to be attributable to natural migration and through trade (Abrahams et al., 2017; Baudron et al., 2019).

2.2.3 Impact of FAW in Africa

FAW is likely to fully establish and continue to cause maize crop losses in the region because of the suitability of the region's climate for the pest's growth and development (Baudron et al., 2019). Additionally, its short life cycle, ability to travel across large geographical areas and its wide host range, promote its rapid multiplication and spread, making it difficult to control (Abrahams et al., 2017; Prasanna et al., 2018). The African Union's sustainable development goal number 7 (G7), targeted at reducing poverty and hunger, may be difficult to achieve in the absence of effective FAW-management strategies (Harrison et al., 2019). FAW is envisaged to be impacting negatively on maize crop production, maize seed production, human health, environmental integrity and, maize trade with regions where the pest has not been reported.

2.2.3.1 Impact on crop production

Available evidence suggests that FAW is difficult to control or manage (Abrahams et al., 2017; Prasanna et al., 2018; Santos-Amaya et al., 2016). This is primarily because of its feeding and sheltering behavior on the host plant. When FAW invaded Africa in 2016, the first affected farmers suffered huge losses because of unpreparedness. This was confirmed by farmers in Zambia, who reported that FAW intensity was less severe in 2017 compared to 2016, and they attributed this to awareness and early response (Kansiime et al., 2019). However, responding with pesticide control reduces profit thresholds for those farmers who grow maize for commercial purposes.

The SSA maize production environment is traditionally burdened by multiple abiotic and biotic stresses (Cairns et al., 2013; CIMMYT, 2019; IITA, 2019). FAW invasion further worsens the burden on the resource-poor SSA smallholder farmers (ACAPS, 2017; Wightman, 2018). Kumela et al. (2019) reported that farmers in Kenya and Ethiopia reported yield losses of 0.77 – 1.0 t ha⁻¹, attributable to FAW infestation. These farmers reported infestation levels that averaged 32% (Ethiopia) and 47.3% (Kenya) during that season, and anticipated a general trend of increasing infestation in future seasons (Kumela et al., 2019). In maize, FAW feeds on foliage, reproductive parts and grain. Feeding on foliage reduces economic yields by causing injury to the plant, including dead heart and reducing the photosynthetic area, whereas feeding on reproductive parts inhibits or reduces fertilization and grain formation, hence reduced final grain yield (Tambo et al., 2019). FAW is also capable of partially or totally devouring maize grain, thereby reducing grain quality and ultimately grain yield (Harrison et al., 2019). In the Americas, FAW infestations have been reported to cause yield losses ranging from 25% to 100%, depending on the severity of infestations (Arias et al., 2011; De Oliveira et al., 2018; Womack et al., 2018).

Earlier reports on impacts of FAW indicate that maize losses could be higher than previously estimated (Abrahams et al., 2017; Sisay et al., 2018). Yield losses were also anticipated in other major African crops, mainly sorghum, millets and legumes (Sibanda, 2017; Harrison et al., 2019). A survey by the FAO (2018a) in Namibia reported yield losses, attributable to FAW in maize, sorghum and millets. The survey showed that in 2017, only a small proportion of farmers (17%) engaged in coping strategies following the negative effects of FAW invasion. Another study by Abrahams et al. (2017) estimated potential annual maize losses in 12 African countries at 21 - 53%, with an economic damage projected at USD 2.48 - 6.19 million. In

contrast, Baudron et al. (2019) suggested that estimates of losses from farmer surveys could have been overestimated, from their studies in Chipinge and Makoni districts in Zimbabwe, they reported FAW-caused losses of 11.57% and 16.39%, respectively, for the two districts. The recorded infestation levels ranged between 32% and 48%. A 2018 study by Rwomushana et al. (2018) reported yield losses of 26 - 40% and 35 - 50% for Ghana and Zambia, respectively, and recently, De Groote et al. (2020) reported similar yield-loss levels, averaging 32 - 34% for Kenya. As reported by Hruska and Gladstone (2014) and De Oliveira et al. (2018), the extent of damage varied with the severity of infestation.

2.2.3.2 Impact on livelihoods

Yield losses reported by Rwomushana et al. (2018), Baudron et al. (2019), Kumela et al. (2019) and others have significant negative impacts on livelihoods of smallholder farmers, given that maize is a subsistence crop in SSA. Most households, including female-headed families in SSA, rely on income from subsistence farming to support payment of key livelihood activities, including school fees for children. Using various socio-economic and agro-ecological data, the FAO estimated food insecurity levels across households in SSA as a function of exposure to FAW invasion risk, and vulnerability and lack of coping strategies among the exposed populations. The study produced a map that is intended to help identify areas where household food insecurity due to FAW is highest, to assist decision makers in deployment of the needed assistance in the region (<http://www.fao.org/emergencies/resources/maps/detail/en/c/1110178/>). However, there is need to carry out additional impact assessment studies on livelihoods of smallholder farmers in SSA to assess the magnitude of the negative impact of FAW on their livelihoods. Even in the absence of such evidence, it is imperative that effective FAW-management strategies be put in place to guard against the pest's potential negative effects on food security and livelihoods of resource-poor farmers in SSA (Goergen et al., 2016; Wightman, 2018; Harrison et al., 2019; Tambo et al., 2019).

2.2.3.3 Impact on human health, non-target organisms and the environment

Use of pesticides to control FAW predisposes farmers to harmful insecticide contamination and also destabilizes the ecosystem by killing non-target organisms (Mihm, 1997; Kumela et al., 2019; Tambo et al., 2020). Hence, development of sustainable and environment-friendly control strategies for FAW is paramount. Initial reports from interactions with farmers and search of the internet have shown that most farmers identify the pest late in their fields and

they usually do panic spraying (Abrahams et al., 2017). As a result, they use different control strategies, including indiscriminate pesticide use, which pre-disposes the farmers, maize grain, livestock and the environment to risk of contamination (Carvalho et al., 2013; Harrison et al., 2019). Indiscriminate use of pesticides has the disadvantage of killing non-target insects, including natural enemies of the intended pest and other agricultural pests (Harrison et al., 2019). This disrupts normal ecosystem functioning and may actually promote the perpetuation of the targeted pest and create outbreaks of other pests that were being naturally suppressed by their natural predators and parasitoids.

Recent studies have shown that most farmers are not aware of, or simply ignore, the dangers of insecticides on human health and non-target insects (Kansiime et al., 2019; Kumela et al., 2019). Abrahams et al. (2017) and Kansiime et al. (2019) reported the use of cheaper, less effective and moderately hazardous insecticides, which might have negative effects on human health, the environment and natural enemies of the target and other pests (Sisay et al., 2018). Farmers in Zambia were reported to have used Monocrotophos, a Class 1b (highly hazardous) insecticide according to the World Health Organization classification (Kansiime et al., 2019). More than 50% of farmers in a study by Kansiime et al. (2019) were reported not to be using personal protective equipment during insecticide spraying. Some farmers spray maize during the grain filling to maturity stages, scenarios which create the risk of pesticide contamination and residual effect on grain intended for consumption.

Many smallholder farmers in Africa are not cautious of human and environmental safety when using synthetic insecticides (Harrison et al., 2019; Kansiime et al., 2019) and there is conclusive evidence of misuse, resulting in toxicity to humans, reduced efficacy and development of insect resistance (Sola et al., 2014; Stevenson et al., 2017; Tambo et al., 2020). This is supported by a report by the United Nations that projected the cost of injury and illness linked to pesticides at USD 90 billion between 2005 and 2020 (Lewis et al., 2016). The practice of using incorrect application rates also promotes the rapid development of insecticide resistance in the pest (Sisay et al., 2018).

2.2.3.4 Impact on seed companies

Farmers in SSA rely mainly on certified maize seed, yet the majority of seed companies supplying most of the seed in a number of countries are still developing (African Centre for Biodiversity, 2015). The sudden emergence of FAW in 2016 and its resurgence and spread in

the following seasons may compromise the economic viability of most small and emerging seed companies. This is worsened by the fact that most of these companies produce their seed with small-scale farmers. Such seed companies may need to invest in extensive grower training on identification and management of FAW.

Studies on smallholder farmers in Kenya and Ethiopia by Kumela et al. (2019), and in Zambia by Kansiime et al. (2019) showed that most farmers were able to observe FAW larvae on infected plants, while a few could identify eggs and adult stages of the pest. This has serious implications for FAW management by farmers, particularly during seed production, as early scouting and identification of eggs and early larval stages are key to ensuring effective control (Nboyine et al., 2020; Prasanna et al., 2018).

In the early years of its invasion in SSA, most farmers could not effectively identify the pest, and most chemicals used were not effective. The most affected stages were the tasseling and silking stages as pollination would be affected by the damaged tassels (personal communication, Peter at Mukushi Seeds, Zimbabwe). FAW's deleterious effects on the covered silks and ears during breeders seed production was noted (personal communication, Simbarashe Chiseko, Crop Breeding Institute, DR&SS, Zimbabwe). The larvae would evade chemical control by going inside the cellophane bags covering the silks as well as the bagged maize ears, destroying the silks and ears.

2.2.3.5 Impact on trade

The pest is likely to affect maize trade, including seed, grain and green maize between Africa and countries without FAW, because of strict and thorough checking at entry points (ACAPS, 2017). Reports suggest that grain consignments contaminated with FAW, coming from Africa, were prevented from entering Europe (Goergen et al., 2016). Lately, South Africa had started shipping maize grain for stock feed to the European Union (<https://www.biznews.com/global-investing/2018/05/23/record-corn-exports-land-debate-key>). There are chances that this may not continue. Seed maize export from Africa to areas without FAW is likely going to be difficult or even impossible because of biosecurity measures across regions.

2.3 Fall armyworm control strategies: past and present

Maize and FAW are both native to the Americas. The two have co-existed in their natural habitat for many years (FAO, 2017). Farmer experiences and research on FAW in maize during

the past 100 years in Mesoamerica have drawn some key lessons that can be used to effectively manage and control FAW in areas where it has recently invaded (Assefa & Ayalew, 2019; Tambo et al., 2019). Traditionally, the Americans have been controlling FAW using host-plant resistance, insecticides (synthetics and botanicals), cultural practices (including early planting, crop rotations and intercropping) and IPM approaches (Abrahams et al., 2017; Womack et al., 2018; Tambo et al., 2019). Farmers and researchers in SSA need to adopt and customize some of these strategies to suit the African farming practices according to farm size and various socio-economic factors (Wightman, 2018; Tambo et al., 2019).

2.3.1 Factors influencing smallholder farmers' choice of FAW control strategies

Farmers' choice of FAW control strategy is affected by various factors, which include availability of a control strategy (including its effectiveness and ease of use) and resources, gender and age among other issues (Kansiime et al., 2019; Constantine et al., 2020). Kansiime et al. (2019) implicated farmers' gender and age as factors affecting control practices; insecticide application was popular among men, and cultural/mechanical methods were mostly practiced by women. Constantine et al. (2020) reported that in Kenya most farmers use chemical pesticides as opposed to biopesticides, because the former is perceived as more effective, fast acting, affordable and having a wide spectrum of target pests.

Sola et al. (2014) reported that farmers in Africa found insecticides unaffordable, as a result many farmers avoided using them. Social settings in most of SSA are such that men have better access to, and control of, finances; hence they tend to use that advantage to make work easier for them. This could explain why synthetic insecticide use was dominated by men. Women, because they usually lack financial resources and are the main labor force in the fields, tend to prefer mechanical control methods. Men used combined control practices more than women across ages, while elderly farmers preferred cultural methods, sometimes combined with synthetic and botanical pesticides, compared to younger farmers, who preferred synthetic pesticides (Kansiime et al., 2019). This is probably because young farmers, and men in general, prefer quick results, which normally come with synthetic insecticides, and they normally have the funds to purchase insecticides. Use of insecticides by elderly farmers may be motivated by age, as they no longer have the strength to use mechanical methods.

Given that FAW is migratory in nature and can quickly build up a population in a short time, pest containment at community level under smallholder farmer setup was seen to be a

challenge, since control strategies are based on individual farmer preferences (Kansiime et al., 2019). Poorly controlled fields harbor the pest, and this causes new infestations, even in fields where farmers effectively control the pest. Kansiime et al. (2019) regressed grain yield against various socio-economic and management practices on FAW infestation levels and the results showed a strong positive correlation between grain yield and use of cultural practices and pesticides in managing this problematic pest. This implied that farmers, who tried to control FAW using one or a combination of methods, would be able to secure grain yield against FAW damage.

2.3.2 Fall armyworm control practices

2.3.2.1 Synthetic and botanical pesticide control practices

Smallholder African farmers rarely use pesticides in maize production. Using data from a survey carried out between 2010 and 2012, Hruska (2019) reported that pesticide use (across all crops) could be as low as 3% in countries without input subsidies, such as Malawi. A 2017 study by the FAO reported that about 1.7% of smallholder farmers in Namibia used pesticides in crop production (FAO, 2018b; Hruska, 2019). In Kenya and Ethiopia, some farmers confused the FAW with some familiar pests such as common African stalk borer [*Busseola fusca* (Fuller)], spotted stalk borer (*Chilo partellus* (Swinhoe)) or African armyworm (*Spodoptera exempta* (Walker)), hence they made wrong choices in pesticide application, which did not help control the pest (Kumela et al., 2019). Appropriate insecticides are usually costly, which tends to push farmers to use cheaper alternatives they come across in trying to eliminate this invasive insect pest. Coupled with incorrect application rates and procedures, this could explain why some farmers in Kenya and Zimbabwe felt insecticides were not being effective in controlling FAW (Baudron et al., 2019; Kumela et al., 2019). In contrast, 97% of farmers in Zambia confirmed that pesticide application helped in controlling FAW, especially when the pesticides were alternated (Kansiime et al., 2019).

As an emergency response strategy to FAW invasion in 2016, most governments in Africa distributed chemical insecticides to farmers through extension. However, most of these were ineffective, since efficacy trials had not been done at that time and the insecticides were used indiscriminately (Abrahams et al., 2017; Sisay et al., 2018). Some of the broad-spectrum pesticides that were being used included Thionex (Endosulfan 50%), Carbaryl (Carbaryl 85WP), Dimethoate (Dimethoate 40EC) and Karate (Lambda cyhalothrin 5EC). These were later replaced by more efficient and eco-friendly pesticides, which included Ecoterex

(Deltamethrin and Pirimiphos methyl), Emamectin benzoate/Macten (Emamectin benzoate 5%), Super dash (Emamectin benzoate and Acetamiprid), Ampligo (Chlorantraniliprole and Lambda-cyhalothrin) and Belt (Flubendiamide).

Governments' intervention promoted the use of insecticides among smallholder farmers in most countries, for instance, it was reported that 72% and 60-62% farmers in Ghana and Zambia respectively, used inorganic insecticides to control FAW in 2017 (Hruska, 2019; Kansiime et al., 2019). The reported increase in pesticide use among smallholder farmers was motivated by the availability of free insecticides distributed by national governments (Abrahams et al., 2017; Kansiime et al., 2019). In those areas where insecticides were not distributed, most farmers simply did not know what to use to control the pest, and some farmers did not use chemical pesticides because of their high cost, as a result farmers suffered yield losses without any control intervention (FAO, 2018b; Rwomushana et al., 2018).

Chemical insecticide control for FAW is a common practice in North and South America (Fatoretto et al., 2017). In contrast, most smallholder farmers in Africa, where there is no government support, cannot afford the repeated spraying required to achieve effective control (Sisay et al., 2018). In some regions of SSA farmers also tried to control FAW using botanical pesticides such as ground chilli pepper, tobacco extracts, neem tree leaves and jatropha leaves (Baudron et al., 2019; Kumela et al., 2019). These botanical pesticides had traditionally been used to control other insect pests in field crops. They seem cheaper alternatives for the resource-poor farmers and are probably less hazardous to the farmers, environment and non-target insects (Roman, 2016; Stevenson et al., 2017; FAO, 2019b). Smallholder farmers in Mesoamerica have been reported to use the same practices in managing FAW (FAO, 2018a).

The relative effectiveness of some of these botanicals on FAW has been studied and reported (Babendreier et al., 2020; A. J. Hruska, 2019). Neem oil and neem seed and leaf powder were reported to have 70% mortality on FAW larvae (Maredia et al., 1992; Silva et al., 2015), and oil from *Eucalyptus urograndis* was effective in protecting maize (Hruska, 2019), while *Carica papaya* seeds ground into powder were found to be as effective as the chemical insecticide malathion (Archundia et al., 2006; Figueroa-Brito et al., 2013). In Ghana, neem oil-based products (0.17 – 0.33%) were found to be almost as effective as Emamectin benzoate (Ema 19.2 EC) in reducing FAW damage in maize (Babendreier et al., 2020). In that study, both the

low and high doses of the neem extracts had the same effect on FAW, hence lower doses were recommended for control.

Though most farmers in SSA are now aware of FAW (Hruska, 2019; Kansiime et al., 2019), the majority are not yet well equipped with knowledge and resources, to effectively control and sustainably manage the pest (Assefa & Ayalew, 2019; Hruska, 2019; Kumela et al., 2019). Kansiime et al. (2019) reported that farmers in Zambia used a total of 22 active ingredients in trying to control FAW, with some of the farmers mixing two to three insecticides in one spray to ensure effectiveness. Other farmers applied insecticides only once in the season, while some applied repeatedly but without a proper spraying schedule. Various rates were used on the basis of crop stage rather than insect stage (Kansiime et al., 2019). In Ethiopia, Assefa and Ayalew (2019) highlighted the fact that there were no registered insecticides for FAW, and that threshold levels were not being implemented to determine the need to spray.

A recent FAW population dynamics study in Ghana by Nboyine et al. (2020) recommended that farmers who used insecticides to control FAW needed to make the best use of the first nine weeks of crop establishment. These nine weeks mark the period in which the foliage of the maize crop will still be soft enough for young neonates, hence moths are attracted by the crop to lay eggs. High-pressure insecticide spray directly on the whorl can give good chemical control, depending on the efficacy of the insecticide used and the larval stage of the FAW. However, the best results are achieved when control is instituted when the larva is young and before it burrows deep into the whorl or enters into the ears of the maize plant.

2.3.2.2 Cultural agronomic practices

Yigezu and Wakgari (2020) summarized different cultural practices that have been utilized across SSA in managing and controlling FAW infestation and maize yield losses. These include handpicking and killing of larvae, placing sand or wood-ash in whorls of maize plants, drenching plants with tobacco extracts, deep plowing to kill overwintering pupae, early planting, destruction of ratoon host plants, burning infested crop residues after harvesting, intercropping with non-host plants, use of multiple cultivars and rotation with non-host crops (Kebede & Shimalis, 2019; Yigezu & Wakgari, 2020).

Studies by Baudron et al. (2019) reported the effectiveness of additional cultural practices, such as weeding and fallow periods against FAW for smallholder farmers in Zimbabwe. Results

showed that repeated weeding reduced FAW damage, probably due to the fact that most of the weeds in the study area were FAW hosts of the graminaceous family. Maize production under zero or minimum tillage was reported to reduce FAW damage in the Americas because it favored population build up for predatory species (Rivers et al., 2016). Kebede and Shimalis (2019) reported that conservation agriculture could reduce the impact of FAW through build-up of natural enemies and boosting of the maize crops' ability to fight the infestation. However, this contradicts the need to deep plow and burn crop residues in infested fields to control worms and pupae, as viewed by Yigezu and Wakgari (2020). Reduced and zero tillage are common practices in Africa; it is therefore important to do further research on this as an option of managing FAW in smallholder farmer systems in SSA.

However, maize intercropping with pumpkin (*Cucurbita spp.*) increased FAW damage, most likely because pumpkin is a known host for FAW (Baudron et al., 2019). Intercropping of maize with legumes, such as cowpea, groundnut and common beans, was also found to be ineffective in reducing FAW damage (Baudron et al., 2019). In contrast, Hailu et al. (2018), reported that intercropping maize with edible legumes significantly reduced FAW and stem-borer infestation and damage. Yigezu and Wakgari (2020) also reported that non-host legumes, such as beans, when intercropped with maize, significantly reduced FAW infestation and damage on maize. Altieri et al. (1978) reported the same findings in Colombia. Intercropping was also reported as one of the control strategies used by farmers in the Americas (FAO, 2017). It is believed that intercropping of two or more crops, or inclusion of non-host crop plants in the field, can reduce FAW oviposition on the maize plant.

Traditionally, smallholder farmers in Central and South America apply sand or soil into the leaf whorls to control the pest. In southern Africa, some farmers used grains of sand, applied together with ammonium nitrate fertilizer, or as separate treatments to control FAW, and this significantly helped control the pest. However, the effectiveness of these and other methods used needs scientific testing (Hruska, 2019). It is thought that sand scarifies the insect's body, predisposing it to infection by natural pathogens, while the ammonium nitrate fertilizer dehydrates the worm, thereby killing it. Kansime et al. (2019) reported that about 19% of the surveyed farmers in Zambia used sand, ashes and detergents to control FAW larvae during the 2016/17 cropping season. The practice of spraying sugar solution and fish soup was also used by farmers in some parts of SSA (Harrison et al., 2019). The strategies are targeted at attracting

and building up populations of natural enemies (predatory ants, parasitoids, solitary wasps and other enemies) in the field (FAO, 2018c).

General good crop management can help in managing FAW. The ability of the maize crop to withstand FAW attack is dependent on the nutritional and water status of the crop. Farmers in Zambia reported that FAW attack was more severe in fields where fertilizer was not applied compared with those where it was applied (Kansiime et al., 2019). The same farmers also reported that early planting and good timing of fertilizer application reduced FAW severity. A well-fertilized and well-watered crop can resist or recover rapidly and much better from FAW attack compared to a water-stressed and nutritionally deficient maize crop. The maize crop can recover from low levels of FAW damage, however this is highly dependent on the crop's growth stage and nutritional status of the crop (Hruska, 2019).

According to Hruska (2019), cultural practices need to play a major role in FAW control in SSA. In view of the small land areas cultivated to maize by smallholder farmers in SSA, Hruska (2019) supported the idea that mechanical control strategies, such as egg squashing and larvae picking can work, citing experiences in Kenya and Ethiopia, where 337 000 ha and 402 000 ha, were satisfactorily controlled in 2017 and 2018, respectively, using this strategy. Wightman (2018) considered the laying of eggs by FAW in large conspicuous clusters, a weakness of the pest itself, as this allowed for easy destruction of the pest through egg squashing or by predatory insects. Tambo et al. (2019) reported that larvae picking and chemical application were the major control strategies utilized in Ghana and Zambia, and a combination of the two practices gave the highest grain yield under FAW infestation. This was also supported by Kansiime et al. (2019), who reported that 36% of farmers in Zambia used cultural/mechanical methods to control FAW, and these were dominated by larvae picking and egg squashing. Physical squashing of larvae, moths and egg masses and use of ashes and liquid detergents in FAW control were also noted in various other countries across Africa (Rwomushana et al., 2018; Wightman, 2018; Baudron et al., 2019).

2.3.2.3 Biological control practices

FAW has several natural enemies, such as predators, parasitoids and pathogens that regulate its population levels. In some cases, intercropping creates an environment that favors development and growth of a population of natural enemies, large enough to control FAW (FAO, 2017). This observation has resulted in popularization of the 'Push-Pull Technology'

(PPT) currently being recommended for FAW control (ICIPE, 2018). The method was developed by the International Centre of Insect Physiology and Ecology (ICIPE) for control of stem borers in maize and is now being promoted and used in several SSA countries to control FAW.

The PPT is based on intercropping maize with greenleaf desmodium, *Desmodium intortum* (Mill.) Urb., and bordering the intercrop with *Brachiaria* cv Mulato II (Midega et al., 2018). The *Desmodium* protects the maize by emitting semiochemicals that repel (push) the moths that are concurrently attracted (pulled) by semiochemicals released by the border crop. ICIPE (2018) and Midega et al. (2018) reported that FAW infestation can be reduced by at least 80% in a field where the technology is being practiced. Hailu et al. (2018), in their studies in Uganda, reported FAW infestation levels of 36-38% on maize under PPT, which were significantly lower compared to 95% infestation observed under sole cropping. PPT reduced FAW infestation in maize better than maize-legume intercropping (Hailu et al., 2018).

Natural parasitism levels of more than 44% have been recorded in unsprayed fields in the Americas (FAO, 2017), which has implications for the development and recommendation of control strategies in SSA. A study by Sisay et al. (2018) in Ethiopia, Kenya and Tanzania, identified five native species of parasitoids, some with parasitism levels as high as 45.3%. These include *Cotesia icipe* (Fernandez-Triana & Fiobe), *Palexorista zonata* (Curran), *Coccygidium luteum* (Brulle), *Charops ater* (Szépligeti) and *Chelonus curvimaculatus* (Cameron). Several other studies have also identified natural enemies of FAW, with the same high levels of parasitism. Kenis et al. (2019) reported the presence of *Telenomus remus* (Dixon) in at least five SSA countries. Agboyi et al. (2020) observed 10 species of parasitoids (*T. remus*, *Chelonus bifeveolatus* (Szpligeti), *Trichogramma* sp., *C. luteum*, *C. icipe*, *Meteoridea* cf. *testacea* (Granger), *Charops* sp., *Metopius discolor* (Tosquinet), *Pristomerus pallidus* (Kriechbaumer), *Drino quadrizonula* (Thomson) in Benin and Ghana. In addition, Koffi et al. (2020) identified seven parasitoids species and three FAW predator species in Ghana. The parasitoids include *C. bifeveolatus*, *C. luteum*, *C. icipe*, *M. testacea*, *Bracon* sp., *Anatrichus erinaceus* (Loew), and an undetermined tachinid fly (Diptera: Tachinidae), while the predator species are *Pheidole megacephala* (F.), *Haematochares obscuripennis* (Stal) and *Peprius nodulipes* (Signoret).

Geographical variation in species occurrence and level of parasitism was noted (Sisay et al., 2018; Kenis et al., 2019; Agboyi et al., 2020; Koffi et al., 2020), which was due to differences in geographical areas, agronomic practices, crop type and stage (Hay-Roe et al., 2016; Ruíz-Nájera et al., 2007). Further studies are required in this area to identify parasitoid species with high parasitism levels, to enable effective biological control in SSA.

In the Americas, though costly, some mass rearing and release of parasitoids and predators are practiced, and are effective in managing the pest FAW and other pests (FAO, 2018c; Parra & Zucchi, 2004; Soares et al., 2012). In SSA, classical bio-control may need government intervention for implementation due to the high cost. However, in light of the recent studies performed in several SSA countries that have identified native parasitoids with good parasitism levels (Agboyi et al., 2020; Kenis et al., 2019; Koffi et al., 2020; Sisay et al., 2018), augmentative bio-control becomes the most appropriate option. Unlike classical bio-control, augmentative bio-control involves periodic release of native species of the pest's natural enemies to augment natural biological control (FAO, 2018c). The Americas have found the parasitoid *Trichogramma* to be effective in controlling FAW through its attack on the pest's egg masses (Prasanna et al., 2018; Soares et al., 2012). Scientists at ICIPE in Kenya and Agboyi et al. (2020) also recommended the parasitoids, *Trichogramma* and *Telenomus*, for augmentative FAW bio-control. Their research proved that the two wasps, when released into maize fields, search for and lay their eggs on the egg masses of FAW, thereby killing FAW before it is even hatched (ICIPE, 2018). Further studies may need to be conducted to determine if this can be implemented cost effectively.

Entomopathogens are pathogens that affect insects and naturally regulate FAW populations in the Americas (Molina-Ochoa et al., 2003). These have also been observed to control FAW in some farmers' fields in Africa (FAO, 2018c). Assefa and Ayalew (2019) reported that FAW was susceptible, in the Americas, to 16 species of entomopathogens, mainly viruses and bacteria. They highlighted that the occurrence and distribution of bio-control agents, including entomopathogens, was dependent on their habit and determined by geographical location, agricultural practices and insecticide use. However, in SSA there is still need to investigate the presence and distribution of these entomopathogens for effective exploitation in FAW control strategies. FAW larvae killed by viruses and fungi are easy to identify. Larvae killed by viruses become soft, usually with head hanging down from the leaves, while those killed by fungi become hard, appearing frozen on leaves with a whitish or light green color (FAO, 2018c).

Farmers in Central America recycle fungal spores and viroid particles through spraying strained entomopathogen filtrate of larvae killed by viruses and fungi into the whorls of maize plants infested by FAW (FAO, 2018c). This promotes continued infection and death of FAW larvae by entomopathogens, which results in reduced FAW populations in maize fields. Virus-based bio-pesticides have also been used in the Americas (Valicente et al., 2010), but these may need testing and registration in SSA. Bio-pesticides that have been tried and showed potential in Africa, including viruses, such as nuclear polyhedrosis virus, bacteria, such as *Bacillus thuringiensis* and fungi, such as *Metarhizium* and *Beauveria* spp. (FAO, 2017, Constantine et al., 2020). However, there is limited use of this in Africa due to several reasons, chief among them is cost and limited knowledge (Constantine et al., 2020).

2.3.2.4 Host plant resistance strategy

The USA uses both native and transgenic FAW resistance to manage FAW in maize, and transgenics have recorded the highest levels of resistance to the pest (Williams et al., 1997; Wightman, 2018). Native resistance is defined as resistance that is naturally available in the gene pool, harnessed through selection for effective use in agricultural production systems (Ni et al., 2014). Native resistance offers significant protection to a crop, but it is usually combined with other management measures in an IPM strategy. This strategy may work better for African farmers, who have limited access to finances to purchase chemical insecticides. Access to cultivars with some level of resistance or tolerance to FAW brings cost-effective control to the resource-poor smallholder farmers in SSA.

Native resistance has not been reported in SSA, because FAW is a new pest and no cultivars with native resistance have been released so far. A study in Zambia by Kansiime et al. (2019) reported greater use of improved cultivars compared to local cultivars, and this is true for most countries in southern Africa. Farmers in Zambia and Zimbabwe reported varying levels of variety susceptibility to FAW (Baudron et al., 2019; Kansiime et al., 2019), improved cultivars being more susceptible as opposed to open-pollinated varieties (OPVs) and local cultivars (Kansiime et al., 2019). In Brazil, FAW was primarily controlled with insecticides until insecticide resistance became a problem, resulting in the introduction of *Bt* maize (Aguirre et al., 2016; Faretto et al., 2017; Sisay et al., 2018). *Bt* maize has effectively managed FAW in the Americas (Womack et al., 2018) but with a 3-4 year cycle of resistance breakdown

(Fatoretto et al., 2017). Adoption of genetically modified (GM) maize in the USA, Brazil and Argentina has surpassed 85% (Hruska, 2019).

Host-plant resistance using transgenic cultivars is one strategy being used by farmers in South Africa (Botha et al., 2019). While most countries in SSA have policy restrictions on the use of GM crops (ISAAA, 2017), farmers in South Africa have been cultivating GM maize cultivars with insect-resistance traits since 1998 (Kruger et al., 2012; 2014). The transgenic maize event 'MON810' was introduced for commercial production in South Africa in 1998 by the then Monsanto company (now Bayer), with the intention to control stem borer. However, the same genes also confer partial resistance to FAW (Prasanna et al., 2018). Another maize transgenic event, MON89034, was introduced in 2010, also by Monsanto (Bonsu & Esterhuizen, 2019). This event contains stacks of insect resistance traits; it is resistant to FAW, common Africa maize stalk borer and spotted stalk borer. For now, the resistance is more durable compared to that in MON810, making it the most preferred maize event in controlling FAW in South Africa (ISAAA, 2017). Botha et al. (2019) reported moderately effective to highly effective field control of FAW with *Bt* events carrying stacks of Cry1A.105 + Cry2Ab2 proteins.

In general, transgenic cultivars carrying monogenic/oligogenic resistance normally exert high selection pressure on insect pests, potentially leading to the development of insect resistance (Hellmich & Hellmich, 2012; Kruger et al., 2012). Stem borer resistance to *Bt* maize was reported by Kruger et al. (2012) and this was thought to have been caused by poor compliance to refugia requirements. Puerto Rico, Brazil and the USA have reported resistance of FAW to Cry1F *Bt* maize, while the same has been reported for Cry1Ab *Bt* maize in Brazil (Botha et al., 2019). Such cultivars, with complete insect pest resistance, should always be planted together with a refuge crop nearby to allow susceptible insect populations to survive and breed with the resistant pest (Onstad, 2014a; Fatoretto et al., 2017). A refuge crop is used to sustain a population of *Bt*-susceptible pest strain (Botha et al., 2019; Kruger et al., 2014). Inter-pest strain breeding between the *Bt*-susceptible and *Bt*-resistant strains can result in dilution of alleles for resistance, thereby slowing down insect pest resistance (Hurley and Mitchell, 2014; Mohankumar and Ramasubramanian, 2014; Onstad, 2014a). The refuge crops are used in South Africa by commercial farmers, who can afford using GM cultivars, and view the practice as more profitable than cultivation of non-GM cultivars (Kruger et al., 2012). In the early years of the introduction of GM maize cultivars in South Africa, many commercial farmers, despite enjoying the benefits of growing GM maize cultivars, continued cultivating large areas of non-

GM maize for export to other African countries that preferred only GM-free maize (Kruger et al., 2012). This implies that native resistance to FAW is the ultimate solution for most of SSA.

2.3.2.5 Integrated pest management (IPM) strategies

Following the invasion of SSA by FAW, key agriculture stakeholders in the region, including governments, international and non-governmental organizations, discussed potential interventions. These included running widespread awareness campaigns, and training of farmers and agricultural stakeholders on building an IPM approach toward controlling and managing FAW (Abrahams et al., 2017; Prasanna et al., 2018). An IPM strategy is based on the principle of controlling a pest using a combination of methods while causing the minimum possible damage to the environment, animals and people. IPM combines cultural, biological, host-plant resistance and safe pesticide control methods (Hurley and Mitchell, 2014; Onstad, 2014a;b). The strategy conveniently aims at slowing down the indiscriminate use of pesticides, which many farmers were employing in trying to manage the pest.

FAW IPM strategies are targeted at preventing or avoiding pest infestations, and management of established infestations. This involves routine scouting to identify and respond to infestations, to suppress the pest using the IPM triangle strategies, i.e., minimum application of safe pesticides, provision of safe, scientifically proven or evidence-based options to farmers, and managing insect resistance to pesticides (Onstad, 2014a; Prasanna et al., 2018). The IPM triangle is a practice that enhances effective application of IPM strategies by considering control as a three-pronged strategy comprising of (i) chemical, (ii) biological and, (iii) cultural control, all based on effective pest monitoring (Zalom, 2010; Onstad, 2014a). The IPM triangle manages resistance through a concept of resistance management that ensures sustainability and eco-friendly pest management strategies (Onstad, 2014a; b).

Monitoring, scouting and early detection are critical in controlling FAW. Pheromone traps are used to monitor the pest's presence and abundance in and around the field, and this can be used to forecast the pest's movements (Prasanna et al., 2018). The traps attract, trap and kill male moths, but they do not sufficiently reduce the male moth population to disrupt mating, hence they should not be used for FAW control purposes (FAO, 2019b), but rather only for monitoring and forecasting. Effective monitoring and forecasting can only be achieved with highly specific cost-effective lures that exclude non-target species, otherwise low specificity leads to overestimation of infestation levels and false movement patterns (Meagher et al.,

2019). Lures are synthetic compounds that mimic natural pheromones and these are put in traps to attract the moths (FAO, 2018d; Knodel et al., 1995). Studies conducted in the USA, Central America and Brazil suggested that there were regional differences in pheromone attractiveness to FAW and also different pheromone-lure compositions showed differential attraction for non-target insects (Meagher, 2001; Batista-Pereira et al., 2006; Meagher et al., 2013; Spears et al., 2016), and this is important for monitoring and surveillance in SSA. FAO has reviewed the commercially available pheromone traps and has made recommendations on the best traps to use for FAW moths (FAO, 2019b). In Togo, Meagher et al. (2019) tested three commercial pheromone blends commonly used in the USA, together with two commercial and one locally made trap for optimal number of moths captured, lure specificity and cost of monitoring. Regardless of lure type, commercial bucket-type traps captured the most moths. The bucket-3C lure trap combination showed the most desirable results, but it is relatively costly (USD 13.50 per trap), which makes the local-3C trap combination a good and affordable (USD 3.50 per trap) choice for smallholder farmers in SSA, as it captured high numbers of moths (Meagher et al., 2019). Its low specificity could be compensated by placing more traps in the target area. Meagher et al. (2019) provides general guidelines regarding the most appropriate trap and lure type suitable for West Africa, but further studies are needed for other regions of SSA.

FAW can have multiple generations in one field and different types of damage can be experienced simultaneously. Control using pesticides is most effective when the larva is still small and young (Nboyine et al., 2020; Prasanna et al., 2018), as older larvae may be difficult to control because of the “frass plug” that deters insecticide penetration into the larva (Bessin, 2004). The pest is usually more destructive on late-planted crops, and in maize, it prefers the whorl stage (V2 – V12 stages) (Bessin, 2004). Random sampling during scouting of the field to check for the pest or signs of infestation is key. It is recommended that at least 10 - 20 consecutive plants should be checked daily for signs of infestation in a field, with the first plant chosen randomly (Bessin, 2004; Prasanna et al., 2018). For scouting to be informative, at least five different spots in a field should be sampled, conforming with FAO’s “W” or “zig-zag” sampling method (Bessin, 2004; FAO, 2018a). Different generations of larvae cause different types of injury to the plant (Harrison et al., 2019; Kumar, 2002). Correctly identifying the type of damage may help in determining the growth stage of the larvae, which can help in choosing an appropriate control strategy. Small larvae cause small ‘pin hole’ and ‘window pane’ damage on leaves, whereas the larger larvae prefer hiding in the whorl and cause foliage damage. During the flowering phase (VT stage = tasseling and silking), large larvae may be pushed out

of the whorl by the tassel as it emerges and they may move to the ears for shelter and food (Bessin, 2004).

It is best for FAW control measures to be instituted when there is evidence of the pest's presence in the field (Onstad, 2014b; Stout, 2014; Prasanna et al., 2018). Effective control is realized when appropriate measures are implemented before damage reaches economic threshold levels (ETLs), i.e., the pest population or pest damage that needs to be controlled so that the damage will not reach and surpass economic injury level (EIL) (Hunt et al., 1995; Paula-Moraes et al., 2013). If the crop damage surpasses EIL, it will no longer be economical to control the pest. At the EIL, yield loss attributable to the pest is equal to the cost of controlling the pest (Paula-Moraes et al., 2013). As a guide, chemical control strategies should be implemented when egg masses are spotted on at least 5% of the crop or when 25% of the crop at early whorl stage (or 40% at late whorl stage) is showing physical damage caused by the pest and when live pests are visible on the crop (Bessin, 2004; Prasanna et al., 2018).

2.4 Prospects for success in breeding for resistance to fall armyworm

The most effective way to manage and control insect pests in crop production is to use insect-resistant crops (Kumar, 2002; Rwomushana et al., 2018). Chemical control provides immediate control, but pesticide resistance can be a problem (Aguirre et al., 2016), and this led to the development of GM maize in the Americas (Aguirre et al., 2016; Gutierrez-Moreno et al., 2019). Host-plant resistance is a phenomenon that is expressed by the degree of the damage by the pest on the host plant. This is influenced by heritable characteristics encoded in the genome of the plant that enables it to suffer minimal damage by the pest (Mihm, 1997).

However, there has not been any systematic study in SSA that has determined and reported maize genetic resources resistant to FAW. Thus far, no research on breeding and release of FAW-resistant maize genetic resources has been conducted in SSA (Prasanna et al., 2018). Reports from recent studies on other aspects of FAW have shown that maize cultivars grown in southern Africa and the SSA region, at large, have succumbed to the pest (Baudron et al., 2019; Kansiime et al., 2019). Various national programmes, working together with CIMMYT and IITA, have initiated breeding programmes for the development of FAW-resistant cultivars in SSA. In Zimbabwe, the national breeding programme, collaborating with CIMMYT and local seed companies, has initiated screening of the diverse maize genetic resources and

commercial cultivars. This strategy will help generate baseline information for advising farmers on cultivar use, or to be used by maize breeders to decide on best lines and/or populations for developing maize breeding populations for FAW resistance.

Breeding for insect pest resistance in maize started around the 1900s (Gernet, 1917; Hinds, 1914) and native FAW resistance was found in crops, such as maize, sorghum, millets, Bermuda grass and peanuts (Wiseman and Davis, 1979; Mihm, 1997; Stout, 2014). There have been considerable efforts to breed maize for native resistance or tolerance to FAW in the Americas (Mihm, 1997; Mihm et al., 1988; Williams et al., 1983; Wiseman et al., 1981), and successes have been reported in literature (Brooks et al., 2005; Kumar, 2002; Stout, 2014). Unfortunately, breeding for native FAW resistance has been quickly overtaken by the advent of *Bt* maize (Hellmich & Hellmich, 2012; Wightman, 2018; Xiao & Wu, 2019). In the 1970s to 1990s, CIMMYT, the USDA-ARS, the Brazilian Agricultural Research Corporation, EMBRAPA, and several US universities identified and developed several improved temperate, tropical and subtropical maize materials with at least partial resistance to FAW (Mihm, 1997; Kumar, 2002; Ni et al., 2008). These materials have been used to breed for resistance to FAW in the Americas, and are potential sources of genes for resistance to FAW, which can be introgressed into current SSA-adapted maize lines, for developing locally adapted hybrids resistant to FAW.

Some of these genetic resources have been introduced into several SSA countries, including Ethiopia, Kenya, Nigeria and Zimbabwe, and crossed to locally adapted lines (Prasanna et al., 2018). New cultivars can be developed through introgression of the FAW-tolerance genes into locally adapted but FAW-susceptible inbred lines, as suggested by Womack et al. (2018). Zimbabwe's national maize breeding programme, collaborating with CIMMYT and the International Atomic Energy Agency, carried out mutation induction in locally adapted materials. New inductions were targeted on selected FAW-tolerant donor lines. It is anticipated that novel lines may be selected for effective breeding of FAW tolerance in the SSA region, potentially leading to production of hybrids for testing and release. Newly developed maize cultivars are often disliked by farmers on account of taste issues (Wightman, 2018). It is therefore very important to include farmer preferences when developing and testing new FAW tolerant cultivars.

Across the years, plants have developed ways to resist/tolerate insect pest herbivory, and these include morphological, biochemical and molecular mechanisms (Womack et al., 2018). Several scientists have classified host-plant resistance into three different categories, which are non-preference, antibiosis and tolerance (Stout, 2014). Previous research has shown that antibiosis is the major mechanism responsible for FAW resistance in resistant genotypes (Wiseman et al., 1981; Williams et al., 1997). Non-preference is the mechanism that confers resistance, mainly on account of hairs on the leaves and stems, thick leaf cuticles, and the shiny leaf texture (Mihm, 1997). Hairs and shiny leaf texture are likely to make the plant an unpleasant habitat, while a thick cuticle makes it hard to bite and chew the leaves. Ni et al. (2008) investigated the resistance of maize inbred lines to both foliar and ear damage by FAW. Included in the study were four CIMMYT inbred lines (CML333, CML335, CML 336, and CML338) with varying levels of silk maysin that confers resistance to corn earworm (*Helicoverpa zea* (Boddie)). Earworm is a close relative of FAW. The study concluded that earworm-resistant maize inbred lines with varying levels of silk maysin could confer cross-resistance to foliage-feeding FAW at the seedling stage (X. Ni et al., 2008). The CIMMYT maize line (CML), CML338, was among the inbred lines with resistance to earworm (Ni et al., 2008).

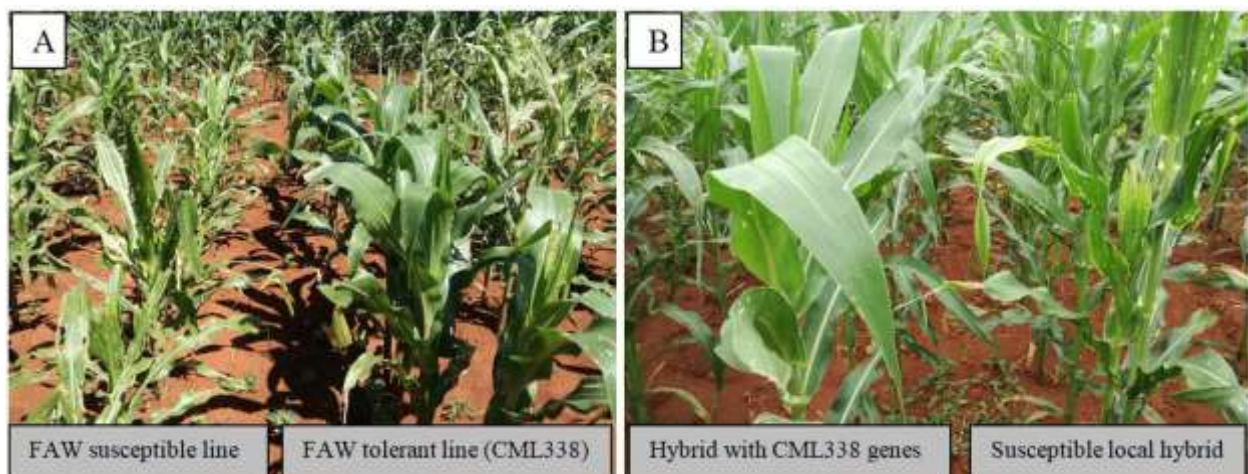


Figure 2.3 Appearances of fall armyworm susceptible and resistant genotypes under fall armyworm infestation. (A) Fall armyworm (FAW) tolerance donor line, CML338, that resists foliar damage by FAW, compared to a susceptible local line, in a field planted under natural infestation in Harare, and (B) A susceptible local hybrid compared side by side with a hybrid with introgressed genes for FAW tolerance from CML338 under natural FAW infestation in Harare in March 2020

The CIMMYT lines, CML338 (Figure 3A), CML67 and CML139 (of Antiguan origin) (Kumar, 2002; Mihm et al., 1988), are among the CIMMYT FAW-tolerance donor lines that

were introduced into SSA for the purpose of introgression of FAW-resistance genes into the locally adapted elite inbred lines to develop FAW-resistant, locally acceptable inbred lines for hybrid development. The hybrids CML67 and CML139 possessed non-preference and antibiosis resistance that was heritable in crosses between susceptible and resistant lines (Kumar, 2002; Kumar & Mihm, 1996). Breeding crosses that have been made so far with FAW-tolerant donor lines and local lines in eastern and southern Africa are yielding promising resistant genotypes (see Figure 3B), and this gives hope for success in breeding locally adapted cultivars that have acceptable resistance to FAW.

In resistance breeding, in general, partial resistance is usually preferred to complete resistance, as partial resistance confers horizontal resistance, which is more durable and takes longer to break down as the pest continues to evolve across time (Storer et al., 2010; Farias et al., 2014; Faretto et al., 2017; Chandrasena et al., 2018). In most cases, native resistance in maize has been found to be polygenic and quantitative in nature and is durable compared to monogenic and oligogenic resistance, typical of transgenics (Chandrasena et al., 2018; Huang et al., 2014). FAW resistance is determined on the modified Davis scale, which measures the extent of damage to foliage or ear on a scale of 1 (most resistant) to 9 (most susceptible) (Davis et al., 1992; Davis and Williams, 1994; Huang et al., 2014; Prasanna et al., 2018). Maize cultivars exhibiting multiple-gene resistance (partial resistance) to FAW, have resistance scores from 3 to 5 on the modified Davis scale. These differ from their genetically modified counterparts carrying Lepidopteran monogenic or oligogenic resistance, which exhibit scores of 1 to 2 on the Davis scale (Aguirre et al., 2016). It is therefore important for breeding programmes to consider durability of resistance as much as the source and strength of the resistance. This is particularly important in Africa, where variety replacement is still slow. African farmers would need a variety that has durable FAW resistance, which they can use for several years without resistance breakdown.

Multiple trait resistance attributable to stacking of native resistance genes or trans-genes into locally adapted maize cultivars with native resistance, can increase durability of FAW resistance (Huang et al., 2011; Prasanna et al., 2018). This works better if breeders combine several traits with different modes of action or toxic proteins (Huang et al., 2014; Faretto et al., 2017). Previous research in the Americas has confirmed that stacking multiple insect-resistance genes effectively controls FAW and manages insect resistance much better (Mohankumar and Ramasubramanian, 2014; Faretto et al., 2017). In South Africa, Botha et

al. (2019) reported high levels of FAW mortality (>99%) with the pyramid toxic event Cry1A.105 + Cry2Ab2 in tolerant and resistant genotypes. Baudron et al. (2019) and Kansiime et al. (2019) reported varying levels of response of different genotypes to FAW infestation in Zambia and Zimbabwe. This creates prospects of improving further maize cultivars for tolerance to FAW.

South Africa has been partnering with Kenya, Mozambique, Tanzania and Uganda in the ‘Water-use Efficient Maize for Africa’ (WEMA) project targeted at developing and disseminating improved maize cultivars for the smallholder farmers (Prasanna et al., 2018). The project was initiated in 2012 and it tested the *Bt* maize event MON810 and other locally adapted maize genotypes that had been stacked with *Bt* and drought-tolerance genes (DT; DroughtGard® or CspB from *Bacillus subtilis*). The cultivars have been tested for safety and efficacy of the transgenic traits against Lepidopteran pests, such as stem borer and FAW, and drought stress under confined environments (ISAAA, 2017). Results from the WEMA project in Kenya, Uganda and Mozambique have shown that introgression of MON810 into locally adapted maize cultivars confers strong stem borer resistance and partial FAW control in maize (Prasanna et al., 2018). Use of these *Bt* events in countries that allow cultivation of GM maize can be a good FAW-management option for the farmers. However, there are significant differences in the status of the biosafety systems in different African countries, with South Africa being one of the few countries having an established biosafety system in place. The African Biosafety Network of Expertise (ABNE) was established to enhance the capacity of African countries to build functional biosafety regulatory systems (ABNE, 2020).

However, studies by Botha et al. (2019) suggest that the FAW introduced in South Africa and probably most of SSA might have resistance alleles against Cry1Ab or the event is a low dose for FAW control. This implies that Cry1Ab *Bt* maize events, such as MON810, require gene stacking for effective FAW control. Gene stacking will also help slow down resistance development regarding the FAW pest. In SSA, the majority of smallholder farmers cannot afford to purchase *Bt* cultivars, as they are usually costly, unless there is government subsidy on the cost of the seed for smallholder farmers. In addition, there is always a refuge crop nearby under smallholder farmer systems. However, development of FAW resistance to present and future *Bt* maize cultivars remains a threat; therefore, insect resistance-management strategies should be put in place. Botha et al. (2019) suggested to begin with a baseline susceptibility study for FAW, as it will guide future assessments. In contrast, Wightman (2018) doubts the

feasibility of use of *Bt* maize in SSA, citing seed cost issues against the low producer price of maize characteristic of the SSA market.

Host-plant resistance is an integral part of an IPM strategy (Stout, 2014; Zalom, 2010). It is environmentally friendly and cost effective, as it reduces production costs by reducing the cost of insecticides (Mohankumar & Ramasubramanian, 2014; Womack et al., 2018). It is of paramount importance that breeders, in their efforts in developing FAW-resistant cultivars, should consider managing insect pest resistance. CIMMYT and its partners reviewed germplasm known to have resistance to FAW, and tagged those as potential sources of FAW-resistance genes, and concluded that there was enough diversity and that conventional breeding could support effective FAW-resistance breeding in SSA (Prasanna et al., 2018). Several breeding programmes in SSA have embarked on intensive FAW-resistance breeding (Kasoma et al., 2020; Prasanna et al., 2018). Mutation induction and conventional crosses are being employed to create and introgress new alleles for FAW resistance into locally adapted maize materials. The focus is on developing elite hybrids that combine FAW resistance with farmer- and industry-preferred traits.

At present, in most of these efforts, selection is conducted mainly under natural infestations, as there are few insect-rearing and screen-house facilities for artificial infestation trials in most countries, an exception being CIMMYT in Kenya and perhaps a few private seed companies. Testing protocols for screening cultivars and inbred lines under natural FAW infestations have been developed and well documented, and these can provide effective screening (Prasanna et al., 2018). In addition, efforts are underway at CIMMYT in Zimbabwe and probably other countries, to develop insect-rearing and testing facilities for selection of lines and cultivars with resistance to FAW. Womack et al. (2018) recommended the use of molecular markers to aid phenotypic selection for FAW resistance. The latter is believed to effectively achieve genetic gains in the shortest time. This implies that selection pressure will be applied only to validate selections done through marker-assisted selection. However, this option will only be feasible upon release of validated markers for FAW-resistance selection in maize. FAW resistance is polygenic, but no quantitative trait loci (QTL) studies for FAW resistance has been done in African maize germplasm yet. Currently, genome-wide association studies (GWAS) is the most advanced strategy for mapping of genome regions associated with traits of interest, such as FAW resistance (Chakradar et al., 2017). The first GWAS study for FAW and maize weevil (MW) resistance in African maize germplasm was carried out by Badji et al. (2020), in a diverse

association mapping panel of maize inbred and doubled haploid lines developed in a wide range of African agro-ecologies. They found 62 quantitative trait nucleotides (QTNs) on all 10 maize chromosomes which were associated with FAW and MW resistance of which six were associated with both FAW and MW resistance, showing pleiotropic genetic control of resistance to these pests. Marker-assisted selection strategies for FAW resistance are therefore still in development.

The WEMA project demonstrated that stacking of *Lepidopteran* spp. resistance traits into locally adapted materials can improve FAW resistance (ISAAA, 2017; Prasanna et al., 2018). Effectively, it means that introgression of native FAW-resistance genes into SSA locally adapted materials can create sustainable and policy-acceptable FAW control. This creates the potential to develop lines and cultivars (hybrids and OPVs) that combine high grain yield potential and FAW resistance. CIMMYT is in the process of converting preferred but FAW-susceptible lines into resistant lines, and 10 promising CIMMYT maize inbreds have been identified and validated in Kenya (Rwomushana et al., 2018)..

2.5 Conclusions

FAW is difficult to control, manage or eradicate, because it is polyphagous and trans-boundary, has high multiplication capacity and a short life cycle, harbors a high trans-boundary capacity through trade and natural winds, and lacks the diapause phase in its growth. An IPM control strategy, guided by cultural approaches already being used by farmers and what can be adopted from the Americas, coupled with an insect resistance-management strategy, is the best option to manage this pest in Africa. These strategies will be strengthened by breeding for multi-trait host-plant resistance through stacking of genes for different modes of control of the pest. Maize-breeding teams in SSA need to evaluate new and old commercial cultivars, breeding populations and lines for FAW resistance. CIMMYT and several international research organizations have developed FAW-resistant lines. These FAW resistance trait donors should be introduced into SSA maize-breeding programmes for trait introgression into the locally adapted lines with or without native FAW resistance genetic backgrounds. Mutation breeding is another option that can be used to enhance FAW tolerance and improve agronomic performance in donor lines. Going forward, it may be important for all breeding programmes to consider releasing maize cultivars with a base line tolerance to FAW. In developing such

cultivars, breeders need to introgress both FAW resistance genes and good agronomic traits for high grain yield to bring effective genetic gains to the farmers.

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Chapter 3

Breeding potential of exotic, fall armyworm resistant donor maize lines in combination with elite materials adapted to mid-altitude conditions

Abstract

Lack of effective fall armyworm [*Spodoptera frugiperda* (J.E. Smith); FAW] resistance in maize cultivars is widely regarded as one of the causes of yield losses due to FAW infestation in sub-Saharan Africa (SSA). Here, 13 mid-altitude adapted lines were used as female parents in line x tester crosses with seven FAW resistant exotic donor lines to generate 83 F₁s. The F₁s were evaluated alongside five check varieties at four locations under natural FAW infestation. The study aimed to: (i) identify crosses that combined effective FAW resistance traits with preferred grain yield performance and related agronomic traits; and (ii) select the best exotic FAW donor lines that confer effective FAW resistance attributes in combination with the local lines. Significant genotypic effects were observed for foliar FAW damage (FFAWD), grain yield (GYD), anthesis date (AD), plant height (PH), husk cover (HC), ear rot (ER) and stem lodging (SL) in lines, testers and crosses. Tester variance was, predominantly, larger than line variance for all traits, and there was preponderance of additive variance over dominance variance, suggesting that additive gene action was more important in the inheritance of these traits, including FAW resistance. The best exotic donor lines with low and negative general combining ability (GCA) effects for FFAWD resistance scores were CML139; CML67; CML121 and CML345. Interestingly, lines CML139 and CML67 showed good GYD *per se* performance, which was greater or equal to the mean trial GYD and CML67, CML121 and CML345 exhibited partial FFAWD resistance. Again, the lines CML67 and CML121 showed low and negative GCA effects for HC and ER. Locally adapted lines showing similar positive attributes included CimExp1, CimExp4, CimExp5, CimExp8 and CimExp10. However, only CimExp10 expressed partial FFAWD resistance. This suggests that FAW resistance genes can potentially be harnessed from materials within breeding programmes in SSA. In addition, F₁s with low and negative specific combining ability effects (SCA) for FFAWD resistance scores, combined with high GYD and good agronomic performance attributes, were identified as CimExp1/CML331, CimExp1/CML345 and CimExp10/CML331. F₁s with the best SCA effects for GYD combined with partial FFAWD resistance and desired agronomic traits included CimExp5/CML331, CimExp7/CML346, and CimExp5/CML345. Overall, results

demonstrated that effective FAW resistance breeding can be achieved using the exotic and locally-adapted breeding resources.

3.1 Introduction

Maize is the main staple food and livelihood crop for more than 300 million families in sub-Saharan Africa (SSA) (Edmeades et al., 2017; VIB, 2017). The crop is highly adaptive to a varied range of production environments and it is also relatively easy to produce (Machida et al., 2010; Shiferaw et al., 2011; Santpoort, 2020). Unfortunately maize production in SSA is constrained by quite a range of socio-economic and bio-physical factors (CIMMYT, 2019; IITA, 2019). Of interest in this study are insect pests, but in particular fall armyworm [*Spodoptera frugiperda* (J.E. Smith), FAW]. Invasion of the SSA region by this invasive, trans-boundary and maize prolific feeder, threatens food and nutrition security, especially in smallholder farming systems, where mitigation strategies are limited (Abrahams et al., 2017; FAO, 2018; Harrison et al., 2019; Kansiime et al., 2019). FAW invaded Africa in 2016, and since then it has caused significant crop damage on maize cultivars grown across the region (Abrahams et al., 2017; Rwomushana et al., 2018). Evidence suggests that maize cultivars grown in SSA are succumbing to the pest (Baudron et al., 2019; Kansiime et al., 2019; Kumela et al., 2019). Therefore, measures to minimize FAW's devastating effects on livelihoods in SSA need to be urgently developed.

Host plant resistance against FAW leaf and ear feeding damage is a safe method of minimising yield losses due to FAW attacks (Goldman, 2020; Matova et al., 2020). For example, various studies in the Americas have reported on success stories in which both exotic materials, with novel resistance alleles, along with native maize breeding materials were effectively used to develop varieties with FAW resistance attributes (Kumar, 2002; Mihm, 1997; Womack et al., 2018). However, similar studies have not yet been done in SSA as FAW is still a new problem in the region. Recently, maize lines bred for FAW resistance at CIMMYT-Mexico were introduced into the CIMMYT-Zimbabwe programme, but it is yet to be established if these exotic lines will adapt to the local climate and if their breeding values will be realised when combined with the locally adapted breeding materials. Therefore, the objectives of the study were to: (i) identify best exotic FAW donor lines that confer effective FAW (foliar and ear) resistance attributes when combined with the locally adapted lines; and (ii) identify F₁s that combined effective FAW resistance attributes, with desirable characteristics for grain yield

performance and related agronomic traits. The selected lines and crosses will be used in further breeding for FAW resistance in SSA.

3.2 Materials and Methods

3.2.1 Germplasm and crossing nursery

A total of 13 mid-altitude adapted lines developed within the CIMMYT-tropical maize breeding programmes, were used as female parents in line x tester crosses with seven FAW exotic donor lines sourced from the CIMMYT-Mexico breeding programme (Table 3.1). The line x tester nursery was established at the CIMMYT-Muzarabani Experiment station (GIS = -16°39'S, 31°01'E, Altitude = 334 masl, Soil type = Red clay soils, average minimum winter temperature = 14 °C, average maximum winter temp = 28 °C), during the 2017 winter season. The mating scheme yielded a total of 84 F₁s (Appendix 3.1).

3.2.2 Hybrid and inbred line trial designs and management

The 83 nicked F₁s obtained from the line x tester crossing scheme were evaluated together with four SeedCo commercial check hybrids and one CIMMYT internal check hybrid (Appendix 3.1) across four natural FAW-infested sites in Zimbabwe (Table 3.2).

The 88 hybrid genotypes were laid out in the field using an alpha (0, 1) lattice design, replicated twice, with 22 incomplete blocks which had block sizes of four plots during the 2017-18 summer season. The 20 inbred line parents (13 local and seven exotic lines) were established side by side with the hybrid trials (Kadoma excluded) during the same season. The inbred lines were also laid out in the field using an alpha (0, 1) lattice design, with two replications nesting eight incomplete blocks each. The experimental unit for all environments was a one 4 m row plot, with inter-row and intra-row spacing of 0.75 m and 0.25 m, respectively. Maize plants (lines and hybrids) were thinned to one plant per planting station at two leaf stage (approximately three weeks after planting) to give a crop population density of about 53000 plants ha⁻¹. The crops in the experiments were raised using standard agronomic practices for maize production. Optimal fertiliser rates of 400 kg ha⁻¹ for both compound D (7N:14P:7K) basal application and ammonium nitrate (AN) (34.5) for top dressing were applied at all environments. Weeds were controlled using herbicides and hand weeding where it was necessary.

Table 3.1 Description of the local lines and the exotic FAW resistance donor lines inter-mated in a line x tester crossing scheme at the CIMMYT-Muzarabani Station during the 2017 winter season

Local line name/code	Line code	GC and texture	Source	HG	Donor line/tester	Tester code	GC and texture	Source	HG
CimExp1	1	WF	Local/Exp	B	CML121	1	YD	Exotic/FAW-resistance donor	A
CimExp2	2	WD	Local/Exp	A	CML139	2	WF	Exotic/FAW-resistance donor	B
CimExp3	3	WDL	Local/Exp	A	CML331	3	WF	Exotic/FAW-resistance donor	B
CimExp4	4	WDL	Local/Exp	A	CML334	4	WFL	Exotic/FAW-resistance donor	B
CimExp5	5	WF	Local/Exp	A	CML345	5	WF	Exotic/FAW-resistance donor	B
CimExp6	6	WF	Local/Exp	A	CML346	6	WF	Exotic/FAW-resistance donor	B
CimExp7	7	WF	Local/Exp	A	CML67	7	RF	Exotic/FAW-resistance donor	B
CimExp8	8	WFL	Local/Exp	B					
CimExp9	9	WF	Local/Exp	A					
CimExp10	10	WD	Local/Exp	A					
CML312	11	WF	Local/Elite	A					
CML566	12	WF	Local/Elite	B					
CML571	13	WD	Local/Elite	B					

GC, grain colour; HG, heterotic group; WF, white and flint; WD, white and dent; WDL, white and dent like; WFL, white and flint like; YD, yellow and dent; RF, red and flint; Exp, experimental

Table 3.2 Description of experimental sites used in the evaluation of the F₁s and inbred lines

Location	Management	Altitude (m)	Latitude	Longitude	Rainfall 2018/19 (mm)	Fertilisers (NPK) ha ⁻¹
CIM-Hre	NI	1506	17°48'S	31°85'E	557.2	166:24.5:23.2
RARS	NI	1341	17°14'S	31°14'E	631.8	166:24.5:23.2
ART-Farm	NI	1527	17°74'S	31°05'E	560.9	166:24.5:23.2
KRC	NI	1149	18°94'S	29°25'E	555.6	166:24.5:23.2

CIM-Hre, CIMMYT-Harare; RARS, Rattray-Arnold Research Station; ART-Farm, Agriculture Research Trust Farm; KRC, Kadoma Research Centre; NI, natural infestation

3.2.3 Data collection and exploitation

Agronomic performance trait data were recorded per plot, including: average foliar damage to plants due to FAW (FFAWD) at 4, 8 and 12 week stages, number of days to male flowering (AD), number of plants with open husk cover (HC), plant height (PH) in cm measured from the base of the plant to the internode holding the tassel; number of plant with broken stems below the ear (SL); number of ears with ear rot (ER); grain colour (GC); ear damage due to FAW (EFAWD) at harvest; grain moisture content (MOI), and grain yield (GYD). GYD was adjusted to t ha⁻¹ at 12.5% moisture content. FAW scoring for both foliar and ear damage was done according to the modified Davis Scale (Figure 3.1) as described by Prasanna et al. (2018). SL, HC and ER were expressed as a percentage. Analysis of variance (ANOVA) was performed for individual sites and across environments on all measured traits using the Genstat Discovery Software V18.0 (VSN International, 2017). Best linear unbiased predictions (BLUPs) and broad sense heritability estimates (H^2) were done using the Multi-environment Trials Analysis in R (META-R) V2.1 R package software (Alvarado et al., 2020). The relative importance of general (GCA) and specific (SCA) combining ability effects were calculated as a proportion of cross effect sum of squares using the Line-by-Tester analysis model in the Analysis of Genetic Designs in R (AGD-R) V3.0 R software (Rodríguez et al., 2015). In the analysis, genotypes were considered to be fixed, while both replications within environments and the environments were considered to be random.

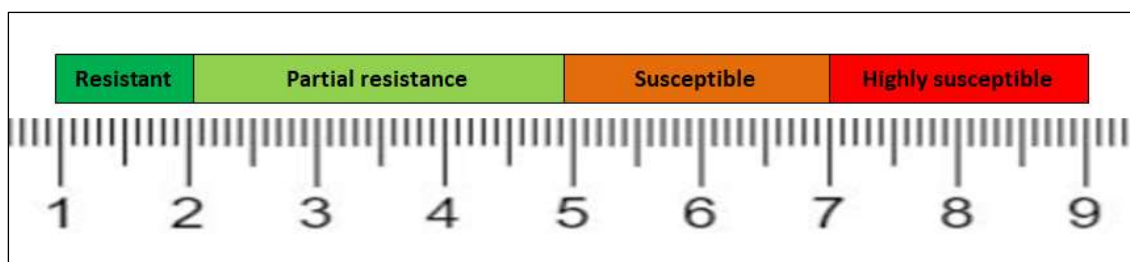


Figure 3.1 Modified Davis Scale showing scores for resistant, partially resistant, susceptible and highly susceptible genotypes across the scoring scale of 1 – 9

3.3 Results

3.3.1 Performance of the hybrids, lines and testers under natural FAW infestation

Line x tester analysis (Table 3.3) showed significant ($P < 0.05$) effects due to lines and testers for GYD, AD, FFAWD, PH, HC, ER and SL, however, line-by-tester interaction effects were absent for all traits except for GYD and AD. Tester variances were generally higher than line variances for all traits except for HC and SL. Similarly, genotypic variances were larger than line-by-tester variances for all traits. For all traits, additive variance was larger than dominance variance. The total contribution of both the additive and dominance variances was larger than that of environmental variances of all traits except for SL, where environmental variance was 28.1 against a total of 21.1 for AV and DV. For FAW resistance traits (FFAWD and EFAWD), it is important to note that environmental variance was larger than both the additive and dominance variances for FFAWD while for EFAWD additive dominance was much larger than both dominance and environmental variances.

On the other hand, the inbred line parents (local and exotic FAW donor lines) showed significant ($P < 0.0001$) genotypic effects for GYD, AD, FFAWD, PH, HC and ER. Genotype-by-environment interaction effects were present for GYD, FFAWD, PH, HC and ER, but absent for AD and EFAWD. Broad-sense (H^2) heritability estimates were high ($\geq 50\%$) for GYD, AD, FFAWD, EFAWD and HC. PH and ER showed low H^2 (Table 3.4).

Table 3.3 Line x tester analysis of crosses developed using exotic FAW resistance donor lines and locally adapted lines, evaluated across four naturally infested fall armyworm sites in Zimbabwe during the 2018-19 cropping season

Source	DF	Mean square							
		GYD	AD	FFAWD	EFAWD	PH	HC	ER	SL
Environment	3	299.51***	8495.79***	172.71***	11.71***	72087.90***	529.50***	2.31	5165.0***
Rep (Environment)	4	11.82*	14.37**	1.97***	0.43	1012.70**	82.88	237.57***	576.20**
Block (Rep x Env)	168	6.32***	8.97**	0.49***	0.31*	375.50***	73.05	48.77***	202.80*
Line	12	15.44***	41.79***	0.78**	0.28	910.10***	251.95***	26.94	522.80***
Tester	6	41.02***	151.99***	0.93**	0.26	4126.10***	222.77**	85.87**	470.00**
Line x Tester	63	5.95*	5.18***	0.30	0.29	268.20	77.69	31.99	158.70
Error		4.08	4.11	0.30	0.24	232.70	61.70	26.62	151.60
Line variance		0.05	0.86	0.0018	0	8.32	3.43	0.21	2.95
Tester variance		0.34	2.16	0.0019	0	44.85	2.68	1.85	0.14
Line x Tester variance		0.51	0.16	0.0086	0.00016	7.18	3.33	0.30	1.14
Genotype variance		0.87	2.81	0.0104	8.45	57.69	8.90	1.80	4.13
Additive variance (AV)		3.49	11.22	0.042	3.38	230.77	35.60	7.19	16.53
Dominance variance (DV)		2.04	0.64	0.035	0.00062	28.73	13.33	1.21	4.58
Environment variance (EV)		0.71	0.59	0.052	0.05	31.57	8.51	4.36	28.10
Broad sense heritability		0.89	0.95	0.60	0.01	0.89	0.85	0.66	0.43
Narrow sense heritability		0.56	0.90	0.33	6.80E-14	0.79	0.62	0.56	0.34

* P < 0.05; ** P < 0.01; *** P < 0.001; Env, environment; Rep, replication; DF, degrees of freedom; GYD, grain yield; AD, anthesis date; FFAWD = foliar fall armyworm damage; EFAWD, ear fall armyworm damage; PH, plant height; HC, husk cover; ER, ear rot; SL, stem lodging

Table 3.4 Analysis of variance pooled over environments for seven quantitative traits in maize inbred lines (13 locally-adapted and seven exotic FAW resistance donors) trials, evaluated during the 2018-19 cropping season

		Mean squares												
Source	DF	GYD	DF	AD	DF	FFAWD	DF	EFAWD	DF	PH	DF	HC	DF	ER
Environment	3	0.62***	2	386.65***	3	14.50***	3	3.78*	2	211.20	1	559.93***	3	3622.30***
Rep (Env)	4	0.67***	3	68.48*	4	1.17*	4	3.92*	3	2011.70***	2	38.47	4	1007.50*
Block (Rep x Env)	24	0.19*	18	33.76	24	2.87***	24	2.29*	18	474.20***	12	103.43**	24	1246.40***
Genotype	31	0.64***	31	77.25***	31	9.78***	31	1.86	31	364.30***	31	125.38***	31	1746.60***
Genotype x Env	81	0.19**	53	19.37	91	0.79***	84	0.91	60	222.60*	31	86.28**	84	1356.30***
Error	67	0.10	47	22.83	94	0.41	74	1.23	70	139.60	47	34.19	63	406.00
LSD (0.05)	210	0.64	154	8.64		1.25		2.01		22.89		11.15	209	45.40
Heritability (H^2)		0.73		0.81		0.92		0.5		0.46		0.58		0.35

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; Env, environment; Rep, replication; LSD, least significant difference; DF, degrees of freedom; GYD, grain yield; AD, anthesis date; FFAWD, foliar fall armyworm damage; EFAWD, ear fall armyworm damage; PH, plant height; HC, husk cover; ER, ear rot

3.3.2 Exotic donor lines that confer effective FAW resistance attributes in combination with the locally adapted parental lines

The best exotic donor lines with low and negative GCA effects for FFAWD resistance scores were: CML139 ($GCA_{FFAWD} = -0.02$, $PSP_{FFAWD} = 5.70$, $PSP_{GYD} = 0.58 \text{ t ha}^{-1}$); CML67 ($GCA_{FFAWD} = -0.014$, $PSP_{FFAWD} = 2.30$, $PSP_{GYD} = 0.66 \text{ t ha}^{-1}$) (Figure 3.2B); CML121 ($GCA_{FFAWD} = -0.0076$, $PSP_{FFAWD} = 2.8$, $PSP_{GYD} = 0.51 \text{ t ha}^{-1}$) (Figure 3.2A) and CML345 ($GCA_{FFAWD} = -0.0052$, $PSP_{FFAWD} = 3.80$, 0.39 t ha^{-1}). Interestingly, the lines CML139 and CML67 showed good GYD *per se* performance, which was greater or equal to the mean GYD (0.58 t ha^{-1}) for the trials. In addition, lines CML67 and CML121 showed low and negative GCA effects for HC and ER, i.e., CML67 ($GCA_{HC} = -1.16$; $GCA_{ER} = -0.19$) and CML121 ($GCA_{HC} = -0.61$; $GCA_{ER} = -1.00$). Again, CML139 had the best negative GCA effects for ER. The line CML121 expressed high and positive GCA effects for PH, while the other selected lines had low and negative GCA effects for the same trait. The GCA effects for PH for CML67 were significant, while those for CML334 were high, positive and significant. CML334 was not selected among the best combiners for FFAWD resistance. All the exotic FAW resistance donor lines showed partial resistance to FFAWD, except CML139 which exhibited a modified Davis score *per se* performance of 5.7.

Some of the locally adapted lines showed low and negative GCA effects for FFAWD. Local lines that combined low GCA effects for FFAWD, HC and ER with high *per se* GYD and FFAWD performance were identified. These included: CimExp1 ($GCA_{FFAWD} = -0.0269$, $PSP_{GYD} = 0.46 \text{ t ha}^{-1}$, $GCA_{HC} = -0.68\%$, $GCA_{ER} = -0.21\%$) and CimExp8 ($GCA_{FFAWD} = -0.0005$, $PSP_{GYD} = 0.43 \text{ t ha}^{-1}$, $GCA_{HC} = -0.99\%$, $GCA_{ER} = -0.0561\%$). The lines CimExp10 ($GCA_{FFAWD} = -0.0104$, $PSP_{GYD} = 0.68 \text{ t ha}^{-1}$, $GCA_{HC} = 0.17\%$, $GCA_{ER} = -0.12\%$) and CimExp5 ($GCA_{FFAWD} = -0.0073$, $PSP_{GYD} = 0.74 \text{ t ha}^{-1}$, $GCA_{HC} = 2.75\%$, $GCA_{ER} = -0.11\%$) combined low and negative GCA effects for FFAWD and ER with high GYD *per se* performance.

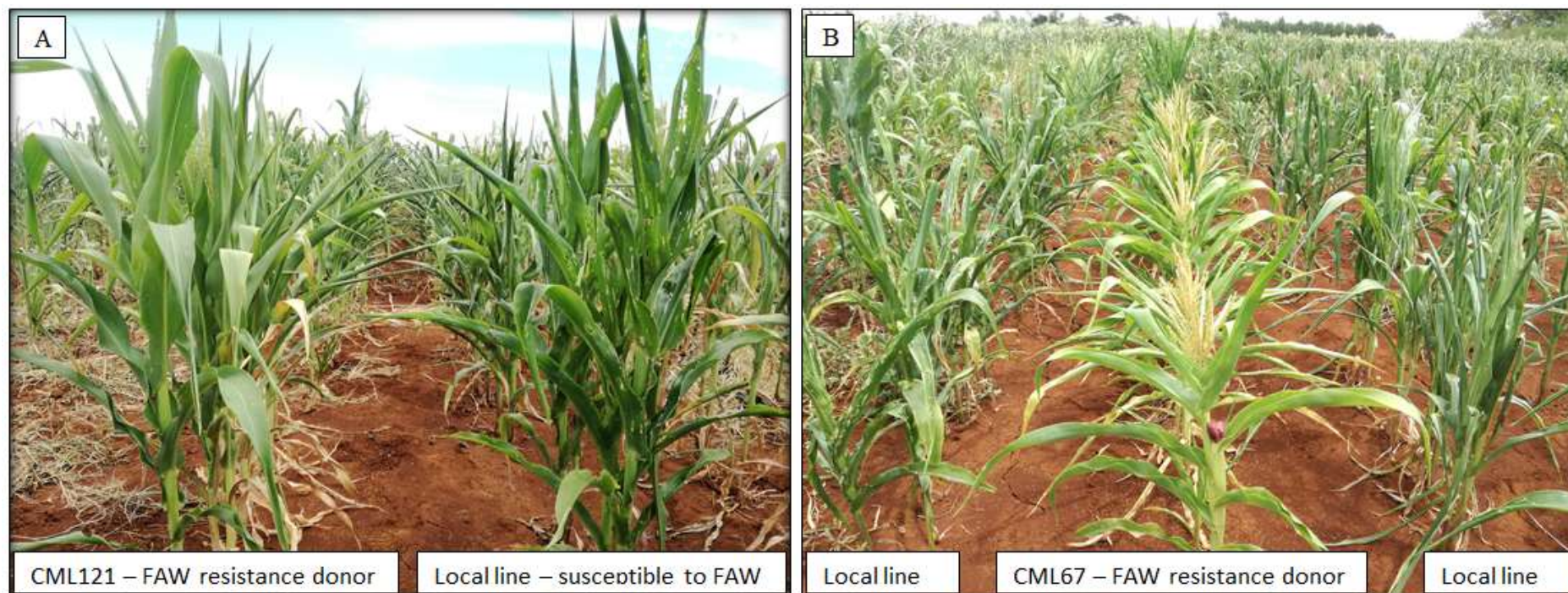


Figure 3.2 Physical appearances of the local lines and exotic fall armyworm resistance donor lines evaluated under natural fall armyworm infestation at Kadoma Research Centre, during the 2017/18 summer season. (A) The FAW resistance donor line CML121 showing FAW resistance compared to a local line showing susceptibility, (B) Two local lines showing significant leaf damage due FAW compared to the resistance donor line CML67 showing no damage from the pest (photographs produced and edited by Prince M. Matova)

Table 3.5 Estimates of general combining ability effects of lines and testers and line/tester *per se* performance in maize during the 2018-19 cropping season

Parent	GYD			AD			FFAWD			PH			HC			ER		
	PSP t ha ⁻¹	GCA	GCA Rank	PSP	GCA	GCA Rank	PSP	GCA	GCA Rank	PSP	GCA	GCA Rank	PSP %	GCA	GCA Rank	PSP	GCA %	GCA Rank
<i>Lines</i>																		
CimExp1	0.46	-0.0026	7	76.08	-0.3545	6	5.48	-0.0269	2	106.61	-2.0690	11	3.05	-0.6831	5	34.2	-0.2103	1
CimExp2	0.51	0.0948	3	76.74	-0.0683	8	5.69	0.0018	7	110.38	2.5176	2	2.04	2.4948	12	35.7	-0.1681	2
CimExp3	0.92	-0.0332	9	70.47	-0.6318	4	4.57	0.0088	9	109.1	1.1068	5	2.63	-0.5757	7	31.3	0.1923	12
CimExp4	0.62	-0.0214	8	76.89	1.4244***	12	6.29	-0.0041	5	103.19	-1.3695	9	2.04	-1.1205	2	29.6	0.1735	11
CimExp5	0.74	0.1539	1	74.33	0.1564	9	5.46	-0.0073	4	105	1.4637	4	8.59	2.7486*	13	32.8	-0.1085	5
CimExp6	0.83	-0.0765	13	72.47	-0.6675	3	5.69	0.0137	12	110.06	0.2364	7	14.28	0.0544	9	39.5	-0.1098	4
CimExp7	.	0.1100	2	.	0.6294	11	.	0.0215	13	.	-1.9182	10	.	-0.4312	8	.	0.3202	13
CimExp8	0.43	0.0558	4	77.02	-0.1366	7	5.62	-0.0005	6	105.88	2.8820	1	4.06	-0.9936	4	47.3	-0.0561	7
CimExp9	0.37	-0.0537	10	76.02	-0.6895	2	5.58	-0.0303	1	98.87	-2.7519	13	2.25	1.8247	11	45.8	0.0513	9
CimExp10	0.68	0.0162	5	72.92	-0.6292	5	4.67	-0.0104	3	110.16	0.8061	6	3.16	0.1743	10	36.7	-0.1203	3
CML312	.	-0.0728	12	.	0.5962	10	.	0.0103	10	.	-0.7216	8	.	-1.8071	1	.	0.1410	10
CML566	0.61	-0.0669	11	77.89	1.6425***	13	6.76	0.0063	8	106.81	2.3629	3	2.04	-0.6324	6	39.9	-0.0732	6
CML571	0.51	0.0104	6	70.42	-1.2715***	1	5.2	0.0106	11	114.75	-2.5451	12	2.04	-1.0531	3	39.7	-0.0319	8
<i>Testers</i>																		
CML121	0.51	-0.1174	4	72.42	-0.8639*	2	2.83	-0.0076	3	106.9	3.3132	2	2.04	-0.6057	3	29.1	-0.9987	2
CML139	0.58	-0.4859	7	76.14	-1.8320***	1	5.73	-0.0184	1	110	-1.6640	6	4.64	0.7192	5	43.5	-1.1217	1
CML331	0.49	0.0101	3	74.79	1.3522***	6	4.57	0.0211	7	108.1	-1.6256	5	2.04	-0.4371	4	45.5	0.2698	5
CML334	0.76	0.6061	2	79.34	2.4089	7	4.3	0.0171	6	108.1	11.2428***	1	2.04	2.0486	7	32.7	1.8814	7
CML345	0.39	0.6316	1	75.02	-0.0759	5	3.77	-0.0052	4	107	-0.5001	3	2.25	1.0835	6	33.8	0.2776	6
CML346	0.49	-0.3354	6	76.81	-0.1622	4	3.89	0.0072	5	108	-1.5068	4	2.04	-1.6435	1	30.6	-0.1135	4
CML67	0.66	-0.3090	5	72	-0.8271*	3	2.32	-0.0141	2	100.6	-9.2596**	7	5.19	-1.1649	2	40	-0.1949	3
LSD (0.05)	0.63			8.63			1.24			22.89			11.15			4.39		
H ²	0.73			0.81			0.92			0.46			0.58			0.35		

* P < 0.05; ** P < 0.01; *** P < 0.001; PSP, *per se* performance; GCA, general combining ability; GYD, grain yield; FFAWD, foliar fall armyworm damage; PH, plant height; AD, anthesis date; ER, ear rot; HC, husk cover

CimExp4 ($GCA_{FFAWD} = -0.0041$, $PSP_{GYD} = 0.62 \text{ t ha}^{-1}$, $GCA_{HC} = -1.12\%$, $GCA_{ER} = 0.17\%$) combined low and negative GCA effects for FFAWD and HC with high GYD *per se* performance (Table 3.5). A further look on just FFAWD *per se* performance of the local lines revealed that among the lines identified for combining low and negative GCA effects for FFAWD with high GYD and resistance to ER and HC opening, CimExp10 was the only line that exhibited partial resistance to FAWD with a modified Davis score of 4.7 (Table 3.5). Figure 3.2 clearly shows the superiority of donor lines over local lines on FFAWD

3.3.3 F₁s with effective FAW resistance attributes combined with desirable characteristics for grain yield performance and agronomic performance traits

F₁s with low and negative specific combining ability effects (SCA) for FAW resistance scores, combining GYD and good agronomic performance attributes included CimExp1/CML331 ($SCA_{FFAWD} = -0.067$; $PSP_{FFAWD} = 3.23$, $PSP_{EFAWD} = 2.21$, $PSP_{GY} = 7.35 \text{ t ha}^{-1}$, $PSP_{HC} = 2.31\%$, $PSP_{ER} = 5.28\%$) (Fig 2B); CimExp1/CML345 ($SCA_{FFAWD} = -0.0014$; $PSP_{FFAWD} = 3.24$, $PSP_{EFAWD} = 2.15$, $PSP_{GY} = 7.72 \text{ t ha}^{-1}$, $PSP_{HC} = 2.31\%$, $PSP_{ER} = 6.37\%$) and CimExp10/CML331 ($SCA_{FFAWD} = -0.00011$; $PSP_{FFAWD} = 3.33$, $PSP_{EFAWD} = 3.31$, $PSP_{GY} = 6.58 \text{ t ha}^{-1}$, $PSP_{HC} = 2.59\%$, $PSP_{ER} = 7.90\%$). The F₁s with the best positive SCA effects for GYD combined with partial FAW resistance and good agronomic traits were identified as CimExp5/CML331 ($SCA_{GYD} = 0.92 \text{ t ha}^{-1}$, $PSP_{GYD} = 8.29 \text{ t ha}^{-1}$); CimExp7/CML346 ($SCA_{GYD} = 0.89 \text{ t ha}^{-1}$, $PSP_{GYD} = 8.48 \text{ t ha}^{-1}$), and CimExp5/CML345 ($SCA_{GYD} = 0.87 \text{ t ha}^{-1}$, $PSP_{GYD} = 8.79 \text{ t ha}^{-1}$). *Per se* performance H^2 for GYD, AD, ER and HC were high (> 0.50) (Table 3.6). The hybrid CimExp10/CML67 showed good resistance to FFAWD as well as to EFAWD (Figure 3.3A; Table 3.6). The GYD and agronomic performance of the 83 F₁ hybrids, four commercial check cultivars and one CIMMYT internal genetic check variety is shown in Appendix 3.2.

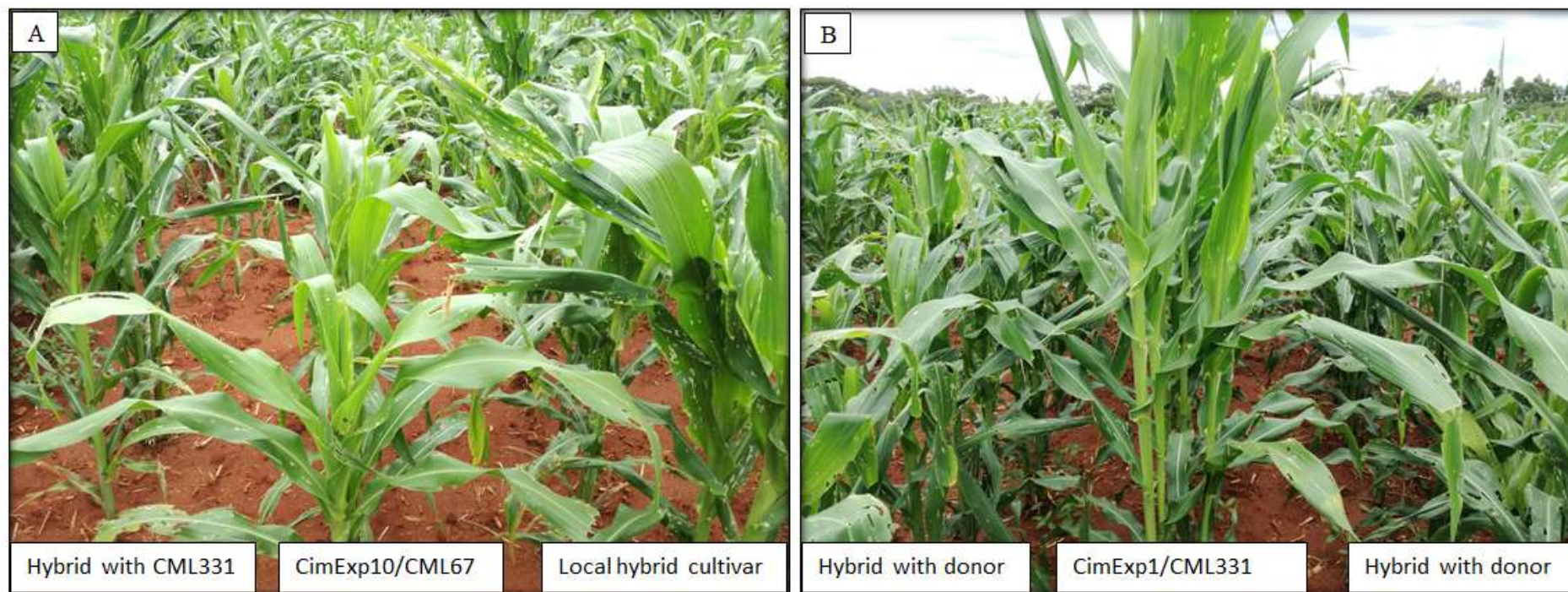


Figure 3.3 Physical appearances of the LxT hybrids evaluated under natural fall armyworm infestation at Rattray-Arnold Research Station, during the 2017/18 summer season. (A) Hybrid constituted with a local line CimExp10 and the FAW resistance exotic donor line CML67 compared to another LxT hybrid and a local cultivar, (B) The hybrid CimExp1/CML331 compared with two other LxT tester hybrids (photographs produced and edited by Prince M. Matova)

Table 3.6 Best F₁s combining fall armyworm resistant attributes with good grain yield and agronomic performance under natural fall armyworm infestation

Trait	Hybrid/SCA effects	Hybrid/cross <i>per se</i> performance (<i>PSP</i>) and rank					
		GYD (t ha ⁻¹)/Rank	FFAWD	EFAWD	AD	ER	HC
GYD	CimExp5/CML331 (0.923)	8.29 (7)	3.41	2.29	73.34	5.89	4.36
	CimExp7/CML346 (0.893)	7.84 (11)	3.36	2.17	69.53	6.67	1.52
	CimExp5/CML345 (0.865)	8.79 (2)	3.39	2.21	70.29	5.91	11.39
FFAWD	CML566/CML346 (-0.083)	5.68 (82)	3.23	2.19	73.03	5.86	1.52
	CimExp1/CML331 (-0.067)	7.35 (26)	3.23	2.21	71.44	5.28	2.32
	CimExp6/CML334 (-0.066)	6.56 (57)	3.17	2.23	72.34	6.17	5.25
EFAWD	CimExp1/CML345 (-0.0014)	7.72 (15)	3.24	2.15	70.19	6.37	2.31
	CML566/CML331 (-0.00013)	6.73 (45)	3.43	2.15	73.93	6.52	1.52
	CimExp10/CML67 (-0.00011)	7.58 (12)	3.18	2.16	69.17	4.76	1.86
AD	CimExp7/CML346 (-0.416)	7.84 (11)	3.36	2.17	69.53	6.67	1.52
	CimExp6/CML121 (-0.389)	6.78 (44)	3.36	2.24	67.97	4.91	3.38
	CML566/CML139 (-0.380)	5.30 (88)	3.53	2.20	69.07	4.73	4.03
Trials mean		6.85	3.34	2.21	70.91	6.07	3.31
<i>H</i> ²		0.65	0.46	0.18	0.85	0.58	0.54

SCA, specific combining ability; GYD, grain yield; FFAWD, foliar fall armyworm damage; EFAWD, ear fall armyworm damage

3.4 Discussion

In any breeding programme effective selection is largely dependent on the existence of sufficient genetic variability. Plant breeding relies on existing genetic variability, and in cases where the required variation is non-existent in the mainstream programme materials, introductions can be sourced for use in introgressing the required genes (Cobb et al., 2019). However, exotic materials, including wild relatives and landraces, need to be verified for their suitability for use in a breeding programme. This prevents contamination of the elite mainstream breeding materials by parents of average or low breeding value (Cobb et al., 2019; Ragot et al., 2018). Breeders use combining ability studies to assess the breeding potential of lines in breeding programmes. In this study, two sets of germplasm, inbred lines and hybrids constituted from local and exotic inbred lines, were evaluated for their combining ability effects and *per se* performance under natural FAW infestation. The results of the study were encouraging as they revealed substantial phenotypic and genetic variability particularly for FFAWD, GYD, AD, PH, HC and ER in both parents (lines and testers) and crosses. This indicates that desirable genotypes encompassing FAW resistance, high GYD and other desirable agronomic traits can be selected as hybrids for potential release or for isolation of desirable lines for further breeding and hybrid constitution. No differences were observed for EFAWD (Table 3.3; Table 3.4).

The study showed predominance of tester variance over line variance as well as prevalence of additive variance over dominance variance suggesting that additive gene action was more important in the inheritance of traits studied, including FAW resistance. Again, this suggests that GCA effects prevailed over SCA effects implying that early generation testing for FAW resistance may be effective in selecting resistant segregants. This concurs with Fasahat et al. (2016) who reported that when GCA effects prevail over SCA effects, efficient early generation testing of crosses or populations can be done, and promising hybrids can be predicted and selected based on the GCA effects of the crosses. Additive genetic variance is genotype controlled and heritable, hence reflects on the breeding value of the parent (Cobb et al., 2019; Xu et al., 2017). In this study, the high additive variance suggests that the parents used in this study were of high breeding value, hence quick genetic gains in development of desirable high yielding FAW resistant genotypes can be realised.

The proportion of additive to non-additive gene action was observed to be 99% to 1% for FFAWD. Parallel to that, the study noted the importance of dominance variance in the inheritance of GYD and FFAWD. The ratio of additive to dominance variance was 63.1% to 36.9% for GYD, while it was 54.5% to 45.5% for FFAWD (Table 3.3). This meant that for GYD and FFAWD both additive and dominance gene action were important.

Looking at the three best hybrids selected for GYD performance, additive-by-additive gene action was noted on CimExp5/CML331 and CimExp5/CML345 while CimExp7/CML346 showed additive-by-dominance gene action (Tables 3.5 and 3.6). The same gene actions were noted for FFAWD, however, interesting complimentary gene action was noted in the cross CimExp6/CML334 where both parents had high and positive GCA effects, implying susceptibility. The hybrid CimExp6/CML334 resulted in low and negative SCA effects for FFAWD, suggesting the hybrid was resistant to FFAWD and its *per se* performance supports that (Table 3.6). Studies by Derera et al. (2008) and Fasahat et al. (2016) observed the same, and reported that both additive and non-additive gene action were important in the control of insect pest and disease resistance in major field crops, including maize. Furthermore, Derera et al. (2014) found that resistance to weevils was controlled by both additive and non-additive genetic effects in maize. Meseka et al. (2018) reported that both additive and non-additive variance were important in the inheritance of aflatoxin resistance in maize, however, they noted that GCA effects were more important than SCA effects.

GCA effects were not significant for most parents for most of the traits evaluated in this study. This could be because the local lines and the exotic lines from the Americas were too diverse and could not combine well for most traits. This may mean that most of the F₁s produced by the crosses may be carrying undesirable genes that may result in linkage drag. A series of backcrosses of selected F₂ populations with the recurrent parent will be required in generation advancement of the selected populations to increase the frequency of favourable alleles. Doubled haploid induction can be applied on the backcrossed populations to produce homozygous lines for screening. In the future when markers for FAW resistance become available, they can be used to isolate lines carrying the FAW resistance genes before field evaluations.

For AD, lines CML566 and CimExp4 had highly significant and positive GCA effects, implying they were good combiners with late maturing testers, while the line CML571 was a good combiner with early maturing testers as it had highly significant and negative GCA effects for AD. The parental testers CML121, CML139 and CML67 had negative and significant GCA effects for AD. This suggests that the three testers were good combiners with early maturing lines. The line CML571 and other early maturing lines such as SV1P and CML539 that have been reported to have FAW resistance in Chapter 4 of this study can be crossed with CML121, CML67 and CML139. The FAW resistance or ability to yield better under FAW infestation by SV1P and CML539 is supposedly linked to their earliness and vigour, as was the case for an extra early OPV-Pool 16 reported in Zambia by Kasoma et al. (2020). In contrast, the line CML331 exhibited highly significant and positive GCA effects for AD suggesting that CML331 combined well with late maturing lines. The line CML331 can be crossed with the line CML491 identified to be resistant to the pest in Chapter 4 and by Kasoma et al. (2020). The parental tester CML334 expressed highly significant positive GCA effects for PH while CML67 exhibited significant and negative GCA effects for the same trait. This implies that CML334 combined well with tall lines as opposed to CML67 that combined better with short lines. Line CimExp5 combined poorly with testers on HC, it had significant positive GCA effects for HC.

For disease and insect pest resistance, negative GCA effects imply resistance while positive GCA effects are associated with susceptibility (Adenike et al., 2017). Yallou et al. (2009) observed that negative GCA effects were more important in the inheritance of *Striga spp* control in maize and Kagoda et al. (2011) reported the same in the inheritance of nematode control in maize. Ongom et al. (2012) and Meseka et al. (2018) suggested that negative GCA and SCA effects are preferred for the inheritance of disease resistance and aflatoxin resistance, respectively. This should be equally true for the inheritance of insect pest resistance. As such, this study observed both negative and positive GCA effects for FFAWD and ER in both lines and testers, meaning that there was wide genetic variability. Negative GCA effects for FFAWD and ER imply that the genotypes expressed desirable performance against FAW infestation and ER development. The parental line CimExp1 showed negative GCA effects for AD, FFAWD, HC and ER, which was desirable, as it suggests that the line is early maturing and had little or no open

husks and had resistance to FFAWD and ER. Unfortunately, the same line had negative GCA effects for GYD and PH, which is undesirable.

Lines CimExp1, CimExp4, CimExp5, CimExp8 and CimExp10 combined low and negative GCA effects for FFAWD, HC, ER and AD with high GYD *per se* performance but only CimExp10 expressed partial FAW resistance *per se* performance. This suggests that amongst the local parental lines used in this study, line CimExp10 was the best, combining high GYD with FAW and ER resistance, earliness and other good agronomic traits. The study identified the exotic FAW resistant lines CML139, CML121, CML67 and CML345 as the best donors as they expressed low and negative GCA effects for FFAWD. However, FFAWD *per se* performance of CML139 was not pleasing as it indicated susceptibility opposed to the other donors that showed partial resistance. This means that the lines CML67, CML121 and CML345 can be used effectively in introgression crosses with local lines while CML139 needs further improvement to enhance its resistance to FAW. These findings partly agree with Kumar (2002) and Kumar and Mihm (1996) who reported that CML67 and CML139 possessed non-preference and antibiosis resistance that was heritable in crosses between FAW susceptible and resistant lines (Kumar, 2002; Kumar & Mihm, 1996). The current study noted robust FAW resistance from the line CML67 while CML139 showed susceptibility to the pest. This may imply that the resistance in CML139 has broken down or FAW has evolved over the years.

Line CML139 may require crossing with other donor or local lines such as CimExp10 or CML491, SV1P, CLHP0005 and CML304 identified to be FAW resistant in Chapter 4 of this study. These are potential breeding lines that can be used in gene pyramiding schemes with exotic lines. Gene pyramiding through crossing exotic-by-exotic or exotic-by-local FAW resistant lines in double or three way crosses can enhance the resistance to FAW. Another strategy may be to subject line CML139 to gamma irradiation with the anticipation that it may enhance its FAW resistance.

Hybrid selection based on SCA effects identified CimExp5/CML331, CimExp7/CML346 and CimExp5/CML345 as the best three hybrids for GYD potential (Table 3.6). Among the three hybrids CimExp5/CML345 (8.79 t ha⁻¹) was the highest yielding, followed by CimExp5/CML331 (8.29 t ha⁻¹) and lastly CimExp7/CML346 (7.84

t ha⁻¹) (Table 3.6). Line CimExp5 was common in two of the hybrids, suggesting that the high GYD potential of the two hybrids may have been contributed by line CimExp5. CimExp5 ranked 1st on GYD performance based on GCA effects, while it ranked third based on *per se* performance with a GYD performance of 0.74 t ha⁻¹ (Table 5). CimExp7 ranked 7th based on GCA effects, the line was not evaluated in the inbred line trials for *per se* performance (Table 3.5). The corresponding tester lines CML345, CML331 and CML346 were ranked 1st, 3rd and 6th based on GCA effects with respective *per se* performance of 0.39 t ha⁻¹ for CML345 and 0.49 t ha⁻¹ for CML331 and CML346. These three tester lines performed below the trial mean of 0.58 t ha⁻¹ (Table 3.5).

All the local lines that constituted the hybrids selected as the best for FFAWD and EFAWD based on SCA effects, were identified as susceptible, except the line CimExp10 (Tables 3.5 and 3.6). This supports the findings of this study that both additive and dominance gene action were involved in the inheritance of FAW resistance (Table 3.3), as well as suggesting that there was over-dominance and positive heterosis for FAWD resistance. A clear case is for hybrid CimExp6/CML334 that was selected among the best three hybrids for FFAWD resistance based on SCA effects, and it ranked 5th on *per se* performance ($PSP_{FFAWD} = 3.2$) (Table 3.6). The female parent CimExp6 had a modified Davis score of 5.69, signifying susceptibility, while the male parent CML334 had a modified Davis score of 4.3 which indicates partial resistance to FFAWD (Table 3.5). This implied that there was dominance gene action and good SCA between CimExp6 and CML334 with regards to FFAWD. The exotic donor lines CML345 and CML67 were the only two identified for combining low and negative GCA effects for FFAWD that appeared in the hybrids with the best SCA effects for FAW resistance. The other donors that constituted the hybrids include CML331, CML346 and CML334 (Table 3.6). Overall, this suggests that the seven exotic FAW resistant donor lines used in this study can be effectively used for breeding for FAW resistance with SSA breeding lines.

3.5 Conclusions

This study demonstrated that the exotic FAW resistance lines from CIMMYT Mexico can be effectively used for breeding for FAW resistance with locally adapted SSA lines. The line CimExp10 was identified as the best, combining high GYD and FAW resistance with other good agronomic traits among the local lines. However, the lines CimExp1,

CimExp4, CimExp5 and CimExp8 showed desirable performance as well. The exotic donor lines CML67, CML331, CML334, CML345 and CML346 showed potential for use in breeding for FAW resistance while CML139 needs further improvement. Crosses constituted with the identified local and exotic lines should be tracked for extraction of desirable lines combining FAW resistance with high GYD potential. However, one or two backcrosses are recommended for the recovery of desirable traits of the local female parents. Crosses with desirable SCA effects, high GYD and acceptable FAW resistance such as CimExp5/CML345, CimExp5/CML331 and CimExp7/CML346 can be targeted for further testing and release. Though there was preponderance of additive gene action, both additive and dominance gene action were important for the inheritance of GYD potential and FAW resistance. Breeding methods that harness both additive and non-additive gene action should be employed for effective selection. Preponderance of additive variance indicates that effective early generation testing of crosses or populations for GYD and FAW resistance can be done, and promising hybrids can be predicted and selected for extraction of desirable lines based on the SCA effects of the crosses. There is need to hasten marker development and validation for FAW resistance breeding to save on time and cost. Rapid pure line development techniques such as DH induction should be integrated in FAW resistance breeding programmes to accelerate the development of resistant hybrids.

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Chapter 4

Response of maize parental lines, experimental hybrids, and commercial cultivars to fall armyworm infestation in southern Africa

Abstract

Fall armyworm [*Spodoptera frugiperda* (J.E. Smith); FAW] is negatively impacting sustainable maize production, particularly in smallholder farming systems in sub-Saharan Africa. In this study, two sets of germplasm (commercial cultivars and experimental hybrids, and local and exotic inbred lines) were evaluated for FAW resistance under managed and natural FAW infestation. The objectives were to identify exotic and locally adapted materials (commercial cultivars, experimental hybrids and inbred lines) with good FAW resistance and superior grain yield performance under FAW infestation, determine agronomic traits correlated with FAW resistance, and estimate the impact of natural FAW infestation on grain yield. Significant genotypic effects were observed for foliar FAW damage, ear FAW damage and grain yield. Commercial cultivars were significantly more affected by FAW infestation than experimental hybrids, as evidenced by high foliar and ear damage scores, but they out-yielded experimental genotypes. The introduced FAW donor lines (CML338, CML67, CML121 and CML334) showed better resistance to FAW damage, individually and in hybrid combinations. Local inbreds SV1P, CML491 and CML539, also showed great potential for FAW resistance. Local and exotic materials with sufficient FAW resistance for production and breeding were evident. Husk cover, ear rot, anthesis date and plant height were correlated with FAW resistance.

4.1 Introduction

Maize is one of the most important food security crops in Africa, and in SSA alone, approximately 38 million metric ton of maize per year is produced to feed and sustain over 300 million families (Kumela et al., 2019; Nyaga et al., 2020). While maize production in SSA is dominated by smallholder farmers, production is confounded and compromised by an array of challenges which include drought, poor soil fertility, insect pests and diseases, inappropriate seed and limited financial resources (Smale et al., 2011; Edmeades et al., 2017; CIMMYT, 2019). The world population is projected to increase by 25% in the next 30 years (Wang et al., 2019) and there is growing demand for maize

in SSA, driven by population growth, rapid urbanization and per capita demand growth (Ekpa et al., 2018; Shiferaw et al., 2011). Unlike in the developed countries, more than 63% of maize produced in SSA is for food consumption (Santpoort, 2020).

The smallholder farmers of SSA have poor mitigation strategies to the various stresses affecting maize production. In 2016, SSA was invaded by a trans-boundary, polyphagous insect pest, fall armyworm [*Spodoptera frugiperda* (J.E. Smith); FAW] (Goergen et al., 2016; Nagoshi et al., 2018; Prasanna et al., 2018; Wightman, 2018). FAW has caused significant crop yield losses across SSA since its arrival on the continent (Abrahams et al., 2017; Baudron et al., 2019; Kansiime et al., 2019). Maize is FAW's most preferred crop and several reports have indicated that most cultivars currently in production across most of SSA are susceptible to the pest (Baudron et al., 2019; Kansiime et al., 2019; Kasoma et al., 2021). However, there has not been a deliberate study to investigate the response of cultivars under production in SSA to FAW infestation (Keno et al., 2018; Matova et al., 2020). This information is important in guiding the smallholder farmers, breeders, seed companies and policy makers on the right cultivars for smallholder farmers in the region. Therefore, the objectives of this study were to: (i) identify locally adapted materials (commercial cultivars, experimental hybrids and inbred lines) with good FAW resistance and superior yield performance under FAW infestation, (ii) determine agronomic traits correlated with FAW resistance in maize hybrids, open pollinated varieties (OPVs) and inbred lines, and (iii) estimate the impact of natural FAW infestation on grain yield. This information can guide seed supply systems and breeding in the wake of FAW.

4.2 Materials and Methods

4.2.1 Germplasm for testing

A collection of 60 genotypes consisting of old and new commercial cultivars registered for cultivation in Zimbabwe, and experimental hybrids (Table 4.1) and 63 inbred lines, some of which are parents in the commercial hybrids (Table 4.2), were used. The inbred lines were developed by the Crop Breeding Institute (CBI), the International Maize and Wheat Improvement Center (CIMMYT) and HarvestPlus, while the cultivars and experimental hybrids were sourced from CBI, CIMMYT and various seed houses in Zimbabwe. The inbred lines used in the inbred line trial constituted the most prominent

parental materials for hybrids developed by CBI and CIMMYT. The commercial cultivars included OPVs and hybrids developed or introduced by CBI since 1909, as well as cultivars developed and released by CIMMYT and different seed houses in Zimbabwe. Some of the cultivars are grown in various countries across the East and Southern African regions (ESA).

4.2.2 Trial sites, experimental design and agronomic management

The trials were established under managed FAW (FAW control) and natural FAW infestation across different sites in Zimbabwe during the 2019 and 2020 summer seasons. Under managed FAW environments, chemical insecticides were used to control FAW. The chemicals used included Ecoterex (Deltamethrin and Pirimiphos methyl), Emamectin benzoate/Macten (Emamectin benzoate 5), Super dash (Emamectin benzoate and Acetamiprid), Ampligo (Chlorantraniliprole and Lambda-cyhalothrin) and Belt (Flubendiamide). Despite this there were still low levels of infestation, as some of the chemicals did not prove effective.

The lowveld research sites (Chiredzi and Chisumbanje) have been traditionally used for maize stalk borer screening as they naturally have a high infestation and active population of stem borers and other insect pests and recently, the FAW due to their inherent high temperature and low rainfall characteristic (Table 4.3). The other sites in Harare, Gwebi and Kadoma represent major maize production areas of Zimbabwe, hence they are expected to have significant FAW populations during maize growing seasons (Table 4.3). The sites DR&SS-Harare and Gwebi VTC were used in both years, while CIMMYT Harare and Chisumbanje were used only in 2019 and Chiredzi, RARS and Kadoma-CRI were used during 2020.

The commercial cultivars experiment was laid out in a $10 \times 6 \alpha (0, 1)$ lattice design, while the inbred line experiment was laid out in a $9 \times 7 \alpha (0, 1)$ lattice design, with both experiments having two replications at each testing site. The experimental unit for all environments was a one 4 m row plot (17 planting stations) except at DR&SS-Harare (DR&SS-Hre) and CIMMYT-Harare (CIM-Hre) that had 2 m row plots (eight planting stations), with inter-row and intra-row spacing of 0.75 m and 0.25 m, respectively.

Table 4.1 Description of commercial cultivars evaluated for resistance to fall armyworm under natural infestation in Zimbabwe

Code	Name	Source	Year of release	Production region	Grain	Market status
1	Salisbury white	CBI	Not Clear	Zimbabwe and ESA	WD	Inactive
2	Southern cross	CBI	Not Clear	Zimbabwe and ESA	W	Inactive
3	Hickory king	CBI	Introduced	Zimbabwe and ESA	W	Inactive
4	R200	CBI	1971	Zimbabwe	Y	Inactive
5	R201	CBI	1971	Zimbabwe	W	Active
6	R215	CBI	1974	Zimbabwe	W	Active
7	ZS107	CBI	1985	Zimbabwe	W	Inactive
8	ZS240	CBI	1992	Zimbabwe	Y	Inactive
9	ZS255	CBI	1998	Zimbabwe	W	Inactive
10	ZS259	CBI	2005	Zimbabwe	W	Inactive
11	ZS261	CBI	2006	Zimbabwe	W	Active
12	ZS263	CBI	2011	Zimbabwe	W	Active
13	ZS265	CBI	2011	Zimbabwe	W	Active
14	ZS269	CBI	2014	Zimbabwe	W	Active
15	ZS271	CBI	2014	Zimbabwe	W	Active
16	ZS273	CBI	2014	Zimbabwe	W	Active
17	ZS275	CBI	2014	Zimbabwe	W	Active
18	ZS225	CBI	2016	Zimbabwe	W	Active
19	SR52	CBI	1962	Zimbabwe and ESA	WD	Inactive
20	ZS242A	CBI	2015	Zimbabwe and ESA	OF	Active
21	ZS246A	CBI	2016	Zimbabwe and ESA	OF	Active
22	093WH03	CBI	Experimental	Zimbabwe	WD	NA
23	093WH123	CBI	Experimental	Zimbabwe	WD	NA
24	113WH330	CBI	Experimental	Zimbabwe	WF	NA
25	ZM309	CIMMYT	2009	Zimbabwe and ESA	WF	Active
26	ZM401	CIMMYT	2009	Zimbabwe and ESA	W	Active
27	ZM421	CIMMYT	2002	Zimbabwe and ESA	W	Active
28	ZM521	CIMMYT	2002	Zimbabwe and ESA	W	Active
29	CZH1258	CIMMYT	Experimental	N/A	W	N/A
30	NTS51	NTS	2014	Zimbabwe	W	Active
31	PAN53	PANNAR	2007	Zimbabwe and ESA	W	Active
32	PAN4M-23	PANNAR		Zimbabwe and ESA	W	Active
33	PAN-7M-81	PANNAR	2013	Zimbabwe and ESA	W	Active
34	PHB30G19	PIONEER	2008	Zimbabwe and ESA	W	Active
35	Shasha301	Champion	Experimental	N/A	W	N/A
36	Shasha302	Champion	Experimental	N/A	W	N/A
37	SeedCo Exp1	SeedCo	Experimental	N/A	W	N/A
38	SeedCo Exp2	SeedCo	Experimental	N/A	W	N/A
39	Manjanja MN421	Mukushi	2015	Zimbabwe, South	W	Active
40	Mutsa MN521	Mukushi	2014	Zimbabwe, South	W	Active
41	Maka MN625	Mukushi	2018	Zimbabwe, South	W	Active
42	Mukwa	Mukushi	2016	Zimbabwe, South	W	Active
43	Pris601	Pristine	2010	Zimbabwe and ESA	W	Active
44	ZAP61	Agriseeds	2008	Zimbabwe and ESA	W	Active
45	ZAP63	Agriseeds	2015	Zimbabwe and ESA	W	Active
46	ZAP43	Agriseeds	2015	Zimbabwe and ESA	W	Active
47	ZAP55	Agriseeds		Zimbabwe and ESA	W	Active
48	CML338/CML67	CIMMYT	Experimental	N/A	YF	N/A
49	CML338/CML334	CIMMYT	Experimental	N/A	YFL	N/A
50	CML331/CML67	CIMMYT	Experimental	N/A	WF	N/A
51	DJ271-28	CIMMYT	Experimental	N/A	W	N/A
52	CIM52/CML139	CIMMYT	Experimental	N/A	WF	N/A
53	CIM53/CML345	CIMMYT	Experimental	N/A	WF	N/A
54	CIM54/CML334	CIMMYT	Experimental	N/A	WDL	N/A
55	CIM55/CML334	CIMMYT	Experimental	N/A	WDL	N/A
56	CIM56/CML334	CIMMYT	Experimental	N/A	WDL	N/A
57	CIM57/CML345	CIMMYT	Experimental	N/A	WF	N/A
58	CIM58/CML121	CIMMYT	Experimental	N/A	YD	N/A
59	CML543/CML334	CIMMYT	Experimental	N/A	WDL	N/A
60	CML571/CML338	CIMMYT	Experimental	N/A	YDL	N/A

WD, White and Dent; WF, White and Flint; WDL, White and Dent like; WFL, White and Flint like; YD, Yellow and Dent; YF, Yellow and Flint; YDL, Yellow and Dent like; YFL, Yellow and Flint like; OD, Orange and Dent; OF, Orange and Flint; ODL, Orange and Dent like; OFL, Orange and Flint like

Table 4.2 Description of inbred lines evaluated for fall armyworm resistance in Zimbabwe

Name	Source germplasm	Adaptation / Programme	Maturity	Grain Colour/Texture	Heterotic Group
2Kba, SV1P,	CBI	Africa MA/ST	Very Early	W	
N3.2.3.3; NAW5885, K64R, RA214P, RA150P, WCoby1P, YCoby7P, QRD69P, RS98P, RS61P, PR15P, RA267P, RA294P, GQL5, WW01408	CBI	Africa MA/ST	Early/Interm/Late	W	
RL17P, EL77P, HX482P, HX439, HS253, BC108P	CBI	Africa MA/ST	Interm/Late	Y	
CLHP0003, CLHP0005, CLHP00306, CLHP00478, DPTY9...*9, CLHP00476, CLHP0286, CLHP00448	HarvestPlus	Africa MA/ST	Early/Interm/Late	O	
CZL1112, CZL12010, CZL1227, CZL1315, CZL1311, CZL15025		Africa MA/ST			
DJL173833, DJL173527, CIMExp60		Africa MA/ST			
CML67	Antigua	Lowland	Late	Y, SD	B
CML334	P590	Subtropical	Late	W, F	B
CML139		Subtropical	Interm	Y, SF	B
CML181		Subtropical		W, D	A
CML300	SintAmTSR	Lowland	Early	Y, F	B
CML312	P500	Subtropical	Interm	W, SF	A Tester
CML331	SUWAN1	Subtropical	Early	W, SD	B
CML338	P590B	Subtropical	Early	Y, SF	B
CML346	P390	Lowland		W, F	B
CML395	IITA	Africa MA/ST	Late	W, SF	B Tester
CML442	REC	Africa MA/ST	Interm	W, D	A Tester
CML444	P43	Africa MA/ST	Late	W, SD	B Tester
CML491	REC	Lowland	Late	W, F	A
CML511	P63Recycled	Africa MA/ST	Early/Interm	W	B
CML539	P500	Africa MA/ST	Early/Interm	W, SF/SD	A
CML121	P47	Subtropical	Interm	Y,D	A
CML297	SintAmTSR	Lowland	-	Y, SD	B
CML304	SintAmTSR	Lowland	-	Y,F	B
CML541	ZEWD	Africa MA/ST		W, F	
CML543		Africa MA/ST		W, SD	B
CML547		Africa MA/ST		W	B
CML566	P43	Africa MA/ST		W, SF	B
CML571		Africa MA/ST		W, SD	B

W, White; Y, Yellow; O, Orange; D, Dent; F, Flint; SD, Semi-dent; SF, Semi-flint; MA, Mid-altitude; ST, Sub-tropical; Interm, Intermediate; NA, Not available

Table 4.3 Description of experimental sites used in the evaluation of commercial cultivars and inbred lines

Location	Management	Altitude	Latitude	Longitude	Precipitation		Fertilisers (NPK) ha ⁻¹
					2018/19	2019/20	
		m			-mm-		
CIM-Harare	NI	1506	17°48'S	31°85'E	557.2	547.3	166:24.5:23.2
RARS	NI	1341	17°14'S	31°14'E	631.8	543.8	166:24.5:23.2
Chisumbanje	NI	421	20°05'S	32°15'E	441.9	434.8	166:24.5:23.2
Chiredzi	NI	1409	21°01'S	21°25'E	416.5	419.2	166:24.5:23.2
DR&SS-Harare	NI+Managed	1506	17°48'S	31°03'E	502.7	436.3	166:24.5:23.2
Gwebi VTC	NI	1448	17°41'S	30°32'E	571.5	542.5	166:24.5:23.2
KD-CRI	NI	1149	18°04'S	29°25'E	555.6	474.8	28:24.5:23.2

CIM-Harare, CIMMYT-Harare; RARS, Rattray-Arnold Research Station; ART-Farm, Agriculture Research Trust Farm; CHS, Chisumbanje; CHZ, Chiredzi; DR&SS-Hre, DR&SS Harare, Gwebi VTC, Gwebi Variety Testing Centre; KD-CRI, Kadoma Cotton Research Institute; NI, Natural Infestation

The experimental plants were thinned to one plant per planting station at two leaf stage (approximately three weeks after planting) to give a crop population density of about 53 000 plants ha⁻¹. The plants in the experiments were raised using standard agronomic practices for maize production.

Optimal fertiliser rates of 400 kg ha⁻¹ for both compound D (7N:14P:7K) basal applications and ammonium nitrate (AN) (34.5N) for top dressing were applied at all environments. Weeds were controlled using herbicides and hand weeding where necessary.

4.2.3 Data collection and analysis

For trials at each site, the following characteristics were recorded per plot: (i) foliar FAW damage (FFAWD) at 4, 8 and 12 week intervals after crop emergence, (ii) anthesis date (AD, number of days), (iii) plant height (PH, cm) at harvesting, (iv) husk cover (HC, number of ears with open tips), (v) ear FAW damage (EFAWD), (vi) ear rots (ER, %) and (vii) grain yield (GYD) per plot adjusted to 12.5% moisture content. FFAWD and EFAWD damage were recorded following the modified Davis scale as described by Prasanna et al. (2018) and shown in Chapter 3, where scores 1-2 = resistant, 2-5 = partial resistance, 5-7 = susceptible, 7-9 = highly susceptible. All the other agronomic traits were recorded as described by Magorokosho et al. (1998) and Masuka et al. (2017).

The collected phenotypic data were subjected to general ANOVA using Genstat Discovery Software V18.0 (VSN International, 2017). Best linear unbiased predictions (BLUPs) and broad sense heritability estimates (H^2) were estimated using the Multi-environment Trials Analysis in R (META-R) v2.1 R package software (Alvarado et al., 2020). For each trait, sites with H^2 lower than 20% were dropped from the combined analysis. This was done to reduce the confounding effect of error and environmental variances. Means were separated using Tukey's multiple comparison test in Genstat Discovery Software (VSN International, 2017). In the ANOVA model, genotypes were considered fixed, while replications within environments and environments were considered random. The META-R v2.1 R package software (Alvarado et al., 2020) was used to estimate genetic correlations between agronomic traits as well as identifying traits correlated with FAW resistance.

4.3 Results

4.3.1 Performance of the commercial cultivars and their corresponding inbred line parents under natural FAW infestation

Significant ($P < 0.05$) genotype effects were seen for FAW infestation on both foliar and ear damage across cultivars and inbred lines evaluated (Tables 4.4 and 4.5). Grain yield and yield related traits (anthesis date, plant height and ear rot), were significantly different ($P < 0.05$) across cultivars and inbred lines evaluated under FAW infestation. The minimum average foliar fall armyworm damage (Avg-FFAWD) modified Davis score for cultivars and experimental hybrids was 3.35 while the highest score was 5.73 (Table 4.4), whereas for inbred lines, Avg-FFAWD ranged from 2.62 to 6.34 (Table 4.5). Generally, FFAWD was higher than EFAWD for both cultivars and inbred lines.

Table 4.4 Analysis of variance for leaf and ear fall armyworm damage scores and other important agronomic traits of commercial cultivars and experimental hybrids under natural FAW infestation sites in Zimbabwe, during the 2019 and 2020 summer seasons

Source of variation	DF	GYD	DF	Avg-FFAWD	DF	EFAWD	DF	AD	DF	ER
Environment	8	104.96***	10	138.99***	5	78.364***	6	2244.24***	8	26140.2***
Replication (Environment)	9	4.06***	11	1.04	6	3.15*	7	466.06***	9	1517.2***
Block (Replication x Site)	162	2.59***	198	2.09***	108	2.08***	126	62.37***	161	660.2***
Genotype	59	10.32***	59	4.77***	58	2.71***	58	76.37***	58	2088.3***
Genotype x Environment (GxE)	448	2.09***	570	0.77**	280	1.39	332	22.96**	439	514.3***
Residuals	296	1.02	397	0.62	197	1.13	239	17.11	277	284.7
Phenotypic (P) variance		3.11		2.20		2.12		41.52		792.69
Genotypic (G) variance		0.57		0.24		0.12		5.35		111.85
GxE variance		0.57		0.12		0.19		3.30		107.71
Environmental variance		0.95		1.21		0.68		15.77		288.44
PCV (%)		68.57		30.35		53.02		9.50		88.94
GCV (%)		29.48		10.13		12.67		3.36		33.41
Broad-sense heritability (%)		0.82		0.87		0.49		0.76		0.78
Least significance difference		2.09		1.52		2.08		8.15		36.56
Grand mean		2.57		4.88		2.74		67.83		31.66
Minimum		0.94		3.36		2.20		64.04		20.14
Maximum		3.85		5.73		3.27		72.15		60.48

* P < 0.05; ** P < 0.01; *** P < 0.001; DF = degrees of freedom; GYD = grain yield; Avg-FFAWD = average foliar fall armyworm damage; EFAWD = ear fall armyworm damage; AD = anthesis date; ER = ear rot; PCV = phenotypic coefficient of variance; GCV = genotypic coefficient of variance

Table 4.5 Analysis of variance for fall armyworm damage scores and various agronomic traits of inbred lines evaluated across natural fall armyworm infestation sites during the 2019 and 2020 seasons

Across natural FAW infestation environments														
Source	DF	GYD	DF	FFAWD Avg	DF	EFAWD	DF	PH	DF	AD	DF	ER	DF	HC
Environment (E)	6	3.43***	9	130.95**	4	21.92***	5	16905.8***	6	2293.32***	4	56525.00***	2	394.73***
Rep (Env)	7	0.13	10	5.55***	5	1.93	6	1145.8*	7	235.63***	5	807	3	5.87
BLK (Rep x Site)	110	0.25	160	2.97***	80	3.23**	96	822.7***	112	108.97***	78	2062	48	60.33*
Genotype (G)	60	0.77***	61	10.18***	58	4.26***	62	970.2***	62	260.86***	59	2916.00*	60	90.15***
GE	275	0.19	524	0.95***	195	1.9	297	477.7	316	150.59***	173	1304	111	60.82*
Residuals	103	0.19	371	0.69	95	1.94	240	412.3	153	27.77	70	1774	96	38.41
P-Variance		0.31		2.54		2.85		648.95		180.33		2840.34		56.96
G-Variance		0.06		0.58		0.62		61.98		15.51		328.78		7.31
GxE-Variance		0.02		0.17		0.05		42.27		114.55		122.75		8.36
Env-Variance		0.04		1.10		0.23		132.39		22.50		614.80		2.88
PCV (%)		126.03		32.67		55.50		27036.00		17.81		108.14		241.42
GCV (%)		54.94		15.54		25.97		8.46		5.23		36.79		86.48
Heritability (%)		0.79		0.92		0.77		0.60		0.46		0.68		0.42
LSD		0.82		1.62		2.63		39.44		10.42		71.12		12.83
Grand mean		0.44		4.88		3.04		93.10		75.38		49.29		3.13
Minimum		0.20		2.62		1.89		79.08		69.57		23.62		1.84
Maximum		1.18		6.34		5.18		106.28		90.79		86.29		12.12
<i>SEm</i> (\pm)														

* P < 0.05; ** P < 0.01; *** P < 0.001; DF = degrees of freedom; GYD = grain yield; Avg-FFAWD = average foliar fall armyworm damage; EFAWD = ear fall armyworm damage; PH = plant height; AD = anthesis date; ER = ear rot; HC = husk cover; Rep = replication; Env = environment; P-Variance = phenotypic variance; G-Variance = genotypic variance; PCV = phenotypic coefficient of variance; GCV = genotypic coefficient of variance; LSD = least significant difference

4.3.2 Private and public sector hybrids and OPVs with substantial levels of FAW resistance and superior yield performance

Table 4.6 describes GYD performance, FAW scores and parental composition of the hybrids that exhibited good GYD performance and acceptable FAW resistance. Among the private sector commercial cultivars, the hybrids PAN53 (Avg-FFAWD = 4.73, EFAWD = 2.65; GYD = 3.85 t ha⁻¹), Mutsa MN521 (Avg-FFAWD = 4.58, EFAWD = 2.88; GYD = 3.63 t ha⁻¹), ZAP61 (Avg-FFAWD = 4.77, EFAWD = 3.18; GYD = 3.13 t ha⁻¹) and Manjanja MN421 (Avg-FFAWD = 4.74, EFAWD = 2.95; GYD = 3.09 t ha⁻¹) had good grain yield potential and showed partial resistance to FAW (Table 4.6). Within the public sector cluster (national breeding programme), the DR&SS registered varieties, ZS246A (Avg-FFAWD = 4.51, EFAWD = 2.73; GYD = 3.24 t ha⁻¹) and ZS242A (Avg-FFAWD = 4.38, EFAWD = 2.92; GYD = 3.04 t ha⁻¹), as well as an experimental hybrid 113WH330 (Avg-FFAWD = 4.81, EFAWD = 2.72; GYD = 3.23 t ha⁻¹) were the best in terms of FAW resistance and grain yield performance (Table 4.6).

Additionally, in the public sector (CIMMYT breeding programme), a total of eight experimental hybrids showing FAW resistance and good grain yield performance under FAW infestation were identified (Table 4.6). With the exception of CZH128 (Avg-FFAWD = 4.78, EFAWD = 2.59; GYD = 3.60 t ha⁻¹), the other seven hybrids were crosses between a FAW resistant donor inbred line parent with a CIMMYT elite line designated as CIMMYT maize line (CML) or an experimental inbred line parent. For example, genotype 55 (CIMExp55/CML334) (GYD = 3.35 t ha⁻¹), a cross between a CIMMYT experimental inbred line and a late flowering FAW resistant donor inbred line parent, CML334, ranked 7th for grain yield performance among the 60 evaluated genotypes under natural FAW infestation.

There was a general trend of decreasing FFAWD scores across FAW resistant hybrids from 4 to 12 weeks after crop emergence (Table 4.6). All commercial cultivars and experimental hybrids had the lowest scores at 12 weeks after crop emergence. FFAWD resistance of some of the genotypes is likely due to non-preference resulting from increased pubescence on stems (Figure 4.1B) and leaves (Figure 4.1C). This may particularly be true for the experimental hybrids that were constituted from crosses between FAW resistant donor inbred line parents (such as genotype CML338/CML67; Figure 4.1D) that had minimal damage on leaves, silks and ears.

Table 4.6 Grain yield performance, fall armyworm resistant scores and parental information of identified resistant genotypes among the 60 entries evaluated across natural fall armyworm infested sites in Zimbabwe during the 2019-20 seasons

	Cultivar name	Genotype	GYD t ha ⁻¹	Rank	FFAWD 4wks	FFAWD 8wks	FFAWD 12wks	FFAWD Avg	EFAWD	Respective parental inbred lines
Private Sector Cultivars	PAN53	31	3.85	1	5.31	5.06	3.81	4.73	2.65	Confidential
	Mutsa MN521	40	3.63	4	5.15	4.79	3.93	4.58	2.88	Confidential
	Manjanja MN421	39	3.09	15	5.25	5.02	4.17	4.74	2.95	Confidential
	ZAP61	44	3.13	13	5.23	4.98	4.25	4.77	3.18	Confidential
Public Sector (DR&SS) Cultivars	ZS246A	21	3.24	9	5.26	4.90	3.72	4.51	2.73	CLHP0003/CLHP0005//CLHP00478
	ZS242A	20	3.04	20	5.17	4.60	3.59	4.38	2.92	CLHP0003/CLHP0005//CML304
	113WH330	24	3.23	10	5.37	5.04	4.09	4.81	2.72	CML312/CML395//SM-236-15
Public Sector (CIMMYT) Experimentals	CZH128	29	3.60	5	4.97	5.10	4.13	4.78	2.59	CZL395/CML444//CZL1227
	CIMExp55/334	55	3.35	7	5.35	4.66	3.65	4.40	2.54	CIMExp55/CML334
	CML571/CML338	60	3.13	12	4.88	4.17	3.39	4.09	2.39	CML571/CML338
	CIMExp54/CML334	54	3.08	16	5.33	4.68	3.87	4.48	2.70	CIMExp54/CML334
	CIMExp52/CML139	52	3.06	17	5.32	5.02	3.61	4.55	2.47	CIMExp52/CML139
	CML338/CML334	49	3.03	21	5.16	4.15	3.46	4.02	2.24	CML338/CML334
	CIMExp58/CML121	58	3.00	22	4.76	3.74	3.54	3.78	2.20	CIMExp58/CML121
	CML543/CML334	59	3.00	23	5.26	4.64	4.19	4.49	2.50	CML543/CML334
Heritability			0.82		0.52	0.82	0.77	0.87	0.49	
Trials Mean			2.57		5.38	5.10	4.26	4.88	2.74	
LSD			2.09		1.24	1.95	1.97	1.52	2.08	

GYD = grain yield; FFAWD 4 wks = foliar fall armyworm damage at 4 weeks after crop emergence; FFAWD 8 wks = foliar fall armyworm damage at 8 weeks after crop emergence; FFAWD 12 wks = foliar fall armyworm damage at 12 weeks after crop emergence; Avg-FFAWD = average foliar fall armyworm damage; EFAWD = ear fall armyworm damage

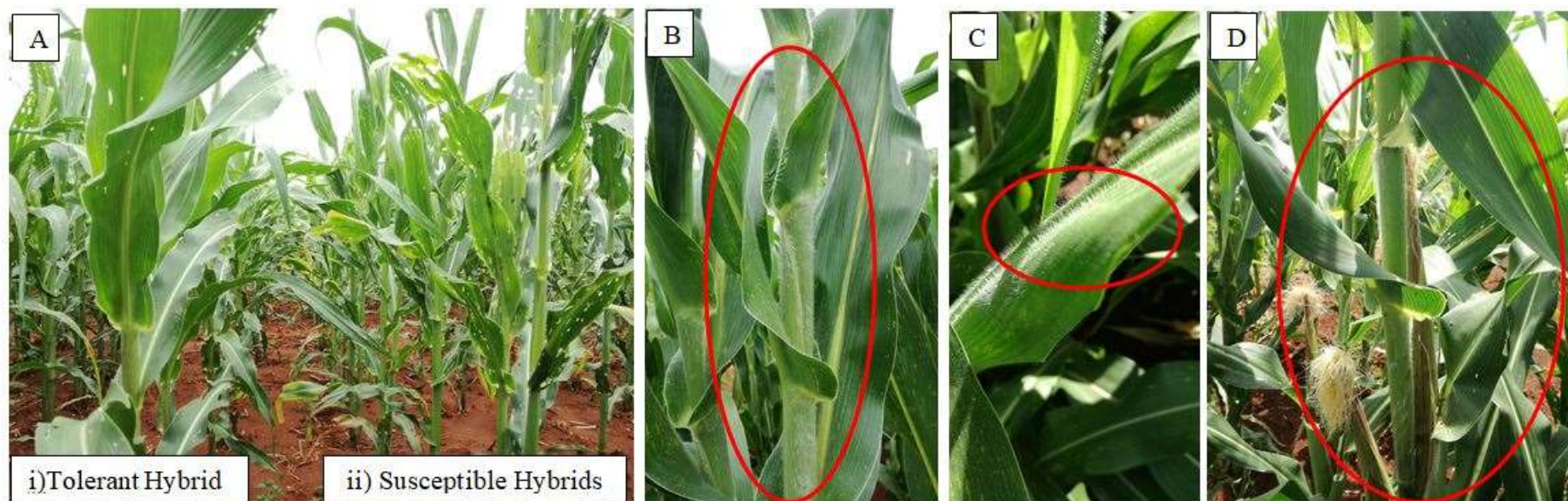


Figure 4.1 Physical appearances of maize hybrids exposed to natural fall armyworm infestation and characteristics of resistant varieties. (A) Physical appearance of maize hybrids exposed to fall armyworm (FAW) infestation (i) Tolerant hybrid and (ii) Susceptible hybrid, (B) Hybrid with pubescence on stem, (C) Hybrid with pubescence on leaves, (D) Experimental hybrid with stacked FAW donor genes, showing pubescence on stems, minor window-pane damage on leaves and undamaged silks (photographs produced by Prince M. Matova)



Figure 4.2 Physical appearance of ears of fall armyworm susceptible and resistant genotypes. (A) Old commercial cultivar ears damaged by fall armyworm (FAW), (B) Recently released commercial cultivar ears not damaged by FAW, (C) Commercial cultivars currently active on the market showing FAW ear damage and ear rots, (D) Experimental hybrid formed by crossing two FAW resistant donor inbred lines showing no ear damage from FAW (photographs produced by Prince M. Matova)

Among the hybrids selected for FAW resistance and good grain yield performance, genotypes with flint-like grains were higher yielding compared to dent-like genotypes and the former had lower scores for ASI compared to the latter (Figure 4.2).

4.3.3 Inbred line parents with FAW resistance in public sector breeding programmes

For the selected public sector (National and CIMMYT breeding programmes) FAW resistant genotypes (listed in Table 4.6), parental inbred lines making up the hybrids were tracked in inbred line trials in order to explore sources of resistance among the publicly available maize germplasm pools in Zimbabwe (Table 4.7). From the national breeding programme registered cultivars, the parental inbred line CLHP0005 (Avg-FFAWD Rank = 9; Avg-FFAWD = 4.39; EFAWD = 4.61; GYD = 0.5 t ha⁻¹), which is a parental line in the hybrids ZS246A and ZS242A, proved to be the best source for FAW resistance. Both ZS242A and ZS246A showed good resistance to FAW (Table 4.6). From the CIMMYT breeding programme, an inbred parent line CML334 (Avg-FFAWD Rank = 8; Avg-FFAWD = 4.35; EFAWD = 2.01; GYD = 0.48 t ha⁻¹), a parental line in the experimental hybrid CIMExp55/CML334, was identified as the best source of FAW resistance. The other potential sources of FAW resistance, but not involved as parents in the identified most resistant hybrid genotypes, were CML67 (Avg-FFAWD Rank = 1; Avg-FFAWD = 2.75; EFAWD = 3.48; GYD = 0.50 t ha⁻¹), CML121 (Avg-FFAWD Rank = 2; Avg-FFAWD = 3.05; EFAWD = 2.33; GYD = 0.57 t ha⁻¹), CML338 (Avg-FFAWD Rank = 3; Avg-FFAWD = 3.63; EFAWD = 2.82; GYD = 0.62 t ha⁻¹), CML346 (Avg-FFAWD Rank = 4; Avg-FFAWD = 3.79; EFAWD = 2.47; GYD = 0.44 t ha⁻¹), SV1P (Avg-FFAWD Rank = 5; Avg-FFAWD = 3.89; EFAWD = 2.46; GYD = 1.05 t ha⁻¹) and CML331 and CML491 (respective scores shown in Table 4.7), with the majority of them being CIMMYT FAW resistant donor lines. The most susceptible lines were WW01408 (Avg-FFAWD Rank = 61; Avg-FFAWD = 6.04; EFAWD = 3.02; GYD = 0.28 t ha⁻¹) and HX482P (Avg-FFAWD Rank = 62; Avg-FFAWD = 6.39; EFAWD = 3.17; GYD = 0.28 t ha⁻¹) (Table 4.7). The inbred lines SV1P (Figures 4.3, 4.4A and Figure 4.5A) and CML491 (Figure 4.4B) were parents of commercial cultivars. Further to that, the evaluated genotypes showed significant differences ($P < 0.05$) for two of the yield related traits, ER and HC. Genotypes that had higher EFAWD had corresponding higher levels of ER. Generally, ER increased with increasing levels of FFAWD, EFAWD and open HC.

Table 4.7 Fall armyworm resistance and grain yield performance of inbred parental lines of FAW resistant public commercial and experimental hybrids and other FAW resistant inbred lines evaluated under natural FAW infested sites in Zimbabwe during the 2019-20 seasons

	Genotype Name	Genotyp Code	FFAWD Avg	Rank	FFAWD 4 wks	FFAWD 8 wks	FFAWD 12 wks	EFAWD	GYD t ha ⁻¹	ER %	AD	HC	PH
Parental inbred lines	CLHP0005	25	4.39	9	4.61	4.61	4.93	3.47	0.50	41.77	73.4	4.88	102.58
	CML304	27	4.60	10	4.43	5.13	4.67	2.41	0.51	35.14	74.0	4.18	104.94
	CZL1227	42	4.86	16	4.53	5.06	5.33	2.48	0.61	35.50	77.3	4.47	97.08
	CML444	28	5.67	52	4.67	6.22	6.04	2.80	0.35	61.78	76.1	3.50	92.80
	CML543	57	6.02	60	4.95	6.58	6.49	2.36	0.23	36.56	76.9	2.08	88.51
	CML395	34	5.81	54	5.03	6.51	6.19	2.39	0.39	35.45	75.8	2.04	91.21
	CML334	48	4.35	8	4.46	4.66	4.96	2.01	0.48	42.08	77.7	2.32	99.74
	CML312	33	5.19	29	4.05	5.53	5.84	2.72	0.39	46.26	75.8	4.61	98.92
	CLHP00478	36	5.19	30	4.73	5.50	5.43	2.73	0.35	34.74	73.0	4.24	94.61
	CML139	51	5.34	35	4.66	6.00	5.71	1.96	0.30	46.97	76.7	1.86	98.22
	CML571	52	4.65	11	4.17	5.23	4.46	3.82	0.30	48.33	74.4	1.96	97.53
	CLHP0003	24	4.91	18	4.50	5.26	5.11	3.23	0.45	42.81	73.1	5.03	97.10
	CIMExp54	60	5.08	24	4.47	5.57	5.11	2.60	0.61	33.04	74.1	2.88	92.70
Other good lines	CML67	50	2.75	1	3.44	2.97	2.83	3.48	0.50	23.62	73.0	2.66	76.63
	CML121	55	3.05	2	3.69	3.01	3.78	2.33	0.57	29.06	73.7	1.96	92.84
	CML338	47	3.63	3	4.29	3.66	4.10	2.82	0.62	35.30	72.1	1.87	93.50
	CML346	53	3.79	4	4.09	4.10	4.04	2.47	0.44	26.25	73.8	2.42	96.68
	SV1P	9	3.89	5	4.12	4.07	4.38	2.46	1.05	29.75	69.6	2.53	100.57
	CML331	49	4.26	6	4.26	4.64	4.80	2.81	0.59	43.84	74.9	4.55	89.04
	CML491	30	4.30	7	4.29	4.67	4.88	2.89	0.99	28.53	73.4	1.86	92.15
Most susceptible	WW01408	23	6.04	61	4.72	6.56	7.00	3.02	0.28	45.31	75.3	3.03	82.84
	HX482P	18	6.39	62	4.42	7.08	7.23	3.17	0.28	61.81	76.3	2.33	80.63
	Heritability		0.90		0.59	0.88	0.86	0.72	0.74	0.68	0.40	0.42	0.66
	Trials Mean		5.14		4.50	5.52	5.59	2.95	0.39	49.29	75.4	3.13	89.93
	LSD		1.60		1.51	2.21	2.26	2.73	0.69	71.12	10.4	12.83	36.58

Avg-FFAWD = average foliar fall armyworm damage; FFAWD 4 wks = foliar fall armyworm damage at 4 weeks after crop emergence; FFAWD 8 wks = foliar fall armyworm damage at 8 weeks after crop emergence; FFAWD 12 wks = foliar fall armyworm damage at 12 weeks after crop emergence; EFAWD = ear fall armyworm damage; GYD = grain yield; ER = ear rot; AD = anthesis date; HC = husk cover; PH = plant height

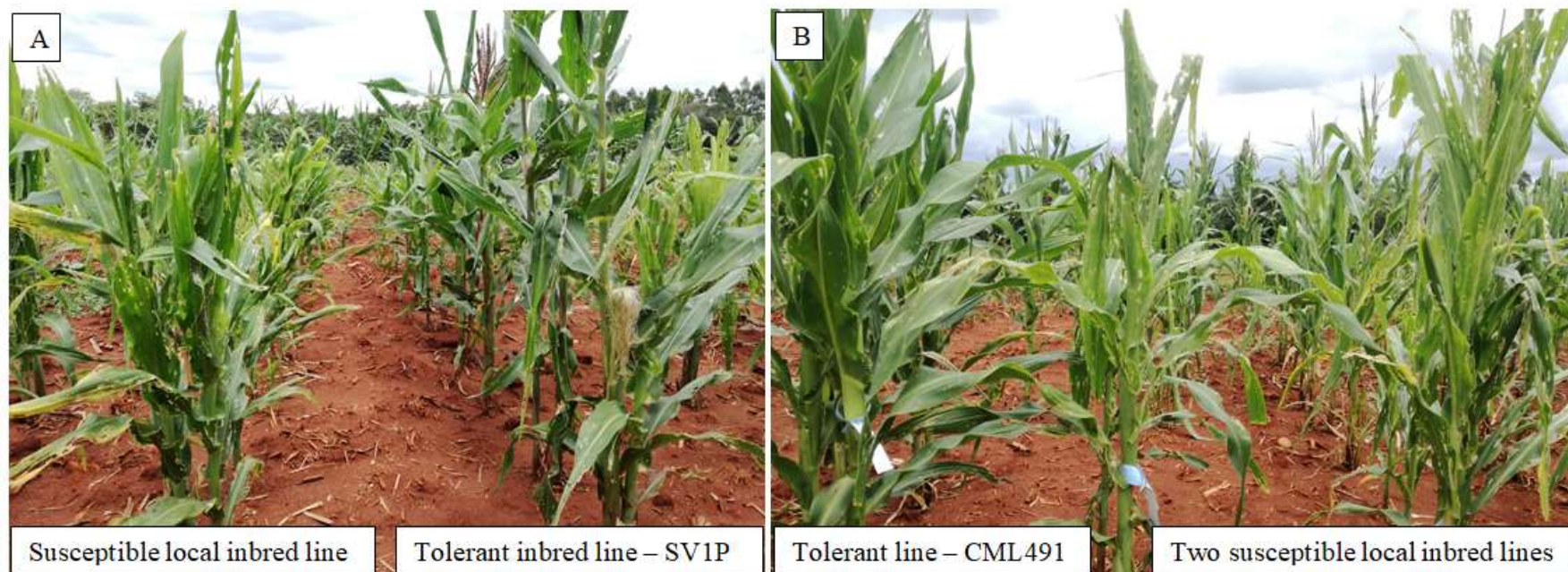


Figure 4.3 Physical appearances of fall armyworm susceptible and resistant inbred lines under natural FAW infestation. (A) Physical appearance of two maize inbred lines exposed to fall armyworm infestation, one susceptible locally adapted commercial inbred line and SV1P, a fall armyworm resistant local line, (B) Physical appearance of three maize inbred lines exposed to fall armyworm infestation, one resistant locally adapted line, CML491 and two local commercial inbred lines susceptible to fall armyworm (photographs produced by Prince M. Matova)

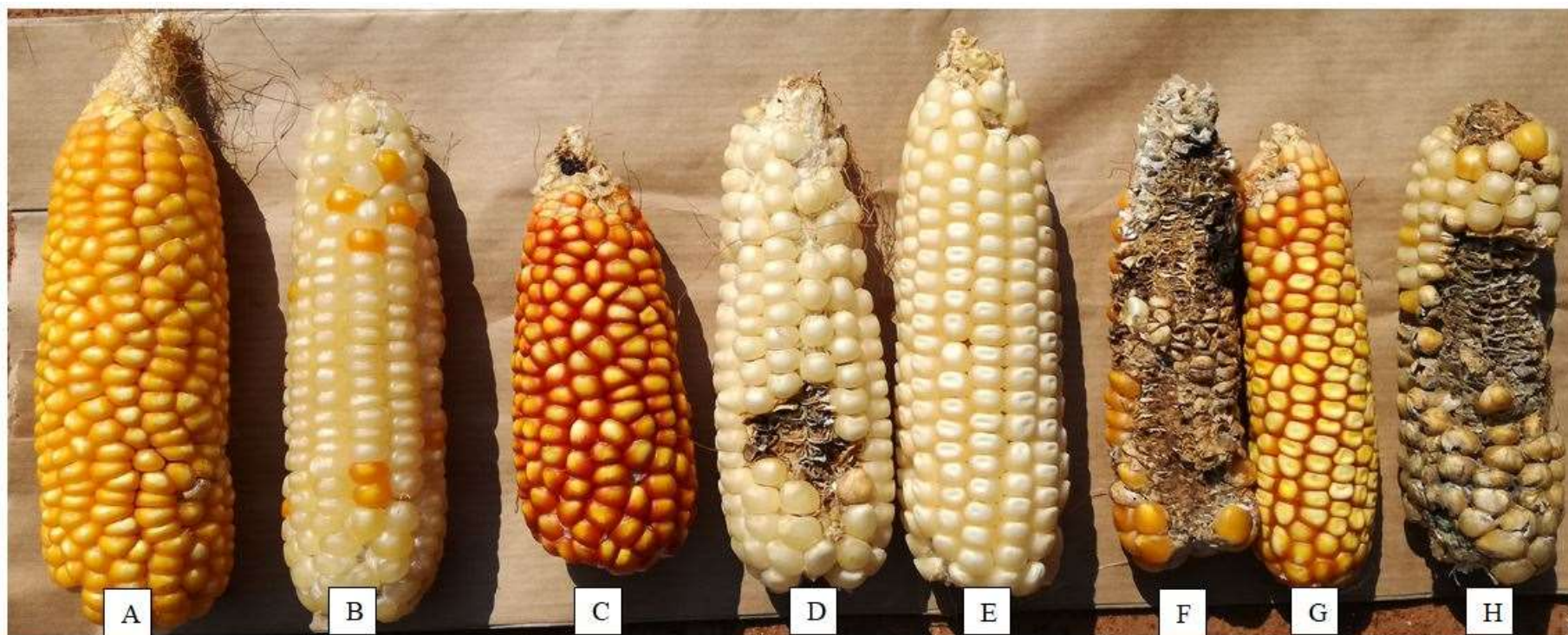


Figure 4.4 Physical appearances of ears of different inbred lines exposed to fall armyworm infestation. (A) Undamaged CML338 ear, (B) Undamaged ear of CML346, (C) Slightly damaged ear of CML67, (D) Moderately damaged ear of a local inbred line, (E) Undamaged ear of a local line, SV1P, (F) Extensively damaged ear of a local yellow inbred line, (G) Slightly damaged ear of CML121, (H) Extensively damaged and rotten ear of a local commercial inbred line (photographs produced by Prince M. Matova)



Figure 4.5 Ear appearances of some locally adapted inbred lines exposed to natural fall armyworm infestation. (A) Undamaged ears of the inbred line SV1P, (B) Fall armyworm damaged ears of an orange maize inbred line, CLHP00448, (C) Slightly damaged ears of an orange maize inbred line, DPTY...*9, (D) Damaged ears of a local commercial inbred line (photographs produced by Prince M. Matova)

CML67 had the lowest FFAWD scores, lowest incidence of ER and lower levels of open HC compared to HX482P which had higher FFAWD and EFAWD scores and ER counts (Table 4.7). Four of the FAW resistant donor inbred lines (CML67, CML121, CML346 and CML338) had good HC ranging between 1.86 – 2.66, which was comparable to that of SV1P and CML491. Line CML331 had HC counts that were comparable to those of CML304, CLHP0003, CLHP0005 and CML543. The ears of some of the FAW resistant donor lines and commercial inbred lines are shown in Figure 4.4.

Contrary to the observation on commercial cultivars and experimental hybrids, inbred line evaluation showed a general trend of increasing FFAWD from 4 – 12 weeks under FAW infestation across genotypes (Tables 4.6 and 4.7). EFAWD was significantly different ($P < 0.05$) across lines though most genotypes had lower levels of EFAWD (Figure 4.5). Ear rots were generally high, and they were significantly higher ($P < 0.05$) in older inbred lines, particularly those with higher FFAWD scores such as HX482P and WW01408 (Table 4.7). Similarly higher levels of poor HC were associated with high levels FFAWD and EFAWD.

4.3.4 Grain yield and agronomic performance of cultivars, experimental hybrids and inbred lines under managed fall armyworm conditions

The mean grain yield performance under managed FAW (FAW free) conditions in the commercial cultivar/hybrid trial was 5.99 t ha⁻¹, while the mean Avg-FFAWD and EFAWD scores were 0.36 and 0.44 respectively (Table 4.8). Grain yields were significantly different ($P < 0.05$) across cultivars. The best performers were PAN-7M-81 (GYD = 8.96 t ha⁻¹, Avg-FFAWD = 2.46, EFAWD = 2.51), PHB30G19 (GYD = 8.87 t ha⁻¹, Avg-FFAWD = 2.44, EFAWD = 1.94), PAN-4M-23 (GYD = 8.62 t ha⁻¹, Avg-FFAWD = 2.63, EFAWD = 2.14), PAN53 (GYD = 8.40 t ha⁻¹, Avg-FFAWD = 2.70, EFAWD = 1.92), Mukwa (GYD = 8.39 t ha⁻¹, Avg-FFAWD = 2.52, EFAWD = 2.28), ZS265 (GYD = 7.78 t ha⁻¹, Avg-FFAWD = 2.62, EFAWD = 1.90), ZS269 (GYD = 7.65 t ha⁻¹, Avg-FFAWD = 2.63, EFAWD = 2.16) and NTS51 (GYD = 7.64 t ha⁻¹, Avg-FFAWD = 2.47, EFAWD = 2.38). The hybrids CIMExp/CML345 and CML338/CML334 were the only two experimental hybrids that were among the best 10 grain yielders under controlled FAW conditions (Table 4.8).

Table 4.8 Grain yield and agronomic performance of the best ten cultivars and experimental hybrids evaluated under managed fall armyworm conditions in Zimbabwe during the 2019-20 seasons

Cultivar name	Genotype	GYD	Rank	PH	AD	FFAWD 4wks	FFAWD 8wks	FFAWD 12wks	FFAWD Avg	EFAWD	ER
PAN-7M-81	33	8.96	1	192.01	71.02	2.43	2.36	2.64	2.46	2.51	17.36
PHB30G19	34	8.87	2	184.03	68.18	2.63	2.26	2.52	2.44	1.94	8.99
PAN4M-23	32	8.62	3	174.09	70.07	2.65	2.37	2.76	2.63	2.14	20.44
PAN53	31	8.40	4	184.53	69.13	2.70	2.47	2.64	2.70	1.92	15.66
Mukwa	42	8.39	5	174.64	69.60	2.46	2.48	2.64	2.52	2.28	19.42
CIMExp/345	53	7.95	6	175.50	68.83	2.49	2.33	2.61	2.46	2.04	14.78
CML338/CML334	49	7.82	7	195.12	69.29	2.52	2.27	2.64	2.46	2.01	25.83
ZS265	13	7.78	8	178.15	69.13	2.49	2.58	2.87	2.62	1.90	14.57
ZS269	14	7.65	9	189.93	70.55	2.64	2.49	2.64	2.63	2.16	13.95
NTS51	30	7.64	10	185.38	68.66	2.50	2.47	2.52	2.47	2.38	21.69
Heritability		0.80		0.65	0.63	0.18	0.42	0.24	0.36	0.44	0.68
Trial mean		5.99		176.45	69.36	2.60	2.45	2.69	2.62	2.22	23.81
LSD		2.73		29.09	4.92	1.48	1.10	1.56	0.97	1.32	25.74

GYD = grain yield; PH = plant height; AD = anthesis date; FFAWD 4 wks = foliar fall armyworm damage at 4 weeks after crop emergence; EH = ear height; FFAWD 8 wks = foliar fall armyworm damage at 8 weeks after crop emergence; FFAWD 12 wks = foliar fall armyworm damage at 12 weeks after crop emergence; FFAWD-Avg = average foliar fall armyworm damage; EFAWD = ear fall armyworm damage; ER = ear rot

In contrast to this, grain yields were not significantly different for inbred lines under managed FAW conditions at Harare during the 2019 and 2020 summer seasons (Table 4.9). However, genotypes showed differential performance ($P < 0.05$) for Avg-FFAWD, FFAWD at 12 weeks, EFAWD, AD and DS while there were no differences across genotypes for FFAWD at 8 weeks and grain texture (Table 4.9). The mean GYD for inbred lines under managed FAW was 0.77 t ha^{-1} , and the means for Avg-FFAWD and EFAWD were 3.88 and 3.37 respectively (Table 4.9).

Comparing mean grain yields attained under natural FAW infestation (2.57 t ha^{-1}) against 5.99 t ha^{-1} realised under managed (controlled) FAW conditions, FAW infestation caused a yield loss of 57.1% on hybrids and OPVs evaluated (Table 4.6 and Table 4.8). A slightly lower but similar yield damage was also observed on inbred lines where the average grain yield performance under FAW stress was 0.39 t ha^{-1} while it was 0.77 t ha^{-1} under managed FAW conditions (Table 4.7 and 4.9). This translates to a yield penalty of 49.4%.

Table 4.9 Grain yield and agronomic performance of the top ten grain yielder inbred lines evaluated under managed fall armyworm conditions in Zimbabwe during the 2019-20 seasons

Name	Genotype	GYD	Rank	FFAWD Avg	FFAWD 8 wks	FFAWD 12 wks	EFAWD	AD
CML121	55	1.16	1	2.69	2.62	2.97	1.78	86.47
CML304	27	1.09	2	3.13	3.08	3.32	3.15	83.22
SV1P	9	1.05	3	3.06	3.23	3.06	3.22	70.87
CML334	48	1.05	4	3.09	2.83	3.55	2.77	86.16
CML491	30	1.01	5	3.40	3.62	3.49	3.70	80.45
CML338	47	0.95	6	2.78	2.75	2.89	1.63	76.28
CZL1112	61	0.95	7	3.98	4.00	4.21	2.47	80.44
DPTY9...*9	38	0.94	8	3.25	3.52	3.07	3.45	78.80
CML539	46	0.92	9	3.49	3.49	3.54	3.48	76.70
CZL1315	40	0.91	10	3.24	3.48	3.36	2.84	79.08
Heritability		0.20		0.66	0.63	0.66	0.68	0.69
Trials Mean		0.77		3.88	3.96	4.12	3.37	81.94
LSD		1.35		1.81	2.03	2.48	1.96	9.34

GYD = grain yield; FFAWD-Avg = average foliar fall armyworm damage; FFAWD 8 wks = foliar fall armyworm damage at 8 weeks after crop emergence; FFAWD 12 wks = foliar fall armyworm damage at 12 weeks after crop emergence; EFAWD = ear fall armyworm damage; AD = anthesis date

4.3.5 Genetic correlations between fall armyworm damage parameters and grain yield and yield related variables across genotypes and environments

In both hybrids/OPVs and inbred lines trials, FAW damage had significantly negative effects ($P < 0.05$) on grain yield performance across genotypes except for EFAWD on inbred lines, where the correlation was very small, positive and insignificant (Table 4.10). For hybrids/OPVs the negative correlation between GYD and FAW damage was highest between GYD and EFAWD ($r = -0.57$; $P < 0.0001$) and FFAWD at 12 weeks ($r = -0.56$; $P < 0.0001$) (Table 4.10). ER had the highest negative effect on grain yield of $r = -0.90$, which was highly significant ($P < 0.0001$). The associations between the different FAWD parameters were all positive and highly significant ($P < 0.0001$), ranging from a lowest of $r = 0.52$ between EFAWD and FFAWD at 8 weeks, and a highest of $r = 0.99$ between FFAWD at 4 and 8 weeks as well as between Avg-FFAWD and FFAWD at 8 weeks (Table 4.10).

In addition, ER showed high positive and highly significant ($P < 0.0001$) correlations with FAWD parameters, similarly PH had positive and significant ($P < 0.001$) associations with GYD and AD. For inbred lines, the associations between FAWD parameters were all positive and highly significant ($P < 0.0001$) except for Avg-FFAWD with FFAWD at 4 weeks ($r = 0.03$) and EFAWD with FFAWD at 8 weeks ($r = 0.14$). EFAWD and PH had high negative ($r = -0.74$) and significant ($P < 0.0001$) associations, in contrast EFAWD showed high, positive and highly significant associations with HC ($r = 0.46$; $P < 0.0001$) and ER ($r = 0.49$; $P < 0.0001$). Plant height was negatively correlated with GYD and all FAW damage parameters, however this negative association was only significant with EFAWD ($r = -0.74$; $P < 0.0001$). Plant height was positively correlated with AD, though not significant (Table 4.10).

Table 4.10 Genetic correlations between grain yield and yield related traits with fall armyworm damage scores at different crop growth stages determined under natural fall armyworm infestation in Zimbabwe during the 2019-20 seasons

A) Hybrids/OPVs									
Traits	GYD	FFAWD 4 wks	FFAWD 8 wks	FFAWD 12 wks	Avg FFAWD	EFAWD	AD	PH	HC
FFAWD_4_wks	-0.47***								
FFAWD_8_wks	-0.31*	0.66***							
FFAWD_12_wks	-0.56***	0.99***	0.98***						
Avg_FFAWD	-0.43***	0.70***	0.99***	0.89***					
EFAWD	-0.57***	0.55***	0.52***	0.53***	0.43***				
AD	-0.29*	0.73***	0.16	0.13	0.20	-0.38**			
PH	0.56***	-0.46***	-0.27*	-0.14	-0.18	-0.25	0.38**		
HC	NA	NA	NA	NA	NA	NA	NA	NA	NA
ER	-0.90***	0.44***	0.53***	0.89***	0.58***	0.46***	0.56***	-0.05	NA
B) Inbred lines									
Traits	GYD	FFAWD 4 wks	FFAWD 8 wks	FFAWD 12 wks	Avg FFAWD	EFAWD	AD	PH	HC
FFAWD 4 wks	-0.99***								
FFAWD 8 wks	-0.48***	0.09							
FFAWD 12 wks	-0.44**	0.54***	0.99***						
Avg FFAWD	-0.52***	0.03	1.00***	0.99***					
EFAWD	0.03	0.83***	0.14	0.62***	0.31*				
AD	-0.54***	0.99***	0.72***	0.67***	0.63***	-0.21			
PH	-0.03	-0.07	-0.23	-0.13	-0.22	-0.74***	0.21		
HC	-0.83***	-0.01	0.04	-0.07	-0.09	0.46***	0.09	0.02	
ER	-0.67***	1.00***	0.68***	1.00***	0.75***	0.49***	0.12	-0.32*	0.99***

* P < 0.05; ** P < 0.01; *** P < 0.001; GYD = grain yield; Avg-FFAWD = average foliar fall armyworm damage; FFAWD 4 wks = foliar fall armyworm damage at 4 weeks after crop emergence; FFAWD 8 wks = foliar fall armyworm damage at 8 weeks after crop emergence; FFAWD 12 wks = foliar fall armyworm damage at 12 weeks after crop emergence; EFAWD = ear fall armyworm damage; PH = plant height; AD = anthesis date; ER = ear rot; HC = husk cover

4.4 Discussion

This study evaluated two sets of germplasm for their resistance to FAW and superior grain yield performance on sites with naturally moderate to high FAW infestation, designated as natural infestation environments as well as under controlled FAW conditions. Moderate infestation was noted on sites in Harare and Gwebi while high infestation was observed at RARS, Chisumbanje, Chiredzi and Kadoma. FAW population was not quantified but infestation pressure in all environments was sufficient to cause differential response across genotypes. Under natural infestation conditions, the lowest Avg-FFAWD score in the hybrid/OPV set was 4.49, while the highest was 5.98 (Table 4.6). In contrast, 2.75 was the lowest Avg-FFAWD score in the inbred lines set and 6.39 was the highest (4.7). Again, the study noted that higher FAWD scores were observed under natural infestation conditions as opposed to managed FAW conditions. For the hybrid/OPV set, the mean Avg-FFAWD scores was 2.62 while it was 2.22 for EFAWD (Table 4.8). The lines showed a mean Avg-FFAWD score of 3.88 and 3.37 for EFAWD (Table 4.9). This implies that varietal screening for FAW resistance can be effectively implemented under natural FAW infestation.

The current study is the second reported study that has evaluated germplasm resources in SSA under natural FAW infestation after the one by Kasoma et al. (2020). In that regard, the findings are encouraging for national research programmes and other breeding programmes across SSA that have no access to artificial screening environments for FAW resistance breeding, as they can effectively evaluate their breeding materials under natural FAW infestation. Again, the highly significant differences between genotypes demonstrated that there is sufficient genetic variability for effective FAW resistance breeding. Generally FFAWD scores were lowest and highest on inbred lines compared to commercial cultivars and experimental hybrids. The lowest scores were exhibited by FAW resistant donor lines while the highest scores came from old local inbred lines. Hybrids/OPVs showed better resistance to FAWD compared to inbred lines primarily because the former are generally vigorous and tend to tolerate FAW attack better than inbred lines. This concurs with Fu et al. (2014) who reported that vigorous genotypes, particularly those showing heterosis, can out-perform their inbred line counterparts that are affected by slow growth and inbreeding depression.

Unlike inbred lines, these vigorous genotypes showed a general tendency to grow out of FFAWD as they grow from young to mature plants. Higher FFAWD scores were observed at 4 weeks after crop emergence and the scores improved from 8 – 12 weeks after crop emergence. Genotype ZS246A had a modified Davis score of 5.26 at 4 weeks after crop emergence. The same genotype recorded 4.90 and 3.72 at 8 and 12 weeks after crop emergence, respectively (Table 4.6). In contrast, inbred line FFAWD scores generally increased over time of 4, 8 and 12 weeks after crop emergence (Table 4.7). This further supports the fact that inbred lines are less vigorous, weaker and have slower growth compared to hybrids and landraces (Azeez et al., 2018; Ibraheem & El-Ghareeb, 2019), hence they tend to suffer more foliar FAW damage compared to hybrids and OPVs. Hruska (2019) reported that maize generally has the capacity to recover from moderate to average FAW foliar damage. However, this is only possible under good moisture and nutrient conditions. In the current study, the maize crop at Kadoma failed to give measurable yields due to the confounding effects of high FAW infestation and excessive drought stress, hence top dressing fertiliser could not be applied. The site was not included for grain yield analysis across sites.

Lower FFAWD scores were noted on hybrids constituted from CIMMYT lines and FAW donor lines as well as crosses between donor lines (Table 4.6). This indicates that FAW donor lines included in this study have the potential to resist FAW damage and they can be used to quickly develop hybrids that can be used in the interim to protect smallholder farmers' maize crop from FAW damage. Wightman (2018) reviewed the experiences from the Americas as possible help in reducing the impact of FAW in Africa and Asia, which highlighted varietal acceptance concerns due to preferences. In the light of that, the cultivars/experimental hybrids and inbred line trials suggested that the most resistant donor lines were CML67, CML121 and CML338. However, these have red and yellow grains and may not be readily accepted by farmers and consumers in Zimbabwe and most of ESA due to colour preference for white maize (Hruska, 2019). In contrast, the lines CML346, CML139 and CML334 showed acceptable FAW resistance both as hybrid parents and inbred lines (Table 4.7). The three have white flint-like to flint grains, hence hybrids constituted from these may be quickly accepted by farmers in the region. It is therefore imperative that maize breeders consider these in developing white maize hybrids that can be quickly released to counter the effects of FAW attack on maize. In addition, as was suggested by the water use efficient maize for Africa (WEMA) project

findings (ISAAA, 2017; Prasanna et al., 2018), gene stacking through introgression crosses among FAW resistant donor lines as well as together with elite and adapted FAW resistant lines such as SV1P and CML491 can result in robust resistance against FAW.

Two orange maize cultivars ZS242A and ZS246A and four white grain cultivars, which include the very early - early maturing hybrids, Manjanja MN421 and Mutsa MN521 and the medium maturity hybrids PAN53 and ZAP61, were the only commercial hybrids that were among the top performers under FAW infestation (Table 4.6). The list of the least resistant cultivars to FFAWD was dominated by most of the hybrids that are currently active and dominant on the market, as well as some old OPVs released by DR&SS (Appendix 4.1). This suggests that most smallholder farmers who have limited capacity to control FAW using chemicals may suffer significant FFAWD damage from the pest. However, GYD rankings of cultivars and experimental varieties evaluated under FAW infestation showed that the pool of current commercial cultivars, despite being susceptible to FAW damage, still out-yield most experimental varieties constituted from FAW donor lines (Table 4.6). This was also previously reported in studies done by Kumar (2002) in the Americas. His study reported that agronomically good genotypes were susceptible to FAW, but they still yielded better than the resistant, but agronomically poor genotypes.

In southern Africa, Kansiime et al. (2019) and Baudron et al. (2019) reported that cultivars in commercial production are susceptible to FAW, citing yield losses in the range of 11.5 – 16.4%. There is need to introgress FAW resistance in parental lines of commercial cultivars so that they can perform better under FAW infestation. The three hybrids PAN53, ZS246A and Mutsa MN521 that were identified among the most FFAWD resistant cultivars, were also among the top 10 grain yielders under FAW infestation (Table 4.6). Inbred lines CLHP0005 and CML304 are parental lines for ZS242A, and again CLHP0005 is a parent of the hybrid ZS246A. The two hybrids (ZS242A and ZS246A) exhibited superior grain yield performance and low FFAWD scores under natural FAW infestation (Table 6). This implies that the superior performance of ZS242A and ZS246A under FAW infestation was due to the superiority of their parental inbred lines under FAW infestation conditions, particularly CLHP0005. Further improvement through FAW resistance introgression on these lines will likely enhance FAW resistance in these improved cultivars.

The inbred lines SV1P and CML491 are commercial inbred lines developed and registered by DR&SS and CIMMYT respectively. In this study, these two inbred lines demonstrated outstanding resistance to FAW damage and the ability to yield significantly better under FAW infestation compared to most of the commercial inbred lines evaluated (Table 4.7). SV1P is a parent of a commercial cultivar ZS259 that is currently off the market in Zimbabwe and was not included in this study. The quality protein maize (QPM) inbred line, CML491 is a parent of a released QPM maize hybrid in Zimbabwe, ZS225Q. The hybrid was included in the study but it was omitted from the analysis due to poor germination. The superior resistance to FAW of CML491 was also noted and reported in a study conducted by Kasoma et al. (2020) in Zambia. Further breeding on the two inbred lines poses good potential for the development of elite, adapted and productive lines with enhanced FAW resistance.

SV1P is an extra early maturing genotype. This may suggest that most of its FAW resistance could have been due to early growth and development. This inbred line has the ability to rapidly grow, therefore flowering and maturing early (Figure 4.4A). This might allow its rapid growth through the most vulnerable and preferred growth stage by FAW as suggested by Azeez et al. (2018) and Prasanna et al. (2018). Similarly a study by Kasoma et al. (2020) in Zambia identified an extra early OPV, Pool 16, among the genotypes selected for good resistance to FAW. The current study noted that AD was highly significant and positively correlated with FFAWD (Table 4.10), this may mean that genotypes that mature early have the capacity to escape FAW damage as observed in this study as well as the one by Kasoma et al. (2020). Again, Kasoma et al. (2020) selected CML539 among the genotypes that exhibited low levels of FAW damage during early stages of growth. CML539 is an early maturing inbred line developed by CIMMYT. In the current study, the inbred line CML539 was again identified among the top 10 grain yielders under FAW infestation, with a grain yield of 0.92 t ha⁻¹. Another local commercial line, DPTY..*9 was among the best grain yielders under FAW infestation. The line had a grain yield performance of 0.9 t ha⁻¹ and an Avg-FFAWD modified Davis score of 4.94 (Appendix 4.1).

A number of studies have reported that, depending on level of infestation, FAW damage can cause yield losses of up to 100% (Arias et al., 2011; De Groote et al., 2020; Hruska & Gould, 1997; de Oliveira et al., 2018; Womack et al., 2018). Comparing the grain yields

realized under FAW natural infestation with those attained under managed FAW conditions, the current study noted that FAW infestation caused a yield penalty of between 49 – 57%. This concurs with De Groote et al. (2020) who reported 53 – 54% yield losses in Kenya and Hruska and Gould (1997) who again reported 15 – 73% yield losses from 55 – 100% infestation at mid to late whorl stages in Nicaragua. In addition, Hruska and Gould (1997) observed that maize is more tolerant to FAW infestation at early vegetative growth stages. This contradicts with observations from the current study that hybrids, OPVs and inbred lines are more vulnerable during early growth stages. However, hybrids and OPVs tend to grow out of FAW damage as they grow through mid to late whorl stages while inbred lines, particularly the susceptible ones such as WW01408 and HX482P showed a trend of increasing damage as they grew to maturity (Tables 4.6 and 4.7).

Relationships between traits help in making selection decisions. A pair of traits with either negative or positive genetic correlations can allow selection using only one of the traits. In contrast, traits with negative correlations do not allow simultaneous selection and may make it difficult to realise gain from selection for two traits simultaneously. In the current study, the different FAWD parameters, which included FFAWD at 4 weeks, FFAWD at 8 weeks, FFAWD at 12 weeks and EFAWD, have shown high positive correlations among and between them and ER. This suggests that varietal selection for FAW resistance can be done using only one of these traits. For hybrids and OPVs, PH showed high and positive associations with GYD and AD (Table 4.8). There is need to further test if selection for PH can be used to select for FAW resistance under FAW infestation. The inbred lines showed high and positive associations of EFAWD with HC and ER. This suggested that genotypes with poor HC are likely to have high EFAWD and ER (Table 4.8). Future studies on these correlations may need to consider path coefficient and stepwise multiple regression analysis. These have the capacity to further decompose the correlations and identify the factors contributing to yield loss the most.

4.5 Conclusions

This study demonstrated that screening for FAW resistance can be effectively performed under natural infestation conditions. Most cultivars currently in production have poor resistance to FAW, except for a few that exhibited better performance. These include PAN53, ZS242A, ZS246A, Mutsa MN521, Manajanja MN421 and ZAP61. The

commercial inbred lines SV1P and CML491 exhibited acceptable FAW resistance, and together with CML539, CLHP0005, CML304 and DPTY...⁹ they produced high grain yields under FAW infestation. These lines have been recommended as potential resources for further breeding for FAW resistance. HC, ER, AD and PH were identified to be correlated with FAW resistance, further testing is required to conclude if they can be used to select for FAW resistance. FFAWD and EFAWD were found to be highly correlated, hence one can be used to select for the other. The study also noted that FAW infestation has the potential to reduce grain yield by 49 – 57%.

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Chapter 5

Adaptability and stability analysis of commercial cultivars, experimental hybrids and lines under natural fall armyworm infestation in Zimbabwe using AMMI and other stability models

Abstract

Fall armyworm [*Spodoptera frugiperda* (J.E. Smith); FAW] resistant cultivars and breeding lines have been identified in sub-Saharan Africa. However, these materials have not been evaluated for their stability across environments with natural FAW infestation. The objectives of this study were to: (i) identify hybrids/OPVs combining high grain yield (GYD) and stability across environments with natural FAW infestation, (ii) select inbred lines with high GYD and stable FAW resistance, and (iii) identify the most discriminating environments for GYD performance and FFAWD under natural FAW infestation. The additive main effect and multiplicative interaction (AMMI) model was used to detect the presence of genotype-by-environment interaction for GYD, and foliar and ear FAW damage. Several stability analysis models were used to analyse adaptation and stability of genotypes across environments. The hybrids Mutsa-MN521 and CimExp55/CML334 were the best, combining adaptation and stability across FAW infested environments. Other acceptable hybrids were identified as 113WH330, Manjanja-MN421, CML338/CML334 and PAN53. The local inbred lines SV1P and CML491 combined adaptability and stable FAW resistance across environments. The best exotic donor lines exhibiting stable FAW resistance were CML67, CML346, CML121 and CML338. Harare and Gwebi were identified as the most discriminating sites for GYD performance, while Kadoma and Rattray-Arnold Research Stations were the most discriminating for FFAWD among inbred lines.

5.1 Introduction

Invasion of the SSA region by fall armyworm [*Spodoptera frugiperda* (J.E. Smith); FAW] continues to threaten food security and livelihoods in the region (Abrahams et al., 2017; Kansiime et al., 2019). Breeding efforts against the maize eating pest are currently underway in SSA, and locally adapted materials with significant resistance to FAW have been identified (Kasoma et al., 2020; Matova et al., 2020; Chapter 4 of this study). CIMMYT recently released hybrids with partial resistance to the pest (CIMMYT, 2020).

Again, several studies in SSA have identified potential materials for use in breeding as well as recommendation to farmers in mitigating the effects of FAW in maize production (Kasoma et al., 2020; Matova et al., 2020). However, varietal performance is largely determined by its genetics, production environment and the interaction between the two. This is commonly referred to as genotype-by-environment interaction (GEI) and in most cases it affects breeding decisions (de Oliveira et al., 2014). The same applies to the FAW resistant hybrids and lines that have been identified and released in SSA.

Breeding aims to improve yield, quality and other desirable agronomic traits, and this is referred to as adaptation. Wilsie (1962) defined adaptation as any characteristic of a living organism that gives it value under the prevailing environmental conditions. In the present scenario, adaptation will therefore mean a variety that is able to give the highest yield in a given production environment. This may not necessarily be across a set of different environments and that makes adaptation easier to compute compared to stability. However, superior yield performance should be stable across environments. Stability is described as the ability of a genotype to perform consistently across a range of environments (Becker and Léon, 1988). Naturally the interaction of a genotype with a number of environments tends to result in differential performance across the environments. Genotypes that perform well and produce good yields across environments are considered adapted and stable. Resistance breeding is targeted at improving adaptation and stability of performance across environments. Testing of adaptation is relatively easy and straight forward compared to stability. Stability of performance is a complex trait that is often negatively affected by several production factors, chief among them being stresses in the production environment.

Several biometrical models have been developed for use in the analysis of GEI and partitioning of yield performance and adaptation with stability across environments (Becker and Léon, 1988; Pacheco et al., 2015). However, one analysis model may not be enough to explain the variation and identify the ideal genotype combining adaptation and stability across environments. In this study different statistical models were used to evaluate and dissect GEI, adaptation and stability of performance of candidate genotypes for FAW resistance and other local cultivars and lines across environments. The objectives of the study were to: (i) detect the presence of GEI among FAW resistant genotypes, (ii) identify the most adapted and stable resistant genotypes across

environments with natural FAW infestation and (iii) identify the most discriminating environment for yield performance and FFAWD under natural FAW infestation. This information can guide breeding of stable FAW resistance in southern Africa.

5.2 Materials and Methods

5.2.1 Germplasm for testing

Fifty two genotypes consisting of 26 hybrids/OPVs and 26 inbred lines were evaluated. The genotypes were selected for FAW resistance and good GYD performance under FAW infestation, showing superior GYD potential under managed FAW conditions and, some for being susceptible to FAW. Thirteen of the inbred lines were parental lines of the hybrids evaluated in this study. These were evaluated together with 11 other local and exotic lines identified to be high yielding and resistant to FAW, and two local FAW susceptible lines (Table 5.1).

The germplasm used were developed by the Crop Breeding Institute (CBI), CIMMYT, HarvestPlus and various seed houses in Zimbabwe. Some of the lines and hybrids evaluated included cultivars and parental materials produced not only in Zimbabwe but across the East and Southern African (ESA) regions (Table 5.1).

5.2.2 Trial sites, experimental design and agronomic management

Materials evaluated were established under natural FAW infestation across different sites in Zimbabwe during the 2019 and 2020 summer seasons, except for Harare that had both natural infestation and managed FAW environments. Managed FAW environments were included for inbred lines because some inbred lines tend to suffer FAW damage even under FAW control.

Table 5.1 Description of genotypes evaluated for adaptation and stability of performance under natural fall armyworm infestation in Zimbabwe during the 2019-20 summer seasons

Hybrid/Cultivar		Source	Year of release	Production region	Line	Line name	Source	Status/Origin
Code	Name				Code			
1	Salisbury white	CBI	Not Clear	Zimbabwe and ESA	25	CLHP0005	HarvestPlus	local
6	R215	CBI	1974	Zimbabwe	27	CML304	CIMMYT	local
13	ZS265	CBI	2011	Zimbabwe	42	CZL1227	CIMMYT	local
14	ZS269	CBI	2014	Zimbabwe	28	CML444	CIMMYT	local
19	SR52	CBI	1962	Zimbabwe and ESA	57	CML543	CIMMYT	local
20	ZS242A	CBI	2015	Zimbabwe and ESA	34	CML395	CIMMYT	local
21	ZS246A	CBI	2016	Zimbabwe and ESA	48	CML334	CIMMYT	local
24	113WH330	CBI	Experimental	Zimbabwe	33	CML312	CIMMYT	local
29	CZH1258	CIMMYT	Experimental	N/A	36	CLHP00478	HarvestPlus	local
30	NTS51	NTS	2014	Zimbabwe	51	CML139	CIMMYT	local
31	PAN53	PANNAR	2007	Zimbabwe and ESA	52	CML571	CIMMYT	local
32	PAN4M-23	PANNAR	-	Zimbabwe and ESA	24	CLHP0003	HarvestPlus	local
33	PAN-7M-81	PANNAR	2013	Zimbabwe and ESA	60	CimExp54	CIMMYT	local
34	PHB30G19	PIONEER	2008	Zimbabwe and ESA	50	CML67	CIMMYT	Exotic
39	Manjanja MN421	Mukushi	2015	Zimbabwe, South Africa, Zambia	55	CML121	CIMMYT	Exotic
40	Mutsa MN521	Mukushi	2014	Zimbabwe, South Africa, Zambia	47	CML338	CIMMYT	Exotic
42	Mukwa	Mukushi	2016	Zimbabwe, South Africa, Zambia	53	CML346	CIMMYT	Exotic
44	ZAP61	Agriseeds	2008	Zimbabwe and ESA	9	SV1P	CBI-DR&SS	local
49	CML338/CML334	CIMMYT	Experimental	N/A	49	CML331	CIMMYT	Exotic
52	CIM52/CML139	CIMMYT	Experimental	N/A	30	CML491	CIMMYT	local
53	CIM53/CML345	CIMMYT	Experimental	N/A	61	CZL1112	CIMMYT	local
54	CIM54/CML334	CIMMYT	Experimental	N/A	38	DPTY... *9	HarvestPlus	local
55	CIM55/CML334	CIMMYT	Experimental	N/A	46	CML539	CIMMYT	local
58	CIM58/CML121	CIMMYT	Experimental	N/A	40	CZL1315	CIMMYT	local
59	CML543/CML334	CIMMYT	Experimental	N/A	23	WW01408	CBI-DR&SS	local
60	CML571/CML338	CIMMYT	Experimental	N/A	18	HX482P	CBI-DR&SS	local

Table 5.2 Description of experimental sites used in the evaluation of commercial cultivars, experimental hybrids and inbred lines

Location	Management	Altitude	Latitude	Longitude	Precipitation		Fertilisers (NPK) ha ⁻¹
					2018/19	2019/20	
		m			-mm-		
CIM-Harare	NI	1506	17°48'S	31°85'E	557.2	547.3	166:24.5:23.2
RARS	NI	1341	17°14'S	31°14'E	631.8	543.8	166:24.5:23.2
Chisumbanje	NI	421	20°05'S	32°15'E	441.9	434.8	166:24.5:23.2
Chiredzi	NI	1409	21°01'S	21°25'E	416.5	419.2	166:24.5:23.2
DR&SS-Harare	NI+Managed	1506	17°48'S	31°03'E	502.7	436.3	166:24.5:23.2
Gwebi VTC	NI	1448	17°41'S	30°32'E	571.5	542.5	166:24.5:23.2
KD-CRI	NI	1149	18°04'S	29°25'E	555.6	474.8	28:24.5:23.2

CIM-Harare, CIMMYT-Harare; RARS, Rattray-Arnold Research Station; ART-Farm, Agriculture Research Trust Farm; CHS, Chisumbanje; CHZ, Chiredzi; DR&SS-Hre, DR&SS Harare, Gwebi VTC, Gwebi Variety Testing Centre; KD-CRI, Kadoma Cotton Research Institute; NI, Natural Infestation

The trials under natural FAW infestation were raised without chemical control for the pest. Chiredzi and Chisumbanje research stations are situated in the lowveld (altitude <600 masl, average temperature 30°C). These sites are characterized by low rainfall and high temperatures, hence they naturally have a high and active infestation population of stem borers, FAW and other insect pests and have been traditionally used for maize stalk borer screening. Harare, Gwebi and Kadoma are active maize production zones and they tend to have high and active FAW populations during maize growing seasons. The sites CIMMYT-Harare and Chisumbanje were used during the 2019 summer season, while Chiredzi, RARS and Kadoma-CRI were used in the 2020 summer season. The sites DR&SS-Harare and Gwebi VTC were used in the summer seasons of both years (Table 5.2).

The hybrid/OPV experiment was laid out in a 10 x 6 α (0, 1) lattice design, while the inbred line experiment was laid out in a 9 x 7 α (0, 1) lattice design. Both experiments had two replications at each testing site and one 4 m row plot for all environments except at DR&SS-Harare and CIMMYT-Harare that had 2 m row plots. Inter-row and intra-row spacing were 0.75 m and 0.25 m, respectively. Plants were thinned to one per planting station at two leaf stage (approximately three weeks after planting) to give a crop population density of 17 and 9 plants per row for the 4 m and 2 m rows, respectively, which translates to about 53 000 plants ha⁻¹. The plants in the experiments were raised using standard agronomic practices for maize production. Optimal fertiliser rates of 400

kg ha⁻¹ for both compound D (7N:14P:7K) basal applications and ammonium nitrate (34.5N) for top dressing were applied at all environments. Weeds were controlled using herbicides and hand weeding where necessary.

5.2.3 Data collection and analysis

The following data were recorded per plot: (i) foliar FAW damage (FFAWD) averaged for scores at 4, 8 and 12 week intervals from date of planting, (ii) ear FAW damage (EFAWD) and (iii) grain yield (GYD) per plot adjusted to 12.5% moisture content. FFAWD and EFAWD damage were recorded following the modified Davis scale as described by Prasanna et al. (2018) where scores 1-2 = resistant, 2-5 = partial resistance, 5-7 = susceptible, 7-9 = highly susceptible. All the other agronomic traits were recorded as described by Magorokosho et al. (1998) and Masuka et al. (2017).

Individual site ANOVA for each trait was done to determine the existence of differences between genotypes using Genstat Discovery Software V18.0 and Multi-environment Trials Analysis in R (META-R) V2.1 R package software. Best linear unbiased predictions (BLUPs) and broad sense heritability estimates (H^2) were done with META-R. To reduce the confounding effect of error and environmental variances sites with H^2 lower than 20% were excluded from the combined analysis. The Bartlett's test was used to test for homogeneity of error variances for the evaluated traits in each environment. Across site ANOVA was done to test the effects and magnitude of genotypes (G), environments (E) and GE interactions using the additive main effect and multiplicative interaction (AMMI) analysis model in Genstat. Genotypes were considered fixed, while replications within environments and environments were considered random (VSN International, 2017; Alvarado et al., 2020).

Both the Genotype-by-Environment Analysis with R (GEA-R) V4.1 R package software and Genstat Discovery Software V18.0 were used to estimate adaptability and stability parameters of the genotypes across environments (Pacheco et al., 2015; VSN International, 2017). The AMMI model was used to assess GEI, adaptation and stability of the genotypes and environments. The first two principal components (PCs), interaction principal component axes (IPCA1 and IPCA2) of the AMMI model and PC1 and PC2 for GGE biplots were computed to visualise the GEI and adaptation of the genotypes to the

test environments. However, the AMMI model on its own cannot effectively identify stable genotypes as it does not encompass a quantitative measure for stability (Gauch and Zobel, 1996; Gauch, 2006). Therefore, the AMMI stability value (ASV) proposed by Purchase et al. (2000) was employed to further analyse stability. The ASV measures stability in two dimensions using PC analysis of the scores of IPCA1 and IPCA2. It denotes the distance from zero in a scatter plot of IPCA1 and IPCA2. The IPCA1 contributes more to the total GEI sum of squares compared to IPCA2. There is therefore a proportional difference between the two PC scores, hence the need to balance the contribution of the two to the total GEI sum of squares. A genotype with the lowest ASV is the most stable (Purchase et al., 2000).

Further to that, the yield stability index (YSI) that gives a simultaneous single measure of yield and yield stability was used. Genotypes with the lowest YSI are considered the most stable and high yielding (Purchase et al., 2000; de Oliveira et al., 2014). The YSI sums up the ranks of yield and ranks of yield stability as follows:

$$YSI = \text{Rank of ASV} + \text{Rank of Yield}.$$

Further analysis for adaptation and stability was done with the GGE biplots, Cultivar superiority index, Eberhart and Russel's coefficient of regression and Wricke's ecovalence models (Yan and Tinker, 2006; Pacheco et al., 2015; VSN International, 2017). The GGE biplots were used to visualise the most adapted and stable genotypes, the most discriminating environments as well as clustering the genotypes and environments based on the effects of FAW infestation on the GYD and FAW damage parameters.

5.3 Results

5.3.1 Analysis of genotype by environment effects for grain yield, fall armyworm resistance and related traits of hybrids/OPVs using the AMMI model

The AMMI across environment ANOVA showed significant ($P < 0.001$) differences for genotypes, environments and GEI. The contribution of environmental variance to the total variance was higher than that of genotypes and GEI for all traits. The two interaction principal component axes (IPCA1 and IPCA2) were significant ($P < 0.05$) for all traits. For GYD the highest contribution to total variance came from the GEI (44.85%), while

environments and genotypes contributed 36.97% and 18.18% respectively (Table 5.3). For FFAWD, environments made the largest contribution to total variance of 52.88% followed by GEI with 30.26% and lastly genotypes with 16.89%. Similarly for EFAWD, environments made the largest contribution to the variance which amounted to 42.22% while GEI and G contributed 41.61% and 16.17% respectively (Table 5.3).

5.3.2 Mean grain yield performance of hybrids/OPVs and stability analysis

GGE biplot analysis showed that the most adaptable and stable genotypes were G40 (Mutsa MN521), G42 (Mukwa) and G58 (CIM58/CML121) (Figure 5.1A). These combined high grain yield performance and stability, reflective of their large PC1 values and small PC2 values on the biplot. The genotype Mutsa MN521 was located on the first concentric ring, close to the position of the most ideal genotype, indicating that it is the most acceptable genotype, combining high grain yield performance and stability, as identified by the biplot. The ideal genotype is the most preferred, it combines adaptation and stability. The most stable genotypes were G54 (CIM54/CML334), G49 (CML338/CML334) and G53 (CIM53/CML345). These were located near the origin of the biplot, implying they had low PC1 and PC2 values. Genotype G49 had GYD that was equal to the trial means, while CIM53/CML345 and CIM54/CML334 performed below the trial means as they were located below the average environmental coordination axis. The biplots explained 65.05% of the total variation observed, with PC1 contributing 46.72% and PC2 contributing 18.33% (Figure 5.1A).

The ranking biplot showed that the best grain yielder was G31 (PAN53), followed by Mukwa, Mutsa MN521 and G32 (PAN4M-23) (Figure 5.1B). However, genotypes PAN53 and PAN4M-23 were highly unstable despite being high yielding as they were located further away from the x -axis. In contrast, genotypes Mutsa MN521 and Mukwa were located closer to the x -axis, indicating low PC2 values. Combining that with their large PC1 values, the two were more stable and adaptable. Genotype G19 (SR52) was identified to be stable but it was very low yielding (Figure 5.1B).

Table 5.3 Analysis of genotype by environment effect for grain yield, fall armyworm resistance and related traits using the AMMI model for commercial cultivars, experimental hybrids and inbred lines under natural FAW infestation sites in Zimbabwe, during the 2019 and 2020 summer seasons

A) Hybrids/OPVs			GYD			FFAWD			EFAWD		
Source of variation	DF		SS	MS		DF	SS	MS	DF	SS	MS
Treatments	233		1405.5	6.03***		285	49044	172.10***	155	565.6	3.65***
Genotypes	25		255.5	10.22***		25	8283	331.30***	25	91.5	3.66***
Environments	8		519.6	64.95***		10	25920	2592.00***	5	238.8	47.75***
Block	9		18	2		11	355	32.3	6	9.6	1.6
Interactions	196		630.4	3.22***		250	14841	59.40**	123	235.4	1.91***
IPCA 1	32		283.7	8.86***		34	4604	135.40**	29	97.2	3.35***
IPCA 2	30		117.8	3.93***		32	2901	90.60***	27	61.8	2.29**
Residuals	134		229	1.71		184	7337	39.9	67	76.3	1.14
Error	199		342.6	1.72		275	11339	41.2	147	150.9	1.03
B) Inbred lines											
Treatments	181		99.47	0.55***		259	1206.5	4.66***	129	375.3	2.91**
Genotypes	25		39.31	1.52***		25	524.2	20.97***	25	137	5.48***
Environments	6		23.2	3.87***		9	427.8	47.54***	4	60.4	15.11***
Block	7		3.08	0.44		10	18.4	1.84*	5	0.9	0.19
Interactions	136		36.96	0.27		224	254.4	1.36*	94	177.8	1.89
IPCA 1	30		14.71	0.49*		33	84.7	2.57***	28	104.2	3.72**
IPCA 2	28		9.43	0.37		31	42.6	1.37*	26	40	1.54
Residuals	78		12.81	0.16		160	127.1	0.8	40	33.6	0.84
Error	124		37.43	0.3		233	194.6	0.84	102	186.8	1.83

GYD = grain yield; FFAWD = foliar fall armyworm damage; EFAWD = ear fall armyworm damage; * P < 0.05; ** P < 0.01; *** P < 0.001; interaction principal component axes = IPCA

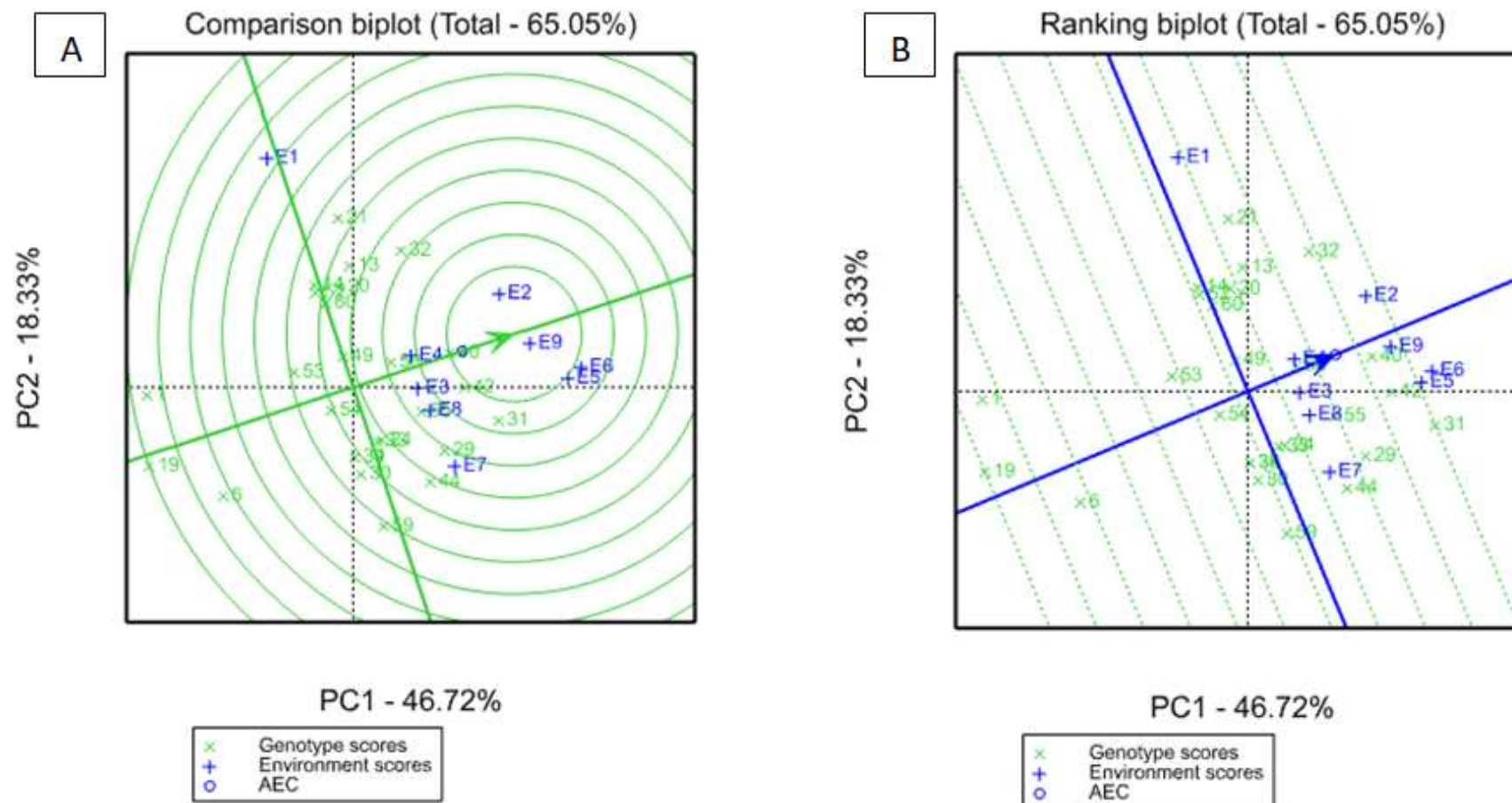


Figure 5.1 GGE biplots showing adaptation and stability of genotypes across nine environments. (A) A comparison GGE biplot (genotype scaling) showing adaptation and stability of genotypes across nine environments, (B) A ranking GGE biplot showing the mean grain yield performance of 26 maize hybrids/OPV produced across nine environments in Zimbabwe. Genotypes are identified by a code prefixed by an 'x' shown in Table 1. Environments are identified by a number prefixed by a '+E': +E1 = Harare-DR&SS-2019; +E2 = Harare-CIMMYT-2019; +E3 = Gwebi-2019; +E4 = Chisumbanje-2019; +E5 = Panmure-2019; +E6 = Rattray-Arnold-2020; +E7 = Gwebi-2020; +E8 = Chiredzi-2020; +E9 = Harare-DR&SS-2020

Further analysis with the covariance percentage (CV %) and coefficient of regression models identified G13 (ZS265), PAN53, Mutsa, MN521 and G55 (CIM55/CML334) as the best genotypes selected by both models for combining good GYD performance with stability across environments. The plot of CV% vs mean GYD placed high yielding and stable genotypes in the 4th quadrant (Figure 5.2A). The plot of coefficient of regression (*bi*) vs variability (S^2di) separates genotypes into three categories (adapted, stable and, stable and adapted). When *bi* is close to 1 the genotypes are adaptable, and when S^2di is near zero, the genotypes are stable. If S^2di is low and the *bi* is high the genotypes will be adaptable and stable (Figure 5.2B). Simultaneous selection using AMMI mean yield performance and stability parameters (*ASV* and *YSI*) together with the Standard deviation (*Sd*), Cultivar superiority (*Cs*), Eberhart and Russel (*ER*) and Wricke's ecovalence (*We*) models identified the best genotypes as G24 (113WH330), Mutsa MN521, G39 (Manjanja MN421), CIM55/CML334 and CML338/CML334. The yield performance and stability ranks of the genotypes are shown in Table 5.4. The cultivar G6 (R215) showed good stability with the *ASV*, *Sd*, *Ss* and *We* models, but failed to perform well on *YSI* and *Cs* indices, and had poor *per se* performance for GYD. PAN53 and Mukwa were the best on GYD *per se* performance across natural FAW environments but they lacked good stability (Table 5.4).

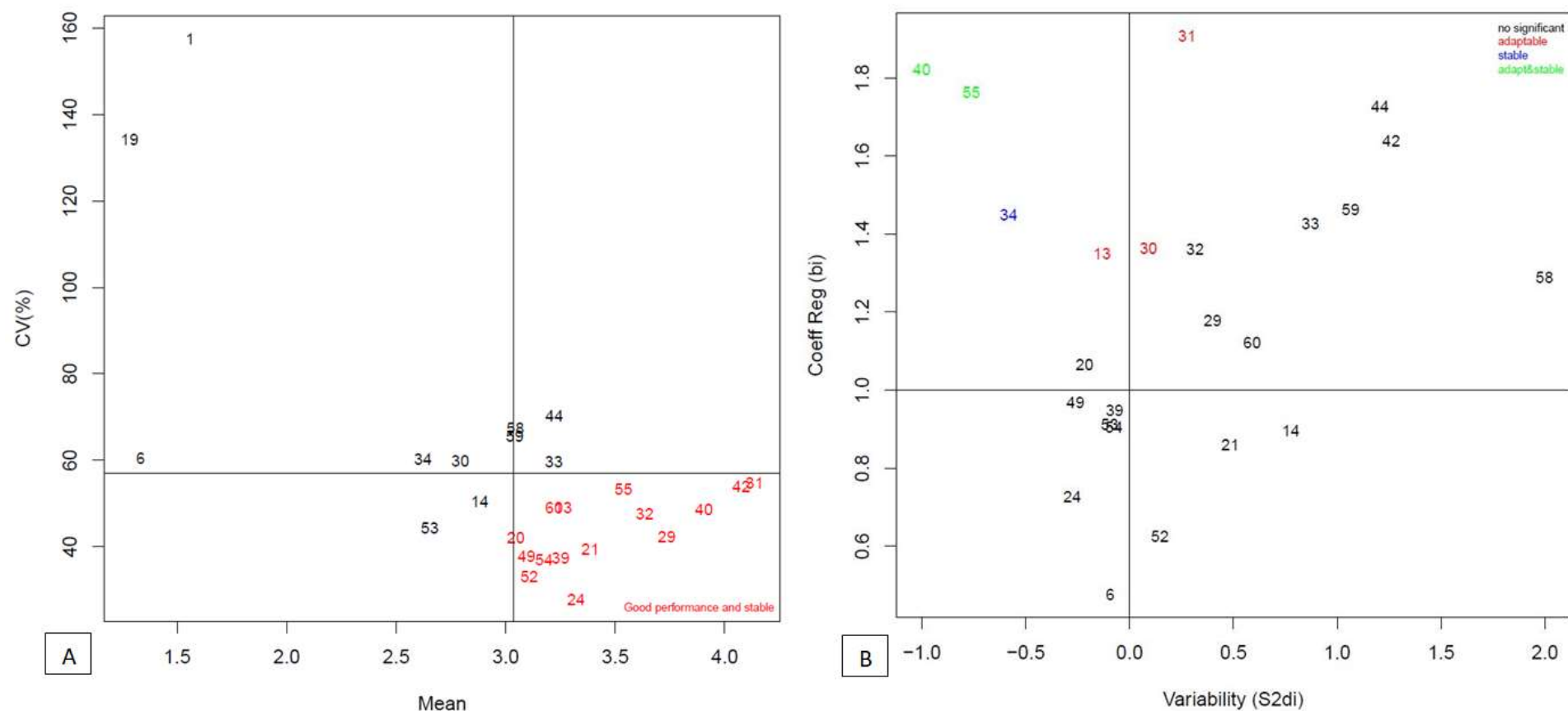


Figure 5.2 Covariance percentage and coefficient of regression biplots showing adaptation and stability of genotypes across environments. (A) A biplot showing covariance percentage (CV %) against mean grain yield performance of 26 maize genotypes evaluated across nine environments in Zimbabwe. (B) A graphical presentation of the Eberhart and Russel coefficient of regression (*bi*) vs variability (S^2di) of mean grain yield for 26 maize genotypes evaluated across nine environments in Zimbabwe. The numbers represent the genotypes evaluated and these correspond with the genotype codes in Table 5.1.

Table 5.4 Assessment of grain yield stability of hybrids and OPVs evaluated across nine natural fall armyworm infestation environments in Zimbabwe during the 2019-20 seasons using different stability models. The shaded rows in green and grey highlight the selections made.

AMMI Stability Model										Mean Square Deviation Model			Lin and Binns Model		Eberhart and Russel Model		Wricke's ecovalence Model	
Genotype Number	Genotype code	Name	IPCAg1	IPCAg2	Mean	GYD Rank	ASV	ASV Rank	YSI	YSI Rank	Sd	Sd Rank	Cultivar superiority	Cs Rank	Static stability	Ss Rank	Wricke's ecovalence	We Rank
1	1	Salisbury White	-2.10	0.32	1.68	24	3.27	26	50	26	2.45	26	10.79	24	*	*	53.19	26
2	6	R215	-0.07	-0.20	1.30	25	0.23	1	26	13	0.81	1	11.43	25	0.65	1	6.63	10
3	13	ZS265	-0.45	-0.46	3.29	9	0.84	12	21	9	1.60	14	3.42	5	2.55	14	6.73	11
4	14	ZS269	-0.58	-0.63	2.88	20	1.10	17	37	22	1.45	10	5.14	17	2.11	10	11.64	18
5	19	SR52	-0.24	1.48	0.95	26	1.53	23	49	25	1.72	16	13.13	26	*	*	19.95	23
6	20	ZS242A	-0.43	-0.56	3.05	17	0.86	13	30	18	1.28	8	4.21	12	1.65	8	4.90	3
7	21	ZS246A	-0.80	-0.36	3.39	7	1.30	20	27	15	1.33	9	3.51	7	1.78	9	10.56	16
8	24	113WH330	0.20	0.27	3.30	8	0.41	3	11	1	0.93	2	4.49	14	0.86	2	5.14	4
9	29	CZH128	0.75	0.04	3.72	4	1.17	19	23	10	1.58	11	3.90	9	2.49	11	9.66	14
10	30	NTS51	0.35	-0.17	2.77	21	0.57	6	27	16	1.67	15	5.50	19	2.80	15	7.69	12
11	31	PAN53	1.03	-0.22	4.14	1	1.62	24	25	12	2.26	24	3.12	4	5.12	23	16.75	21
12	32	PAN4M-23	-0.23	-0.96	3.64	5	1.02	15	20	6	1.73	17	3.01	3	2.98	16	10.13	15
13	33	PAN7M-81	0.42	0.49	3.23	10	0.82	10	20	7	1.92	20	4.93	16	3.69	19	13.93	19
14	34	PHB30G19	0.44	-0.09	2.60	23	0.68	7	30	19	1.58	12	5.87	22	2.50	12	3.53	1
15	39	Manjanja-MN421	0.07	0.44	3.22	13	0.45	4	17	3	1.22	7	4.20	11	1.48	7	6.07	6
16	40	Mutsa-MN521	0.44	-0.01	3.91	3	0.68	8	11	2	1.90	19	2.41	1	3.61	18	6.32	7
17	42	Mukwa	0.56	0.75	4.08	2	1.15	18	20	8	2.20	23	2.95	2	4.82	22	19.98	24
18	44	ZAP61	1.01	-0.44	3.22	11	1.63	25	36	21	2.27	25	5.43	18	5.14	24	19.16	22
19	49	CML338/CML334	-0.17	0.31	3.10	16	0.41	2	18	5	1.17	4	4.43	13	1.37	4	4.77	2
20	52	CimExp52/CML139	-0.66	0.18	3.11	15	1.03	16	31	20	1.03	3	4.53	15	1.06	3	9.12	13
21	53	CimExp53/CML345	-0.31	0.08	2.64	22	0.49	5	27	17	1.18	5	5.71	21	1.38	5	5.39	5
22	54	CimExp54/CML334	-0.48	0.03	3.14	14	0.75	9	23	11	1.18	6	3.87	8	1.39	6	6.42	8
23	55	CimExp55/CML334	0.53	0.02	3.54	6	0.83	11	17	4	1.89	18	3.43	6	3.56	17	6.57	9
24	58	CimExp58/CMC121	0.50	-1.16	3.02	18	1.40	21	39	23	2.05	22	6.05	23	4.22	21	20.66	25
25	59	CML543/CML334	0.80	0.73	3.02	19	1.43	22	41	24	2.00	21	5.67	20	3.98	20	15.37	20
26	60	CML571/CML338	-0.58	0.10	3.22	12	0.91	14	26	14	1.58	13	3.92	10	2.50	13	11.03	17

IPCAg1 = interaction principal component axes for genotypes 1; IPCAg2 = interaction principal component axes for genotypes 2; GYD = grain yield; ASV = AMMI stability value; YSI = yield stability index; Sd = standard deviation; We = Wricke's ecovalence.

5.3.3 Identification of the best screening environments for grain yield potential under natural fall armyworm infestation in Zimbabwe

The AMMI model biplot and the GGE biplot (Scatter plot) shown in Figure 5.3A and Figure 5.3B, respectively, identified E1 as the most discriminating environment, followed by E7. The two had the longest vectors showing their high discriminating power. Environment E1 (Harare-DR&SS-2019) and E7 (Gwebi-2020) were not strongly associated with genotypes, while the other environments had associations with specific genotypes. The environments E2 (Harare-CIMMYT-2019), E3 (Gwebi-2019) and E4 (Chisumbanje-2019) were stable as they had short vectors and most of the genotypes were clustered around these environments (Figure 5.3A). This implies that these environments (E2, E3 and E4) may not be the best in screening genotypes for FAW resistance under natural FAW infestation conditions.

Further analysis with the scatter plot showed that genotypes Mutsa MN521, Mukwa, PAN53, G29 (CZH1258), G44 (ZAP61), CIM55/CML334, CIM58/CML121, Manjanja MN421 and CIM54/CML334 were clustered within the mega-environment including all the other environments except E1. The genotypes that were outside the mega-environments were G1, G19, G6, G59, G30, G54, G53, G19, G32, G21, G13, G14, G20 and G60. E2 formed its own mega-environment, however, this was circulated by the bigger mega-environment covering all the other environments besides E1. The mega-environment covering E1 was positioned further away from the other two mega-environments (Figure 5.3B).

5.3.4 Inbred lines exhibiting high adaptation and foliar fall armyworm resistance stability across environments with natural fall armyworm infestation

The genotypes G9 (SV1P), G30 (CML491) and G38 (DPTY...*9) were the best for GYD performance across environments with mean yields of 1.37 t ha⁻¹, 1.30 t ha⁻¹ and 1.15 t ha⁻¹, respectively (Table 5.5).

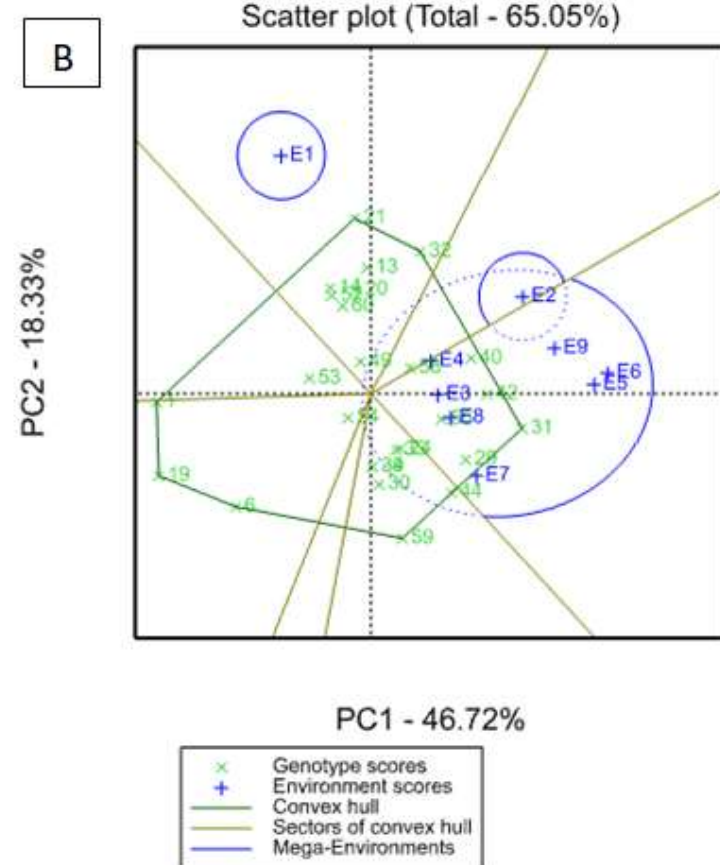
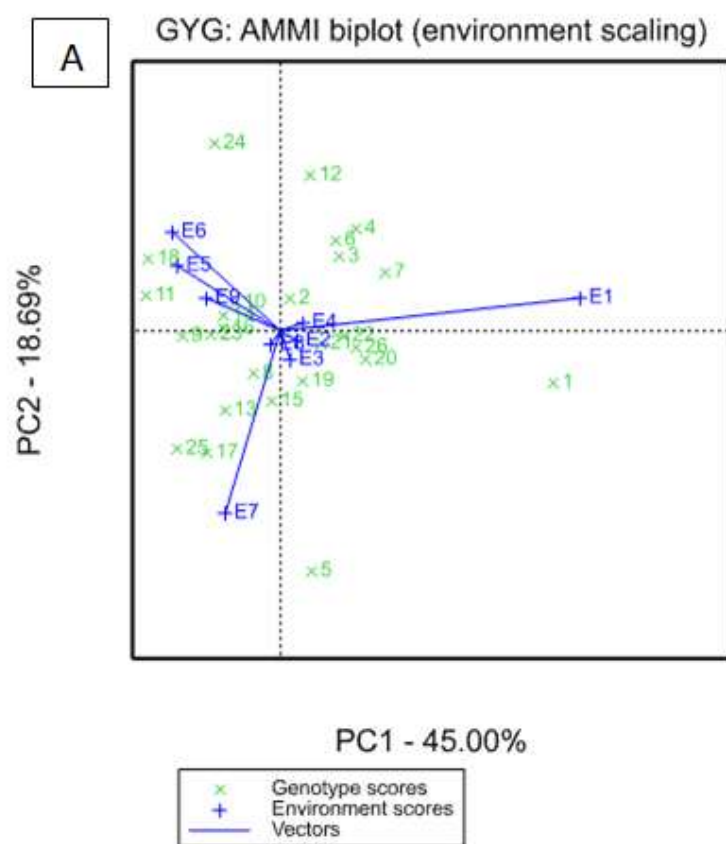


Figure 5.3 Biplots showing the positions of genotypes and environments on the scatter-gram. (A) A comparison AMMI scatter biplot for grain yield (environment scaling) showing the positions of the 26 genotypes and nine environments on the two dimensional scatter-gram, (B) A GGE biplot showing mega-environments depicted by grain yield scores of 26 maize genotypes evaluated across nine environments in Zimbabwe during 2019-20 seasons. Genotypes are identified by a number (for Figure 5.3A) and a code (for Figure 5.3B) prefixed by an 'x' all shown in Table 4.5. Environments are identified by a number prefixed by a '+E', +E1 = Harare-DR&SS-2019; +E2 = Harare-CIMMYT-2019; +E3 = Gwebi-2019; +E4 = Chisumbanje-2019; +E5 = Panmure-2019; +E6 = Rattray-Arnold-2020; +E7 = Gwebi-2020; +E8 = Chiredzi-2020; +E9 = Harare-DR&SS-2020

Table 5.5 Assessment of grain yield potential of inbred lines evaluated across six environments with natural fall armyworm infestation and one managed fall armyworm environment in Zimbabwe during the 2019-20 seasons

Genotype	Genotype code	Name	Grain yield	Grain yield rank
G1	9	SV1P	1.37	1
G2	18	HX482P	0.10	25
G3	23	WW01408	0.07	26
G4	24	CLHP0003	0.52	15
G5	25	CLHP0005	0.60	12
G6	27	CML304	0.79	5
G7	28	CML444	0.31	21
G8	30	CML491	1.30	2
G9	33	CML312	0.45	18
G10	34	CML395	0.37	19
G11	36	CLHP00478	0.31	20
G12	38	DPTY...*9	1.15	3
G13	40	CZL1315	0.71	8
G14	42	CZL1227	0.67	10
G15	46	CML539	0.49	17
G16	47	CML338	0.78	6
G17	48	CML334	0.71	7
G18	49	CML331	0.59	13
G19	50	CML67	0.63	11
G20	51	CML139	0.30	22
G21	52	CML571	0.26	23
G22	53	CML346	0.50	16
G23	55	CML121	0.88	4
G24	57	CML543	0.13	24
G25	60	Cim60Exp	0.69	9
G26	61	CZL1112	0.54	14

The ANOVA of the AMMI model showed significant ($P < .001$) effects of genotypes and environments for GYD, FFAWD and EFAWD, while GEI was significant for FFAWD only. For this reason, only FFAWD was included for further analysis. The IPCA1 was significant for all traits while the IPCA2 was significant for FFAWD only. Dissection of the GEI variance for FFAWD showed that the genotypes made the largest contribution to total variance which amounted to 43.45%, while environments and GEI contributed 35.46% and 21.09% respectively (Table 5.3).

The most discriminating environments for FFAWD were identified as +7 (Kadoma) and +5 (Rattray-Arnold) for the 2020 season whilst +1 (Harare-DR&SS) and +2 (Harare-CIMMYT) were identified for the 2019 season. These had the longest vectors indicative of the high discriminating power of these environments. The environment +4 (Gwebi-2019) had the shortest vector implying it was the least discriminating (Figure 5.4A).

Figure 5.4B showed that the inbred line G50 (CML67) had the lowest FFAWD scores, it had the smallest PC1 value followed by G53 (CML346), G55 (CML121), G9 (SV1P), G47 (CML338) and G30 (CML491) as some of the best performers for resistance to FFAWD. The highest stability for FFAWD across the environments was exhibited by G53, followed by G55, G47, G30, G50 and G9. The inbred lines G33 (CML312) and G49 (CML331) showed average performance on FFAWD resistance, but they were unstable as shown by their large PC2 values. The poor performers included genotypes G18 (HX482P), G57 (CML543), G28 (CML444) and G34 (CML395), these had large PC1 values indicating large FFAWD scores.

The biplot clustered the testing environments into three mega-environments based on FFAWD scores that were scored in those environments. The first mega-environment covered +2 (Harare-CIMMYT-2019), the second covered +1 (Harare-DR&SS-2019) and +3 (Harare-Managed FAW-2019) and the third mega-environment encompassed environments +4, +5, +6, +7, +8, +9 and +10 (Figure 5.4B).

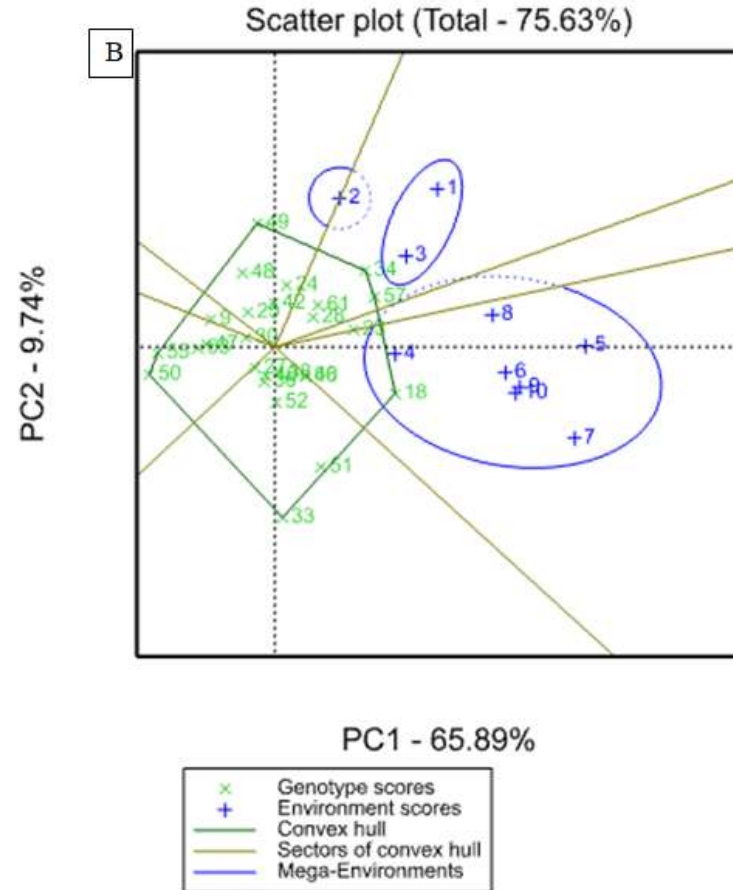
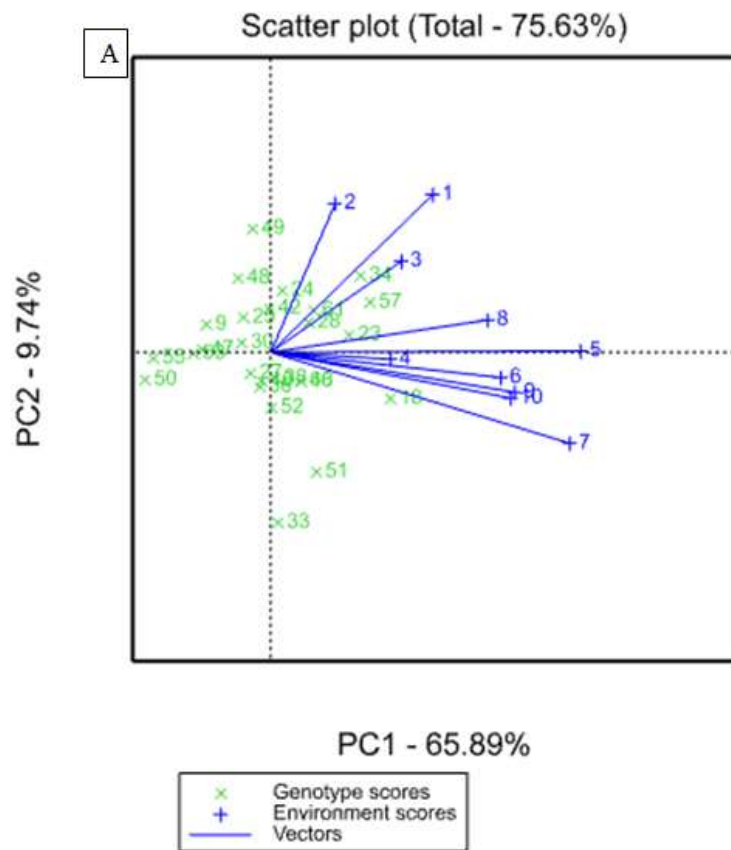


Figure 5.4 Biplots showing the positions of inbred lines and environments on the scatter-gram. (A) A GGE scatter biplot (environment scaling) showing the position of environments and genotypes on the biplot, (B) A GGE biplot showing mega environments depicted by foliar fall armyworm damage scores of 26 maize genotypes evaluated across ten environments in Zimbabwe during 2019-20 seasons. Genotypes are identified by a number prefixed by an 'x', the numbers represent genotypes evaluated, the numbers correspond to the genotype codes in Table 5.5. Environments: +1 = Harare-DR&SS-2019; +2 = Harare-CIMMYT-2019; +3 = Harare-Managed FAW-2019; +4 = Gwebi-2019; +5 = Ratray-Arnold-2020; +6 = Gwebi-2020; +7 = Kadoma-2020; +8 = Chiredzi-2020; +9 = Harare-Managed FAW-2020; +10 = Harare-DR-SS-2020.

5.4 Discussion

Breeding for yield stability in FAW infestation environments is important, as it aims to guarantee the performance of cultivars and varieties recommended for production in such environments. Chapter 4 of this PhD study identified commercial cultivars, experimental hybrids and inbred lines with acceptable levels of FAW resistance. However, the performance of these genotypes needed to be evaluated for stability across environments with natural FAW infestation. These genotypes were evaluated in this study, and the significant GEI that was observed for hybrids/OPVs for all traits and for FFAWD for inbred lines indicates differential performance of the genotypes. This implied that selection of the best genotypes across environments was not going to be easy, hence the need for a more refined analysis for increased screening efficiency and effective selection and cultivar recommendations.

Refined analysis for cultivar performance when there is GEI aims to check the adaptability and stability of genotypes across environments, and this has been recommended by Lin and Binns (1988) and Becker and Léon (1988), among others. Most of the variation observed for FFAWD and EFAWD on hybrids/OPVs across the environments was contributed by the environments, as they showed the largest percentages of the total sum of squares. This indicates that there were large differences in the mean performance of these traits for most of the environments. However, for GYD the greatest contribution to the observed variation came from GEI, implying that GYD performance was highly dependent on the response of the genotype to the production environment. This concurs with Becker and Léon (1988) who suggested that genotypic performance is determined by the environmental conditions.

Contrary to the above, the genotypes were responsible for most of the variation observed across inbred lines for GYD and FFAWD. This suggests that varietal performance was highly distinct and explicit such that the effects of the environments and GEI were overshadowed by genotypic effects. This could probably be the same reason for the lack of significance on GEI for GYD and EFAWD. However, though not significant, GEI contributed the largest effects to the variation that was observed for EFAWD on the inbred lines. This may relate to factors such as husk cover that may depend on genotypes and environmental factors that stress the plants or make them more attractive to the pest.

Observations from Chapter 4 have noted that genotypes with open husk cover tend to have more damage on the ears by the FAW. The GEI was significant for FFAWD only on inbred lines. This suggested the need to focus on only FFAWD for stability analysis. With regards to that, genotypes contributed 43.45% to the total sum of squares of the GEI, while environments and GEI contributed 35.46% and 21.09% respectively (see Table 5.1).

The GGE comparison and ranking biplots (PC1 vs PC2) for hybrids and OPVs in Figure 5.1 showed that genotype effect scores were more scattered compared to the environmental effect scores. The same was observed on inbred lines (see Figure 5.4). This suggests that variability due to genotypes was greater than variability due to the environments as was shown by the contributions of the genotypes to total sum of squares of the variance components (Table 5.3). According to Yan and Tinker (2006), adaptability is measured by PC1 in the positive direction of the *x*-axis while stability is evaluated by PC2 along the *y*-axis on either side of the *x*-axis. Accordingly, the hybrids PAN53, Mukwa, Mutsa MN521 and PAN4M-23 were the highest yielders as they had the largest PC1 values. With regards to stability, genotypes Mutsa MN521 and Mukwa were more stable, hence the two combined both stability and adaptation and that makes them acceptable. Becker and Léon (1988) recommended that cultivars should not only be high yielding but should have sustained yield superiority across environments.

The environments Harare and Gwebi were observed to be highly discriminating for GYD performance in the hybrids/OPVs as they had the longest vectors. This implied that the sites Harare and Gwebi were able to differentiate GYD varietal performance under natural FAW infestation environments better than other sites. Similar results were observed by Matova and Gasura (2018) in their studies on cowpea, in which Harare was identified to be the most discriminating and representative site. A study by Gasura et al. (2015) on sorghum identified Rattray-Arnold Research Station as the most discriminating and representative site. The findings by Matova and Gasura (2018) and (Gasura et al., 2015) suggest that high potential environments are the best in discriminating genotypic performance for GYD potential. Again, these seem to concur with the findings of this study that observed Harare and Gwebi as the most discriminating environments. The two environments are in natural region 11, characterised by good soils and high rainfalls.

The hybrids CIM54/CML334, CML338/CML334 and CIM53/CML345 were the most stable for GYD performance across environments with natural FAW infestation, however, they had average to below average GYD performance, hence are not preferred. This concurs with de Oliveira and de Godoy (2006) and Becker and Léon (1988) who reported that the most stable genotypes are not necessarily the highest yielders. Genotypes that combined both adaptability (high GYD performance) and stability across environments are the most preferred by both seed producers and farmers. The GGE biplot analysis in the current study identified genotypes Mutsa MN521 and Mukwa as the most preferred hybrids combining adaptability and stability. The hybrids PAN53 and CIM55/CML334 were also identified as acceptable genotypes. PAN53 had high GYD performance and relatively good stability, while CIM55/CML334 had good stability and acceptable GYD performance (see Figure 5.1).

These four hybrids (CIM55/CML334, Mutsa MN521, Mukwa and PAN53) were again identified as the best by the CV% stability model. The quadrant position of the hybrid CIM55/CML334 showed that the genotype is stable but its GYD performance was relatively low compared to Mutsa MN521, Mukwa and PAN53. This was also displayed by the GGE biplot in Figure 5.1. The Eberhart and Russel Coefficient of Regression model identified genotypes Mutsa and CIM55/CML334 as the best, combining adaptability and stability (Figure 5.2B). These results suggest that quick genetic gains for FAW resistance in locally adapted materials can be achieved if breeders focus on improvement of parents of the hybrids.

Different stability analysis methods were used in this study as it is quite difficult to use only one method and come up with a correct conclusive decision. The same sentiments were echoed by Becker and Léon (1988) and Yan and Tinker (2006) who reported that stability analysis is a complex phenomenon that remains a challenge to breeders in variety evaluation and recommendations. Additional stability methods were used to conclude the findings from the previous models that had collectively identified genotypes G55, G40, G42 and G31 as the most adapted and stable performers under natural FAW infestation. These models included the ASV, YSI, Mean square deviation, Cultivar superiority index, Static stability and Wricke's ecovalence models (see Table 5.4) (Lin and Binns, 1988; Purchase et al., 2000). The use of different stability models helped in reaching conclusive results, breeders should strive to use different analysis models in stability analysis.

A simultaneous analysis of the results of the above models shown in Table 5.4 identified genotypes G24 (113WH330), G39 (Manjanja MN421), G40 (Mutsa MN521), G49 (CML338/CML334) and G55 (CIM55/CML334) as the most adapted and stable hybrids. Selection was primarily based on the ranks of *ASV* and *YSI* which, according to Purchase et al. (2000) and de Oliveira et al. (2014), have the advantage of simultaneous selection for *GYD* performance and yield stability. Rank inversions were noted across different models. A good example was cultivar Mutsa-MN521 which was ranked second on the *YSI* of the AMMI model and was ranked number 18 with the static stability model (Table 5.4). Such rank inversions have also been reported in studies by de Oliveira et al. (2014) on fruit yield of yellow passion fruit. The models, AMMI1 and AMMI2 were giving opposing stability ranks of the yellow passion fruit varieties. However, the rank inversions exhibited by Mutsa-MN521 and G55 (CimExp55/CML334) suggests that the two may have dynamic stability. This implies that they are adapted to a wide range of environments hence they exhibit low GEI but they are not as stable as genotypes with static stability. Genotypes with static stability have consistent performance across environments hence they tend perform better in stressful environments as suggested by Weedon and Finckh (2019).

The stability models shown in Table 5.4 brought in four new candidates that were not visible among the most adapted and stable genotypes with the first analysis models. These included G6 (R215), G24 (113WH330), G39 (Manjanja MN421) and G49 (CML338/CML334). The mean *GYD* performances of these genotypes were generally low, mostly average to below average. These were therefore easily eliminated from the top performers, initially by the GGE biplots which placed them near or below the y-axis of the biplot (Figure 5.1). The CV% model identified them among the performers that combined good *GYD* and stability. However, their *GYD* performance was not preferred, as there were many cultivars with better *GYD* performance and stability (see Figure 5.2A). The coefficient of regression plot excluded these genotypes as they were labelled non-significant implying they were not different from the other poor performers (see Figure 5.2B). Overall, this identifies the genotypes G40 (Mutsa MN521) and G55 (CIM55/CML334) as the most adapted and stable genotypes under natural FAW infestation, selected by all models.

With regards to the inbred lines, the genotype G9 (SV1P) exhibited the best GYD performance across the environments. The genotypes G30 (CML491) and G38 (DPTY...*9) were second and third in terms of grain yield rankings. The three genotypes are locally adapted lines bred by CBI-DR&SS, CIMMYT and HarvestPlus respectively. The lines SV1P and CML491 combined high GYD performance and FAW resistance, and this was reported by previous studies (Kasoma et al., 2020). Again, the current study noted that the lines SV1P and CML491 combined high GYD performance with stable FAW resistance across environments (see Table 5.5 and Figure 5.4). This suggests that the two local lines can be effectively used in further breeding for FAW resistance as they are likely to produce progenies that combine enhanced stable FAW resistance with adaptation. The exotic donor lines G50 (CML67), G53 (CML346), C55 (CML121) and G47 (CML338) exhibited very low FFAWD damage scores and their performance were consistent across environments (see Figure 5.4). The lines can be good FAW donor lines in introgression of FAW resistance into local lines.

5.5 Conclusions

The commercial cultivar Mutsa-MN521 and the experimental hybrid CimExp55/CML334 were identified as the FAW resistant hybrids combining adaptation and stability across FAW infested environments. Other acceptable hybrids were identified as 113WH330, Manjanja-MN421, CML338/CML334 and PAN53. The local inbred lines SV1P and CML491 combined adaptability and stable FAW resistance across environments. The best exotic donor lines combining good FFAWD resistance with stable FFAWD resistance across environments were identified as CML67, CML346, CML121 and CML338. Harare and Gwebi were identified as the most discriminating and representative sites that can be used for quick screening of good GYD performers under natural FAW infestation for both lines and hybrids/OPVs. Kadoma and Rattray-Arnold Research Stations were identified as the most discriminating environments for FFAWD among inbred lines. Harare was also identified as a discriminating environment both under natural infestation as well as under managed FAW conditions.

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Chapter 6

Exploring the use of mutation breeding in maize for the development novel maize genotypes with resistance to fall armyworm

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Abstract

Mutation breeding has been used successfully worldwide to generate crop varieties with various traits, including pest resistance. Before any mutation breeding is initiated, radio-sensitivity tests need to be conducted to determine optimum doses for mutagenesis. In this study, radio-sensitivity tests were conducted on three maize (*Zea mays* L.) genotypes with six gamma irradiation doses. Highly significant effects of mutagenesis on days to seedling emergence, emergence percentage and seedling height were observed. Regressing seedling height on gamma ray doses estimated the lethal dose 50 for the three varieties. The study showed that maize seeds are responsive to gamma irradiation and optimal doses can be used to generate novel genetic variability for effective breeding. Doses with high relative biological effectiveness for mutation breeding ranged from 160 gy – 275 gy.

6.1 Introduction

Maize (*Zea mays* L.) is the most important cereal crop cultivated and consumed in Zimbabwe and other sub-Saharan Africa (SSA) countries (Magorokosho et al. 2003; Edmeades et al. 2017). Globally, maize is cultivated on an average of 181 million hectares annually (VIB, 2017), with an estimated production of more than one billion metric tons (Kornher, 2018). In SSA, the crop is planted on 25 to 29 million hectares out of the estimated 200 million hectares (Badu-Apraku & Fakorede, 2017; IITA, 2020). Approximately 38 million metric tons is produced annually in SSA (Setimela et al. 2017; Nyaga et al. 2020). Regardless of its importance as a food-security crop, the majority of

farmers in Africa often attain very low yields, averaging around 1.5 to 2.0 t ha⁻¹ (Lyddon, 2018; Setimela et al., 2017).

Despite decades of research and crop improvement efforts on maize, production constraints continue to cause significant economic losses (CIMMYT, 2019; IITA, 2019). Biotic stresses (particularly weeds and insect pests) and abiotic stresses (especially heat, drought and low soil fertility) are the major constraints reducing maize productivity and ultimately affecting food security (Fahad et al., 2017; Lamaoui et al., 2018). Demand for maize is estimated to increase with the rise in global population and the reduction in area that is suitable for agriculture (Cairns et al., 2013; Ekpa et al., 2018; Santpoort, 2020), yet maize production constraints are expected to surge because of climate change. Climate change is a factual and pressing global problem affecting crop production (Mulungu & Ng'ombe, 2019). Currently, fall armyworm (*Spodoptera frugiperda*; FAW) is considered the worst insect pest of maize in SSA, since it was first observed in 2016 (Abrahams et al., 2017; Kasoma et al., 2020; Matova et al., 2020) and maize lethal necrosis (MLN), the most devastating disease in East Africa (Nyaga et al., 2020). Therefore, developing maize suitable for these production challenges is vital.

Deployment of innovative techniques, such as mutation breeding, may be a viable option to develop novel maize genotypes resistant to emerging production stresses. Mutation breeding creates chances for development of new alleles, new allelic combinations or enhancement of those currently existing in the maize gene pool (Mba et al. 2010; Spencer-Lopes et al. 2018). Mutations are the primary source of evolution and they happen spontaneously with very low frequencies (Oladosu et al., 2016; Shu, 2009; van Harten, 1998). Nuclear techniques in plant mutation breeding play a key role in enhancing the occurrence and frequency of beneficial mutations. Mutation breeding has been practiced in many crops across the globe and more than 3000 crop varieties with resistance to insect pests and other desirable agronomic traits, have been released for commercialization in 50 countries worldwide (IAEA, 2019; Oladosu et al., 2016). Gamma mutation induction can be used to enhance resistance of breeding materials to biotic and abiotic stresses or improve their agronomic performance.

Before engaging in a full-fledged mutation breeding programme for any crop, it is important to conduct radio-sensitivity tests to determine the optimum dose to use for

mutagenesis (Mba et al. 2010; Spencer-Lopes et al. 2018). Determination of optimal mutagen doses for use in mutagenesis is a critical step in mutation breeding programmes (Gnankambary et al., 2019). The optimum dose for mutagenesis can be described as a mutagen concentration that gives the highest number of mutations with the least number of unintended mutations, or damage (Oladosu et al., 2016). Optimum doses are also described as the mutagen quantities that give high relative biological effectiveness from a mutagenesis process (Spencer-Lopes et al. 2018). Radio-sensitivity tests have been performed on cowpea (*Vigna unguiculata* [L.] Walp) (Gnankambary et al., 2019; Horn & Shimelis, 2013), sorghum (*Sorghum bicolor* [L.] Moench) (Wanga et al., 2020), pearl-millet (*Pennisetum glaucum* [L.] R. Br.) (Ousmane et al. 2013), rice (*Oryza sativa* L.) (Gowthami et al., 2017) and other field crops, but there is no report of such studies in maize. Furthermore, there is little information on mutation breeding in maize and no optimal doses have been reported for gamma irradiation on maize seeds. The International Atomic Energy Agency (IAEA) has suggested a gamma irradiation dose range of 100 - 300 Gy for practical use (Shu et al. 2012), but there is a need to optimize gamma irradiation doses for effective use in mutation breeding for maize. This information is vital in designing an effective mutation breeding programme. In this study, the aims were to: (i) estimate the optimal dose range for gamma mutation induction in maize mutation breeding for two inbred lines and one open-pollinated variety (OPV) maize; and (ii) compare the response of the two inbred lines and one OPV to gamma irradiation. The information is critical for use in running optimized mutation breeding projects on maize particularly where there is need to develop new traits or enhance the performance of what is already there.

6.2 Materials and methods

6.2.1 Plant material, preconditioning of seeds and gamma irradiation

Elite inbred lines, WCoby1P and CLHP0003, developed by the Crop Breeding Institute (CBI) (an institute under the Department of Research and Specialist Services, DR&SS, in Zimbabwe) and HarvestPlus, respectively, and OPV ZM309 bred by CIMMYT, were used in the study. The grains of the inbred line WCoby1P are white and flint-like, whereas those of CLHP0003 are orange and hard flint. The seeds of the OPV ZM309 are white and flint to semi-flint in texture. The inbred line WCoby1P is a parental line for several hybrids in Zimbabwe and CLHP0003 is a parental line for most of the released orange

maize cultivars in Eastern and Southern Africa (ESA). The OPV ZM309 is a maize variety cultivated across many countries in southern Africa.

For each genotype, six 20 g packets, containing approximately 50 maize seeds each, were packed and dried in desiccators for three days to pre-condition them for gamma irradiation at a grain moisture content of 8%, following the method given by Spencer-Lopes et al. (2018). The six packs of seed for each genotype were labeled as 0 gy, 150 gy, 200 gy, 250 gy, 300 gy and 350 gy, and each pack was irradiated with its labeled gamma radiation dose. The 0 gy pack for each genotype was used as the control (not irradiated). Irradiation was done at the Agriculture and Biotechnology Laboratories of the Food and Agriculture Organization/International Atomic Energy Agency, as per IAEA protocols (Spencer-Lopes et al. 2018). The source of gamma rays was Cobalt 60 (^{60}Co , gamma cell model no. 220).

6.2.2 Trial site, experimental design and agronomic management

The preliminary radio-sensitivity test was performed in a greenhouse at DR&SS, Harare Research Station (HRS) in Zimbabwe in June 2018. Temperature in the greenhouse ranged from 30 to 35°C during the three-week period in which the trial was conducted. Three trials were laid out in a randomized complete block design (RCBD) with two replications. Two wooden box plots measuring 130 cm × 100 cm × 10 cm were used for each genotype. The wooden boxes were filled to a depth of 9 cm with red clay medium-grain topsoil found at HRS, mixed with compound D fertilizer (7N:14P:7K) at a rate of 400 kg ha⁻¹. For each genotype, one box constituted a replication with all six treatments (the different doses), which were randomized in each box. For each treatment, 10 seeds were planted in one-row plots, with 10 planting stations each; there were six rows per box. The boxes were watered to field capacity a day before planting; and after planting, watering was done three times a week.

6.2.3 Data collection and analysis

The following parameters were recorded per trial for each dose: (i) days to seedling emergence (DSE), (ii) number of emerged seedlings (NES) recorded at five-day intervals for 15 days, (iii) seedling height (SH), (iv) number of albino seedlings (NAS), and (v) number of abnormal seedlings (NAbS). Albino seedlings represent young plantlets

without chlorophyll in their leaves or in both the leaves and stem, giving them a characteristic yellow color. Abnormal seedlings usually fail to develop or open leaves, and do not grow. The collected phenotypic data were expressed as a percentage of the parental control (0 gy). Data were subjected to general ANOVA using Genstat Discovery Software V18.0 (VSN International, 2017). Where results were significant, means were separated using a Tukey multiple comparison test in the Genstat Discovery Software (VSN International, 2017). Box plots were also generated for DSE, NES and SH data in response to irradiation using the mutant generation 1 mutants of the three different maize genotypes (ZM309, CLHP0003 and WCoby1P), using the 'ggplot' function in the ggplot2 v3.0.0 R package (Wickham, 2016). SH data as a percentage of the control (0 gy dose) were regressed against gamma ray doses. The lethal dose 50 (LD₅₀) for each genotype was estimated using the following simple linear regression model: $y = mx + c$ where y is the response variable (SH as a percentage of the control), x is the independent variable (irradiation dose), m is the gradient (regression coefficient) and c is a constant (y -intercept).

6.3 Results

6.3.1 Effects of gamma mutation induction on M1 plants of three maize genotypes

Results showed significant effects of gamma irradiation (GI) ($P < 0.05$) on SH, NES and DSE in all three maize genotypes across all the doses (Table 6.1). Effects of gamma radiation on plant height were more severe at high doses than at the low doses, with the highest dose (350 gy) causing zero germination for the inbred line WCoby1P (Figure 6.1) and 100% weak and abnormal seedlings for the inbred line CLHP0003 and the OPV ZM309. The gamma irradiation dose of 200 gy caused 5% and 10% albino seedlings in genotypes CLHP0003 and ZM309, respectively.



Figure 6.1 Height differences of mutant plants of three different varieties. (A) CLHP0003, (B) ZM309 and (C) WCoby1P irradiated with five different gamma ray doses compared with the un-irradiated parental control (M0). RS test, radio-sensitivity test.

Table 6.1 Combined ANOVA for seedling heights, number of seedlings that emerged and number of days to seedling emergence expressed as a percentage of the control for three maize genotypes irradiated with six gamma ray doses

Source of variation	WCoby1P		CLHP0003		ZM309	
	DF	Mean squares	DF	Mean squares	DF	Mean squares
A. Seedling height						
Replication	1	1.87	1	0.26	1	0.52
GI doses	5	2603.99***	5	1462.60***	5	1769.66***
Residual	5	0.87	5	0.49	5	0.42
Total	11		11		11	
B. Number of seedling that emerged						
Replication	1	127.34	1	227.26	1	5.79
GI doses	5	3574.94***	5	365.78**	5	2107.64***
Residual	5	47.67	5	54.67	5	33.56
Total	11		11		11	
C. Number of days to seedling emergence						
Replication	1	0.00	1	33.33	1	0.00
GI doses	5	1134.99***	5	773.33**	5	1053.50***
Residual	5	16.53	5	33.33	5	24.69
Total	11		11		11	

GI, gamma irradiation; **, *** significant at <0.01 and <0.001 probability level, respectively.

6.3.2 Response of inbred lines and open-pollinated variety (OPV) to gamma radiation

Regression analysis of SH on gamma ray doses showed responses of ZM309, WCoby1P and CLHP0003 to the different gamma radiation doses; the respective equations were (Figure 6.2):

$$y = -0.215x + 100.059 \text{ (for ZM309; } R^2 = 0.97\text{)}$$

$$y = -0.2853x + 100.0081 \text{ (for WCoby1P; } R^2 = 0.96\text{)}$$

$$y = -0.2361x + 101.1892 \text{ (for CLHP0003; } R^2 = 0.96\text{)}$$

For each genotype, the respective equation can be used to determine the irradiation dose for a target lethal dose. The regression coefficients (slopes) for the three equations were significant ($P < 0.0001$). The estimated LD₅₀ dose was 232.83 gy for genotype ZM309, 216.81 gy for CLHP0003 and 175.28 gy for WCoby1P.

For all three genotypes, gamma irradiation delayed seedling emergence as the doses increased from 150 gy. The delay was lowest at 250 gy (10%) and highest at 350 gy (45%) (Figure 6.3). Comparing the DSE between the irradiated and the un-irradiated plants showed that the 150 gy irradiation dose enhanced germination and seedling emergence by 5% in the inbred line CLHP0003 (Figure 6.3). However, genotypes ZM309 and WCoby1P showed contrasting results to those for CLHP0003; irradiation at 150 gy showed similar effects on DSE for the irradiated and the un-irradiated treatments (Fig. 3). The general trend for the two genotypes (ZM309 and WCoby1P) was that the number of days to seedling emergence increased as gamma irradiation dose increased above 150 gy (Figure 6.3).

However, the rate of change was higher, with a steady increase of 15 - 20% DSE, as the doses increased from 200 gy to 350 gy for ZM309, whereas DSE was slightly reduced and steady for WCoby1P for the doses 200 gy, 250 gy and 300 gy (Figure 6.3). An approximate 53% delay in DSE was, however, noted as the dose increased from 300 gy to 350 gy for WCoby1P. The dose 350 gy had its peak at approximately 65% delayed emergence compared with the control WCoby1P (dose 0 gy).

Gamma irradiation dose of 150 gy increased the NES in genotypes CLHP0003 and WCoby1P by more than 20% and 10%, respectively, compared to the respective controls (0 gy) (Figure 6.4). The same dosage reduced the NES by about 5% in ZM309. The results showed a general decrease in NES with increasing gamma irradiation dose. The pattern was, however, smooth for ZM309, whereas it varied around the parental control for WCoby1P, and it decreased NES by about 4 - 20 %, as doses increased from 200 gy to 350 gy for CHLP0003 (Figure 6.4). Irradiation doses 200 gy and 250 gy showed the same effect as the control (0 gy) on NES in CLHP0003. The irradiation dose of 300 gy did not have any effect on the NES of WCoby1P, and this result was similar to the control treatment. However, doses of 150 gy and 250 gy increased the NES by about 10% and 15%, respectively. A dose of 350 gy resulted in no seedling emergence for WCoby1P (Figure 6.4).

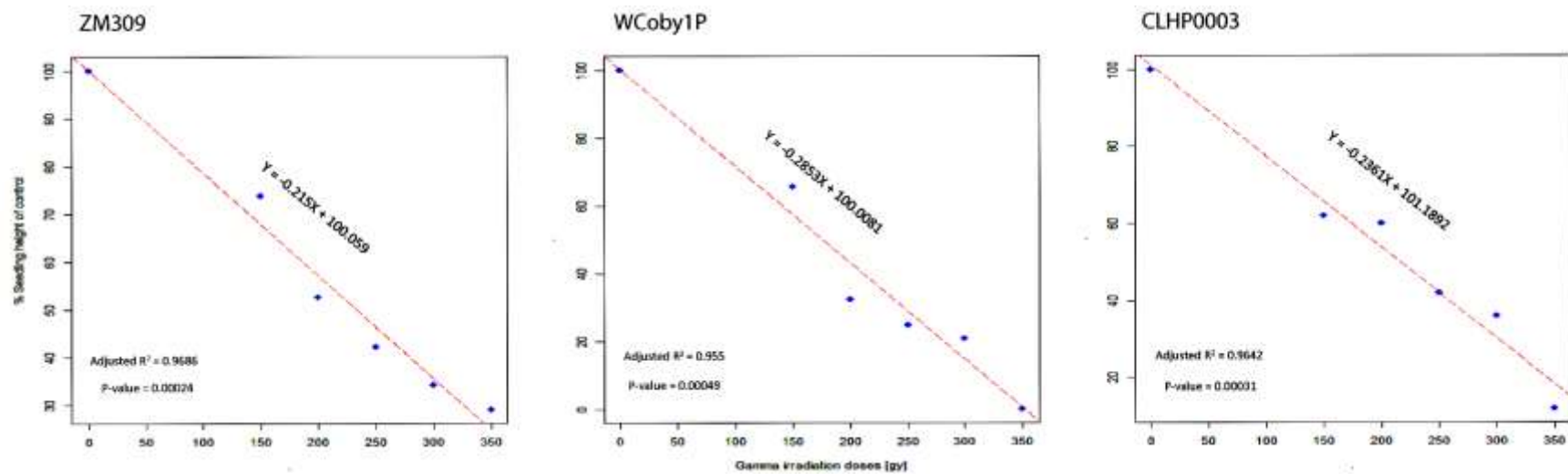


Figure 6.2 Determination of LD50 gamma ray doses on three maize varieties irradiated with 0, 150, 200, 250 and 300 gy. The blue squares are the points of convergence between the six levels of gamma irradiation doses and the percent seedling height of control. The red dotted line is the line of best fit, for interactions between gamma irradiation doses and percent seedling height of control.

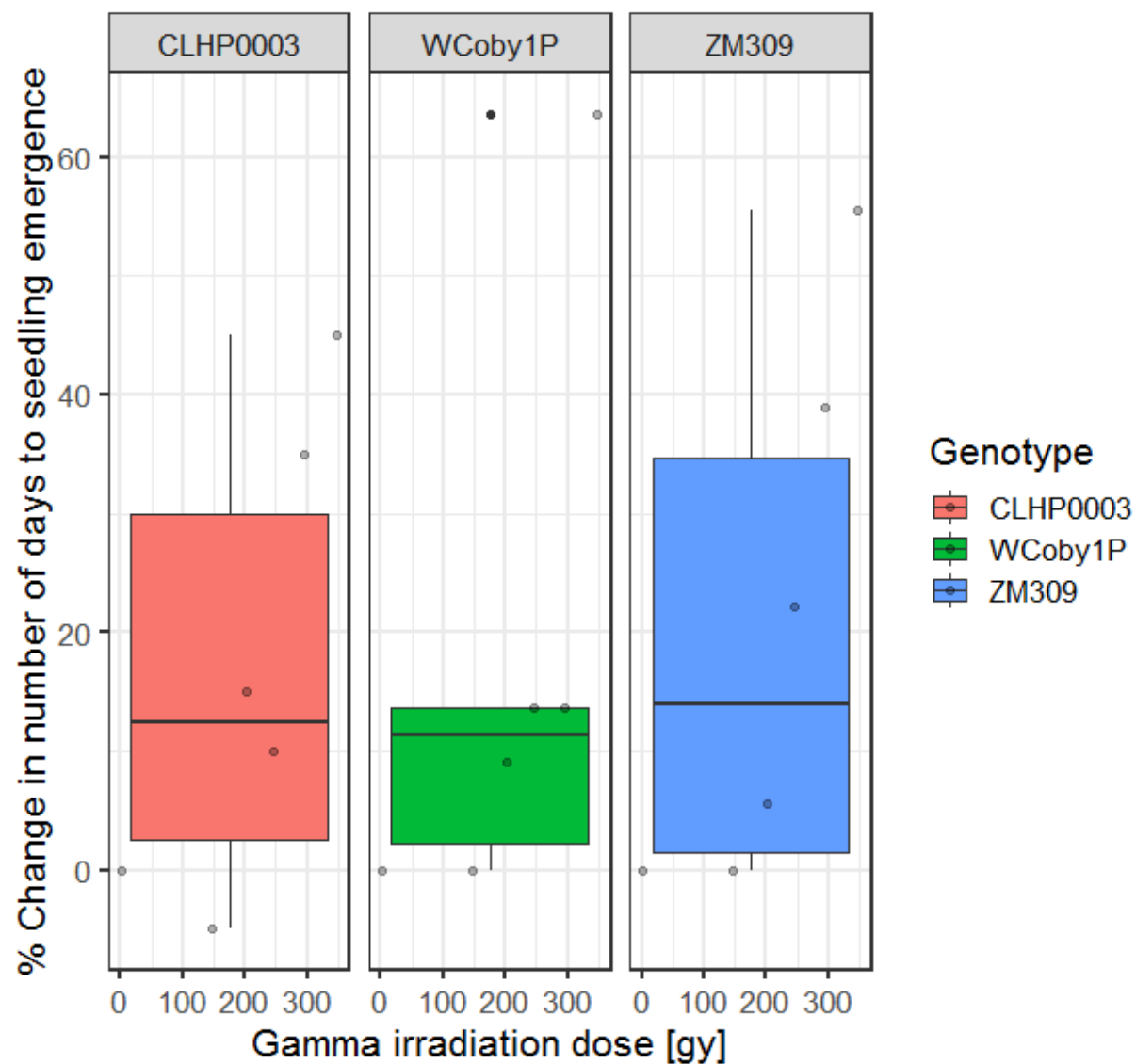


Figure 6.3 Schematic illustration of the effect of gamma irradiation on the number of days to seedling emergence of the genotypes CLHP0003, WCoby1P and ZM309. The grey dots in the boxplots denotes points of convergence between the six levels of gamma irradiation doses with the percent change in number of days to seedling emergence. The black dots represent the outlier values.

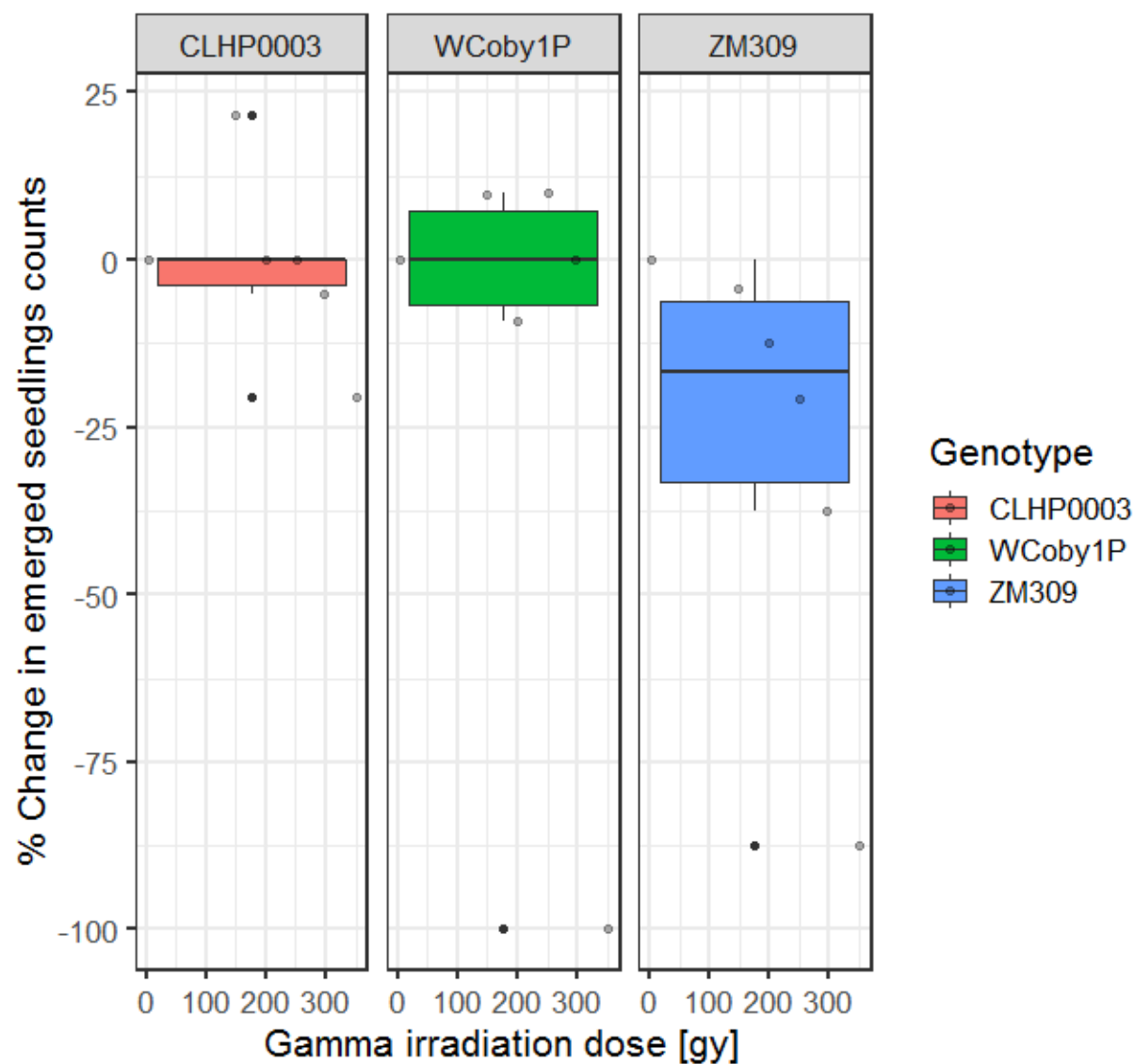


Figure 6.4 Schematic illustration of the effect of gamma irradiation on the number of seedlings that emerged after irradiation for genotypes CLHP0003, WCoby1P and ZM309. The grey dots in the boxplots denote points of convergence between the six levels of gamma irradiation doses with the percent change in emerged seedlings counts. The black dots represent the outlier values

6.4 Discussion

In this study, results from a radio-sensitivity test on three maize genotypes demonstrated that maize seeds were responsive to gamma ray mutagenesis and that maize inbred lines had a lower LD₅₀ than the OPV. Optimal gamma radiation doses for the two inbred lines and one OPV variety were also established, which were 216.81 gy (for CLHP0003) and 175.28 gy (for WCoby1P), and 232.83 gy (for genotype ZM309), respectively.

Firstly, the responsiveness of maize seeds to gamma radiation was encouraging, as it indicated the possibility of using mutation breeding techniques in generating new variation. Gamma irradiation on the three maize genotypes resulted in a general trend of decreasing relative biological effectiveness of mutant plants with increasing gamma ray doses. Similar results were also observed in cowpea by Horn and Shimelis (2013) and rice by Gowthami et al. (2017). In the current study, there was a general trend of decreasing SH, increasing DSE and decreasing NES across the three genotypes, as the irradiation doses increased from 0 gy to 350 gy. Gowthami et al. (2017) reported a reduction in germination percentage in rice, as doses increased from 100 gy to 500 gy. Similarly, Gnankambary et al. (2019) noted a decrease in germination and plant survival in cowpea, as doses increased from 150 gy to 300 gy.

The lower LD₅₀ observed for inbred lines compared to the OPV is not surprising, probably because inbred lines are generally less vigorous compared to OPVs; hence, inbred lines tended to be more sensitive to irradiation than the OPV. Again, a general lack of a consistent pattern for the NES was observed in the two inbred lines (CLHP0003 and WCoby1P), which was not the case for the OPV (ZM309). This demonstrated that inbred lines were more sensitive and less resilient to gamma irradiation, hence tended to have unstable and erratic behavior after irradiation. The gamma ray dose of 350 gy resulted in zero germination for the inbred line WCoby1P, whereas the same dose resulted in weak and abnormal seedlings in CLHP0003 and ZM309. This suggests that WCoby1P was the weakest among the genotypes. This could be attributable to its physical properties (grain color, texture and size) in contrast to those of the other two genotypes.

Physical properties including grain texture/type, size and color could have an influence on the different gamma irradiation responses obtained in this study. The large grained white flint-like

inbred line, WCoby1P, had a lower LD₅₀ of 175.28 gy compared to 216.81 gy, which was noted for the orange and hard-flint small-grained inbred line, CLHP0003. Comparing the two inbred lines (CLHP0003 and WCoby1P), it can be suggested that (i) orange colored grains were more tolerant to gamma irradiation compared to the white colored grains, (ii) flint grains were more tolerant to gamma irradiation compared to flint-like grains, and (iii) large grains were less tolerant to gamma irradiation compared to small grains. OPVs, because of their greater vigor compared to inbred lines, are naturally supposed to be more tolerant to gamma irradiation; hence, ZM309 had a higher LD₅₀. The OPV had 32.8% and 7.5% gamma ray tolerance advantage over the white flint-like inbred line WCoby1P and the orange hard flint inbred line CLHP0003, respectively.

Gamma irradiation is also influenced by target tissue factors, the genetic makeup of a variety and the process itself, which is purely random. This could have caused the differences in radio-sensitivity noted among the three maize genotypes in this study. Based on the current findings, where genotype vigor, grain color, grain size and grain texture are believed to have an effect on the radio-sensitivity of maize seeds, we suggest that future gamma irradiation in maize be guided by type of genotype, and grain colour, size and texture, among other factors, as these could affect response to irradiation. Though our results suggested that orange, small flint grains were more tolerant to gamma irradiation than flint-like white large grains, further investigations on the effect of gamma irradiation on dent compared to flint grains, grain color and size are necessary.

The overall LD₅₀ for the three maize genotypes used in this study ranged from 175 gy to 233 gy. Doses around a determined LD₅₀, as those obtained in this study, are believed to work best for mutation breeding (Mba et al. 2010; Horn and Shimelis 2013). With reference to the current study, doses ranging from 160 gy to 250 gy could be best applied for gamma ray mutation induction on maize inbred lines, whereas doses of 200 - 275 gy could be recommended for OPVs in maize mutation breeding programmes.

The current study was aimed at optimising gamma irradiation doses for inbred lines and an OPV. Optimising induction doses raises the chance of getting mutants with high relative biological effectiveness in a mutation breeding project. Higher irradiation doses are known to have highly damaging effects (Gnankambary et al., 2019), which include destruction of systems for growth

promoters, chromosomal aberrations and up-regulation of growth inhibitors (Spencer-Lopes et al., 2018). Such lethal mutations limit the success of a mutation breeding programme. Our data suggested that doses from 300 gy to 350 gy had more negative effects than beneficial ones.

On the other hand, lower mutagenesis doses have been shown to induce early germination and seedling emergence, increase germination capacity, vigor and survival, although this is normally associated with low mutation frequencies (Mba et al., 2010). Low mutation frequencies generally do not support effective breeding efforts (Spencer-Lopes et al., 2018). The current study has shown a gamma irradiation dose of 150 gy to cause a reduction in DSE and an increase in NES (Figure 6.3), demonstrating that lower level irradiation doses may enhance agronomic performance, but may not necessarily be good for effective breeding progress and genetic gains because of their low mutation inductive nature (Mba et al. 2010; Spencer-Lopes et al. 2018). However, this may not be the case in other crop species. Studies by Gwata et al. (2016) and Horn and Shimelis (2013) showed that some cowpea genotypes had a requirement of an optimal dose as low as 200 gy, and others genotypes had the same as high as 600 gy. This could have been caused by seed coat color, texture and thickness, which affect the penetration of the radiation energy into the genetic material.

Previous studies have shown that trait improvement with mutation induction is possible (Kenzhebayeva et al., 2019; Oladosu et al., 2016; Tomlekova et al., 2017). A study by Tomlekova et al. (2017) reported that x-ray mutation induction in pepper increased beta-carotene content while maintaining good levels of the other nutritional attributes of the fruits. Mutation breeding has created quite a number of novel plant traits for the benefit of mankind since the 1930s (Oladosu et al., 2016), and >3,200 elite mutant varieties have been released and registered in the IAEA mutant variety database, MVDB (IAEA, 2019). Gamma irradiation of maize materials with preferred genetic backgrounds creates chances for improvement of such genotypes into more acceptable phenotypes with enhanced resistance or tolerance to biotic and abiotic stresses and emerging challenges, such as FAW and MLN.

The current PhD study has identified donor lines that require FAW resistance enhancement such as CML139 that has been reported in Chapter 4. Spencer-Lopes et al. (2018) and Mba et al. (2010) recommended the use of mutagenesis for trait enhancement on already improved or adapted lines.

Gamma irradiation on CML139 and other exotic donor lines has potential to enhance the FAW resistance or improve disease resistance in some of the better adapted lines which includes CML334 and CML121. Again, the locally adapted lines such as SV1P and CML491 that exhibited superior grain yield performance and stable FAW resistance across environments (see Chapter 4 and 5 for details) can be irradiated to increase their FAW resistance. Genetic variation is the primary requirement for crop improvement and effective selection but sometimes it is simply not there (Cobb et al., 2019; Xu et al., 2017). Mutation breeding harbors potential to create such needed genetic traits and this has been reported in several crops (Shu et al., 2012; Shu, 2009), and there is potential to create effective FAW resistance in maize with gamma ray mutation induction.

6.5 Conclusions

This study demonstrated that gamma mutation induction can be used to generate novel variation in maize. Radio-sensitivity studies performed suggested that gamma irradiation doses of 160 gy to 250 gy can be used on maize inbred lines, whereas doses of 200 - 275 gy may be used for OPVs. It is important to recognize that different types of breeding materials require different irradiation doses and that induced mutations are random events. Grain texture, color and size may have an effect on the sensitivity of the genotype to gamma irradiation.

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Chapter 7

General conclusions and recommendations

This study concluded that fall armyworm [*Spodoptera frugiperda* (J.E. Smith); FAW] is difficult to eradicate but it can be managed. This is mainly because of its biology, physiology and ecology. The pest is polyphagous, trans-boundary and has a short life cycle which enables it to multiply fast in appropriate environments such as the SSA region. The best management strategy was suggested to be an integrated pest management (IPM) approach. The IPM strategy should involve cultural methods already being used by local farmers and strategies adopted from the Americas, all anchored by multi-trait host-plant resistance breeding. FAW resistance should be considered as a basic trait in all varieties developed for release. In breeding of such varieties, breeders need to consider not just FAW resistance but also taste and other good agronomic performance traits such that varieties developed will be market attractive. Breeding programmes across SSA need to invest in modern breeding strategies as these enable quick responses to emerging challenges such as FAW. Again, there is a need to explore new ways of enhancing genetic diversity and resistance to FAW among local and exotic materials in breeding for resistance to this pest (Matova et al., 2020, 2021).

The overall aim of the study was to investigate the potential of breeding for FAW resistance in southern Africa. This study, conducted on exotic FAW resistant lines from CIMMYT Mexico and locally adapted SSA lines proved that effective breeding for resistance to the pest is possible. Good crosses between the identified local and exotic inbred lines should be used for extraction of desirable populations/lines that combine FAW resistance and high GYD potential. Additive and dominance gene action were found to be important for the inheritance of GYD and FAW resistance. Therefore breeding methods that harness both additive and non-additive gene action should be employed for effective selection, including early generation testing for the two traits during breeding. However, a general lack of significant combining ability effects between the exotic lines and the local lines for most traits was noted with concern and it was thought to be due to their diverse backgrounds. It is therefore recommended that at least two backcrosses of the selected lines with the recurrent parent, under selection pressure will be ideal for the recovery of

desirable traits of the local female parents. Marker assisted backcrossing will be the most ideal, however this can only be possible after deployment of the markers.

Crosses that showed desirable SCA effects, high GYD and acceptable FAW resistance, such as CimExp5/CML345, CimExp5/CML331 and CimExp7/CML346, are recommended for further testing and possible release. There is need to hasten marker development and validation for FAW resistance breeding to save on time and cost. These could be used in forward breeding or marker assisted backcrossing (MABC) or marker assisted recurrent selection (MARS) which helps to reduce linkage drag. Rapid pure line development techniques such as doubled haploid (DH) induction should be integrated in FAW resistance breeding programmes to accelerate the development of resistant hybrids. Most countries and institutions in SSA do not have facilities for artificial infestation in screening genotypes for resistance to FAW. This has been viewed as a drawback to breeding progress on FAW resistance, however the current study has demonstrated the effectiveness of natural infestation environments. In the interim, national breeding programmes and seed houses across SSA who do not have artificial screening facilities are encouraged to make use of the natural infestation environments in the fight against FAW. It is recommended to use sites in active maize growing zones as well as areas known to have high and active FAW populations.

Most conventional cultivars currently in production in Zimbabwe and southern Africa at large have shown poor resistance to FAW. The few that exhibited better performance include PAN53, ZS242A, ZS246A, Mutsa-MN521, Manajanja-MN421 and ZAP61. However, despite being susceptible to the pest, most commercial cultivars tend to yield satisfactorily under natural FAW infestation. This was a result of their vigour that enables them to grow fast and out of FAW damage over time. The commercial inbred lines SV1P, CML491, CML539, CLHP0005, CML304 and DPTY...^{*9} were identified to have good FAW resistance and are recommended for potential use in breeding for resistance to the pest. Husk cover, ear rot, anthesis date and plant height were identified to be correlated with FAW resistance. Potentially this can be used in screening genotypes with resistance to the pest. The study also noted that FAW infestation has the potential to reduce grain yield by 49 – 57%.

Stability analysis identified the commercial cultivar Mutsa-MN521 and the experimental hybrid CimExp55/CML334 as the most FAW resistant hybrids combining adaptation and stability across FAW infested environments. The hybrids 113WH330, Manjanja-MN421, CML338/CML334 and PAN53 were noted to have acceptable adaptation and stability across the same environments. The local inbred lines SV1P and CML491 had stable resistance to foliar FAW damage. Good and stable FFAWD resistance was not noted in the exotic donor lines: CML67, CML346, CML121 and CML338. Breeding populations from crosses between SV1P, CML491, CML67, CML346, CML121 and CML338 has the potential to produce locally adapted materials with enhanced FAW tolerance. Harare and Gwebi were identified as the most discriminating and representative sites for use in quick screening of maize hybrids/OPVs for good GYD performance under natural FAW infestation. Kadoma and Rattray-Arnold were identified as the most discriminating environments for FFAWD among inbred lines. Harare was also identified as a discriminating environment for FFAWD in inbred lines, both under natural infestation as well as under managed FAW conditions.

Maize mutation breeding with gamma irradiation was optimised and optimal doses were recommended as 160 gy to 250 gy for maize inbred lines and 200 - 275 gy for OPVs. Gamma mutation induction is recommended on the local lines and the exotic donor lines from CIMMYT Mexico that have been identified to be FAW resistant in this study. Breeding crosses between these inbred lines can also be irradiated with gamma rays to enhance their FAW resistance and perhaps to improve their agronomic traits and adaptation to SSA. The inbred line CML139 is agronomically good but it is slightly susceptible to the pest hence there is a chance of improvement with gamma irradiation.

List of Appendices

Appendix 3.1 - Description of F1 hybrids generated by LxT mating design

Entry#	Source	Code	Pedigree	Grain colour
1	CIMMYT	DJH172867	CML571/CML121	Yellow
2	CIMMYT	DJH172868	CML566/CML121	Yellow
3	CIMMYT	DJH172871	CimExp10/CML121	Yellow
4	CIMMYT	DJH172872	CimExp7/CML121	Yellow
5	CIMMYT	DJH172873	CimExp8/CML121	Yellow
6	CIMMYT	DJH172874	CimExp9/CML121	Yellow
7	CIMMYT	DJH172878	CimExp4/CML121	Yellow
8	CIMMYT	DJH172880	CimExp5/CML121	Yellow
9	CIMMYT	DJH172882	CimExp6/CML121	Yellow
10	CIMMYT	DJH172883	CimExp2/CML121	Yellow
11	CIMMYT	DJH172884	CimExp1/CML121	Yellow
12	CIMMYT	DJH172885	CimExp3/CML121	Yellow
13	CIMMYT	DJH172889	CML571/CML139	White
14	CIMMYT	DJH172890	CML566/CML139	White
15	CIMMYT	DJH172891	CML566/CML67	Yellow
16	CIMMYT	DJH172893	CML312/CML139	White
17	CIMMYT	DJH172894	CML312/CML67	Yellow
18	CIMMYT	DJH172896	CimExp10/CML67	Yellow
19	CIMMYT	DJH172897	CimExp7/CML139	White
20	CIMMYT	DJH172898	CimExp8/CML67	Yellow
21	CIMMYT	DJH172900	CimExp9/CML67	Yellow
22	CIMMYT	DJH172901	CimExp9/CML139	White
23	CIMMYT	DJH172907	CimExp4/CML67	Yellow
24	CIMMYT	DJH172908	CimExp4/CML139	White
25	CIMMYT	DJH172910	CimExp5/CML67	Yellow
26	CIMMYT	DJH172911	CimExp5/CML139	White
27	CIMMYT	DJH172914	CimExp6/CML139	White
28	CIMMYT	DJH172915	CimExp2/CML139	White
29	CIMMYT	DJH172917	CimExp1/CML139	White
30	CIMMYT	DJH172920	CML571/CML334	White
31	CIMMYT	DJH172922	CML566/CML334	White
32	CIMMYT	DJH172924	CML312/CML334	White
33	CIMMYT	DJH172926	CimExp10/CML334	White
34	CIMMYT	DJH172928	CimExp7/CML334	White
35	CIMMYT	DJH172930	CimExp8/CML334	White
36	CIMMYT	DJH172932	CimExp9/CML334	White
37	CIMMYT	DJH172937	CimExp4/CML334	White
38	CIMMYT	DJH172939	CimExp5/CML334	White
39	CIMMYT	DJH172942	CimExp6/CML334	White
40	CIMMYT	DJH172944	CimExp2/CML334	White
41	CIMMYT	DJH172946	CimExp1/CML334	White
42	CIMMYT	DJH172949	CML571/CML67	Yellow
43	CIMMYT	DJH172951	CimExp9/CML67	Yellow
44	CIMMYT	DJH172952	CimExp6/CML67	Yellow

Appendix 3.1 continued - Description of F1 hybrids generated by LxT mating design

Entry#	Source	Code	Pedigree	Grain colour
45	CIMMYT	DJH172953	CimExp2/CML67	Yellow
46	CIMMYT	DJH172916	CimExp1/CML67	Yellow
47	CIMMYT	DJH172954	CimExp3/CML67	Yellow
48	CIMMYT	DJH172957	CML571/CML331	White
49	CIMMYT	DJH172958	CML566/CML331	White
50	CIMMYT	DJH172959	CimExp10/CML331	White
51	CIMMYT	DJH172961	CimExp8/CML331	White
52	CIMMYT	DJH172966	CimExp4/CML331	White
53	CIMMYT	DJH172968	CimExp5/CML331	White
54	CIMMYT	DJH172970	CimExp6/CML331	White
55	CIMMYT	DJH172971	CimExp2/CML331	White
56	CIMMYT	DJH172972	CimExp1/CML331	White
57	CIMMYT	DJH172973	CimExp3/CML331	White
58	CIMMYT	DJH172976	CimExp3/CML334	White
59	CIMMYT	DJH172978	CML571/CML345	White
60	CIMMYT	DJH172979	CML566/CML345	White
61	CIMMYT	DJH172981	CML312/CML345	White
62	CIMMYT	DJH172982	CimExp10/CML345	White
63	CIMMYT	DJH172983	CimExp7/CML345	White
64	CIMMYT	DJH172984	CimExp8/CML345	White
65	CIMMYT	DJH172989	CimExp4/CML345	White
66	CIMMYT	DJH172990	CimExp5/CML345	White
67	CIMMYT	DJH172992	CimExp6/CML345	White
68	CIMMYT	DJH172993	CimExp2/CML345	White
69	CIMMYT	DJH172994	CimExp1/CML345	White
70	CIMMYT	DJH172995	CimExp3/CML345	White
71	CIMMYT	DJH172997	CML571/CML346	White
72	CIMMYT	DJH172998	CML566/CML346	White
73	CIMMYT	DJH173000	CML312/CML346	White
74	CIMMYT	DJH173001	CimExp10/CML346	White
75	CIMMYT	DJH173002	CimExp7/CML346	White
76	CIMMYT	DJH173003	CimExp8/CML346	White
77	CIMMYT	DJH173004	CimExp9/CML346	White
78	CIMMYT	DJH173009	CimExp4/CML346	White
79	CIMMYT	DJH173011	CimExp5/CML346	White
80	CIMMYT	DJH173012	CimExp6/CML346	White
81	CIMMYT	DJH173013	CimExp2/CML346	White
82	CIMMYT	DJH173014	CimExp1/CML346	White
83	CIMMYT	DJH173015	CimExp3/CML346	White
84	SEEDCO	SC608	SC608	Yellow
85	SEEDCO	SC633	SC633	White
86	SEEDCO	SC727	SC727	White
87	SEEDCO	SC719	SC719	White
88	CIMMYT	CZH15429	CZH15429	White

Appendix 3.2 – Grain yield and agronomic performance of LxT hybrids and check cultivars

Code	Genotype	GYG	AD	ASI	PH	EH	EPO	RL	SL	EPP	HC	ER	TEX	FFAWD	EFAWD
SC727	86	9.48	73.84	1.07	240.83	123.28	0.51	7.37	4.26	1.08	6.38	5.25	3.55	3.65	2.28
SC719	87	8.71	73.95	1.09	237.99	129.45	0.52	6.39	4.00	1.10	1.82	7.52	3.44	3.52	2.26
DJH172939	38	8.35	73.77	1.15	234.39	122.14	0.51	6.69	4.26	1.14	10.42	5.55	3.36	3.54	2.18
DJH172976	58	7.45	72.57	1.35	233.08	120.52	0.51	7.38	4.77	1.08	3.36	7.12	2.80	3.36	2.17
DJH172930	35	8.47	72.52	1.19	233.05	111.02	0.49	8.10	5.30	1.08	5.19	9.55	2.66	3.39	2.16
DJH172944	40	7.62	71.98	1.15	230.94	116.11	0.50	6.19	4.16	1.08	7.98	7.25	3.23	3.46	2.24
DJH172942	39	6.56	72.34	1.19	230.42	116.76	0.50	6.73	4.32	1.11	5.25	6.17	2.76	3.17	2.23
DJH172922	31	7.83	74.73	1.03	230.15	117.01	0.50	6.79	5.29	1.08	5.48	7.92	3.47	3.51	2.23
DJH172868	2	6.92	70.74	1.00	228.66	119.00	0.51	9.52	5.22	1.14	1.52	4.47	3.76	3.38	2.23
CZH15429	88	8.22	73.26	1.03	228.34	116.97	0.51	5.46	4.40	1.11	11.24	5.41	3.18	3.40	2.28
DJH172946	41	8.01	72.23	1.11	227.92	111.85	0.49	8.93	4.68	1.10	5.48	6.75	3.04	3.38	2.22
DJH172937	37	6.69	73.78	1.09	227.09	110.07	0.49	7.67	4.57	1.09	2.14	9.99	3.35	3.25	2.20
SC608	84	7.77	69.58	1.03	226.14	111.05	0.50	7.19	4.11	1.09	3.88	5.18	3.33	3.72	2.31
DJH172926	33	6.60	73.04	1.11	224.97	114.30	0.50	6.48	3.78	1.10	5.80	5.63	3.14	3.15	2.21
DJH173003	76	7.66	70.87	1.15	224.89	108.95	0.49	6.03	4.13	1.10	1.52	5.84	2.18	3.37	2.21
DJH172885	12	6.85	69.69	1.09	224.69	112.56	0.50	7.81	5.81	1.14	1.88	6.34	3.48	3.35	2.21
DJH172883	10	6.32	70.02	1.03	224.57	111.61	0.50	7.06	4.94	1.17	1.97	4.34	3.08	3.38	2.22
DJH173015	83	6.14	71.17	1.24	224.24	115.16	0.50	6.25	6.19	1.10	1.90	5.17	2.47	3.36	2.20
DJH172924	32	6.98	73.11	1.09	223.50	116.38	0.51	6.50	3.83	1.09	1.52	5.57	2.99	3.31	2.21
DJH172867	1	6.62	68.02	1.86	223.13	108.61	0.49	10.41	4.32	1.11	2.27	4.84	3.61	3.43	2.20
DJH172961	51	6.61	71.13	1.17	222.37	111.23	0.50	8.13	4.46	1.08	1.52	5.29	2.70	3.33	2.21
DJH172928	34	7.79	74.50	1.09	222.34	105.29	0.49	6.47	4.12	1.10	4.85	9.36	3.15	3.57	2.23
DJH173001	74	6.35	69.63	1.17	222.24	106.15	0.49	6.67	3.96	1.14	2.72	4.69	2.39	3.18	2.21
DJH172971	55	6.59	72.17	1.09	221.42	106.22	0.49	6.88	4.06	1.08	4.62	5.55	2.76	3.41	2.22
DJH172992	67	6.50	71.07	1.24	220.99	107.67	0.49	6.29	4.01	1.09	6.20	6.69	2.76	3.38	2.19
DJH172882	9	6.78	67.97	1.09	220.68	110.85	0.50	6.60	6.49	1.14	3.38	4.91	3.32	3.36	2.24
DJH172871	3	6.94	69.82	1.13	220.68	113.35	0.51	9.71	3.91	1.11	4.06	5.04	3.76	3.28	2.25
DJH173013	81	7.28	71.26	1.15	220.60	105.31	0.49	6.63	4.00	1.11	1.97	5.23	2.51	3.26	2.22
DJH172911	26	6.57	69.18	1.11	220.39	106.28	0.49	8.08	5.49	1.21	3.36	4.39	3.33	3.24	2.22
DJH172995	70	6.20	69.46	1.11	220.20	105.92	0.49	6.94	3.99	1.08	3.45	6.62	2.32	3.29	2.19
DJH172993	68	8.15	71.07	1.15	220.05	106.48	0.49	7.78	4.04	1.11	9.82	5.81	2.43	3.27	2.21
DJH172873	5	6.55	70.50	1.11	219.66	109.22	0.50	7.24	5.72	1.12	1.52	4.31	3.61	3.27	2.19
DJH172889	13	6.07	68.88	1.17	219.61	117.47	0.51	7.09	4.66	1.11	4.51	4.71	3.47	3.25	2.22
DJH172878	7	6.31	72.14	1.00	219.56	106.97	0.50	6.57	4.04	1.13	1.52	7.94	3.61	3.28	2.21
DJH172979	60	7.42	72.70	1.09	219.19	115.59	0.51	6.07	4.20	1.09	1.83	5.67	2.52	3.26	2.18
DJH172953	45	7.49	69.93	1.09	219.19	111.48	0.50	8.13	4.21	1.18	2.01	5.18	2.44	3.27	2.23
DJH172901	22	6.24	68.58	1.11	219.06	112.00	0.50	7.14	4.45	1.15	7.80	4.99	3.52	3.14	2.21
DJH172968	53	8.29	73.34	1.07	218.89	108.06	0.50	6.14	4.12	1.10	4.36	5.89	2.95	3.41	2.29
DJH172890	14	5.30	69.07	1.13	218.83	112.46	0.51	9.42	4.74	1.07	4.03	4.73	3.57	3.53	2.20
DJH172880	8	7.16	69.53	1.02	218.74	104.36	0.49	6.47	4.03	1.17	2.46	4.73	3.38	3.43	2.19
DJH173011	79	6.61	71.19	1.23	218.44	110.97	0.50	6.35	3.64	1.16	2.17	5.34	2.79	3.42	2.26
DJH172978	59	7.60	70.39	1.13	218.26	106.14	0.49	8.23	4.37	1.09	1.86	5.69	2.90	3.34	2.20
DJH172982	62	7.49	69.88	1.17	218.04	108.67	0.50	7.65	3.99	1.11	2.09	6.45	2.66	3.38	2.26
DJH172984	64	7.19	69.96	1.25	217.95	102.51	0.49	6.59	3.79	1.10	1.52	3.74	2.38	3.24	2.18
DJH172958	49	6.73	73.93	1.13	217.90	110.29	0.50	6.08	4.08	1.12	1.52	6.52	3.61	3.43	2.15
DJH172970	54	5.64	71.18	1.17	216.99	108.23	0.50	6.57	4.14	1.11	2.01	6.06	2.34	3.50	2.17
DJH172874	6	6.52	69.35	1.13	216.89	109.71	0.50	8.13	6.95	1.12	8.12	5.91	3.23	3.24	2.19
DJH172981	61	6.82	71.41	1.15	216.86	103.65	0.49	7.40	4.01	1.08	1.52	7.43	2.86	3.26	2.19

GYD = grain yield; AD = anthesis date; ASI = anthesis silking interval; PH = plant height; EH = ear height; EPO = ear position; RL = root lodging; SL = stem lodging; EPP = ears per plant; HC = husk cover; ER = ear rot; FFAWD = foliar fall armyworm damage; EFAWD = ear fall armyworm damage

Appendix 3.2 continued– Grain yield and agronomic performance of LxT hybrids and check cultivars

Code	Genotype	GYG	AD	ASI	PH	EH	EPO	RL	SL	EPP	HC	ER	TEX	FFAWD	EFAWD
DJH173002	75	7.84	69.53	1.13	216.22	109.33	0.50	5.95	4.08	1.10	1.52	6.67	2.51	3.36	2.17
SC633	85	6.80	71.22	1.15	216.17	108.68	0.50	7.01	3.86	1.12	8.12	13.63	3.42	3.94	2.35
DJH172972	56	7.35	71.44	1.19	216.14	102.70	0.49	6.72	5.69	1.08	2.32	5.28	2.86	3.23	2.21
DJH172894	17	6.56	71.86	1.13	215.97	115.49	0.51	8.38	4.33	1.08	1.52	8.51	3.00	3.35	2.28
DJH172966	52	6.62	72.57	1.13	215.87	102.43	0.49	7.11	4.09	1.10	4.88	6.11	3.27	3.34	2.20
DJH172891	15	5.74	72.27	1.11	215.76	110.55	0.50	8.23	5.24	1.08	2.09	5.08	3.09	3.35	2.22
DJH172990	66	8.79	70.28	1.11	215.69	110.34	0.50	6.47	4.00	1.10	11.39	5.91	2.51	3.39	2.21
DJH172897	19	5.41	69.68	1.11	215.68	108.87	0.50	7.86	4.12	1.22	2.75	6.33	3.28	3.38	2.17
DJH172932	36	7.10	71.81	1.09	215.45	104.63	0.49	6.21	4.20	1.07	2.01	7.98	2.52	3.23	2.19
DJH172998	72	5.68	73.03	1.13	215.44	109.24	0.50	5.87	3.98	1.13	1.52	5.86	2.66	3.23	2.19
DJH172884	11	5.61	71.21	1.05	215.30	110.59	0.50	9.85	5.72	1.16	1.52	4.47	3.23	3.29	2.21
DJH173009	78	5.52	72.06	1.09	215.22	110.07	0.50	7.64	4.03	1.11	1.52	6.32	2.57	3.30	2.22
DJH172983	63	8.48	71.67	1.14	215.20	104.94	0.49	8.29	4.17	1.10	3.03	7.95	2.51	3.30	2.25
DJH172994	69	7.72	70.19	1.18	215.10	104.45	0.49	6.17	4.71	1.09	2.31	6.37	2.07	3.24	2.15
DJH172896	18	7.58	69.17	1.13	214.84	100.52	0.48	6.76	4.04	1.09	1.86	4.76	3.26	3.19	2.16
DJH172917	29	6.25	68.63	1.05	214.59	109.48	0.50	8.61	5.94	1.17	2.14	5.66	3.33	3.24	2.26
DJH172957	48	5.79	71.36	1.11	214.22	103.54	0.49	6.36	4.02	1.07	1.52	5.03	2.95	3.47	2.19
DJH172898	20	5.97	70.64	1.15	213.84	103.77	0.49	8.58	5.91	1.08	1.52	6.13	2.53	3.25	2.21
DJH173004	77	6.41	70.44	1.11	213.82	106.90	0.50	6.32	4.19	1.46	1.52	6.99	2.14	3.21	2.20
DJH172920	30	6.81	71.01	1.25	213.60	101.92	0.49	6.57	4.65	1.06	2.27	6.07	3.38	3.41	2.25
DJH172908	24	6.86	71.56	1.09	212.95	108.86	0.50	9.05	4.09	1.11	1.52	5.35	3.57	3.25	2.22
DJH172959	50	6.58	71.27	1.23	212.94	101.69	0.49	6.21	3.99	1.08	2.59	7.90	3.13	3.33	2.19
DJH172914	27	6.89	69.19	1.13	212.91	107.72	0.50	8.99	6.21	1.19	2.20	5.53	3.18	3.39	2.28
DJH173012	80	5.76	70.01	1.19	212.79	102.80	0.49	6.03	4.74	1.10	1.52	5.07	2.09	3.29	2.17
DJH172893	16	5.78	69.53	1.07	212.39	106.71	0.50	7.90	4.09	1.17	1.52	4.21	3.33	3.25	2.22
DJH173000	73	5.78	70.51	1.17	212.10	105.60	0.50	7.00	3.99	1.10	1.52	7.27	2.29	3.62	2.24
DJH172872	4	7.26	71.24	1.07	211.89	104.12	0.50	8.85	4.64	1.17	2.20	5.55	3.57	3.24	2.26
DJH172989	65	7.30	71.42	1.07	211.82	108.03	0.51	7.15	4.01	1.09	1.52	5.92	2.75	3.36	2.18
DJH172915	28	6.79	68.80	1.05	211.72	108.33	0.50	7.89	4.56	1.19	8.24	5.19	3.28	3.22	2.23
DJH172973	57	7.42	71.06	1.07	210.98	109.55	0.51	8.99	3.97	1.07	2.25	7.81	2.91	3.44	2.22
DJH172910	25	6.22	69.48	1.21	210.51	103.06	0.49	6.61	3.95	1.15	3.96	7.84	3.08	3.29	2.19
DJH173014	82	6.55	69.88	1.05	210.33	105.65	0.50	7.23	4.33	1.06	2.27	4.32	2.14	3.31	2.22
DJH172952	44	6.85	69.48	1.15	210.27	101.77	0.49	6.80	4.19	1.08	1.52	5.07	2.80	3.25	2.20
DJH172900	21	5.86	70.27	1.13	207.82	104.97	0.50	6.50	4.65	1.07	1.52	6.13	2.87	3.09	2.18
DJH172907	23	7.35	71.48	1.05	207.19	101.59	0.49	6.48	4.09	1.09	1.97	3.71	3.49	3.17	2.18
DJH172997	71	5.75	69.07	1.21	205.88	102.85	0.50	7.26	4.84	1.09	1.52	7.90	2.95	3.42	2.16
DJH172916	46	5.79	69.65	1.11	204.17	101.94	0.50	10.11	3.96	1.14	1.52	5.14	2.57	3.14	2.20
DJH172949	42	5.50	68.46	1.17	203.92	101.15	0.50	7.59	4.80	1.08	1.52	6.75	3.09	3.37	2.21
DJH172954	47	6.08	68.85	1.09	203.01	105.59	0.51	7.72	4.79	1.09	2.27	7.09	2.77	3.25	2.22
DJH172951	43	6.02	68.47	1.05	201.72	101.05	0.50	6.70	4.46	1.09	6.60	4.16	3.03	3.29	2.21
n Locs		4	4	4	4	4	4	4	4	4	4	4	4	4	4
n Reps		2	2	2	2	2	2	2	2	2	2	2	2	2	2
Error Var		2.92	3.52	2.71	221.48	153.75	0.00	122.72	87.86	0.23	60.16	27.12	0.18	0.24	0.20
Genotypic Var		1.23	3.08	0.06	80.15	46.43	0.00	6.42	3.90	0.01	11.20	6.03	0.26	0.04	0.01
GenxEnv Var		1.25	0.50	0.00	15.24	10.21	0.00	39.35	63.10	0.00	8.23	4.13	0.22	0.07	0.08
Location Var		1.71	51.83	0.64	437.19	162.95	0.00	65.02	24.70	0.02	3.39	0.00	0.24	1.03	0.07
Heritability		0.65	0.85	0.16	0.72	0.68	0.28	0.20	0.13	0.28	0.54	0.58	0.77	0.46	0.18
Grand Mean		6.85	70.91	1.14	218.36	108.93	0.50	7.31	4.49	1.11	3.31	6.07	2.98	3.34	2.21
LSD		3.35	3.68	3.23	29.17	24.30	0.11	21.71	18.37	0.94	15.20	10.21	0.84	0.96	0.88
CV		24.97	2.64	144.82	6.82	11.38	11.43	151.56	208.53	43.19	234.57	85.84	14.39	14.68	20.29

GYD = grain yield; AD = anthesis date; ASI = anthesis silking interval; PH = plant height; EH = ear height; EPO = ear position; RL = root lodging; SL = stem lodging; EPP = ears per plant; HC = husk cover; ER = ear rot; FFAWD = foliar fall armyworm damage; EFAWD = ear fall armyworm damage; LSD = least significant difference; CV = coefficient of variance

**Appendix 4.1 - Agronomic performance of commercial cultivars and experimental hybrids
evaluated under natural fall armyworm infestation in Zimbabwe during 2019-20 seasons**

Genotype	Name	Avg FFAWD	EFAWD	GYD t ha ⁻¹	ER	AD	PH
48	CML338/CML67	3.2	2.1	3.0	28.3	65.3	162.4
58	CimExp58/CML121	3.6	1.9	3.2	27.6	67.3	180.2
57	CimExp57/CML345	3.8	2.2	2.9	32.1	68.9	172.0
49	CML338/CML334	3.9	2.0	3.5	27.1	69.5	182.7
60	CML571/CML338	3.9	2.2	3.6	33.9	65.9	178.6
53	CimExp53/CML345	4.1	2.0	3.2	31.9	67.6	172.8
56	CimExp56/CML334	4.2	2.3	3.0	29.4	70.6	179.0
20	ZS242A	4.2	2.7	3.3	26.8	67.3	178.7
55	CimExp55/CML334	4.2	2.2	3.8	30.8	71.9	179.1
51	DJ271-28	4.2	2.2	3.0	28.0	66.5	174.8
54	CimExp54/CML334	4.3	2.4	3.3	27.2	71.2	173.7
59	CML543/CML334	4.3	2.3	3.5	42.5	71.0	188.8
21	ZS246A	4.3	2.6	3.5	28.9	66.1	173.1
52	CimExp52/CML139	4.4	2.2	3.5	29.8	68.1	175.2
40	Mutsa MN521	4.4	2.8	4.0	29.4	67.5	176.5
39	Manjanja MN421	4.5	2.7	3.4	29.1	64.5	160.2
14	ZS269	4.5	2.5	3.3	30.8	70.5	173.8
9	ZS255	4.5	2.9	2.4	37.8	67.7	171.2
10	ZS259	4.5	3.1	1.9	37.4	64.6	162.9
27	ZM421	4.6	2.5	2.2	30.8	65.4	165.3
31	PAN53	4.6	2.4	4.4	29.5	68.2	181.9
24	113WH330	4.6	2.5	3.5	25.2	69.4	177.9
29	CZH128	4.6	2.3	4.0	28.8	66.3	176.4
44	ZAP61	4.6	2.9	3.5	28.2	66.2	183.5
15	ZS271	4.6	2.7	3.2	31.1	70.9	182.4
18	ZS225	4.7	2.6	2.4	31.4	72.9	155.3
28	ZM521	4.7	2.4	2.3	31.3	63.8	171.1
50	CML331/CML67	4.7	2.4	2.7	32.7	70.1	168.6
36	Shasha302	4.7	2.6	2.6	30.6	69.3	172.4
34	ComCultivar1	4.7	2.4	3.3	29.4	67.5	187.3
25	ZM309	4.7	2.8	2.2	27.4	66.1	156.7
26	ZM401	4.8	2.8	2.2	31.4	64.3	153.8
38	SeedCo-Exp2	4.8	2.7	4.0	29.8	66.1	180.8
13	ZS265	4.8	2.5	3.7	26.0	69.5	172.0
23	093WH123	4.8	2.6	2.3	30.1	68.7	169.1
47	ComCultivar2	4.8	2.5	3.5	29.2	68.6	171.0
17	ZS275	4.8	2.8	2.5	34.0	68.7	174.6
30	ComCultivar3	4.8	2.9	3.3	29.2	66.3	179.4
7	ZS107	4.8	2.7	1.6	44.9	72.0	183.0
45	ComCultivar4	4.9	2.3	3.7	26.5	68.8	186.1
43	ComCultivar5	4.9	2.5	3.1	29.0	68.7	168.1
19	SR52	5.0	2.6	1.5	39.5	71.3	169.2
35	ComCultivar6	5.0	2.5	2.1	33.9	66.2	148.3

Appendix 4.1 Continued - Agronomic performance of commercial cultivars and experimental hybrids evaluated under natural fall armyworm infestation in Zimbabwe during 2019-20 seasons

Genotype	Name	Avg FFAWD	EFAWD	GYD t ha ⁻¹	ER	AD	PH
4	R200	5.0	2.5	1.0	38.3	69.9	153.8
2	Southern cross	5.0	2.9	1.8	46.7	71.7	156.4
37	SeedCo-Exp1	5.0	2.4	2.7	30.2	66.6	180.4
12	ZS263	5.0	3.0	3.0	33.8	67.6	168.7
42	ComCultivar7	5.0	2.6	4.4	26.8	69.6	168.6
3	Hickory king	5.1	3.0	1.4	50.4	70.5	180.2
22	093WH03	5.1	2.8	2.8	28.7	69.6	171.1
11	ComCultivar8	5.1	2.8	3.1	30.9	69.4	169.1
33	ComCultivar9	5.1	2.7	3.8	27.7	70.2	180.8
46	ComCultivar10	5.1	2.3	3.3	32.1	68.2	174.3
32	ComCultivar11	5.1	2.4	4.1	31.5	68.7	172.6
41	ComCultivar12	5.2	2.3	3.5	30.2	69.9	174.9
5	R201	5.2	2.8	2.0	38.7	69.0	165.7
16	ComCultivar13	5.2	2.4	2.7	34.6	69.8	174.1
6	R215	5.2	3.0	1.9	42.1	67.8	169.4
8	ZS240	5.3	NA	2.5	NA	NA	154.4
1	Salisbury white	5.5	2.8	1.5	47.5	70.6	178.0
No. Locations		12	8	10	6	10	10
No. Replications		2	2	2	2	2	2
Heritability		0.87	0.62	0.85	0.50	0.85	0.80
Grand Mean		4.70	2.54	2.90	32.63	68.45	171.48
LSD		1.47	1.77	2.16	35.50	7.46	37.07
CV		15.98	35.61	38.02	55.52	5.56	11.03

Avg-FFAWD = average foliar fall armyworm damage; EFAWD = ear fall armyworm damage; GYD = grain yield; AD = anthesis date; ER = ear rot; PH = plant height; CML = CIMMYT maize line; CimExp = CIMMYT Experimental line; ComCultivar = commercial cultivar