INVESTIGATION OF THE GENETIC BASIS OF HIGH YIELD POTENTIAL OF A NEW MAIZE HYBRID, “ExpHybrid6”

By

Phanuel Farai Senzere

Diploma in Agriculture (Chibero College of Agriculture, Zimbabwe)
B.Sc. Hons, Crop Science (University of Zimbabwe, Zimbabwe)

A dissertation submitted in fulfilment of the requirements for the degree of
Master of Science in Plant Breeding

School of Agricultural, Earth and Environmental Sciences
College of Agriculture, Engineering and Science

UNIVERSITY OF KWAZULU-NATAL
INYUVESI YAKWAZULU-NATALI

South Africa
December 2023

ABSTRACT

With the world population expected to reach 9 billion by 2050, implying that crop yields must be increased to meet the demand for more food due to this population increase. However, space for agricultural activities is shrinking, hence expanding area under cultivation will not be possible to solve food shortages. Increased maize yields, for example, can be realized through increased genetic gain through the development of new hybrids. It is, thus, important to determine the basis for genetic gain in maize hybrids in order to devise suitable breeding strategies for continuous improvement of yield. The first experiment, was aimed at confirming the comparative advantage of new maize hybrids over the old ones by running a trial involving eight commercial hybrids; two old (control) and six new hybrids. These were evaluated in a randomised complete block design (RCBD) replicated twice across two sites in Zimbabwe, during the 2021/2022 summer season. The hybrids were significantly different ($P<0.05$) for grain yield and other traits. There were no significant differences ($P >0.05$) among hybrids for anthesis-silking interval, and grey leaf spot (GLS). Old hybrids were inferior in terms of foliar diseases rating. The new hybrid, ExpHybrid6, displayed the highest grain yield and cultivar superiority index (CSI). It exhibited 2.41% yield advantage with respect to the trial mean and 7.59% over the old hybrids. This hybrid was, therefore, subjected to a generation mean analysis (GMA) in the second experiment to determine the basis of its advantages. The experiment was undertaken to specifically understand the gene action governing grain yield and secondary traits in this best performing new single cross hybrid, designated as ExpHybrid6. Six populations including parents (P_1 and P_2), F_1, F_2, and backcross generations (BCP_1 and BCP_2) were evaluated in a RCBD, during 2020/2021 and 2021/2022 summer seasons, in Zimbabwe. Analysis of the generations using the PROC GLM function in the SAS computer software program version 9.4 showed significant differences among generations for all the traits. The dominance and additive gene effects were highly significant ($P<0.01$) for both grain yield and secondary traits. Epistatic gene effects were significant ($P<0.001$) in the additive x additive form for grain yield. Duplicate type of epistasis was observed for most traits. However, dominance gene effects were the most prominent. Mid-parent heterosis for grain yield potential was confirmed at 171%. It was, therefore, established that the basis for high grain yield potential of the ExpHybrid6 is dominance gene action, implying that heterosis breeding should be continued in developing new productive hybrids in the maize breeding program.

DECLARATION

I, Phanuel Farai Senzere, declare that:

1. The research reported in this dissertation, unless indicated otherwise, is my original research.
2. This dissertation has not been submitted for any degree examination at any other university.
3. This dissertation does not contain other person's data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other researchers. Where other published sources have been quoted, then:
    a. Their words have been rewritten with the general information attributed to them being referenced.
    b. Where their exact words have been used, their writings has been placed in italics and inside quotation marks, and referenced.
4. This dissertation does not contain text, graphics or tables copied and pasted from the internet, unless specifically acknowledged, and the source being acknowledged.

Signed

[redacted]

…………………………………………………Date: 05 December 2023
Phanuel Farai Senzere

As the candidate's supervisor, I agree to submission of this thesis:

[redacted]

16/12/2023

…………………………………………………Date…………………………………………
Professor Julia Sibiya (Supervisor)

…………………………………………………Date…………………………………………..
Professor John Derera (Co-Supervisor)

ACKNOWLEDGEMENTS

I am grateful and indebted to Seed Co Limited management, heads of departments and support staff at Seed Co Stapleford, Stapleford Research Centre (SRC) and Rattray Arnold Research Station (RARS) who assisted with trial management. I appreciate the love, support and encouragement from my dear wife Lixieter Senzere, my daughters Mikayla and Alisha, parents (Mrs G Senzere; Mr and Mrs Khumalo), colleagues, siblings Kevin, Stanford and Sylvia, and friends. Special mention goes to Professor Sibiya and Professor Derera for guidance throughout the study period, and Dr Cousin Musvosvi for assisting with analysis of data and interpretation.

DEDICATION

Dedicated with affection to my spouse *Lixieter* and daughters *Mikayla* and *Alisha.*

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

LIST OF ABBREVIATIONS

A	Additive
AA	Additive-Additive
AD	Additive-Dominance
ANOVA	Analysis of Variance
BCP1	Backcross to parent one
BCP2	Backcross to parent two
BPH	Better Parent Heterosis
Bt	*Bacillus thuringiensis*
CD	Cob diameter
CIMMYT	International Maize and Wheat Improvement Center
CSI	Cultivar Superiority index
D	Dominance
DD	Dominance-Dominance
DPS	Days to pollen shedding
DSE	Days to silk emergence
DTMA	Drought Tolerant Maize for Africa
ED	Ear diameter
EH	Ear Height
EL	Ear Length
F1	First filial generation
F2	Second filial generation
FAO	Food and Agricultural Organization of the United Nations
FW	Field weight
GCA	General combining ability
GLS	Grey Leaf Spot
GM	Genetically Modified
GMA	Generation Mean Analysis
GW	Grain weight
HKW	Hundred Kernel weight
HT	Herbicide Tolerant
KD	Kernel depth
KER	Kernels per row

KPE	Kernels per ear
KRN	Kernel row number
LAI	Leaf Area Index
LCC	Leaf Chlorophyll Concentration
MLND	Maize Lethal Necrosis Disease
MOI	Moisture content
MPH	Mid-Parent Heterosis
MSV	Maize streak virus
N	Nitrogen
NCLB	Northern Corn leaf Blight
NL	Number of leaves
NLAE	Number of leaves above uppermost ear
OPV	Open-pollinated variety
PH	Plant height
QTL	Quantitative Trait Loci
RARS	Rattray Arnold Research Station
SADC	Southern Africa Development Community
SCA	Specific combing ability
SHL	Shelling percentage
SRC	Stapleford Research Centre
SSA	Sub-Saharan Africa
TBN	Tassel branch number
USA	United States of America
WEMA	Water Efficient Maize for Africa

CHAPTER 1
INTRODUCTION

1.1 Background

Maize (*Zea mays* L.) is a staple and principal crop for food security in Zimbabwe, South Africa, and the rest of sub-Saharan Africa (SSA). Despite maize being introduced in Africa in the 16th century it is grown throughout the continent over approximately 35 million hectares (Ndebeh and Akromah, 2017), which constitutes 50% of total cropping land in the region (Musundire et al. 2021). It is also the number one yielding cereal in the world (Musimwa and Derera, 2017) and according to Erenstein et al. (2022), maize will be the most grown cereal crop by 2030.

Maize is capable of growing in diverse conditions making it popular in Africa (Haruna et al. 2017). In Zimbabwe, it is grown throughout the country (Setimela et al. 2014), irrespective of whether the conditions are suitable or not. However, Zimbabwe's average maize yield was reported to be 1.4 t ha^{-1} (ZimFact 2021), which falls below the SSA average of 1.5 t ha^{-1} (Erenstein et al. 2022). Cairns et al. (2013) cautioned that some decrease in yield gains due to various factors are threatening future food security, especially in SSA. Low average maize yield has been attributed to factors such as poor quality germplasm presently used to develop new varieties in maize breeding programs and the effect of various stresses, both biotic and abiotic (Mushayi et al. 2020).

Maize production and productivity varies among countries. For example, in 2021, Zimbabwe produced 1.4 million tonnes from 957 000 hectares (1.5 t ha^{-1}), while South Africa harvested 16.8 million tonnes from 3.1 million hectares (5.4 t ha^{-1}), and Ethiopia harvested 10.7 million tonnes from 2.5 million hectares (4.3 t ha^{-1}) (FAOStat 2023). These observed production and productivity gaps have been attributed to varying soil types, low soil nutrient status, failure by farmers to follow good agronomic practices and failure to adopt new technologies in some instances (Bernard et al. 2011; Kafle, 2010; Sileshi et al. 2010). Furthermore, most rural farmers are resource poor and as such cannot meet the requirements of improved hybrids. On the other hand, the adoption of genetically modified (GM) maize by Republic of South Africa has greatly improved yields (Ala-Kokko et al. 2021). However, not all countries are fully supportive of this GM technology due to myths surrounding it (Engel et al. 2002). With the world population expected to rise to 9 billion by 2050, implying that maize yields have to increase double to meet the demand for more food to match the population increase. In addition, land for agricultural activities continues to decrease, as urbanization increases, hence expanding area under cultivation will not be possible to solve maize shortages (van Dijk et al. 2021). Therefore, increased food yields can be realized through increased genetic gain in new hybrids. It is, thus, important to determine the basis for genetic gain in these high yielding emerging maize hybrids, to devise suitable breeding strategies for continuous improvement of yield. Various mating designs, including generation mean analysis (GMA), North Carolina Design II, diallel and line by tester methods can be used for this purpose. It is, however, preferable in this case to utilize GMA, since it provides a measure of the relative importance of the average effects of the genes (additive effects), dominance deviations, and effects due to non-allelic gene interactions (Pujar et al. 2022; Viana, 2000), separating the effects into fixable and non-fixable ones. Furthermore, GMA enables selection of an appropriate breeding procedure and estimation of genetic advance since the genetic system governing traits will be unmasked. Measuring genetic gain will enable breeders to evaluate their breeding programs and make informed decisions.

1.2 Problem statement

The world's first commercial single cross maize hybrid was SR52 bred in Zimbabwe (then Rhodesia) (Alumira and Rusike, 2005) and it succeeded in east and southern Africa. Its parents form the basis of major heterotic patterns in SSA (Musimwa and Derera, 2017; Sibiya et al. 2011). The single cross hybrid, ExpHybrid6, under study possesses similar attributes to those of SR52 but the basis for its exceptional yield has not been studied yet. Both hybrids are late maturing and high yielding. For that reason, the genetic and yield basis needs to be exploited since no such information is available at the moment in spite of its exceptional yield potential.

Understanding the genetic basis of yield for single cross hybrids will enable breeders to use the parental lines in developing better new lines and creating new combinations. Investigating gene actions would provide information valuable in reviewing the breeding approaches with the objective of developing new lines from this hybrid. Direct selections for maize is difficult, as yield is a complex trait, polygenically inherited and influenced greatly by the environment and genotype x environment x management interactions. Selection of secondary traits associated with grain yield can, therefore, be employed to improve selection efficiency for the grain yield (Tengan et al. 2012).

Both inter and intra-allelic interactions can be examined using generation mean analysis (GMA). For GMA to be effective, divergent homozygous parents are needed, that is, all the favourable alleles should be in one parent and unfavourable alleles in the other (Mather and Jinks, 1977). The hybrid understudy fulfils the requirements of GMA as it was developed using inbred lines which are both different and homozygous.

1.3 Research objectives and justification

The principal objective was to compare ExpHybrid6's yield ability relative to other old and new commercial hybrids and to further examine the genetic effects contributing to its yield by means of GMA. Results from this study shall be used in the selection of superior cross combinations in the hybrid maize breeding. Results shall also be exploited in creating high yielding and modified versions of the same hybrid. Information on gene interactions governing yield would be used to exploit effectiveness of breeding programs.

1.3.1 Specific objectives

The specific objectives of the study were:

1. To confirm the relative yield advantage of ExpHybrid6 over eight commercial hybrids comprising old and new hybrids.
2. To determine the gene action governing grain yield and secondary traits in the new single cross hybrid ExpHybrid6.
3. To determine the role of epistasis in performance of ExpHybrid6.
4. To review literature on relevant topics related to maize production, gene action and epistasis.

1.3.2 Research hypotheses

The following hypothesis were tested:

1. ExpHybrid6 has a yield advantage over old and other new commercial hybrids.
2. Dominance gene effects are responsible for ExpHybrid6's high yield performance.
3. There is high heterosis in ExpHybrid6 single cross maize hybrid, influenced by epistasis.

1.4 Dissertation outline

This dissertation consists of five standalone chapters (introduction, literature review, two experimental chapters and general discussion/conclusion). As such unavoidable repetitions may be found with ideas and concepts overlapping mainly on introductions and references. Style of referencing used is based on the Crop Breeding and Applied Technology as found in Mendeley reference manager and references appear at the end of each chapter. Table 1.1 gives a brief outline of the chapters.

Table 1- 1: Dissertation outline

Chapter	Title
1	Introduction to dissertation
2	Review of literature
3	Relative yield advantage of ExpHybrid6 over old hybrids.
4	Generation mean analysis for yield and yield components of maize hybrid ExpHybrid6.
5	Summary of research findings and recommendations.

References

Ala-Kokko K, Lanier Nalley L, Shew AM, Tack JB, Chaminuka P, Matlock MD and D'Haese M (2021) Economic and ecosystem impacts of GM maize in South Africa. Global Food Security 29: 100544.

Alumira J and Rusike J (2005) The Green Revolution in Zimbabwe. The Electronic Journal of Agricultural and Development Economics 2: 50–66.

Bernard M, Hellin J, Nyikal R and Mburu J (2011) Determinants for Use of Certified Maize Seed and the Relative Importance of Transaction Costs. Journal of Gender, Agriculture and Food Security 1: 1–22.

Cairns J., Hellin J, Sonder K, Araus J., Macrobert JF, Thierfelder C and Prasanna BM (2013) Adapting maize production to climate change in sub-Saharan Africa. Food Security 5: 345–360.

Engel K, Frenzel T and Miller A (2002) Current and future benefits from the use of GM technology in food production. 127: 329–336.

Erenstein O, Jaleta M, Sonder K, Mottaleb K and Prasanna BM (2022) Global maize production, consumption and trade: trends and R&D implications. Food Security 14: 1295–1319.

FAOStat (2023) Food and Agriculture Statistics | FAO | Food and Agriculture Organization of the United Nations. Available at <https://www.fao.org/food-agriculture-statistics/en/> Accessed on April 11, 2023.

Haruna A, Adu GB, Buah SS, Kanton RAL, Kudzo AI, Seidu AM and Kwadwo OA (2017) Analysis of genotype by environment interaction for grain yield of intermediate maturing drought tolerant top-cross maize hybrids under rain-fed conditions. Cogent Food and Agriculture 3: 1–13.

Kafle B (2010) Determinants of Adoption of Improved Maize Varieties in Developing

Countries: a Review. International Research Journal of Applied and Basic Sciences 1: 1–7.

Mather K and Jinks JL (1977) Introduction to Biometrical Genetics Introduction to Biometrical Genetics. Chapman and Hall, London.

Meng EC, Hu R, Shi X and Zhang S (2006) Maize in China: Production Systems,Constraints and Research Priorities. 1–77p.

Mushayi M, Shimelis H, Derera J, Shayanowako AIT and Mathew I (2020) Multi-environmental evaluation of maize hybrids developed from tropical and temperate lines. Euphytica 216: 1–14.

Musimwa T and Derera J (2017) Why SR52 is such a great maize hybrid? II. Heritability, correlation and path-coefficient analyses. Euphytica 213: 1–14.

Musundire L, Derera J, Dari S and Tongoona P (2021) Assessment of genetic gains for grain yield and components from introgression of temperate donor inbred line into tropical elite maize inbred lines: II. Performance inter se. Euphytica 217: 1–25.

Ndebeh J, Akromah R and Obeng-Antwi K (2017) Genotype by environment interaction and yield stability of early maturing maize single cross hybrids at three locations in Southern Ghana. African Journal of Agricultural Research 12: 2807–2816.

Ndhlela T, Herselman L, Magorokosho C and Setimela P (2014) Genotype × Environment Interaction of Maize Grain Yield Using AMMI Biplots. Crop Science 54: 1992–1999.

Sibiya J, Tongoona P, Derera J, van Rij N and Makanda I (2011) Combining ability analysis for Phaeosphaeria leaf spot resistance and grain yield in tropical advanced maize inbred lines. Field Crops Research 120: 86–93.

Sileshi G, Akinnifesi FK, Debusho LK, Beedy T, Ajayi OC and Mong'omba S (2010) Variation in maize yield gaps with plant nutrient inputs, soil type and climate across sub-Saharan Africa. Field Crops Research 116: 1–13.

Tengan KL., Obeng-Antwi K and Akromah R (2012) Genetic variances , heritability , and correlation studies on selected phenotypic traits in a backcross breeding program involving normal and Opaque-2 maize. Agriculture And Biology Journal Of North America 3: 287–291.

Xu Y, Li P, Zou C, Lu Y, Xie C, Zhang X, Prasanna BM and Olsen MS (2017) Enhancing Genetic Gain in the Era of Molecular Breeding. Journal of experimental botany 68: 2641–2666.

ZimFact (2021) Yes, Zimbabwe’s maize yield among region’s lowest, despite increased harvest . p. 2. ZimFact. Available at <https://zimfact.org/yes-zimbabwes-maize-yield-among-regions-lowest-despite-increased-harvest/> Accessed on April 26, 2023.

CHAPTER 2

LITERATURE REVIEW

2.1 Introduction

The purpose of this review is to provide information needed to understand the study and expose gaps in the area, thereby supporting the logic behind the study. Topics relevant to the research focus are thus discussed and these include the significance of maize and maize production trends in Zimbabwe and South Africa. Furthermore, challenges affecting maize productivity in SSA are summarised. Further topics related types of maize hybrids grown in SSA, brief history of maize breeding, generation mean analysis, heterosis, heritability and genetic gain were discussed.

2.2 Significance of maize

Maize is a major staple crop used as food by almost a billion people worldwide (Mushayi et al. 2020). Musundire et al. (2019) indicated that maize has been particularly important in the SSA region where its commercial value determines the socio-political economy and political behaviour of the region. Since its introduction in Africa around 1500 AD, maize has spread across the continent over the past six centuries becoming the major source of calories and successfully replacing sorghum and millets even in areas where maize does not perform well (Haruna et al. 2017).

According to Smale et al. (2011), total land area used for maize production is approximately 25 million hectares in the SSA with a huge potential for expansion. Erenstein et al. (2022) reported that 41.2 million hectares were under maize worldwide from 2017 to 2019, producing a total of 84.7 million metric tonnes. In advanced nations, 70% is processed into stock feed, 3% consumed by humans and 27% is used as either seed, bioethanoor for industrial purposes

(Smale et al. 2011). The maize usage trend is, however, different in SSA where 80% is consumed directly by humans either as maize meal, boiled or roasted and only 12% is used for stock feed and the remaining 8% is used for industrial purposes (Ekpa et al. 2019). In America, 40% of maize is used for ethanol production and less than 10% is consumed directly by people (Ranum et al. 2014). By year 2050, food demand will surge by 60% thereby putting further burden on farming, hence the need for better yielding and climate smart maize hybrids (FAOSTAT 2022). The data in Tables 2-1 and 2-2 shows the top 20 maize growing nations in the world and in Africa, respectively. Figure 2-1 and 2-2 show the 10-year production trends in Zimbabwe and South Africa, respectively. Figure 2-3 shows the 10-year production comparison between Zimbabwe and South Africa.

Table 2- 1: Top 20 maize growing countries in the world**.**

Country	**Area harvested (ha)**	**Production (tonnes)**	**Average yield (t ha$^{-1)}$**
1. United States of America	34555670	383943000	11.11
2. China	43355859	272762124	6.29
3. China, mainland	43324100	272552000	6.29
4. Brazil	19024538	88461943	4.65
5. Argentina	8146596	60525805	7.43
6. Ukraine	5481800	42109850	7.68
7. India	9860000	31650000	3.21
8. Mexico	7139621	27503478	3.85
9. Indonesia	3495981	20010000	5.72
10. South Africa	3118300	16870705	5.41
11. France	1549520	15358300	9.91
12. Russian Federation	2901612	15239865	5.25
13. Romania	2554680	14820690	5.80
14. Canada	1390500	13983859	10.06
15. Nigeria	6000000	12745000	2.12
16. Ethiopia	2530000	10722000	4.24
17. Pakistan	1652501	10634831	6.44
18. Philippines	2564383	8300322	3.24
19. Egypt	1027057	7500000	7.30
20. Poland	998470	7321910	7.33

Source: (FAOSTAT, 2022)

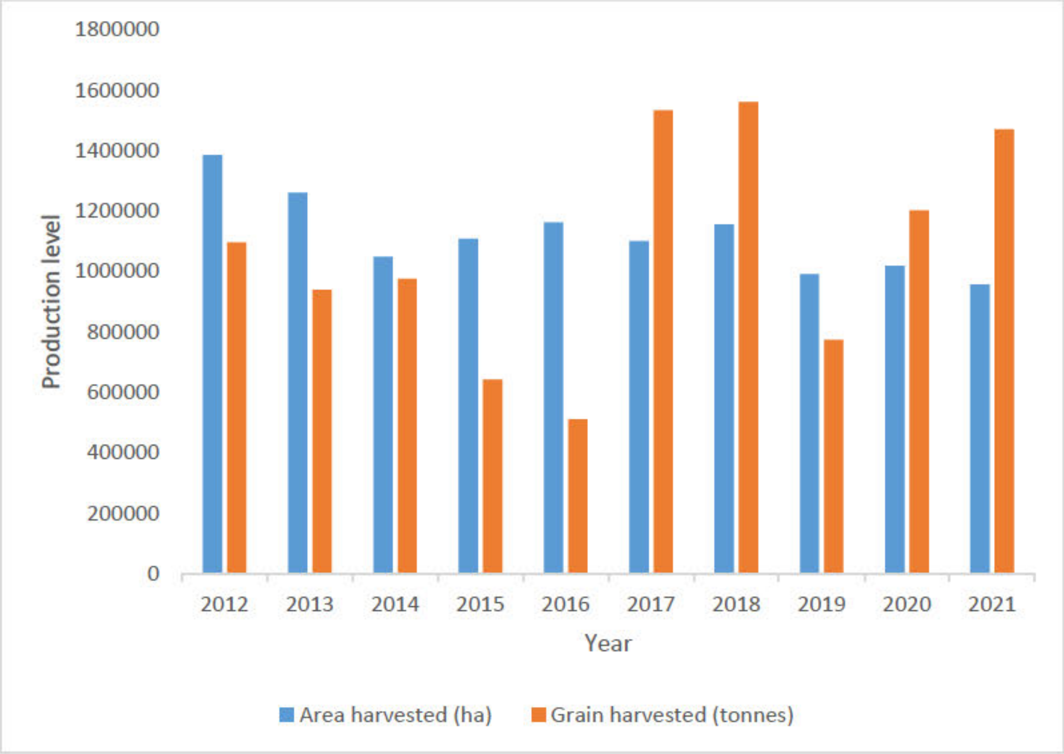
The United States of America is the global maize superpower mainly because of advanced technologies, extensive use of GM maize and the use of single cross hybrids, and improvements in agronomic practice. China's production success is largely due to technology advancement, affordability of inputs like fertilizers as well as a well-organized government support scheme (Meng et al. 2006). The adoption of improved agricultural technologies has enabled South Africa to produce more maize than France, Russia, Romania, and Canada and make it a top ten producer of maize in the world.

Table 2- 2: Top 20 maize growing countries in Africa

Country	Area Harvested (ha)	Production (tonnes)	Average yield (t ha^{-1})
1. South Africa	3118300	16870705	5.41
2. Nigeria	6000000	12745000	2.12
3. Ethiopia	2530000	10722000	4.24
4. Egypt	1027057	7500000	7.30
5. Tanzania	4400000	7039000	1.60
6. Malawi	1750000	4581000	2.62
7. Zambia	1410102	3620240	2.57
8. Mali	1536189	3603000	2.35
9. Ghana	1300000	3500000	2.69
10. Kenya	2168603	3303000	1.52
11. Angola	2741091	2970208	1.08
12. Uganda	984995	2800000	2.84
13. Democratic Republic of Congo	2903683	2243379	0.77
14. Cameroon	1186193	2100150	1.77
15. Mozambique	1870000	2100000	1.12
16. Burkina Faso	1109744	1913000	1.72
17. Benin	1349543	1628149	1.21
18. Zimbabwe	957793	1469664	1.53
19. Côte d'Ivoire	518794	1140000	2.20
20. Togo	750000	929000	1.24

Source: (FAOSTAT, 2022)

According to Musundire et al. (2021) most South African farmers grow single cross maize hybrids and this has resulted in high productivity. Nigeria's productivity is mainly driven by the large acreage planted to maize, due to its high population. Despite having the highest area under maize in Africa, Nigeria's production is hindered by low average yields per hectare (2.2 t ha^{-1}) against South Africa's 5.4 t ha^{-1}and Ethiopia's 4.2 t ha^{-1}(FAOSTAT 2022). About 43% of Nigerian farmers continue to use OPVs, and this has also been cited as a hindrance to improved productivity, thus adoption of improved hybrids would improve the yields (Abdoulaye et al. 2018). Ethiopian maize productivity success story has been mainly attributed to an increase in production and not land expansion, although sorghum and teff *(Eragrostis tef)* growers in the rift valley have diversified into maize farming (Abate et al. 2015). Favourable economic and production conditions, availability of modern varieties developed from home-grown improved germplasm supported by better farmer-extension linkage and use of fertilizers are some of the factors contributing to high maize production in Ethiopia (Abate et al. 2015). Chivasa et al. (2022) reported that Ethiopia had a successful variety replacement story every five years, for example BH661 released in 2011 replacing BH660, which was released in 1993. Egypt's productivity journey is mainly due to the use of modern varieties and fertilizers complimented by a very good irrigation system where water is drawn from the Nile Basin (James 2010). Egypt has approximately 2.5 million hectares of arable land which can be irrigated. Tanzania, Kenya and Uganda have largely benefited from the bimodal rainfall pattern resulting in increased productivity since farmers have the opportunity to plant twice within one year (Palmer et al. 2023).



Source: (FAOSTAT, 2022)

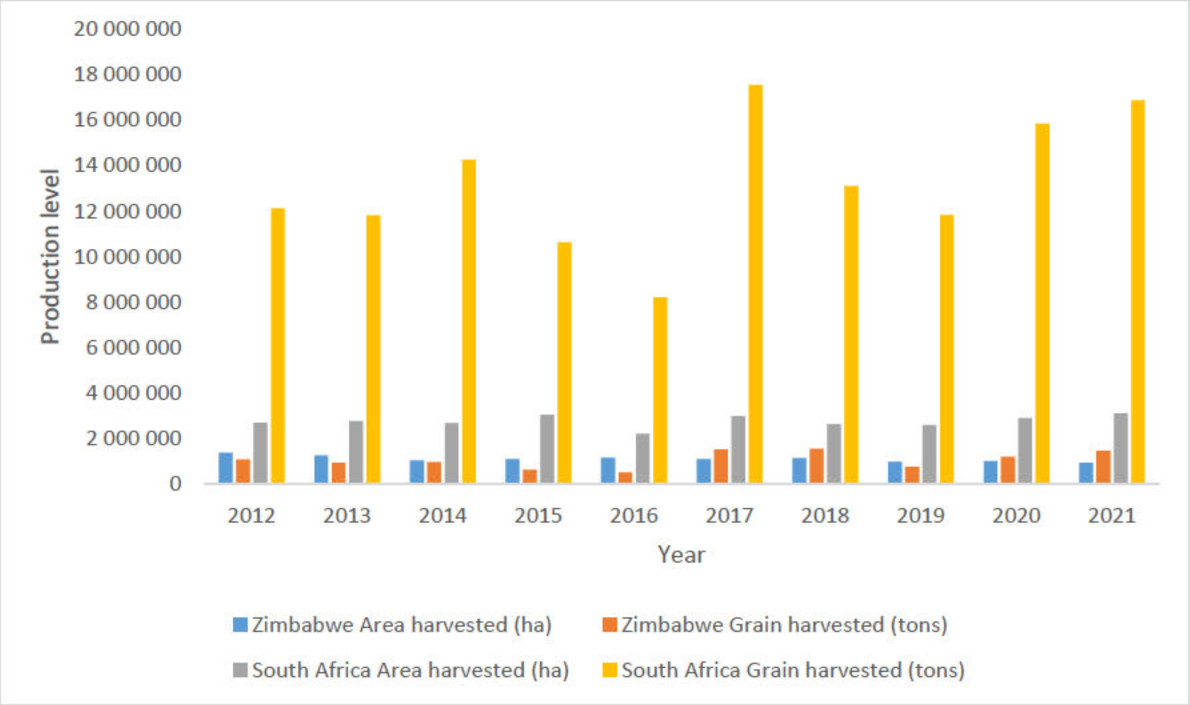
Figure 2- 1: Ten-year maize production trend for Zimbabwe

Zimbabwe has the potential to increase its productivity by refining land tenure policies as well as offering competitive prices to the farmers to encourage more maize production. Most farmers are shunning maize production due to uncompetitive market prices. Farmers with limited resources often resort to seed recycling due to high cost of certified seed and by so doing they lose out on yield. The ten-year average yield for the period up to 2021 was 1.2 tonnes per hectare (Figure 2-1) even though seed of high yielding hybrids available on the market. This shows that farmers are not taking advantage of hybrids that produce high yields, which could be due to a lack of knowledge about the benefits of hybrids, or a lack of access to high-quality hybrids. Most of the country's maize is produced by small, subsistence farmers who cannot afford fertilizers, resulting in low yields. A sufficient level of support and motivation could greatly increase maize yields from the current levels. Investing in agricultural extension services, agricultural technologies, and improved access to credit could be key factors to increase maize yields. Additionally, providing incentives for farmers to adopt improved management practices could also be beneficial.

Source: (FAOSTAT, 2022)

Figure 2- 2: Ten-year maize production trend for South Africa

South Africa's maize yield per hectare (>5 t ha^{-1}) is very encouraging and SSA should thrive to reach this tonnage for Africa to be food secure. The use of modern farming techniques and hybrids has been behind this high productivity. Single cross maize hybrids, be it conventional and genetically modified, are intensively used in South Africa, thereby contributing significantly to maize yields (Musundire et al. 2019). The ten-year average yields for South Africa up to 2021 are very encouraging (Figure 2-2). Yields averaged 4.75 t ha^{-1}, a higher level than the SSA average, which is around 1.5 t ha^{-1}. This improvement in yields can be attributed to the use of improved agricultural techniques, such as the use of fertilizers andirrigation systems. These techniques have helped to increase crop production, resulting in higher yields. As SSA countries strive to increase yields and become self-sufficient in food, they should learn from South Africa's success story. South Africa's success in increasing yields is due to its emphasis on investing in agricultural technology and infrastructure. SSA countries should also focus on investing in agricultural technology and infrastructure if they hope to increase their yields and become self-sufficient in food.



Source: (FAOSTAT, 2022)

Figure 2- 3: Comparison of Zimbabwe and South Africa production levels 2012-2021.

South Africa’s maize production level is way above that of Zimbabwe, especially in terms of grain yield per ha. This is largely attributed to the favourable economic environment prevalent in the former as well as good land tenure policies. It can be observed from Figure 2.3 that between 2012 and 2016, Zimbabwe’s total maize grain yield harvested was lower than the area planted to the crop. There was a slight improvement in 2017, 2018 2020 and 2021.

2.3 Limitations in maize production

Despite the importance of maize for food security, productivity is low in SSA (Badu-Apraku and Oyekunle, 2012) compared to the rest of the world. Abiotic and biotic stress factors, as well as socio-economic constraints have been linked to low productivity (Lobulu et al. 2019).

2.3.1 Abiotic factors limiting maize production

Drought stress, and cost of inputs have significantly contributed to food shortages in Africa. Majority of maize in SSA is rain fed and this exposes it to unfavourable effects of the ever changing weather patterns (Mulungu and Ng'ombe, 2019). Soils have low fertility especially in northern Guinea savanna and areas with high altitude (Badu-Apraku and Fakorede 2017). Majority of the farmers cannot afford fertilizers and little fertilizer input use is a major contributor to below average maize yields in SSA (Leitner et al. 2020).

2.3.2 Biotic stress factors limiting maize production

Biotic factors such as insect pests like Fall army worm (FAW) and foliar diseases like Maize lethal necrosis disease (MNLD) have resulted in huge grain losses in the horn of Africa (Keno et al. 2018). Lobulu et al. (2019) stated that Tanzania recorded losses of 20-100% due to *Striga* infestations.

The other constraints in maize production include slow adoption of modern technologies by societies, poor maize grain prices resulting in farmers not being motivated to grow maize due to socio-economic factors as well as ever changing government policies (Badu-Apraku and Fakorede 2017). Post-harvest losses are prevalent in smallholder farming communities and have a negative effect on productivity by reducing quantity and quality (Musundire et al. 2015; Saeed and Laing 2023). Loses occur in the fields, during processing and in storage due to lack of knowledge on post-harvest management practices (Abass et al. 2014). Storage loses due to grain weevil *Sitophilus zeamais* and the larger grain borer *Prostephanus truncatus* have resulted in heavy loses of between 40-90% (Saeed and Laing 2023). Poor yielding hybrids have also contributed to constraints in maize production as well as failure by seed producing companies to deploy varieties adapted to specific environments, and poor variety turnover/replacement (Chivasa et al. 2022).

Additional key challenges that maize farmers encounter that contribute to limited maize productivity and potential are climate variability, limited access to quality seeds, soil degradation,, limited access to agricultural inputs, and lack of knowledge and skills. Addressing these constraints requires a multi-faceted approach that includes promoting climate-smart agriculture, improving seed systems, implementing sustainable soil management practices, enhancing pest and disease control measures, increasing farmers' access to agricultural inputs, and providing training and extension services. Achieving maximum productivity and ensuring food security for millions of people can be achieved by resolving these limitations.

2.4 History of maize improvement in Zimbabwe

Maize is one of the most important staple crops in Zimbabwe. It has played a significant role in the country's agricultural development and food security. Over the years, efforts have been made to improve maize production in Zimbabwe through various breeding and cultivation practices.

The history of maize breeding in Zimbabwe can be traced back to the early 20th century when the government recognized the need to enhance maize yields and quality. The first step towards this was the introduction of improved maize varieties from other countries, such as the United States and South Africa (Rusike and Donovan 1995). Prior to the green revolution, open pollinated varieties (OPVs) were being grown in Asia, however, by the 1940s double cross hybrids were gaining momentum in USA. Zimbabwe, then Rhodesia, released the first commercial double cross in 1949 and went on to produce what would become the world's first commercialized single cross (SR52) in 1960 (Havazvidi and Tattersfield, 2006; Smale and Jayne, 2004). According to Derera and Musimwa (2015), the single-cross maize hybrid went on to become a sought after hybrid across Africa. Derera and Musimwa (2015) reported that the hybrid is still being grown by farmers in South Africa and Eswatini. McCann (2009) reported that some farmers in Zimbabwe recorded yields of SR52 which were better than those obtained by farmers who were in the US corn-belt.

The SR52 parental lines, N3 and SC form the basis of major heterotic groups in maize breeding programs across East and Southern Africa. Ever since, numerous single cross hybrids have been produced and are preferred by modern farmers. These achievements led Zimbabwe to be one of the countries with the highest usage of maize hybrids in SSA (Abate et al. 2017). Efforts are being made to develop drought-tolerant and climate-resilient maize varieties to mitigate the impact of changing climatic conditions on maize production. In the face of climate change, these varieties aim to guarantee food security and sustainability.

The history of maize improvement in Zimbabwe has been characterized by the introduction of improved varieties, the adoption of hybrid maize, and the development of programs to support farmers and seed companies. The continuous efforts to enhance maize production have played a vital role in ensuring food security and contributing to the country's agricultural development.

2.5 Types of maize hybrids commonly grown

2.5.1 Single cross maize hybrids

Single crosses are formed after crossing two homozygotic lines with a greater genetic distance (MacRobert et al. 2014). The harvested seed expresses heterosis when planted due to genetic distance. They yield better than other hybrids due to equal contribution of alleles from both parents. Single cross hybrids are generally uniform due to equal distribution of alleles from both parents and they are not easily affected by changes in weather patterns since they have better adaptability to variable environments (Sain Dass et al. 2009). The genetic uniformity of hybrids makes them better yielders. However, yield of single crosses is low at seed production level due to absence of heterosis in inbred lines. This makes seed more expensive to produce and subsequently costly to the farmer (Macrobert et al. 2014). Under stressful conditions, single crosses have poor pollen-silk synchronization because pollen shedding occurs for a short period since the plants are genetically the same. This makes them more vulnerable to drought especially during flowering.

South African maize is largely dominated by single crosses, whether genetically modified or conventionally bred (Musundire et al. 2019). These single crosses have enabled farmers to produce higher yields. Single cross hybrids have been bred and grown in Zimbabwe with great success. After SR52, many other single cross hybrids were produced, and these include SC701 and SC709, which were developed by Seed Co Private limited. The average yield of these hybrids was 8.0 t ha^{-1} under good farming practices.

2.5.2 Three-way maize hybrids

When a single cross is crossed onto an inbred line, it becomes a three-way hybrid. The single cross will be the female parent while the inbred line is the male parent. The male inbred line should not be related to any of the parents constituting the single cross female. A three-way hybrid is made up of three unrelated inbred lines. The inbred line contributes 50% of the alleles with each parent of the single cross contributing 25% of the genetic make-up (Macrobert et al. 2014).

Three way hybrids cost less to produce compared to single cross hybrids (Makinde et al. 2021). This means that more seed will be harvested per unit area at seed production owing to the high yield obtained from the female single cross (Khalil et al. 2010). The higher the seed yield, the lower the production costs, the lower the price to the farmer. With three-way hybrids there is a longer pollen shedding period since the plants are not uniform. This enables pollen-silk synchronisation to be achieved even under stressful conditions (Araus et al. 2012). Three-way hybrids have stable performance across diverse environments (Makinde et al. 2021). According to Joshi and Gautam (2021) there is more phenotypic variability in three way hybrids than single crosses due to the presence of three sources of alleles. The major drawback of three-ways is in seed production because of the need to maintain and bulk three inbred lines as opposed to two as is the case of single crosses.

Majority of seed breeding in Zimbabwe is done by private companies such as Seed Co Private limited. The aim of these companies is to make profit. This has led to the production of three-way hybrids because they are cheaper to produce than single cross hybrids. The early maturing basket of maize hybrids is mainly dominated by three-way hybrids as the target market are small holder farmers with limited finances. Average yields of 4.0 t ha^{-1} were recorded for the three-way hybrids.

2.5.3 Double cross maize hybrids

Crossing two single crosses produces a double cross. They are unique in the sense that they are constituted by four different inbred lines each contributing 25% of the alleles resulting in more phenotypic variation. Since double crosses use single cross as male, more pollen is shed. This entails that a greater female: male ratio (8:1) is appropriate in seed production. A high female: male ratio means more rows of the female will be harvested per unit area. Double cross hybrids are highest yielders in seed production and least expensive for the farmer. However, grain yield is usually less than three-way hybrids (Macrobert et al. 2014). Double cross hybrids have been successfully used in India. After the first double cross commercial hybrids in 1961, maize annual productivity increased from 0.9 t ha^{-1} to 1.1 t ha^{-1} (Kumar et al. 2012). Katragadda et al. (2020) reported that since inbreds are succumbing to emerging pests and diseases as well as their low yield potential, utilization of double cross hybrids will benefit both the farmer and the seed growers and more seed will be harvested per unit area resulting in reduced costs incurred by the farmer. Sujiprihati et al. (2003) reported that double cross hybrids performed better than single cross hybrids in Malaysia. This is, however, contrary to what other researchers reported. A study by Lynch et al. (1973) and Taj et al. (2012) found that single cross hybrids outperformed both three-way and double cross hybrids. Utilization of double cross hybrids is not known in Africa as private seed companies are not willing to share this information due to intellectual property rights.

2.5.4 Open-pollinated (OPVs) and synthetic varieties

A considerable number of farmers across SSA are still growing OPVs despite introduction and deployment of hybrids (Masuka et al. 2017) mainly because they are less priced compared to hybrids and are fairly yielding in some cases (Kutka, 2011). Usage of OPVs is more prevalent in West Africa (41%) compared to East Africa (27%) and Southern Africa (8%) (Abate et al. 2017). This is because of low budgetary provision and investment in research and development in SSA particularly in West Africa (Siziba et al. 2013).

Open-pollinated varieties are developed by selecting phenotypically good ears. The selected ears are then randomly mixed before multiplication. There is no controlled pollination during seed multiplication. This is due to a cheap breeding procedure and a shorter development cycle compared to hybrids. The OPVs tend to have a larger ecological plasticity which means they have good yield stability. The OPVs yields lower than hybrids under optimum conditions.

Synthetic varieties are developed through crossing of numerous genotypes with good combining ability. They are a product of random mating involving selected genotypes and may be sources of germplasm in maize programs, they could be a good source of pest and disease resistance (Lonnquist 1961; Márquez-Sánchez and Sahagún-Castellanos 2002; Welu 2015). They are maintained through routine mass selection using full sibs and half sibs in some cases. Reconstitution of synthetic variety should be done regularly, failure of which will result in it becoming an OPV (Welu, 2015). Performance of synthetics depends on the number of parental components constituting it (Gasim and Link, 2007). Synthetic populations have better performance than OPVs (White and Connolly, 2011). Synthetic varieties are not very popular in Zimbabwe it could be due to high rate of hybrids adoption as reported by Abate et al. (2017). In South Africa, there is Nelson's Choice variety which is a synthetic variety (Capstone Seeds 2023). Sibiya et al. (2013) and Derera et al. (2006) reported that OPVs and local landraces were being preferred over hybrids because farmers are slow to adopt change and would rather prefer irrespective of their low yields.

2.5.5 Genetically modified (GM) maize

Progress in biotechnology has made it possible for introgression of genetic material amongst and within species (Eckhoff et al. 2003). This has resulted in the development of maize which resist pests attack known as Bt (*Bacillus thuringiensis*) maize which was released over two and half decades ago in the United States of America. South Africa commercially adopted genetically modified (GM) maize, yellow Bt maize, in 1998 and this was followed by herbicide tolerant (HT) white maize which was commercialized in 2003-2004. In 2016, more than 70% of total maize grown in South Africa was GM (Ala-Kokko et al. 2021). Despite numerous advantages of GM maize like high yield potential, pest resistance and herbicide tolerance, its adoption is still lagging in Africa. South Africa is the only country to commercialise GM maize production, while in the rest of African countries are still in confined trials or nothing has been done to regulate them (Gbadegesin et al. 2022). Slow adoption is because of potential concerns on health, biosafety and limited public acceptance in Africa (Ojuederie et al. 2011; Qaim, 2020). Gbadegesin et al. (2022) argued that limited public acceptance in Africa is generally because of inadequate awareness.

The Water Efficient Maize for Africa (WEMA) and Drought Tolerant Maize for Africa (DTMA) are projects co-funded by CIMMYT and other organizations. The mandate of these projects to develop climate smart varieties capable of withstanding heat and drought stress. DTMA initiatives have led to the release of more than 150 drought tolerant varieties across participating countries in six years from 2007 (Fisher et al. 2015). Through WEMA initiatives GM maize hybrids which had the Bt gene were released (Sujiprihati 2014). However the project faced a lot of criticism as it was accused of having an “ulterior motive” (accused of having a hidden agenda) by activists (anti-GM technology groups) (African Centre for Biodiversity (ACB) 2017; Wamatsembe et al. 2017).

2.6 Grain yield

a product of dry matter and/or moisture content at harvest, and accumulation of dry matter followed by allocation of photo-assimilates to grain (Evans and Fisher, 1999; Tollenaar and Lee, 2002). Grain yield constitutes the target trait in crop genetic improvement (Jiaqin et al. 2009). According to Acquaah (2015), yield is the amount a part of the crop which is of importance to the producer. This can be roots, leaves, flowers, and oil content. Interaction among various yield constituents, genetic makeup (G), environmental conditions (E) and interaction amongst these (G*E) makes grain yield inheritance very complex (Baenziger et al. 2010; Evans and Fisher, 1999). The overall crop performance is best measured using its yield (Acquaah, 2015).

Yield gap is the difference between what farmers get and what a variety is capable of producing (Assefa et al. 2020). Yield potential is what a variety yields when grown with all yield defining factors, that is, carbon dioxide, radiation, temperature and cultivar features (Assefa et al. 2020). Potential yield is the ceiling obtained from a crop in the absence of yield limiting factors and yield reducing factors such as pollutants, weeds, pests and diseases, adequate moisture regime and nutrients coupled with good agronomic practices (Liu et al. 2016; Lobell et al. 2009). Yield gap is large in SSA versus developing countries, even though improved maize hybrids have been adopted across various maize growing areas within the region (Assefa et al. 2020). Yield gaps cannot be reduced due to socio-economic constraints especially amongst small scale resource poor farmers in SSA (Liu et al. 2016). However, yield gaps can be narrowed by taking corrective action on yield limiting and yield reducing factors, observing the correct time of planting, good agronomic practices, varietal choice, proper usage of soil nutrient enhancers (Fischer et al. 2009; Kihara et al. 2016; Neumann et al. 2010). Management practices such as planting population, time of planting, seed dressing, fertilizer use and time of application were found to be useful in increasing yields (Jiang et al. 2019; Salama et al. 2021). Adoption of improved maize varieties positively changed the food security situation for small scale farmers in South Africa, Tanzania and Zambia (Manda et al. 2018; Sinyolo 2020). Researchers like Kassie et al. (2011) and Bezu et al. (2014) reported that farmers' productivity was greatly improved following adoption of improved maize varieties.

2.7 Grain yield components

A breeding program focuses on improving the yield trait since it is of economic significance to breeders and producers (Greveniotis et al. 2021).Yield components for maize include cobs per plant, kernel row number, and grains per row and grain weight. Thus desired yield components have to be exploited indirectly (Viola et al. 2003). Several factors influence grain yield and yield components (Băşa et al. 2016). Total plants per unit area, cobs per plant, rows per cob, kernels per row and kernel weight are the five major yield components in maize (Acquaah 2015). Haarhoff and Swanepoel (2018) reported plant population and row spacing as major agronomic factors with strong influence on grain. Grain yield is correlated to the number of kernels obtained per unit (Otegui and Bonhomme, 1998; Ritchie and Alagarswamy, 2003; Tandzi and Mutengwa, 2020). However, Acquaah (2007) stated that days to physiological maturity and the ability to tolerate biotic and abiotic stress factors determine yield of maize. Physiological conditions during anthesis and grain filling period affect yield (Andrade et al. 1999). Yield increase is the major target in plant breeding although such traits like disease resistance, yield stability and drought tolerance are also are also key traits (CIMMYT 2021).

2.8 Genetic analysis using generation mean analysis

When designing breeding programs breeders should have prior understanding of the gene action governing expression of traits (Chemeda et al. 2015). To improve yields and yield components, plant breeders must understand gene action, heterosis, inbreeding depressions, and genetic gain (Said 2014; Acquaah 2015). Generation mean analysis is a statistical method of estimating gene effects in different crops (Mather and Jinks, 1977). This type of analysis is mainly used for preliminary studies (Hallauer and Miranda, 1988). Information on fixable and non-fixable gene effects is obtained using generation mean analysis (Acquaah 2007). This method is credited for exposing the role of epistasis in hybrid performance (Kaeppler 2012). Lyimo et al. (2011) reported that generation mean analysis (GMA) takes advantage of gene interactions and provide vital information required in designing breeding strategies. Plant breeders normally use generation mean analysis as a tool for selecting appropriate crop improvement procedures, estimation of genetic advance, explaining heterosis and calculation of heritability of a trait (Gaur 2018). Generation mean analysis was used in both field and horticultural crops such as wheat (Farshadfar et al. 2001), rice (Sharifi et al. 2013), cotton (Srinivas and Genet, 2015), pearl millet (Jog et al. 2016), dry beans (Salegua et al. 2021) and horticultural crops like okra (Naveed et al. 2009).

When parents have remarkably different alleles with regard to favourable traits, generation mean analysis can be useful (Sibiya 2010). A major application of the technique has been in disease resistance studies, in which one parent is highly susceptibility to a disease while the other is highly resistant to it (Acquaah 2007; Sibiya 2010; Alam et al. 2014; Salegua et al. 2021). Lyimo et al. (2011) and Sibiya (2010) studied resistance of maize to grey leaf spot (GLS) using this technique. In addition to using generation mean analysis for estimating effect in relation to genotype and environment, it can also be used for estimating effects in relation to linkage, epistasis, and the interaction of them (Acquaah, 2007; Mather and Jinks, 1977). Hallauer and Miranda (1988), analysed inbred lines using generation mean analysis to confirm whether the alleles were homozygous and homogeneous.

Generating means assumes that there are two alleles per locus, most negative alleles are present in F1 and vice versa in no linkage at interacting loci, and t higher order epistatic relationships do not. (Mather and Jinks, 1977). The F2 is the base population or reference population as defined by Hayman (1960) and has maximum segregation (Hallauer and Miranda, 1988). According to Bernardo and Woodbury (2020) the recommended minimum number of progenies from populations is 50 to 100. Furthermore, sampling of segregating generations must be done for valid estimates of generation means.

Several studies have been done using generation mean analysis. Mushongi et al. (2013) used GMA on leaf chlorophyll concentration (LCC) at different N regimes and reported that different gene effects were governing the gene expression at different stages during the grain filling period. The general conclusion was that fixable gene effects were low under high N dosage while non-fixable gene effects were high under low N dosage. Derera and Musimwa (2015) used GMA on a single cross maize hybrid, SR52, and observed high levels of heterosis (>300%) and confirmed the presence of epistasis. Dominance gene action was found to be the basis of this extraordinary heterosis.

Breeding programs can be evaluated using GMA because it provides detailed information on population parameters, such as whether or not the trait is controlled by additive or non-additive gene effects within a given population the population (Campbell et al. 1997). As well as cross-pollinated plants, self-pollinated plants can also be analysed using GMA. A first order statistical analysis, which is usually the minimum of a sample, is used to analyse the data, this results in fewer sampling errors when compared with a second order statistical analysis, that is, the next sample value after the first, (Campbell et al. 1997). According to Mbogo et al. (2015), generation means analysis was performed to estimate genetic parameters associated with *Striga hermonthica* resistance in maize and reported that to determine the most advantageous method for breeding *Striga* tolerance, it was crucial to investigate the method of gene action.

2.9 Gene action

A good understanding of gene action is essential in selecting parents and breeding procedures for hybridization. It is therefore essential for breeders to be aware of the type of expression before beginning breeding activities. There are several genes influencing grain yield, which is an extremely important but also a very complex it many genes for its expression (Kayaga et al. 2017). It is also important to mention that genes can have additive, dominant, and epistatic effects, which are described as gene interaction (Mather and Jinks 1977). An additive gene effect occurs when different genes contribute independently to a specific trait expression. If the heterozygote performs in a significantly different manner from its homozygote parent, dominant genes are acting, and usually the heterozygote will be closer to one parent than the other. Over dominance occurs when individual alleles at a locus have separate effects on the phenotype, but their combined effect exceeds individual effects. A partial dominance occurs when all the alleles at a locus are partially expressed, resulting in a completely different or intermediate phenotype (Acquaah 2007).

When epistasis gene action exists, some genes interact positively with one another and others prevent the expression of other genes in different loci (Miko 2011). An epistatic interaction occurs when a few genes act together rather than independently and their effects depend on the allelic state of the other genes (Brown et al. 2014). There are two types of epistasis: fixable and non-fixable. The additive-dominance form of epistasis is non-fixable, while the additive-additive form of epistasis is fixable.

The additive-dominance form of epistasis is caused by a single gene that masks the effect of one or more other genes. This form of epistasis is not fixable because it is caused by interactions between alleles of the same gene, which can be eliminated by crossing with unrelated individuals (Acquaah 2007) and should be avoided when selecting for desired traits.
Additive-dominance epistasis occurs when the effects of one gene on another are equal to the additive effects of both genes together (Acquaah 2007). This type of epistasis can be eliminated by removing or modifying the gene that is masking the other genes. The additive-additive form of epistasis is caused by interactions between alleles of different genes (Acquaah 2007). This type of epistasis is detectable and preventable through QTL mapping and genetic analysis, and can be avoided when selecting for desired traits (Crawford et al. 2017). Epistasis should be detected and eliminated from breeding programs to ensure optimal genetic gain. This can be done through QTL mapping and genetic analysis. QTL mapping and genetic analysis can detect the presence of epistasis, while marker-assisted selection can be used to identify and exclude

individuals with epistasis (Crawford et al. 2017). These methods can be used to prevent epistasis from interfering with breeding programs and ensure optimal genetic gain. As epistasis is unlikely to have breeding value, its presence in breeding as it affects the response to selection.

The gene action that determines grain yield inheritance varies across environments. In a single cross maize hybrid, dominance effects were found to be more important than additive effects for grain yield (Shahrokhi et al. 2011). A similar finding was reported by Derera and Musimwa (2015) when studying SR52, where dominance effects impacted grain yield more than additives. These findings support the idea that environment plays an important part in the inheritance of grain yield. Genotype-by-environment interactions are important to consider when breeding maize varieties (Gupta et al. 2022). However, studies by other researchers like Betrán et al. (2003) reported that non-additive gene action was important in controlling yield under sub-optimal conditions. These findings were further validated by Derera et al. (2008) and Chandel and Mankotia (2014) who reported similar findings in which additive effects were superior to dominance effects in controlling grain yield under drought and non-drought situations.

2.9.1 Breeding implications due to gene action

When the breeding objective is not hybrid breeding, dominance genes are not liked by breeders as they cannot be easily fixed (Billiard et al. 2021). Breeders, therefore, prefer to use recessive genes, which are easier to control. Because selection in the short term is impossible, and makes breeding very difficult. Compared to other interactions, breeders prefer additive-additive interactions since they have a high likelihood of success (Novoselovic et al. 2004). According to Zdunić et al. (2008), fixable epistatic effects can be exploited in intra-population improvement, whereas non-fixable effects can be exploited using heterosis in hybrid breeding. Due to the fixability of additive gene action, Mushongi et al. (2013) suggest that recurrent selection could be most effective if the key mode of inheritance is additive gene action. The purpose of this study was to determine the genetic effects of the population coming out of ExpHybrid6 and make recommendations.

2.10 Heterosis

It was Shull who coined the term heterosis between 1908 and 1912 while working with hybrid maize (Shull 1952). An individual hybrid performs better than its parents as a result of heterosis (Acquaah 2015). As Brown et al. (2014) showed, heterosis is more likely to occur when the genetic distance between two parents is larger. The exploitation of heterosis in maize breeding boosts yields and has a great economic value (Kaeppler, 2012; Yi et al. 2019). The basis of modern maize breeding programs and the high productivity of maize hybrids is a function of the performance of the inbred lines and the vigour of the hybrids (Brown and Caligari 2008). Therefore, the performance of parental maize inbred lines *per se* can be improved by choosing appropriate germplasm and proper selection for establishing these inbred lines. There are three levels of heterosis: standard heterosis, mid-parent heterosis, and better parent heterosis. Standard hybrid vigour is the dominance of F1 over standard commercial check varieties (Acquaah 2015). This is also called useful heterosis or economic heterosis and is calculated as follows:

$$\text{Standard Heterosis} = [(F_1 - \text{Check}) \div \text{Check}] \text{ X } 100$$

Mid-parent hybrid vigour is the dominance of a hybrid over the average performance of its constituents. Mid-parent heterosis is calculated using the following formula:

$$MPH = 100*(\frac{[MF_1 — (MP_1+MP_2)/2]}{(MP_1+ MP_2)/2)}$$

Where: MF1 = mean performance of F_1; MP_1 = mean performance of P_1; MP_2 = mean performance of P_2.

Better parent heterosis is when heterosis is calculated over the better parent (Singh, 2016). It is calculated using the following formula;

$$((F_1 - BP)/BP))*100$$

Where BP = mean of better parent

Heterosis results in an increase in quality, overall vigour, and yield, increasing resistance to disease and insects (Brown and Caligari 2008). The desirable heterosis is positive for the majority of the characters (Mai et al. 2021). Negative heterosis, on the other hand, is found in characters like earliness, plant height, and lethal substances and create superior hybrids (Derera and Musimwa 2015).

Varying values have been recorded by various researchers. Derera and Musimwa (2015) reported 311% mid parent heterosis and 996% better parent heterosis for yield whilst studying a single cross maize hybrid. Atif et al. (2012) in a study on maize heterosis reported MP and BP heterosis of 131% and 126% for grain yield respectively, while Gissa et al. (2007) reported 89% MPH on maize inbred lines.

Heterosis has long been explained by dominance and over dominance theories. These theories suggest that heterosis is caused by the crossing of different alleles that produce a dominant or over dominant phenotype in the offspring (Kotkar and Giri 2020). The dominance theory suggests that heterosis is a result of dominant alleles masking the deleterious effects of recessive alleles, while the over dominance theory suggests that heterosis is a result of heterozygosity resulting in higher trait values than homozygosity (Lamkey and Edwards 1999; Kotkar and Giri 2020). These theories suggest that heterosis results from the combining of different alleles, where the dominant allele of one genotype masks the effect of the recessive allele of another genotype (Singh et al. 2021). This leads to the expression of the traits of the heterozygous genotype, which is greater than either parent. According to the dominance theory, heterosis results from dominant alleles and recessive alleles cause deleterious effects. As a result, heterosis will occur when there are more dominant alleles than recessive alleles (Acquaah 2015). On the other hand, the over dominance theory assumes that heterozygosity produces higher trait values when compared with homozygosity, that is, when the alleles of two parents are combined and the resultant offspring are produced (Acquaah 2015).

2.11 Genetic gains in maize breeding

Genetic gains realized over time should be assessed regularly as a way of measuring the effectiveness of breeding programs in order to devise new strategies (Badu-Apraku et al. 2013). According to Xu et al. (2017), performance growth realized over an identified period through artificial selection is genetic gain. Genetic gain is basically genetic improvement or breeding progress (Laidig et al. 2017). Upsurge in demand for superior products, plant breeders must enrich genetic gain potential of their products to match the demand and address the decline in average yield focus should be on producing market driven maize inbred lines and market-oriented hybrids (Musundire et al. 2021). Demand led breeding, entails stakeholders along the value chain to incorporate their different needs in breeding programs (Demand-Led Breeding 2020; Lobulu et al. 2019). Inclusive and consultative breeding encourages farmer preferred traits to be incorporated in development of new hybrids. Masuka et al. (2017) highlighted that genetic gain assessment facilitates breeders to measure and fine-tune breeding programmes centred on their performance.

Maize genetic gains in SSA were not absolutely quantified until 2017 (Masuka et al. 2017). However, Badu-Apraku et al. (2013) did studies on genetic gains using OPVs and reported gains of 13.5 kg ha^{-1} year^{-1} under ideal growing environments and 11.4 kg ha^{-1} year^{-1} suboptimal situations in West and Central Africa. In East and Southern Africa, genetic gain assessments were done for hybrids released from 2000 to 2010 and it was discovered that gains were 109.4 kg ha^{-1} $year^{-1}$ under good conditions, 32.5 kg ha^{-1} $year^{-1}$ under heat and drought stress (Masuka et al. 2017). Most recently Asea et al. (2023) reported 81 kg ha^{-1} $year^{-1}$ on varieties released between 2008 and 2020 in Uganda. Genetic gains showed variation across environments, with higher genetic gains in stress free environments and lower in stressful environments (Masuka et al. 2017).

Genetic gain is influenced by genetic variation in germplasm, time to complete a breeding cycle and heritability of important traits (Xu et al. 2017). Adoption of modern breeding techniques like genomic and molecular tools, doubled haploid technology and marker assisted selection are some of the ways which can be adopted to improve genetic gain (Xu et al. 2019). Furthermore, selection intensity can be enhanced through precision genotyping and phenotyping (Xu et al. 2019). The knowledge of genetic gain is the yard stick for breeding programmes to measure progress. Breeders should, from time to time, assess genetic gains realised in their breeding programmes. This aids them to appraise breeding techniques and come up with new approaches (Badu-Apraku et al. 2021). Measuring genetic gain is vital in gauging breeding performance. Genetic gain can be improved by enabling high selection intensity. This can be achieved by broadening the program. Some ways of increasing genetic gain include fast tracking breeding cycles, sufficient genetic variation and proper phenotyping (Masuka et al. 2017). Maize breeding programs succeed was due to the superiority of the hybrids released.

2.12 Conclusion

While maize is an exotic crop to Africa, it has established itself as a strategic food security and staple crop in Zimbabwe and the rest of SSA. This is because maize is relatively easy to grow, highly nutritious, and its yields are significantly higher than other crops. It is relatively inexpensive to produce, making it an important source of food for many people in the region.

There have been numerous successes in the improvement of maize since the mid-twentieth century. Single cross hybrids are improving yields in countries that are developing and deploying them, so their promotion and application is necessary in order to increase yields. There are a variety of factors that affect SSA yields, according to a literature review. The literature review further demonstrated that grain yield inheritance depends on all forms of gene action, with dominance gene effects greater than additive gene effects. In terms of heterosis, most hybrids have high levels of heterosis for yield and yield components like kernel weight, ear length, and grain mass. Breeding progress can be evaluated through genetic gains assessments. This study examined the genetic basis of ExpHybrid6 as well as the genetic gains of new single cross hybrids against old single cross hybrids.

References

Abass AB, Ndunguru G, Mamiro P, Alenkhe B, Mlingi N and Bekunda M (2014) Post-harvest food losses in a maize-based farming system of semi-arid savannah area of Tanzania. Journal of Stored Products Research 57: 49–57.

Abate T, Fisher M, Abdoulaye T, Kassie GT, Lunduka R, Marenya P and Asnake W (2017) Characteristics of maize cultivars in Africa: How modern are they and how many do smallholder farmers grow? Agriculture and Food Security 6: 1–17.

Abate T, Shiferaw B, Menkir A, Wegary D, Kebede Y, Tesfaye K, Kassie M, Bogale G, Tadesse B and Keno T (2015) Factors that transformed maize productivity in Ethiopia. Food Security 7: 965–981.

Abdoulaye T, Wossen T and Awotide B (2018) Impacts of improved maize varieties in Nigeria: ex-post assessment of productivity and welfare outcomes. Food Security 10: 369–379.

Acquaah G (2015) Conventional Plant Breeding Principles and Techniques. Springer International Publishing, Cham, 115–158p.

Acquaah G (2007) Principles of Plant Genetics and Breeding, Second. Wiley-Blackwell, Chichester.

African Centre for Biodiversity (ACB) (2017) The Water Efficient Maize for Africa Project: Profiteering not Philanthropy. p. 59.

Ala-Kokko K, Lanier Nalley L, Shew AM, Tack JB, Chaminuka P, Matlock MD and D'Haese M (2021) Economic and ecosystem impacts of GM maize in South Africa. Global Food Security 29: 100544.

Alam A, Somta P and Srinives P (2014) Generation mean and path analyses of reaction to mungbean yellow mosaic virus (MYMV) and yield-related traits in mungbean (Vigna radiata (L.) Wilczek). Society for the Advancement of Breeding Research in Asia and Oceania 46: 150–159.

Andrade FH, Vega C, Uhart S, Cirilo A, Cantarero M and Valentinuz O (1999) Kernel number determination in maize. Crop Science 39: 453–459.

Araus JL, Serret MD and Edmeades GO (2012) Phenotyping maize for adaptation to drought. Frontiers in Physiology 3: 1–20.

Asea G, Kwemoi DB, Sneller C, Kasozi CL, Das B, Musundire L, Makumbi D, Beyene Y and Prasanna BM (2023) Genetic trends for yield and key agronomic traits in pre- commercial and commercial maize varieties between 2008 and 2020 in Uganda. Frontiers in Plant Science 14: 1–13.

Assefa BT, Chamberlin J, Reidsma P, Silva JV and van Ittersum MK (2020) Unravelling the variability and causes of smallholder maize yield gaps in Ethiopia. Food Security 12: 83–103.

Atif I, Awadalla A, Khalafalla M, Idris A and Osman A (2012) Combining Ability and Heterosis for Yield and Yield Components in Maize. Australian Journal of Basic and Applied Sciences 6: 36–41.

Badu-Apraku B and Fakorede MAB (2017) Advances in genetic enhancement of early and extra-early maize for sub-Saharan Africa. Advances in Genetic Enhancement of Early and Extra-Early Maize for Sub-Saharan Africa 1–604.

Badu-Apraku B, Obisesan O, Abiodun A and Obeng-Bio E (2021) Genetic Gains from Selection for Drought Tolerance during Three Breeding Periods in Extra-Early Maturing Maize Hybrids under Drought and Rainfed Environments. Agronomy 11: 831.

Badu-Apraku B and Oyekunle M (2012) Genetic analysis of grain yield and other traits of extra-early yellow maize inbreds and hybrid performance under contrasting environments. Field Crops Research 129: 99–110.

Badu-Apraku B, Yallou C and Oyekunle M (2013) Genetic gains from selection for high grain yield and Striga resistance in early maturing maize cultivars of three breeding periods under Striga-infested and Striga-free environments. Field Crops Research 147: 54–67.

Baenziger PS, Dweikat I, Gill K, Eskridge K, Berke T, Shah M, Campbell BT, Ali ML, Mengistu N, Mahmood A, Auvuchanon A, Yen Y, Rustgi S, Moreno-Sevilla B, Mujeeb-Kazi A and Morris MR (2010) Understanding Grain Yield: It Is a Journey, Not a Destination. Czech Journal of Genetics and Plant Breeding 47: 77–84.

Băşa AG, Ion V, Dumbravă M, Temocico G, Epure LI and Ştefan D (2016) Grain Yield and Yield Components at Maize under Different Preceding Crops and Nitrogen Fertilization Conditions. Agriculture and Agricultural Science Procedia 10: 104–111.

Bernardo R and Woodbury SP (2020) Breeding For Quantitative Traits in Plants, Third Edit. Stemma Press, Minnesota, 327–328p.

Betrán FJ, Beck D, Bänziger M and Edmeades GO (2003) Secondary traits in parental inbreds and hybrids under stress and non-stress environments in tropical maize. Field Crops Research 83: 51–65.

Bezu S, Kassie GT, Shiferaw B and Ricker-Gilbert J (2014) Impact of improved maize adoption on welfare of farm households in Malawi: A panel data analysis. World Development 59: 120–131.

Billiard S, Castric V and Llaurens V (2021) The integrative biology of genetic dominance. Biological Reviews 96: 2925–2942.

Brown J and Caligari PDS (2008) An Introduction to Plant Breeding. Blackwell Publishing Ltd, Oxford, UK.

Brown J, Caligari PDS and Campos H (2014) Plant Breeding, Second. Wley Blackwell, West Sussex, UK.

Campbell KW, Hamblin AM and White DG (1997) Inheritance of resistance to aflatoxin production in the cross between corn inbreds B73 and LB31. Phytopathology 87: 1144–1147.

Capstone Seeds (2023) Capstone Seeds South Africa. Available at <https://www.capstoneseeds.com/> Accessed on July 20, 2023.

Chandel U and Mankotia BS (2014) Combining Ability in Local and CIMMYT Inbred Lines Of Maize (Zea mays L.) For Grain Yield and Yield Components Using Line × Tester Analysis. Society for the Advancement of Breeding Research in Asia and Ocenia Journal of Breeding and Genetics 46: 256–264.

Chemeda D, Amsalu A, Habtamu Z and Adugna W (2015) Generation Means Analysis for Quantitative Traits in Sesame (Sesamum indicum L.). Ethiopian Journal of Science 38: 75–84.

Chivasa W, Worku M, Teklewold A, Setimela P, Gethi J, Magorokosho C, Davis NJ and Prasanna BM (2022) Maize varietal replacement in Eastern and Southern Africa: Bottlenecks, drivers and strategies for improvement. Global Food Security 32: 100589.

CIMMYT (2021) Maize research – CIMMYT. CIMMYT. Available at <https://www.cimmyt.org/work/maize-research/> Accessed on February 10, 2022.

Crawford L, Zeng P, Mukherjee S and Zhou X (2017) Detecting epistasis with the marginal epistasis test in genetic mapping studies of quantitative traits. 1–37p.

Demand-Led Breeding (2020) Demand-Led breeding |. Available at <https://www.demandledbreeding.org/> Accessed on February 24, 2022.

Derera J and Musimwa TR (2015) Why SR52 is such a great maize hybrid? I. Heterosis and generation mean analysis. Euphytica 205: 121–135.

Derera J, Tongoona P, Langyintuo A, Laing M and Vivek B (2006) Farmer Perceptions On Maize Cultivars In The Marginal Eastern Belt of Zimbabwe and Their Implications for Breeding. African Crop Science Jurnal 14: 1–15.

Derera J, Tongoona P, Vivek BS and Laing MD (2008) Gene action controlling grain yield and secondary traits in southern African maize hybrids under drought and non-drought environments. Euphytica 162: 411–422.

Eckhoff S, Paulsen M and Yang S (2003) Maize. Elsevier Science 1: 3647–3657.

Ekpa O, Palacios-Rojas N, Kruseman G, Fogliano V and Linnemann AR (2019) Sub-Saharan African Maize-Based Foods - Processing Practices, Challenges and Opportunities. Food Reviews International 35: 609–639.

Erenstein O, Jaleta M, Sonder K, Mottaleb K and Prasanna BM (2022) Global maize production, consumption and trade: trends and R&D implications. Food Security 14: 1295–1319.

Evans LT and Fisher RA (1999) Yield Potential: Its Definition, Measurement, and Significance. Crop Science 39: 1544–1551.

FAOSTAT (2018) Statistical database of the Food and Agriculture Organization. Statistics Division, Food and Agriculture Organization of the United Nations, Rome, Italy.

FAOSTAT (2022) Statistical database of the Food and Agriculture Organization. Statistics Division, Food and Agriculture Organization of the United Nations, Rome, Italy.

Farshadfar E, Ghanadha M, Zahravi M and Sutka J (2001) Generation mean analysis of drought tolerance in wheat (Triticum aestivum L.). Acta Agronomica Hungarica Hungary 49: 59–66.

Fischer RA, Byerlee D and Edmeades GO (2009) Can technology deliver on the yield challenge to 2050? FAO, Rome, Italy, p. 46. In Expert Meeting on How to feed the World in 2050?

Fisher M, Abate T, Lunduka RW, Asnake W, Alemayehu Y and Madulu RB (2015) Drought tolerant maize for farmer adaptation to drought in sub-Saharan Africa: Determinants of adoption in eastern and southern Africa. Climatic Change 133.

Gasim S and Link W (2007) Agronomic performance and the effect of self-fertilization on german winter faba beans. Journal of Central European Agriculture 8: 121–127.

Gaur A (2018) Analysis of Basic generation means and variances and its utility in plant breeding.

Gbadegesin LA, Ayeni EA, Tettey CK, Uyanga VA, Aluko OO, Ahiakpa JK, Okoye CO, Mbadianya JI, Adekoya MA, Aminu RO, Oyawole FP and Odufuwa P (2022) GMOs in Africa: Status, adoption and public acceptance. Food Control 141: 109193.

Gissa DW, Zelleke H, Labuschagne MT, Hussien T, Singh H, Zelleke H, Labuschagne MT, Hussien T and Singh H (2007) Heterosis and combining ability for grain yield and its components in selected maize inbred lines. South African Journal of Plant and Soil 24: 133–137.

Greveniotis V, Bouloumpasi E, Zotis S, Korkovelos A and Ipsilandis CG (2021) Estimations on trait stability of maize genotypes. Agriculture (Switzerland) 11: 1–16.

Gupta V, Kumar M, Singh V, Chaudhary L, Yashveer S, Sheoran R, Dalal MS, Nain A, Lamba K, Gangadharaiah N, Sharma R and Nagpal S (2022) Genotype by Environment Interaction Analysis for Grain Yield of Wheat (Triticum aestivum (L.) em.Thell) Genotypes. Agriculture (Switzerland) 12: 1–15.

Haarhoff SJ and Swanepoel PA (2018) Plant population and maize grain yield: A global systematic review of rainfed trials. Crop Science 58: 1819–1829.

Hallauer AR and Miranda JBF (1988) Quantitative genetics in maize breeding. Iowa State University Press, 468p.

Haruna A, Adu GB, Buah SS, Kanton RAL, Kudzo AI, Seidu AM and Kwadwo OA (2017) Analysis of genotype by environment interaction for grain yield of intermediate maturing drought tolerant top-cross maize hybrids under rain-fed conditions. Cogent Food and Agriculture 3: 1–13.

Havazvidi E and Tattersfield R (2006) Development of Seed Industry. p. 235–240. In Zimbabwe Agriculture Revolution Revisited.

Hayman BI (1960) The separation of epistatic from additive and dominance variation in generation menas. II - World Vegetable Center. Genetica.

James C (2010) A global overview of biotech (GM) crops: adoption, impact and future prospects. GM crops 1: 8–12.

Jiang R, He W, Zhou W, Hou Y, Yang JY and He P (2019) Exploring management strategies to improve maize yield and nitrogen use efficiency in northeast China using the DNDC and DSSAT models. Computers and Electronics in Agriculture 166.

Jiaqin S, Ruiyuan L, Dan Q, Congcong J, Yan L, Morgan C, Bancroft I, Jianyi Z and Jinling M (2009) Unraveling the Complex Trait of Crop Yield With Quantitative Trait Loci Mapping in Brassica napus. Genetics 182: 851–861.

Jog K, Kachhadia V, Vachhani J and Lalwani H (2016) Generation mean analysis and inbreeding depression in pearl millet. Electronic Journal of Plant Breeding 7: 469–481.

Joshi P and Gautam D (2021) Genetic insights on single cross maize hybrid and its importance on maize self-sufficiency in Nepal. Archives of Agriculture and Environmental Science 6: 218–226.

Kaeppler S (2012) Heterosis: Many Genes, Many Mechanisms—End the Search for an Undiscovered Unifying Theory. International Scholary Research Network Botany 2012: 1–12.

Kassie M, Shiferaw B and Muricho G (2011) Agricultural Technology, Crop Income, and Poverty Alleviation in Uganda. World Development 39: 1784–1795.

Katragadda S, Pradeep T and Sravani D (2020) Identification of potential parental lines for single, three-way and double crosses in maize (Zea mays L.). Maydica 65: 65.

Kayaga HN, Kagoda F, Ochwo-ssemakula M, Mahulé B, Alladassi E, Asea G, Gibson P and Edema R (2017) Inheritance of Yield and Yield-related Traits in Highland Maize Hybrids of Uganda. The Korean Society of Crop Science 2017: 255–262.

Keno T, Azmach G, Wegary D, Worku M, Tadesse B, Wolde L, Deressa T, Abebe B, Chibsa

T and Suresh L (2018) Major biotic maize production stresses in Ethiopia and their management through host resistance. African Journal of Agricultural Research 13: 1042–1052.

Khalil AI, Rahman H, Saeed N and Khan NU (2010) Combining Ability in Maize Single Cross Hybrids for Grain Yield : A Graphical Analysis. Plant Breeding 26: 373–379.

Kihara J, Huising J, Nziguheba G, Waswa BS, Njoroge S, Kabambe V, Iwuafor E, Kibunja C, Esilaba AO and Coulibaly A (2016) Maize response to macronutrients and potential for profitability in sub-Saharan Africa. Nutrient Cycling in Agroecosystems 105: 171–181.

Kotkar H and Giri A (2020) Plant epigenetics and the 'intelligent' priming system to combat biotic stress. Elsevier Inc., 25–38p.

Kumar R, Kumar B, Kaul J, Karjagi CG, Jat SL, Parihar CM and Kumar A (2012) Maize research in India -historical prospective and future challenges. Maize Journal 1: 1–6.

Kutka F (2011) Open-pollinated vs. hybrid maize cultivars. Sustainability 3: 1531–1554.

Laidig F, Piepho HP, Rentel D, Drobek T, Meyer U and Huesken A (2017) Breeding progress, variation, and correlation of grain and quality traits in winter rye hybrid and population varieties and national on-farm progress in Germany over 26 years. Theoretical and Applied Genetics 130: 981–998.

Lamkey KR and Edwards JW (1999) The Genetics and Exploitation on Heterosis in Crops: Quantitative Genetics of Heterosis. The Genetics and Exploitation on Heterosis in Crops 31–48.

Leitner S, Pelster DE, Werner C, Merbold L, Baggs EM, Mapanda F and Butterbach-Bahl K (2020) Closing maize yield gaps in sub-Saharan Africa will boost soil N2O emissions. Elsevier 47: 95–105.

Liu Z, Yang X, Lin X, Hubbard KG, Lv S and Wang J (2016) Narrowing the Agronomic Yield Gaps of Maize by Improved Soil, Cultivar, and Agricultural Management Practices in

Different Climate Zones of Northeast China. Earth Interactions 20: 1–18.

Lobell DB, Cassman KG and Field CB (2009) Crop yield gaps: Their importance, magnitudes, and causes. Annual Review of Environment and Resources 34: 179–204.

Lobulu J, Shimelis H, Laing M and Mushongi AA (2019) Maize production constraints, traits preference and current Striga control options in western Tanzania: farmers' consultation and implications for breeding. Acta Agriculturae Scandinavica Section B: Soil and Plant Science 69: 734–746.

Lonnquist JH (1961) Progress from recurrent selection procedures for the improvement of corn populations. University of Nebraska- Lincoln 197: 36.

Lyimo HJF, Pratt RC and Mnyuku RSOW (2011) Heritability and gene effect estimates for components of partial resistance to grey leaf spot of maize by generation mean analysis. Plant Breeding 130: 633–639.

Lynch P., Hunter R. and Kannenberg L. (1973) Relative performance of single cross, three-way cross, and double cross corn hybrids recommended in Ontario, 1968-72. Canadian Journal of Plant Science 53: 805–810.

Macrobert JF, Setimela P, Gethi J and Worku M (2014) Maize Hybrid Seed Production Manual. Mexico, D.F: CIMMYT, 2–3p.

Mai C, Wen C, Xu Z, Xu G, Chen S, Zheng J, Sun C and Yang N (2021) Genetic basis of negative heterosis for growth traits in chickens revealed by genome-wide gene expression pattern analysis. Journal of Animal Science and Biotechnology 12: 1–14.

Makinde SA, Olukemi J, Olayiwola RO, Ariyo O, Makinde AS, Porbeni JB, Oluseyi R, Omolayo O, Ariyo J, Oluseyi Olayiwola R and Ariyo OJ (2021) Performance of three-way maize hybrids across different agro-ecologies. Taylor and Francis 36: 582–592.

Manda J, Gardebroek C, Kuntashula E and Alene AD (2018) Impact of improved maize varieties on food security in Eastern Zambia: A doubly robust analysis. Review of

Development Economics 22: 1709–1728.

Márquez-Sánchez F and Sahagún-Castellanos J (2002) Synthetic varieties or composite varieties? Maydica 47: 103–105.

Masuka Benhildah, Atlin GN, Olsen M, Magorokosho C, Labuschagne M, Crossa J, Bänziger M, Pixley K V., Vivek BS, Von Biljon A, Macrobert J, Alvarado G, Prasanna BM, Makumbi D, Tarekegne A, Das B, Zaman-Allah M and Cairns JE (2017) Gains in maize genetic improvement in eastern and southern Africa: I. CIMMYT hybrid breeding pipeline. Crop Science 57: 1–12.

Masuka B, Magorokosho C, Olsen M, Atlin GN, Bänziger M, Pixley K V., Vivek BS, Labuschagne M, Matemba-Mutasa R, Burgenõ J, Macrobert J, Prasanna BM, Das B, Makumbi D, Tarekegne A, Crossa J, Zaman-Allah M, Van Biljon A and Cairns JE (2017) Gains in maize genetic improvement in eastern and southern Africa: II. CIMMYT open-pollinated variety breeding pipeline. Crop Science 57: 180–191.

Mather K and Jinks JL (1977) Introduction to Biometrical Genetics Introduction to Biometrical Genetics. Chapman and Hall, London.

Mbogo PO, Dida MM and Owuor B (2015) Generation Means Analysis for Estimation of Genetic Parameters for Striga hermonthica Resistance in Maize (Zea mays L.). Journal of Agricultural Science 7: 143–155.

McCann J (2009) Maize and grace : Africa’s encounter with a New World crop, 1500-2000. Harvard University Press, Cambridge.

Meng EC, Hu R, Shi X and Zhang S (2006) Maize in China: Production Systems,Constraints and Research Priorities. 1–77p.

Miko I (2011) Epistasis : Gene Interaction and Phenotype Effects. Nature Education 6: 1–6.

Mulungu K and Ng’ombe JN (2019) Climate Change Impacts on Sustainable Maize Production in Sub-Saharan Africa: A Review. Intechopen 1: 1–11.

Mushayi M, Shimelis H, Derera J, Shayanowako AIT and Mathew I (2020) Multi-environmental evaluation of maize hybrids developed from tropical and temperate lines. Euphytica 216: 1–14.

Mushongi AA, Derera J, Tongoona P and Lyimo NG (2013) Generation mean analysis of leaf chlorophyll concentration from mid-silking to physiological maturity in some tropical maize (Zea mays L.) genotypes under low and high nitrogen dosages. Euphytica 189: 111–122.

Musundire L, Dari S and Derera J (2015) Genetic analysis of grain yield performance and weevil [Sitophilus zeamais (Motschulsky)] resistance in southern African maize hybrids. Maydica electronic publication 60: 1–9.

Musundire L, Derera J, Dari S and Tongoona P (2021) Assessment of genetic gains for grain yield and components from introgression of temperate donor inbred line into tropical elite maize inbred lines: II. Performance inter se. Euphytica 217: 1–25.

Musundire L, Derera J and Tongoona P (2019) Genetic Variation and Path Coefficient Analysis of Introgressed Maize Inbred Lines for Economic Traits. Euphytica 11: 1–15.

Naveed A, Khan A and Khan I (2009) Generation mean analysis of water stress tolerance in okra (Abelmoschus esculentus L.). Pakistan Journal of Botany 41: 195–205.

Neumann K, Verburg P, Stehfest E, Systems CM-A and 2010 U (2010) The yield gap of global grain production: A spatial analysis. Elsevier 103: 316–326.

Novoselovic D, Baric M, Drezner G, Gunjaca J and Lalic A (2004) Quantitative inheritance of some wheat plant traits. Genetics and Molecular Biology 27: 92–98.

Ojuederie OB, Ogunmoyela O, Omidiji O and Oyedeji SI (2011) Agricultural Biotechnology the Panacea for Food Security in Sub-Saharan Africa. Libyan Agriculture Research Center Journal Internation 2: 123–132.

Otegui ME and Bonhomme R (1998) Grain yield components in maize: I. Ear growth and kernel set. Field Crops Research 56: 247–256.

Palmer PI, Wainwright CM, Dong B, Maidment RI, Wheeler KG, Gedney N, Hickman JE, Madani N, Folwell SS, Abdo G, Allan RP, Black ECL, Feng L, Gudoshava M, Haines K, Huntingford C, Kilavi M, Lunt MF, Shaaban A and Turner AG (2023) Drivers and impacts of Eastern African rainfall variability. Nature Reviews Earth and Environment 4.

.

Qaim M (2020) Role of New Plant Breeding Technologies for Food Security and Sustainable Agricultural Development. Applied Economic Perspectives and Policy 42: 129–150.

Ranum P, Peña JP, Peña-Rosas P, Garcia-Casal MN and Nieves Garcia-Casal M (2014) Global maize production, utilization, and consumption. Annals of the New York Academy of Sciences 1312: 105–112.

Ritchie JT and Alagarswamy G (2003) Model Concepts to Express Genetic Differences in Maize Yield Components. Agronomy Journal 95: 4–9.

Rusike J and Donovan PA (1995) The maize seed industry in Zimbabwe. Development Southern Africa 12: 189–196.

Saeed MB and Laing MD (2023) Biocontrol of Maize Weevil, Sitophilus zeamais Motschulsky (Coleoptera: Curculionidae), in Maize over a Six-Month Storage Period. Microorganisms 11.

Said AA (2014) Generation mean analysis in wheat (Triticum aestivum L.) under drought stress conditions. Annals of Agricultural Sciences 59: 177–184.

Sain Dass K, Manivannan A and Chikkappa GK (2009) Single cross hybrid maize – A viable solution in the changing climate scenario. Indian Journal of Genetics and Plant Breeding 69: 331–334.

Salama HSA, Nawar AI, Khalil HE and Shaalan AM (2021) Improvement of maize productivity and n use efficiency in a no-tillage irrigated farming system: Effect of cropping sequence and fertilization management. Plants 10.

Salegua V, Melis R, Fourie D, Sibiya J and Musvosvi C (2021) Generation mean analysis for resistance to bacterial brown spot disease in dry bean. New Zealand Journal of Crop and Horticultural Science 1: 1–14.

Sharifi P, Dehghani H, Momeni A and Moghaddam M (2013) Genetic evaluation of some morphological traits in rice by mean generation analysis. Iranian Journal of Field Crop Science 42: 1–13.

Shull G (1952) Beginnings of the Heterosis concept. Princeton University. Available at <https://scholar.google.com/scholar> Accessed on March 22, 2022.

Sibiya J (2010) Breeding Investigations for Resistance to Phaeosphaeria Leaf Spot (PLS) and other Important Folira Diseases and a Study of Stability in African Maize Germplasm. PhD Thesis. University of KwaZulu-Natal.

Sibiya J, Tongoona P, Derera J and Makanda I (2013) Smallholder farmers perceptions of maize diseases, pests, and other production constraints, their implications for maize breeding and evaluation of local maize cultivars in KwaZulu-Natal, South Africa. African Journal of Agricultural Research 8: 1790–1798.

Singh B (2016) Plant Breeding: Principles and Methods. Kaylani, Mumbai, India.

Singh DP, Singh AK and Singh A (2021) Inbreeding depression and heterosis. Plant Breeding and Cultivar Development 291–303.

Singh R, Ram L and Srivastava RP (2012) A Journey of Hybrids in Maize : An Overview. Indian Research Journal of Extension Education Special Issue I: 340–344.

Sinyolo S (2020) Technology adoption and household food security among rural households in South Africa: The role of improved maize varieties. Technology in Society 60: 101214.

Siziba S, Nyikahadzoi K, Nyemeck JB, Diagne A, Adewale A and Oluwole F (2013) Estimating the impact of innovation systems on maize yields: The case of Iar4d in southern Africa. Agrekon 52: 83–100.

Smale M, Byerlee D, Jayn T and Jayne TS (2011) Maize Revolutions in Sub-Saharan Africa. Nairobi, 3–5p.

Smale M and Jayne TS (2004) Maize Breeding in East and Southern Africa, 1900–2000. Washington DC, USA.

Srinivas B and Genet DB (2015) Estimation of genetic parameters through generation mean analysis for fiber quality traits in upland cotton. Society for the Advancement of Breeding Research in Asia and Oceania 47: 238–247.

Sujiprihati S (2014) Convergence of Food Security, Energy Security and Sustainable Agriculture. Biotechnology in Agriculture and Forestry 67: 173–196.

Sujiprihati S, Saleh G and Ali E. (2003) Performance and yield predictions in double cross hybrids of tropical grain maize. Pertanika Journal of Tropical Agricultural Science 26: 27–34.

Taj N, Ajmal S and Saleem R (2012) Yield Performance of Single / Double Crosses and F2 Progenies in Maize (Zea mays L.). Journal of Agricultural Science and Technology 50: 469–476.

Tandzi LN and Mutengwa CS (2020) Estimation of Maize (Zea mays L.) Yield Per Harvest Area: Appropriate Methods. Agronomy 10: 29.

Tollenaar M and Lee EA (2002) Yield potential, yield stability and stress tolerance in maize. Field Crops Research 75: 161–169.

Viola G, Ganesh M, Reddy SS and Kumar CVS (2003) Heritability and Genetic Advances studied of Elite baby corn (Zea mays L.) lines-Indian Journals. Progressive Agriculture 3: 127–128.

Wamatsembe IM, Asea G and Haefele SM (2017) A survey: Potential impact of genetically modified maize tolerant to drought or resistant to stem borers in Uganda. Agronomy 7: 1–

16.

Welu G (2015) Synthetic Varieties : History , Development and Applications in Crop Improvement. Advances in Life Science and Technology 32: 23–29.

White R and Connolly B (2011) Breeding Organic Vegetables: A Step-by-Step Guide for Growers, 1st ed. Dyck E (ed). Northeast Organic Farming Association of New York, New York, 39p.

Xu Y, Li P, Zou C, Lu Y, Xie C, Zhang X, Prasanna BM and Olsen MS (2017) Enhancing Genetic Gain in the Era of Molecular Breeding. Journal of experimental botany 68: 2641–2666.

Xu Y, Liu X, Fu J, Wang H, Wang J, Huang C, Prasanna BM, Olsen MS, Wang G and Zhang A (2019) Enhancing Genetic Gain through Genomic Selection: From Livestock to Plants. Plant Communications 1: 1–21.

Yi Q, Liu Y, Hou X, Zhang X, Li H, Zhang J, Liu H, Hu Y, Yu G, Li Y, Wang Y and Huang Y (2019) Genetic dissection of yield-related traits and mid-parent heterosis for those traits in maize (Zea mays L.). BMC Plant Biology 19: 392–411.

Zdunić Z, Nastasić A, Jocković D, Ivanović M, Dalović I, Mijić A and Jocković M (2008) Genetic analysis of grain yield and oil content in two maize populations. Periodicum Biologorum 114: 495–500.

CHAPTER 3

ANALYSIS OF THE RELATIVE YIELD ADVANTAGE OF ExpHybrid6 OVER OLD AND NEW HYBRIDS

Abstract

Continuous improvement of crops is of paramount importance for food security to be achieved. Rising global population entails that food demand must escalate by the corresponding proportion. This study examined the relative yield advantage of new hybrids (developed post-2000) over old hybrids (developed pre-2000). The trial was made up of eight commercial hybrids; two old and six new hybrids and planted across two sites in Zimbabwe, that is, Stapleford Research Centre (SRC) and Rattray Arnold Research Centre (RARS) during the 2021/22 summer season. The experimental design was a randomised complete block design (RCBD) with two replications at each site. Traits measured were days to mid silking (DMS), days to mid pollen (DMP), foliar diseases rating (maize streak virus, *Phaesophaeria* leaf spot, Northern Corn Leaf Blight), grain yield among other traits. The hybrids were significantly different ($P<0.05$) for grain yield. Statistically insignificant differences ($P >0.05$) were observed on anthesis-silking interval, Grey Leaf Spot (GLS) among other traits at RARS. Old hybrids were inferior in terms of foliar diseases rating. The mean grain yield forthe new hybrids was superior to that of the old hybrids. Entry six, ExpHybrid6, had superior grain yield mean across sites and the smallest Cultivar Superiority Index (CSI), the smaller the number the superior the cultivar. Its yield advantages were 2.41% with respect to the grain yield mean of the trial and 7.59% over the old hybrids. It is therefore recommended that farmers should tap into ExpHybrid6's exceptional yield potential and improve productivity and food security.

3.1 Introduction

Over 1.2 billion people in Africa and Latin America use maize as staple food and by 2030 it will be the most traded crop on the planet (Erenstein et al. 2022). It is vital for plant breeders to continuously improve crop yields to match and sustain the growing population. Not solely is production threatened by population growth, new diseases such as maize lethal necrosis disease (MLND), pests like fall armyworm (FAW) and frequency of droughts due to climate change also contribute to reduced productivity and production. Against this background, it is crucial for breeders to evaluate genetic gains and measure progress in their breeding programs for crop improvement.

In order to develop new breeding strategies, it is crucial to measure genetic gains achieved over time (Badu-Apraku et al. 2013). The process of artificial selection that results in performance growth over a defined period of time was described by Xu et al. (2017) as genetic gain. For plant breeders to match the ongoing demand for superior products, they must continuously enhance their genetic gain potential. Musundire et al. (2021) recommend that breeders focus on developing market-oriented hybrids to counter the decline in average yields (Musundire et al. 2021). This then entails that the relative yield advantage of current of new hybrids over old hybrids should be assed. The relative yield advantage of maize refers to the improvement in yield achieved by using improved maize varieties compared to traditional or local varieties. It represents the difference in yield between the improved varieties and the baseline or reference varieties. A successful maize breeding program is directly related to the supremacy of the new hybrids released. The objective of this study was to estimate relative yield advantage of ExpHybrid6 over other new and old single cross maize hybrids bred and produced in Zimbabwe.

3.2 Materials and methods

3.2.1 Experimental design and description of sites

The experiment was made up of eight commercial hybrids, two of which are old hybrids while the other six are new hybrids. The hybrids were evaluated for genetic gain over two sites in Zimbabwe during the 2021/22 summer cropping season. The experimental design was a RCBD with two replications at each site. The sites were Stapleford Research Centre (SRC) and Rattray Arnold Research Station (RARS). The two sites were classified as sites as mid-altitude environments (Magorokosho et al. 2008). RARS generally receives more annual rainfall than SRC (Table 3-2). Soils at RARS are reddish clay while those at SRC are clay loam. There is high disease pressure at SRC due a higher altitude than RARS. Planting at SRC was done on 25 November 2021 while at RARS it was done on 18 December 2021. Spacing of 0.75 m between rows and 0.25 m between plants was used, giving a population of 53000 plants/ha. Consisted of two rows of eight plants per row. The standard agronomic practices were done as per recommendation for each site. Description of hybrids and detailed climatic data for the sites are given in Tables 3-1 and 3-2, respectively.

Table 3- 1: Description of varieties for the 2021-22 experiment

Entry	Hybrid description	Maturity	Year of release
ExpHybrid1	New	Medium	2015
ExpHybrid2	New	Medium	2017
ExpHybrid3	New	Medium	2017
ExpHybrid4 (SC701)	Old	Late	1994
ExpHybrid5 (SC709)	Old	Late	1997
ExpHybrid6	New	Late	2009
ExpHybrid7	New	Late	2017
ExpHybrid8	New	Medium	2016

Table 3- 2: Climatic data for the sites

Site name	Altitude (m)	Mean annual rainfall (mm)	Longitude	Latitude
RARS	1360	800	17° 16′ S	31° 31′ E
SRC	1466	700	17° 42′ S	30° 54′ E

RARS = Rattray Arnold Research Station; SRC = Stapleford Research Centre

3.2.2 Data collection

Following the CIMMYT Zimbabwe protocol, agronomically important traits were measured per plot basis (CIMMYT 1985). Traits measured and their brief description are presented in Table 3-3.

3.3 Data Analysis

Analysis of variance for both individual and across sites was done using Breeding Management Software (BMS) version 3.0.8 2021 (https://seedco.bmspro.io/ibpworkbench). Across site analysis was done for the two sites using the same software. The same software was used to calculate the Cultivar Superiority Index (CSI). Generally, CSI describe the variation in genotype performance in each environment in relation to the genotype with maximum performance (Bakare et al. 2022). As a result, performing CSI on each site proved challenging.

3.3.1 Estimation of relative yield advantage of ExpHybrid6, and new versus old hybrids

The relative yield advantage of ExpHybrid6 over all the other hybrids and that of new hybrids over old hybrids was calculated using the following formulae:

I. *Relative Yield Advantage of Hybrid6 over Hybrid1 =*
*((Mean of Hybrid6 – Mean of Hybrid1)/Mean of Hybrid1)) * 100*

II. *Relative Yield Advantage of Hybrid6 over Hybrid2 =*
*((Mean of Hybrid6 – Mean of Hybrid2)/Mean of Hybrid2)) * 100*

III. *Relative Yield Advantage of Hybrid6 over Hybrid3 =*
*((Mean of Hybrid6 – Mean of Hybrid3)/Mean of Hybrid3)) * 100*

IV. *Relative Yield Advantage of Hybrid6 over Hybrid4 =*
*((Mean of Hybrid6 – Mean of Hybrid4)/Mean of Hybrid4)) * 100*

V. *Relative Yield Advantage of Hybrid6 over Hybrid6 =*
*((Mean of Hybrid5 – Mean of Hybrid6)/Mean of Hybrid5)) * 100*

VI. *Relative Yield Advantage of Hybrid6 over Hybrid7 =*
*((Mean of Hybrid6 – Mean of Hybrid7)/Mean of Hybrid7)) * 100*

VII. *Relative Yield Advantage of Hybrid6 over Hybrid8 =*
*((Mean of Hybrid6 – Mean of Hybrid8)/Mean of Hybrid8)) * 100*

VIII. *Relative Yield Advantage of New hybrids over Old hybrids =*
*((Mean of new hybrids – Mean of old hybrids)/Mean of old hybrids)) * 100*

Table 3- 3: List of traits recorded

Trait	Abbreviation	Criteria used
Anthesis	AD	Measured as the number of days from effective planting date to 50% pollen shed.
Silking day	SD	Measured as the number of days from planting to 50% silking.
Anthesis silking interval	ASI	Calculated as the difference between AD and SD.
Plant height	PH	Determined by randomly selecting 10 plants from a plot and measuring the distance between the base of the plant and where the tassel starts to branch.
Ear height	EH	Determined on those plants whose heights were measured by measuring the distance in centimetres from the plant base to the node that bears the upper ear.
Total lodging	TL	Determining by adding the number of plants that lodged as a result of root and stalk lodging.
Root lodging %	RL%	Root lodging incidence
Husk cover	HC	Obtained by counting the number of bare tips then express them as a percentage of the total number of plants in a plot.
Shelling percentage	SH%	Determined by calculating the weight of shelled grain as percentage of unshelled cob weight.
Number of plants	NP	Determined by recording the number of plants per plot after thinning.
Number of ears harvested per plot	EHP	Determined by recording the number of ears harvested per plot.
Moisture content	MOI	Determined by recording moisture percentage of grain after shelling.
Grain yield	GY	Determined by adjusting grain weight to 12.5% moisture content and converting to tonnes ha^{-1}.
Grey leaf spot	GLS	Scores were taken for severity of GLS (*Cercospora zeae maydis*) using a disease rating scale where 1 = 0% and 9 = 75–100% leaf area showing disease symptoms.
Northern corn leaf blight	NBLT	Records were taken for the severity of Northern corn leaf blight (*Exserohilum turcicum*) using a disease rating scale where 1 = 0% and 9 = 75–100% leaf area showing disease symptoms
Maize streak virus	MSV	Records were taken for the severity of MSV symptoms using a disease rating scale where 1 = 0% and 9 = 75–100% leaf area showing disease symptoms.
Rust	RST	Records were taken for the severity of rust symptoms (*Puccinia sorghi*) using a disease rating scale where 1 = 0% and 9 = 75–100% leaf area showing disease symptoms.
Phaeosphaeria leaf Spot	PLS	Records were taken for the severity of *Phaeosphaeria* Leaf Spot symptoms using a disease rating scale where 1 = 0% and 9 = 75–100% leaf area showing disease symptoms.
Ear position ratio	EPR	Determined by dividing plant height by ear height.

Source: (CIMMYT 1985)

3.3.2 Heritability

The BMS statistical package (The Breeding Management System Version 3.0.8 2021) generates generalized heritability. This type of heritability differs with standard heritability in that it uses average pairwise predictions error to obtain genetic and error covariance matrices thereby allowing estimation of unbalanced data with complicated error and genetic structures.

3.4 Results

At both SRC and RARS sites, heritability estimates of > 0.5 were observed grain yield. ExpHybrid6 had highest yield of 10.3 t h^{-1}. ExpHybrid3 and ExpHybrid7 had the lowest yield at SRC and RARS, respectively. Generally, most traits were statistically significant ($P<0.05$) except for number of plants, maize streak virus and root lodging percentage. Combined analysis of variance indicated that ExpHybrid6 was the highest, while entries ExpHybrid7 and ExpHybrid8 were the lowest in grain yield. Grain yield mean was 8.3 t ha^{-1} and only three hybrids had yields above the overall trial mean. Tables 3-4, 3-5 and 3-6 show results from RARS, SRC and combined (RARS and SRC), respectively. In terms of other traits, entry ExpHybrid6 had the lowest disease scores, especially grey leaf spot, whereas ExpHybrid4 and ExpHybrid5 had the highest disease score.

Table 3- 4: Trial mean (RARS)

Genotypes	GY	MOI	AD	SD	PH	EH	EPR	GLS	NBLT	PLS	SHpct
ExpHybrid1	9.3	16.2	69.5	69.0	3.0	1.4	0.4	6.1	1.4	2.0	77.8
ExpHybrid2	10.9	15.4	72.5	72.5	3.0	1.3	0.4	3.8	1.3	1.5	81.4
ExpHybrid3	10.0	17.1	70.0	70.0	3.2	1.5	0.5	5.4	1.6	1.0	84.0
ExpHybrid4	9.1	15.7	67.5	67.5	3.0	1.3	0.4	5.2	0.7	1.5	81.7
ExpHybrid5	8.3	16.3	68.0	68.5	3.0	1.3	0.4	5.3	2.3	2.0	80.9
ExpHybrid6	12.0	15.2	67.5	68.0	3.1	1.5	0.5	3.4	2.1	1.5	81.8
ExpHybrid7	7.0	15.6	68.5	69.5	2.9	1.3	0.4	5.7	1.2	1.0	81.5
ExpHybrid8	8.0	15.0	70.0	70.0	3.1	1.3	0.4	4.1	2.9	1.0	64.6
Mean	9.1	15.8	69.2	69.4	3.0	1.4	0.4	4.9	1.7	1.4	79.2
CV	13.5	8.3	2.7	3.4	5.5	10.8	8.2	35.8	78.9	66.2	5.7
Heritability	0.6	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.8
Variance	3.5	1.7	4.0	4.7	0.0	0.0	0.0	3.2	1.3	0.5	43.5
SD	1.9	1.3	2.0	2.2	0.2	0.1	0.0	1.8	1.1	0.7	6.6
P-value	0.003	0.708	0.057	0.429	0.909	0.576	0.654	0.682	0.743	0.872	0.000

GY = Grain yield; MOI = Grain moisture content; AD = Anthesis Day; SD = Silking Day; EH = Ears Harvested; PH = Plant Height; EH = Ear Height; EPR = Ear Position Ratio; GLS = Grey Leaf Spot; NBLT = Northern Leaf Blight; PLS = *Phaeosphaeria* Leaf Spot; SHpct = Shelling percentage.

Table 3- 5: Trial mean (SRC)

Genotypes	GY	MOI	AD	SD	PH	EH	GLS	MSV	PLS	RST	SHpct
ExpHybrid1	7.5	19.9	73.5	73.5	3.1	1.8	2.1	1.0	1.5	1.0	78.1
ExpHybrid2	6.8	17.5	71.7	72.9	3.1	1.7	3.5	1.0	1.0	1.0	80.3
ExpHybrid3	6.5	18.1	71.5	72.5	3.0	1.5	1.9	1.0	4.0	2.0	78.7
ExpHybrid4	6.8	16.3	75.8	77.1	3.1	1.7	6.0	2.0	2.0	2.5	82.4
ExpHybrid5	7.4	18.9	71.7	72.9	2.8	1.5	5.0	1.0	1.0	3.0	84.0
ExpHybrid6	8.6	16.9	77.0	77.5	3.0	1.7	1.9	1.0	1.0	1.0	78.9
ExpHybrid7	7.9	15.7	74.3	74.1	2.9	1.6	2.0	1.0	2.0	1.0	77.9
ExpHybrid8	7.0	17.4	74.5	75.0	3.1	1.8	1.6	1.0	2.0	1.0	77.6
Mean	7.3	17.6	73.8	74.4	3.0	1.7	3.0	1.1	1.8	1.6	79.7
CV	9.4	5.6	1.1	1.7	2.4	4.1	39.0	48.0	47.4	36.4	0.7
Heritability	0.6	0.8	0.9	0.8	0.8	0.8	0.8	0.0	0.7	0.8	1.0
Variance	0.6	2.2	3.8	4.3	0.0	0.0	3.2	0.3	1.2	0.8	5.3
SD	0.8	1.5	1.9	2.1	0.1	0.1	1.8	0.5	1.1	0.9	2.3
P-value	0.017	0.000	0.000	0.000	0.000	0.000	0.000	0.429	0.003	0.000	0.000

GY = Grain yield; MOI = Grain moisture content; AD = Anthesis Day; SD = Silking Day; PH = Plant Height; GLS = Grey Leaf Spot; PLS = *Phaeosphaeria* Leaf Spot; SHpct = Shelling percentage.

Table 3- 6: Combined analysis for SRC and RARS.

Genotypes	**GY**	**CSI**	**MOI**	**AD**	**SD**	**PH**	**EH**	**GLS**	**PLS**
ExpHybrid1	8.37	2.22	18.10	71.52	71.26	3.05	1.58	4.11	1.75
ExpHybrid2	8.86	1.13	16.45	72.12	72.70	3.06	1.50	3.66	1.25
ExpHybrid3	8.28	2.09	17.58	70.73	71.24	3.08	1.52	3.64	2.50
ExpHybrid4	7.96	2.93	16.00	71.63	72.30	3.06	1.48	5.59	1.75
ExpHybrid5	7.82	3.91	17.62	69.87	70.70	2.87	1.41	5.16	1.50
ExpHybrid6	10.32	0.00	16.03	72.23	72.74	3.04	1.59	2.64	1.25
ExpHybrid7	7.45	6.43	15.68	71.38	71.80	2.92	1.44	3.84	1.50
ExpHybrid8	7.50	4.69	16.22	72.27	72.51	3.08	1.57	2.86	1.50
Mean	8.32		16.71	71.47	71.91	3.02	1.51	3.94	1.63
CV	18.00		8.71	2.89	2.87	4.69	8.39	29.22	36.68
P-value	0.09		0.01	0.00	0.00	0.41	0.00	0.00	0.85

GY = Grain yield; CSI = Cultivar Superiority Index; MOI = Grain moisture content; AD = Anthesis Day; SD = Silking Day; PH = Plant Height; EH = Ear Height; GLS = Grey Leaf Spot; PLS = *Phaeosphaeria* Leaf Spot.

3.4.1 Relative yield advantage of ExpHybrid6

The grain yield advantage of new hybrids versus old hybrids was 7.59%, and for EH, 7.14%. Of particular interest is GLS, which had relative yield advantage of -35.19%. Due to its yield, which was higher than all other hybrids, most of the analysis on centred ExpHybrid6. Table 3-7 summarises the relative percentage yield advantage of ExpHybrid6 with respect to trial mean, mean of new hybrids, mean of old hybrids and mean of medium hybrids on selected traits. The ExpHybrid6 had highest yield and lowest GLS rating score. Table 3-8 shows means of ExpHybrid6, trial mean, old hybrids, and new hybrids, late and medium maturing hybrids. ExpHybrid6 had the highest mean grain yield of 10.3 t ha^{-1}. Compared to the other hybrids studied, it is very late and has the highest ear height position. The relative yield advantage of ExpHybrid6 over the other seven hybrids is presented in Table 3-9. The relative Percentage yield advantages ranged from 15.73% (ExpHybrid2) to 37.33% (ExpHybrid7). .

Table 3- 7: Relative yield advantage of ExpHybrid6 on selected traits.

Traits	**RY$_A$**	**RY$_B$**	**RY$_C$**	**RY$_D$**
GY	2.41	7.59	7.06	1.20
AD	0.28	1.41	-1.39	-0.56
SD	0.14	0.70	-0.69	0.00
PH	0.00	0.00	0.00	-3.23
EH	0.00	7.14	-6.67	0.00
GLS	-10.26	-35.19	54.29	0.00

GY = Grain yield; AD = Anthesis Day; SD = Silking Day; PH = Plant Height; EH = Ear Height; GLS = Grey Leaf Spot; RY$_A$= Relative yield advantage with respect to trial mean; RY$_B$ = Relative yield advantage with respect to mean of old hybrids; RY$_C$ = Relative yield advantage with respect to mean of new hybrids; RY$_D$ = Relative yield advantage with respect to mean of medium hybrids.

Table 3- 8: Summary of means for selected traits on ExpHyrid6, trial mean, new, old, medium and late hybrids across two sites.

Traits	**Mean of ExpHybrid6**	**Trial Mean**	**Mean of New hybrids**	**Mean of Old hybrids**	**Mean of late hybrids**	**Mean of medium hybrids**
GY	10.3	8.3	8.5	7.9	8.40	8.30
AD	72.2	71.5	71.7	70.7	71.30	71.70
SD	72.7	71.9	72.0	71.5	71.90	71.90
PH	3.0	3.0	3.0	3.0	3.00	3.10
EH	1.6	1.5	1.5	1.4	1.50	1.50
GLS	2.6	3.9	3.5	5.4	3.60	3.60

GY = Grain yield; AD = Anthesis Day; SD = Silking Day; PH = Plant Height; EH = Ear Height; GLS = Grey Leaf Spot.

Table 3- 9: Relative yield advantage of ExpHybrid6 over other hybrids.

Hybrid	**Mean Grain yield**	**Relative Yield advantage (%)**
ExpHybrid1	8.4	22.62
ExpHybrid2	8.9	15.73
ExpHybrid3	8.3	24.10
ExpHybrid4	8.0	28.75
ExpHybrid5	7.8	32.05
ExpHybrid6	10.3	0.00
ExpHybrid7	7.5	37.33
ExpHybrid8	7.5	37.33

3.4.2 Heterosis

High heterosis levels for the F_1 with respect to the parents was detected in all traits (Table 3-10).

Table 3- 10: Heterosis of the maize hybrid ExpHybrid6

	Heterosis for F1 (%)			**Heterosis for F2 (%)**		
Parameter	**MPH**	**P1**	**P2**	**MPH**	**P1**	**P2**
DPS	-8	-5	-11	-6	-3	-9
DSE	-7	-4	-10	-5	-2	-8
PH	70	81	60	26	45	28
EH	76	76	76	29	41	41
NL	11	16	7	6	11	3
NLAE	6	20	-5	5	19	-6
TBN	49	80	28	23	56	11
FW	157	184	135	42	89	57
GW	171	212	139	42	100	53
MOI	9	8	11	9	9	12
SHL	11	15	7	2	6	-2
EL	34	64	13	12	39	-4
KER	59	60	59	24	32	31
KRN	9	0	19	3	-5	14
HKW	50	114	15	16	69	-9
KPE	79	62	100	28	26	56
ED	29	32	27	14	19	14
CD	17	20	14	9	13	7
KD	48	49	46	20	27	25

DPS= days to pollen shed; DSE= days to silk emergence; PH = plant height (from the soil to flag leaf); EH = ear height (from soil to base of upper most ear); NL= total number of leaves; NLAE = number of leaves above uppermost ear; TBN=total number of tassel branches; FW= Field weight; GW = grain weight; MOI= grain moisture content; SHL= shelling percentage; EL = ear length; KER = Kernels per row; KRN = kernel row number; HKW = hundred kernel weight; KPE = kernels per ear; ED= ear diameter; CD = cob diameter; KD = kernel depth.

The highest heterosis values were 171% and 157% for grain yield and ear mass, respectively. With respect to better parent, P_1, highest heterosis values were 212% and 184% for grain yield and ear mass respectively. P_2 had 139% for grain yield and 135% for ear mass. Mid-parent heterosis values of above 50% were observed on plant height (70%), ear height (76%), grains per cob (79%), grains per row (59%) and hundred kernel weight (50%). On the other end, days to mid pollen and days to mid silking had negative mid-parent heterosis values which means hybrids were early to shade pollen than silk. Traits like the total leaves above the top most cob, and grains per row had single digit heterosis values of 6% and 9%, respectively. Heterosis values dropped in the F_2 generation across all traits.

ExpHybrid6 was the only hybrid in the study that had heterosis measured due to its involvement in the analysis of generation means. Furthermore, the parents of the other hybrids were not available for this study.

3.5 Discussion

The objective of this trial was to measure the relative yield advantage of "ExpHyrid6" over old and new hybrids. The results showed that the experimental hybrid ExpHybrid6 yield advantage over the other hybrids. The ExpHybrid6 had 15.73% advantage over the experimental hybrid and 37.33% over the experimental hybrid "ExpHybrid7" and "ExpHybrid8". This is an indication it is a good hybrid. Genetic variability determines the extent to which maize breeding populations can improve traits through genetic improvement. Agronomic and grain yield differences among the hybrids tested revealed significant differences. A significant amount of variation was found for the majority of the secondary traits, which indicates that the traits used in the study had adequate genetic diversity.

As a result of genetic diversity, plant breeders are able to select new and improved maize varieties with desirable economic traits (Badu-Apraku et al. 2021). The results have shown that ExpHybrid6 is superior to old hybrids due to its outstanding yield. This was further confirmed by the cultivar superiority index (CSI), which is a non-parametric stability analysis whereby the mean square differences between a cultivar observed value and that of the best variety within a given environment (Lin and Binns 1988). The closer the CSI is to zero, the superior the hybrid. The superiority of ExpHybrid6 means that the hybrid was a good candidate for replacing old hybrids. Varietal replacement entails that old hybrids should be replaced when revenue realized begins to decline (Chivasa et al. 2022).

An effective evaluation of genetic gains needs to be conducted over a specified time frame, known as an era trial (Rutkoski 2019). The realised yield advantage for ExpHybrid6 with respect to mean of old hybrids and trial mean for grain yield were 7.59% and 2.41% respectively. The realised genetic gains were in favour of new hybrids for many traits except for AD and SD. New hybrids including the hybrid under study had better resistance to disease than older hybrids, as evidenced by negative gains in GLS. This shows that new hybrids had more resistance to GLS than old hybrids mainly due a combination of improved genetic resources and breeding methods (conventional). GLS caused massive yield losses in the late 90s resulting in decommissioning of many commercial hybrids. It has been reported that grey leaf spot results in yield losses of up to 25% (Sibiya et al. 2012).

Heterosis was confirmed for the hybrid ExpHybrid6. Different traits had varying values of heterosis and this is consistent with other studies like Kaeppler (2012) who reported that heterosis depends largely on the trait under study with yield having greatest heterosis. Positive heterosis is desirable since it is an indicator of high yield (Duvick 2005). Heterosis was considerably larger for grain yield than other traits, this corroborates with the position that highly complex traits such as grain yield often have greater heterosis (Kaeppler 2012). Heterosis values of ExpHybrid6 relative to the parental lines were quite high. The high mid-parent heterosis values are consistent with Derera and Musimwa (2015) who reported mid parent heterosis (311%) values between 14 % – 996 %.

Negative heterosis values were obtained for days to pollen shed and days to silk emergence. This corroborates with findings by Derera and Musimwa (2015) and Ndaruhutse (2016) who both reported negative heterosis for days to pollen shed and days to silk emergence. This indicates that F_1 hybrid flowers earlier than parental lines. Derera and Musimwa (2015) further reported high values for better parent heterosis, similar to the findings of this study. Heterosis values of 108.61% for grain yield were observed in a study on combining ability and heterosis for yield and yield components in maize (Atif et al. 2012). Vivek et al. (2009) reported grain yield mid parent heterosis of 33.5 % while Gissa et al. (2007) reported 89.2% on a study on maize. Oyekunle and Badu-Apraku (2014) and Shahrokhi et al. (2011) reported heterosis values of 102.6% and 112.75%, respectively in maize grain yield Li et al. (2001) reporting 324.7 % in rice research.

In this study heterosis levels severely decreased at F_2 in relation to F1. Mid-parent heterosis for grain yield was 171% at F1 but dropped to 42 % at F_2, this corroborate with Falconer (1989) who reported that heterosis declines by 50% in the F_2 generation. This drop in heterosis vindicates the position that farmers will suffer yield losses by planting F_2 seed. The use of recycled seeds is prevalent in some parts of SSA mainly because of lack of resources to buy hybrid seeds every season. Poor distribution frameworks for hybrids, especially in remote areas and inaccessible areas also contributes to the continued use of recycled seed resulting in the farmers losing out on yield advantage even in a good season.

3.6 Conclusion

Relative advantages were observed for grain yield relative to both the mean of trial and old hybrids. Relative yield advantage with respect to trial mean were 2.41% whilst relative to olds hybrids were 7.59%. Secondary traits such as anthesis day and silking day also had advantages of 0.28% and 0.14% with respect to mean of trial, whilst with respect to old hybrids the gains were 0.70% and 1.41% respectively. Based on the results obtained it can be concluded that ExpHybrid6 is indeed a highly productive hybrid. This hybrid was bred using conventional breeding methods and underwent vigorous testing before getting registered for commercial release. Its performance against old hybrids showed that new hybrids are better than old hybrids. Maize breeding programs in Africa should invest in breeding of single crosses as they have the potential of reducing the yield gap. Furthermore, heterosis was confirmed through generation mean analysis with different traits having varying values.

References

Asea G, Kwemoi DB, Sneller C, Kasozi CL, Das B, Musundire L, Makumbi D, Beyene Y and Prasanna BM (2023) Genetic trends for yield and key agronomic traits in pre- commercial and commercial maize varieties between 2008 and 2020 in Uganda. Frontiers in Plant Science 14: 1–13.

Atif I, Awadalla A, Khalafalla M, Idris A and Osman A (2012) Combining Ability and Heterosis for Yield and Yield Components in Maize. Australian Journal of Basic and Applied Sciences 6: 36–41.

Badu-Apraku B, Obisesan O, Abiodun A and Obeng-Bio E (2021) Genetic Gains from Selection for Drought Tolerance during Three Breeding Periods in Extra-Early Maturing Maize Hybrids under Drought and Rainfed Environments. Agronomy 11: 831.

Badu-Apraku B, Yallou C and Oyekunle M (2013) Genetic gains from selection for high grain yield and Striga resistance in early maturing maize cultivars of three breeding periods under Striga-infested and Striga-free environments. Field Crops Research 147: 54–67.

Bakare MA, Kayondo SI, Aghogho CI, Wolfe MD, Parkes EY, Kulakow P, Egesi C, Rabbi IY and Jannink JL (2022) Exploring genotype by environment interaction on cassava yield and yield related traits using classical statistical methods. PLoS ONE 17: 1–24.

Chivasa W, Worku M, Teklewold A, Setimela P, Gethi J, Magorokosho C, Davis NJ and Prasanna BM (2022) Maize varietal replacement in Eastern and Southern Africa: Bottlenecks, drivers and strategies for improvement. Global Food Security 32: 100589.

CIMMYT (1985) Managing Trials and Reporting Data for CIMMYT's International Maize Testing Program, 5th ed. CIMMYT, Mexico, 11–16p.

Demand-Led Breeding (2020) Demand-Led breeding |. Available at <https://www.demandledbreeding.org/> Accessed on February 24, 2022.

Derera J and Musimwa TR (2015) Why SR52 is such a great maize hybrid? I. Heterosis and generation mean analysis. Euphytica 205: 121–135.

Duvick DN (2005) The Contribution of Breeding to Yield Advances in maize (Zea mays L.). Advances in Agronomy 86: 83–145.

Erenstein O, Jaleta M, Sonder K, Mottaleb K and Prasanna BM (2022) Global maize production, consumption and trade: trends and R&D implications. Food Security 14: 1295–1319.

Gissa DW, Zelleke H, Labuschagne MT, Hussien T, Singh H, Zelleke H, Labuschagne MT, Hussien T and Singh H (2007) Heterosis and combining ability for grain yield and its components in selected maize inbred lines. South African Journal of Plant and Soil 24: 133–137.

Kaeppler S (2012) Heterosis: Many Genes, Many Mechanisms—End the Search for an Undiscovered Unifying Theory. International Scholary Research Network Botany 2012: 1–12.

Laidig F, Piepho HP, Rentel D, Drobek T, Meyer U and Huesken A (2017) Breeding progress, variation, and correlation of grain and quality traits in winter rye hybrid and population varieties and national on-farm progress in Germany over 26 years. Theoretical and Applied Genetics 130: 981–998.

Li Z, Luo LJ, Mei HW, Wang DL, Shu QY, Tabien R, Zhong DB, Ying CS, Stansel JW, Khush GS and Paterson AH (2001) Overdominant Epistatic Loci Are the Primary Genetic Basis of Inbreeding Depression and Heterosis in Rice . I . Biomass and Grain Yield. Genetics Society of America 158: 1737–1753.

Lin CS and Binns MR (1988) A Superiority Measure of Cultivar Performance for Cultivar × Location Data. Canadian Journal of Plant Science 68: 193–198.

Lobulu J, Shimelis H, Laing M and Mushongi AA (2019) Maize production constraints, traits preference and current Striga control options in western Tanzania: farmers' consultation and implications for breeding. Acta Agriculturae Scandinavica Section B: Soil and Plant

Science 69: 734–746.

Magorokosho C, Vivek B and MacRobert J (2008) Characterization of Maize Germplasm Grown in Eastern and Southern Africa: Results of the 2007 Regional Trials Coordinated by CIMMYT. Harare, Zimbabwe. CIMMYT., 5–7p.

Masuka B, Atlin GN, Olsen M, Magorokosho C, Labuschagne M, Crossa J, Bänziger M, Pixley K V., Vivek BS, Von Biljon A, Macrobert J, Alvarado G, Prasanna BM, Makumbi D, Tarekegne A, Das B, Zaman-Allah M and Cairns JE (2017) Gains in maize genetic improvement in eastern and southern Africa: I. CIMMYT hybrid breeding pipeline. Crop Science 57: 1–12.

Musundire L, Derera J, Dari S and Tongoona P (2021) Assessment of genetic gains for grain yield and components from introgression of temperate donor inbred line into tropical elite maize inbred lines: II. Performance inter se. Euphytica 217: 1–25.

Ndaruhutse F (2016) Generation Mean Analysis for Diplodia Ear Rot Resistance in Tropical Maize Inbred Lines. University of Nairobi, Kenya. University of Nairobi, 55–58p.

Oyekunle M and Badu-Apraku B (2014) Genetic Analysis of Grain Yield and Other Traits of Early-Maturing Maize Inbreds under Drought and Well-Watered Conditions. Journal of Agronomy and Crop Science 200: 97–107.

Rutkoski JE (2019) A Practical Guide to Genetic Gain. Advances in Agronomy 157: 217–249.

Shahrokhi M, Khorasani, Saeed K and Ebrahimi A (2011) Generation Mean Analysis for Yield and Yield Components in Maize (Zea mays L .). Journal of Plant Physiology and Breeding 1: 59–72.

The Breeding Management System Version 3.0.8 (2021) The Integrated Breeding Platform. Available at <https://www.integratedbreeding.net/breeding-management-system> Accessed on June 11, 2023.

Vivek BS, Crossa J and Alvarado G (2009) Heterosis and Combining Ability Among Cimmyt

’ S Mid-Altitude Early To Intermediate Maturing Maize (Zea Mays L .) Populations. Maydica 54: 97–107.

Xu Y, Li P, Zou C, Lu Y, Xie C, Zhang X, Prasanna BM and Olsen MS (2017) Enhancing Genetic Gain in the Era of Molecular Breeding. Journal of experimental botany 68: 2641–2666.

Xu Y, Liu X, Fu J, Wang H, Wang J, Huang C, Prasanna BM, Olsen MS, Wang G and Zhang A (2019) Enhancing Genetic Gain through Genomic Selection: From Livestock to Plants. Plant Communications 1: 1–21.

CHAPTER 4

GENERATION MEAN ANALYSIS FOR YIELD AND YIELD COMPONENTS OF MAIZE HYBRID ExpHybrid6

Abstract

ExpHybrid6 is a single cross hybrid bred in Zimbabwe and produces exceptional yield both in farmers' fields and research plots. However, the genetic basis of its outstanding yield and heterosis has not be quantified. The goal of this study was to determine gene action controlling yield and yield components in ExpHybrid6 using generation means analysis. Six generations developed from two divergent, highly homozygous maize lines, that is, parents (P_1 and P_2), and its progenies F_1, F_2, BCP_1 and BCP_2, were evaluated in Zimbabwe at Stapleford Research Centre during 2020/21 and 2021/22 summer seasons. A randomized complete block design (RCBD) was used, and the data was analysed using SAS9.4 package following the PROC mixed protocols. The lack of fit test confirmed significant dominance and additive effects. Furthermore, epistasis was investigated by partitioning it into additive x additive, additive x dominance and dominance x dominance gene effects. The presence of epistasis of the dominance nature for grain yield was confirmed. With respect to relative importance of gene effects, non-fixable dominance effects contributed 95.54% to yield. Yield components such as ear weight, kernels per cob, ear diameter, cob diameter and kernel depth all contributed over 90%. The results are an indication that dominance gene action is the basis of superior performance of ExpHybrid6 yield. This implies that breeding focus should be on selecting superior lines based on their performance in crosses. The current maize breeding initiatives will be designed and improved using the information obtained this study.

4.1 Introduction

Maize production occupied 41.3 million hectares across SSA in 2020, which is 16.2% of estimated crop area and by 2030 it is expected that 50.9 million hectares will be under maize, representing 18.3% of the estimated crop area (Erenstein et al. 2021). Despite being a strategic crop to food security, maize yields across Africa have remained relatively low. Maize grain yield in SSA is the lowest with less than 1.8 t ha^{-1} compared to the global average of 5.8 t ha^{-1} (Masuka et al. 2017; Beyene et al. 2017; Erenstein et al. 2021). Low yields are attributed to poor yielding varieties, low usage of inputs, biotic and abiotic stress factors were among other contributing factors (Bello et al. 2010).

Due to changing weather patterns, new pests and diseases emerge, necessitating the development of new hybrids to improve yield and tolerance to biotic and abiotic stress factors. A single cross maize hybrid developed in Zimbabwe in 1960 became the first to be commercialized in the world (Seed Co Limited 2017). Since then, various single cross maize hybrids have been developed throughout the world. Top maize producers in the world like China and the USA grow single cross maize hybrids with great success (Makore et al. 2022). According to Musundire et al. (2021), South Africa's maize seed business is dominated by single crosses, both conventional and genetically modified. The maize breeding programs in SSA, with the exception of South Africa, have been focused on the production of three-way hybrids because they are inexpensive and can thrive in constrained growing conditions common in Africa, due to of the genetic buffer effect (Makore et al. 2022). The success story of maize improvement in the USA suggested that it is possible to improve productivity in SSA by developing and deploying single cross hybrids (Troyer 2004).

The future of maize hinges on yield improvement and stability across Africa and not on land expansion alone. Plant breeding efforts should be designed in a way to enhance food security in SSA. Maize breeding in Zimbabwe started in 1932 leading to the development of SR1 the first double cross commercial hybrid in 1949, followed by SR52 a single cross hybrid in 1960 (Eicher, 1995; Mashingaidze, 2006). These achievements led to increases in yield potential as well as drought and disease tolerance, which was beneficial to both small, medium and large-scale farmers. The second half of the 20th century was characterised by a noticeable jump in average maize yield per hectare. The maize yields went up three-fold within ten years following the release of SR52 (McCann, 2009). The world's top maize producers such as the USA, China and Brazil, heavily rely on single cross maize hybrids development.

Breeders can improve the traits and maximize the efficiency of breeding programmes through an understanding of the gene action governing the target traits (Mather and Jinks, 1982). Gene action can be studied using biometrical techniques such as biparental cross and triple test cross analysis, line x tester analysis, quadriallel analysis, triallel analysis, partial diallel cross, diallel analysis and generation mean analysis (Katragadda et al. 2020). This study used GMA to explore the basis of yield in a single cross maize hybrid ExpHybrid6. Generation mean analysis is preferred because, it gives information on the importance of additive and dominance, as well as epistatic gene effects, that is, additive x additive, dominance x dominance and additive x dominance (Said 2014). Moreover, it provides comprehensive analysis of a cross (Hayman 1960) and the populations developed usable in breeding programs (Coates and White, 1998).

The hybrid under study satisfied the requirements for generation mean analysis as proposed by Mather and Jinks, (1977). It was developed using inbred lines which were highly homozygous and divergent in terms of maturity. Estimation of gene effects is key in any breeding program as it helps in the formulation of new improved breeding programs (Said 2014). The hybrid under study phenotypically resembles SR52 by which its genetic basis of heterosis was investigated by Derera and Musimwa (2015). Just as the case with SR52, information obtained will be used to design and/or modify existing breeding strategies for breeding of productive inbred lines that will be used to produce better yielding hybrids. Heterosis has been exploited by maize breeders over many years and hybrid breeding programmes. This study investigated the yield basis ExpHybrid6 as a way of formulating approaches for further breeding and developing modified versions of the parental lines involved. The detailed information of the parental inbred lines are not going to be disclosed due to intellectual property issues.

4.2 Materials and methods

4.2.1 Germplasm and crosses for generation mean analysis

The genetically pure inbred seed and the F_1 generation were obtained from Seed Co Private Limited. For the purposes of this study, the actual names of the inbred lines used shall not be revealed due to intellectual property rights, and therefore, they will be referred to as parent 1 (P_1) and parent 2 (P_2). The F_1 was self-pollinated to produce F_2 in the winter of 2021 (off-season), May to October at Muzarabani Research Centre in Zimbabwe. Simultaneously, the two parents, P_1 and P_2, were backcrossed to F_1 to produce BCP_1 and BCP_2, respectively at the same site. The parental lines are maintained by Seed Co through self-pollination and they are homozygous and very divergent in maturity, and height, thus satisfying the requirements of generation mean analysis (Mather and Jinks, 1977).

4.2.2 The hybrid ExpHybrid6

The maize hybrid ExpHybrid6 is a late maturing tropical mid-altitude single cross hybrid which was bred by Seed Co Limited, one of the leading seed producers in Africa. Before it was commercially released, it was evaluated in various yield trials at the turn of the millennium across Zimbabwe, Zambia, Malawi, and Tanzania among other countries. Yield trials conducted by independent institutions like International Maize and Wheat Improvement Centre

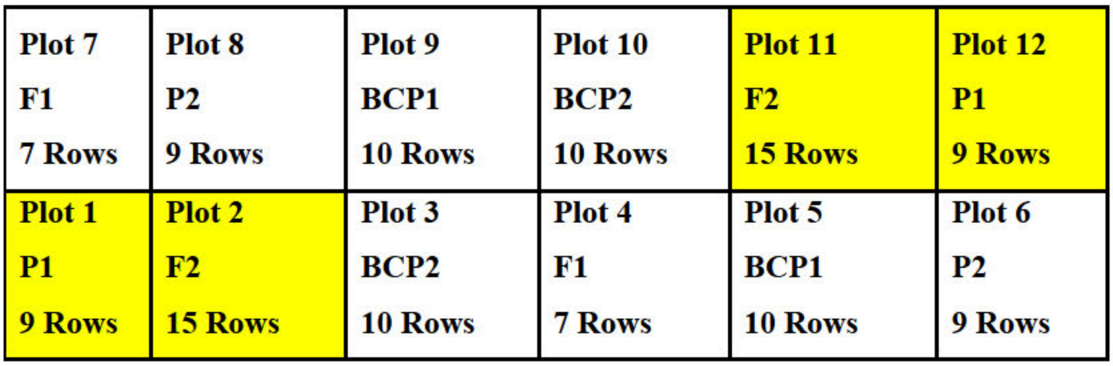
(CIMMYT) and Agricultural Research Trust (ART) showed that this hybrid can yield up to 18 t ha^{-1} under optimum conditions (unpublished). The hybrid has long cobs, deep kernels and high shelling percentage. It is also resistant to foliar diseases such as grey leaf spot (GLS), maize streak virus (MSV) and Northern Corn Leaf Blight (NCLB).

4.2.3 Experimental design and management

The six populations (P_1, P_2, BCP_1, BCP_2, F_1 and F_2) were evaluated over two successive seasons, 2020/21 and 2021/22 season at Stapleford Research Centre (SRC) located at 17° 42′ S (longitude) and 30° 54′ E (latitude) at 1466 meters above sea level. Randomised complete block design (RCBD) was used with two replications each season and different randomization. Two border rows of inbred lines between plots of vigorous generations, to minimise the effects of shading. For the non-segregating populations, P_1, P_2 and F_1, seven rows per plot were planted, however, in situations where the inbred line was next to a hybrid, two extra rows were planted to minimize shading. As a result, P_2 had 9 rows in replication 1 and P_1 had 9 rows in replication 2. Field layouts during both seasons are presented in Figures 4.1 and 4.2. Ten rows were planted for the segregating populations, BCP_1 and BCP_2. For the F_2, 15 rows were planted since maximum segregation is obtained in this generation. This resulted in variable number of plants per generation.

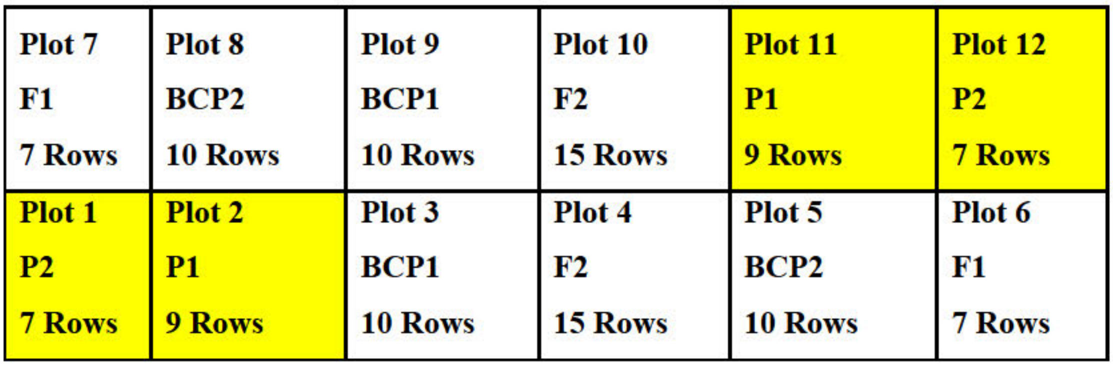
Row length was 3.5 m, intra and inter row spacing were 0.25 m and 0.75 m, respectively. At planting, three seeds were placed at each planting hill and later thinned down to one. Thinning was done three weeks from the date of planting. The trials were rain-fed during both seasons. The trials were planted in 19 November 2020 and 25 November 2021 for season 1 and 2, respectively. . The two seasons were very different in terms of total rainfall received, and the distribution in each season is illustrated in Figure 4-2. During 2020/21 season, more rains were received between December and February, whereas during 2021/22 season, more rainfall was received from January to March.

Prior to planting, the land was first ploughed using a tractor mounted disc plough. Then a tractor mounted harrow was used to break big clods and produce a fine tilth to enable good seed emergence. The planting stations were then marked using pre marked cables with the desired intra and inter row spacing. Basal fertilizer 7:14:7 (NPK) and 8.5% S (i.e. 28 kg N: 56 kg P_2O_5: 28 kg K_2O + 34 kg S) was applied manually at every planting station. The trial was irrigated for establishment. Pre-emergence herbicides were used to control weeds and manual weeding was done as and when necessary. Various pesticides were applied in rotation to control fall army worm (FAW) once every fortnight.



Plot 7 **F1** **7 Rows**	**Plot 8** **P2** **9 Rows**	**Plot 9** **BCP1** **10 Rows**	**Plot 10** **BCP2** **10 Rows**	**Plot 11** **F2** **15 Rows**	**Plot 12** **P1** **9 Rows**
Plot 1 **P1** **9 Rows**	**Plot 2** **F2** **15 Rows**	**Plot 3** **BCP2** **10 Rows**	**Plot 4** **F1** **7 Rows**	**Plot 5** **BCP1** **10 Rows**	**Plot 6** **P2** **9 Rows**

Figure 4- 1: Trial field layout at Stapleford Research Centre 2020/21 season



Plot 7 **F1** **7 Rows**	**Plot 8** **BCP2** **10 Rows**	**Plot 9** **BCP1** **10 Rows**	**Plot 10** **F2** **15 Rows**	**Plot 11** **P1** **9 Rows**	**Plot 12** **P2** **7 Rows**
Plot 1 **P2** **7 Rows**	**Plot 2** **P1** **9 Rows**	**Plot 3** **BCP1** **10 Rows**	**Plot 4** **F2** **15 Rows**	**Plot 5** **BCP2** **10 Rows**	**Plot 6** **F1** **7 Rows**

Figure 4- 2: Trial layout at Stapleford Research Centre 2021/22 season

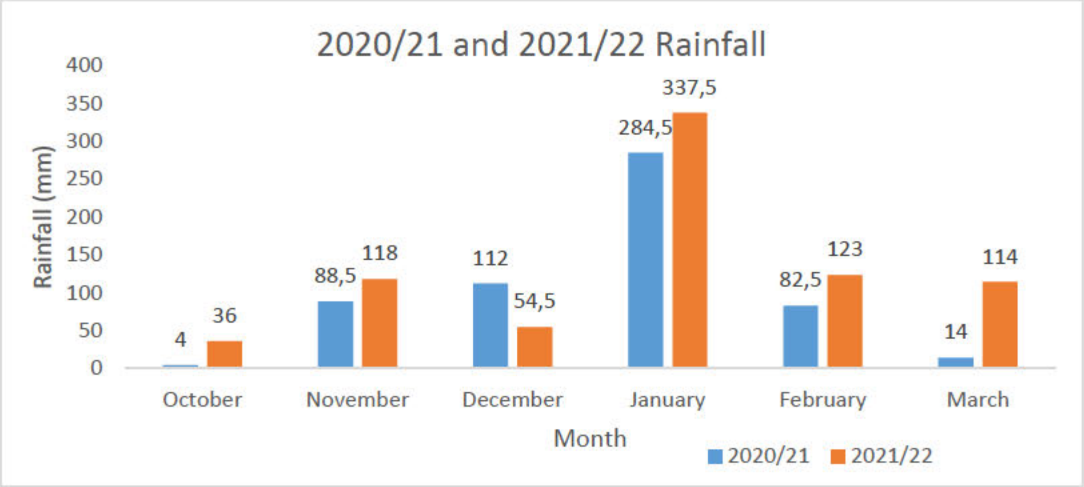


Figure 4- 3 : Total rainfall received during the two seasons

4.2.4 Data collection

Data were collected per individual plant from all plots. Each generation had different number of plants as shown in Table 4-1. The segregating populations had the highest number of plants. The traits measured were number of days from planting to initial silk emergence, number of days from planting to the first pollen shedding, plant height (from the surface of the soil to the tip of the highest tassel branch, ear height (from the soil surface to the primary ear), number of leaves above primary ear, number of rows per ear, ear length, ear mass (which was taken as single plant yield and in the case of ear prolificacy, the combined mass of all the ears was taken as the yield), 100-kernel mass and grain moisture content. Even though all these traits were measured, for generation mean analysis only divergent traits were further analysed.

Table 4- 1: Total plants per each replication over the two season

	Season 1		**Season 2**	
	Number of plants		**Number of plants**	
Generation	**Rep 1**	**Rep 2**	**Rep 1**	**Rep 2**
P1	83	73	124	95
P2	76	72	79	71
F1	71	66	112	102
F2	125	128	212	211
BCP1	128	137	138	131
BCP2	133	132	123	131

4.3 Data Analysis

4.3.1 Analysis of variance

All the data were analysed using SAS9.4 software (SAS Institute Inc. 2013). Given that the number of plants were different for each generation, it was necessary to do the PROC mixed procedure. This is in agreement with what other researchers like Piepho and Möhring (2010). Data analysis was done using the following model:

Response = population mean+ block effects + generation effects + random error effects.

$\mathbf{Y}ijk = \boldsymbol{\mu}i + \mathbf{b}j + \mathbf{g}ijk + \mathbf{e}ij$

$\mathbf{Y}ijk$ = response

$\boldsymbol{\mu}i$ = population mean

$\mathbf{e}ij$ = experimental error

$\mathbf{g}ijk$ = plant specific errors

$\mathbf{b}j$ =effect of the j^{th} block on the k^{th} plant

Blocks, block x generation effects, were treated as random effects and the generations were fixed effects. In situations where data was significant ($P \leq 0.05$), the traits were further subjected to the mean separation tests. It is important to note that the Bartlett's test of homogeneity of error variance (Hossein and Lovric 2011) across the two seasons to determine whether to combine the years or deal with them separately was not done.

4.3.2 Mean separation

The significance of the means of the generations were separated using the Tukey's studentized Range test (HSD). The mean separation test was done to determine significant differences at $P \leq 0.05$ between P_1 and P_2 for the measured traits. Mather and Jinks (1982), highlighted the use of dissimilar parents as one of the preconditions for performing generation mean analysis. Previous studies by Mushongi et al. (2013), Musimwa and Derera (2017) and Salegua et al. (2021) showed that the mean separation procedure was done to identify traits suitable for subjecting traits to generation mean analysis.

4.3.3 The GMA model and epistasis testing

$Y = m + \alpha a + \beta d + \alpha^2 aa + 2\alpha\beta ad + \beta^2 dd$

- α and β are the coefficients for a and d, respectively
- Y = the observed mean
- m = mean = mean of the F2 (i.e., the base population)
- a = pooled additive effects
- d = pooled dominance effects
- aa = additive x additive gene interaction effects
- ad = additive x dominance gene interaction effects
- dd = dominance x dominance gene interaction effects

This model was analysed using the GLM models using SAS Macros. The procedure was necessary since it takes care of data collected on a plant basis. This model is also capable of detecting and partitioning epistasis into its respective forms, that is, additive, dominance, additive-additive, additive-dominance and dominance-dominance.

4.4 Results

4.4.1 Analysis of variance

Analysis of variance (ANOVA) was done to evaluate the genotypic effects. Mean comparisons among trait means were estimated by the least significant difference (LSD) test at 5% levels of significance. The analysis of variance across generations showed data were highly significant (P<0.001) for most traits across seasons.

4.4.2 Mean separation

All trait means were subjected to generation mean analysis. A total of 19 traits were analysed. This, however, is contrary to what Derera and Musimwa (2015) did. In their study, traits that were similar to the inbred lines were not subjected to generation mean analysis. The F_1 generation showed means which were superior to other generations on most traits (68.4%) measured. The parents, P_1 and P_2 were significantly different for all the traits except ear height and kernel depth F_1 and F_2 means were significant for all the traits except for grain moisture. No significant difference between F_1 and BCP_1, F_2 and BCP_2 on days to mid pollen, days to silk emergence and cob diameter. The means of F_1 and segregating populations as well as the parents showed high levels of significance. Ear height had similar means for P_1 and P_2. On plant height F_2 and BCP_1 had similar means. Populations F1, BCP1 and BCP2 had similar means on days to silking. F_1 and BCP_1 and F_2 and BCP_2 had similar means on days to pollen shed.

Table 4- 2: Trait Means for six generations over two seasons

Generation	**N**	**DPS**	**DSE**	**PH**	**EH**	**NL**	**NLAE**	**TBN**	**FW**	**GY**	**EL**	**KRN**	**HKW**
P_1	375	84.3b	84.45b	159.94e	91.06e	13.63e	5.22d	8.91e	109.61f	85.32f	12.55e	14.11ab	23.76d
F_1	351	80.45d	80.71de	289.34a	91.12e	15.78a	6.28b	16.02a	311.48a	266.24a	20.61a	14.06ab	50.95a
F_2	676	82.12c	82.61c	231.46c	159.97a	15.07c	6.21bc	13.94c	207.69d	170.72d	17.44cd	13.41b	40.25bc
BCP_1	534	79.58d	79.57de	235.70c	128.45d	15.20bc	6.12c	14.95b	225.90c	184.80c	16.99d	14.53a	36.37c
BCP_2	519	82.17c	82.03cde	254.24b	137.84b	15.44b	6.60d	14.08ac	247.53b	202.44b	19.48b	13.41b	44.03abc
P_2	298	89.93a	89.31a	181.38d	133.68c	14.69d	6.61a	12.56d	132.60e	111.52e	18.24c	11.78c	44.24ab
Statistics													
Mean		82.57	82.65	228.79	126.14	15.02	6.18	13.59	210.48	173.57	17.56	13.63	39.76
CV (%)		10.31	10.66	31.30	15.50	8.60	12.02	29.80	34.83	37.76	28.05	32.32	100.26
P-value		***	***	***	***	***	***	***	***	***	***	Ns	ns
MSE		72.45	77.62	5128.63	382.48	1.67	0.55	16.41	5374.65	4294.94	24.27	19.41	1589.19

*** significant at $P<0.001$; ** significant at $P<0.01$; * significant at $P<0.05$; ns = not significant; DPS= days to pollen shed; DSE= days to silk emergence; PH = plant height (from the soil to flag leaf); EH = ear height (from soil to base of upper most ear) NL= total number of leaves; NLAE = number of leaves above uppermost ear; TBN=total number of tassel branches; FW= Field weight; GY = grain yield; EL = ear length; KRN = kernel row number; HKW = hundred kernel weight;

Table 4- 3: Trait Means for six generations over two seasons (continuation)

Generation	N	MOI	SHL	KER	KPE	CD	ED	KD
P1	375	11.76bc	77.96bc	26.13ad	354.83de	24.31d	40.85ef	16.54de
P2	298	11.36bd	83.80ab	26.26cd	287.78ef	29.09a	42.46de	16.86de
F1	351	12.65ab	89.95aa	41.76a	575.51a	27.47b	53.75a	24.66a
F2	676	12.76ab	82.52abc	34.43c	448.63cd	29.02a	48.46cd	20.99c
BCP1	534	12.84a	81.84bc	35.85bc	506.48b	27.55b	49.28bc	20.25cd
BCP2	519	12.46ab	81.14bc	36.35b	475.53bc	25.60c	50.03b	22.49b
Statistics								
Mean		12.46	82.59	33.99	450.91	27.36	47.90	20.54
CV (%)		22.65	48.06	28.06	37.65	14.45	9.68	18.43
P-value		ns	ns	***	***	***	***	***
MSE		7.91	1575.74	90.97	28821.30	15.63	21.50	14.34

***significant at P>0.001; ** significant at P>0.01; * significant at P<0.05; ns = not significant; MOI= grain moisture content; SHL= shelling percentage; CD = cob diameter; KER = Kernels per row; KPE = kernels per ear; ED= ear diameter; KD = kernel depth

Table 4- 4: Gene effects for measured traits and their respective standard errors (±SE)

Parameter	Mean	A	D	AA	AD	DD	Type of interaction
DPS	91.90±1.59***	-2.82±0.30***	-28.23±3.91***	-4.99±1.55**	0.23±0.57 ns	16.57±2.51***	Duplicate
DSE	93.89±1.62***	-2.43±0.31***	-32.48±3.98***	-7.20±1.58***	-0.03±0.58 ns	19.12±2.55***	Duplicate
PH	124.45±14.15***	-10.49±2.72***	284.03±24.86***	53.80±13.80***	-7.94±5.1 ns	-111.75±22.35***	Duplicate
EH	66.91±3.85***	0.11± 0.74**	166.60±9.50***	29.10±3.76***	4.10±1.39**	-68.76±6.09***	Duplicate
NL	13.33±0.26***	-0.52±0.05**	4.98±0.64***	1.00±0.25***	0.28±0.09**	-2.36±0.41***	Duplicate
NLAE	5.35±0.15***	-0.69±0.03***	2.59±0.37***	0.60±0.15***	0.21±0.05**	-1.62±0.23***	Duplicate
TBN	8.3 ±0.80***	-1.83±0.15**	14.49±1.98***	2.31±0.78**	2.70±0.29***	-6.89±1.27***	Duplicate
FW	0.64±14.53 ns	-11.66±2.79***	506.07±35.80***	116.23±14.18***	-10.05±5.24 ns	-199.30±22.95***	Duplicate
GY	3.50±13.00***	-13.20±2.50***	397.25±32.05***	91.68±12.70***	-4.49±4.69 ns	-137.67±20.55***	Duplicate
MOI	11.45 ± 0.55***	0.18±0.11*	2.55±1.35 ns	-0.43±0.54 ns	0.20±0.20 ns	-1.878±0.87*	Duplicate
SHL	84.61±7.81***	-2.933±1.50 ns	-14.75±19.24 ns	-4.12±7.62 ns	3.63±2.81 ns	19.71±12.33 ns	Complimentary
EL	12.00±0.99***	-2.85±0.19***	12.54±2.44***	3.17±0.97**	0.36±0.36 ns	-4.14±1.57 **	Duplicate
KER	19.42±2.06***	-0.07±0.40 ns	37.42±5.07***	6.67±2.00**	-0.44±0.74 ns	15.18±3.25***	Complimentary
KRN	10.60±0.87***	1.16±0.17***	7.51±2.15**	2.24±0.85**	-0.05±0.31 ns	-4.15±1.38**	Duplicate
HKW	32.12±7.82***	-10.30±1.50**	8.07±19.28 ns	-0.17±7.63 ns	2.62±2.82 ns	8.77±12.36 ns	Duplicate
KPE	154.05±35.87***	33.59±6.89***	762.87±88.40***	169.45±35.00***	-2.62±12.93 ns	-339.28±56.68***	Duplicate
ED	37.09±0.94***	-0.80± 0.18***	29.40±2.33***	4.77±0.92***	0.04±0.34 ns	-12.54±1.49***	Duplicate
CD	21.45±0.77***	0.65±0.15***	15.78±1.89***	3.26±0.75***	2.12±0.28***	-8.39±1.21***	Duplicate
KD	15.65±0.76***	-0.14±0.15 ns	13.62±1.86***	1.52±0.74*	-2.08±0.27***	-4.15±1.19**	Duplicate

*** significant at P<0.001; ** significant at P<0.01; * significant at P<0.05; ns = not significant; DPS= days to pollen shed; DSE= days to silk emergence; PH = plant height (from the soil to flag leaf); EH = ear height (from soil to base of upper most ear); NL= total number of leaves; NLAE = number of leaves above uppermost ear; TBN=total number of tassel branches; FW= Field weight; GW = grain weight; MOI= grain moisture content; SHL= shelling percentage; EL = ear length; KER = Kernels per row; KRN = kernel row number; HKW = hundred kernel weight; KPE = kernels per ear; ED= ear diameter; CD = cob diameter; KD = kernel depth, A= additive, D= dominance, AA = additive-additive, AD = additive-dominance, DD = dominance-dominance.

4.4.3 Genetic effects estimation

Most of the gene effects for different traits were significant (P<0.001). However, the additive-dominance (AD) gene effects was not significant for 68.4% of the traits including grain weight (Table 4-4). The additive (A) gene effects were non-significant on shelling percentage and kernel per row and kernel number while additive x additive (AA) was not significant for grain moisture, shelling percentage, hundred kernel weight. Dominance (D) effects were not significant for moisture and shelling percentage and 100 kernel weight while dominance x dominance effects did not show significant differences on shelling percentage and hundred kernel weight. Amongst the main effects the dominance effect (D) was superior to the additive (A) on all traits except kernel per row and kernel per ear. On the other hand, interactions AA had larger values than DD on 68.4% of the traits while AD had two large values with DD having five highest values.

The dominance (D) and dominance x dominance (DD) were in opposite direction, that is D is positive whereas DD is negative on most traits except for shelling percentage, kernels per row and hundred kernel weight, however on days to pollen shed and days to silk emergence, D was negative while DD was positive. When dominance (D) and dominance x dominance (DD) have contrasting signs, it means that the nature of epistasis is duplicate.

Additive gene effects were negative on 14 of the 19 traits tested and three traits were not significant. All the traits with positive additive effects were significant. With regards to dominance gene effects, negative significant values were observed on days to silk emergence, days to pollen shed and shelling percentage. Positive (DD) and non-significant (AD) gene effects were observed on grain moisture and shelling percentage. Additive x dominance effects were positive and significant on 11 traits. With respect to dominance x dominance type of gene action, 14 of the 19 variables were negative and significant while the remaining were positive with two not significant.

4.4.4 Additive-dominance model

The lack of fit test was conducted on 12 traits. Lack of fit is the equivalent to the Joint scaling Test of Mather and Jinks (1971) and is performed to determine the adequacy of the additive-dominance model. An analysis of lack of fit was conducted to determine if the additive-dominance model adequately explained the dependent variables.

As a result, the following model was used:

$\mu i= m + [a]X_{i1} + [d]X_{i2} + \lambda i$

Where: i = (1,…..,G)
m = an intercept
[a] = the additive effect
[d] = the dominance effect
$X_{i1}$and X_{i2} = the corresponding coefficients
λi= a lack-of-fit effect

The coefficients of α and β used in the construction of models in generation mean analysis as proposed by Piepho and Möhring (2010) are presented in Table 4-5.

Table 4- 5: Coefficients of α and β used in the construction of models in generation mean analysis

Generation	m	a	d	aa	ad	dd
P_1	1	1	0	1	0	0
P_2	1	-1	0	1	0	0
F_1	1	0	1	0	0	1
F_2	1	0	0.5	0	0	0.25
BCP_1	1	0.5	0.5	0.25	0.25	0.25
BCP_2	1	-0.5	0.5	0.25	-0.25	0.25

m = mean effects; **a** = additive; **d** = dominance; **aa** = additive x additive; **ad** = additive x dominance; **dd** = dominance x dominance)

Source: (Piepho and Möhring, 2010)

Among the two traits fitted to the additive-dominance model, kernel row number and hundred kernel weight were the only traits that provided good fit. This indicates the presence of epistatic gene interactions. (Table 4-6).

Table 4- 6: Lack of fit, F-values and their significance for several traits of the maize hybrid ExpHybrid6

	Additive (a)		**Dominance (d)**		**Lack of fit for additive-dominance model**	
Parameter	**F value**	**P value**	**F value**	**P value**	**F value**	**P value**
DPS	288.1	<.0001	895.17	<.0001	38.38	<.0001
DSE	236.55	<.0001	541.43	<.0001	29.12	<.0001
PH	32.37	<.0001	314.37	<.0001	33.26	<.0001
NL	162.07	<.0001	518.34	<.0001	15.65	<.0001
NLAE	806.8	<.0001	118.62	<.0001	27.69	<.0001
TBN	120.47	<.0001	789.61	<.0001	44.42	<.0001
FW	98	<.0001	2811.59	<.0001	16.98	<.0001
GY	98.52	<.0001	2123.24	<.0001	11.25	<.0001
KPE	27.47	<.0001	1489.21	<.0001	15.04	<.0001
KRN	109.97	<.0001	102.49	<.0001	3.99	<0.01
HKW	37.14	<.0001	20.59	<.0001	1.07	0.3591
CD	2.14	0.1433	502.46	<.0001	40.29	<.0001

4.4.5 Influence of genetic effects

Table 4- 7: Percentage contribution of gene effects to the different traits of the hybrid ExpHybrid6

Parameter	Additive	Dominance	Additive x Additive	Additive x Dominance	Dominance x Dominance	Fixable	Non-Fixable
DPS	22.78	59.95	5.94	0.01	11.32	28.71	71.29
DSE	20.03	58.76	4.08	0.02	17.12	24.10	75.90
PH	6.94	89.73	0.07	0.25	3.07	7.01	92.99
EH	0.16	95.62	0.42	0.29	3.51	0.58	99.42
NL	23.34	69.26	0.62	1.58	5.20	23.95	76.05
NLAE	81.18	10.36	1.42	1.80	5.24	82.60	17.40
TBN	13.31	69.04	1.73	11.98	3.94	15.03	84.97
FW	4.35	91.52	0.11	0.15	3.87	4.46	95.54
GY	5.17	91.89	0.46	0.03	2.45	5.63	94.37
MOI	3.54	62.96	27.67	1.10	4.74	31.21	68.79
SHL	13.82	51.81	13.10	8.10	13.18	26.91	73.09
EL	53.63	44.46	0.60	0.18	1.12	54.24	45.76
KER	0.93	95.39	0.28	0.04	3.37	1.21	98.79
KRN	67.84	21.95	0.01	0.01	10.19	67.85	32.15
HKW	57.96	39.66	1.16	0.76	0.46	59.12	40.88
KPE	2.55	91.38	0.06	0.00	6.01	2.61	97.39
ED	3.59	91.99	0.81	0.01	3.60	4.40	95.60
CD	0.82	74.43	2.26	12.66	9.83	3.07	96.93
KD	5.58	88.81	0.21	4.46	0.94	5.79	94.21

DPS= days to pollen shed; DSE= days to silk emergence; PH = plant height (from the soil to flag leaf); EH = ear height (from soil to base of upper most ear); NL= total number of leaves; NLAE = number of leaves above uppermost ear; TBN=total number of tassel branches; FW= Field weight; GW = grain weight; MOI= grain moisture content; SHL= shelling percentage; EL = ear length; KER = Kernels per row; KRN = kernel row number; HKW = hundred kernel weight; KPE = kernels per ear; ED= ear diameter; CD = cob diameter; KD = kernel depth

The percentage contributions to the different traits for hybrid ExpHybrid6 are shown in Table 4-7. Proportion of fixable gene effects (additive and additive x additive) to non-fixable effects (dominance, additive x dominance, and dominance x dominance) relative to the generation sum of squares differed from trait to trait. Non-fixable effects were observed for most traits. While number of leaves above the uppermost ear, ear length, kernel row number and hundred kernel weight had fixable effects of more than 50%. Interestingly ear length which had nearly equal contribution of fixable and non-fixable effects at 54.24 % and 45.76% respectively.

4.5 Discussion

4.5.1 Analysis of variance and mean comparisons

Significant differences were observed in most of the traits studies. Suggesting the existence of wide variation among generations. The fact that F1 hybrids revealed higher performance in most of the traits indicates that F1 exhibit heterosis, while parents (P1 and P2) show inbreeding depression. Generally, means of F1 hybrids tend to be superior to those of F2 and backcross. According to Falconer (1960) heterosis drops by at least half in the F2 generation. With regards to flowering phenology (days to pollen shed and days to silking emergence) significant difference were observed between parental line 1 and parental line 2. No significant differences were observed the between F1 and BCP1 and F2 and BCP2 on days to pollen shed and silk emergence. Indicating the pollen-silk synchronization for these generations. In these generations, silk emergence and pollen shedding occurred simultaneously. This flowering behaviour is beneficial under heat and drought stress and pollinations will occur over a short space of time. Furthermore, good pollen-silk synchronization is preferred by seed growers since both the male and female parent will be planted at the same time as opposed to staggered planting. With regards to yield F_1 was the best performer and P_1 was the worst. The difference in yield between the parental lines is an indication that heterosis could be due to dominance.

The means for P_1 and P_2 were not significantly different ($P \geq 0.05$) for ear height. Generally short plants are less susceptible to root and stem lodging; thus, they can withstand high plant populations. The two parental lines were significantly different on the number of leaves and number of leaves above the uppermost ear. P_2 had more leaves than P_1. Liu et al. (2020) reported that leaves above ear are more conducive for grain filling. Number of leaves per plant affects leaf area, which in turn affects leaf area index (LAI). The LAI is essential for the formation of dry matter and yield. Dry matter and yield will therefore be affected indirectly by leaf number per plant. The more the leaves above the ear, the greater the leaf area, the greater the grain filling period (Liu et al. 2020; Pinter et al., 2011). This could be the reason why P_2 had a higher grain yield than P_1 and may be responsible for the higher yield of ExpHybrid6. The genetic makeup of P_2 may also be responsible for the higher grain yield of ExpHybrid6.

As such, P_2 may be a better candidate for further research and breeding programs. Furthermore, since P_2 yields better than P_1, therefore, the performance in ExpHybrid6 is as a result of heterosis. The P_2 proved to be a better parent than P_1 in terms of its overall performance. Yet again, as was expected, F_1 performed better than all the other generations. This is because heterosis is highest in the F_1 generation and lowest in inbred lines due to inbreeding depression effects (Azizi et al. 2006; Kaeppler, 2012; Samayoa et al. 2017).

The moisture levels of grain for P_1 and P_2 were greater than those for F_1, F_2, BCP_1 and BCP_2. This confirms that the parental lines mature late, while maturity declines in subsequent generations. However, there were no significant differences between F_1 and F_2. In terms of shelling percentage, ear length, kernels per ear, and hundred kernel weight, P_2 was superior to P_1. Low shelling percentage indicates low yield, and vice versa. Overall yield is positively influenced by ear length, kernels per ear, and hundred kernel weight. On the other hand, P_1 outperformed P_2 on kernel depth, kernels per ear, ear and cob diameter. This is further testimony that P_2 yields better than P_1. The F_1 hybrid, as expected, was superior to all the other generations on all traits this because of heterosis which is highest in the F_1 generation (Azizi et al. 2006).

4.5.2 Gene effects

The study showed significant differences between P_1 and P_2 in almost all traits studied. Brown et al. (2014) argued that if parental lines show great diversity, levels of heterosis will be high. Phenotypic variances amongst the parental lines could be an indication of genetic divergence. However, genotypic divergence was not measured in this study as was the case with the study done by Derera and Musimwa (2015). Phenotypically the lines under study are diverse based on the studied traits. Mather and Jinks (1977) reported that genetic divergence is key in performing generation mean analysis. Therefore, ExpHybrid6 qualified as a candidate due to presence of significant phenotypic differences between the parental lines.

Tests of mean separation usually determines the number of traits to be used. Statistically significant differences were found between P_1 and P_2 for traits at $P<0.001$. In this study, all traits were subjected to generation mean analysis even though some were not divergent unlike Mushongi et al. (2013) and Derera and Musimwa (2015). for example While studying cucumber, Kere et al. (2013) conducted mean separation tests on four traits, of which two were not significantly different, but went on to analyse all four traits by generation means. The process of obtaining extreme phenotypes typically results in all traits being subjected to generation mean analysis, as described by Derera and Musimwa (2015).

Only four traits such as the number of leaves above the uppermost ear, the ear length, the number of kernel rows, and the weight of a hundred kernels had additive genetic effects. These traits included the number of leaves above the uppermost ear, the ear length, the number of kernel rows, and the weight of a hundred kernels. The dominant genetic effects were predominant in most of the traits. Traits with dominant genetic effects are usually difficult to select for (Zdunić et al. 2008). However, breeders can achieve more from the presence of dominance gene effects through heterosis exploitation (Derera and Musimwa, 2015). Greater chance of breeding success is found from additive and additive x additive effects than other interactions. These gene effects are more useful to the breeders, especially when relying on phenotypic selection. Several epistatic factors were observed in this research.

Similar signs on D and DD estimates means that gene action is complimentary, different signs mean that gene action is duplicate (Mather and Jinks, 1982). In this study, only two traits, that is, shelling percentage and kernels per row had complimentary type of interaction while the rest had duplicate type of interaction. The findings corroborates with Azizi et al. (2006) whose study confirmed duplicate association on grain yield, kernel row number, plant height, field weight, and kernel depth among other traits. Mbogo et al. (2015) reported complimentary type of gene interaction on plant height. Dominant gene effects contributed more than other effects and interactions with respect to grain yield. The importance of dominance effects is therefore confirmed by duplicate type of interaction. This implies that dominance gene action is the basis of high yield for ExpHybrid6. This corroborates with the findings of Derera and Musimwa (2015) who reported that dominance gene effect was the basis of yield in SR52 maize hybrid. Similar results confirming the contribution of dominant gene action have been shared by several other investigators (Amer et al. 2002; Azizi et al. 2006; Oyekunle and Badu-Apraku, 2014).

4.5.3 Fixable and Non fixable gene effects

Estimation of non-fixable and fixable effects was done through assigning gene effects into their respective groups (Gianola et al. 2009,Gregorio 2001 and Mushongi et al. 2013). Fixable effects are also known as additive effects and consisted of A and AA. Non-additive gene effects are also non-additive gene effects and are made up of D, AD and DD. In this study non-fixable gene action had 94.37% for grain yield, 95.54% for grain field weight, 98.79% for kernels per row, 95.6% for ear diameter, 96.9% for cob diameter and 94.21% for kernel depth. The high percentage on yield and yield components are an indication that yield of ExpHybrid6 is largely contributed by non-fixable genes. Natol et al. (2018) reported that non-additive gene effects are superior to additive gene effects on yield. Fixable genetic effects control the inheritance mechanism of grain yield with a pronounced dominant effect (Haq et al. 2013). Number of leaves above uppermost ear, ear size, grain row number and hundred kernel weight had greater additive gene value than the non-additive ones. The rest of the traits had values of non-additive gene effects greater than additive gene effects.

4.6 Conclusion

Generation mean analysis revealed high heterosis in the hybrid ExpHybrid6, which is controlled by dominance gene action. Furthermore, it was revealed that majority of ExpHybrid6's yield related traits were controlled by dominant gene action. This means that breeding through hybridization can be effective, thus breeders can get better results through heterosis exploitation. It can therefore be concluded that ExpHybrid6 is an exceptional hybrid because of dominance gene effects that confers heterosis.

References

Adhikari S, Joshi A, Kumar A and Singh NK (2021) Diversification of maize (*Zea mays* L.) through teosinte (Zea mays subsp. parviglumis Iltis & Doebley) allelic. Genetic Resources and Crop Evolution 68: 2983–2995.

Amer E, El-Shenawy A and Mosa H (2002) A comparison of four testers for the evaluation of maize yellow inbreds. Egyptian Journal of Applied Science 2: 573–578.

Atif I, Awadalla A, Khalafalla M, Idris A and Osman A (2012) Combining Ability and Heterosis for Yield and Yield Components in Maize. Australian Journal of Basic and Applied Sciences 6: 36–41.

Azizi F, Rezaei A and Saeid G (2006) Generation mean analysis to estimate genetic parameters for different traits in two crosses of corn inbred lines at three planting densities. Journal of Agricultural Science and Technology 8: 153–169.

Bello O, Abdulmaliq S, Afolabi M and Ige S (2010) Correlation and path coefficient analysis of yield and agronomic characters among open pollinated maize varieties and their F 1 hybrids in a diallel cross. African Journal of Biotechnology 9: 2633–2639.

Beyene Y, Gowda M, Suresh LM, Mugo S, Olsen M, Oikeh SO, Juma C, Tarekegne A and Prasanna BM (2017) Genetic analysis of tropical maize inbred lines for resistance to maize lethal necrosis disease. Euphytica 213: 224.

Brown J, Caligari PDS and Campos H (2014) Plant Breeding, Second. Wley Blackwell, West Sussex, UK.

Coates ST and White DG (1998) Inheritance of resistance to gray leaf spot in crosses involving selected resistant inbred lines of corn. Phytopathology 88: 972–982.

Derera J and Musimwa TR (2015) Why SR52 is such a great maize hybrid? I. Heterosis and generation mean analysis. Euphytica 205: 121–135.

Eicher CK (1995) Zimbabwe’s maize-based Green Revolution: Preconditions for replication. World Development 23: 805–818.

Erenstein O, Chamberlin J and Sonder K (2021) Estimating the global number and distribution of maize and wheat farms. Global Food Security 30.

Falconer D. (1960) Introduction to quantitative genetics. London.

Gianola D, De Los Campos G, Hill WG, Manfredi E and Fernando R (2009) Additive Genetic Variability and the Bayesian Alphabet. Genetics 183: 347–363.

Gregorio GB (2001) Progress in Breeding for Trace Minerals in Staple Crops. American Society for Nutritional Sciences 13: 500–5002.

Haq MIU, Ajmal S, Kamal N, Khanum S, Siddique M and Kiani MZ (2013) Generation mean analysis for grain yield in maize. Journal of Animal and Plant Sciences 23: 1146–1151.

Hossein A and Lovric M (2011) Bartlett ' S Test Bartlett ' S Test. International Journal of Ecological Economics & Statistics 1–3.

Kaeppler S (2012) Heterosis: Many Genes, Many Mechanisms—End the Search for an Undiscovered Unifying Theory. International Scholary Research Network Botany 2012: 1–12.

Katragadda S, Pradeep T and Sravani D (2020) Identification of potential parental lines for single, three-way and double crosses in maize (Zea mays L.). Maydica 65: 65.

Kere GM, Guo Q, Shen J, Xu J and Chen J (2013) Heritability and gene effects for salinity tolerance in cucumber (Cucumis sativus L.) estimated by generation mean analysis. Scientia Horticulturae 159: 122–127.

Li Z, Luo LJ, Mei HW, Wang DL, Shu QY, Tabien R, Zhong DB, Ying CS, Stansel JW, Khush GS and Paterson AH (2001) Overdominant Epistatic Loci Are the Primary Genetic Basis of Inbreeding Depression and Heterosis in Rice . I . Biomass and Grain Yield. Genetics Society of America 158: 1737–1753.

Makore F, Magorokosho C, Dari S, Gasura E, Mazarura U and Kamutando CN (2022) Genetic Potential of New Maize Inbred Lines in Single-Cross Hybrid Combinations under Low-

Nitrogen Stress and Optimal Conditions. Agronomy 12: 2205.

Mashingaidze K (2006) Maize Research and Development. University of Zimbabwe Publications, Harare, p. 363–376. In Zimbabwe Agriculture Revolution Revisited.

Mashingaidze AB, Werf W Van Der, Lotz LAP, Mudita I, Nyakanda C and Kropff MJ (2012) Leaf stripping and detasselling increase ear growth rate and maize grain yield. p. 820–834. In Scientific Conference Proceedings.

Masuka B, Magorokosho C, Olsen M, Atlin GN, Bänziger M, Pixley K V., Vivek BS, Labuschagne M, Matemba-Mutasa R, Burgenõ J, Macrobert J, Prasanna BM, Das B, Makumbi D, Tarekegne A, Crossa J, Zaman-Allah M, Van Biljon A and Cairns JE (2017) Gains in maize genetic improvement in eastern and southern Africa: II. CIMMYT open-pollinated variety breeding pipeline. Crop Science 57: 180–191.

Mather K and Jinks JL (1982) Biometrical Genetics: The Study of Continuous Variation, 3rd ed. Chapman and Hall.

Mather K and Jinks JL (1977) Introduction to Biometrical Genetics Introduction to Biometrical Genetics. Chapman and Hall, London.

Mbogo PO, Dida MM and Owuor B (2015) Generation Means Analysis for Estimation of Genetic Parameters for Striga hermonthica Resistance in Maize (Zea mays L.). Journal of Agricultural Science 7: 143–155.

Mushongi AA, Derera J, Tongoona P and Lyimo NG (2013) Generation mean analysis of leaf chlorophyll concentration from mid-silking to physiological maturity in some tropical maize (Zea mays L.) genotypes under low and high nitrogen dosages. Euphytica 189: 111–122.

Musimwa T and Derera J (2017) Why SR52 is such a great maize hybrid? II. Heritability, correlation and path-coefficient analyses. Euphytica 213: 1–14.

Musundire L, Derera J, Dari S and Tongoona P (2021) Assessment of genetic gains for grain yield and components from introgression of temperate donor inbred line into tropical elite maize inbred lines: II. Performance inter se. Euphytica 217: 1–25.

Natol B, Berhanu A and Mandefero N (2018) Genetic analysis for grain yield and yield related traits in maize (Zea mays L.) inbred lines in line tester mating design. Journal of Agricultural Biotechnology and Sustainable Development 10: 132–139.

Naveed A, Khan A and Khan I (2009) Generation mean analysis of water stress tolerance in okra (Abelmoschus esculentus L.). Pakistan Journal of Botany 41: 195–205.

Ndaruhutse F (2016) Generation Mean Analysis for Diplodia Ear Rot Resistance in Tropical Maize Inbred Lines. University of Nairobi, Kenya. University of Nairobi, 55–58p.

Oyekunle M and Badu-Apraku B (2014) Genetic Analysis of Grain Yield and Other Traits of Early-Maturing Maize Inbreds under Drought and Well-Watered Conditions. Journal of Agronomy and Crop Science 200: 97–107.

Pallavi, Singh A and Chaudhary S (2019) Generation Mean Analysis using Six Parameters Genetic Model for Quantitative Traits in Cowpea [(Vigna unguiculata (L.) Walp.]. Int.J.Curr.Microbiol.App.Sci 8: 1967–1973.

Piepho HP and Möhring J (2010) Generation means analysis using Mixed models. Crop Science 50: 1674–1680.

Pinter J, Glenn F, Pen S, Pok I, Hegyi Z, Zsubori Z-ZT, Hadi G and Marton CL (2011) Utilizing Leafy genes as resources in quality silage maize breeding. Maydica 56: 243–250.

Said AA (2014) Generation mean analysis in wheat (Triticum aestivum L.) under drought stress conditions. Annals of Agricultural Sciences 59: 177–184.

Salegua V, Melis R, Fourie D, Sibiya J and Musvosvi C (2021) Generation mean analysis for resistance to bacterial brown spot disease in dry bean. New Zealand Journal of Crop and Horticultural Science 1: 1–14.

Samayoa LF, Malvar RA and Butrón A (2017) QTL for maize midparent heterosis in the heterotic pattern American dent × European flint under corn borer pressure. Frontiers in Plant Science 8: 1–8.

SAS Institute Inc. (2013) The SAS System for Windows, Release 9.4. SAS Institute, Inc., Cary.

Seed Co Limited (2017) Seed Co Limited. Hybridization. Available at <https:www.seedcogroup.com/innovations/hybridization> Accessed on March 31, 2022.

Shahrokhi M, Khorasani, Saeed K and Ebrahimi A (2011) Generation Mean Analysis for Yield and Yield Components in Maize (Zea mays L .). Journal of Plant Physiology and Breeding 1: 59–72.

Sibiya J, Tongoona P, Derera J and van Rij N (2012) Genetic analysis and genotype × environment (G × E) for grey leaf spot disease resistance in elite African maize (*Zea mays* L.) germplasm. Euphytica 185: 349–362.

Srinivas B and Genet DB (2015) Estimation of genetic parameters through generation mean analysis for fiber quality traits in upland cotton. Society for the Advancement of Breeding Research in Asia and Oceania 47: 238–247.

Troyer AF (2004) Background of U.S. Hybrid Corn II: Breeding, Climate, and Food. Crop Science 380: 370–380.

Zdunić Z, Nastasić A, Jocković D, Ivanović M, Dalović I, Mijić A and Jocković M (2008) Genetic analysis of grain yield and oil content in two maize populations. Periodicum Biologorum 114: 495–500.

CHAPTER 5
RESEARCH OVERVIEW

5.1 Introduction

This study sought to understand the genetic basis of a single cross hybrid ExpHybrid6 and the genetic gain of newly developed hybrids versus old ones. The tropical single cross maize hybrid was evaluated using generation mean analysis to ascertain its genetic base and gene action responsible for its exceptional yield as well as to confirm heterosis of ExpHybrid6. Furthermore, eight single cross hybrids, including the generation mean analysis candidate, were separately evaluated with the objective of measuring relative yield advantage of the new hybrids against old hybrids. A brief overview of the research results is presented in this chapter, along with recommendations based on the previous chapters' examination of the hybrid ExpHybrid6's yield. In addition, the results' impact and notable shortcomings are discussed. Finally, insights into the potential application of the ExpHybrid6 hybrid are provided.

The objectives of the study were;

1. To measure relative yield advantage of new hybrids against old hybrids and confirm heterosis of the single cross maize hybrid ExHybrid6.
2. To determine the gene action governing grain yield and secondary traits in the new single cross hybrid ExpHybrid6.
3. To ascertain the role of epistasis in ExpHybrid6.

5.2 Summary of research findings

It was established that ExpHybrid6 has exceptional mid parent heterosis of 171% of grain yield. With respect to relative yield advantage, the study showed that Exphybrid6 had advantage over old hybrids. Both individual and across site analysis substantiated that ExpHybrid6 is indeed a high yielding hybrid, which is better than old hybrids and its yield potential is not by chance hence its basis should be explored. The generation mean analysis showed that dominance gene action was the main mode of gene action responsible for grain yield and associated traits in the hybrid ExpHybrid6 although additive effects showed significance on some traits. The presence of epistasis was also confirmed. Duplicate type of epistasis was dominant compared to complimentary for the majority of traits. The implication of this is that improvement can only be done through heterosis breeding. Alternatively, recurrent selection for specific combining ability can be employed for population improvement.

5.5 Conclusion and recommendations

The relative yield advantage study confirmed that emerging hybrids are performing better than old hybrids. The main objective of this research was to measure relative yield advantage in newly developed maize hybrids. Through generation mean analysis it was established that dominance gene effects are behind the hybrid's high yield. Dominance was also found to have direct contribution to plant height, ear height, kernel row number, kernel per ear and ear diameter. African maize breeding should invest in single cross breeding, because they have the potential to reduce yield gaps. Since non additive gene action is the main mode of gene action, it is therefore recommended that improvements be done through heterosis exploitation.

It is further recommended that correlation and path analysis be done on the same hybrid. This will expose the role of secondary traits in yield. Path coefficients analysis will help in partitioning correlation coefficients into direct and indirect effects.