A RETROSPECTIVE ANALYSIS OF MAIZE SYSTEMS TOLERANCE TO COMBINED DROUGHT WITH HEAT STRESS AND LOW SOIL NITROGEN IN ZIMBABWE

By

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A thesis submitted in partial fulfilment of the requirements for the degree of **Doctor of Philosophy** (PhD) in Plant-Breeding

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DECLARATION

I, Stanley Gokoma, declared that:

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Signed …  …30 July 2025

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For my daughters Shumirai and Shamiso

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LIST OF ABBREVIATIONS AND SYMBOLS

%	Percent
AATF	African Agriculture Technology Foundation
AGG	Accelerated genetic gains
ANOVA	Analysis of variance
ARC	Agriculture Research Council
ASI	Anthesis to silking interval
BLUE	Best linear unbiased estimations
BLUPS	Best linear unbiased predictors
CA	Conservation agriculture
CDHS	Combined Drought and Heat stress
CIMMYT	International Centre for the Improvement of Maize and Wheat
CRISPR	Clustered regularly interspaced short palindromic repeat
CRMA	Climate Resilient Maize for Asia
DMS	Dextrinised maize starch filler
DNA	Deoxy-ribonucleic acid
DTMA	Drought tolerant maize for Africa
FAO	Food and Agricultural organisation of the United Nations
FAOSTAT	Food and Agriculture Organisation statistics
GDD	Growing degree days
GHG	Greenhouse gas
GWAS	Genome wide association studies
HSP	Heat shock proteins
HSTMA	Heat Stress Tolerant Maize for Asia
HTP	High throughput phenotyping
IFDC	International Fertiliser Development Centre
IITA	International Institute of Tropical Agriculture
IPCC	Inter Governmental Panel on Climate Change
LNS	Low nitrogen stress
LSD	Least significant difference
MARB	Marker assisted recurrent backcrossing

MARS	Marker assisted recurrent selection
META	Multi environmental trial analysis
N	Nitrogen
N_2O	Nitrous oxide
NARS	National Agriculture Research systems
NUE	Nitrogen use efficiency
^oC	Degrees Celsius
OPV	Open pollinated variety
QTL	Quantitative trait loci
REML	Restricted maximum likelihood
RNA	Ribo-nucleic acid
SDG	Sustainable development goal
SSA	Sub Saharan Africa
TALEN	Transcription activator-like effector nucleases
UAV	Unmanned aerial vehicle
V11	Vegetative phase eleventh leaf stage
V6	Vegetative phase sixth leaf stage
VPD	Vapour pressure deficit
WEMA	Water efficient Maize for Africa
WMO	World Meteorological Organisation of the United Nations
WUE	Water Use Efficiency
ZFN	Zinc finger nucleases

ABSTRACT

Climate change and variability have resulted in emergence of new constraints to maize production putting at risk the livelihoods of millions of people in Zimbabwe. Drought and heat stresses have increased in occurrence, intensity and severity threatening food and nutrition security. Over the years, grain yield losses were mainly linked to drought and poor soil fertility especially low soil nitrogen, but in recent times, reports have also attributed it to heat stress, occurring simultaneously with drought. Unfortunately, most smallholder farmers are resource-poor and cannot rescue their crops from the vagaries of these stresses. Crop improvement is highly regarded as the most cost effective and sustainable approach to building climate change resilience. However, the potential of integrating improved varieties in farming systems threatened by combined drought and heat, and low nitrogen stress is still poorly quantified. Therefore, this study aimed to make a retrospective analysis of maize systems tolerance to combined drought with heat stress and low soil nitrogen in Zimbabwe. The specific objectives were i) to identify sub-tropical maize inbred lines with combined drought and heat stress adaptation attributes among maize populations developed within the CIMMYT maize breeding program and the Crop Breeding Institute of the government of Zimbabwe, ii) to identify pre-release maize hybrids developed within CIMMYT maize breeding program with combined drought and heat stress adaptation attributes, and iii) to do the retrospective analysis of maize performance under low nitrogen stress conditions related to combined drought and heat stress in sub-Saharan Africa. Managed low nitrogen experiments were conducted in Eastern and Southern Africa, and combined drought and heat stress experiments were conducted at Chiredzi research station in Zimbabwe. The combined drought and heat stress experiments were conducted in Zimbabwe during the dry, hot, and rain-free season to ensure simultaneous occurrence of drought and heat stress. Drought at reproduction phase was simulated by withdrawing irrigation three weeks before flowering. The results showed important traits, number of ears per plant, number of kernels per row and cob girth that could be prioritised for selecting germplasm and revealed maize inbred lines and hybrids with adaptive attributes under these conditions. These will be recommended for incorporation and advancement in the national maize breeding program in Zimbabwe. Genetic correlation analysis showed that the number of ears per plant, number of kernels per row, and cob girth were highly associated with grain yield ($p<0.05$) of hybrids under combined drought and heat stress. In the inbred lines experiment, anthesis to silking interval, plant height, ear height, husk cover, grain moisture content at harvest, number of leaves above the ear and internode length were the key traits associated with grain yield under combined drought and heat stress. The newly developed pre-release maize hybrids, DJ65-32, DJ65-1 and DJ65-28 predominantly and significantly outperformed the old and widely grown commercial varieties by 34.97% under both combined drought and heat, whereas OPVs performed well under low nitrogen conditions. These hybrids and their parents will be advanced in the breeding program DJ65-32, DJ65-1 and DJ65-28. The study demonstrated the potential benefits of integrating

improved maize varieties in farming systems under threat from climate change-induced abiotic stresses. Overall findings from this study have implications for improving the maize breeding program to continuously churn out new varieties with enhanced adaptation to low nitrogen and combined drought and heat stress in Zimbabwe.

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CHAPTER 1

INTRODUCTION TO THE THESIS

1.1 Background and justification

Zimbabwe increasingly faces food security challenges in a climate change crisis. Climate change has resulted in the emergence of new constraints to maize production putting to risk the livelihoods of millions of people especially in sub-Saharan Africa (SSA) who largely rely on this crop for survival (Ereinstein et al., 2022). Over the years, both biotic (e.g. pests and diseases) and abiotic (especially, drought and heat) stresses have increased in frequency, intensity, severity and duration due to climate change (Lobell and Gourdji, 2012, Challinor et al., 2016) rendering most households food insecure. Grain yield losses in maize production due to climate change have been linked to drought (Badu-Apraku et al.,2017; Cairns et al., 2021; Arambu-Merlos et al., 2024) and poor soil fertility (Banzigger et al., 2000; Govindasamy et al., 2023; Oliveira et al., 2023), but in recent times, reports have also attributed heat stress (Wahid et al., 2007; Cairns et al., 2012; Dong et al., 2021) especially when it occurs simultaneously with drought stress (Rizhsky et al., 2004; Mittler, 2006; Zandalinas et al., 2017) as major factors contributing to decline in yield in SSA. This is usually the case because most farmers in SSA are resource poor (Exenberger and Pondorfer, 2011; van Ittersum et al., 2016) and cannot rescue their crops from the vagaries of these stresses.

There is a vicious cycle whereby climate change induced cocktail of abiotic stresses which then interact to cause low productivity of crops. For instance, drought and heat stress effects are much stronger if these stresses occur simultaneously together (Rizhsky et al., 2004; Barnabas et al., 2008; Cairns et al., 2012; Zandalinas et al., 2017), a phenomenon now widely referred to combined drought and heat stress (CDHS) in plant breeding circles. But drought and heat stress also reduced soil microbial diversity and functions (Hui et al., 2024; Li et al., 2024) which are vital for nutrient cycling

activities (e.g. Nitrogen cycle) (UNEP, 2024), subsequently altering nutrient availability to the plants resulting in reduced plant productivity (Torres-Rodriguez et al., 2021; Prabha-Sigh et al., 2022). To counteract the reduced nutrient availability because of climate change, more fertilisers are used in the cropping systems, and this has resulted in positive nutrient balances in the developed countries. The use of nitrogenous fertilisers fortuitously results in the emission of nitrous oxides both in the production and use of the fertilisers. Nitrous oxides are highly potent, persistent greenhouse gases (UNEP, 2024). However, in the developing countries, (most of which are in SSA) fertiliser use is still very low averaging less than 20 kg ha^{-1} (Sheahan and Barret, 2017). In addition, most farmers in developed countries can afford to supplement natural rainfall with irrigation and thereby drastically minimising the effects of drought and heat stress on their crops (Osteen et al., 2012; Zhang et al., 2015). But this is not the case in SSA where most farmers grow maize under rainfed conditions without any of irrigation system (Makore et al., 2022). As a result, maize productivity is curtailed by both CDHS as well as low soil fertility particularly low soil nitrogen stress (LNS). Addressing this problem requires a holistic approach which involves the breeding of maize genotypes that are adaptable to current and future climatic conditions and has high nitrogen use efficiency (NUE). Crop improvement programs have recently succeeded in combating climate change-linked production challenges such as the maize lethal necrosis disease by breeding maize varieties resistant to the disease (Zhan et al., 2022). In the past, breeding of more productive crop varieties has averted starvation in many countries (van Ittersum et al., 2021). Banking on these past experiences, it was hypothesised that the current and predicted climate change induced abiotic stresses can be ameliorated through crop breeding.

As a result, crop productivity in most developing countries is curtailed by combined drought and heat stress as well as low soil fertility especially low nitrogen stress. Low nitrogen causes yield losses ranging from 10 to 80% (Etiro et al., 2020). Addressing these problems requires a holistic approach which includes the breeding of crop varieties that are adaptable to current climatic conditions and have high nitrogen use efficiency.

1.2 Summary of the problem

Over the past years, significant strides have been made in the plant breeding space to develop maize varieties adapted to climate change induced factors (Makumbe et al., 2011: Cairns et al., 2013; Prasanna et al., 2022). For example, Drought Tolerant Maize for Africa (DTMA) project, the International Maize and Wheat Improvement Centre (CIMMYT) developed more than 120 maize inbred lines and more than 160 drought tolerant maize hybrids which were reported to have impacted positively on people's lives in SSA (Fisher et al., 2015; Setimela et al., 2018). Furthermore, the Water Efficient Maize for Africa (WEMA) project, which was a collaborative research effort between CIMMYT, Monsanto (now Bayer Crop Science), African Agricultural Technology Foundation (AATF), National Agricultural Research Systems (NARS) and the Agricultural Research Council (ARC) of South Africa resulted in the release of more than 120 water use efficient (WUE) maize hybrids, which showed to be productive under drought stress conditions (Edge et al., 2018). Elsewhere, in the Climate Resilient Maize for Asia (CRMA) and Heat Stress Tolerant Maize for Asia (HSTMA) projects, several maize inbred lines and hybrids adapted to drought and heat stress were released (Zaidi et al., 2020). Despite these achievements the potential of integrating improved maize genotypes in farming systems are still threatened by the combined drought and heat stress (CDHS) and low nitrogen stress (LNS) which are still poorly quantified. The status quo makes it impossible to solely recommend adoption of improved maize varieties as a solution to boost food security in agro-ecologies threatened by these climate-induced stresses.

1.3 Objectives of the study and hypotheses

This study aimed to depict the potential benefits of incorporating plant breeding innovations in farming systems under threat from climate-induced abiotic stresses for improved food security in Zimbabwe. The specific objectives were to:

(i) Identify sub-tropical maize inbred lines with combined drought and heat stress adaptation attributes among maize populations developed within the Crop Breeding Institute of Zimbabwe national maize breeding program and the CIMMYT Zimbabwe maize breeding program,

(ii) Identify pre-release maize hybrids developed within the CIMMYT maize breeding program with combined drought and heat stress adaptation attributes and,

(iii) Retrospective analysis of genetic variability for grain yield performance under low nitrogen conditions among pre-commercial and commercial hybrids as well as OPVs related to combined drought and heat stress in Eastern and Southern Africa.

The study was centred on the hypothesis that, maize developed for adaptation to drought or heat can also withstand these two stresses as they occur simultaneously. The new varieties with combined drought and heat stress tolerance will perform better than the old commercial varieties under these conditions. The old commercial hybrids were not intentionally bred for tolerance to the combination of these abiotic stresses which are prevalent in the target environments or ecologies, especially in Zimbabwe. The study also investigated the existence of genetic variability for yield performance under low soil nitrogen in Easten and Southern Africa.

1.4 Structure of the thesis

The thesis is structured as follows:

Chapter 1: Introduction to the thesis. The foregoing has provided the background and justification for devoting research investments in developing breeding germplasm that has combined drought and heat resistance traits. The objectives of the current study were also laid.

Chapter 2: Review of the Literature. The pertinent literature on climate change, heat and drought is reviewed and synthesised. Progress and challenges in breeding maize for drought tolerance is also

discussed as well as implications of low soil fertility and nitrogen use efficiency on maize productivity.

Chapter 3: This is a research chapter that is dedicated to the identification of sub-tropical maize inbred lines with combined drought and heat stress adaptation attributes among maize populations developed within the CIMMYT maize breeding program.

Chapter 4: This is a research chapter that covers the identification of pre-release maize hybrids developed within the CIMMYT maize breeding program with combined drought and heat stress tolerance attributes.

Chapter 5: The chapter is dedicated to the retrospective analysis of maize performance under low nitrogen stress conditions in relation with combined drought and heat stress in sub–Saharan Africa.

Chapter 6: Research overview. This summarises the research findings.

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CHAPTER 2

LITERATURE REVIEW

2.1 Introduction

This review discusses the global maize production trends and the major constraints with emphasis on the abiotic stresses that are affecting maize productivity under small-holder farming systems in sub–Saharan Africa (SSA). The different types of droughts are briefly discussed as well as heat stress as they affect maize production under natural conditions. The strategies that can be implemented to improve maize productivity are highlighted. Maize is produced worldwide on approximately 40.7 million hectares with a total production of about 1.16 billion tonnes in 2022 (Global yield gap atlas, 2023). Maize production is strongly linked to the seasonal weather conditions especially under rainfed production with droughts causing major yield loss shocks. In SSA, smallholder farmers are the major producers of maize under rainfed conditions (Giller et al., 2021), and the production is exposed to the vagaries of climate variability. Due to the stochastic occurrence of drought and variations in intensity, severity and duration, it is difficult to quantify the effects of drought on crop production each season. However, it is agreed that drought intensity, frequency and severity is projected to increase due to declining rainfall and rising temperatures (Wanders and Wada, 2015: Mahajan et al., 2025: Tang et al.,2025).

2.1.2 Definition of concepts

A clear understanding of heat and drought is prudent in devising a breeding strategy that emphasizes on combined drought and heat stress (CDHS) tolerance as the core of the breeding and pre-breeding objectives in Zimbabwe. There is no universally accepted definition of drought, and this has led to different types of droughts being defined depending on the impacts. Various authors have defined both drought and heat stress in maize and other crops. There are five different types of droughts, and these are meteorological drought, hydrological drought, agricultural drought, socio-economic drought as well as ecological drought (Zhang et al., 2023). All droughts emanate from insufficient

precipitation, when the supply of water fails to meet demand resulting in various short and long-term impacts on both plants and the whole ecosystem (Cavalcante et al., 2024). The impacts of drought on maize production depend on the duration, severity and intensity of the drought as well as the crop genotype, and developmental stage (Barnabas et al., 2008). Total crop failure can occur if the drought is of a long duration. However, the most common scenarios are short duration droughts occurring at the critical developmental stages (Gourdji et al., 2013).

Meteorological drought is the most prevalent type and is defined on the basis of dryness and the length of the dry period in comparison to some long term average for the region or area (Panagoulia and Dimou, 1998; Tate and Gustard, 2000; Mishra and Singh, 2010). The period is defined as the number of days during which precipitation is below a given threshold (Panagoulia and Dimou, 1998). The severity of the meteorological drought is therefore defined by the number of days during which the precipitation is below the established long-term average. The other types of droughts are a result of the meteorological drought thus the severity of the meteorological drought directly affects the intensity and severity of the other droughts.

An agricultural drought occurs when soil moisture is depleted to the extent that crop and pasture yields are significantly affected (Wang et al., 2023). The agricultural drought creates a linkage between the meteorological drought and the shortages that occur in plants because of low precipitation. An agricultural drought therefore refers to a period during which crop plants are unable to get sufficient water for plant physiological processes due to inadequate precipitation or irrigation. The agricultural drought may occur during a critical developmental stage of the crop and negatively impact crop yield thus the distribution of the precipitation during the growing seasonal is critical. An agricultural drought therefore determines the occurrence of food scarcity as it affects crop yields (Wang et al., 2023). Plant water requirements depend on the crop stage and the prevailing weather conditions. When the crop enters the reproductive stage, the crop water requirements get to the peak.

The occurrence of an agricultural drought during the reproductive stage is extremely detrimental to grain yield (Liu et al 2021). The occurrence of high temperatures may accentuate the onset and intensity of the agricultural drought (Zhang et al., 2023). Due to the high-water requirements and the sensitivity of the reproductive tissues, the flowering stage of maize has been determined as the most vulnerable stage (Edmeades et al., 1993: Magorokosho et al., 2003).

The hydrological drought is concerned with the impacts of precipitation shortfalls on surface and sub-surface water rather than with the meteorological explanation of the event (Wang et al., 2023). The onset of a hydrological drought takes long to manifest in the form of reduced stream flow, ground water and reservoir levels. As a result, the hydrological drought is a long-term result of the meteorological drought.

Socio-economic drought occurs when the supply of an economic good is affected by the meteorological drought (American Meteorological Society, 2004). The disturbance in the production system causes a failure in meeting the demand, for example, poor generation of electricity due to low water levels. An ecological drought occurs due to a prolonged and widespread deficit in naturally available water supplies which causes multiple stresses across the ecosystems (Tate and Gustard, 2000). Zambia and Zimbabwe are experiencing long hours of load shedding because of the El Niño phenomenon of 2023 to 2024 which is an example of a socio-economic drought (Dube and Nhamo, 2023).

Even though there is no universally accepted definition of drought, Lipiec et al. (2013) postulated that drought stress occurs when soil and atmospheric humidity is low, and the ambient air temperature is high. It is related to the changes in soil and meteorological conditions and not with plant and tissue hydration. This definition appears to work succinctly for agricultural crop production and indicates that drought and heat stress cannot be easily separated hence a strategy that looks at improving

drought and heat stress tolerance of crops as they occur simultaneously together in the farmers' fields would be more effective than looking at the two stresses separately.

The occurrence of drought accompanied by high temperatures has become a common phenomenon as climate change surges. Heat stress is defined as the rise in soil and air temperature beyond a threshold level for a minimum amount of time such that permanent injuries occur that hinder the growth and development of the crop plants (Rizhsky et al., 2002; Wahid et al., 2007; Cairns et al., 2012; Lipiec et al., 2013; Lamaoui et al., 2018). The threshold temperature is the temperature above which growth and development of a crop cease. Heat stress is a complex function of duration, intensity as well as the crop developmental stage (Rizhsky et al., 2002; Wahid et al., 2007; Cairns et al., 2012). The optimal mean air temperature for maize growth is between 25^{o}C and 37.3^{o}C (Porter and Semenov 2005; Cicchino et al. 2010; Cairns et al., 2012). The wide range of temperature may be due to the differences in the measurements and the prevailing environmental conditions when the measurements were taken. In hot dry areas, the vapour pressure deficit (VPD) is usually high, and this results in lower temperatures being detrimental to crop growth. Gradual increase in temperature over an extended period allows plants to acclimate whereas a rapid elevation of temperature causes a sudden death of plant tissues, a phenomenon called leaf firing (Chen et al., 2012). The combination of accelerated leaf senescence and leaf firing reduces the photosynthetic area of the crop plants as well as making the stored assimilates unavailable for remobilisation.

Tassel blasting is a result of heat stress occurring during tasselling and results in the desiccation of tassels before pollen shedding (Chen et al., 2012). Tassel blasting reduces pollen availability and usually results in poor pollination as well as poor seed set. Heat stress affects the quantity and viability of pollen grains due to the impact of high temperatures on the tassels and moisture content of the pollen grains (Begcy et al., 2019) as well as the moisture content of silks. Extreme heat denatures the pollen grains. Tassel blasting is an important secondary trait which is used for the elimination of

genotypes from trials because susceptible genotypes will fail to pollinate when grown in isolation (Badu-Apraku et al., 2023). Combined drought and heat stress may result in poor or no silk extrusion making them unavailable for pollination (Badu-Apraku and Fokorede, 2017). This results in complete crop failure. The anthesis to silking interval (ASI) is a secondary trait which indicates stress tolerance among genotypes. Poor partitioning of assimilates to the ear under stress results in a large anthesis to silking interval (Bolaños and Edmeades, 1993; Araus et al., 2012; Chapman and Edmeades, 2014; Monneveux et al., 2014)

Climate change has severely affected the frequency, duration, and severity of the major abiotic and biotic stresses in agricultural production. A change in the state of climate that can be identified by changes in the mean and or the variability of its properties that persists for an extended period, typically decades or longer, is referred to as climate change (IPCC, 2007). Human activity has greatly contributed to climate change by altering the composition of the global atmosphere (El Bilali et al., 2020). The long-term impacts of these alterations are attributed to the changes in climatic conditions and agriculture is one of the major contributors of greenhouse gases. Since the 1980s each successive decade has been warmer than any preceding decade hence the decade 2011 to 2020 was the warmest on record (WMO, 2020). The year 2023 is the warmest year on record beating the year 2016 which was heavily influenced by a strong El Nino (WMO, 2024). Climate change impacts are occurring faster than was initially projected (Hansen et al., 2025), hence the urgency required to tackle both the impacts and causes of climate change. Agriculture is a contributor and a victim of climate change. The use of nitrogenous fertilisers results in the release of nitrous oxides which are potent and persistent greenhouse gases (Deng et al., 2015). Nitrous oxide is the third most important greenhouse gas which depletes the ozone layer (Feng and Li, 2023). According to the United Nations Environmental Program (UNEP, 2024), 75% of the nitrous oxide originates from synthetic fertilisers and manures. Animal production results in the release of methane (CH_4) which is a more potent greenhouse gas than carbon dioxide. As a result, agriculture is directly responsible for the production of two important greenhouse gases.

2.1.2 Main uses of maize in areas where it is domesticated

Processing of maize into various products depends on the region and culture of the people. Maize can be processed into a variety of food and industrial products including starch, sweeteners, grits, flour, tortillas, snacks, breakfast cereals, oil, beverages, glue, industrial alcohol and fuel ethanol (Ranum et al., 2014; Shah et al., 2016). Maize is the basis for food security in some of the world's poorest regions in Africa, Asia and Latin America, where it is the source of food for about 4.5 billion people in 94 developing countries (Shiferaw et al., 2011; Erenstein et al., 2022). Maize consumption is expected to increase by 16% by 2027, driven by the rapidly expanding livestock sectors in developing countries as well as human populations in SSA (OECD/FAO, 2019; Sah et al., 2020). Maize is a major carbohydrate source for feed production and the rapid increase in the populations of pigs, cattle and chicken poses a major strain on feed production. As affluence increases with the rising incomes, the consumption of meat and dairy products increases. Meat production has more than doubled in the past 50 years (Ritchie, 2017), thereby requiring more feed for the intensive production.

The use of maize in the pharmaceutical industry as a filler in tablet production either in combination with lactose or alone as dextrinised maize starch filler (DMS) (Shah et al., 2016) has eased the problems associated with lactose intolerance in some individuals.

Many countries have increased the use of ethanol as a biofuel as a way of reducing the import bill for petroleum-based fuels. Maize is one of the crops that is used in ethanol production, especially in the developed countries. The starch in the maize grain is readily convertible to monosaccharide upon treatment and hydrolysis (Schwietzke et al., 2009). Cellulose conversion technology which involves pre-treatment and hydrolysis offers the prospect of increasing ethanol production from maize as other parts of the maize plant are utilised in the production of ethanol (Schwietzke et al., 2009). However, the advent of electric cars and the need to reduce use of fossil fuels as a way of combating global

warming has resulted in a decline in the demand for biofuels and consequently, the demand for maize used in biofuel production (Malode et al., 2021; Amaya et al., 2024).

2.1.3 Challenges for food security

The rapidly increasing human population in SSA demands a sharp increase in food production and this must happen in a rapidly changing climate and on degraded soils. Area expansion has been the major driver of increased maize production in SSA rather than an increase in productivity (Jayne et al., 2023). Maize production in Africa is strongly tied to the area harvested (Epule et al., 2022), but because of population increase and urbanisation, the prospects for increased area expansion have declined. The SSA region has the highest rate of population increase in the world and crop production has been pushed into marginal areas. Area expansion is associated with environmental degradation as well as loss of biodiversity and reduction of carbon dioxide sequestration. Without a commensurate increase in crop productivity there will be an increase in hunger and poverty in areas where the greatest warming is predicted to occur. It is estimated that more than 800 million people worldwide experienced hunger in 2022 (OECD/FAO, 2023). The high prevalence of hunger indicates that its elimination by 2030 seems more unlikely (OECD/FAO, 2023). The rate of population increase in SSA outstrips the rate of crop production increase heightening the need to increase maize productivity to avert starvation.

The impacts of climate change are not uniform and poor countries and the relatively poor within countries are extremely vulnerable (Barrett et al., 2008: Benjamin et al., 2025). The simultaneous occurrence of a myriad of climate disasters greatly diminishes their coping capacity and recovery. The SSA region is projected to experience multiple stresses during a single cropping season, and this will drastically impact crop productivity (Benjamin et al., 2025: Mahajan et al., 2025). The occurrence of drought combined with heat stress is already a common feature. The outbreak of pests and diseases increases the stress factors associated with crop production. Due to the occurrence of multiple stresses

and the associated crop failures, farmers have become risk averse. Risk aversion leads to under-investment and under adoption of improved agricultural production technologies (Hansen et al., 2019). As a result, agricultural investment in the technologies that enhance crop productivity by the small-holder farmers is low resulting in large yield gaps. The use of inorganic fertilisers and adoption of improved hybrid varieties remains low (Aramburu-Merlos et al., 2024) hence yields have stagnated around 2 tha^{-1} in most countries in SSA. Continuous breeding of new stress resilient crop varieties is at the centre of crop adaptation. Crop breeding may not be the panacea to all productivity challenges faced by smallholder farmers, but adaptable stress resilient crop varieties are a sustainable means to counteract the challenges. The persistent use of low yielding obsolete varieties is common among smallholder farmers partly due to lack of new varieties because of low varietal turnover and lack of knowledge among the smallholder farmers on the latest available technologies to counteract climate change.

Agronomic practises such as improved weed and pest control, and correct use of inorganic and organic fertilisers will enhance crop productivity among smallholder farmers. SSA region is the only region in the world that is experiencing negative nutrient balances that continue to increase (IFDC, 2023). Low fertiliser use especially nitrogen, has resulted in persistent low yields among smallholder farmers even where improved varieties are available. Closing the existing grain yield gaps will be crucial in attaining the sustainable development goal (SDG) number two, which is eradication of hunger. Doubling fertiliser usage and ensuring weed and pest control would potentially increase grain yields by 70% (Aramburu-Merlos et al., 2024). However, the production and use of nitrogenous fertilisers is associated with emission of nitrous oxides which are highly potent greenhouse gases (GHG) (Feng and Li, 2023; UNEP,2024). Increased use of nitrogenous fertilisers should be coupled with improved agronomic practises to minimise emissions from the fertilisers through denitrification. Proper management of nitrogenous fertilisers has the potential to improve air quality through the concurrent reduction of ammonia and the oxides of nitrogen that form harmful particulates and ground ozone (UNEP, 2024). Contamination of water bodies is a major environmental concern

associated with the use of nitrogenous fertilisers. Breeding of varieties capable of utilising low soil nitrogen has been pursued at the International Centre for Maize and Wheat Improvement (CIMMYT) (Bänziger and Cooper, 2001; Bänziger et al., 2002), resulting in the release of several maize varieties with high nitrogen use efficiency (NUE).

There are still disagreements on the predicted trends of climate change due to the different outputs from different climate models. However, it is generally agreed that the impact of climate change on agricultural production will be greatest in the tropics and sub tropics (Boutejka et al., 2024). Sub-Saharan Africa is particularly vulnerable to climate change due to the range of projected impacts, multiple stresses that occur simultaneously and its low adaptive capacity (Hellin et al., 2012; Pereira, 2017). There has been an increase in the number of extreme warm days and a decrease in the number of extreme cold days in Africa leading to about 34% decline in agricultural productivity (WMO, 2023). Closing the existing grain yield gaps will be crucial in attaining the sustainable development goal (SDG) number two, which is eradication of hunger causing crop plants to have little or no reserves for use during the grain filling stage. The warming trend in Africa is the largest in all regions of the world. Areas experiencing deficit rainfall have increased since 1978 and are now more than the areas experiencing excessive rainfall (WMO, 2023). The greatest threat to crop production will likely come from intermittent temperature spikes at the critical growing stages rather than the general increase in mean temperatures (Gourdji et al., 2013).

The threshold temperature for maize growth is 35ºC (Cairns et al., 2012; Chen et al., 2012; Waqas et al., 2021). Temperatures above the threshold temperature during the vegetative phase can result in extensive leaf firing causing a rapid decline in the photosynthetic area. A reduction in the photosynthetic area negatively affects the accumulation and storage of photo-assimilates. High temperatures during the reproductive stages results in tassel blasting (Chen et al., 2012), and desiccation of the silks and pollen grains (Begcy et al., 2019; Prasanna et al., 2021) which can cause

severe decline in grain yield due to the perturbation of the reproductive processes. The damage caused by the high temperatures during the reproductive stages is irreversible and cannot be compensated in the later stages resulting in devastating grain yield losses.

Smallholder agriculture is mostly rainfed and under-developed, but it is responsible for food security in sub–Saharan Africa. Small scale farmers are financially poor and have limited access to infrastructure and information (Pereira, 2017). Due to limited access to information, there is limited forward planning for drought mitigation before and during the cropping season. Information from the early warning systems may not reach the farmers in time and hence, occurrence of drought usually has devastating effects. The effects of climate variability and drought conditions are further accentuated by the lack of machinery to speed up farming operations that may help in timeliness of critical operations such as planting. As a result, planting may be delayed causing the crop to coincide with adverse weather conditions during the critical growing period. Sub-Saharan Africa agriculture has been summarised as a low technology, labour intensive, capital scarce endeavour (Exenberger and Pondorfer, 2011) indicating that farmers have limited options to condition the production environment. Early planting which may be possible with use of machinery for both land preparation and planting may be beneficial where terminal droughts are frequent. However, this is not always possible because farmers depend on the rain to plant the crop.

2.1.4 Global maize production trends

Globally, maize is grown on over 197 million hectares with an annual production of about 1.16 billion tonnes (Erenstein et al., 2022). The United States of America, China and Brazil are the largest maize producers respectively. The three account for 48% of the total global maize area (Ranum et al., 2014). In Africa, South Africa is the biggest maize producer followed by Nigeria and Egypt (FAOSTAT, 2024). The Southern Africa region is maize self-sufficient as South Africa takes care of the shortfalls which occur among other countries (OECD/FAO, 2024). In South Africa maize is predominantly

produced by resourced large scale commercial farmers. Maize production in South Africa is highly mechanised and mostly done under irrigation with grain yields per hectare competing with the developed countries. Figure 2.1 summarises maize productivity in the major producing countries, highlighting the low grain yields obtained in Zimbabwe compared to South Africa, Brazil China, Mexico and the USA. The impact of the 2012 meteorological drought which affected even the intensively managed regions is illustrated by a dip in the grain yields in the USA. However, despite this dip, the grain yields recorded in the USA are still relatively higher than the grain yields obtained prior to 2000 indicating significant improvements in breeding for drought tolerance in new maize hybrids in the USA. The USA grows temperate maize which cannot be directly introduced into tropical sub-Saharan Africa.

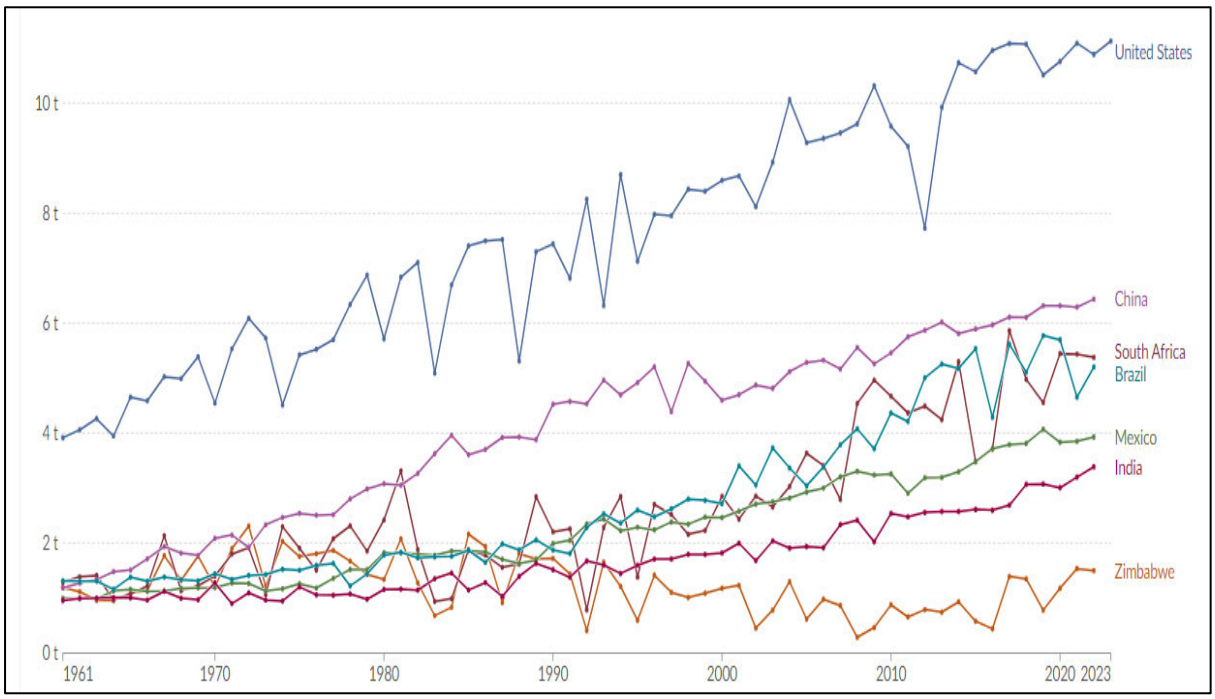

Figure 2. 1. Summary of maize productivity in selected countries in tonnes per hectare from 1961 to 2022. (Source: FAOSTAT, 2024).

Global agricultural production will have to increase by 70% to cater for the ever-increasing world population even though the required increase depends on the base year used for the estimation (Giller

et al., 2021). The rising world demand for maize is coupled with the general stagnation of grain yields on 24-39% of the cropland areas (Ray et al., 2012). Africa is a continent of contrasts with regards to rates of maize yield change (Ray et al., 2013). Yields are increasing in some states in Nigeria, isolated areas in Ethiopia, Angola, Madagascar and South Africa, but maize yields are decreasing in Morocco, Rwanda and Zambia (Ray et al., 2013). In Zimbabwe, maize yields have increased from 0.8tha^{-1} to 1.53 tha^{-1} (FAOSTAT, 2024). There is rapid population growth in SSA, and to cater for the increasing demand for maize grain, there is an urgent need to increase maize productivity to ensure food and nutritional security in the region which is highly dependent on maize as the major staple cereal.

2.1.5 Major maize production trends in SSA

Maize production in SSA is mostly rainfed with minimal application of both organic and inorganic fertilisers as well as pesticides. Unlike in the developed countries where most of the maize is intensively managed, rainfed maize production in the developing countries is extensively managed and exposed to the hazards of climate variability. Climate variability is exacerbated by the surging climate change which has resulted in the high frequency of intense drought and heat stress. In Southern Africa, maize is grown on about 2.6 million hectares producing about 13 million tonnes of grain. In Zimbabwe, about 1.2 million hectares are devoted to maize production producing about 1.2 million tonnes of grain (FAOSTAT, 2020), indicating that the average national yield is just about one tonne per hectare. This is far below the world average yield of about 5.92 t ha^{-1}. In Zimbabwe, production is dominated by the small-scale farmers with land holdings less than a hectare and have limited resources to counteract the effects of climate change hence their yields are strongly tied to the yearly climatic conditions. As a result, the 2023/2024 El Nino had devastating effects on maize production. The low average yields in Zimbabwe are comparable to other SSA countries (Figure 2.2).

The smallholder farmers who dominate maize production in SSA cultivate small pieces of land which are often degraded and have no access to reliable irrigation (AGRA, 2014). Maize production in SSA

is more severely limited by poor soils than low rainfall (OECD/FAO, 2024), thus the increased use of inorganic fertilisers will potentially result in higher grain yields. The production systems are labour intensive lacking mechanisation with very little or no addition of inorganic fertilisers. As a result, nutrient mining is rampant leading to low productivity and high exploitable yield gaps. The average maize yields for some of the countries in Eastern and Southern Africa (ESA) are summarised in Figure 2.2.

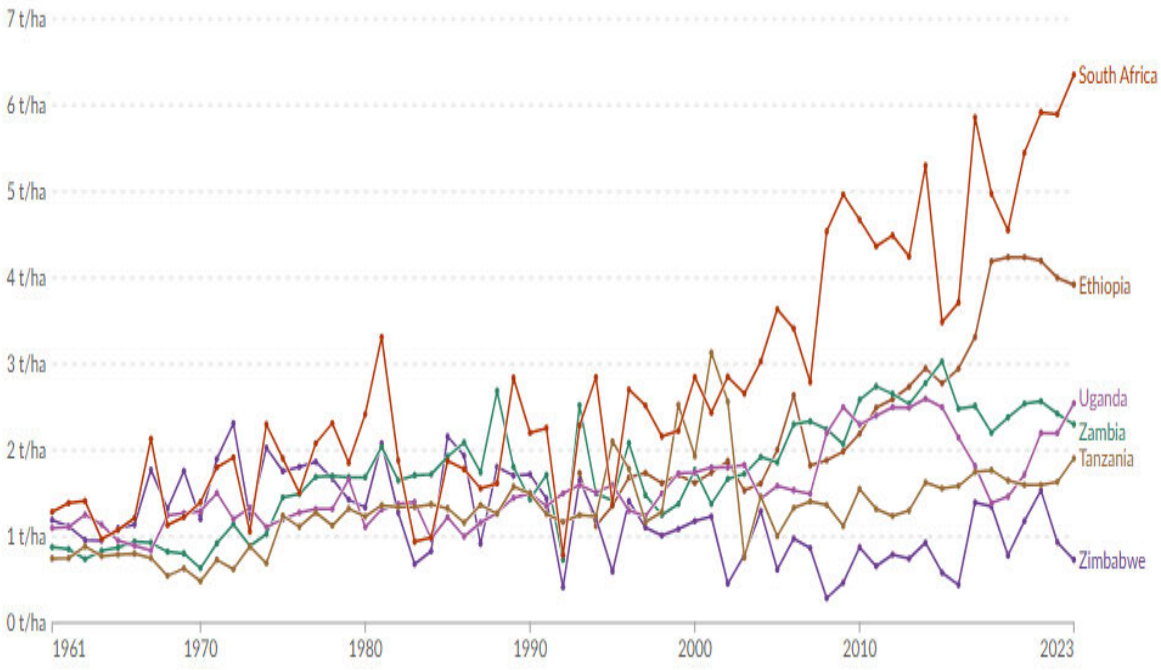

Figure 2. 2. Maize grain yields (t ha^{-1}) for selected countries in Eastern and Southern Africa, from 1961 to 2022 (Source: FAOSTAT 2024).

2.2 Climate change

Long term weather variability is occurring worldwide and has severely affected agricultural production especially rainfed smallholder agriculture. Climate variability is attributed mostly to anthropogenic greenhouse gas emission. The severity of climate change is related to the magnitude of changes in mean temperatures, rainfall and carbon dioxide (CO_2) concentrations, even though methane (CH4) and nitrous oxides (N_2O) are more potent gases than carbon dioxide (UNEP, 2024).

There is greater certainty in temperature change than there is in rainfall variability (Kumar et al., 2021). Increase in temperature has a wide range of effects on both plants and insect pests and these include altering the phenology, increased respiration rates, reduced pollen grain germination ability and silk receptivity, reduced grain filling duration and ultimately reduced crop yields (Ahmed et al., 2018; Prasanna et al., 2021).

Rising temperatures make the once unfavourable climates favourable for new pests, for example, the emergence of Fall armyworm, (*Spodoptera frugiperda* J.E. Smith) in Africa which has resulted in annual maize yield losses of more than 50% (Day et al., 2017). Change in mean temperatures result in rapid multiplication of pests due to the shortening of each stage of the life cycle (Barfield and Ashley, 1987; Deutsch et al., 2018; Tigchelaar et al., 2018). As a result, many generations of pests occur during the crop's most vulnerable stage leading to extensive crop damage. The short life cycle and emergence of many generations during the crop duration increases the possibility of development of pesticide resistance as farmers respond by increasing the frequency and dosage of pesticide sprays. Farmers may also resort to the use of more toxic pesticides which may affect the safety of the crop for human and animal consumption. Some of the pesticides used end up being washed into the water bodies thereby affecting aquatic life. Post harvest losses due to maize weevils *(Sitophilus zeamais)* damage has increased as insects proliferate rapidly under the warmer climate conditions.

The rising temperatures have resulted in high incidences of viral, fungal and bacterial diseases. Incidences and severity of these diseases depend on the prevailing weather conditions. Warm humid conditions tend to favour the development of fungal, viral and bacterial diseases. Fusarium stalk and ear rots have been associated with 13% to 70% yield losses in maize (Ouko et al., 2020; Benjamin et al., 2024) while maize streak viruses are associated with 30% to 100% yield loss in maize (Benjamin et al., 2024). Infection of maize grain by mycotoxin producing fungi species make the grain unsuitable for both human and animal consumption. Maize ears damaged by pests are more

vulnerable to fungal infections than intact ears resulting in high aflatoxins in the affected grains. Maize lethal necrosis (MLN) a synergistic infection between maize chlorotic mottle virus (MCMV) and several maize infecting viruses in the *Potyviridae*, like sugarcane mosaic virus (SMV), has caused severe damage to maize crops in East Africa with estimates of between 30% and 100% grain yield loss (Zhan et al., 2022).

Rainfall distribution has become more erratic such that the critical growth stages of crop plants are coinciding with drought and high temperatures resulting in drastic yield reduction. Sometimes it is not the total rainfall but the distribution during the growing season which affects the crop. Mid-season droughts have become a common feature such that research for drought tolerance targets flowering time water stress (Lu et al., 2011; Tesfaye et al., 2016). In the developed countries, drought stress is mitigated by irrigation. However, in SSA, inadequate irrigation infrastructure development as well as the high costs associated with pumping irrigation water has resulted in most of the maize being produced under rainfed conditions. Dry spells during the critical reproductive stages cause drastic reduction of yield through the perturbation of both pollination and fertilisation, either by delaying the emergence of the silks or by affecting the water potential of the pollen grains and the silks or a combination of both. The asynchrony in pollen shed and silk emergence causes a large anthesis to silking interval. Low water potential of pollen grains and silks causes poor seed set because of reduced silk receptivity and impaired pollen grain germination (Prasanna et al., 2022). Due to the increased frequency of combined drought and heat stress, there is an increase in the yield losses attributed to climate change and variability. More than 50% of the total variation in maize yields is attributed to climate change (Cairns and Prasanna, 2018).

2.2.1 Impacts of climate change induced stresses

Climate change and variability affect crops directly and indirectly. The direct impacts are through the destabilisation of plant physiological and reproductive processes whereas indirect effects occur

through its influence on raising the atmospheric evaporative demand (VPD) (Lennart et al., 2024) as well as increasing the incidences of pests and disease outbreaks. The impacts of heat stress on crop production are already significant and will get worse with the surging climate change (Lennart et al., 2025).

High temperatures affect photosynthesis before respiration, and this results in high photorespiration. Respiration exponentially increases with increasing temperature from 0 to 40^{o}C, (Prasad et al., 2008). Above 50^{o}C, respiration ceases due to the damage of the respiratory mechanism (Prasad et al., 2008). As a result, respiration depletes the photo-assimilates leading to poor plant growth or death in extreme cases. Combined drought and heat stress result in the shortening of the phenological stages without a commensurate increase in assimilate accumulation. As a result, less photosynthates are accumulated for each developmental stage and when the demand for the photosynthates increases during grain filling period, there will be insufficient reserves due to both poor accumulation as well as low photosynthetic activity. Photosynthesis is reduced by both excessively high temperature as well as the reduction in photosynthetic area due to leaf firing and rapid leaf senescence. Inadequate assimilate production and availability results in developmental defects such as fewer, malformed and or smaller organs (Stone and Nicolas, 1995; Maestri et al., 2002).

Reproductive organs do not have the potential to acclimate because of their inability to produce osmolytes that can either provide protection or increase acclimation potential (Prasad et al., 2008). As a result, the reproductive phase is the most vulnerable crop developmental stage. Temperatures above 35^{o}C are lethal to maize pollen viability and even a short exposure of maize plants beyond the threshold temperature during flowering results in a significant loss of yield (Kaushal et al., 2016). Low relative humidity and high temperatures associated with combined drought and heat stress result in high vapour pressure deficit (VPD). High vapour pressure deficit causes high evapotranspiration rates which hasten the onset and severity of drought stress especially in rain fed drylands.

The water potential of both the pollen grains and the silks is critical for successful pollination and fertilisation. The water potential of the pollen grains is determined by the environmental conditions during the time of pollen shedding (Westgate and Boyer 1986) and time of silk extrusion. Drought stress causes a delay in the silk extrusion resulting in a large anthesis to silking interval (Bolaños et al., 1993; Edmeades et al., 1999; Monneveux et al., 2006; Beyene et al., 2016). Pollen grains must absorb water from the silks in order to germinate (Westgate and Boyer 1986), however, because of the high vapour pressure deficit under combined drought and heat stress, there is usually inadequate water on the silks for pollen germination thereby impairing the fertilisation process. Heat stress also affects the water potential and specific gravity of pollen grains (Badu-Apraku and Fakorede, 2017) thereby affecting their ability to land on the silks and germinate. Synchronisation of pollen shedding and silk emergence is a desirable trait as it ensures successful pollination which is critical for fertilisation even though post pollination processes such as pollen tube growth, fertilisation, formation of the endosperm and embryo development are sensitive to heat stress (Barnabás et al., 2008). Heat stress affects all developmental stages of maize crop, but the reproductive stage is the most vulnerable. Maize is more sensitive to temperature change than changes in rainfall. As a result an increase in temperature by 2^{o}C is projected to have more deleterious effects than a 20% decline in rainfall (Lobell et al., 2010).

Climate change has resulted in an increase in the proliferation of insect pests and disease incidences. The drying of the atmosphere may result in decreased incidences of foliar fungal diseases but losses due to fungal infections may rise as ear infections may increase. About 70% of maize yield losses are from ear rot diseases in SSA (Benjamin et al., 2024), especially mycotoxin producing fungi for example *Aspergillus flavus* and ear rot causing fungi of the *Fusarium* spp. Insect vectored viral diseases are projected to increase with the increase in the population of insects. Maize yield losses associated with Maize streak virus (MSV) were estimated at 30-100% (Benjamin et al., 2024). Maize lethal necrosis disease is a devastating disease whose damage depends on the variety and stage of crop

when infected. In Kenya, all commercial varieties were susceptible and damages ranged from 30 to 100% (Zhan et al., 2022).

Climate change influences population dynamics of pests by affecting the reproduction cycles as well as the survival of the pests at different stages. An increase in temperature of 1^{o}C is associated with an additional 10-25% yield reduction due to insects pests either as vectors or herbivory (Trębicki and Finlay, 2018).The feeding habits of insects are highly influenced by the ambient temperatures (Tigchelaar et al., 2018), with warmer temperatures resulting in high feeding by phytophagous pests. The changes in precipitation have resulted in the changes in the migratory habits of the desert locust (*Schistocerca gregaria)* (Deutsch et al., 2018).

Post-harvest losses from storage pests such as the maize weevil *(Sitophilus zeamais)* may increase due to the increased feeding. To counteract the rising populations of insects, farmers respond by increasing the frequency and dosages of spray which affects the development of resistant pests and the safety of the food produced.

2.2.2 Strategies to enhance maize productivity under drought and heat stress and low soil nitrogen

Crop breeding and adaptation is one of the major strategies that can be pursued to ensure food and nutrition security in SSA. The success of the green revolution was underpinned by the development and deployment of higher grain yielding varieties which were resistant to lodging and foliar diseases. Most maize breeding programs screen against the common occurring diseases such as grey leaf spot, common rust and turcicum leaf blight diseases as well as stem lodging. The ability to develop quickly and disseminate new improved varieties with tolerance to complex biotic and abiotic stresses is one of the major strategies to improve the resilience of maize cropping systems (Cairns and Prasanna 2018; Prasanna et al., 2021). The outbreak of the maize lethal necrosis disease in East Africa was combated

using new varieties tolerant to the disease (Zhan et al., 2022). There is little doubt that new germplasm which is more suited to future climates is critical along with improved agronomic and crop management practises (Hellin et al., 2012). However, there is low varietal turnover in SSA (Abate et al., 2017; Atlin et al., 2017; Chivasa et al., 2022), such that most of the current commercial varieties are no longer suitable for the current climatic conditions. Choice of variety, suitable for the target environment is an important aspect in increasing maize productivity. Crop breeding provides a sustainable way to counteract the impacts of climate change by producing crop varieties that are suited to the current climatic conditions and resistant to pests and diseases.

Various yield gaps exist, especially among smallholder farmers in SSA. Reducing the yield gaps will be fundamental in meeting the rising demand for maize as expected from the rapidly increasing population in SSA. An increase of about 184% in the area under maize will be required to cater for the rising population if there is no increase in yield on the current maize area (van Ittersum et al., 2016). Since 2000, 74% of Africa's crop production growth has been attributed to area expansion (Jayne and Sánchez, 2021). Area expansion is not sustainable because land is a finite resource. Crop production has already been pushed into marginal areas due to both urbanisation and population expansion. Crop intensification on the current maize area will reduce area expansion thereby helping in combating desertification and greenhouse gas emissions. The conversion of forests to agricultural lands negates the carbon sequestration of forests and results in the release of carbon dioxide which is one of the major greenhouse gases and is a major primary source of indirect greenhouse gas emissions from the agricultural sector (OECD/FAO, 2024).

Along with the reduction of yield gaps, there is a need to reduce post-harvest losses along the food crop value chain especially in storage. Abass et al. (2014), estimated that between 15% and 25% of maize grain yield is lost in storage because of maize weevils (*Sitophilus zeamais* and *S. granaries* (L), the larger grain borer (*Prostephanus trunctus* (Horn)) and the lesser grain borer (*Ryzopertha dominica*

(L)). These storage pests cause extensive damage resulting in both qualitative and quantitative losses to maize grain in storage. Chemical control is widely used but availability and affordability are a major challenge among smallholder farmers. There are concerns of the residual effects of the chemicals as well as the environmental impacts especially with the use of fumigants like Aluminium phosphide. Breeding interventions have been pursued but there has been limited progress in SSA (Derera et al., 2014), despite the existence of a wide genetic variability for resistance. However, several insect resistant varieties have been released in South America, (Jiménez et al., 2023). This strategy may need to be pursued in sub-Saharan Africa to reduce post-harvest grain losses.

Crop intensification entails increased use of synthetic fertilisers which has stagnated between 13 and 20 kg ha^{-1} (Sheahan and Barrett, 2017) in SSA. Proper management of synthetic nitrogenous fertilisers is critical to avoid excessive emission of nitrous oxides. Nitrous oxides are 300 times more potent than carbon dioxide and persists longer in the atmosphere (Pasha et al., 2016). This implies that the use of inorganic fertilisers must be properly managed to ensure that the emission of nitrous oxides is minimised. Synthetic fertilisers are expected to contribute about 34% to the direct greenhouse gas emissions during the next decade (OECD/FAO, 2024). However, more environmental damage is associated with non-use of fertilisers than use of fertilisers (Giller et al., 2021), because without the addition of both organic and inorganic fertilisers, excessive nutrient mining occurs resulting in serious marginalisation. Implementing efficient use of inorganic fertilisers involves the four principal techniques, that is, right source, right rate, right placement and right timing (4Rs) which minimise loss to the environment and increases nutrient accessibility by crops. Increased use of fertilisers is a critical condition for improved crop production.

Irrigation alleviates the impacts of drought and heat stress. However, under rainfed conditions, the occurrence of midseason drought is detrimental to crop production as the stress tends to coincide with the critical flowering period. Efficient irrigation systems enhance crop productivity in the developed

countries and minimise yield gaps by ensuring that crop water requirements are met during the critical periods. Even though heat stress may occur at any time during the crop life cycle, the impacts of heat stress are minimised when there is adequate moisture in the soil because plants dissipate heat through transpiration (Barnabas et al., 2008). Without irrigation the occurrence of drought and heat stress simultaneously, results in crop plants failing to meet the physiological water requirements as well as the evaporative demand of the atmosphere resulting in reduced productivity. Lack of irrigation and technological advancement including efficient information system result in farmers making uninformed decisions on varieties to grow as well as expected weather conditions. As a result, the occurrence of drought under rainfed conditions has severe impacts on crop production.

In addition to combined drought and heat stress, low soil nitrogen stress is a constant stress severely constraining maize grain yield among smallholder farmers in sub-Saharan Africa. The impact of low nitrogen stress on crop plants depends on the magnitude and duration of exposure, the genotype response and soil moisture (Oliveira-Santos et al., 2023). In sub–Saharan Africa, due to the general inadequate application of inorganic fertilisers, especially nitrogenous fertilisers, crop productivity is low. Nitrogen is the second largest requirement after water in crop production and nitrogen is the most common limiting factor in crop production (Govindasamy et al., 2023). The available organic and inorganic fertilisers are usually inadequate to meet the recommended application rates resulting in severe nutrient mining in most areas. The removal of the maize stover for use as a stock feed exacerbates nutrient mining thereby accentuating low nitrogen stress among smallholder farmers. Low soil nitrogen use efficiency of most maize varieties is associated with low soil nitrogen hence there is a need to breed varieties with higher nitrogen use efficiency (NUE). About 50% of the applied nitrogen is utilised by the plant and the rest is wasted through volatilisation, as ammonia gas (NH_3) and nitrous oxides (N_2O), leaching when dissolved as nitrates (NO_3^-) and as surface run-off (Govindasamy et al., 2023). There is a linear relationship between the emission of soil nitrous oxide and mean annual temperature (Hui et al., 2024), thus as the temperatures are rising due to global warming, soil nitrogen loss is increasing.

The recommended application rate for manure is about 25 tonnes per hectare (Dunjana et al., 2014), and this quantity is rarely available for most smallholder farmers in sub-Saharan Africa. There has been an emphasis on the quality of the manure rather than the quantity (Gudeta et al., 2016). High quality manure will increase the availability of nutrients especially nitrogen which may be fixed in poor quality manure. Due to insufficient quantities of manure, smallholder farmers use various combinations of organic and inorganic fertilisers to mitigate low soil nitrogen stress. Like the nitrogenous fertilisers, manure is also a source of greenhouse gases accounting for about 25% of methane and 31% of nitrous oxide released from agricultural activities (Gudeta et al., 2016). Both methane and nitrous oxide are highly potent, persistent greenhouse gases. As a result, agriculture is a victim and contributor of climate change.

The need to increase crop productivity has resulted in increasing use of inorganic fertilisers which leads to increased emission of greenhouse gases emanating from nitrogenous fertilisers. Reducing the consumption of nitrogenous fertilizers will result in the abatement of nitrous oxide emissions. Crop breeding and deployment of genotypes with high nitrogen use efficiency will make agriculture more sustainable (Santos et al., 2023). There are wide genotypic variations for nitrogen use efficiency among maize inbred lines and the hybrids as well as open pollinated varieties (Li et al., 2022). The ability of the genotype to utilise the absorbed nitrogen efficiently is called the nitrogen internal use efficiency (NIE) and this has been noted to be higher in the newer hybrids than the older varieties (Li et al., 2022). High nitrogen internal use efficiency is exhibited through early establishment of pre-anthesis structures, high leaf senescence scores during grain filling and reduced grain nitrogen concentrations at harvest (Li et al., 2022). It has been estimated that an increase of about 1% in the nitrogen use efficiency of crop plants will result in a saving of about $2.3 billion (Santos et al., 2023). Nitrogen use efficiency has two major components which are uptake from the soil and utilisation of the absorbed nitrogen (Santos et al., 2023). Absorption of nitrogen from the soil depends on the soil moisture content as well as the root architecture. Due to the increased occurrence of drought, the

absorption of soil nitrogen is severely hampered, by both reduced root growth and low soil moisture to dissolve the nitrogenous compounds. Organic nitrogen in manures must be converted into the absorbable forms, and the processes are intermediated by soil microbes. The activities of the soil microbes involved in the mineralisation of nutrients depend on the soil moisture content and prevailing soil temperatures (Li et al., 2024).

Crop breeding interventions have mainly focused on the utilisation of the absorbed nitrogen due to the difficulties associated with studying the root architecture. However, genotypes with high nitrogen use efficiency tend to have extensive root coverage for increased soil exploration and absorption of nitrogen (Prabha-Sigh et al., 2022). Conventional breeding has been pursued to improve nitrogen use efficiency of crop plants and recent studies have involved gene editing to enhance nutrient response (Wei et al., 2018). However, there has been no significant improvement over the control plants (Sathee et al., 2022). Transgenic approaches are being explored to transfer the symbiotic trait in legumes to cereals to equip cereals with the ability to associate with the nitrogen fixing bacteria (Bailey-Serres et al., 2019).

2.2.3 Approaches in breeding maize for combined drought and heat stress

Drought stress has been one of the most devastating abiotic stresses affecting maize productivity in sub–Saharan Africa and this has threatened the livelihoods of millions of people in this region. Between 2005 and 2015, about USD29 billion worth of crops was lost directly because of drought stress (FAO, 2021). Most of the technological advancements intended to increase crop productivity such as increased use of inorganic fertilisers and improved maize varieties are negated by drought stress (Lobell et al., 2011). As a result, breeding efforts are mainly focused on the production of germplasm tolerant to drought stress, in addition to higher grain yields under low nitrogen fertilisation (Raza et al., 2023). Breeding and dissemination of drought tolerant maize varieties was noted as one of the most economic and sustainable ways of stabilizing maize yields in sub-Saharan Africa (Badu-

Apraku et al., 2023). However, because of climate change, the incidences of drought combined with high temperatures have increased enormously and hence the need to focus on germplasm combining drought and heat stress tolerance in addition to other biotic stress tolerances.

Conventional breeding has resulted in the release of many hybrids, inbred lines and open pollinated varieties (OPVs) which have overcome various stress factors. The success of conventional breeding depends on availability and diversity among available germplasm (Musundire et al., 2019). However, progress in breeding and delivery of drought tolerant maize varieties has been slow because grain yield is a complex quantitative trait controlled by many genes and several correlated traits which makes it difficult to manipulate. Gene linkages and epistatic effects tend to reduce the speed of breeding as unfavourable traits may be inherited together with the favourable traits. As a result, conventional breeding tends to be slow due to linkage drag and the low heritability estimates exhibited by grain yield under abiotic stresses. Under field conditions, there is variability in the severity, duration and intensity of the drought stress at different locations and from year to year. To counteract the slow speed of breeding and faced by the surging climate change and variability, various breeding tools have been developed and used in breeding climate resilient germplasm (Prasanna et al., 2012). However, each breeding technique has its own limitations, and conventional breeding remains the most utilized method in the developing world due to low technological advancements and various regulatory requirements for the adoption and deployment of transgenic varieties.

The use of biotechnology and advanced breeding tools in untangling the molecular and physiological mechanisms of drought tolerance will enhance the breeding of drought tolerant varieties (Sheoran et al., 2022). Advanced molecular breeding techniques like the marker assisted selection (MAS), marker assisted recurrent selection (MARS) marker assisted recurrent backcrossing (MARB), transgenics and genome editing may compliment conventional breeding in delivering stress resilient germplasm (Sheoran et al., 2022). Marker assisted selection was proposed to achieve accelerated genetic gains for

the improvement of grain yield under drought stress (Ribaut and Ragot, 2007), and it has been extensively used in the identification of quantitative trait loci (QTL) (Sheoran et al., 2022). The identified quantitative trait loci can be manipulated through various means such as gene editing or deoxy-ribonucleic acid (DNA) methylation resulting in new genotypes. The advent of advanced sequencing tools has disentangled ultra-high density genetic maps to discover massive molecular markers and precisely locate the position of quantitative trait loci (Yu et al., 2011). The major setback of marker assisted selection is the need for large populations for fine mapping of quantitative trait loci. This is expensive to carry out due to the large land requirement and the resources for phenotyping (Gedi and Menkir 2019). Due to the associated costs, there has been limited successful application of the identified quantitative trait loci (Leema, 2018; Kumar et al., 2024). The number of quantitative trait loci regulating the trait of interest and the distribution of the alleles within the quantitative trait loci greatly affects progress of using marker assisted recurrent selection (Badu-Apraku et al., 2023). A trait which is controlled by many quantitative trait loci tends to be more difficult to manipulate.

Genomic selection was proposed to increase the precision of molecular markers in the identification of genotypes with genes for drought tolerance (Sikha et al., 2017; Badu -Apraku et al., 2023). Genomic selection identifies the genomic regions associated with the specific drought tolerant trait in a wider population unlike marker assisted selection which considers recombinant inbred lines from a bi-parental cross (Badu-Apraku et al., 2023). Genomic selection enables breeders to dissect quantitative traits into specific genes which can be improved through marker assisted recurrent selection (Oladasu et al., 2019). The identified genes can be genetically engineered to improve the targeted traits through various means such as genome editing. Genomic selection has resulted in higher genetic gains under drought stress than pedigree selection (Beyene et al., 2016). Genome wide association studies (GWAS) have been widely used to effectively and efficiently identify quantitative trait loci in diverse populations (Schard et al., 2018) and it has become the most widely used tool for studying genotypic and phenotypic correlations (Sheoran et al., 2022). But because of the complexity

of drought tolerance, dissecting it through genome wide association studies has not resulted in major genetic gains and to counteract this, correlation studies of metabolic traits has been utilized (Zhang et al., 2016). However, quantitative trait loci associated with drought and heat stress tolerance have been identified even though the information has not been adequately utilized in the development of maize cultivars (Gedi and Menkir, 2019; Badu-Apraku et al., 2023). Genotype by environmental interactions, epistatic interactions and the need for high-throughput phenotyping have been some of the major setbacks for the use of quantitative trait loci in maize breeding (Madhuri, 2020). Studies on the performance of hybrids produced through genomic selection have been inconclusive. Beyene et al., (2016) reported higher genetic gains than conventional breeding whereas Badu-Apraku et al., (2023) reported no difference in genetic gains between conventional breeding and genome wide association studies. However, there is full agreement on the cost reduction of producing the hybrids using genomic selection compared to the conventional breeding techniques.

Recent advances in scientific plant studies have revealed a new field which elucidates plant cell components and how they change in response to environmental conditions. The study involves sequencing genomes, proteins, transcripts and metabolites and this has been aided by the next generation sequencing (NGS) (Yang et al., 2021). This new field is commonly referred to as omics, and these studies include genomics, epigenomics, proteomics and metabolomics (Budak et al., 2015).

Genomics identifies the key genes involved in conferring certain adaptive or functional processes whereas transcriptomics reveal how the genes are expressed under certain conditions (Singh et al., 2022). Proteomics deals with the proteins in a sample whereas metabolomics identifies metabolites which are synthesised in response to environmental conditions. The study of ‘omics’ has been used to identify the genes, quantitative trail loci, gene networks, and the regulatory pathways associated with drought stress tolerance in maize and have revealed several drought-related biomarkers (Sheoran et al., 2022) including heat shock proteins (HSP) (Wang et al., 2019). The application of ‘omics’ in the

developing countries is hindered by the high costs associated with infrastructure requirements, the complexity of translating research findings into practical application. The data generated is often complex and requires sophisticated computational skills (Sanooja et al., 2025) The overall plant performance under stress involves various stages of tolerance which include acclimation, injury and recovery. However, under laboratory conditions, the recovery is often ignored because of limited space in the greenhouses. As a result, the metabolites produced during the acclimation and recovery processes are not captured and determined (Obata et al., 2015). The stress in greenhouses is usually applied as a single rapid event or for a short duration therefore it does not adequately mimic field conditions. The application of omics is still limited (Sheoran et al., 2022).

Phenotyping has been one of the major bottlenecks in maize breeding (Araus et al., 2012). This was due to the high cost, lack of adequate and suitable equipment and the need to record the same trait at different locations at the same time. However, high throughput phenotyping (HTP) aided by unmanned aerial vehicles (UAV) and drones are contributing to the study of omics that has gained popularity and extensive use in maize breeding. High throughput phenotyping enables accurate, labour and cost-effective phenotyping of complex morpho-physiological traits (Khadka et al., 2020). Phenotypic expression of traits is highly influenced by the environment which vary from one location to the other and from one year to the other as the stress intensity and duration varies. As a result, phenotyping multi-location trials under field conditions is affected by the lack of timing and yearly variations in the severity of the stress factor. Under greenhouse conditions, standardized and automated procedures are often used, and these provide unbiased recordings (Sheoran et al., 2022). However, these controlled environments do not adequately mimic field conditions and the initial capital investment for purchasing high throughput phenotyping equipment is still high thereby reducing their application in most of the developing countries.

Epigenetic modification of gene action has emerged as an important way of modulating the expression of specific genes without changing the deoxyribonucleic acid (DNA) sequence (Sheoran et al., 2022). These modifications are common in response to environmental changes such as drought and heat stress and are heritable and long lasting possibly through plant stress memory (Sheoran et al., 2022). Epigenetic changes alter gene action through small ribonucleic acid (RNA) (miRNA or siRNA) to cause non-expression or over-expression of DNA through either DNA methylation or histone changes (Wojtyla et al., 2020). These modifications improve stress resistance in crop plants by either up-regulating or down-regulating small ribonucleic acids which affect the production of plant hormones, reactive oxygen species (ROS) and transcriptional factors (Banerjee et al., 2017). Post translational and post transcriptional changes such as phosphorylation, ubiquitination, DNA methylation, RNA interference chromatin modification and post-translational modifications are some of the applications of epigenetic modifications (Thibaut et al., 2019). The methylation of DNA in maize inbred lines has shown that there are distinct drought responses among drought tolerant and drought sensitive germplasm (Sheoran et al., 2022: Li et al., 2025). These indications make it easier and accurate to distinguish between the susceptible and tolerant germplasm without the extensive costs associated with field trials.

Genome editing involves the rapid and precise manipulation of the DNA sequence by changing the sequence of major genes either through deletion or addition of a particular region for the development of the targeted ideotype. This is achieved by using sequence specific DNA nucleases which can be used for manipulating any plant genes (Takasu et al., 2010). Genome editing tools such as zinc finger nucleases (ZFN), transcription activator-like effector nucleases (TALEN) and the clustered regularly interspaced short palindromic repeat (CRISPR) or the CRISPR associated protein 9 (Cas9) system, have provided targeted gene modification in plants (Khalil, 2020; Hisano et al., 2021). Gene editing has been utilized to improve the nutrient response of crop plants, for example nitrogen use efficiency (Wei et al., 2018). The ability to edit the zygote in doubled haploids has provided another window through which rapid development of stress tolerant maize inbred lines can be done (Sheoran et al.,

2022). However, the success of genome editing depends on the ability to use molecular markers or techniques capable of discovering the desired quantitative trait loci (Sheoran et al., 2022).

Prime gene editing technology has vastly improved gene editing by offering precise large variations such as deletions, replacements and inversions of gene sequences (Yidi et al., 2024). Genome editing technology is used for making small variations in the genome such as insertions and deletions (indel) (Yidi et al., 2024), but prime editing allows the insertion of the desired DNA sequence at a specific position thereby creating the desired variation in the traits of interest. These can be small insertions or deletions to enhance grain yield or disease resistance or nutritional improvements. The application of prime gene editing is still minimal but has great potential in creating the desired variations from which selections can be made.

There has been remarkable progress in genetic engineering which has culminated in the transfer of both artificial and natural favourable genes into the desired crop plants. The inserted gene sequence is known as the transgene and it may come from an unrelated plant or from a completely different species (Jhansi and Usha, 2013), for example *Bacillus thuringiensis* genes inserted in the maize genome to confer insect pest resistance. The genes which are introduced may be responsible for signalling or regulating pathways or encoding enzymes in pathways leading to the synthesis of functional and structural protectants (Hisano et al., 2021). Genetic engineering has increased the options available for the rapid production of drought and heat stress tolerant maize germplasm (Martignago et al., 2020). For example, the genes TsVp and Bet A from *Thellungiella halophila* and ZnaTIP1, ZmPLC1, ZMVPP1 and ZMC111 from *Escherichia coli* have been used (Zhang et al., 2020). The drought tolerant plants arise from the over-expression of these genes (Yu et al., 2021) and the high synthesis of glycine betaine (GB) which is one of the major osmo-protectants in maize (Li et al.,2024). Transgenic plants provide production advantages by being pest resistant which reduces

spraying costs or being resistant to herbicides for example Roundup ready maize, which reduces the cost of weed control (Jhansi and Usha, 2013).

2.2.4 Progress in breeding for combined drought and stress tolerant maize

Various breeding projects have been launched in different regions with the aim of producing adaptable maize germplasm to different stresses in sub-Saharan Africa. The drought tolerant maize for Africa (DTMA) which was launched in 2006 aimed to develop and promote commercialization of maize hybrids and varieties with stable yields. The Stress Tolerant Maize for Africa (STMA) followed the Drought Tolerant Maize for Africa project, and the project sought to produce maize varieties with multiple stress tolerance to counteract the impacts of climate change. These two mega projects produced new maize varieties which yielded 20-30% more than the commercial checks across stressful and favourable field conditions (Badu-Apraku et al., 2023). About 254 new stress resilient maize hybrids and open pollinated varieties (OPVs) were produced between 2006 and 2017 (Badu-Apraku et al., 2023). The International Institute of Tropical Agriculture (IITA) produced about 44 hybrids and 54 OPVs which were tolerant to drought and *Striga* spp (Badu-Apraku et al., 2023). The combination of drought and heat stress has synergistic deleterious effects and hence the need to produce maize germplasm capable of tolerating a combination of stresses rather than a single stress at a given growth stage.

The Accelerated Genetic Gains (AGG) project followed the Stress Tolerant Maize for Africa project, and it focused on improving varietal turn over and increased use of technology in breeding to produce multiple stress tolerant maize varieties. About 69 maize varieties were released with the highest number of maize varieties being released in Nigeria and Zambia (Badu-Apraku et al., 2023). Of the 69 new maize varieties, 17 were yellow maize varieties and 52 were white maize varieties. The varieties had various combinations of stress tolerances including tolerance to *Striga* spp., Maize Lethal Necrosis disease (MLN), fall army worm (FAW) drought, heat, and low soil nitrogen.

The Water Efficient Maize for Africa (WEMA) project was launched in 2008, and it was a public-private sector collaboration endeavour to produce hybrid maize varieties with about 35% yield advantage over the commercial hybrids (Edge et al., 2018). The project operated in Kenya, Mozambique, South Africa, Tanzania, Uganda, Zambia and Zimbabwe. The project used conventional breeding, marker assisted recurrent selection and other biotechnology tools in the development of hybrids, that were marketed free from royalties (Obunyali et al., 2019). More than 70 hybrids were released in Kenya, the most widely grown transgenic variety was W1101 (Willy et al., 2021). At the conclusion of The Water Efficient Maize for Africa project, the African Agricultural Technology Foundation (AATF) coordinated the continuation of the project under the name TELA maize using transgenic approaches to produce maize hybrids resistant to both biotic and abiotic stresses. The main objective of the TELA project was to improve food security among smallholder maize farmers through the commercialisation of transgenic drought-tolerant and insect resistant maize varieties (Willy et al., 2021). The transgenic varieties have shown adaptability and have yielded about 53% more than the commercial hybrids at the research sites and about 188% more than the Kenyan national average (Obunyali et al., 2019). The increased use of transgenics has resulted in higher grain yield, reduced crop failure and reduced inter-seasonal yield variations among smallholder farmers resulting in many ripple effects including poverty reduction, reduced chemical usage and improved environmental safety due to reduced spraying against insect pests (Willy et al., 2012). In Nigeria, four transgenic drought tolerant and insect resistant maize varieties have been adopted and have resulted in a saving of about $256 million in pesticides imports (Obunyali et al., 2019).

Despite the advances in breeding technologies, most breeding programmes are still using conventional breeding methods due to an array of factors, chief among them being the lack of adequate funding to acquire the necessary equipment and infrastructure. The doubled haploid technology is being utilised by CIMMYT in Kenya (Prasanna et al., 2012) and SEEDCO in Zimbabwe to cut down the number of years required for the development of maize inbred lines which represents a huge saving. Despite

these efforts breeding of maize hybrids is still a costly venture, and this has contributed to the low varietal turn over in sub-Saharan Africa.

Field trials are still the most used means of assessing the performance of new genotypes under the targeted stress conditions. The omics revolution has brought a new perspective in analysing the various molecules that are synthesised by plants in response to different stress conditions. However, combining the omics and field trialling should enhance both technologies.

The transgenic approach has had major impacts on yield protection and on the environment. The insect pest resistant varieties are important in areas where stem borers and fall armyworm are prevalent (Thansi and Usha, 2013). The transgene controls the pests while the reduction in spraying reduces environmental pollution and at the same time reducing the import bill for the pesticides (Hellmich and Hellmich, 2012). The use of drought tolerant transgenics will help in food security under the extremely variable climatic conditions ensuring stable harvests from season to season. Transgenic varieties with high nutrient use efficiency will alleviate the impacts of low soil fertility which is rampant in sub–Saharan Africa (Sathee et al., 2022). There are still widespread fears on the safety of transgenic crops. Government policies have not favoured the use of transgenics in some countries in sub–Saharan Africa. The use of a combination of various breeding methods for the development of climate adapted germplasm including conventional, molecular and transgenic is important to produce climate adapted varieties (Hellin et al., 2012; Prasanna, 2015; Cairns and Prasanna, 2018), which will counteract the impacts of climate change and reduce food insecurity and prevalence of hunger.

2.3 Conclusion

Conventional breeding has relied on genetic variation both in the current germplasm and wild relatives to produce new varieties that are tolerant to different types of stresses. Grain yield tends to exhibit low heritability estimates under stressful conditions hence genetic gains under stress tend to be low. A variety of secondary traits have been utilised to improve selection efficiency under stress and various methods have been used to determine the contribution of each trait towards grain yield. Correlation studies and path coefficient studies have been applied in maize breeding to determine the traits to target under given stress factors. Phenotyping is one of the major bottlenecks in maize breeding because of the cost involved in measurement of traits at different times in multi-locational trials.

Advanced breeding tools have been developed and mostly seek to reduce the breeding cycles as well as the costs associated with phenotyping. There have been major successes in breeding for both biotic and abiotic stress tolerance using the advanced breeding techniques. The ability to edit any gene has greatly enhanced both the suppression and expression of genes within a given variety. The application of gene editing remains low but would potentially make breeding faster and cheaper. However, genetic engineering using transgenics, intragenics and cisgenics has had tremendous success in the production of varieties tolerant to biotic and abiotic as well as various combinations of these stresses. Transgenic varieties have potential economic and environmental benefits emanating from reduced spraying and high yields under stress. The major issues affecting the adoption of the genetic engineering innovations are the affordability of the seed and the safety concerns of the farmers. A holistic approach is required to enlighten the farmers on the benefits of the transgenics at the same time enlightening the public to dispel the perceived health concerns.

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CHAPTER 3

Identification of sub-tropical maize inbred lines with combined drought and heat stress adaptation attributes among maize populations developed within the CIMMYT and Crop Breeding Institute maize breeding program

ABSTRACT

There is an urgent need to widen the genetic base for hybrid development to counteract climate change and focus breeding programs on the development of crop varieties that are resilient to both inter and intra seasonal weather conditions. This study aimed to: (i) identify sub-tropical maize inbred lines with combined drought and heat stress adaptation attributes, and (ii) identify agronomic traits that can be used to indirectly select for high grain yield performance under combined drought and heat stress conditions in maize.

A total of 40 inbred lines (24 elite experimental lines, 10 combined drought and heat stress released lines and six drought tolerant released lines) developed within the CIMMYT maize breeding program were evaluated together with six maize inbred lines released from the Zimbabwe National breeding program, the Crop Breeding Institute (CBI). The 40 maize inbred lines were planted in an 8 x 5 α-lattice design at Chiredzi Research Station, in Zimbabwe. Chiredzi Research Station is in the southeast lowveld of Zimbabwe and is characterised by hot dry periods between September and November with temperatures exceeding the 35^{o}C during the day. Managed combined drought and heat stress (CDHS) trials were planted in July to ensure flowering occurred during the hottest days. The two trials were differentiated by planting dates. The trials were replicated three times. Irrigation was withdrawn six weeks after seedling emergence to induce drought and heat stress conditions in the experiments. Combined analysis of variance (ANOVA) showed significant differences among the genotypes for grain yield (GYD), number of days to anthesis (AD), anthesis to silking interval (ASI), plant and ear height (PH and EH), number of ears per plant (EPP), number of leaves above the ear

(NLAE), internode length (IL), chlorophyll content (CC) and early plant vigour (EPV). There were no significant site main effects on AD and CC. The best yielding (18 maize inbred lines) were not significantly different from each other for grain yield. They consisted of four maize inbred lines identified in an earlier study, one from the CBI and eleven were new maize inbred lines developed from CIMMYT maize breeding program. Among the CIMMYT maize inbred lines identified in earlier studies as candidates for combined drought and heat stress breeding in maize, CML444 was also identified. The agronomic traits EPP and CC were significantly and positively correlated with grain yield and appear to be prime traits in yield determination under combined drought and heat stress conditions. AD and ASI were significantly and negatively correlated with grain yield, and these traits determine the success of the pollination and ultimately fertilisation success. Overall, the study successfully identified target traits and maize inbred lines for utilisation in breeding new maize varieties adapted to combined drought and heat stress in sub-Saharan Africa.

3.1 Introduction

There is an urgent need to widen maize genetic base for hybrid development to counteract climate change and variability induced crop production threats. These production threats are both biotic and abiotic. The frequency and intensity of combined drought and heat stress has increased with increasing climate variability. It is therefore imperative that crop breeding focuses on the development of crop varieties that are resilient to variable weather conditions within seasons rather than tolerance to individual stresses at a specific crop growth stage (Zaidi et al., 2020). The new maize varieties should be adaptable to different climatic conditions as well as withstand various biotic stresses. Maize breeding for drought stress tolerance focused on reproductive stage drought tolerance (Monneveux et al., 2006; Ainsworth and Ort, 2010; Worku et al., 2016) which is the most susceptible crop developmental stage (Monneveux et al., 2006; Prasanna et al., 2021). However, the emergence of heat stress and drought stress and their combination have added another complex challenge to crop breeding. Heat stress affects all crop developmental stages including photosynthetic respiratory enzymatic activities leading to energy deficiencies (Li et al., 2025). New tolerant maize inbred lines must be developed and selected for tolerant high yielding hybrids suited to the current and future climates.

Multiple stresses occur in the resource constrained smallholder farmer's fields. During summer cropping, lack of irrigation facilities exposes the crop to drought stress and accentuates high temperature stress due to lack of adequate water for transpiration which would result in the dissipation of heat. The occurrence of two or more stresses has a synergistic effect and the impacts greatly exceed the impacts of each stress when occurring alone (Rizhsky et al., 2002; Wahid et al., 2007; Cairns et al., 2013). The metabolic and physiological responses to two different stresses may require antagonistic responses (Barnabás et al., 2008). For example, drought stress causes the plant to close the stomata to conserve moisture whereas heat stress requires the plant to open the stomata to dissipate heat through transpiration (Barnabas et al., 2008). Due to inadequate moisture availability,

plants fail to open their stomata and leaf temperature remains high resulting in the perturbation of the photosynthetic system and injury of cell membranes.

Crop improvement for drought tolerance has been a long-term goal of most breeding programs and in response mega-projects like Drought Tolerant Maize for Africa (DTMA), have released various maize inbred lines, hybrids and open pollinated varieties (OPVs) (Badu-Apraku et al., 2023) widely used across the continent. However, the surging climate change has resulted in the occurrence of drought stress combined with heat stress and hence the need to produce and identify germplasm that combine both as they occur simultaneously together. Cairns et al., (2012) noted that drought tolerance is genetically distinct from heat stress or combined drought and heat stress. Therefore, there is an urgent need to widen the genetic base and identify genotypes which are tolerant to combined drought and heat stress. The success of any breeding programme depends on the availability and variability of the genetic materials (Musundire et al., 2019). The identification of the combined drought and heat stress genotypes can be successfully undertaken under the desired stress conditions. Various studies have been conducted in greenhouses to screen genotypes for combined drought and heat stress, but the conditions do not adequately simulate field conditions. Various processes are involved in conferring plant tolerance to stresses and these include acclimation and recovery from the stress. However, under greenhouse conditions, stress is usually applied as a single rapid event or for short periods (Li et al., 2025), giving the crop plants no time to acclimate. Due to limited space in greenhouses, the cop plants usually do not grow to maturity hence recovery processes are not adequately studied. However, open field studies are affected by the variations in the stress occurrence and intensity from year to year and the differences in the climatic conditions from one location to another. Sometimes the stress occurs when the crop has grown past the most susceptible stage and hence expected phenotype may not manifest. It would be important to breed and select inbred lines under the targeted stresses. Heat stress induces deoxy-ribonucleic acid (DNA) methylation in maize kernels (Li et al., 2025). These alterations are heritable and form the basis of tolerance to the stress that would have caused the methylation in the future generations. In this study, maize inbred lines were grown under open field

conditions to encompass all the processes conferring tolerance to combined drought and heat, allowing the expression of the combined drought and heat stress phenotype.

The present study aimed to: (i) identify local and exotic maize inbred lines with combined drought and heat stress adaptation attributes, and (ii) identify agronomic traits that can be used to indirectly select for high grain yield performance under CDHS conditions in maize. The research was centred on the hypothesis that there is wide genetic variability for tolerance to CDHS among various maize inbred lines being used for hybrid production in the CIMMYT maize program in Southern Africa and the national breeding program of Zimbabwe, (i.e., Crop Breeding Institute (CBI).

3.2 Materials and methods

3.2.1 General research design

The experiment was conducted during the dry season of 2016, at Chiredzi Research Station in Zimbabwe (21º1`10``S, 31º34`23``E, 432 meters above sea level). There are less chances of rainfall disruption of drought screening trials during that period (May-October) in Zimbabwe. Planting was done at two different intervals: (i) First planting 23rd of August 2016, and (ii) Second planting 30th of August 2016. This was done to ensure that flowering coincided with the hottest and dry months (October to November). Irrigation was withdrawn six weeks after planting to impose drought stress conditions on the crop. Heat stress set in naturally as the temperatures are predominantly above the growing threshold for maize during that period in the lowveld areas of Zimbabwe, (Figure 3. 1).

3.2 2 Plant materials

A total of 40 maize inbred lines (24 elite experimental lines, two combined drought and heat stress tolerant released maize inbred lines and eight drought tolerant released maize inbred lines) developed within the CIMMYT maize breeding program were evaluated together with six maize inbred lines from the Zimbabwe National breeding program, the Crop breeding institute (CBI). Two maize inbred lines with combined drought and heat stress tolerance were identified by Cairns et al., (2012). The 24 elite experimental lines from CIMMYT and six maize inbred lines from CBI were not previously evaluated for combined tolerance to combined drought and heat stress (Table 3.1).

3.2.3 Experimental design and field management

The trials were laid out in a 5 x 8 α-lattice (0.1) design, replicated three times. Each plot was made up of two rows 4-m long with 0.25m interplant distance and 0.75m between rows, with a final density of 53, 333 plants ha^{-1}. Two kernels were planted at each planting station and were thinned to one at three-leaf stage. All plots received 400 kg ha^{-1} as compound D (7%N, 14% P_2O_5 and 7% K_2O) at

sowing. Nitrogen (N) 60 kg $ha^{-1}$was split applied as Ammonium Nitrate at four and six weeks after planting. All agricultural practices which are recommended for weed and pest control were followed to minimise crop damage (Kamara, 2017). Daily weather records were taken to ascertain if the temperature exceeded the growing temperature threshold for maize.

Table 3. 1. List of sub-tropical maize inbred lines developed from the CIMMYT and CBI maize breeding programs evaluated for tolerance to combined drought and heat stress tolerance at Chiredzi Research station during the 2016 dry season.

ENTRY No.	NAME	PEDIGREE	ORIGIN	SOURCE	HETEROTIC GROUP
1	CL114305	(CML395-B/[(CML395/CML444)-B-4-1-3-1-B/CML395//DTPWC8F31-1-1-2-2]-5-1-2-2-BBB)DH1-B*5	ELITE EXPERIMENTAL	CIMMYT	B
2	CL114315	(CML444-B/[LZ956441/LZ966205]-B-3-4-4-B-5-B*8) DH2-B*5	ELITE EXPERIMENTAL	CIMMYT	B
3	CL114316	(CML444-B/[LZ956441/LZ966205]-B-3-4-4-B-5-B*8) DH3-B*4	ELITE EXPERIMENTAL	CIMMYT	B
4	CL114302	([SYN-USAB2/SYN-ELIB2]-35-2-3-1-B*6/[CML442/CML197/[TUXPSEQ]C1F2/P49-SR]F2-45-7-3-2-BBB]-2-1-1-1-1-B*5)DH-B*4	ELITE EXPERIMENTAL	CIMMYT	A
5	DJ91-5	[MAS[MSR/312]-117-2-2-1-B*5/ZM621A-10-1-1-1-2-B*7]-B-10-1-BB	ELITE EXPERIMENTAL	CIMMYT	A
6	DJ71-280	[MAS[206/312]-23-2-1-1-B*5/MAS[MSR/312]-117-2-2-1-B*5]-B-10-1-BB	ELITE EXPERIMENTAL	CIMMYT	A
7	DJ71-276	[[INTA-2-1-3/INTA-155-2-2]-X-3-2-B-11-B-5-B/EliteBulkA]-B(bal)-9-1-1-1-B*4	ELITE EXPERIMENTAL	CIMMYT	A
8	CL107248	([[EV7992#/EV8449-SR]C1F2-334-1(OSU8i)-1-4-X-X-2-B/[SC/ZM605-1-2-5-2/CML395]-B-14-3-2-1-3-1/[[EV7992#/EV8449-SR]C1F2-334-1(OSU8i)-10-4(I)-X-X-B/[MSRXPOOL9]C1F2-205-1-3-1-2/CML202]-B-5-1-1-2-B-4)-1-4-3-2-B*4	ELITE EXPERIMENTAL	CIMMYT	A
9	DJ88-6	[[CML444/CML395//DTPWC8F31-1-1-2-2-BB]-4-2-2-2-2-BB/[MSRXPOOL9]C1F2-205-1(OSU23i)-5-3-X-X-1-B//EV7992/EV8449-3-2-2-2-B*5]-B-1-1-BB	ELITE EXPERIMENTAL	CIMMYT	B
10	DJ88-8	[[LZ956441/LZ966205]-B-3-4-4-B-5-B*5/[CML390/CML206]-BB-2-4-B*4]-B-1-1-1-B*7	ELITE EXPERIMENTAL	CIMMYT	A
11	CL115339	(CML537/[[KILIMA(ST94)-S5:101/CML442]-BB-1-1/CML390]-3-3-1-1-1)-B-5-3-2-BB	ELITE EXPERIMENTAL	CIMMYT	A
12	CL1013722	(CML444-B/LaPostaSeqC7-F180-1-2-2-1-BBB)-B-246-2-1-BBB	ELITE EXPERIMENTAL	CIMMYT	B
13	CL1013613	(CML444-B/LaPostaSeqC7-F180-1-2-2-1-BBB)-B-74-1-1-BBB	ELITE EXPERIMENTAL	CIMMYT	B
14	CL1013701	(CML444-B/LaPostaSeqC7-F180-1-2-2-1-BBB)-B-217-1-2-BBB	ELITE EXPERIMENTAL	CIMMYT	B
15	C447-4	[DTPWC8F31-4-2-1-6-B2/CML395//[CML445/ZM621B]-2-1-2-3-1-BB]-3-2-1-1-2-1-B*4	ELITE EXPERIMENTAL	CIMMYT	B
16	CL106622	[P501SRc0-F2-47-3-2-1-B/[CML442/CML197//[TUXPSEQ]C1F2/P49-SR]F2-45-7-3-2-BBB]-2-1-1-1-2-BBB]-B-11-1-2-B*6	ELITE EXPERIMENTAL	CIMMYT	A

17	CL115324	([[CML388/CML391]-BB-5-2/CML390]-2-1-2-1-1-B/SYNTemperateA-SR-F2-40-2-1-1-1-B)-B-6-1-2-BBB	ELITE EXPERIMENTAL	CIMMYT	A
18	CL108623	(CML269/TX114-BBB-1-1-B*6/[(CML395/CML444)-B-4-1-3-1-B/CML395//DTPWC8F31-1-1-2-2]-5-1-2-2-B*5)-1-1-2-1-BB	ELITE EXPERIMENTAL	CIMMYT	B
19	C447-41	[[EV7992#/EV8449-SR]C1F2-334-1(OSU8i)-1-4-X-X-2-B/[SC/ZM605-1-2-5-2/CML216]-B-17-1-1-1-BB	ELITE EXPERIMENTAL	CIMMYT	A
20	C529-43	[CML444/CML395//ZM521B-66-4-1-1-1-BB]-3-3-1-1-B*5	ELITE EXPERIMENTAL	CIMMYT	B

21	CL102321	AdvancedB08(BalBulk)-135-4-2-1-B	ELITE EXPERIMENTAL	CIMMYT	A
22	C1008-1	([LZ956441/LZ966205]-B-3-4-4-B-5-B*7/LaPostaSeqC7-F71-1-2-1-1-BBB)-1-7-1-1-BB	ELITE EXPERIMENTAL	CIMMYT	B
23	CL106477	[CML444/CML395//DTPWC8F31-1-1-2-2-BB]-4-2-2-2-1-B*4	ELITE EXPERIMENTAL	CIMMYT	B
24	DJ96-27	[[LZ956441/LZ966205]-B-3-4-4-B-5-B*5/[CML390/CML206]-BB-2-4-B*4]-B-4-1-3-B*6	ELITE EXPERIMENTAL	CIMMYT	A
25	JC18-1	LaPostaSeqC7-F18-3-2-1-1-BBB	DROUGHT TOLERANT RELEASED	CIMMYT	B
26	JC18-2	DTPWC9-F24-4-3-1-BB	DROUGHT TOLERANT RELEASED	CIMMYT	B
27	JC18-3	DTPYC9-F46-1-2-1-1-BB	DROUGHT TOLERANT RELEASED	CIMMYT	B
28	JC18-4	DTPYC9-F46-1-2-1-2-BB	DROUGHT TOLERANT RELEASED	CIMMYT	B
29	JC18-5	POB502c3F2-10-3-2-1-BB	DROUGHT TOLERANT RELEASED	CIMMYT	B
30	JC18-6	LaPostaSequiaC7-F64-2-6-2-2-BB	DROUGHT TOLERANT RELEASED	CIMMYT	B
31	JC18-7	LaPostaSequiaC7-F180-3-1-1-1-BB	DROUGHT TOLERANT RELEASED	CIMMYT	B
32	CML312	CML312	DROUGHT TOLERANT RELEASED	CIMMYT	A
33	CML444	CML444	DROUGHT TOLERANT RELEASED	CIMMYT	B
34	CML571	CML571	DROUGHT TOLERANT RELEASED	CIMMYT	B
35	DR&SS	K64R	HEAT TOLERANT RELEASED	CBI	B
36	DR&SS	M162W	ELITE RELEASED	CBI	A
37	DR&SS	N3	ELITE RELEASED	CBI	A
38	DR&SS	SC	ELITE RELEASED	CBI	B
39	DR&SS	NAW5867	ELITE RELEASED	CBI	A
40	DR&SS	M37W	ELITE RELEASED	CBI	B

CBI = Crop Breeding Institute

3.2.4 Data collection

Comprehensive data were collected for various traits. Measurements were done according to the, CIMMYT, (1985) procedures. The traits that were measured and the measurement procedure were:

a. Number of days to anthesis (AD) were recorded when 50% of the plants in a plot were shedding pollen.
b. Number of days to silking (SD) were recorded when 50% of the plants in a plot had silks emerged.
c. Plant height (PH) (cm) measured as the distance between the base of the plant to the auricle of the flag leaf using a Laser distance metre (DISTO)
d. Ear height (EH) (cm) measured as the distance between the base of the plant to the node bearing the primary ear.
e. Stalk lodging (SL) percentage of plants per plot that had stalks broken below the ear.
f. Root lodging (RL) percentage of plants per plot which had stalks inclined by more than 45^{o}.
g. Leaf senescence (Sen) percentage of dead leaves in a plot on a scale of 1 -10 where 1 is no leaf senescence and 10 was all leaves dead.
h. Bad husk cover the number of plants in a plot with exposed ear tips
i. Chlorophyll content measurements were done using a SPAD meter (Konica Minolta, Japan) from the topmost fully developed leaf ding the vegetative phases and from the ear bearing leaf during the reproductive phases.
j. Tassel branches were counted from five randomly picked plants from each plot and the mean was taken as the number of tassel branches for each plot.
k. Tassel size was visually scored on a scale of one to five where one was small and five was large.
l. Internode length the length of the ear bearing node was measured in centimetres
m. Number of leaves above the ear the leaves above the topmost ear were counted.
n. Number of rows on the ear were counted for five selected cobs from each plot

o. Cob girth was measured using a tap measure wound around five randomly selected cobs from each plot
p. One hundred kernel weight, one hundred kernels were randomly picked from the shelled grain from each plot and the weighed using a scale.
q. Grain weight, at harvest the four plants in the alleys were discarded and the cobs from the remaining plants were harvested and the grain shelled and weighed using a scale. Grain yield per hectare was calculated adjusted to 12.5% moisture content.

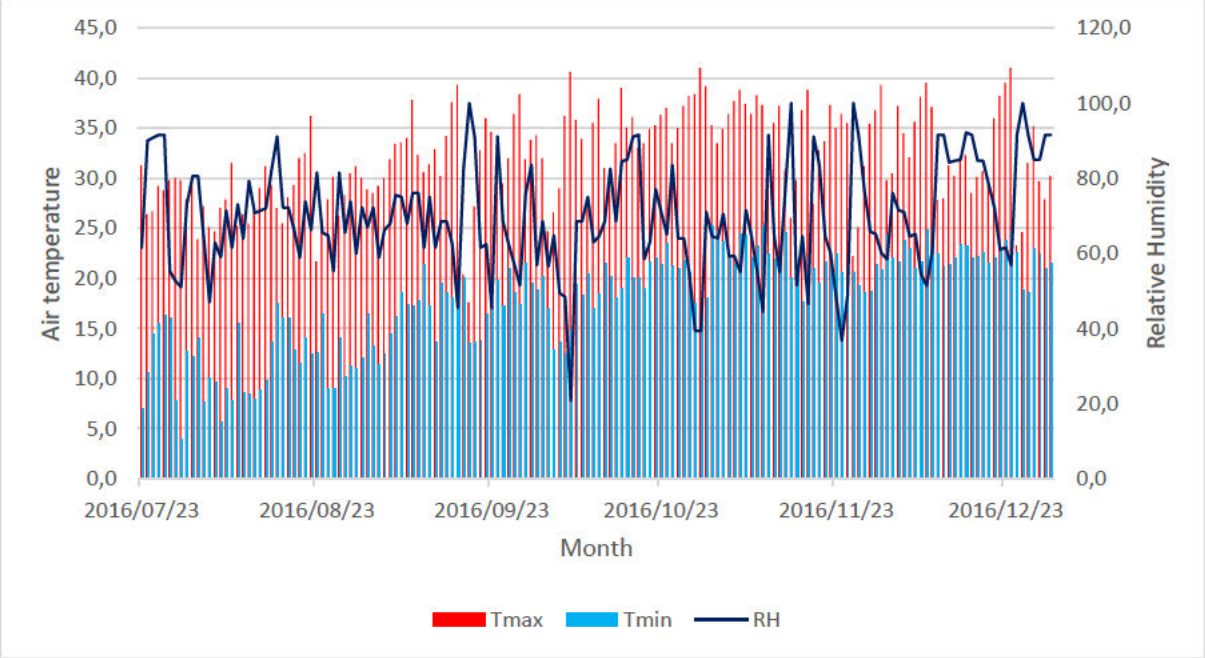
3.2.5 Data analysis

The morpho-agronomic data collected were analysed using the restricted maximum likelihood (REML) procedure in the CIMMYT-Field book software (CIMMYT, 1999), for individual site analysis. Combined analysis was done using GenStat v17 (VSN, International, 2010). Heritability estimates and genetic correlations among traits were estimated using the Multi Environmental Trial Analysis with R (META-R) software V6.0 (Rodriguez et al., 2016). Correlation among traits and grain yield were estimated using the Performance analytics R (V 2.0.4) in R. (Patterson et al., 2004)

3.3 Results

3.3.1 Weather conditions

The growing period was characterised by high temperatures especially during flowering and grain filling. This resulted in severe combined drought and heat stress resulting in low grain yield. The daily maximum and minimum temperatures are shown in Figure 3.1 below.



. Figure 3. 1. Daily maximum and minimum temperatures for the period July to December 2016.

Tmax =maximum temperature, Tmin= minimum temperature and RH = relative air humidity,

(Source; Zimbabwe Sugar Association Experiment Station, (ZSAES) in Chiredzi located 4km from Chiredzi Research Station and had full weather data.)

3.3.2 Identification of sub-tropical maize inbred lines with combined drought and heat stress adaptation attributes

Combined analysis of variance (ANOVA) revealed highly significant ($P<0.001$) planting date main effects for grain yield (GYD), anthesis to silking interval (ASI), plant height (PH), ear position (EPO), internode length (IL), number of ears per plant (EPP), number of leaves above the ear (NLAE), tassel

branches (TB), and grain texture (TEX) (Table 3.2). No planting date main effects were detected for the number of days to anthesis (AD), chlorophyll content (CC) and early plant vigor (EPV).

The heritability estimates for the number of days to anthesis (AD), plant heights (PH), internode length (IL), the number of ears per plant (EPP), number of leaves above the ear (NLAE), tassel blasting (TB), grain texture (TEX), root lodging (RL), and stalk lodging (SL) were high (> 50%) (Table 3.2). The heritability estimate for combined analysis for grain yield was below threshold and could not be detected. Plant height (PH), ear position (EPO) and number of ears per plant (EPP) exhibited low genotypic variance. These traits exhibited low genotypes by location interactions like the number of days to anthesis (AD), the number of leaves above the ear (NLAE) and grain texture (TEX).

The best performing 12 maize inbred lines and their traits are summarized in Table 3.3. together with the six maize inbred lines from the Crop Breeding Institute. K64 exhibited protogyny and flowered early which resulted in good pollination.

Table 3. 2. Combined analysis of variance (ANOVA) means of squares for grain yield and secondary traits of the 40 maize inbred lines for the two experiments conducted at Chiredzi Research Station in Zimbabwe during the 2016 dry season.

Source of variation	**DF**	**GYD**	**AD**	**ASI**	**PH**	**EPO**	**INTER**	**EPP**	**NLAE**	**SL**	**CHLO**	**RL**	**T_B**	**EPV**	**TEX**
		11.71	9.05	722.04		6.62	245.88	4.58	4.65	123.55	1.86	543.81		24.81	58.68
Site	1	(***)	(ns)	(***)	3.42 (***)	(***	(***)	(***)	(***)	(**)	(ns)	(*)	57.68 (***)	(ns)	(***)
		0.19	58.64	14.01		0.03	14.69	0.11	0.88	4.22	52.91	39.77	18.66	747.64	0.22
Replication (Site)	4	(ns)	(ns)	(*)	0.20 (***)	(***)	(**)	(**)	(**)	(ns)	(***)	(ns)	(*)	(***)	(ns)
		0.16	40.74	20.95	0.05	0.01	5.83	0.09	0.42	28.09	30.70	216.76	17.14		0.90
Blocks (Replication x Site)	37	(ns)	(ns)	(***)	(***)	(ns)	(*)	(***)	(**)	(***)	(***)	(***)	(***)	167.06 (***)	(***)
		0.51	109.45	19.72	0.14	0.01	18.21	0.19	1.10	65.14	64.51	534.34	26.43	317.47	1.95
Inbred lines	39	(***)	(***)	(***)	(***)	(**)	(***)	(***)	(***)	(**)	(***)	(***)	(***)	(***)	(***)
		0.21	23.11	13.74	0.02	0.01	6.10	0.02	0.35	178.50	9.15	178.50	5.31	110.78	
Inbred line x Site	14	(ns)	(ns)	(***)	(ns)	(ns)	(*)	(ns)	(*)	(**)	(ns)	(**)	(ns)	(ns)	0.31 (*)
												98.47			
Residual	44	0.18	29.02	5.36	0.02	0.01	3.60	0.03	0.21	16.57	7.95		5.49	75.79	0.18
												215.77			
Total	137	0.351	44.480	16.447	0.06	0.04	8.02	0.10	0.45	12.43	22.68		11.39	148.99	0.87
										25.03					
												0.75			
Heritability		0.65	0.79	0.43	0.80	0.22	0.65	0.88	0.72	0.74	0.93		0.81	0.75	0.72
												84.75			
Genotypic Variance		0.13	18.93	2.18	0.02	0.00	2.10	0.04	0.16	9.30	22.67		4.53	50.43	0.17
												25.23			
Genotype x Location Variance		--	0.62	4.08	0.00	0.00	1.02	0.00	0.05	2.48	0.50		0.48	8.21	0.00
Residual		0.21	28.42	5.36	0.02	0.00	3.66	0.02	0.22	12.02	8.07	103.25	5.14	77.34	0.40
Grand mean		0.87	63.27	2.69	1.57	0.62	8.88	0.40	6.58	2.95	44.70	9.51	8.39	49.92	3.57
LSD		0.48	4.21	2.34	0.14	0.03	1.76	0.18	0.43	3.21	2.69	9.33	1.99	7.21	0.51

***, **, * significant at 0.001, 0.01, 0.05 level, ns is non-significant. GYD= grain yield, AD= number of days to anthesis, ASI= anthesis to silking interval, PH= plant height, EPO= ear position, Inter=Internode length, NLAE= number of leaves above the ear, Chlor= chlorophyll content, T_Branches = number of tassel branches

Table 3. 3. Summary performance means of the 12 highest yielding maize inbred lines developed from the CIMMYT maize breeding program in comparison with the maize inbred lines from the Crop breeding Institute of the Government of Zimbabwe.

ENTRY	CODE	STATUS	GYD (mean t ha^{-1})	RANK (grain yield)	AD	ASI	PH	SL	RL	EPP	HC	ER	SEN	TEX	NLAE	EPV
30	JC18-6	RELEASED	1.90	1	61.71	-1.69	152.84	6.43	1.59	1.25	0.83	35.99	5.94	2.97	6.68	62.95
25	JC18-1	RELEASED	1.80	2	61.11	-0.23	195.59	3.55	9.56	1.15	1.04	19.05	6.68	3.01	7.37	67.42
18	CL108623	NEW	1.54	4	58.13	0.39	188.68	5.58	3.75	0.71	28.12	32.60	8.21	3.62	7.44	57.84
12	CL1013722	NEW	1.51	5	59.80	-0.72	196.32	21.48	1.08	0.50	0.30	38.57	7.62	3.55	6.47	47.07
4	CL114302	NEW	1.45	6	63.26	-1.28	181.32	2.50	0.57	0.71	3.06	23.01	7.49	3.14	6.50	65.64
15	C447-14	RELEASED	1.33	7	55.56	1.19	151.99	4.26	1.16	0.69	0.09	19.06	7.06	3.28	6.60	57.28
27	JC18-3	RELEASED	1.28	8	56.16	0.01	174.98	3.91	8.28	0.97	11.48	28.63	8.10	3.08	6.47	45.07
5	DJ91-6	RELEASED	1.27	9	61.04	0.61	184.83	1.07	1.60	0.66	0.17	62.01	6.96	3.76	7.00	52.80
11	CL115339	NEW	1.25	10	60.03	-1.54	168.57	6.20	9.50	0.67	18.74	52.08	8.30	3.63	7.37	37.16
8	CL107248	NEW	1.22	11	61.5	0.5	140.0	1.0	3.3	0.7	1.6	16.1	8.4	3.2	6.0	46.01
23	CL106477	RELEASED	1.21	12	58.2	-2.1	170.0	5.0	2.2	0.75	0.5	49.9	7.5	4.3	6.0	50.69
6	DJ71-280	NEW	1.21	13	61.60	0.0	168.0	1.33	3.79	0.71	9.7	55.0	7.5	4.4	6.8	51.23
Crop Breeding Institute released lines																
35	K64R	RELEASED	1.74	3	59.90	-1.57	162.71	11.08	2.99	0.80	24.87	47.26	7.66	3.94	6.37	62.88
40	M37W	RELEASED	0.53	29	63.66	2.82	181.55	3.36	4.00	0.34	2.75	35.55	7.70	3.98	7.29	51.53
37	N3	RELEASED	0.30	32	63.38	1.06	167.57	28.67	3.87	0.56	-0.04	70.98	7.66	4.86	6.41	45.21
39	NAW5867	RELEASED	0.27	34	69.74	3.35	178.38	14.16	2.93	0.14	0.21	89.10	7.50	4.95	5.96	46.12
36	M162W	RELEASED	0.28	38	82.56	0.51	116.82	5.38	0.88	0.06	-0.44	61.47	8.26	3.78	5.81	50.15
						11.3										
38	SC	RELEASED	0.00	40	67.05	0	213.52	23.85	3.71		0.96		8.49		6.46	43.12
LSD (0.05)			**0.80**	**11**	**3.46**	**3.16**	**21.00**	**12.47**	**7.62**	**0.30**	**9.21**	**31.62**	**0.76**	**0.90**	**0.84**	**13.67**

GYD= grain yield, AD= number of days to anthesis, ASI= anthesis to silking interval, PH= plant height (cm), SL stem lodging, RL = root lodging, EPP = number of ears per plant, HC = Husk cover, ER = number of rotten ears in a plot, SEN = leaf senescence, TEX = grain texture, NLAE= number of leaves above the ear, EPV = early plant vigour

3.3.2 Identification of agronomic traits that can be used to indirectly select for high grain yield performance under combined drought and heat stress conditions in maize

Most of the traits measured exhibited significant and positive correlations with grain yield. The number of ears per plant exhibited the highest highly significant and positive correlation with grain yield followed by grain moisture content at harvest and ear height. Leaf chlorophyll content was positively correlated with grain yield as well as bad husk cover. However, grain yield was significantly and negatively correlated with the anthesis to silking interval and root lodging. The correlation matrix (Figure 3.2) shows the correlation of the measured traits with grain yield and among the traits.

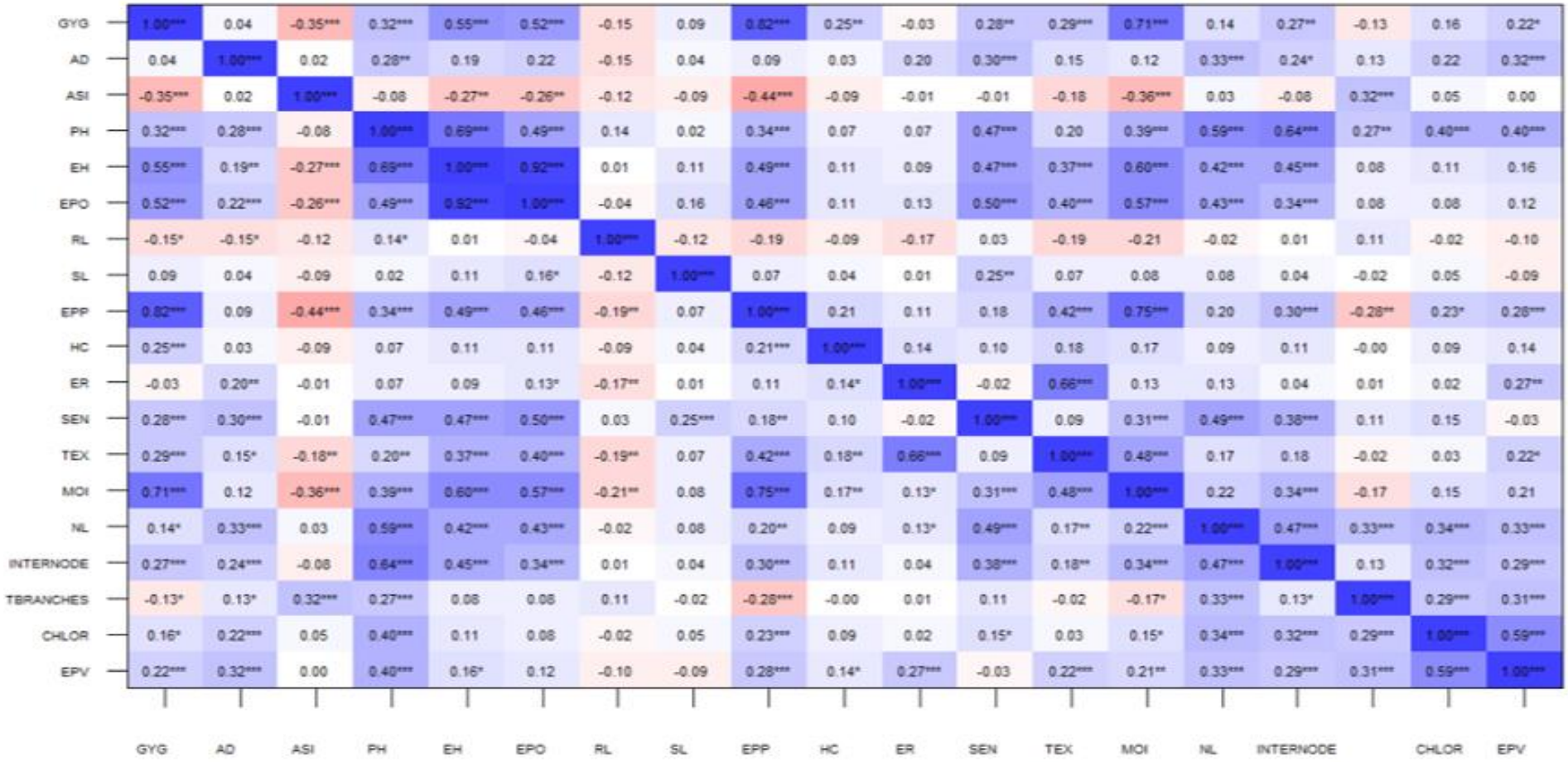


Figure 3. 2. Correlation matrix showing associations among traits of maize inbred lines grown at Chiredzi during dry months of 2016.

GYG = grain yield, AD = number of days to anthesis, ASI = anthesis to silking interval, PH = plant height, EH = ear height, EPO = ear position, RL= root lodging, SL = stem lodging, EPP = number of ears per plant, HC = Bad husk cover, ER = number of rotten ears per plot, SEN = leaf senescence, Tex = grain texture, MOI = grain moisture at

harvest, NL = number of leaves above the ear, INTERNODE = Internode length, TBRANCHES = number of tassel branches, CHLO = chlorophyll content, EPV= canopy cover. ***, **, * significant at 0.001, 0.01, 0.05 respectively.

3.4. Discussion

The year 2016 was the warmest on record for the decade ending 2020, even though it was highly influenced by a strong El Nino. However, due to surging climate change, the year 2024 has surpassed all the records for high temperatures, with a record 1.55^{o}C above pre-industrial period (WMO, 2025). The high temperatures and absence of rainfall allowed for the full expression of the combined drought and heat stress phenotype. This enabled the identification of tolerant inbred lines as well as the susceptible inbred lines. Yearly weather variations present major maize production challenges under rainfed conditions. Temperature affects most plant processes, by increasing the rate of enzymic reactions within the optimal ranges and ultimately altering and denaturing the enzymes thereby halting the reactions

The success of a maize breeding program depends on the availability and variability of the inbred lines as well as the diversity in the base germplasm. The emergence of new biotic and abiotic stresses due to climate change requires continuous breeding of new varieties that are adaptable to the emerging maize production challenges. Crop improvement and adaptation is a major tool for enhancing productivity under the current and future climates. The maize inbred lines in this study exhibited wide variability and high heritability estimates for most of the traits except ear position. The existence of genetic variability enhances selection and may lead to the production of new improved varieties that are suited to the current and future climates. The occurrence of highly significant differences among the maize inbred lines for all the traits measured indicated the prevalence of wide genetic variability among the maize inbred lines. The exploitation of the variability results in the production of different varieties with different stress tolerance capabilities. The low genotypic variances exhibited by plant height, ear position and number of ears per plant indicated that the traits were highly influenced by environmental factors and hence progress in improving these traits through selection would be slow.

There were no detectable planting date main effects on the number of days to anthesis dates and chlorophyll content which could be an indication of the stability of these traits and low responsiveness to environmental conditions. The Entries were at the same developmental stage when the stress occurred since they were not separated according to the number of days to anthesis. Genotypes were classified according to their maturity groups depending on the number of days to anthesis. However, the number of days to anthesis decreased with the increase in mean temperatures and the accumulation of growing degree days (GDD). This often results in the reduction of the crop duration which is one of the major causes of yield reduction under combined drought and heat stress (Chen et al., 2012). The number of days to anthesis and the anthesis to silking interval, often determined the success of the pollination and fertilisation processes. When maize crop plants are subjected to abiotic stresses, the partitioning of assimilates tend to favour the tassel and this is exhibited by the delay in the extrusion of the silks easily noticed by the large anthesis to silking interval (Monneveux et al., 2016). Genotypes with a large anthesis to silking interval often have poor grain yield due to poor seed set. This is attributed to the exhaustion of pollen grains before the silks emerge hence such genotypes are eliminated because they will fail to pollinate when grown in isolation. Silks may emerge when the pollen grains have been exhausted or may have lost viability due to high temperatures. The high vapour pressure deficit (VPD) often associated with combined drought and heat stress caused the silks to dry out quickly before pollination and fertilisation resulting in poor seed set and grain yield. The impacts of a large anthesis to silking interval were masked in experimental blocks because genotypes flower at different times thereby enhancing the availability of pollen grains. The anthesis to silking interval is used for the elimination of genotypes (Badu-Apraku and Fakorede, 2017).

The best yielding entries flowered early and exhibited good flowering synchrony. LaPostaSequia-C7-F64, a released line from CIMMYT, had a small anthesis to silking interval (1,89 days) and had the highest yield whereas SC flowered late and exhibited poor flower synchronization resulting in poor grain yield. Under optimal conditions, the male and female flowers mature at the same time showing complete synchrony. However, under abiotic stress conditions, the male flowers mature before the

female flowers, a condition referred to as protandry. Protogyny is a situation whereby the female flowers mature earlier than male flowers (Bassetti and Westgate, 1994). Protogynous genotypes are highly desirable when breeding for abiotic stress and its expression is independent of the differences between genotypes in different maturity groups (Bolaños and Edmeades, 1996). Genotypes with large anthesis to silking interval had poor and grain yield. CML 312 had large anthesis to silking interval, but it flowered early thus it benefitted from the late flowering entries thereby exhibiting high grain yield. However, genotypes with large anthesis to silking interval failed to pollinate themselves when grown in isolation and hence were undesirable. The significant and negative correlation between grain yield and the anthesis to silking interval indicated the need to select against genotypes exhibiting a large anthesis to silking interval.

LaPostaSequia-C7-F64 and LaPostaSequia-C7-F18 were highly prolific as indicated by the high number of ears per plant which was highly positively correlated with grain yield. The number of ears per plant is a measure of barrenness (Monneveux et al., 2006) and the higher the value, the lower the degree of barrenness. Genotypes with a high number of ears per plant tend to have high grain yield due to the increased number of grains per unit area (He et al., 2021). Due to poor grain filling because of poor assimilate supply and shortened grain filling period (Ren et al., 2022), the number of kernels per unit area is more important than the weight of individual kernels (Ruiz et al., 2022). Various researchers reported a high correlation between grain yield and the number of ears per plants (Bolaños and Edmeades 1993; Araus et al., 2012; Mhike et al., 2012). The highly significant and positive correlation between grain yield and number of ears per plant showed the importance of this trait in yield determination. At the same time, the number of ears per plant was significantly and negatively correlated with the number of days to anthesis and the anthesis to silking interval. The conditions which influence high grain yield also influence the number of ears per plant. This would imply that selecting genotypes with a small anthesis to silking interval would result in genotypes with high number of ears per plant. The heritability estimates for the number of ears per plant was high and remained almost constant under increasing stress intensity which may be an indication that it can be

used in the selection of genotypes with tolerance to combined drought and heat stress when the heritability of grain yield is low.

The amount and quality of radiation reaching the lower leaves is determined by the incidences of mutual leaf shading within the canopy as well as the size of the tassel. Internode length determines the spatial arrangement of leaves. Short internodes result in leaves being close to each other causing high mutual shading which often results in thin weak stems (Xu et al., 2004), which are prone to stem lodging. The penetration of radiation into the canopy is reduced especially to the lower leaves resulting in low photosynthetic activity. The significant and positive correlation between internode length and plant height as well as ear height is indicative of the direct relationship of these traits. However, there was no significant correlation between internode length and grain yield, contrary to Xu et al., (2004) who reported a decline in ear development with increased internode elongation suggesting a decrease in assimilate partitioning to the ear.

The heritability estimates for the number of tassel branches were high (0.81) in agreement with Sangoi, (1996) and Brewbaker (2015). Under abiotic stresses, tassel growth takes precedence over ear growth resulting in a large anthesis to silking interval (Monneveux et al., 2006). Breeding in the temperate regions has succeeded in selecting for small tassels resulting in high grain yield (Duvick et al., 2004). A small tassel would reduce the amount of assimilates used for tassel development thereby promoting ear development. However, Brewbaker (2015) showed that there is no evidence that large tassels reduce grain yield. The current results showed no significant correlation between grain yield and the number of tassel branches. In the temperate regions, large tassels reduced the penetration and quality of radiation into the crop canopy thereby resulting in low photosynthesis rates unlike, in the tropics, where leaf firing and tassel blasting may occur due to high temperatures. Tassel blasting may result in severe shortage of pollen grains leading to poor yields. As a result, large tassels were desirable as some tassel branches may produce pollen grains after tassel blasting may have occurred.

Tassels with many branches tend to have a wider window for pollen shedding since the maturity of the anthers is not synchronised resulting in the pollination of the ears even with flowering asynchrony. Small tassels are more vulnerable to tassel blasting and tend to have a narrow pollen shedding period compared to large tassels with many tassel branches. The tassel may provide shade which may shield the flag leaf from leaf firing. The number of tassel branches were negatively correlated with grain yield and the number of ears per plant. This might corroborate with the finding that tassel formation competes with the ear development resulting in lower grain yields. As a result, it would be worthwhile to select for tassels with fewer branches for inbred lines.

Leaf chlorophyll content exhibited high heritability (0.93) and this was in agreement with Xiong et al., (2023), but in contrary to the findings of Edmeades et al., (1997) and Ghimire et al., (2015). Leaf chlorophyll content was significantly and positively correlated (0.16) with grain yield in agreement with Ghimire et al., (2015). Chlorophyll content influences the length of the grain filling period (Yang et al., 2002) by enhancing the green leaf duration (Ren et al., 2023) as assimilates in the leaves are remobilised to the development of the ear. These results showed a significant and negative correlation between chlorophyll content and leaf senescence (0.15) suggesting that an increase in chlorophyll content would result in an increase in leaf senescence. In the absence of leaf firing, leaf senescence is a well programmed process leading to the remobilisation of assimilates into the sink (Gregersen et al., 2013). However, under combined drought and heat stress, leaf firing may occur and the assimilates stored in the leaves become unavailable for grain filling. Direct selection for chlorophyll content in maize was not widely practised (Araus et al., 2012), however recent evidence has indicated the importance of chlorophyll content in maintaining high grain yield (Mazloom et al., 2025; Brkic et al., 2025). The studies to exploit new traits for further development of genotypes adaptable to the current climatic conditions have focused on the importance of chlorophyll content as it affects leaf senescence (Sade et al., 2018; Ahmed et al., 2020; Monteoliva et al., 2021; Xiong et al., 2023). Génotypes with stable chlorophyll under stress have low senescence levels and increased green leaf duration (Brkic et al., 2025).

Root lodging exhibited high heritability, and this could indicate that the trait can be improved through selection. The use of maize inbred lines with low root lodging scores may result in the formation of hybrids resistant to root lodging. Root lodging is an undesirable trait because it distorts canopy structure thereby disturbing photosynthesis. Mechanical harvesting becomes inefficient resulting in yield losses as some cobs remain behind. The cobs of lodged plants tend to get in contact with the ground resulting in cob rots and poor grain quality. The resulting yield losses due to root lodging are huge. Root architecture is a difficult trait to study because roots are underground which may require destructive sampling. As a result, phenotypic expression of root strength and density is used.

The inbred line K64R is mostly used as a male parent in hybrid combinations as a drought tolerant donor. The exhibition of combined drought and heat stress tolerance traits is an indication of the spill-over effects of breeding for drought tolerance which could be due to complimentary or epistatic gene effects. However, SC was highly susceptible to combined drought and heat stress as there was no grain yield. The inbred line is commonly used in hybrid combinations to produce some of the highest yielding late maturing hybrids in Zimbabwe. DJ71-276 exhibited excellent stay green characteristics, but it was completely barren, it could be used as a donor of tolerance traits to be introgressed into the high yielding susceptible inbred lines. Continuous production and testing of maize inbred lines under the desired stress will aid in the production of hybrids adapted to current and future climates.

3.5. Conclusions

The maize inbred line K64R from the Crop Breeding Institute, showed tolerance to combined drought and heat stress as well as four maize inbred lines viz JC18-1, JC18-2, JC18-3 AND JC18-4, which were identified by Cairn's et al., (2012). The new maize inbred lines identified as tolerant to combined drought and heat stress were DJ53-9, DJ91-5, DJ71-280, DJ53-17, DJ53-37, DJ53-21, C727-425, C1008-1 and C27-18. These eleven maize inbred lines and four that were previously identified by Cairns et al., (2013) can be recommended for utilisation in breeding new hybrids with tolerance to combined drought and heat stress. DJ71-276 and SC were identified as potential donors for combined drought and heat stress tolerance and high grain yield respectively.

Plant height, ear height, ear position, the number of ears per plant, grain moisture at harvest, internode length and early plant vigour were the traits that were positively and significantly correlated with grain yield. These traits can be used for the identification of combined drought and heat stress tolerant maize inbred lines ideotypes.

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CHAPTER 4

Identification of maize hybrids with combined drought and heat stress tolerance attributes in the CIMMYT- breeding program

ABSTRACT

Crop adaptation plays a major role in determining productivity among small-holder farmers. The main objectives of this study were to: (i) identify experimental maize hybrids developed within the CIMMYT maize breeding program with combined drought and heat stress, and (ii) identify agronomic traits that can be indirectly used to select grain yield performance for maize hybrids under combined drought and heat stress conditions. A total of 55 maize hybrids consisting of five commercial hybrids widely grown in Zimbabwe, 13 pre-release hybrids from CIMMYT breeding program and 37 experimental hybrids which were constituted from inbred lines also evaluated under combined drought and heat stress (CDHS) conditions during the 2016 dry season. The results showed that significant differences were found on the planting date main effects for most of the traits including grain yield, number of days to anthesis and leaf senescence indicating the strong influence of the planting date. Significant genotypes by environmental interactions were detected for leaf senescence, and number of kernel rows on the ear indicating that these traits would be expressed differently in a different site. The association of the measured traits with grain yield under combined drought and heat stress were estimated and the traits number of ears per plant (EPP), husk cover (HC), grain texture (TEX), grain moisture content at harvest (MOI), number of kernels per row (KERN), cob girth and one hundred kernel weight (KENGW) could be used for indirect selection. Under combined drought and heat stress, the highest phenotypic direct effects were exhibited by the traits EPP, KERN, and cob girth whereas at the genotypic level, the highest total effects were exhibited by number of kernel rows, cob girth and plant heights, these traits are vital in selection for high yielding

hybrids under combined drought and heat stress. Hybrids with combined drought and heat stress tolerance traits were successfully identified and these were Entries DJ65-1, DJ65-28, DJ65-32, DJ65-35 and DJ65-37.

4.1 INTRODUCTION

There has been an increase in the frequency, intensity and severity of climate change induced crop production disasters. The occurrence of drought, heat as well as their co-occurrences has increased in sub–Saharan Africa yet there is a devastating increase in population within this region that relies heavily on maize as a major source of calories thereby deepening food insecurity (Grote et al., 2021). To counteract the reduction in crop productivity due to climate change linked disasters, there has been an increase in the area under maize production (Jayne and Sanchez, 2022). Global maize production has increased due to increased productivity as well as area expansion. However, in sub-Saharan Africa area expansion has accelerated since the year 2000 (Erenstein et al., 2022), and this has led to a doubling of the area under maize production. The use of hybrid seed, increased use of mineral fertilisers as well as improved pest and disease control has led to high productivity in the developed countries. Conversely, in the developing countries, yields are still low mainly because of low use of mineral fertilisers averaging about $20kgha^{-1}$ (Sheahan and Barrett, 2017), poor disease and pest control as well as the use of old varieties which are no longer suitable for the current climatic conditions. There is low varietal turnover in the developing countries (Abate et al., 2017; Atlin et al., 2017). As a result, farmers in these countries are growing varieties that were selected under past climatic conditions resulting in poor yields.

Climate variability and climate change have resulted in substantial yield losses in maize. For every $1^{o}C$ increase in global temperature, maize yields decrease by between 7 and 10% (Zhao et al., 2017; Dong et al., 2021). The projected temperature increases due to climate change will result in yield losses of about ten million tonnes per year (Tesfaye et al., 2016). Climate change influences the emergence and the spread of crop pests and diseases. The increase in frequency, duration and severity of combined drought and heat stress especially in tropical environments is a major constraint that has emerged recently because of climate change. Phytophagous pests and diseases accentuate the impacts of combined drought and heat stress by reducing the photosynthetic area of the crops resulting in poor yields. The occurrence of drought and heat stress simultaneously is a major hindrance to maize

productivity. Combined drought and heat stress tolerance is now being considered together in breeding programs (Barnabás et al., 2008; Fahad et al., 2017; Makore et al., 2021).

The persistent occurrence of high temperatures has made it imperative to produce varieties which combine tolerance to various abiotic and biotic stresses. Varieties which are tolerant to combined drought and heat stress as well as low nitrogen stress and fall army worm will play a critical role in boasting productivity in SSA. Under combined drought and heat stress, photorespiration tends to occur at high rates draining the energy reserves of the plant which results in poor productivity or even plant death (Sheoran et al., 2022). Heat stress affects the transportation of water and inorganic minerals through the plant stem hence it is important to target the whole plant tolerance rather than reproductive stage tolerance (Li et al., 2025).

Temperatures above 35^{o}C affect pollination as well as germination of the pollen tube (Dupuis and Dumas, 1990). Various studies have identified pollen viability as the major constraint under heat stress, however, a recent study by Li et al., (2025) showed that there were no differences in pollen survival between susceptible and tolerant maize genotypes. Thus, maternal factors tend to determine survival under heat stress. Kernel abortion after pollination was found to be variety specific (Niu et al., 2021), thus the development of varieties with combined drought and heat stress tolerance will result in higher yields due to reduced kernel abortion. After pollination and fertilisation, heat stress disrupts the metabolism of sugars by impairing the synthesis of starch required for grain filling (Li et al., 2025). Thus, breeding for combined drought and heat stress tolerant varieties should target both pollen survival and maternal properties that confer tolerance before and after fertilisation. The tolerant maize varieties could alleviate the impacts of combined drought and heat stress in the farmers' fields. Improved maize varieties with tolerance to combined drought and heat stress can increase yields by up to 62% compared to the benchmark varieties under hotter and drier climate scenarios (Tesfaye et

al., 2016), and any extent of combined drought and heat stress tolerance is vital to increase maize grain yields (Lennart et al., 2025).

The potential of integrating improved maize genotypes in farming systems threatened by combined drought and heat stress is still poorly quantified. The status quo makes it impossible to solely recommend adoption of improved maize varieties as a solution to boost food security in agro ecologies threatened by combined drought and heat stress. The main objectives of this study were to (i) identify maize hybrids from the CIMMYT maize breeding program which combine drought and heat stress adaptation attributes, and (ii) to select agronomic traits that can be indirectly used to select for grain yield performance of maize hybrids under CDHS conditions. It was hypothesised that high yielding experimental hybrids can be identified from those that were developed within the CIMMYT Zimbabwe breeding pipeline which can alleviate the impacts of climate change on maize productivity, and that the agronomic traits highly correlated with grain yield within the newly developed hybrids can be used in identifying combined drought and heat stress ideotypes.

4.2 MATERIALS AND METHODS

4. 2.1 Plant materials

The total of 55 hybrids comprising five commercial hybrids widely grown in Zimbabwe, 13 pre-release hybrids from the CIMMYT breeding program and 37 experimental hybrids constituted from inbred lines which were also evaluated for combined drought and heat stress (CDHS) (in Chapter 3) were evaluated in two field trials differentiated by planting dates, under managed combined drought and heat stress conditions during the 2016 dry season. The experimental maize hybrids and the commercial hybrids were of different maturity groups (Table 4.1).

Table 4. 1. List of experimental and commercial hybrids evaluated for combined drought and heat stress tolerance at Chiredzi Research station during the 2016 dry season.

ENTRY	PEDIGREE	PARENT 1	PARENT 2	STATUS
1	CML312/CML442//CZL1311	CML312/CML442	CZL1311	EXPERIMENTAL HYBRID
2	CML545/CML548//K64R	CML545/CML548	K64R	EXPERIMENTAL HYBRID
3	CML545/CML548//[NAW5867/P49-SR(S2#)//NAW5867]FS#-48-2-1-BBB	CML545/CML548	[NAW5867/P49-SR(S2#)//NAW5867]FS#-48-2-1-BBB	EXPERIMENTAL HYBRID
4	CZH0837	.	.	PRE-RELEASE
5	CML545/CML548//([CML444/CML395//DTPWC8F31-4-2-1-6]-3-1-2-1-1-B*5/[LZ956441/LZ966205]-B-3-4-4-B-5-B*7)-2-4-2-1-BBB	CML545/CML548	([CML444/CML395//DTPWC8F31-4-2-1-6]-3-1-2-1-1-B*5/[LZ956441/LZ966205]-B-3-4-4-B-5-B*7)-2-4-2-1-BBB	EXPERIMENTAL HYBRID
6	CZL1311/K64R	CZL1311	K64R	EXPERIMENTAL HYBRID
7	CML571/CZL1311	CML571	ZL1311	EXPERIMENTAL HYBRID
8	CML571/K64R	CML571	K64R	EXPERIMENTAL HYBRID
9	CZH0616	.	.	PRE-RELEASE
10	00SADVEB-#-74-1-1-1-2-BB/CZL1311//K64R	00SADVEB-#-74-1-1-1-2-BB/CZL1311	K64R	EXPERIMENTAL HYBRID
11	PHB30G19	.	.	COMMERCIAL HYBRID
12	00SADVEB-#-74-1-1-1-2-BB/CZL1311//([CML444/CML395//DTPWC8F31-4-2-1-6]-3-1-2-1-1-B*5/[LZ956441/LZ966205]-B-3-4-4-B-5-B*7)-2-4-2-1-BBB	00SADVEB-#-74-1-1-1-2-BB/CZL1311	([CML444/CML395//DTPWC8F31-4-2-1-6]-3-1-2-1-1-B*5/[LZ956441/LZ966205]-B-3-4-4-B-5-B*7)-2-4-2-1-BBB	EXPERIMENTAL HYBRID
13	CML571/CZL1311//CZL1311	CML571/CZL1311	CZL1311	EXPERIMENTAL HYBRID
14	CML571/CZL1311//CML571	CML571/CZL1311	CML571	EXPERIMENTAL HYBRID
15	CML571/CZL1311//K64R	CML571/CZL1311	K64R	EXPERIMENTAL HYBRID

16	CML571/CZL1311//([CML444/CML395//DTPWC8F31-4-2-1-6]-3-1-2-1-1-B*5/[LZ956441/LZ966205]-B-3-4-4-B-5-B*7)-2-4-2-1-BBB	CML571/CZL1311	([CML444/CML395//DTPWC8F31-4-2-1-6]-3-1-2-1-1-B*5/[LZ956441/LZ966205]-B-3-4-4-B-5-B*7)-2-4-2-1-BBB	EXPERIMENTAL HYBRID
17	CZL1311/CML543//CZL1311	CZL1311/CML543	CZL1311	EXPERIMENTAL HYBRID
18	CZL1311/CML543//([CML444/CML395//DTPWC8F31-4-2-1-6]-3-1-2-1-1-B*5/[LZ956441/LZ966205]-B-3-4-4-B-5-B*7)-2-4-2-1-BBB	CZL1311/CML543	([CML444/CML395//DTPWC8F31-4-2-1-6]-3-1-2-1-1-B*5/[LZ956441/LZ966205]-B-3-4-4-B-5-B*7)-2-4-2-1-BBB	EXPERIMENTAL HYBRID
19	CZL1311/CML543//CML571	CZL1311/CML543	CML571	EXPERIMENTAL HYBRID
20	CZL1311/CML543//K64R	CZL1311/CML543	K64R	EXPERIMENTAL HYBRID
21	CZL1311/CML543//[NAW5867/P49-SR(S2#)//NAW5867]FS#-48-2-1-BBB	CZL1311/CML543	[NAW5867/P49-SR(S2#)//NAW5867]FS#-48-2-1-BBB	EXPERIMENTAL HYBRID
22	CZL1311/CML543//([CML444/CML395//DTPWC8F31-4-2-1-6]-3-1-2-1-1-B*5/[LZ956441/LZ966205]-B-3-4-4-B-5-B*7)-2-4-2-1-BBB	CZL1311/CML543	([CML444/CML395//DTPWC8F31-4-2-1-6]-3-1-2-1-1-B*5/[LZ956441/LZ966205]-B-3-4-4-B-5-B*7)-2-4-2-1-BBB	EXPERIMENTAL HYBRID
23	((KU1403x1368)-7-2-1-1-BB/CML444)-B-8-5-5-1-1-1-1-B/CLWN201//CZL1311	((KU1403x1368)-7-2-1-1-BB/CML444)-B-8-5-5-1-1-1-1-B/CLWN201	CZL1311	EXPERIMENTAL HYBRID
24	((KU1403x1368)-7-2-1-1-BB/CML444)-B-8-5-5-1-1-1-1-B/CLWN201//([CML444/CML395//DTPWC8F31-4-2-1-6]-3-1-2-1-1-B*5/[LZ956441/LZ966205]-B-3-4-4-B-5-B*7)-2-4-2-1-BBB	((KU1403x1368)-7-2-1-1-BB/CML444)-B-8-5-5-1-1-1-1-B/CLWN201	([CML444/CML395//DTPWC8F31-4-2-1-6]-3-1-2-1-1-B*5/[LZ956441/LZ966205]-B-3-4-4-B-5-B*7)-2-4-2-1-BBB	EXPERIMENTAL HYBRID
25	((KU1403x1368)-7-2-1-1-BB/CML444)-B-8-5-5-1-1-1-1-B/CLWN201//K64R	((KU1403x1368)-7-2-1-1-BB/CML444)-B-8-5-5-1-1-1-1-B/CLWN201	K64R	EXPERIMENTAL HYBRID
26	((KU1403x1368)-7-2-1-1-BB/CML444)-B-8-5-5-1-1-1-1-B/CLWN201//CML571	((KU1403x1368)-7-2-1-1-BB/CML444)-B-8-5-5-1-1-1-1-B/CLWN201	CML571	EXPERIMENTAL HYBRID

27	((KU1403x1368)-7-2-1-1-BB/CML444)-B-8-5-5-1-1-1-B/CLWN201//K64R	((KU1403x1368)-7-2-1-1-BB/CML444)-B-8-5-5-1-1-1-B/CLWN201	K64R	EXPERIMENTAL HYBRID
28	((KU1403x1368)-7-2-1-1-BB/CML444)-B-8-5-5-1-1-1-B/CLWN201//K64R	((KU1403x1368)-7-2-1-1-BB/CML444)-B-8-5-5-1-1-1-B/CLWN201	K64R	EXPERIMENTAL HYBRID
29	((KU1403x1368)-7-2-1-1-BB/CML444)-B-8-5-5-1-1-1-B/CLWN201//[NAW5867/P49-SR(S2#)//NAW5867]FS#-48-2-1-BBB	((KU1403x1368)-7-2-1-1-BB/CML444)-B-8-5-5-1-1-1-B/CLWN201	[NAW5867/P49-SR(S2#)//NAW5867]FS#-48-2-1-BBB	EXPERIMENTAL HYBRID
30	((KU1403x1368)-7-2-1-1-BB/CML444)-B-8-5-5-1-1-1-B/CLWN201//([CML444/CML395//DTPWC8F31-4-2-1-6]-3-1-2-1-1-B*5/[LZ956441/LZ966205]-B-3-4-4-B-5-B*7)-2-4-2-1-BBB	((KU1403x1368)-7-2-1-1-BB/CML444)-B-8-5-5-1-1-1-B/CLWN201	([CML444/CML395//DTPWC8F31-4-2-1-6]-3-1-2-1-1-B*5/[LZ956441/LZ966205]-B-3-4-4-B-5-B*7)-2-4-2-1-BBB	EXPERIMENTAL HYBRID
31	CML444/CML536//[[LZ956441/LZ966205]-B-3-4-4-B-5-B*5/[CML390/CML206]-BB-2-4-B*4]-B-4-1-1-B*7	CML444/CML536	[[LZ956441/LZ966205]-B-3-4-4-B-5-B*5/[CML390/CML206]-BB-2-4-B*4]-B-4-1-1-B*7	EXPERIMENTAL HYBRID
32	CZL1311/CML444//P44c10MH7-19-3-2-1-B*4	CZL1311/CML444	P44c10MH7-19-3-2-1-B*4	EXPERIMENTAL HYBRID
33	[[LZ956441/LZ966205]-B-3-4-4-B-5-B*5/[CML390/CML206]-BB-2-4-B*4]-B-4-1-3-B*7//CZL1112/(TZMI101-x-TZMI501)-31-1-3-1-1-1-B--B*6	[[LZ956441/LZ966205]-B-3-4-4-B-5-B*5/[CML390/CML206]-BB-2-4-B*4]-B-4-1-3-B*7	CZL1112/(TZMI101-x-TZMI501)-31-1-3-1-1-1-B--B*6	EXPERIMENTAL HYBRID
34	CML444/[[LZ956441/LZ966205]-B-3-4-4-B-5-B*5/[CML390/CML206]-BB-2-4-B*4]-B-4-1-3-B*6//ECAVL18-113-3-1-2-3-1-BB	CML444/[[LZ956441/LZ966205]-B-3-4-4-B-5-B*5/[CML390/CML206]-BB-2-4-B*4]-B-4-1-3-B*6	ECAVL18-113-3-1-2-3-1-BB	EXPERIMENTAL HYBRID
35	CZL1112/(TZMI101-x-TZMI501)-31-1-3-1-1-1-B--B*6//[[LZ956441/LZ966205]-B-3-4-4-B-5-B*5/[CML390/CML206]-BB-2-4-B*4]-B-4-1-3-B*7	CZL1112/(TZMI101-x-TZMI501)-31-1-3-1-1-1-B--B*6	[[LZ956441/LZ966205]-B-3-4-4-B-5-B*5/[CML390/CML206]-BB-2-4-B*4]-B-4-1-3-B*7	EXPERIMENTAL HYBRID
36	CML536/CML539	CML536	CML539	EXPERIMENTAL HYBRID
37	CML537/CML197	CML537	CML197	EXPERIMENTAL HYBRID
38	CML571/CZL1311//[[LZ956441/LZ966205]-B-3-4-4-B-5-B*5/[CML390/CML206]-BB-2-4-B*4]-B-4-1-3-B*6-B	CML571/CZL1311	[[LZ956441/LZ966205]-B-3-4-4-B-5-B*5/[CML390/CML206]-BB-2-4-B*4]-B-4-1-3-B*6-B	EXPERIMENTAL HYBRID

39	CML539/CML540//CML571	CML539/CML540	CML571	EXPERIMENTAL HYBRID
40	CM545/CML548//CML571	CM545/CML548	CML571	EXPERIMENTAL HYBRID
41	CM545/CML548//([SYN-USAB2/SYN-ELIB2]-12-1-1-1-B*5/CIMCALI8843/S9243-BB-#-B-5-1-BB-4-1-2-3-2-B)-B-5-1-1-B*4	CM545/CML548	([SYN-USAB2/SYN-ELIB2]-12-1-1-1-B*5/CIMCALI8843/S9243-BB-#-B-5-1-BB-4-1-2-3-2-B)-B-5-1-1-B*4	EXPERIMENTAL HYBRID
42	CML537/CML312//[[LZ956441/LZ966205]-B-3-4-4-B-5-B*5/[CML390/CML206]-BB-2-4-B*4]-B-1-1-1-B*6	CML537/CML312	[[LZ956441/LZ966205]-B-3-4-4-B-5-B*5/[CML390/CML206]-BB-2-4-B*4]-B-1-1-1-B*6	EXPERIMENTAL HYBRID
43	CML545/CML548//[[CML444/CML395//DTPWC8F31-1-1-2-2-BB]-4-2-2-2-2-BB/[MSRXPOOL9]C1F2-205-1(OSU23i)-5-3-X-X-1-B//EV7992/EV8449-3-2-2-2-B*5]-B-1-1-BBB	CML545/CML548	[[CML444/CML395//DTPWC8F31-1-1-2-2-BB]-4-2-2-2-2-BB/[MSRXPOOL9]C1F2-205-1(OSU23i)-5-3-X-X-1-B//EV7992/EV8449-3-2-2-2-B*5]-B-1-1-BBB	EXPERIMENTAL HYBRID
44	CML536/CML395//[MAS[MSR/312]-117-2-2-1-B*5/ZM621A-10-1-1-1-2-B*7]-B-10-1-B*4-B	CML536/CML395	[MAS[MSR/312]-117-2-2-1-B*5/ZM621A-10-1-1-1-2-B*7]-B-10-1-B*4-B	EXPERIMENTAL HYBRID
45	CML444/CML539//[[LZ956441/LZ966205]-B-3-4-4-B-5-B*5/[CML390/CML206]-BB-2-4-B*4]-B-1-1-1-B*7	CML444/CML539	[[LZ956441/LZ966205]-B-3-4-4-B-5-B*5/[CML390/CML206]-BB-2-4-B*4]-B-1-1-1-B*7	EXPERIMENTAL HYBRID
46	CML539/CML540//([[EV7992#/EV8449-SR]C1F2-334-1(OSU8i)-1-4-X-X-2-B/[SC/ZM605-1-2-5-2/CML395]-B-14-3-4-1-1-2/[[EV7992#/EV8449-SR]C1F2-334-1(OSU8i)-10-4(I)-X-X-B/[MSRXPOOL9]C1F2-205-1-3-1-2/CML202]-B-5-1-1-1-B-1)-2-1-2-1-B*4	CML539/CML540	([[EV7992#/EV8449-SR]C1F2-334-1(OSU8i)-1-4-X-X-2-B/[SC/ZM605-1-2-5-2/CML395]-B-14-3-4-1-1-2/[[EV7992#/EV8449-SR]C1F2-334-1(OSU8i)-10-4(I)-X-X-B/[MSRXPOOL9]C1F2-205-1-3-1-2/CML202]-B-5-1-1-1-B-1)-2-1-2-1-B*4	EXPERIMENTAL HYBRID

47	CML444/CZL068//[MAS[MSR/312]-117-2-2-1-B*5/ZM621A-10-1-1-1-2-B*7]-B-10-1-B*5	CML444/CZL068	[MAS[MSR/312]-117-2-2-1-B*5/ZM621A-10-1-1-1-2-B*7]-B-10-1-B*5	EXPERIMENTAL HYBRID
48	CML444/CZL068//[MAS[206/312]-23-2-1-1-B*5/MAS[MSR/312]-117-2-2-1-B*5]-B-10-1-B*6	CML444/CZL068	[MAS[206/312]-23-2-1-1-B*5/MAS[MSR/312]-117-2-2-1-B*5]-B-10-1-B*6	EXPERIMENTAL HYBRID
49	CML312/CML444//[[CML312/[TUXPSEQ]C1F2/P49-SR]F2-45-3-2-1-BB//INTA-F2-192-2-1-1-1-B*4]-1-5-1-1-2-BB/[CML442/CML197//[TUXPSEQ]C1F2/P49-SR]F2-45-7-3-2-BBB]-2-1-1-1-2-BBB]-B-1-1-BBB	CML312/CML444	[[CML312/[TUXPSEQ]C1F2/P49-SR]F2-45-3-2-1-BB//INTA-F2-192-2-1-1-1-B*4]-1-5-1-1-2-BB/[CML442/CML197//[TUXPSEQ]C1F2/P49-SR]F2-45-7-3-2-BBB]-2-1-1-1-2-BBB]-B-1-1-BBB	EXPERIMENTAL HYBRID
50	PAN413	.	.	COMMERCIAL HYBRID
51	PAN53	.	.	COMMERCIAL HYBRID
52	SC403	.	.	COMMERCIAL HYBRID
53	SC513	.	.	COMMERCIAL HYBRID
54	SC637	.	.	COMMERCIAL HYBRID
55	SC727	.	.	COMMERCIAL HYBRID

4. 2.2 Experimental design, establishment and field management

The trials were planted during the 2016 dry season at Chiredzi Research station (21°1`10``S, 31°34`23``E, 430 meters above sea level) in Zimbabwe. First trial was established on the 23rd and the second on the 30th of August 2016. The trials were planted using the 5 x 11 α-lattice design, replicated two times. Each plot consisted of two-row 4-m long with 0.25m interplant distance and 0.75m between the rows, with a final density of 53, 333 plants ha^{-1}. Two kernels were planted at each planting station and were thinned to one, two weeks after seedling emergence. All plots received 400kgha^{-1} as compound D (7%N, 14% P_2O_5 and 7% K_2O) at sowing. Nitrogen (N) 66 kg $ha^{-1}$was applied as Ammonium Nitrate at the V6 and V11 stages. All recommended weed and pest control measures were followed (Kamara, 2017).

4.2.3 Data collection

Comprehensive data were collected for various agronomic traits. Measurements were done according to the International Maize and Wheat Improvement Centre, CIMMYT (1985) procedures. The growth and yield traits collected were:

Number of days to anthesis (AD), number of days to silking (SD), plant height (PH) (cm), ear height (EH) (cm), stalk lodging (SL), root lodging (RL), leaf senescence (Sen), bad husk cover (HC), chlorophyll content measurements were done using a SPAD meter (Konica Minolta, Japan) Tassel branches were counted, tassel size was visually scored on a scale of one to five where one was small and five was large, internode length the length of the ear bearing node was measured in centimetres, number of leaves above the ear the leaves above the topmost ear were counted, number of rows on the ear were counted for five selected cobs from each plot, cob girth, one hundred kernel weight.

4. 2.4 Statistical analysis

The data collected were analysed in CIMMYT-Fieldbook software using the Restricted Maximum Likelihood (REML) procedure, for individual site analysis to determine if there were any significant

differences among the hybrids. The adjusted means from the individual site analyses were merged and subjected to combined ANOVA using GENSTAT software v17, (VSN, International, 2009) and the Multi Environmental Trial Analysis (META-R software (v3.3.1 (Rodriguez et al., 2018)), in order to estimate genetic correlations, repeatability, and the best linear unbiased predictors (BLUPs). The correlations among traits were estimated using the package the Psych in R v2.4.6.26 R package (Revelle, 2024). Genotypic and phenotypic path coefficient analysis was done using the Variability v 0.1.0 in R package (Popat, 2020).

4. 3 RESULTS

4. 3.1 Identification of pre-release maize hybrids within the CIMMYT maize breeding program with combined drought and heat stress adaptation attributes.

4.3.1.1 Mean square and heritability estimates of the tested hybrids for the various traits collected in the experimental sites.

There were highly significant planting date main effects on all the measured traits except for ear position, number of ears per plant and the number of kernel rows on the ear (Table 4.2). The hybrids exhibited significant differences ($p<0.001$) for grain yield, leaf senescence, number of ears per plant, bad husk cover, number of rotten ears per plot, grain texture and grain moisture content at harvest.

Significant genotypes by environmental interactions were detected for leaf senescence (Table 4.2). The heritability estimates for grain yield, number of ears per plant and bad husk cover were high (>50%) whereas the heritability estimates for the number of days to anthesis, plant height, ear position, leaf senescence, number of kernel rows on the ear, grain texture and grain moisture content at harvest were low ranging from 0 to 0.19 (Table 4.2)

4.3.1.2 Mean performance of the tested hybrids for the various traits collected in the experimental sites.

As for adaptation under CDHS conditions, generally the newly developed experimental hybrids performed better than the commercial hybrids. For grain yield, the best ten hybrids consisted of nine newly developed experimental hybrids with yield varied from 4.89tonsha^{-1} to 3.73tonsha^{-1} and one commercial hybrid, PAN413 had a grain yield of 3.80tonsha^{-1}. Interestingly, five of the best ten experimental hybrids DJ65-32, DJ65-1, DJ65-28, DJ65-35 and DJ65-37, were constituted using the newly developed experimental inbred lines that were identified as tolerant to CDHS in Chapter 3. The

identified best performing experimental hybrids also exhibited a smaller anthesis to silking interval ranging from -0.1 to 3.5 days and higher number of ears per plant ranging from 0.46-0.76 (Table 4.3).

4.3.2 Identification of morpho-agronomic traits that can be used for the selection of combined drought and heat stress ideotypes.

Number of ears per plant, number of kernels in a row and the cob girth exhibited positive phenotypic direct effects of 0.46,0.15 and 0.17 respectively whereas the number of days to anthesis and leaf senescence, revealed negative phenotypic direct effects of 0.04 and 0.06 respectively on grain yield Table 4.4. At the genotypic level, the number of days to anthesis, plant height, number of kernels in a row exhibited negative direct effects of 0.42, 0.24 and 0.39 respectively but the total effects were positive 0.12, 1.02 and 0.75 respectively. Leaf senescence was the only trait that exhibited negative direct and total effects on grain yield at the genotypic level with values of 0.16 and 0.09 respectively, Table 4. 5. The correlation matrix, (Figure 4.1) showed that the number of ears per plant, bad husk cover and grain texture were positively and significantly correlated with grain yield with values of 0.75, 0.30 and 0.38 respectively. The anthesis to silking interval, number of rotten ears per plot and leaf senescence were significantly and negatively correlated with grain yield with values of 0.04, 0.39 and 0.22 respectively.

Table 4. 2. Combined ANOVA for agronomic traits recorded in maize hybrid trials conducted at the Chiredzi Research Station during the 2016 dry months under managed combined drought and heat stress conditions.

Source of variation	**DF**	**GYD**	**AD**	**ASI**	**PH**	**EPO**	**SEN**	**EPP**	**HC**	**ER**	**ROWS**	**MOI**	**TEX**
Site	1	20.689 (***)	11463.290 (***)	180.685 (***)	3404.8 (***)	0.01 (ns)	2224.651 (***)	0.00 (ns)	1401.9 (**)	5043.81 (***)	0.00 (ns)	243.118 (***)	0.875 (*)
Replication (Site)	4	0.723 (ns)	14.477 (*)	0.280 (ns)	1018.0 (***)	0.127 (ns)	0.9364 (***)	0.030 (ns)	287.2 (ns)	162.74 (ns)	12.40 (ns)	5.670 (*)	0.048 (ns)
Block (Replication x Site)	60	5.272 (***)	13.566 (***)	6.002 (*)	429.8 (***)	0.108 (ns)	0.2374 (***)	0.075 (***)	297.4 (***)	268.91 (***)	113.11 (***)	2.751 (*)	0.644 (***)
Hybrid	54	2.862 (***)	6.492 (ns)	4.102 (ns)	161.2 (ns)	0.007 (ns)	0.4110 (***)	0.049 (***)	416.8 (***)	194.03 (***)	33.00 (*)	3.644 (***)	0.970 (***)
Hybrid x. Site	54	0.697 (ns)	8.198 (ns)	3.205 (ns)	156.6 (ns)	0.006 (ns)	0.3015 (***)	0.013 (ns)	97.3 (ns)	119.50 (ns)	36.08 (*)	2.142 (ns)	0.221 (ns)
Residual	147	0.887	5.777	3.724	134.1	0.007	0.1161	0.016	127.3	86.89	22	1.805	0.209
Total	320	2.07	42.756	4.685	216.7	0.007	7.1709	0.032	206.8	160.81	43.24	3.152	0.81
Heritability		0.74	0	0	0	0.11	0.19	0.72	0.76	0.46	0	0.27	0.16
Genotypic Variance		0.41	8.73	0	0	0	0.01	0.01	63.6	17.96	0	0.15	0
Genotype x Location-Variance		0	0.67	0	12.09	0	0.08	0	0	10.71	4.43	0.22	0.21
Residual		0.84	5.79	0	131.9	0.01	0.12	0.02	120.1	89.98	23.123	1.83	3.35
Grand mean		2.47	49.02	0	152.11	0.54	3.27	0.55	11.51	11.84	28.85	15.26	0.36
LSD		0.71	5.92	0	0	0.02	0.22	0.09	8.14	6.38	0	1.87	13.76

GYD=grain yield, AD= number of days to anthesis, ASI= anthesis to silking interval, PH= plant height, EPO= ear position, SEN= leaf senescence, EPP = number of ears per plant, HUSKCOVER = number of ears with bad husk cover per plot, ER = number of rotten ears per plot, KEN_ROW= number of kernels per row, TEX = grain texture, MOI = grain moisture content at harvest. *** Significant P<0.001, ** significant P=0.01, *significant P<0.05, ns non-significant.

Table 4. 3. List of the 10 highest yielding experimental and pre-release hybrids selected from the hybrid trials conducted at the Chiredzi Research Station during the dry months of 2016 under managed combined drought and heat stress.

ENTRY	SOURCE	HYBRID DESCRIPTION	GYD	RANK	AD	ASI	EH	RL	EPP	HC	ER	TEX
A. Selected experimental and pre-release hybrids												
27	DJ65-32	Experimental	4.89a	1	42.5	-0.1	92.1	18.3	0.66	31.8	3.8	3.2
1	DJ65-1	Experimental	4.51a	2	42.4	2.5	87.3	46.9	0.57	31.3	7.8	3.8
23	DJ65-28	Experimental	4.24a	3	45.5	-1.1	75.6	14.2	0.53	16.6	2.0	3.2
30	DJ65-35	Experimental	4.15a	4	40.8	3.3	85.7	49.0	0.72	16.1	3.2	2.6
32	DJ65-37	Experimental	3.99a	5	44.3	2.4	90.4	18.3	0.65	-0.5	9.7	3.7
39	DJ86-3	Experimental	3.93a	6	39.2	4.3	81.9	16.4	0.61	4.5	5.2	3.8
25	DJ65-30	Experimental	3.82a	7	41.5	0.3	62.1	12.1	0.76	33.0	5.8	3.6
26	DJ65-31	Experimental	3.75a	9	44.8	0.7	81.1	17.0	0.62	-2.0	0.0	3.3
46	DJ87-1	Pre-release	3.73a	10	40.1	3.5	74.9	11.1	0.67	-1.8	2.0	3.0
19	DJ65-23	Experimental	3.62a	11	42.7	3.2	84.9	43.9	0.46	17.8	12.7	3.9
B. Commercial hybrids												
50	PANNAR	Commercial	3.80a	8	43.9	0.9	74.6	23.0	0.67	13.9	5.1	3.8
55	SEEDCO	Commercial	3.18a	21	46.7	0.9	101.5	-3.0	0.61	4.2	16.0	4.3
51	PANNAR	Commercial	3.08a	24	45.4	2.6	84.8	25.0	0.49	0.6	19.2	3.5
53	SEEDCO	Commercial	3.03b	26	42.6	2.7	82.6	47.8	0.45	6.6	9.1	2.9
54	SEEDCO	Commercial	1.79b	49	46.7	0.9	83.1	14.7	0.38	8.2	10.7	3.5
52	SEEDCO	Commercial	1.64b	52	39.4	5.7	74.2	2.5	0.47	18.4	16.7	2.6
LSD (0.05)			**1.82**		**4.0**	**3.5**	**19.3**	**32.0**	**0.23**	**19.0**	**13.1**	**0.8**

GYD=grain yield, AD= number of days to anthesis, ASI= anthesis to silking interval, EH= Ear height, RL root lodging, EPP = number of ears per plant, HC = number of ears with bad husk cover per plot, ER = number of rotten ears per plot, TEX = grain texture,

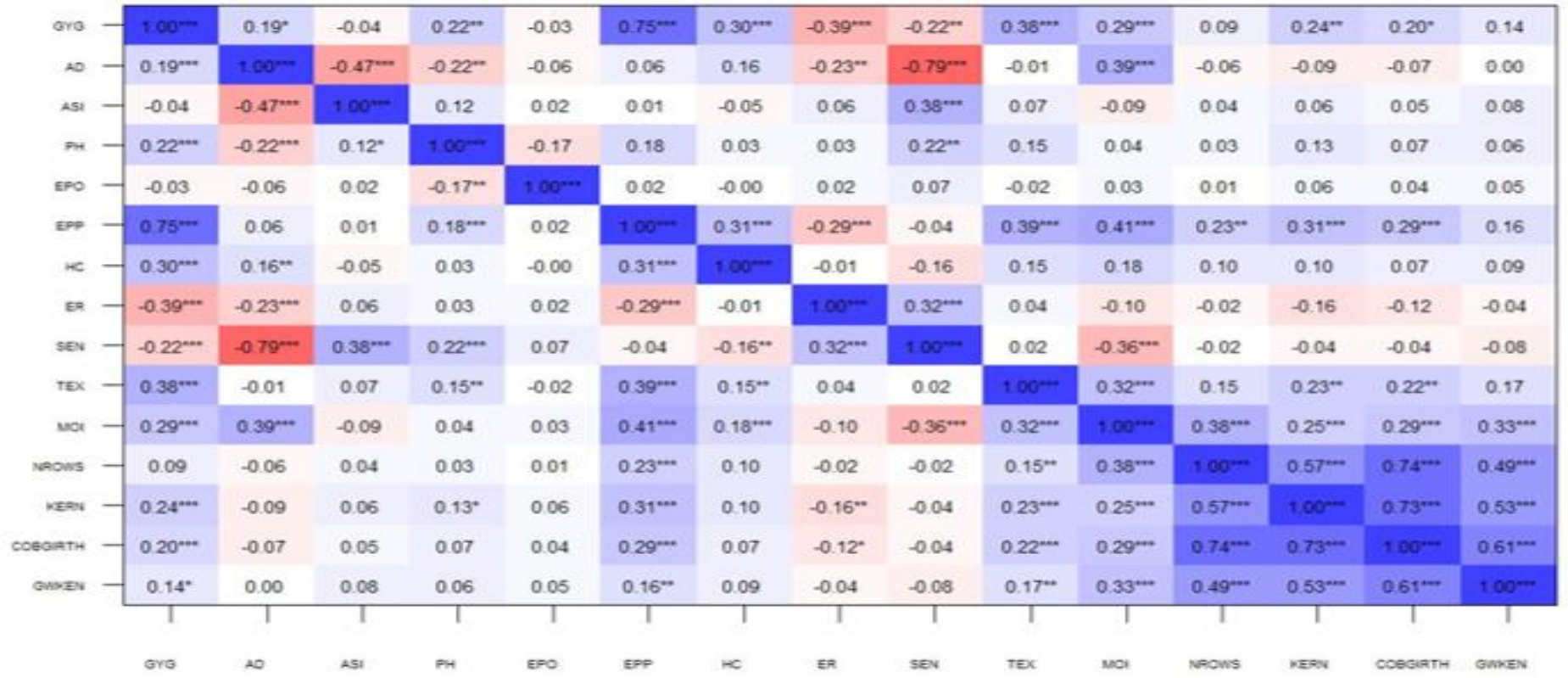

Figure 4. 1. Correlation matrix of traits measured for the experimental hybrids planted at Chiredzi during the dry months of 2016 under combined drought and heat stress.

GYG=grain yield, AD= number of days to anthesis, ASI= anthesis to silking interval, PH= plant height, EPO= ear position, EPP= number of ears per plant, HC = bad husk cover, ER = number of rotten ears per plot, SEN= leaf senescence, NROW= number of kernel rows, TEX = grain texture, MOI = grain moisture content at harvest, KERN = number of kernel rows on the ear, GWKEN = weight of 100 kernels, COBGIRTH = circumference of cobs, *** significant P<0.001, ** significant P=0.01, ns non-significant.

Table 4. 4. Results of the phenotypic path coefficient analysis on grain yield for agronomic data generated from the hybrid trial conducted at the Chiredzi Research Station during the dry months of 2016 under managed combined drought and heat stress con.

	AD	**PH**	**EPP**	**SEN**	**TS**	**KENROW**	**KERN**	**COBGIRTH**	**TOTAL**
AD	**-0.03571**	-0.00476	-0.09976	0.00821	0.00015	-0.0012	-0.04796	-0.0284	-0.22561
PH	0.00314	**0.05459**	0.09008	0.01656	-0.00001	0.00358	0.03683	0.04148	0.29621
EPP	0.00769	0.01055	**0.46192**	0.01427	0.00001	0.00653	0.08991	0.07861	0.73441
SEN	0.00532	-0.01632	-0.11995	**-0.05514**	0.00001	-0.00187	-0.0314	-0.02865	-0.33523
TS	0.00513	0.00062	-0.00347	0.00033	**-0.00102**	-0.00021	0.00307	-0.00319	0.00359
KENROW	0.00189	0.00858	0.1337	0.00455	0.00001	**0.02261**	0.05735	0.11867	0.2445
KERN	0.0115	0.01342	0.27959	0.01161	-0.00002	0.00871	**0.14893**	0.0981	0.681
COBGIRTH	0.00601	0.01335	0.21591	0.00936	0.00002	0.01591	0.08665	**0.16862**	0.46682

Figures in bold are the direct effects of each trait on grain yield, while the indirect effects on yield are above and below the diagonal. AD= days to anthesis, PH = plant height, EPP = number of ears per plant, SEN = leaf senescence, TS = tassel size, KENROW = number of kernel rows on the ear, KERN = number of kernels in a row, COBGIRTH = cob circumference.

Table 4. 5. Results of the genotypic path coefficient analysis on grain yield of agronomic data generated in hybrid trials conducted at the Chiredzi Research station during the 2016 dry season under managed combined drought and heat stress conditions.

	AD	**PH**	**EPP**	**SEN**	**TS**	**KENROW**	**KERN**	**COBGIRTH**	**TOTAL**
AD	**-0.41742**	-0.25928	0.0028	0.21299	-0.09	1.11414	-0.01192	-0.76197	0.1205
PH	-0.45796	**-0.23632**	0.02258	0.1176	-0.01033	0.27952	-0.49163	-0.1043	1.02402
EPP	-0.02625	-0.11992	**0.04445**	-0.0352	0.02484	0.52279	-0.41899	-0.28777	0.79511
SEN	0.555	0.17349	0.00978	**-0.16018**	0.06739	0.11008	-0.25645	-0.08757	-0.14743
TS	0.18584	0.01208	0.00547	-0.05341	**0.20214**	-0.49158	-0.01767	0.20736	0.02146
KENROW	-0.61705	-0.08765	0.03087	-0.0234	-0.13184	**0.75369**	0.09859	-0.33483	0.75464
KERN	-0.01281	-0.29913	0.04801	-0.10577	0.0092	-0.19132	**-0.3884**	0.06861	1.08976
COBGIRTH	-1.51782	-0.11763	0.06112	-0.06694	-0.20003	1.20427	0.12716	**-0.20955**	1.00286

Bold diagonal are the direct effects of each trait on grain yield and off diagonal are the indirect effects of each train on grain yield. AD= days to anthesis, PH = plant height, EPP = number of ears per plant, SEN = leaf senescence, TS = tassel size, KENROW = number of kernel rows on the ear, KERN = number of kernels in a row, COBGIRTH = cob circumference. Figures in bold are the direct effects of each trait on grain yield. Bold diagonal are the direct effects and off diagonal are the indirect effects of each trait.

4. 4. DISCUSSION

Grain yield is the primary objective of most maize breeding programmes, even bio-fortified varieties are tested for grain yield performance after reaching the desired nutritional targets. The experimental hybrids performed better than the commercial hybrids as well as the pre-release hybrids from the CIMMYT maize breeding program. The experimental hybrids yielded 61% more than both the commercial and pre-release hybrids indicating their superiority under combined drought and heat stress conditions. These findings corroborated the findings of Tesfaye et al., (2016). Selection of high performing genotypes under the current climatic conditions is therefore possible, and this augmented the findings of Zaidi et al., (2020). The resource constrained smallholder farmers in sub-Saharan Africa are the major producers and are the key drivers of food and nutrition security in this region. Identification of genotypes that are tolerant to combined drought and heat stress will help to counteract the impacts of combined drought and heat stress as it occurs in the smallholder farmer's fields.

Crop breeding and adaptation as well as increased inorganic fertiliser use, and best management practises will help in reducing the impacts of climate change on maize production. Lack of climate adapted maize varieties results in low yields among smallholder farmers, whereas inadequate application of production nutrients has resulted in huge yield gaps between research plots yields and farmer's yields. Most of the current commercial hybrids being grown in Zimbabwe are outdated and are not adapted to combined drought and heat stress, for example SC513 which was released 26 years ago. The commercial varieties were selected under past climatic conditions and hence are not adapted to the current climates, like worldwide trends where newer varieties are more tolerant to abiotic stresses than older varieties (Tollenaar and Lee, 2006; He at al., 2021; Ren et al., 2021; Su et al., 2022). There is low varietal turnover in most developing countries in SSA (Abate et al., 2017; Atlin et al., 2017; Chivasa et al., 2022), hence experimental hybrids performed better than the commercial varieties. High grain yield among the experimental hybrids could be attributed to stress tolerance

rather than escape mechanisms because the commercial hybrid, Pan 53, in the early maturity group had low grain yield. It is an early maturing variety which was bred for terminal drought stress avoidance. Stress tolerance, rather than escape is the desired trait because heat stress can occur at any time during the crop development cycle and impacts negatively all the crop developmental stages (Wahid et al., 2007). However, the greatest damage occurs during the reproductive stages (Annadurai et al., 2023; Santos et al., 2023).

Accelerated leaf senescence under combined drought and heat stress is common. Genotypes such as PAN 413, DJ65-1 and DJ65-28 that exhibited low leaf senescence tended to have high yields due to the extended grain filling periods and this agreed with the findings of Li et al., (2022) and Wu et al., (2023). The best yielding experimental hybrid, DJ65-32 had a score of 6.0 whereas the best yielding commercial hybrid, Pan 413 had a score of 5.0. Due to the importance of the stay green characteristic in maintaining high yields under abiotic stresses, concerted efforts are being made to reduce leaf senescence through CRISPR-Cas9 technology (Tang et al., 2025). As the soil dries under combined drought and heat stress, the absorption of nutrients from the soil is hampered by both unavailability of water to dissolve the nutrients and poor root elongation. In general, plants tend to mobilise assimilates from the older leaves to the younger leaves, especially nitrogen and this is exhibited through gradual leaf senescence from the bottom to the top (Gregersen et al., 2013: Wu et al., 2023). However, because of the high ambient temperatures, leaf firing may occur causing the desiccation of the younger top leaves severely reducing the photosynthetic area. Accelerated leaf senescence and reduction in photosynthetic area negatively impacts grain filling rate and duration resulting in a yield reduction of about 44% (Djanaguiraman et al., 2020). Yield reduction under combined drought and heat stress may be due to the destabilisation of the photosynthetic machinery (Djanaguiraman et al., 2020), as well as inadequate supply of the raw materials due to stomatal closure and reduced absorption of water from the soil. The combined effects of reduced photosynthetic area and poor supply of raw materials results in poor assimilation. As a result, the plants have inadequate assimilates for the developmental stages. Due to the high photo-respiration rates under combined drought and

heat stress, photo-assimilates may be depleted before the end of grain filling resulting in poorly filled grains or complete ear abortion. Reduced plant developmental stage duration is one of the major causes of low yields under combined drought and heat stress (Chen et al., 2012).

The heritability estimates for grain yield were high, (0.74) and this result was in contrast with the findings of Bänziger et al., (2004) Araus et al., (2012), Ziyomo and Bernardo (2013) and Musundire et al., (2019). Grain yield is a complex trait, which is controlled by many genes, is highly influenced by the environment as well as interactions among other traits, resulting in significant site main effects. However, most researchers (Mhike et al., 2012, Ziyomo and Bernado., 2013: Badu-Apraku et al., 2018) have reported low heritability estimates for grain yield and this tends to reduce the selection efficiency thereby reducing breeding speed. As a result, secondary traits are usually incorporated into the selection index to increase the efficiency of selection of high yielding genotypes. Secondary traits which were highly correlated with high grain yield and easy to measure enhanced selection under low heritability estimates for grain yield for example number of ears per plant and leaf senescence.

Climate change has increased the occurrence of storage pests and concomitantly losses attributed to these pests. Post-harvest losses can reach up to 90% (Saeed and Laing, 2023), however, crop breeding and selection of genotypes resistant to storage pests is possible (Derera, 2014), thereby minimising reliance on chemical control. Grain texture and husk cover were some important traits in conferring resistance to weevil damage. Bad husk cover exhibited high heritability (0.76) indicating the possibility to identify superior genotypes through selection. Well covered ears reduce fungal infections by providing physical barrier to both fungi and maize weevils. Fungal infections may result in high mycotoxin content. The damage resulting from fungal infections have been estimated to reach 70% (Benjamin, 2024) depending on the prevailing conditions. Ears with good husk cover were less prone to bird damage in the field, than ears with exposed tips. Damaged ears are more prone to fungal infections as well as ingression by maize weevils than intact ears.

Highly significant and positive correlations were detected between grain yield and the number of ears per plant (0.75), number of kernels per row (0.24) and cob girth (0.20). These findings were in agreement with most studies on drought stress screening conducted by Monneveux et al., (2006), Edmeades et al., (2015), Musundire et al., (2019), Choudhary et al., (2023) and Yang et al., (2023). Also, the number of ears per plant is an important secondary trait in screening genotypes for abiotic stress tolerance. The number of kernels in a row and the number of rows per ear directly determine the grain yield by affecting the total number of grains on an ear. Under combined drought and heat stress, grain filling was curtailed by both inadequate supply of assimilates as well as short green leaf duration due to accelerated leaf senescence. As a result, the total number of kernels was more important than the weight of individual kernels as shown by a low correlation (0.14) with grain yield. Interestingly, the cob traits were highly correlated indicating that selecting for one will result in the improvement of the others.

Significant and positive genetic correlations were detected for plant height, number of ears per plant, number of kernel rows on the ear, and cob girth with values of 0.22, 0.75, 0.24 and 0.20 respectively. These results corroborated with the findings of Immanuel and Nagarajan, (2011) and Reddy et al., (2022). Highly correlated traits tend to be inherited together. Under combined drought and heat stress, the weight of individual kernels was reduced because of the poor grain filling. Grain filling was affected by the duration and the availability of assimilates. As a result, the total number of kernels was one of the more important factors in determining grain yield than the weight of individual kernels. The cob traits such as the number of kernel rows and the number of kernels in a row which determine the total number of kernels on the ear are crucial in yield determination. Measuring all the cob traits may not be practically feasible hence it is advisable to target one of the correlated secondary traits as suggested by Malosetti et al., (2008).

Leaf senescence was negatively correlated with grain yield. The number of rotten ears were significantly and negatively correlated with grain yield. Coincidentally, leaf senescence and the number of rotten ears were significantly and positively correlated. This suggested that selecting genotypes with low leaf senescence would result in a selection of genotype with reduction in the number of rotten ears.

The correlation matrix showed that cob traits are highly correlated with each other and grain yield. Cob girth was easily assessed visually during harvesting and was found to be an important trait giving an indication of the number of kernel rows. The number of ears per plant was positively and significantly correlated with all the cob traits measured. This suggested that targeting high number of ears per plant and cob girth could accelerate breeding progress yet minimising phenotyping cost in combined drought and heat stress tolerance breeding programs.

Most traits exhibited negligible phenotypic direct effects on grain yield except the number of ears per plant (0.46), number of kernels per row (0.14) and cob girth (0.16). The environment modified the expression of some traits, and this may have resulted in low phenotypic correlations. The number of days to anthesis and leaf senescence exhibited moderate negative total effects on grain yield. These results contrasted with the findings of Singh and Kumar (2017), Gazal et al., (2018), Bankole et al., (2019) and Singh et al., (2020). Tassel size exhibited negligible total phenotypic effects on grain yield. However, several researchers such as Westgate and Boyer (1986), Duvick et al., (2004), Schussler and Westgate (2016), Li et al., (2021) showed that small tassels result in more assimilates being utilised for ear development than larger tassel size. And this was exhibited by the occurrence of small anthesis - silking interval. The heat stress phenotype of rapid, limited time exposure in the greenhouses is different from the heat stress phenotype under field conditions. Under field conditions, the duration of the stress is long, and multiple stresses may occur simultaneously thereby exacerbating the outcome. Consequently, the results from experiments carried out in greenhouses may be different

from field experiments. Under combined drought and heat stress, relatively large tassels with many branches were desirable to ensure pollination. The occurrence of tassel blasting may result in severe yield loss due to inadequate pollen grains. The impacts of tassel blasting may be exacerbated under combined drought and heat stress due to the occurrence of a large anthesis to silking interval. The least yielding genotypes had large anthesis to silking intervals of up to 13 days. However, DJ65-3 had a large anthesis-silking interval even though it had a high grain yield of 2.4 $tonha^{-1}$. The high yield could have been a result of early flowering thereby utilising pollen grains from other genotypes. However, if this genotype is grown in isolation under combined drought and heat stress, complete crop failure may occur due to exhaustion of pollen grains before silk emergence.

4.5 CONCLUSIONS

Seven high yielding experimental hybrids under combined drought and heat stress were identified and these were DJ65-1, DJ65-3, DJ65-28, DJ65-30, DJ65-31, DJ65-32 and DJ65-35. Interestingly, the high yielding inbred lines from Chapter 3 produced high yielding hybrids which is an indication that the stress tolerance traits are heritable. Plant escape mechanism was not effective under combined drought and heat stress conditions. PHB30G19 which is a drought tolerant variety performed poorly indicating that drought tolerance is distinct from combined drought and heat stress tolerance. Hybrids developed using the drought and heat stress tolerant inbred line K64R, from the CBI performed well under combined drought and heat stress. This maize inbred line may be used in the development of more hybrids with high tolerance to combined drought and heat stress tolerance.

The number of ears per plant, anthesis to silking interval, cob girth, and tassel size were detected as key traits for breeding high yielding maize hybrids under combined drought and heat stress. Chlorophyll content requires more research to determine its usefulness in maize breeding.

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CHAPTER 5

A retrospective analysis of maize performance under Low Nitrogen stress conditions related to combined drought and heat stress in Easten and Southern Africa[1]

ABSTRACT

Fertiliser use in sub-Saharan Africa is the lowest in the world and has stagnated around 20kgha^{-1}. The persistent low application of inorganic fertilisers and removal of stover results in low soil nitrogen. Low soil nitrogen (N) stress is one of the principal constraints to maize yields in the Eastern and Southern Africa (ESA). The average maize yield is one tonne per hectare which is below the genetic potential of most hybrids and improved open pollinated varieties (OPVs). The development of maize varieties with a yield advantage under very low nitrogen fertilisation rates will help to provide an immediate benefit to smallholder farmers. Improving the nitrogen use efficiency of maize hybrids will result in higher nitrogen recovery rates resulting in less leaching of nitrogen as well as loss through nitrification and ammonification. The study sought to: 1) Investigate the relationship between grain yield under low and optimal N conditions; and 2) Establish the level of variability in low N tolerance among elite Eastern and Southern African (ESA) maize varieties. Fifty-eight paired trials, each consisting of 40 to 65 experimental maize hybrids, under low N and optimal conditions were conducted in five countries in Eastern and Southern Africa between 2013 and 2015. The level of grain yield reduction as a result of nitrogen stress ranged from 8% to

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91% across the 58 paired trails. Grain yield of hybrids ranged from 1.69 Mg ha^{-1} to 3.44 Mg ha^{-1} in the early maturity group and 1.71 Mg ha^{-1} to 3.35 Mg ha^{-1} in the intermediate to late maturity group, with heritability ranging from 0.25 to 0.53 and 0.29 to 0.76, in the respective two maturity groups. Under low N stress pre-commercial hybrids that were bred for low N tolerance performed better than the old commercial hybrids and open pollinated varieties (OPVs). These results suggest that if more effort is devoted to selecting maize under low N conditions, significant yield gains can be realized with profound impact on maize productivity in SSA under drought with heat and low N stress.

5.1 INTRODUCTION

Intensification of maize production in sub-Saharan Africa (SSA) requires sufficient and efficient use of inorganic fertilisers (Van Ittersum et al., 2019). Maize production is severely impacted by the increasing frequency, intensity and severity of drought combined with heat stress (Wahid et al., 2007; Cairns et al., 2013; Serdeczny et al., 2017; Niu et al., 2021) as well as low soil nitrogen (N) (Holden, 2018; Dimkpa et al., 2023). Poor soil management and inadequate addition of both organic and inorganic fertilisers have resulted in severe nutrient mining in SSA. Therefore, most farmers end up producing maize that are deficient in most soil nutrients especially nitrogen. Average fertiliser application rates in the region have stagnated between 13 and 20kg of nutrient per hectare (Sheahan and Barrett, 2017b; Jayne and Sanchez, 2021), as compared to 120kg and 73 kg ha^{-1} in South Asia and Latin America, respectively (Crawford et al., 2005; Begho et al., 2022). In sharp contrast to other regions of the world, fertiliser use in SSA has decreased over the past decade (Kostandini et al., 2015). Coupled with the low fertiliser application rates in SSA, is the low agronomic efficiency of nitrogen, making the application of inorganic fertilisers unprofitable. The agronomic efficiency of N in SSA is about 33% of the world average (Jayne and Sanchez, 2021), thereby making fertiliser use unattractive to resource constrained farmers. However, fertiliser use in SSA must increase enormously to boost the productivity via yield increase per unit area of land capable of meeting the demand for food by the rapid population increase (Van Ittersum et al., 2019; Cassman and Dobermann, 2022). Low fertiliser use is one of the major causes of the huge yield gaps experienced in SSA despite the genetic gains in maize breeding.

There is a need to change from extensification to intensification of smallholder agriculture to reduce the conversion of marginal lands into agricultural lands. Extensification has been the

major driver of maize production increase in SSA (Giller et al., 2021; Jayne and Sanchez, 2021). Extensification involves the expansion of the area under crop production without a concomitant increase in yield per unit area (Jayne and Sanchez, 2012; Giller et al., 2021). The increase in the farm size is usually not matched by an increase in use of inputs such that low yields may persist but are masked by area expansion (Giller et al., 2021). Whereas intensification with sufficient and efficient use of both organic and inorganic fertilisers coupled with adapted cultivars and best management practises will reduce the environmental impacts (Van Ittersum et al., 2019) while maintaining biodiversity. Improvement in agricultural productivity has many synergistic effects on the environment and the economy due to the downstream industries involved. Transitioning to intensification will require a holistic approach to crop and soil management.

The SSA region is extremely heterogenous ecologically, economically and in-terms of farmer's capacity to adapt to yield-constraining shocks. Technical advancement and innovation are not readily adopted in SSA despite several interventions to increase crop productivity. Only Ethiopia has had a major increase in crop productivity (Abate et al., 2015; Jayne and Sanchez, 2021). Unlike climate-related stresses, such as drought and heat, which vary in occurrence, duration, and severity each season, low N stress is a consistent problem for most smallholder farmers. This is particularly true for many female farmers in SSA, who tend to have less access to inputs, including fertilisers (Kilic et al., 2015; Sheahan and Barrett, 2017), creating a large gender gap in agricultural productivity. In SSA, women farmers produce 30% less than men farmers per hectare and one of the main reasons for the low productivity is the 21% gender gap in the use of inorganic fertilisers in maize production (Patterman et al., 2011; Abdisa et al., 2024). The agricultural productivity gender gap is one of the significant and costly inefficiencies hampering progress in the sub region (Buehren,

2023). Increasing agricultural productivity is an important step in poverty reduction ensuring food and nutrition security.

Improved maize varieties with a yield advantage at less than recommended fertilisation rates would provide an immediate and significant benefit to smallholder farmers. The simultaneous improvement of maize grain yield and the nitrogen use efficiency (NUE) is an important breeding objective which will reduce environmental pollution and fertiliser cost for the resource constrained smallholder farmers. Rongfa et al., (2022) noted an increase in the nitrogen use efficiency of newer hybrids produced between 1990 and 2000 in China compared to the older hybrids. Improved nitrogen use efficiency results from enhanced nitrogen remobilisation from pre-anthesis structures.

Bänziger et al., (1997) first investigated the efficiency of selection for grain yield under low N stress conditions relative to indirect selection under optimal N in 14 trials in Mexico. The genetic correlation between grain yield under low N decreased as the yield decreased. The authors concluded that direct selection for low N tolerance was more efficient under low N conditions where yields were at least 40% less than those under optimal conditions. Presterl et al., (2003) found a similar relationship in temperate maize using 21 experiments under low N and optimal conditions in eight locations across France and Germany where N stress reduced grain yields by 14 to 55%. The current study aimed to: 1) Investigate the relationship between grain yield under low N and under optimal conditions; and 2) Establish the level of variability in low N tolerance among elite Eastern and Southern African (ESA) maize varieties. It was hypothesized that a better understanding of the variability that exists in maize for grain yield performance under low N conditions could guide objective setting of maize

breeding programs which will lead to rapid genetic gains under low nitrogen stress conditions in the sub-region.

5.2 MATERIALS AND METHODS

5.2.1 Study designs, experiment management and data collection

The study was separated into two clusters to answer two major objectives: 1) Investigating the relationship between grain yield under low N and optimal conditions; and 2) Establishing the level of variability in low N tolerance among elite Eastern and Southern African (ESA) maize varieties.

Cluster 1: Investigating the relationship between grain yield under low N and optimal conditions

Germplasm

The germplasm used for this study was from the International Maize and Wheat Improvement Centre (CIMMYT) regional (stage 4) trials that are comprised of advanced elite and pre-commercial hybrids which are tested throughout ESA (Masuka et al., 2017a; Setimela et al., 2017a). Regional trials were separated into two maturity groups: early (less than 68 days to anthesis) and intermediate to late (more than 68 days to anthesis).

Field trials

Experiments were conducted at 13 locations across five countries in ESA between 2013 and 2015 (Table 5. 1). An alpha-lattice design replicated twice was used. At all locations, two seeds per hill were sown. Then thinned to one seed per hill three weeks after emergence. Trials were planted at the same time. Genotypes were planted in two-row plots, with a final plant density of 5.33 plants m^{-2}. In East Africa optimal trials, calcium ammonium nitrate (CAN) fertilizer was used at the rate of 54 kg N ha^{-1}, followed by the top dressing of urea fertilizer at the rate of 138 kg N ha^{-1} three weeks after planting. In Southern Africa, optimal trials had, all plots receiving 400 kg ha^{-1} as compound D (7% N, 14% P_2O_5 and 7% K_2O) at

sowing. A second application of N (66 kg N ha^{-1}) was applied as urea at the six-leaf stage (V6). In East Africa managed low N trials, triple super phosphate (46% P_2O_5) was applied at planting at the rate of 50 kg P_2O_5 ha^{-1}, with no further top dressing. In Southern Africa low N trials, all plots received basal application of P as triple super phosphate at 200 kg ha^{-1} and K as muriate of potash (200 kg ha^{-1}). The number of years of depletion of residual N at each location varied from two to six years. The field site in Harare consisted of five separate blocks that had been N-depleted for different lengths of time. A total of 116 experiments were conducted under optimal and low N conditions giving 58 paired sites (low N and well fertilised). At all sites, the blocks were ploughed using a tractor drawn disc plough and harrowed using a disc harrow to obtain a fine tilth to ensure good crop establishment. All recommended plant, weed, and insect control measures were followed.

Table 5.1 Summary of trial locations and the number of trials per site used to determine the relationship between grain yield under low Nitrogen and optimal conditions.

				Number of paired trials			
Country	Location	Coordinates	Elevation (masl)	2013	2014	2015	**Total**
Ethiopia	Bako	9.094, 37.046	1408	1		1	**2**
Kenya	Embu	-0.503, 37.457	1492			1	**1**
	Kakamega	0.279, 34.767	1526	2		1	**3**
	Kiboko	-2.215, 37.724	990	1		1	**2**
South Africa	Cedara	-29.530, 30.280	1100		1	1	**2**
	Golden	-14.170,					
Zambia	Valley	28.370	1173	1		5	**6**
	Lusaka West	-15.408, 28.329	1300	4	3	3	**10**
		-17.700,					
Zimbabwe	Devonia	31.383	1296		2		**2**
	Gwebi	-17.683, 30.867	1450		1	2	**3**
	Harare	-17.723, 31.023	1498		4	12	**16**
	Kadoma	-18.350, 29.916	1325		1	1	**2**
	Rattray Arnold	-17.670, 31.170	1458	1	2	6	**9**

Masl= metres above sea level

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Data collection

At physiological maturity, all plants were hand harvested and shelled. The shelled grain was weighed using a scale. Grain yield was estimated as ‘shelled grain weight’ per plot adjusted to 12.5% grain moisture content and expressed in $Mgha^{-1}$.

Cluster 2: Establishing the level of genetic variability among elite ESA maize varieties in low N tolerance

Germplasm

Germplasm was selected to represent current commercial varieties available in ESA and experimental varieties. The commercial varieties were selected under optimal conditions and grain yield was the primary trait of interest. CIMMYT experimental hybrids were primarily selected for drought and low N stress tolerance, and yield potential under optimal conditions. Germplasm was separated into two maturity groups: early and intermediate to late maturity. In the early maturity group, a total of 14 varieties were used, comprising of ten hybrids and four OPVs. In the intermediate to late group, a total of 35 varieties (comprised of 28 hybrids and 7 OPVs) were used.

Field trials

Experiments were conducted at five locations in Kenya (Embu, Kakamega and Kiboko), Zambia (GART) and Zimbabwe (Harare) in 2011 (Table 2). Details of site coordinates and elevation are presented in Table 1. Two treatments were used: low N stress and optimal. Experiments were planted and managed as described above under Cluster 1.

Data collected

Days to anthesis and silking were recorded when 50 % of the plants had shed pollen and 50 % of the plants had silks, respectively. The anthesis-silking interval (ASI) was calculated as days to silking minus days to anthesis. At physiological maturity, plant height was measured on five representative plants per plot, all plants were hand harvested, and grain yield measured.

Statistical analysis

Data from the two clusters of experiments were analysed in Meta-R version 3.3 (Lopez et al. 2015). The linear models are implemented in lmer from package lme4 of R using REML to calculate BLUEs and BLUPs and estimate the variance components. For analysis of individual environments, the following model was used:

$$Y_{ijk} = \mu + Rep_i + Block_j(Rep_i) + Gen_k + Cov + \varepsilon_{ijk}$$

Where; Y_{ijk} was the trait of interest, μ was the mean effect, Rep_i is the effect of the $_i$th replicate, $Block_j(Repi)$ is the effect of the $_j$th incomplete block within the $_i$th replicate, Gen_k is the effect of the $_k$th genotype, Cov is the effect of the covariate (plant height), ε_{ijk} is the error associated with the $_i$th replication, $_j$th incomplete block and the $_k$th genotype. Both genotype and covariate were considered as fixed effects.

For combined analysis, the following model was used:

$$Y_{ijk} = \mu + Env_i + Rep_j(Env_i) + Block_k(Env_iRep_j) + Gen_l + Env_i \times Gen_l + Cov + \varepsilon_{ijk}$$

Where, Env_i and $Env_i \times Gen_l$ are the effects of the $_i$th environment and environment x genotype interaction.

Broad-sense heritability (H^2) of a given trait at an individual environment was calculated as:

$$H^2 = \frac{\sigma^2 g}{\sigma^2 g + \sigma^2 e/nreps}$$

Where, $\sigma^2 g$ and $\sigma^2 e$ are the genotype and error variance components respectively, and *nreps* is the number of replicates.

For the combined analysis, H^2 was calculated as:

$$H^2 = \frac{\sigma^2 g}{\sigma^2 g + \sigma^2 ge/nEnvs + \sigma^2 e/(nEnvs\ x\ nreps)}$$

Where; $\sigma^2 ge$ is the genotype x environment interaction variance component and *nEnvs* is the number of environments in the analysis.

Genetic correlations between environments were calculated using equations from Cooper et al. (1996).

$$\rho_{g(jj')} = \frac{\rho_{p(jj')}}{h_j h_{j'}},$$

Where, $P_{p(j\,j')}$ is the phenotypic correlation between environments $_j$ and $_{j'}$ and h_j and $h_{j'}$ are the heritabilities of environments $_j$ and $_{j'}$ respectively.

Regression analysis was conducted to study the relationship between grain yield under low N and optimal conditions using the '*lm*' function in the R statistical package and these relationships were visualised on a regression plots using the '*plot*' function in the R package (R Development Core Team, 2013).

5.3 RESULTS

5.3.1 Relationship between grain yield and heritability under low N and optimal conditions

37 Over two-thirds of low N trials had a yield reduction of over 50% relative to the optimal trials, while one-fifth of low N trials had a yield reduction of over 75%. Broad sense heritability (H^2) ranged from 0.05 to 0.85 under low N stress and 0.28 to 0.95 under optimal conditions (Table 5.3). Although H^2 with yield reduction under low N stress increased (Figure 5.1), over two-thirds of low N stress trials had an H^2 greater than 0.5. For optimal trials, 79% had an H^2 greater than 0.5. Four trials under low N had an H^2 of less than 0.20. In almost two-thirds of paired trials, H^2 was higher under optimal conditions than low N stress. Within these paired trials, H^2 was higher under optimal conditions than under low N stress with an average of 0.38.

5.3.2 Correlation of grain yield under low N and optimal conditions

Genetic correlations between low N and optimal paired trials were generally positive (with only seven trials showing a negative correlation between low N and optimal). The efficiency of indirect selection under optimal N against direct selection under low N (Figure 5. 2). The efficiency of indirect selection for grain yield was significantly decreased with the level of stress intensity ($R^2 = 0.22$, $p<0.05$). The average efficiency of indirect selection at optimal N under low N stress was 58%.

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Table 5. 2. Means for grain yield under low nitrogen (N) and optimal (opt) conditions and the yield reduction under low N stress relative to optimal conditions, repeatability and variance components under low nitrogen and optimal conditions.

				Grain yield (Mg ha^{-1})		Reduction	Repeatability		Variance components: Genotypic		Variance components: Residual	
Country	**Location**	**Entries**	**Year**	**Opt**	**Low N**	**(%)**	**Opt**	**Low N**	**Opt**	**Low N**	**Opt**	**Low N**
Kenya	Embu	56	2015A	6.14	5.39	12	0.76	0.67	0.91	1.00	0.87	1.51
Kenya	Kakamega	56	2015A	7.59	4.75	37	0.45	0.77	0.56	0.92	2.08	0.85
Kenya	Kiboko	56	2015A	6.06	4.97	18	0.72	0.58	0.52	0.56	0.59	1.21
Zimbabwe	Harare	60	2014A	8.57	1.56	82	0.79	0.62	1.01	0.07	0.80	0.14
Zimbabwe	Gwebi	60	2014A	8.05	1.08	87	0.73	0.44	0.95	0.04	1.06	0.16
Zimbabwe	Kadoma	60	2014A	5.55	2.08	63	0.41	0.38	0.10	0.05	0.42	0.27
Zambia	Lusaka West	60	2014A	7.90	2.58	67	0.83	0.38	1.36	0.18	0.83	0.88
Zimbabwe	Harare	55	2015A	9.25	4.50	51	0.85	0.48	1.70	0.11	0.93	0.35
Zambia	Golden Valley	55	2015A	7.63	1.56	79	0.58	0.65	0.46	0.06	0.98	0.09
Zimbabwe	Devonia	55	2015A	7.85	3.60	54	0.78	0.53	1.62	0.12	1.40	0.31
Zimbabwe	Kadoma	55	2015A	8.11	0.79	90	0.44	0.53	0.45	0.07	1.73	0.18
Zimbabwe	Rattray Arnold	55	2015A	6.36	3.80	40	0.80	0.72	1.05	0.30	0.80	0.35
Zimbabwe	Kakamega	65	2013A	10.69	3.68	66	0.76	0.75	4.06	0.44	3.96	0.45
Zambia	Lusaka West	65	2013A	8.26	3.48	58	0.73	0.50	1.02	0.52	1.14	1.56
Zimbabwe	Harare	60	2015A	10.27	3.67	64	0.72	0.51	1.35	0.10	1.04	0.29
Zimbabwe	Rattray Arnold	60	2015A	7.86	4.32	45	0.84	0.56	0.79	0.22	0.44	0.54
Ethiopia	Bako	50	2013	6.88	3.08	55	0.53	0.76	1.11	0.48	0.86	0.65
Zimbabwe	Devonia	50	2014A	7.77	1.66	79	0.49	0.60	1.15	0.16	0.83	0.35
Zambia	Lusaka West	50	2014A	7.29	1.35	82	0.95	0.56	2.14	0.13	0.82	0.31
Zimbabwe	Rattray Arnold	50	2014A	5.20	2.43	53	0.50	0.20	1.21	0.47	0.83	0.82
Ethiopia	Bako	55	2015A	9.31	3.28	65	-	0.70	0.96	0.15	0.47	0.30
South Africa	Cedara	55	2015A	6.65	3.70	44	0.40	-	0.57	0.11	0.74	0.18
Zimbabwe	Harare	55	2015A	6.26	4.32	31	0.74	0.17	0.63	0.25	0.63	0.75
Zimbabwe	Harare	55	2015A	8.36	3.80	55	0.74	0.23	1.31	0.11	0.78	0.49
Zambia	Golden Valley	55	2015A	5.39	1.37	75	0.86	0.17	0.31	0.01	0.42	0.11
Zimbabwe	Gwebi	55	2015A	9.05	2.31	75	0.66	0.18	0.53	0.05	0.61	0.36
Zambia	Lusaka West	55	2015A	6.39	2.02	68	0.70	0.34	0.47	0.44	0.57	0.72
Zimbabwe	Rattray Arnold	55	2015A	7.20	2.12	71	0.66	0.29	0.82	0.16	0.71	0.52
Zambia	Lusaka West	64	2013A	8.78	4.50	49	-	-	0.40	1.50	0.50	0.68
Zimbabwe	Devonia	55	2014A	7.90	0.79	90	0.62	0.45	0.44	0.03	0.54	0.07
Zambia	Lusaka West	55	2014A	8.44	1.31	84	0.53	0.23	0.99	0.08	1.73	0.56
Zimbabwe	Rattray Arnold	55	2014A	5.39	3.19	41	0.72	0.78	1.41	0.58	1.08	0.33
Zimbabwe	Harare	60	2015A	6.64	3.87	42	0.58	0.70	0.44	0.22	0.64	0.19
Zimbabwe	Harare	60	2015A	8.97	4.44	50	0.86	0.64	1.94	0.28	0.66	0.31
Zimbabwe	Harare	60	2015A	9.42	4.84	49	0.89	0.64	2.06	0.24	0.53	0.26
Zimbabwe	Gwebi	60	2015A	9.01	2.35	74	0.28	0.30	0.25	0.04	1.28	0.21

Table 5. 2 Continued. Means for grain yield under low nitrogen (N) and optimal (opt) conditions and the yield reduction under low N stress relative to optimal conditions, repeatability and variance components under low nitrogen and optimal conditions.

Zambia	Lusaka West	60	2015A	6.48	2.53	61	0.55	0.68	0.31	0.67	0.51	0.64
Zimbabwe	Rattray Arnold	60	2015A	7.02	2.68	62	0.82	0.05	0.95	0.02	0.41	0.59
Zambia	Golden Valley	55	2013A	6.52	0.51	92	0.61	0.63	0.41	0.01	0.78	0.02
Kenya	Kakamega		2013A	11.44	4.10	64	0.82	0.00	5.75	0.00	3.68	3.90
Kenya	Kiboko	55	2013A	3.86	3.20	17	0.45	0.49	0.33	0.12	1.19	0.37
Zambia	Lusaka West	55	2013A	8.23	2.93	64	0.76	0.29	1.19	0.16	1.12	1.15
Zimbabwe	Rattray Arnold	55	2013A	5.39	2.73	49	0.74	0.81	0.31	0.29	0.33	0.21
Zimbabwe	Harare	40	2014A	8.66	1.54	82	0.73	0.67	1.16	0.16	1.25	0.23
Zimbabwe	Harare	42	2015A	10.27	3.67	64	0.72	0.51	1.35	0.10	1.04	0.29
Zambia	Golden Valley	42	2015A	7.79	1.37	82	0.47	0.59	0.39	0.04	1.32	0.08
South Africa	Cedara	50	2014A	10.22	5.26	49	0.46	0.56	2.60	1.04	6.04	1.66
Zimbabwe	Harare	50	2014A	6.71	3.25	52	0.86	0.42	2.17	0.18	0.70	0.50
Zimbabwe	Harare	50	2014A	6.47	2.32	64	0.82	0.72	1.91	0.34	0.84	0.26
Zimbabwe	Harare	60	2015A	5.96	4.57	23	0.79	0.77	0.78	0.37	0.42	0.22
Zimbabwe	Harare	60	2015A	6.18	5.69	8	0.45	0.68	0.70	0.39	1.76	0.36
Zambia	Golden Valley	60	2015A	6.80	1.31	81	0.32	0.64	0.23	0.05	1.01	0.06
Zimbabwe	Rattray Arnold	60	2015A	7.39	2.64	64	0.75	0.62	0.75	0.23	0.51	0.28
Zimbabwe	Harare	60	2015A	6.90	4.89	29	0.50	0.77	0.49	0.42	1.01	0.25
Zimbabwe	Harare	60	2015A	8.17	4.63	43	0.74	0.85	1.18	0.54	0.83	0.19
Zambia	Golden Valley	60	2015A	6.65	1.54	77	0.78	0.78	0.59	0.14	0.33	0.08
Zimbabwe	Rattray Arnold	60	2013A	7.54	2.68	64	0.75	0.85	0.74	0.33	0.50	0.12
Zambia	Lusaka West	50	2014A	7.57	4.04	47	0.43	0.55	0.34	1.09	1.34	2.68

Table 5. 3. Summary of locations and grain yield and repeatability (H) of trials under low nitrogen (N) stress and optimal conditions of early and intermediate-late commercial hybrids and OPVs.

Low Nitrogen Stress				Optimal			
		Grain yield (Mg ha^{-1})				Grain yield (Mg ha^{-1})	
Season	**Location**	**Mean**	**H^2**	**Season**	**Location**	**Mean**	**H**
			Early				
A	Embu	3.44	0.53	A	Kiboko	7.31	0.78
A	Kiboko	2.66	0.52	A	Kakamega	4.95	0.90
A	Kakamega	1.69	0.25	A	Embu	3.90	0.81
B	GART	2.96	0.26	B	GART	10.25	0.92
				B	Harare	7.58	0.24
			Intermediate-Late				
A	Kiboko	2.59	0.29	A	Kiboko	6.79	0.78
A	Kakamega	1.97	0.76	A	Embu	5.74	0.74
B	GART	3.35	0.50	A	Kakamega	4.69	0.84
B	Kiboko	2.42	0.46	A	Embu	4.21	0.64
B	Harare	1.71	0.53	B	GART	9.19	0.86
				B	Harare	4.93	0.95

Table 5. 4. Best linear unbiased predictions (BLUPS) for grain yield and best linear unbiased estimates (BLUES) anthesis date, anthesis-silking interval (ASI) and plant height (PH) under low nitrogen (N) and optimal conditions for early maturity variety.

			Grain yield (Mg/ha)		Anthesis date (d)		ASI		PH (cm)	
Variety	**Variety type**	**Breeding program**	**Low N**	**Optimal**	**Low N**	**Optimal**	**Low N**	**Optimal**	**Low N**	**Optimal**
DH 04	Hybrid	Kenya Seed	2.66	7.35	74.5	69.5	3.45	1.62	174.4	216.7
DK 8031	Hybrid	Monsanto	3.20	7.11	73.1	68.2	5.21	3.48	175.3	214.3
PHB3253	Hybrid	Pioneer	3.24	7.14	76.5	70.1	3.23	2.36	174.8	221.6
SC513	Hybrid	SeedCo	2.52	6.60	75.7	70.3	5.79	2.23	161.3	217.8
SC403	Hybrid	SeedCo	2.58	6.82	73.6	68.5	5.43	2.34	162.6	208.8
SC407	Hybrid	SeedCo	2.26	6.58	71.2	65.3	7.29	3.27	165.4	213.4
VP0717	Hybrid	CIMMYT	2.57	5.84	69.9	64.8	4.01	2.51	148.8	196.2
CZH0928	Hybrid	CIMMYT	3.31	7.76	75.7	69.9	4.76	1.50	155.6	201.5
CKPH08028	Hybrid	CIMMYT	2.53	6.12	77.7	72.5	4.64	1.76	177.4	225.1
CKIR07012	Hybrid	CIMMYT	3.06	8.18	76.3	71.6	4.73	2.29	171.0	220.4
ZM523	OPV	CIMMYT	2.50	6.01	74.0	69.3	5.62	2.83	155.0	195.7
09SADVE-F2	OPV	CIMMYT	3.31	6.95	75.4	70.9	4.22	2.63	163.5	204.7
ZM521	OPV	CIMMYT	2.82	5.75	70.4	66.4	3.86	2.07	160.9	194.7
ZM309	OPV	CIMMYT	2.28	5.43	65.9	62.7	4.99	2.92	138.9	177.7
Mean			2.77	6.69	73.6	68.6	4.80	2.41	163.2	207.7
LSD			0.77	1.22	2.92	1.40	2.24	1.41	18.63	12.27
H			0.48	0.71	0.90	0.97	0.47	0.29	0.66	0.90

DM41 = SC403; DUMA 43 = SC407

Table 5. 5. Best linear unbiased predictions (BLUPS) for grain yield, anthesis date, anthesis-silking interval (ASI) and plant height (PH) under low nitrogen (N) and optimal conditions for intermediate-late maturity varieties

			Grain yield (tha^{-1})		Anthesis date (d)		ASI		PH (cm)	
Variety	**Breeding program**	**Variety type**	**Low N**	**Optimal**	**Low N**	**Optimal**	**Low N**	**Optimal**	**Low N**	**Optimal**
KH631Q	FreshCo	Hybrid	1.51	3.49	78.1	80.0	2.91	1.16	164.6	197.2
KSTP94	KALRO	Hybrid	2.07	4.65	70.2	70.5	6.12	2.92	185.6	229.2
H624	Kenya Seed	Hybrid	2.36	6.44	78.2	78.2	5.61	3.35	214.3	258.6
H513	Kenya Seed	Hybrid	2.53	5.87	71.8	71.8	4.84	2.17	174.2	218.1
H516	Kenya Seed	Hybrid	2.57	5.80	72.7	75.0	5.72	2.91	193.6	231.8
H614D	Kenya Seed	Hybrid	1.58	4.77	81.1	80.8	6.35	3.57	210.6	254.4
Pris601	Klein Karoo	Hybrid	2.94	7.53	72.7	73.6	3.42	1.76	180.4	209.9
Pan53	Panaar	Hybrid	2.78	7.83	73.8	74.1	5.90	2.83	189.1	230.5
		Hybrid								
Pan 67	Pannar		2.14	5.94	71.9	71.3	4.79	2.86	179.0	220.7
Pan 691	Pannar	Hybrid	2.73	5.44	79.9	80.6	4.50	4.26	219.5	238.3
PHB 30D79	Pioneer	Hybrid	3.22	6.51	72.4	73.1	6.67	4.52	197.9	220.3
SC627	SeedCo	Hybrid	2.39	5.92	71.9	72.6	5.93	2.78	183.3	221.3
WH505	Western Seed	Hybrid	2.69	6.19	74.9	76.7	4.29	2.05	179.1	215.1
WH403	Western Seed	Hybrid	2.90	6.92	73.6	75.1	4.92	2.80	183.1	219.1
WH504	Western Seed	Hybrid	2.81	6.68	74.5	76.2	5.60	2.21	180.6	215.6
WH105	Western Seed	Hybrid	2.50	5.36	70.5	71.1	4.62	2.69	178.9	210.2
WH507	Western Seed	Hybrid	3.05	6.57	74.0	75.3	3.47	1.95	188.8	217.7
CKH101537	CIMMYT	Hybrid	2.18	6.46	74.5	74.6	4.70	2.05	166.7	208.7
CKH101574	CIMMYT	Hybrid	3.05	6.63	73.1	74.5	4.10	1.31	168.4	209.0
CKH08037	CIMMYT	Hybrid	2.68	6.72	69.8	71.2	6.80	3.07	174.6	204.5
CKH09419	CIMMYT	Hybrid	3.00	6.12	70.7	71.2	4.20	1.95	168.7	194.5
CKH08066	CIMMYT	Hybrid	2.61	5.95	72.5	74.3	4.91	3.09	166.9	212.6
CKH08032	CIMMYT	Hybrid	2.85	7.08	72.2	72.6	4.23	2.75	169.0	207.2
CKH10707	CIMMYT	Hybrid	3.04	6.37	72.7	72.8	4.47	2.82	166.4	201.2
CZH0616	CIMMYT	Hybrid	3.37	8.03	70.4	70.8	3.40	1.54	169.4	203.0
CKPH08043	CIMMYT	Hybrid	1.97	5.68	75.1	76.2	6.25	3.31	183.4	212.8
CKIR07013	CIMMYT	Hybrid	2.72	5.91	73.1	74.1	3.98	2.38	185.4	221.5
CKH101572	CIMMYT	Hybrid	2.59	6.41	72.5	73.8	4.12	1.45	165.5	211.8
ZM627	OPV	CIMMYT	2.66	6.08	72.6	72.2	3.52	1.86	159.4	200.6
ECAVL1/ECAVL18	OPV	CIMMYT	2.03	5.57	72.6	72.4	4.71	2.71	170.8	205.8
ECA-VL43-#	OPV	CIMMYT	2.82	6.12	72.9	72.0	3.13	2.36	175.2	210.8
ECA-VL45-#	OPV	CIMMYT	3.01	6.28	72.0	72.4	2.77	1.88	171.4	205.7
ECAVL1	OPV	CIMMYT	1.88	4.78	73.4	73. 6	4.76	2.65	168.4	205.7
Embu Synthetic	OPV	KALRO	1.78	4.04	69.1	69.6	5.31	3.26	163.6	207.8
Kakamega Synthetic II	OPV	KALRO	2.10	5.50	72.6	72.2	5.39	2.46	164.3	211.5
Mean			2.55	6.05	73.2	73.9	4.75	2.56	178.9	215.5
LSD			0.58	1.04	1.71	1.38	1.92	1.18	13.9	12.8
H^2			0.82	0.85	0.95	0.97	0.61	0.70	0.89	0.90

5.3.3 Variability in low N tolerance among elite Eastern and Southern African maize varieties

Under low N stress, grain yield ranged from 1.69 to 3.44 Mg ha^{-1} in the early maturity group and 1.71 to 3.35 Mg ha^{-1} in the intermediate to late maturity group. Grain yield under optimal conditions ranged from 3.90 to 10.25 Mg ha^{-1} in the early maturity group and 4.21 to 9.19 Mg ha^{-1} in the intermediate-late maturity group (Table 5.3). Under optimal conditions, H^2 ranged from 0.24 to 0.90 and 0.64 to 0.95 in the early and intermediate to late maturity group, respectively. Under low N stress, H^2 ranged from 0.25 to 0.53 and 0.29 to 0.76 in the early and intermediate to late maturity group, respectively.

There was large genetic variability for grain yield under low N stress (Tables 5.4 and 5.5). In the early maturity group, there was 1 Mg ha^{-1} difference in yield for both the hybrids and OPVs, with hybrid CZH0928 and OPV 09ADVE-F2 both yielding 3.31 Mg ha^{-1} (Table 5.4). Two commercial hybrids (PHB3253 and DK8031) yielded more than 3 Mg ha^{-1} under low N stress. OPV 09ADVE-F2 yielded significantly more than the three best yielding hybrids (CKPH08028, SC513 and -SC403), under low N stress. In the intermediate to late maturity group, there was over a one-fold difference in yields under low N stress. Yields ranged from 1.51 Mg ha^{-1} and 1 Mg ha^{-1} to 3.37Mg ha^{-1} and 3.01 Mg ha^{-1} for hybrids and OPVs, respectively (Table 5). Low N stress significantly reduced plant height in both maturity groups, while significantly increasing days to anthesis and anthesis to silking interval (ASI) (Table 5. 4 and 5.5)

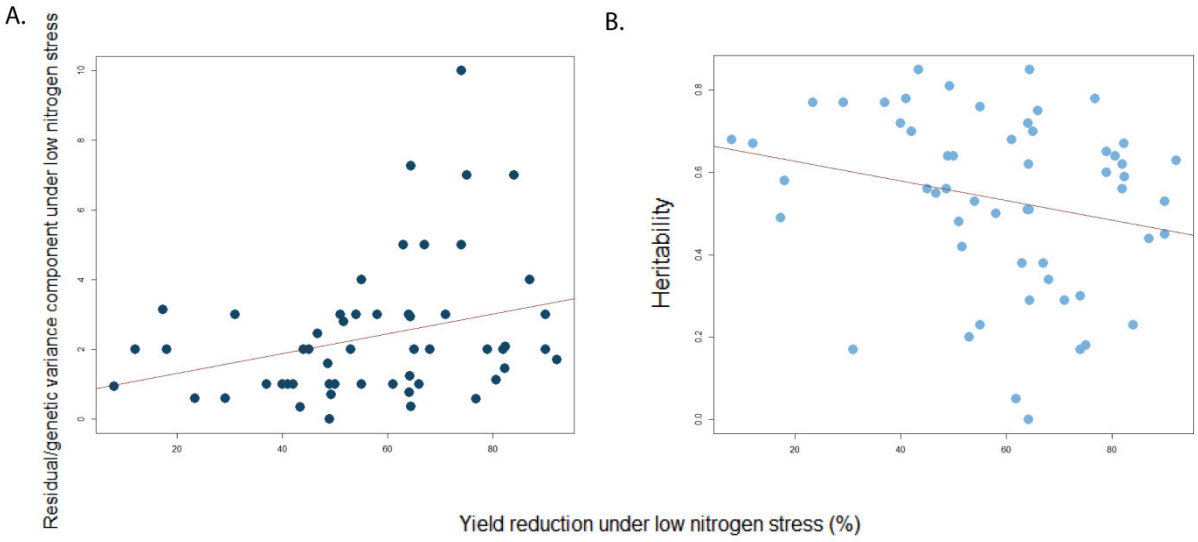

Figure 5. 1. Genetic correlation between grain yield under optimal conditions B. Genetic correlation between heritability and yield reduction under low nitrogen stress.

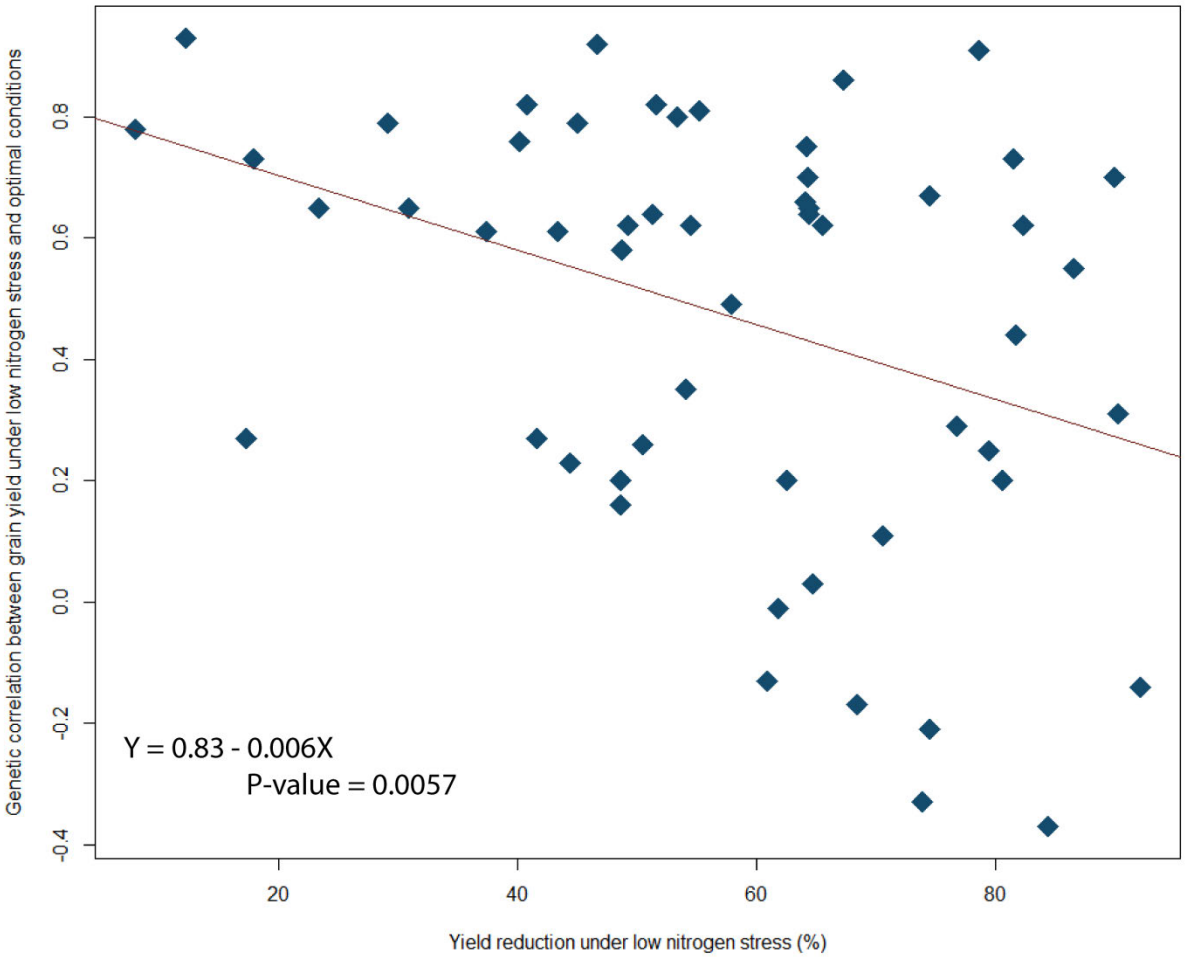

Figure 5. 2. Yield reduction under low nitrogen stress

5.4 DISCUSSION

In this study, as the level of N stress intensity increased the genetic correlation between grain yields under low N and optimal conditions decreased, indicating that the efficiency of indirect selection under optimal conditions for grain yield under low N stress also decreased. This result was concurring with the findings of Bänziger et al., (1997) and Presterl et al., (2003). The obtained results confirmed that rapid genetic gains will be achieved through direct selection under low N rather than through indirect selection under optimal N conditions. The sites of higher yield potential (e.g. Kakamega and Harare), trials yielded between 3-4 Mg ha^{-1} could still have a yield reduction greater than 60% and could be used as low N stress sites as opposed to the established classification of 3$Mgha^{-1}$.

The commercial varieties used in this study were selected to represent genetic diversity in ESA and provide a baseline for low N stress breeding in the region. Varietal replacement in ESA is very slow (Abate et al., 2017; Atlin et al., 2017; Chivasa et al., 2022) and varieties are still widely grown in this region. Several varieties had very low yields under low N stress, particularly within the intermediate to late group (CKPH08043, ECAVL1, Embu Synthetic, H614D and KH631Q all yielded less than 2 $Mgha^{-1}$). However, despite initially limited screening capacity for low N stress tolerance in the public and private sector in ESA, large variability for grain yield under low N stress was observed. This suggested that there were spill-over effects resulting in indirect selection for low N tolerance. Several early and intermediate to late hybrids and OPV varieties yielded over 3 $Mgha^{-1}$ under severe N stress. In the early maturity group, two hybrids (CZH0928 and PHB3253) and one OPV (O9ADVE-F2) yielded over 1 $Mgha^{-1}$ more under severe N stress than the widely grown hybrid SC407 (sold in Kenya as Duma 41). In the intermediate to late maturity group, CZH0616, PHB30D79, WH507 and ECA-VL45-# yielded more than 3 $Mgha^{-1}$ under severe N stress.

These results likely reflected the successes in breeding for drought tolerance. The highest yielding intermediate to late maturity variety, CZH0616, was selected for drought tolerance (Setimela et al., 2017a and b). Similarly, CZH0928 (early maturity variety) and Pris061 (intermediate to late maturity variety) were also developed primarily for drought tolerance. Tolerance to mid-season drought stress is closely related to tolerance to low N stress (Bänziger et al., 1999). Selection for mid-season drought tolerance was associated with changes in the establishment of reproductive structures related to low N stress tolerance (Bänziger et al., 2002). Consequently, selection for drought tolerance tends to result in improved tolerance to low N stress. However genetic gain for low N stress is lower when selection is indirect (Masuka et al., 2017a).

The current study suggested that the use of OPVs in low yield environments could be more beneficial than hybrids because the OPVs yielded more than commercial hybrids. For example, within the early maturity group, O9ADVE-F2 yielded significantly more than two commercial hybrids (SC407 and SC513. O9ADVE-F2 had previously been identified as the highest yielding OPV in regional (stage 4) trials within the medium maturity group for maize mega-environments A and C (Magorokosho et al., 2011). In subsequent on-farm trials, under farmer management, O9ADVE-F2 yielded more than the commercial hybrid SC513 (Setimela et al., 2012). Intermediate to late maturity OPVs, i.e., ECA-VL45-# and ECA-VL43-#, yielded significantly more than four commercial hybrids (Pan67, KSTP64, H614D and KH631Q). This wa9s in direct contrast to studies of experimental hybrids and OPVs which showed that hybrids yield significantly more than OPVs under low N stress (Masuka et al., 2017a and b) However, the commercial hybrids in this study were released up to 30 years ago (H614D was released in 1986 and SC513 in 1999). Thus, in regions of ESA where only obsolete hybrid varieties are available to smallholder farmers, OPVs may offer an important

option for increased food security (Masuka et al., 2017b). Because no hybrid from the private sector out-yielded O9ADVE-F2 under low-N, it is likely to be a cost-effective varietal choice for farmers in ESA managing under low-N conditions (Pixley and Bänziger, 2004). The outstanding performance of the OPV and the low varietal turnover in ESA suggested that more effort should be devoted to developing OPVs for low-N management.

Kostandini et al., (2015) estimated that an increase in yield of 16% under very low N fertiliser application rates (0-29 kg N ha^{-1}) has the potential to deliver a total of US$586 million in gross benefits with US$136 million and US$100 million of benefits to maize producers in Kenya and South Africa respectively within nine years. The results from the present study suggested that breeding for low N stress tolerant maize could have substantial impact in ESA. For example, SC513 (sold as SC Punda Mulia 55 in Kenya) is one of the most widely grown varieties by smallholder farmers in ESA. Under optimal conditions, there was no significant difference in yield between SC513 and all other hybrids and OPVs, except for CKIR07012 (a hybrid which yielded significantly more than SC513). However, under low N stress conditions faced by most smallholders in SSA, SC513 yielded nearly 0.8 tonnes ha^{-1} less than the highest-yielding OPV and hybrid. Replacing this obsolete variety with the OPV 09SADVE-F2 or the hybrid CZ0928 could increase yields for smallholders as much as 30% under low-N conditions.

Given the prevalence of low N stress in ESA and the low genetic correlation between yield under optimal and low N stress, yield under low N stress should be included as a criterion for varietal registration.

5.5 CONCLUSIONS

Low nitrogen stress screening needs to be incorporated into the maize breeding pipelines. There may be need to establish a collaborative screening network since the available screening facilities are limited to a few breeding programs yet progress in breeding is more rapid when screening is done directly. The production of OPVs may be an important strategy as some OPVs had higher grain yield under low nitrogen stress than hybrids.

There is need to improve varietal turnover in sub–Saharan Africa to capitalise on the recent advances from the breeding programs. There is wide genetic variability for low nitrogen stress tolerance among the different varieties hence increasing varietal turnover may result in higher grain yield under smallholder farmers. The continuous use of varieties which were selected in past climates and are no longer suitable for the current conditions negates the genetic gains being achieved by the different breeding programs. Low nitrogen stress tolerance needs to be combined with tolerance to combined drought and heat stress because these stresses are occurring simultaneously together under smallholder farmers conditions.

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CHAPTER 6

OVERVIEW OF THE RESEARCH FINDINGS, CONCLUSIONS AND RECOMMENDATIONS

6.1 Introduction, Research Objectives and hypotheses

This chapter aims to make an overview of the study by summarising the key objectives and findings of the study. The chapter highlights the implications of the findings to the maize breeding programs in Zimbabwe with a view to counteract the adverse effects which may arise due to climate change.

The specific objectives of this study and the hypotheses which were tested were to:

i. Identify local and exotic maize inbred lines with combined drought and heat stress adaptation attributes.

ii. Depict agronomic traits that can be used to indirectly select for high grain yield performance under combined drought and heat stress conditions in maize.

   It was hypothesised that there is wide genetic variability for tolerance to combined drought and heat stress among various maize inbreds being used for hybrid production in the CIMMYT maize program in Southern Africa and the national breeding program of Zimbabwe.

iii. Identify pre-release maize hybrids developed within the CIMMYT maize breeding program with combined drought and heat stress adaptation attributes.

iv. Identify agronomic traits that can be used to indirectly select for grain yield performance for maize hybrids under combined drought and heat stress conditions.

   It was hypothesised that high yielding experimental hybrids and morpho-physiological traits can be identified to use for indirect selection under combined drought and heat stress from experimental hybrids.

v. Assess the genetic variability for grain yield performance under low nitrogen conditions among pre-commercial and commercial maize hybrids. It was hypothesised that better

understanding of the variability that exists in maize for yield performance under low nitrogen conditions could guide objective setting of maize breeding programs which will lead to rapid genetic gains under low nitrogen stress conditions in the region.

6.2 Overview of the research findings

1. Inbred lines with tolerance to combined drought and heat stress were identified in addition to the ones identified in an earlier study, i.e., La Posta Sequia C7-F64-2-6-2-3 and DTPYC9-f46-1-2-1-2.
2. The maize inbred line K64R from the Crop Breeding Institute was among the inbred lines identified with combined drought and heat stress tolerance.
3. Two potential donors for adaptive traits to combined drought and heat stress tolerance were identified and these were Entries 7 ((CML444-B/LaPostaSeqC7-F180-1-2-2-1-BBB)-B-217-1-2-BBB) and entry 14 ([[INTA-2-1-3/INTA-155-2-2]-X-3-2-B-11-B-5-B/EliteBulkA]-B(bal)-9-1-1-1-B*4) which showed adaptive traits like low senescence scores but were poor yielding. These maize inbred lines could be used in gene stacking to come up with tolerant inbred lines.
4. The new experimental hybrids should be advanced in the program and deployed as combined drought and heat stress tolerant varieties that can be used to mitigate the impacts of climate change on smallholder agricultural productivity.
5. The identified secondary traits will help in the identification of ideotypes associated with grain yield under combined drought and heat stress. This will reduce the phenotyping costs and help speed up the breeding process.
6. To broaden the genetic breeding base, twelve new maize inbred lines were identified as being tolerant to combined drought and heat stress. These maize inbred lines will add to the list of inbred lines that were identified in an earlier study (Cairns et al., 2013). The maize inbred line (K64R) from CBI exhibited tolerance to combined drought and heat stress. This maize inbred line was developed a long time ago and this may imply that tolerance genes are scattered in

the maize germplasm and need to be identified and incorporated in the current genotypes to counteract the impacts of climate change.

7. This study revealed that there is wide genetic variability among the inbred lines and breeding for combined drought and heat stress can be achieved using new and old, maize inbred lines after careful evaluation under the intended stress. It is possible to breed hybrids with tolerance to combined drought and heat stress as well as high yield. Hybrids with combined drought and heat stress tolerance need to be quickly developed and deployed for use by small-holder farmers to alleviate the impacts of climate change and achieve the strategic development goal number one.
8. The study re-affirmed that selection for Low nitrogen stress must be done directly under low Nitrogen and hence the need to incorporate Low Nitrogen screening in the breeding pipelines in ESA.

6.3 General conclusions

1. There is wide variability among the maize inbred lines from the Crop Breeding Institute of the Government of Zimbabwe and the CIMMYT maize breeding program. The variability can be utilised to breed hybrids with tolerance to combined drought and heat stress. The hypothesis was accepted.
2. The commercial hybrids are susceptible to combined drought and heat stress and need to be replaced. The hypothesis was accepted because the experimental hybrids outperformed the current commercial hybrids.
3. High yielding experimental hybrids and CIMMYT pre-releases were identified. The identified hybrids should be used in the development of new hybrids with tolerance to combined drought and heat stress. The hypothesis was accepted.
4. Some key traits were identified that can be used for the identification of ideotypes under combined drought and heat stress. The hypothesis was accepted.

5. Selection of hybrids to combat low soil fertility status in most smallholder farmers' fields should be done under low nitrogen stress to speed up genetic gains for nitrogen use efficiency.

6.4 General recommendations

1. There were budgetary constraints such that the experiments could not be repeated during the main season to test performance and disease tolerance. The dry period usually has low disease pressure and hence the hybrids maybe susceptible to important diseases like Gray leaf spot (*Cercospora zeae- maydis*) and Turcicum leaf blight *(Exserohilum turcicum)*.
2. The trials may need to be repeated in several locations to test for stability of the hybrids. This would lead to region specific recommendations on the best varieties to grow under the current climatic conditions.
3. The identified lines tolerant to combined drought and heat stress need to be incorporated in the breeding pipelines to speed up the production of hybrids tolerant to combined drought and heat stress.
4. The formation of inbred lines targeted for the development of combined drought and heat stress should be done under combined drought and heat stress to take advantage of the DNA modifications through methylation which occurs under stress. These modifications are heritable.
5. There is need to encourage increased fertiliser use to reduce yield gaps among smallholder farmers. Increased fertiliser to mitigate low inherent soil fertility could be a cheaper means of increasing productivity than irrigation infrastructure development. However, there is need to increase training on the appropriate use of synthetic fertilisers and manures to abate the release of nitrous oxides into the atmosphere.
6. Advanced breeding techniques need to be incorporated into the breeding schemes to aid the development of varieties with multiple stress tolerance. Transgenic breeding techniques have succeeded in the development of drought and insect resistant maize varieties which have been

beneficial to the farmers and the environment. The combination of epigenetics, genome editing and various omics will result in the development of stress resilient varieties that are more suited to the current and future climates. However, field experiments under the desired stress conditions will continue to play an important role to enable the synthesis of proteins and metabolites which can be analysed using the various omics and for the identification of traits which can be used for the identification of the ideotypes.