

**Combining ability of maize inbred lines for productivity, agronomics, and
nutritional content under different nitrogen fertilizer regimes**

By

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GENERAL ABSTRACT

Maize is a staple crop in sub-Saharan Africa with an average per capita consumption of 100 kg per annum. Despite its importance, maize is rich in starch but deficient in other nutrients leading to malnutrition in many people that heavily depend on maize without other nutrient-rich complementary sources of food. The objectives of this study were to (i) assess genetic variation for agronomic traits, yield and nutritional content among maize inbred lines and hybrids under high and low soil nitrogen availability (ii) determine the combining ability of maize inbred lines and their crosses for agronomic traits, grain yield, and nutritional content, and (iii) deduce the gene action controlling the inheritance of these traits under low and high input conditions. Ten maize inbred lines consisting of five quality protein maize (QPM) and five normal-endosperm maize (non-QPM) inbred lines were crossed using the Griffing's diallel mating design. The resultant hybrids, their parental lines and three control varieties were evaluated under low and high soil nitrogen treatments across two seasons at two locations in South Africa. The hybrids and their inbred line parents exhibited significant genetic variation for plant height, ear height, anthesis days, silking days, anthesis to silking interval, grain moisture, shelling percentage, grain yield, protein, oil and starch content. There were significant genotype x environment interaction effects on grain yield, shelling percentage, grain moisture and anthesis to silking interval. On average, yield and agronomic performances were lower in QPM hybrids under low nitrogen conditions confirming their less adaptation to the low input conditions compared to their normal maize endosperm counterparts. The protein, oil and starch contents of maize decreased under low nitrogen conditions. Both the general (GCA) and specific (SCA) combining ability effects for grain yield, protein and oil contents were significant across nitrogen management conditions. The significance of GCA and SCA effects suggested that both additive and non-additive gene action were involved in the inheritance of grain yield, agronomic traits, protein, and oil content.

DECLARATION

I, **Letlhogonolo Lucky Molefe** declare that:

1. The research reported in this thesis, except where otherwise indicated, is my original research.
2. This thesis has not been submitted for any degree or examination at any other University.
3. This thesis does not contain other persons' data, pictures, graphs, or other information, unless specifically acknowledged as being sourced from other persons.
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Signed 

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DEDICATION

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Chapter 1: General Introduction

1.1 Introduction

This chapter introduces maize as an important crop in the world. The chapter provides a background to the study and outlines the production constraints affecting maize production and factors impacting its nutritional content. Subsequently, the chapter states the justification, research objectives, hypotheses, and questions of the study. Finally, the outline and structure of the thesis is provided in this chapter.

1.2 Background

Maize is an important crop in the world and is vital for food security especially in developing countries. About 4.5 billion people around the world depend on maize for daily calorific intake (Erenstein *et al.*, 2022). However, maize is rich in starch but contains very low amounts of other macronutrients and micro-nutrients that contribute to nutrient deficiency in many people that depend on it as a staple food without access to nutrient rich complementary foods. At least 80% of maize production in Africa is carried out under smallholder farms where the average yield is $<1 \text{ t ha}^{-1}$ compared to a potential of $>5 \text{ t ha}^{-1}$ (Nyoni *et al.*, 2023) due to biotic and abiotic stress factors. Low soil fertility and high frequency of drought are among the most important constraints of maize production factors (Worku *et al.*, 2020; McMillen *et al.*, 2022).

Due to continuous maize production on the same fields, soil fertility declines rapidly as soil nutrients are not adequately replenished. Most smallholder farmers in developing countries cannot afford fertilizers and generally apply below optimal rates of fertilizer leading to poor grain yields (Bojtor *et al.*, 2022). Maize is very sensitive to nitrogen deficiency and consistently produces lower than its potential yield when nitrogen stress occurs during vegetative growth

and reproductive stages. Another major challenge affecting maize production in sub-Saharan Africa is drought. Erratic and below average annual rainfall contribute to significant yield loss leading to poor yield. There is a need to develop maize hybrids that are drought and low nitrogen stress tolerant to improve maize productivity in marginal environments. In addition, the poor nutritional value of maize requires active efforts to develop nutrient-dense varieties to avert malnutrition among many people.

Developing suitable cultivars requires the availability of exploitable genetic variation for grain yield, agronomic traits, and nutritional content (Nyoni *et al.*, 2023). Assessing the available genetic variation is a pre-breeding step conducted to evaluate the relative usefulness of germplasm before designing breeding programs. Assessing genetic variation includes genotype evaluation to identify superior genotypes for use in generating breeding populations. Subsequently, the identified genotypes must be evaluated to determine their ability to pass desirable characteristics to the offspring. This is a phenomenon known as combining ability (Kamal *et al.*, 2023). It allows the breeder to deduce whether the parental lines are good at passing their traits to offspring, helps to identify suitable crosses for developing breeding populations and facilitates the deduction of genetic control of traits. Knowledge of combining ability, genetic control and trait heritability is important to devise suitable breeding strategies to achieve maximum genetic gain. In addition, it is critical to understand genotype by environment interaction as it affects trait expression, complicates the selections and results in differential performance of genotypes over several environments (Alizadeh *et al.*, 2022).

1.3 Problem statement

Maize is an important crop in sub-Saharan Africa but low average yields in this region and its poor nutritional quality hinder its potential use. Under smallholder farming systems in sub-Saharan Africa, maize productivity is a fraction of yields attained in the temperate regions. The main factors affecting maize productivity is poor soil fertility, drought, and a lack of improved maize varieties (Yokamo, 2020; Spurk *et al.*, 2023). Maize is characterized by high starch content but relatively poor values for other macronutrients and micronutrients. The protein, oil and zinc contents of maize are very low, and they contribute to malnutrition in people that rely on maize as a staple food without access to complementary sources of nutrients. The need to develop maize varieties that have high yield potential, low nitrogen and drought stress tolerance and high nutritional content is urgent. Developing new varieties requires availability of genetic variation for grain yield and nutrients, understanding combining ability and genetic control of traits and knowledge of genotype x environment interaction. Currently, there is a lack of genetic variation for nutritional content especially quality protein. Genetic variation can be created through recombination provided that the parental lines have good combining ability. Therefore, this study seeks to develop new breeding populations with high yield potential, high nutritional quality and tolerance to low nitrogen and drought stress.

1.4 Justification

Maize is an important crop in Africa. As part of a staple diet, it is important to improve its nutritional content to reduce malnutrition and supply adequate dietary requirements. Crop improvement entails exploiting genetic variation through recombination of alleles. For maize, which depends on hybridization, genetic variation is created through crossing divergent inbred lines. Therefore, understanding combining ability of lines is important for developing suitable

breeding populations and devising appropriate breeding strategies. The study will contribute to efforts to improve maize productivity especially in marginal environments and in the face of climate change and declining soil fertility. It will contribute to food and nutrition security in developing countries that are heavily reliant on maize for food intake.

1.5 Research Objectives

The aim of this study is to develop breeding populations with high yield potential and high nutritional content for production in marginal conditions of low soil nitrogen.

1.6 Specific Objectives:

The specific objectives of this study are:

1. To evaluate genetic variation in maize inbred lines and their hybrids to select suitable parents for line maintenance and hybrids for breeding population development.
2. To determine the combining ability of maize inbred lines and their hybrid crosses for developing best breeding populations to improve yield, agronomic traits, and oil, starch, and protein quality.
3. To determine the gene action controlling yield, agronomic traits, and protein quality in maize inbred lines and their hybrid crosses.
4. To determine the effects of nitrogen on yield and agronomic performance of maize inbred lines and their hybrid crosses in different locations.

1.7 Research Hypothesis

1. There is genetic variation between inbred lines and their hybrid combinations.

2. The combining ability of maize inbred lines and their crosses is high for grain yield, and agronomic traits and protein content and varies under different soil nitrogen conditions.
3. The inheritance of grain yield, agronomic traits and protein quality in maize inbred lines and their hybrid crosses is controlled by additive genetic effects.
4. Soil nitrogen levels influence grain yield productivity, agronomic performance, and nutritional quality of maize.

1.8 Research Questions

1. Is there adequate genetic variation among the inbred lines and their hybrid combinations for developing improved maize varieties?
2. Does the combining ability of maize inbred lines and their hybrid combinations vary significantly to identify superior parents and breeding populations?
3. Are yield, agronomic traits and protein quality in maize inbred lines and their hybrid crosses controlled by genetic effects relevant to devise breeding strategies for maize improvement?
4. Is there significant genotype by environment interaction effects in maize inbred lines and their hybrid combinations evaluated under low soil nitrogen stress conditions?

1.9 Dissertation structure

Table 1.1 The structure of the dissertation showing the chapter titles and their summary.

Chapter	Title	Description

Chapter 1	General introduction	The chapter introduces the study providing the background, objectives, justification, and research hypotheses.
Chapter 2	Literature review	The literature review provides a context of the study in relation to what is already reported by other researchers and identifies the research gap for the current study.
Chapter 3	Materials and Methods	This chapter details all the plant material used and environments for the experiments, outlines the experimental details for planting, data collection and data analysis.
Chapter 4	Results	The main results obtained from the experiments are summarized in this chapter.
Chapter 5	Discussion of results	The chapter discusses main trends of the results and provides explanations for the observations, contextualizes the observations against literature and provides implications for breeding using the test genotypes.
Chapter 6	Conclusions and Recommendations	The chapter consolidates the findings and conclusions drawn from the study. It also provides recommendations for further studies.

Chapter 2: LITERATURE REVIEW

2.1 Introduction

This chapter introduces maize as an important cereal crop for food in Africa, and the factors affecting its production and nutritional content are discussed. The current literature on breeding

for quality protein maize and improved agronomic performance was reviewed. Finally, the review identifies the research gap as the need to develop suitable maize varieties and contextualizes the study against available knowledge.

2.2 Importance of maize

Maize (*Zea mays*, L.) is ranked among the most important cereal crops in the world alongside rice and wheat. These three crops account for 94% of global cereal consumption (Erenstein *et al.*, 2022). Maize contributes more than 70-98% of energy requirements in southern African countries (Amanjyoti *et al.*, 2024). It is used as human food, animal feed and as biofuel. In sub-Saharan Africa, 77% of maize produced is used as food and 12% for animal feed (Erenstein *et al.*, 2022). For human consumption, it provides daily calorific requirements for many people across the world (Goredema-Matongera *et al.*, 2021). The global consumption of maize is estimated at about 116 million metric tons, with Africa accounting for more than 30% of the consumption (Erenstein *et al.*, 2022). Maize per capita consumption in South Africa is estimated at 100 kg per year compared to the global average of 175 kg (Erenstein *et al.*, 2022). Maize contains about 70 % starch, which is higher than the starch content in rice and wheat (Erenstein *et al.*, 2022). However, maize contains very little protein, essential amino acids (2% lysine) and micronutrients such as iron and zinc (Prasanna *et al.*, 2020). The low nutritional content of maize contributes to malnutrition in people that heavily depend on the crop for food but with less access to complementary food sources of other nutrients.

Maize is an integral component of the cropping systems in sub-Sahara Africa. It is grown across wide agroecological conditions by both subsistence and commercial farmers in low and intensive input cropping systems. Though maize is a tropical plant by origin, it is grown from temperate, subtropical to tropical regions. The grain yield varies widely over these regions

with temperate regions having relatively higher average yield compared to the tropical regions. The differences in yield potential are due to variation in climatic conditions and agronomic practices and access to input resources (Erenstein *et al.*, 2022) in addition to genetic potential of the hybrids.

2.3 Maize production

The global production of maize is estimated at over one billion metric tonnes annually and Africa accounts for only 6.5% (Erenstein *et al.*, 2022). The area under maize production in Africa is estimated at 117 million hectares with a total output of 1137 million tonnes (FAO, 2021)., the majority of which are under small farm holdings (Kumar *et al.*, 2022). Half of the maize harvested in the world is produced by nine countries namely Argentina, Brazil, China, India, Mexico, Romania, South Africa, Ukraine, and United states (FAO, 2021).

Table 2.1 Annual maize production in the top producing countries in 2023/24

Country	Million tons
United States of America	31.54
China	23.37

Brazil	10.28
European union	4.86
Argentina	4.45
India	2.83
Ukraine	2.47
Mexico	2.06
South Africa	1.36
Canada	1.22
Indonesia	1.04

2.4. Production constraints

Given the wide environmental conditions in which maize is grown, several constraints are encountered during production. Poor soil fertility, drought stress, pests and diseases and a lack of improved varieties are among the major constraints of maize productivity in sub-Saharan.

Africa.

2.4.1 Declining Soil Fertility

Declining soil fertility is a major problem to sustainable maize production in SSA (Mutuku *et al.*, 2020). Low soil fertility is partly caused by depletion of soil nutrients without adequate replenishment and inherently nutrient deficient soil formed from igneous and quartz parent rocks (Karki *et al.*, 2021). Nitrogen deficiency is the common problem in poor soils leading to low maize productivity (Lu *et al.*, 2021). Nitrogen is required for plant growth and development and is a major component of chlorophyll pigments required for photosynthesis and forms an

integral part of cell walls, genetic material, root growth and reproductive development (Plett *et al.*, 2020). Many leaf cell components, particularly those associated with the photosynthetic apparatus, including carboxylation enzymes and proteins of cell membranes constitute nitrogen in one form or another (Kaur *et al.*, 2023). Its deficiency leads to young plants that are pale, light green or yellow and underdeveloped. During flowering, nitrogen deficiency leads to kernel abortion, and poor grain filling. The most used strategy to address nitrogen deficiency is the application of inorganic fertilizer. However, there are concerns on the environmental sustainability of nitrogenous fertilizer application. Excessive and inappropriate use of fertilizers in agriculture causes soil acidification and environmental pollution (Zhang *et al.*, 2022).

Also, fertilizer prices are too high for most farmers to apply optimal rates to replenish soil nutrient stocks. Another problem related to fertilizer use in crop production is that it is not readily available in developing countries and among small holder farmers. Consequently, fertilizer application rates in Africa are lower than other countries around the world (BonillaCedrez *et al.*, 2021). Fertilizer application in Africa is only about 10 kg/ha compared to an average of 100 kg/ha applied by farmers in Asia (Gezahegn, 2021). The application rates in Africa are far less than required by plants and to replenish nutrient stocks lost due to leaching or plant absorption. The average minimum required amount of nitrogen to replenish soil nutrients is around 50 kg/ha, which is higher than the average nitrogen applied by farmers in Africa (Chen *et al.*, 2023).

2.4.2 Lack of improved cultivars

Maize is an integral component of cropping systems and human diets in Africa. Improved cultivars are required to provide energy requirements and supplement micronutrients for human

consumption. On the other hand, improved cultivars are required to grow in marginal environments with limited soil nutrients and moisture supply. Most maize cultivars have poor protein content. One nutrient lacking in maize is the tryptophan required in human diet (Goredema-Matongera *et al.*, 2021). There have been efforts to develop quality protein maize (QPM) cultivars to address malnutrition problems. There are very few QPM cultivars currently. A QPM variety is a variety that has tryptophan to protein ratio higher than 0.8% and lysine level of about 4% (Maqbool *et al.*, 2021). QPM varieties development started in the 1960's but success has been relatively low. Quality protein maize (QPM) varieties have been released in about 34 countries around the world. However, the QPM varieties have not been widely adopted due to challenges with adaptation and seed availability in many of the countries. In addition, QPM varieties have been reported to have low seed and grain yield, which are major constraints to their adoption. It is imperative to develop QPM varieties that are high yielding and tolerant to biotic and abiotic stresses. Developing QPM varieties with appropriate agronomic performance will contribute to increased adoption among farmers.

2.5 Breeding Progress in QPM under nitrogen stress tolerance

There are several efforts to develop maize with high lysine and tryptophan and high yield potential. Breeding for QPM began in the early 1970s at International Maize and Wheat Improvement Center (CIMMYT) where researchers developed *Opaque-2* populations (Prasanna *et al.*, 2020). Successful development of QPM varieties with high yield potential depends on the availability of adequate genetic variation to conduct effective selection. The CIMMYT holds a large gene bank of maize and could provide some genetic variation for nutritional content to exploit. The gene bank potentially holds important genes to improve the locally adapted germplasm that lacks in nutritional quality. In South Africa, the Agricultural

Research Council-Small Grain Institute (ARC-SGI) maintains the national gene bank of maize and is at the forefront of breeding efforts to improve maize nutritional value. Genetic variation in nutritional content is not widely reported in maize (Tanumihardjo *et al.*, 2020). This will provide challenges for breeding efforts to improve the nutritional content of maize. On the other hand, genetic variation for drought and low nitrogen stress tolerance has been reported widely in maize (Hammad *et al.*, 2020). The genetic variation can be exploited to develop new and improved varieties of maize. They could be combined with QPM maize to develop varieties that combine high yield potential with good agronomic performance and high nutritional content.

Breeding for high nutritional content, drought tolerance and low nitrogen tolerance is complicated by several factors that include the genetic architecture of these traits, environmental influence, trait correlations, and accuracy of measuring the phenotypic expression (Rosero *et al.*, 2020). Nutritional content is affected by environmental factors that can confound selection. Yadav *et al.* (2020) reported that protein quality and content of QPM was not stable across environments, which complicated selection and identification of superior genotypes. It has also been reported that the *Opaque2* gene in QPM is recessive and can be lost easily when outcrossed to non-QPM maize, which means that only QPM x non-QPM breeding populations were not largely viable (Maqbool *et al.*, 2021). Also, the soft endosperm associated with the *Opaque2* gene caused 25% yield loss during conversion to normal maize (Maqbool *et al.*, 2021).

Nitrogen stress tolerance in maize is also controlled quantitatively, making it difficult to identify and select superior genotypes (Anas *et al.*, 2020). Low genetic variation for tolerance to low nitrogen availability also hinders breeding efforts. As expected with quantitatively controlled traits, nitrogen stress tolerance exhibits crossover ranking across multiple environments in response to environmental effects. One of the main challenges is to simulate

all soil chemical, biological and physical processes that influence nitrogen availability in the field during experiments for phenotyping genotype response to low nitrogen stress in controlled environments (Ghodsi *et al.*, 2020). Evaluating genotypes directly in fields with naturally low nitrogen is often used but the genotype performance is affected by spatial variation in nutrient availability across the whole field leading to inaccurate phenotyping. Selecting for low nitrogen tolerance is further complicated by correlations among the agronomic traits that are associated with tolerance to low nitrogen availability. Some traits are unfavorably correlated, which means that they cannot be selected and improved simultaneously. Finally, measuring traits such as root depth, root length, root architecture and nitrogen uptake is difficult and contribute to a low number of studies, breeding efforts and progress on low nitrogen tolerance (Keimeso and Abakemal, 2020). The quantitative nature of QPM, drought tolerance and low N tolerance has hindered progress in developing QPM maize that incorporates other important traits such as high yield, suitable agronomic performance and drought and low nitrogen stress tolerance.

2.6 Combining ability in maize

Genetic gain can be achieved depending on combining ability of parental lines and their hybrid combinations. The concept of combining ability measures the ability of a parental lines to pass heritable traits to the offspring (Akroun *et al.*, 2021). Combining ability is described as the ability of a genotype to pass desirable characteristics or superior performance to its progenies (Keerthana *et al.*, 2023). Analyzing combining ability of parental lines allows for the identification of the best parents to select for developing breeding populations or hybrids (Rahmani *et al.*, 2023). In addition, it also allows the deduction of heritability estimates and gene action controlling traits, which is required for designing suitable breeding strategies for high genetic gain (Nisarga *et al.*, 2021).

Combining ability is categorized into general combining ability (GCA) effects of parental lines and the specific combining ability (SCA) effects of the hybrid combinations. The GCA of a parental line is its average performance in several hybrid combinations, while the SCA of a hybrid combination is the deviation of its performance from its predicted performance based on the GCA of the parents involved in the hybrid (Synrem *et al.*, 2022). Specific combining ability is used to designate those instances in which certain hybrid combinations do relatively better or worse than would be expected based on the average performance of the parents (Mogesse *et al.*, 2020). The GCA and SCA effects are related to additive and non-additive gene action, respectively (El-Azeem *et al.*, 2021). Parents with favorable GCA effects would be selected for pure line maintenance while hybrids with good SCA effects are useful for developing breeding populations and genetic advancement. There are several genetic designs including diallel mating that can be used to determine combining ability of maize. The choice of the mating design depends on the objectives of the breeding program (Williams-Alanís *et al.*, 2022).

2.7 Combining ability in maize under low and high nitrogen condition.

Combining ability in maize can be affected by management conditions under which the maize is grown. Conditions that promote expression of genetic potential of a genotype are likely to improve its combining ability with other genotypes. Nitrogen management is an important part of production in sub-Saharan Africa due to the inherent deficiency and depletion of nitrogen in the soil. Luz *et al.*, (2024) reported that nitrogen application had significant impact on the expression of all traits in maize. Nitrogen stress decreased yield by about 33% while combining ability x nitrogen input interaction effects for grain yield and anthesis days under low nitrogen were found to be significant (Luz *et al.*, 2024). The general and specific combining ability

effects were stronger under high nitrogen application conditions compared to low nitrogen conditions. Line x tester analysis revealed that GCA effects, primarily from lines, predominantly influenced grain yield and other traits across both nitrogen conditions, except for ear height and plant aspect under low nitrogen, where SCA effects also had significant impact (Aboderin *et al.*, 2024). It has been reported that additive gene effects, which is due to the general combining ability of parents, is more pronounced under high nitrogen content and affects traits such as grain yield, plant height and flowering dates (Noelle *et al.*, 2017). In contrast, specific combining ability effects were found to be more important for grain yield under low nitrogen conditions. There are also reports of significant interaction between GCA and SCA effects in influencing grain yield production under low nitrogen conditions (Luiz *et al.*, 2024). These assertions as elaborated in literature have implications for breeding strategies. Hybrids that exhibit low SCA for grain yield and other agronomic traits under low nitrogen conditions could be used in recycling to create synthetic populations (Luiz *et al.*, 2024) because such hybrids would have less values when deployed as commercial products.

2.8 Diallel crosses in maize.

The diallel crossing design is one of the methods used in determining combining ability in maize breeding programs. The main objectives of using diallel designs are to identify best parental lines, estimate the genetic components and understanding the environment x genotype interaction and deduce the gene effects controlling trait inheritance (Akinyosoye, 2022). The design is based on crossing the available parental lines in all possible combinations. There are different types of diallel designs grouped into complete and incomplete diallel crossing. A complete diallel design is when all possible crosses are generated and can be evaluated with or without the reciprocal crosses or parents in a trial (El-Azeem *et al.*, 2021). In contrast, a half

diallel or incomplete diallel is when half the set of crosses are generated to exclude reciprocal crosses (Onejeme *et al.*, 2020). These can then be evaluated with or without the self-pollinated parental lines.

The methods also vary in their applications and underlying assumptions (Sprague and Tatum, 1942). The Griffing Method 1 proposes to include parents, F1 hybrids and the reciprocal crosses in the analysis and can be used to estimate the GCA, SCA and the reciprocal effects. The second method, Griffing Method 2, uses parents and F1 hybrids without the reciprocals. This is used to determine GCA and SCA effects but cannot be used to deduce reciprocal effects. Griffing Method 3 analyses the GCA, SCA and reciprocal effects based on the F1 hybrids and their reciprocals without the parents. Finally, Griffing Method 4 simplifies the calculation of GCA and SCA based on the F1 hybrids only excluding the parents and reciprocal crosses.

2.9 Summary

Maize is an important crop in the world and especially in sub-Saharan Africa where it is a major component of the human diet. It accounts for a large proportion of daily energy requirements despite its limitations in other nutrients especially proteins and essential oils. In addition, the yield productivity of maize in Africa is generally lower than its potential yield or the global average. Several factors contribute to these challenges. Firstly, maize is inherently poor in nutritional quality and has very narrow genetic variation for nutritional content. Secondly, low soil fertility and moisture are major abiotic factors that limit maize productivity. It is recognized that breeding for nutrient dense, drought tolerant and nitrogen use efficient maize varieties could alleviate these challenges in Africa. However, low genetic variation, the quantitative genetic architecture of these traits and huge environmental effects limit progress in breeding for such superior genotypes. Developing superior hybrids depends on the available genetic

variation for recombination, understanding of combining ability and trait heritability to design appropriate breeding strategies. Therefore, an undertaking to evaluate genetic variation for QPM, response to nitrogen availability and agronomic performance is necessary to deduce combining ability, identify superior parental lines and breeding populations as a step towards developing superior maize hybrids for Africa.

Chapter 3: MATERIALS AND METHODS

3.1 Introduction

This chapter outlines the materials, methods, and design of the experiments in pursuing the objectives of this study. The plant materials, experimental sites, data collection and analysis procedures are outlined. The experiments were adequate to answer the research questions.

3.2 Plant materials and mating design

Ten tropical maize inbred lines described in Table 3.1 were used in this study. Six maize inbred lines were obtained from the International Maize and Wheat Improvement Centre (CIMMYT). Five of the lines obtained from CIMMYT were quality protein maize (QPM) inbred lines. The other four were normal endosperm maize inbred lines obtained from the Agricultural Research Council (ARC) of South Africa. The six CIMMYT inbred lines, CML144, CML176 and CML550 are white-grain lines of the flint grain texture, while CML181, CML182 and CML511 are white grain with a dent texture. The four inbred lines from the ARC were mainly white and dent grain texture. The inbred lines were coded for convenience of the study.

The ten inbred lines were used in a diallel mating design following the Griffing's (1956) method 2 to generate hybrid crosses at the Makhathini Research Station, in KwaZulu-Natal, in South Africa, during the winter season of 2012. The 90 hybrid crosses derived are shown in Table 3.2.

Table 3.1 Description of the 10 maize inbred lines used in the study.

Line Code	Name	Endosperm type	Texture	Source	Heterotic group
L1	CML144	QPM	White flint	CIMMYT	A
L2	CML176	QPM	White flint	CIMMYT	B
L3	CML181	QPM	White dent	CIMMYT	B
L4	CML182	QPM	White dent	CIMMYT	B
L5	CML511	QPM	White flint	CIMMYT	B
L6	CML550	Normal	White flint	CIMMYT	B
L7	CW14	Normal	White dent	ARC	NA*
L8	DT-SR-W	Normal	White dent	ARC	NA
L9	I-43	Normal	White dent	ARC	I
L10	K64R	Normal	White dent	ARC	K

ARC=Agricultural Research Council of South Africa; CIMMYT= International Maize and Wheat Improvement Centre; QPM=quality protein maize. NA* = Heterotic orientation or group is not known.

Table 3.2 The 10 parental lines (**bold**) and their 90 reciprocal crosses generated in a diallel mating design.

Lines	L1	L2	L3	L4	L5	L6	L7	L8	L9	L10
L1	L1 ×L1	L1×L2	L1×L3	L1×L4	L1×L5	L1×L6	L1×L7	L1×L8	L1×L9	L1×L10
L2	L2×L1	L2 ×L2	L2×L3	L2×L4	L2×L5	L2×L6	L2×L7	L2×L8	L2×L9	L2×L10
L3	L3×L1	L3×L2	L3 ×L3	L3×L4	L3×L5	L3×L6	L3×L7	L3×L8	L3×L9	L3×L10
L4	L4×L1	L4×L2	L4×L3	L4 ×L4	L4×L5	L4×L6	L4×L7	L4×L8	L4×L9	L4×L10
L5	L5×L1	L5×L2	L5×L3	L5×L4	L5 ×L5	L5×L6	L5×L7	L5×L8	L5×L9	L5×L10
L6	L6×L1	L6×L2	L6×L3	L6×L4	L6×L5	L6 ×L6	L6×L7	L6×L8	L6×L9	L6×L10
L7	L7×L1	L7×L2	L7×L3	L7×L4	L7×L5	L7×L6	L7 ×L7	L7×L8	L7×L9	L7×L10
L8	L8×L1	L8×L2	L8×L3	L8×L4	L8×L5	L8×L6	L8×L7	L8 ×L8	L8×L9	L8×L10
L9	L9×L1	L9×L2	L9×L3	L9×L4	L9×L5	L9×L6	L9×L7	L9×L8	L9 ×L9	L9×L10
L10	L10×L1	L10×L2	L10×L3	L10×L4	L10×L5	L10×L6	L10×L7	L10×L8	L10×L9	L10 ×L10

CML114=L1, CML176=L2, CML181=L3, CML182=L4, CML511=L5, CML550=L6, CW14=L7, DT-SR-W=L8, I-43=L9, K64R=L10

3.3 Trial Locations and Management Conditions

The experiments were conducted at Potchefstroom and Cedara research stations, in South Africa. The climate of Potchefstroom is temperate with cold winters and warm summers. Its soils are sandy clay loam and irrigation was applied at 8 mm per day to supplement rainfall, during the flowering stage. Cedara is regarded as subtropical humid region within the Natal mist belt. The soils at Cedara are clay, and no supplemental irrigation was applied. At both locations, low soil nitrogen (N) conditions were created by depleting soil nitrogen for three consecutive seasons by planting oats, wheat, and sorghum consecutively at high population densities and uprooting them before flowering. During the depletion period, single super phosphate (SSP) and potassium chloride (KCL) fertilizers were applied at 25 kg ha⁻¹ to supply the required potassium, chloride, phosphate, calcium, and Sulphur. After depletion, all crop residues were removed, and soil samples were taken for analyses of N and other nutrients. Soil analyses results are presented in Table 3.3. No nitrogenous fertilizer was applied throughout the growing season. Optimum nitrogen availability condition was maintained at both locations by planting oats for three consecutive winter seasons and incorporating the residues into the soil where trials were later planted. Before planting, a basal fertilizer was applied at 150 kg ha⁻¹ of NPK+0.5% Zn (3:2:1) supplying 12.5% N, 8.3% P and 4.2% K and 0.5% Zn. At four weeks after planting, top-dressing was conducted with 150 kg ha⁻¹ of Limestone Ammonium Nitrate (LAN). The combination of location, nitrogen treatments and seasons created a total of eight test environments that are summarized in Table 3.4.

Table 3.3: Soil analysis results at the study locations

Property	Potchefstroom Low N		Potchefstroom High N		Cedara Low N		Cedara High N	
	Top soil	Sub soil	Top soil	Sub soil	Top soil	Sub soil	Top soil	Sub soil
% Sand	53.0		58.0		7.0		9.0	
% Silt	9.0		13.0		22.0		25.0	
% Clay	38.0		29.0		71.0		66.0	
pH (H ₂ O)	6.6	6.6	6.8	7.0	5.7	5.5	5.7	5.3
N-NO ₃ (mgkg ⁻¹)	1.1	0.1	4.0	1.0	1.3	2.1	1.4	2.8
N-NH ₄ (mgkg ⁻¹)	0.5	0.5	0.8	0.6	1.0	1.2	0.7	0.9
P (mgkg ⁻¹)	29.0	1.0	18.0	5.0	4.0	7.0	2.0	5.0
K (mgkg ⁻¹)	130.0	63.0	205.0	120.0	38.0	90.0	30.0	58.0
Ca (mgkg ⁻¹)	885.0	1040.0	805.0	830.0	620.0	710.0	623.0	560.0
Mg (mgkg ⁻¹)	383.0	315.0	400.0	410.0	145.0	153.0	108.0	105.0
Na (mgkg ⁻¹)	23.0	30.0	15.0	20.0	5.0	5.0	8.0	5.0
Ca %	55.1	64.2	50.8	52.3	70.2	70.1	75.6	73.0
Mg %	39.4	32.2	41.7	42.7	27.1	25.0	21.7	22.6
K %	4.2	2.0	6.6	3.9	2.2	4.6	1.9	3.9
Na %	1.2	1.6	0.8	1.1	0.5	0.4	0.8	0.6

P=phosphorous, K=potassium, Ca=calcium, Mg=magnesium, N-NO₃=nitrogen nitrate, N-NH₄=nitrogen ammonium nitrate, mgkg⁻¹=milligram per kilogram

Table 3.4: Features of the eight test environments in South Africa, during the trial periods

Environment code	Location	Longitude	Latitude	Long-term average Precipitation (mm)	Long-term Temperature range (°C)	Season	Nitrogen regime
1	Cedara	30.26498	-29.5419	575.5	9.9 – 24.0	2012/13	Low N
2	Cedara	30.26498	-29.5419	575.5	9.9 - 24.0	2012/13	High N
3	Cedara	30.26498	-29.5419	554.4	9.9 - 24.8	2013/14	Low N
4	Cedara	30.26498	-29.5419	554.4	9.9 – 24.8	2013/14	High N
5	Potchefstroom	27.07553	-26.7361	603.0	9.8 – 25.9	2012/13	Low N
6	Potchefstroom	27.07553	-26.7361	603.0	9.8 – 25.9	2012/13	High N
7	Potchefstroom	27.07553	-26.7361	644.3	12.9 – 26.8	2013/14	Low N
8	Potchefstroom	27.07553	-26.7361	644.3	12.9 – 26.8	2013/14	High N

3.4 Experimental Design and Trial Management

The diallel comprising 45 F₁ crosses and their 45 reciprocals, 10 parental lines, and three standard check hybrids (CRN3505, LS8519 and CAP9001) were evaluated using alpha-lattice design with two replications, under low and high nitrogen management conditions at Cedara and Potchefstroom in South Africa, during the 2012/13 and 2013/14 cropping seasons. Each plot was made up of two 4 m rows with inter-row spacing of 0.75 m and intra-row spacing of 0.25 m. The trials were planted by hand and seedlings were later thinned to one plant per station at four leaf stage. Fertilizer and irrigation were applied as previously described under trial locations and management conditions. Hand weeding was done when necessary to keep the fields weed free.

3.5 Data Collection

Measurements and observations were recorded on a plot basis for the following twelve traits. Days to anthesis were determined as the number of days from planting date to the date when 50% of plants in a plot had fully emerged tassels and shedding pollen. Days to silking were determined as the number of days from the planting date to the date when 50% of plants in a plot had silks of about 2 cm long. Anthesis-silking interval was calculated as the difference between days from planting to silking and days to anthesis. Ear height was measured at physiological maturity as the distance in centimeters (cm) from the base of the plant to the insertion of the top ear of the same plant and a mean of six plants was recorded. Plant height was measured at physiological maturity as the distance from the base of the plant to the first tassel branch of the same plant, and a mean of six plants was recorded. Ear prolificacy was counted as number of ears with at least one fully developed grain divided by the number of harvested plants. Shelling percentage and grain moisture content were measured at harvest.

Shelling percentage was determined as the ratio of grain weight from an ear to the total weight of the grain and the cob of the ear and was expressed as a percentage. Grain moisture content was measured as percentage water content of grain measured at harvest using a grain moisture meter. Grain yield was calculated from shelled grain weight per plot and was adjusted to tons ha⁻¹ at 12.5 % moisture. After field data were collected for all traits, 500 g maize grain samples for each genotype were subjected to protein, oil, and starch content analysis by means of nearinfrared spectroscopy method using the FOSS grain analyser (Infratec 1241 Grain analyser, FOSS).

3.6 Data Analysis

The data was tested for homogeneity of variance using the Bartlett's test in Genstat 18th edition (Arsham and Lovric, 2011). Combined ANOVA was done across the seven environments, across high N environments and across low N environments using GenStat software 18th edition. The following model was used: $Y_{ij(k)l} = \mu + b_j(r_k)(E_l) + r_k(E_l) + g_i + E_l + gE_{(il)} + e_{ij(k)l}$ where $Y_{ij(k)l}$ is the response of the i^{th} genotype in the j^{th} incomplete block nested within the k^{th} replication nested in the l^{th} environment; μ is the grand mean, $b_j(r_k)(E_l)$ is the effect of the j^{th} incomplete block nested in the k^{th} replication also nested in the l^{th} environment and $j= 1, 2, \dots, 15.5$; $r_k(E_l)$ is the effect of the k^{th} replication nested in the l^{th} environment and $k=1, 2, 3$; g_i is the effect of the i^{th} genotype and $i= 1, 2, 3, \dots, 93$; E_l is the effect of the l^{th} environment and $l= 7$ across all, 4 for low N and 3 for high N; $gE_{(il)}$ is the interaction effect of the i^{th} genotype and the l^{th} environment and $e_{ij(k)l}$ is the random error term.

The regression between the genotype performance under low nitrogen and high nitrogen conditions was calculated using the lme4 package (Bates 2015) in R (R Core Team 2021). The mean for grain yield, protein, oil and starch contents were used as the independent variables

while their corresponding values under high nitrogen conditions were treated as the response variable. Linear regression analysis was carried out according to the methods of Finlay and Wilkinson (1963) using the following model: $Y = a + bX$, where X is the value of the trait under low nitrogen conditions and Y is the corresponding value of the trait under high nitrogen conditions. The slope of the line is b , and a is the intercept (the value of Y when $X = 0$).

Estimation of general combining ability (GCA), specific combining ability (SCA), and reciprocal effects (REC), and the partitioning of reciprocal effects into maternal (MAT) and non-maternal effects (NMAT) of the 10 parental lines, was done using the DiallelSAS05 program in Statistical Analyses System (SAS) (Pérez *et al.*, 2020). The genotypes were considered as fixed effects, while the environments and replications within environments were considered as random effects. The model used in the analysis was: $Y_{ijkl} = \mu + p + p(r) + pr(b) + g_i + g_j + r_{ij} + s_{ij} + e_{ijkl}$, Y_{ijkl} = observed measurement for the ij^{th} cross in the k^{th} replication, under the i^{th} environment combination, μ = is the population mean; g_i and g_j = general combining ability (GCA) effects for the i^{th} and j^{th} parental lines, respectively; r = reciprocal effects, such that $r_{ij} = -r_{ji}$; s_{ij} = specific combining ability (SCA) effect for the ij^{th} cross; and e_{ijkl} = error term associated with the ij^{th} cross evaluated in the k^{th} replication. The relative significance of the GCA, SCA and reciprocal effects was determined based on the proportion of these factors to the total genetic effects. Variance components were determined by equating mean squares to their respective expectations and solving the equations. Broad sense heritability (H^2) (%) values based on genotype (hybrid) means (Ferrari *et al.*, 2022) for all the traits were calculated as

$$H^2 = \frac{\sigma_g^2}{\sigma_g^2 + \frac{\sigma_{ge}^2}{e} + \frac{\sigma_e^2}{re}} \times 100, \text{ where } \sigma_g^2 \text{ is the genotypic variance, } \sigma_{ge}^2 \text{ is the genotype x}$$

environment interaction variance, and σ_e^2 is the error variance, r is the number of replications, and e is the number of environments.

Chapter 4: RESULTS

4.1 General Analysis of Variance

The data was combined and subjected to analysis of variance (ANOVA) for the traits that were recorded during growth and at harvest. Table 4.1 shows the ANOVA mean squares for the different traits measured in the trials across different locations and soil nitrogen availability conditions. The environment and genotype main effects were significant ($P < 0.05$) for grain yield across the nitrogen regimes. A similar trend was observed for ear prolificacy, shelling percentage, plant height and ear height. The environment mean squares were also significant ($p < 0.05$) for grain oil and protein content. However, the genotype x environment interaction effects were only significant ($p < 0.05$) for anthesis to silking interval, plant height, ear height and ears per plant. The environment main effects were significant ($p < 0.05$) for all traits that were recorded in the trials.

Table 4.2 presents the ANOVA mean squares for traits measured across locations under low nitrogen availability conditions. The environment (comprising 2 locations x 2 seasons) main effects were significant ($p < 0.05$) for all traits under low nitrogen. Genotype main effects had significant ($p < 0.05$) impact on all the traits under low nitrogen conditions except for grain moisture, anthesis to silking interval, plant height, and ear height that did not exhibit significant genotypic variation at $P < 0.05$. Reciprocal hybrid effects were only significant ($p < 0.05$) for anthesis days and oil content. The genotype x environment interaction effects were significant ($p < 0.05$) for anthesis and silk emergence dates, and starch and oil content under low soil nitrogen. Oil content and silking days exhibited significant ($p < 0.05$) variation among crosses due to the environment x reciprocal interaction effects. There were significant ($p < 0.05$) maternal effects for grain moisture and protein and non-maternal effects for anthesis days and

oil. The environment x maternal effects were significant ($p < 0.05$) for plant height and oil, while environment x non-maternal effects were only significant ($p < 0.05$) for grain moisture and silking date.

The environment (comprising two seasons at two locations) main effects significantly ($p < 0.05$) affected the expression of all the traits under high nitrogen availability conditions (Table 4.3). In contrast, the genotypic differences were only significant for grain yield, anthesis days and days to silking. However, the genotypes did not vary significantly for all the nutritional traits. Significant ($p < 0.05$) maternal effects were only detected for shelling percentage and days to silking. The environment x genotype interaction effects were highly significant ($p < 0.01$) for grain yield, grain moisture, anthesis days, silking days and anthesis-silking interval and oil content among the nutritional traits. The environment x reciprocal interaction effects were only significant ($p < 0.05$) for grain yield and grain moisture content.

Table 4.1: Mean squares for traits measured on 90 maize reciprocal crosses evaluated at Cedara and Potchefstroom across different regimes of nitrogen availability.

SOV	Df	GY	EPP	SP	GM	AD	SD	ASI	PH	EH	Starch	Oil	Protein
Environment	7	1166.85***	0.96***	3892.62***	1268.72***	5453.03***	3810.70***	734.95***	339606.7***	213193.4***	227.57***	23.70***	302.31***
Replication (Environment)	8	9.02***	0.05	26.52	4.50*	243.07***	151.16***	30.60***	2441.74***	1995.94***	4.36	0.16	3.59***
Genotype x Environment	89	5.38***	0.06***	109.09**	3.8	26.69***	32.35***	4.05	356.11**	197.66	6.21*	0.82***	1.00**
Genotype	534	2.84**	0.03	73.54*	3.06***	12.33***	14.10***	4.20*	244.86	161.22	4.59	0.20***	0.64
Residual	623	2.3	0.03	62.91	1.94	8.92	9.43	3.49	216.72	156.89	4.42	0.12	0.65

SOV=source of variation, DF=degrees of freedom, GY=grain yield, EPP=ears per plant, SP=shelling percentage, GM=grain moisture, AD=days to anthesis, SD=days to silking, ASI=anthesis silking interval, PH=plant height, EH=Ear height.

Table 4.2 Mean squares for traits measured on 90 maize crosses evaluated at Cedara and Potchefstroom across two years under low nitrogen conditions.

SOV	Df	GY	EPP	SP	GM	AD	SD	ASI	PH	EH	Starch	Oil	Protein
Environment	3	2022.46***	0.22***	1568.34***	1116.19***	2759.07***	3371.32***	647.17***	488629.49***	299945.68***	178.08***	23.48***	120.57***
Replication (Environment)	3	7.73*	0.07**	13.23	5.69*	61.87***	33.93**	12.44**	3503.99***	2572.09***	2.34**	0.11	2.62*
Genotype	89	5.91**	0.03*	91.59*	2.69	17.16***	19.25**	2.82	250.72	198.48	1.81***	0.73***	1.04*
Genotype x Environment	267	3.55	0.02	65.5	3.32***	10.14**	12.39***	2.65	208	163.44	0.81*	0.16***	0.76
Residual	356	3.14	0.02	55.06	2.32	7.77	8.46	2.79	179.88	156.36	0.63	0.08	0.81

SOV=source of variation, ^{Df}=degrees of freedom, GY=grain yield, EPP=ears per plant, SP=shelling percentage, GM=grain moisture, AD=days to anthesis, SD=days to silking, ASI=anthesis silking interval, PH=plant height, EH=Ear height

Table 4.3 Mean squares for traits measured on 90 maize crosses evaluated at Cedara and Potchefstroom across two years under high nitrogen conditions.

Source	Df	GY	EPP	SP	GM	AD	SD	ASI	PH	EH	Starch	Oil	Protein
Environment	3	271.62***	0.62***	8117.8***	2027.76***	7449.85***	2881.81***	1134.76***	277084.42***	182553.87***	265.17***	35.77***	607.62***
Replication (Environment)	4	10.74***	0.03	44.24	2.91	484.67***	307.45***	54.81***	1022.92*	1227.63***	7.06	0.22	4.9***
Genotype	89	2.38*	0.06*	91.91	3.3	23.12**	28.68***	5.88	341.07	177.37	9.79	0.31	0.5
Genotype X Environment	178	1.77**	0.04	85.17	3.11***	14.99**	15.93**	6.28**	304.79	149.41	9.86	0.25**	0.5
Residual	267	1.16	0.04	73.39	1.43	10.45	10.72	4.42	266.01	157.59	9.47	0.17	0.43

SOV=source of variation, ^{Df}=degrees of freedom, GY=grain yield, EPP=ears per plant, SP=shelling percentage, GM=grain moisture, AD=days to anthesis, SD=days to silking, ASI=anthesis silking interval, PH=plant height, EH=Ear height.

4.2 Mean performance of genotypes

The mean performance of the top ten experimental hybrids and checks are presented in Table 4.4. The genotypes showed wide variation in agronomic performance, yield productivity and nutritional content. The days to anthesis varied from 76 to 82 days with a mean of 78. The earliest genotype for anthesis was entry L27, while the latest was entry L40. In comparison, the anthesis days for the three checks were between 76 and 80. The silking days also exhibited variability among the genotypes with a range between 75 and 82 days recorded for entries L19 and L40, respectively. The silking days for the checks were between 77 and 80, while the overall mean for silking was 78 days. The anthesis silking interval showed little variation between -1 and 1. Check 3 was the shortest genotypes with an average plant height of 179 cm while entry L65 was the tallest at 206 cm. The average plant height was 191cm. The ear height for entry L84 was the shortest at 87cm compared to 110 cm recorded for the check 2. On average, the ear height was 100cm. Ear prolificacy was not well pronounced as it ranged between 1.00 and 1.24. The least prolific genotype was entry L42 and the most prolific was entry L18. The grain moisture content exhibited a wider range from 12.82% to 15.79% with an average of 14.05%. Entry L90 had the lowest grain moisture content at harvest while the highest grain moisture was recorded for entry L66. About 75.37% of the ear is retained as grain after shelling on average. Entry L85 had the lowest shelling percentage of 68.76% while check 1 had the highest shelling percentage at 80.87%. The variation in oil content was narrow ranging between 4.47 and 5.69 with a mean of 4.92. The entries with the lowest and highest oil content were entries L35 and L37, respectively. The oil contents for checks 1, 2 and 3 were 4.61, 4.70 and 4.84, respectively. Protein content was between 7.52 recorded for entry L86 and 8.89 recorded for entry L39. The average protein content was 8.08%. In comparison, the checks 1, 3 and 2 had protein contents of 7.88, 7.95 and 8.14%, respectively. The starch content

was between 65.6 and 71.8 with the mean at 70.69. Entries with minimum and maximum starch contents were L48 and L75, respectively. The mean yield of the genotypes varied widely from a minimum of 3.29 and a maximum of 6.02. On average, grain yield was 4.66 t/ha. The lowest yielding entry was L48 compared to entry L11 that had the highest grain yield. Check 1 had grain yield of 5.09 t/ha which was higher than 3.85 t/ha recorded for both checks 2 and 3.

Table 4.4 Means for traits measured on top 10 maize crosses and checks evaluated at Cedara and Potchefstroom across the different nitrogen availability.

Rank	Entry	GY	AD	SD	ASI	PH	EH	EPP	GM	SP	Oil	Protein	Starch
1	L11	6.02	76.79	76.57	0.21	195.5	102	1.11	14.64	78.54	4.64	7.63	71.26
2	L35	5.92	76	75.57	0.43	191.21	98.07	1.06	14.01	78.9	4.47	8.34	70.86
3	L13	5.78	78.21	79.36	-1.14	181.21	103.14	1.2	14.46	72.5	5.28	8.51	70.3
4	L60	5.71	77.57	77.21	0.36	183.64	105	1.09	14.49	74.51	5.11	8.04	70.62
5	L36	5.66	77.43	76.71	0.71	196.86	101.36	1.05	13.86	80.35	4.93	8.3	70.51
6	L83	5.57	77.57	77.14	0.43	183.14	103.14	1.08	13.71	75.16	4.6	7.92	71.27
7	L72	5.54	78.14	78.29	-0.14	191.29	104.29	1.15	14.2	78.1	4.94	8.53	70.14
8	L1	5.51	76.43	76.57	-0.14	194.79	95.21	1.1	14.33	79.19	5.07	8.09	70.69
9	L14	5.49	77.93	78	-0.07	189.43	103	1.15	14.31	75.61	5.02	7.89	70.74
10	L18	5.38	78.86	79.86	-1	196.21	104.36	1.01	14.13	78.93	5.1	8.11	70.5
Check1	L91	5.09	76.64	78.07	-1.43	188.43	96	1.13	13.99	80.87	4.61	7.88	71.09
Check2	L92	3.85	79.5	80.43	-0.93	192.43	110.07	0.99	14.09	78.81	4.7	8.14	70.94
Check3	L93	3.85	76.07	76.71	-0.64	178.57	89.86	0.93	13.46	74.25	4.84	7.95	70.91
Mean of Checks		4.26	77.4	78.4	-1	186.48	98.64	1.02	13.85	77.98	4.71	7.99	70.98
Grand Mean		4.66	77.95	78.06	-0.11	190.68	100.4	1.04	14.05	75.37	4.92	8.08	70.69
SEM		1.53	3.4	3.3	1.92	15.35	13.27	0.17	1.4	7.84	0.34	0.82	2.07
LSD		3	6.68	6.47	3.77	30.15	26.06	0.33	2.75	15.4	0.68	1.61	4.06
CV		32.8	4.4	4.2	1690.4	8.1	13.2	16.4	10	10.4	7	10.2	2.9

SEM=standard error of mean, LSD=least significant difference, CV=coefficient of variation, GY=grain yield, EPP=ears per plant, SP=shelling percentage, GM=grain moisture, AD=days to anthesis, SD= days to silking, ASI=anthesis silking interval, PH=plant height, EH=Ear height

Table 4.5 summarizes mean performance of hybrids under low nitrogen. Yield under low nitrogen ranged from 3.28 to 7.15 t/ha with an average of 5.14 t/ha. The highest yielding genotype under low nitrogen treatment was entry L13 and the lowest was entry L53. Entries L11 and L14 were among the top 10 yielding genotypes with yield of 6.9 and 6.04 with average of 5.14 t/ha. Entry L19 had the highest starch content of 72.15 % but lowest protein content at 7.1%. Some entries had desirable nutritional content but were not among the top in grain yield production. For example, Entry L28 had the highest protein content of 8.6% while entries L2, L75 and L19 had high starch content values above 72% but their grain yield values were less than 6.00 t/ha. Entries L76 and L44 recorded the highest oil content values of 5.4 and 5.9%, respectively. The highest shelling percentages were 84.0, 81.7 and 81.4%, which were recorded for entries L67, L56 and L23, respectively. The tallest genotype was entry L79 with plant height of 211.1cm followed by entry L21 (207.9cm), entry L22 (207.0cm), entry L5 (205.1cm), entry L48 (205.0cm), entry L44 (203.9cm) and entry L87 (203.5cm), which were taller than the tallest check 2 (203.1 cm). The earliest flowering entries were entry L12 and entry L47 with silking days of 77.3, and entries L46 and L77 with anthesis of 77.8 days. Late flowering genotypes were entries L84, which took about 85 days to anthesis and entry L75 which produced silks in 84 days.

Table 4.5 Means for traits measured on top 10 maize crosses evaluated at Cedara and Potchefstroom under low nitrogen availability.

Rank	ENTRY	GY	AD	SD	ASI	PH	EH	EPP	GM	SH	Oil	Protein	Starch
1	L13	7.15	80.3	80.9	-0.63	188.5	102.8	1.12	14.8	75.1	5.4	8.2	70.69
2	L11	6.9	80	79.5	0.5	197.8	106.3	1.02	14.7	79.9	4.5	7.2	71.83
3	L35	6.9	78.3	77.8	0.5	190.5	95.5	1.01	14.5	81.2	4.4	8.1	71.08
4	L83	6.8	80	79.8	0.25	192.1	107.3	1	14.2	79.2	4.6	7.7	71.7
5	L36	6.62	78.8	78.5	0.25	205.1	106.6	1.09	14.4	79.9	4.8	7.9	70.98
6	L60	6.61	81.4	80.4	1	183.8	105.1	1.1	15.3	76.1	5.1	7.6	71.05
7	L72	6.43	81.1	80.1	1	189.8	103.1	1.07	14.5	79.7	4.8	8.4	70.16
8	L1	6.12	78.1	78.3	-0.13	194.6	89.6	1.06	14.8	80.8	5.1	7.7	70.95
9	L68	6.11	80.6	81.1	-0.5	184	95.6	0.95	14.6	76.9	4.9	8.1	70.98
10	L14	6.04	79	78.6	0.38	196.5	104	1.06	14.9	75.8	5	7.6	71.13
Check1	L91	5.69	79.4	79.6	-0.25	190.3	98.8	1.07	14.7	82.4	4.5	7.9	71.53
Check2	L92	4.01	82.3	81.9	0.38	203.1	121.1	0.94	13.9	80.4	4.6	8	71.26
Check3	L93	3.67	80.5	81.1	-0.63	184.5	96.9	0.93	14.6	72.8	4.6	7.8	71.54
Mean of Checks		4.46	80.7	80.9	-0.17	192.6	105.6	0.98	14.4	78.5	4.6	7.9	71.44
Grand Mean		5.14	80.4	80.1	0.25	194	103.4	0.99	14.4	76.6	4.9	7.7	71.12
SEM		1.77	2.8	2.9	1.69	14.3	13.6	0.149	1.5	7.3	0.3	0.9	0.79
LSD		3.49	5.6	5.7	3.32	28.2	26.8	0.293	3	14.4	0.6	1.8	1.55
CV		34.5	3.5	3.6	686.7	7.4	13.2	15.1	10.6	9.6	5.9	11.8	1.1

SEM=standard error of mean, LSD=least significant difference, CV=coefficient of variation, GY=grain yield, EPP=ears per plant, SP=shelling percentage, GM=grain moisture, AD=days to anthesis, SD= days to silking, ASI=anthesis silking interval, PH=plant height, EH=Ear height

Grain yield of the genotypes ranged between 1.96 and 6.00 t/ha with an average of 4.03 t/ha under high nitrogen conditions (Table 4.6) The highest yielding genotypes was entry L1 (average grain yield 6.00 t/ha) and the lowest yielding was entry L90 (1.96 t/ha). Entry L14 was ranked in the top 10 yielding genotypes with a yield of 4.74 t/ha. The range of starch content was between 69 and 71 % while the average was 70.23%. The average protein content was 8.28%. Entry L77 had the

highest protein content amongst the highest yielding entries. The tallest plants under optimum nitrogen conditions ranked 9 and 58, which were entries L20 and L6 with height of 201.67 and 200.17 cm, respectively. Overall, there were no prolific hybrids as the average prolificacy was 1.

Table 4.6 Means and statistics for traits measured on top ten maize crosses evaluated at Cedara and Potchefstroom under high nitrogen availability.

Rank	ENTRY	GY	AD	SD	ASI	PH	EH	EPP	GM	SP	Oil	Protein	Starch
1	L78	6.0	75.7	76.7	-1.0	195.2	102.5	1.1	15.2	76.5	5.0	8.5	69.9
2	L74	5.6	75.8	76.3	-0.5	194.2	102.2	1.1	14.5	78.0	4.8	8.6	70.5
3	L54	5.3	77.8	77.3	0.5	187.8	97.7	1.1	14.8	77.3	5.0	8.8	70.1
4	L23	4.9	72.3	72.8	-0.5	194.3	99.0	1.1	13.6	74.6	4.8	8.5	70.5
5	L77	4.9	75.0	74.7	0.3	183.0	95.0	1.0	15.6	75.2	4.8	8.8	70.0
6	L53	4.9	75.8	74.8	1.0	173.2	95.5	1.1	14.6	74.5	4.9	8.7	70.4
7	L18	4.9	74.5	76.0	-1.5	195.8	102.7	1.1	13.9	80.2	5.3	8.8	69.8
8	L11	4.8	72.5	72.7	-0.2	192.5	96.3	1.2	14.5	76.7	4.8	8.2	70.5
9	L20	4.8	72.8	72.3	0.5	201.7	100.7	1.4	13.5	72.9	5.0	8.7	70.2
10	L14	4.7	76.5	77.2	-0.7	180.0	101.7	1.3	13.6	75.4	5.1	8.3	70.2
Check 1	L91	4.3	73.0	76.0	-3.0	186.0	92.3	1.2	13.1	78.8	4.8	7.8	70.5
Check 2	L92	3.6	75.8	78.5	-2.7	178.2	95.3	1.1	14.4	76.7	4.8	8.3	70.5
Check 3	L93	4.1	70.2	70.8	-0.7	170.7	80.5	0.9	11.9	76.2	5.2	8.2	70.1
Mean Check		4.0	73.0	75.1	-2.1	178.3	89.4	1.1	13.2	77.3	4.9	8.1	70.4
Grand Mean		4.0	74.7	75.3	-0.6	186.2	96.4	1.1	13.6	73.8	4.9	8.6	70.1
SEM		1.1	3.9	3.7	2.1	16.6	12.8	0.2	1.2	8.5	0.4	0.7	3.0
LSD		2.2	7.6	7.3	4.2	32.7	25.2	0.4	2.3	16.7	0.8	1.4	6.0
CV		27.7	5.2	4.9	356.0	8.9	13.3	17.6	8.7	11.5	8.2	8.1	4.3

SEM=standard error of mean, LSD=least significant difference, CV=coefficient of variation, GY=grain yield, EPP=ears per plant, SP=shelling percentage, GM=grain moisture, AD=days to anthesis, SD= days to silking, ASI=anthesis silking interval, PH=plant height, EH=Ear height

4.3 Crossover ranking of genotypes across the different nitrogen management conditions.

A regression analysis was conducted to determine the relationship between performance under low nitrogen and high nitrogen management conditions. In general, genotypes that perform well in grain yield productivity, and nutrients accumulation under low nitrogen conditions also perform

well when nitrogen conditions improve. The regression analysis showed that there was a positive relation between yield productivity and nutrient accumulation under low nitrogen and high nitrogen conditions as exhibited by the positive y-intercepts (Table 4.7). Grain yield and protein content under low nitrogen management conditions exhibited weaker regression on their respective values under high nitrogen management conditions as exhibited by their small R^2 values of 0.05 and 0.09, respectively. On the other hand, oil and starch contents values under low and high nitrogen conditions were strongly correlated as exhibited by the stronger R^2 values of 0.36 and 0.28, respectively.

Table 4.7 Regression estimates of traits means under low N compared to high N conditions.

Trait	Intercept	Estimate	St error	t value	p value	R^2
Grain yield	3.05	0.19	0.07	2.66	0.01**	0.05
Oil content	2.90	0.42	0.06	6.40	0.000***	0.36
Protein content	7.21	0.18	0.09	2.07	0.04*	0.09
Starch content	39.06	0.44	0.07	6.08	0.000***	0.28

R^2 =coefficient of determination.

A further analysis of the regression results to identify genotypes that performed well for grain yield production and nutritional content under both low and high nitrogen management conditions was conducted. Figure 4.1 shows that yield exhibited a positive relationship between low and high nitrogen conditions. For every unit increase in grain yield production under low nitrogen conditions, the same genotype would be expected to produce 0.38 ton/ha more under high nitrogen conditions. In Figure 4.2, the genotypes that produced reasonably high yield under both conditions were genotypes 35, 11, 36, 60, 1 and 14. These hybrids exhibited more stable yield production.

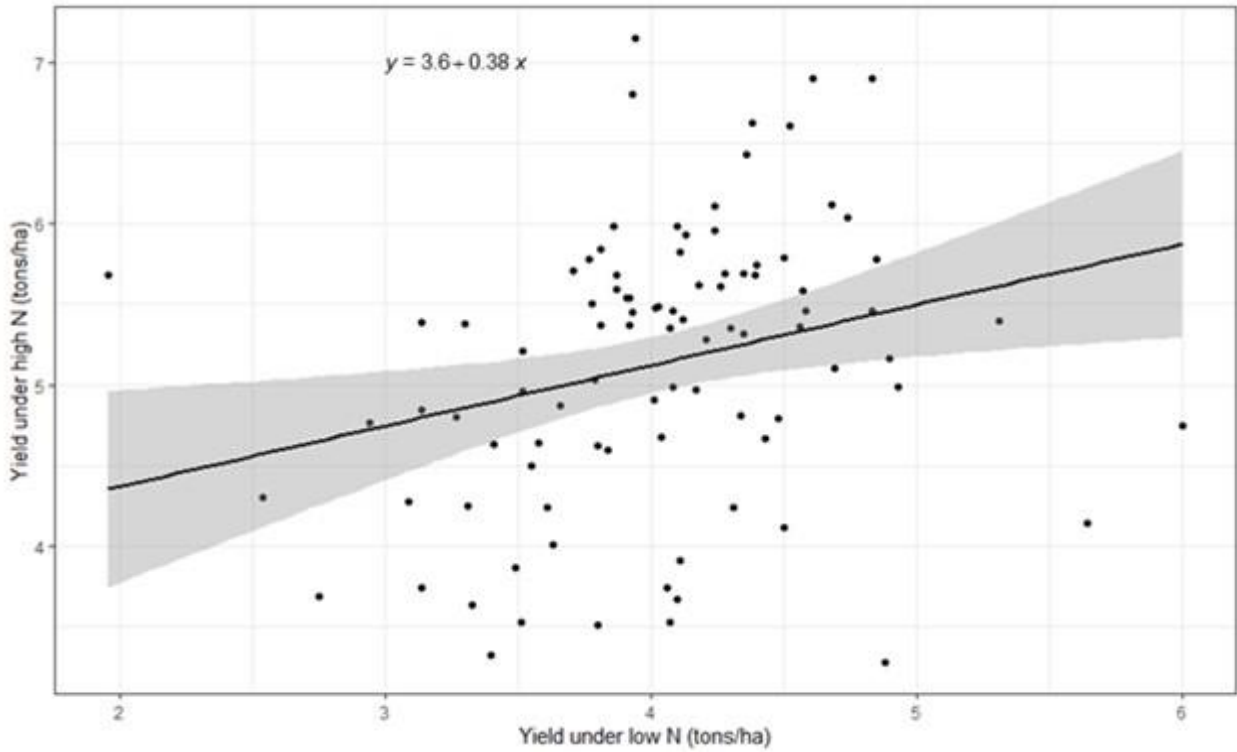


Figure 4.1 Scatterplot showing the linear relationship between genotype yield under low and high N conditions.

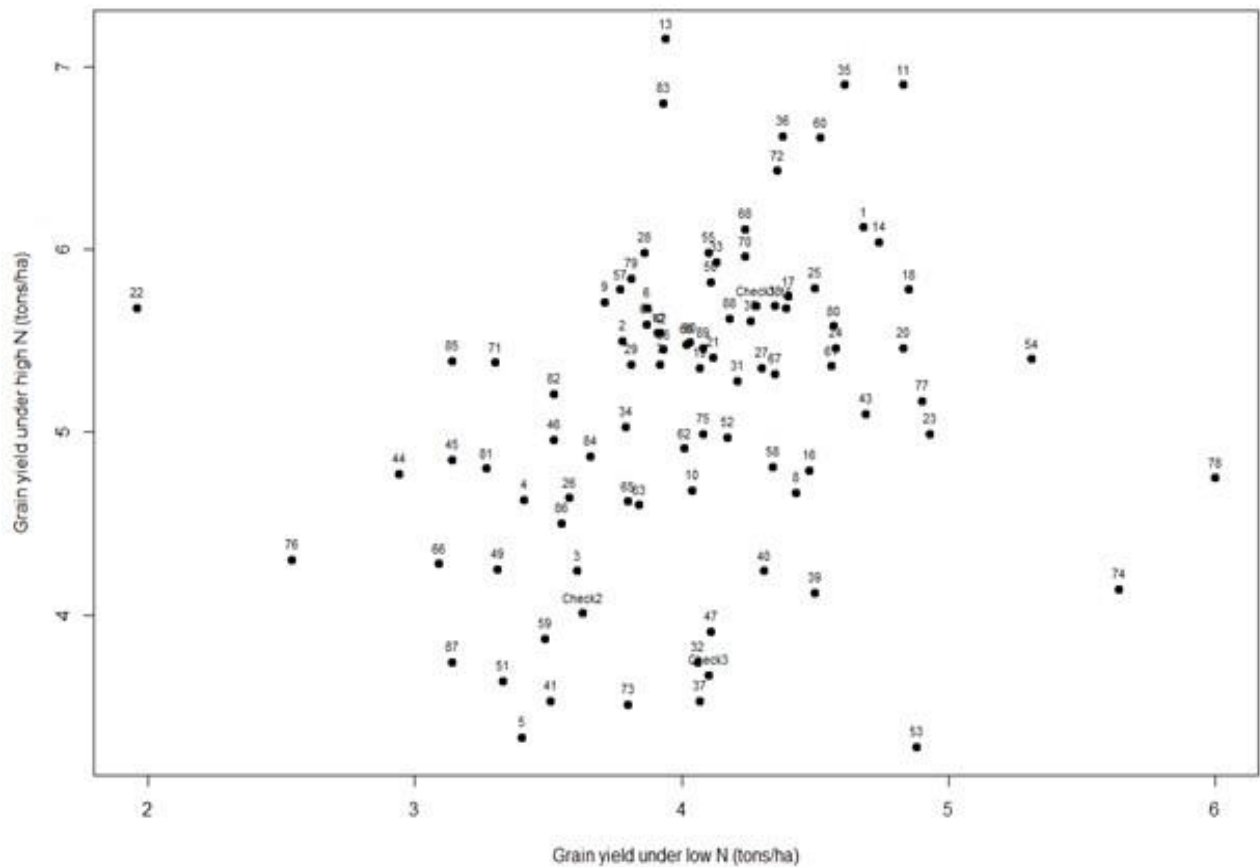


Figure 4.2 Scatterplot showing relations between genotype grain yield under low and high nitrogen conditions.

Figure 4.3 shows that oil content under low nitrogen conditions was positively correlated with oil content under high nitrogen conditions. For every unit increase in oil content under low nitrogen conditions, the same genotype would be expected to contain 0.42% more oil under high nitrogen conditions. In Figure 4.4, the genotypes that had reasonably high oil content under both conditions were genotypes 37, 76, 58, and 40. These hybrids exhibited that they had stable oil content despite differences in nitrogen application.

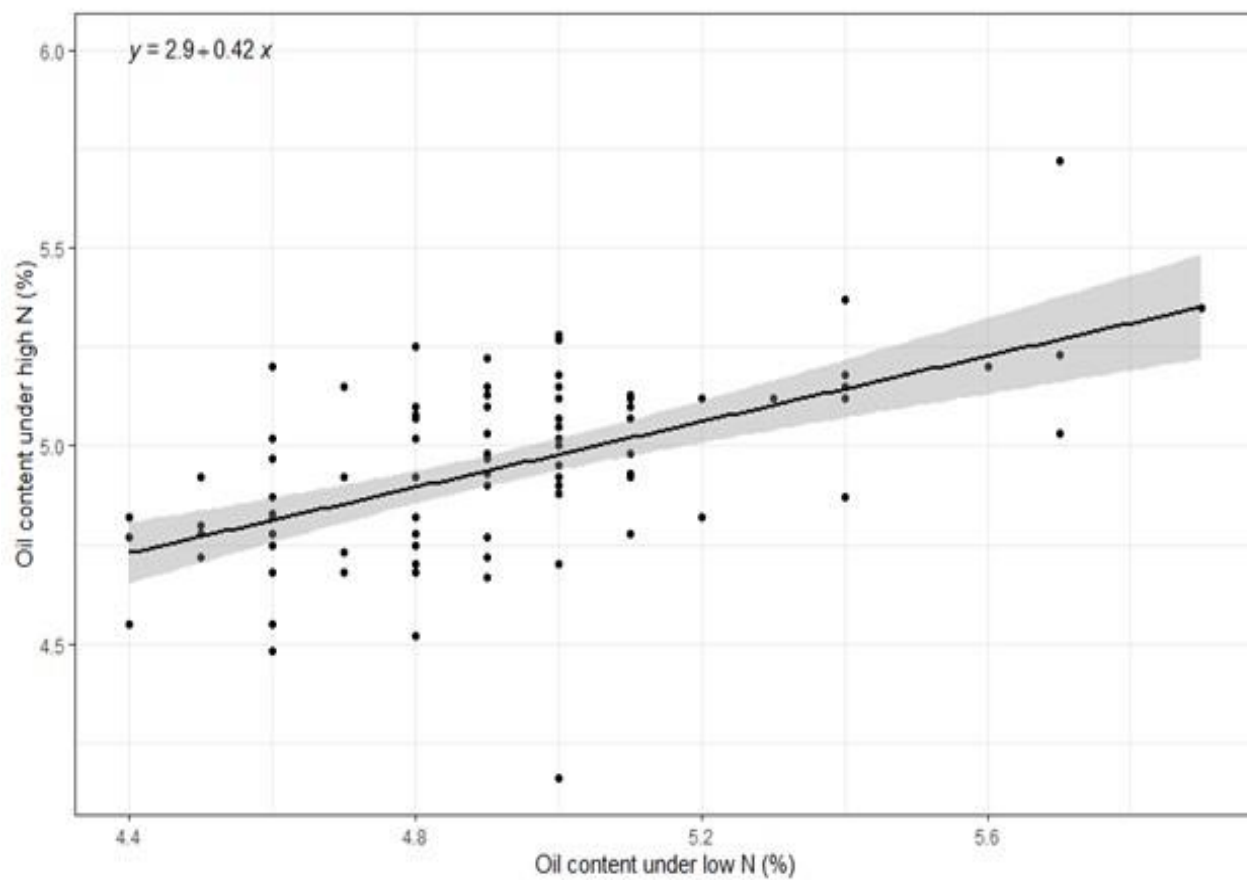


Figure 4.3 Scatterplot showing the linear relationship between genotype oil content under low and high N conditions.

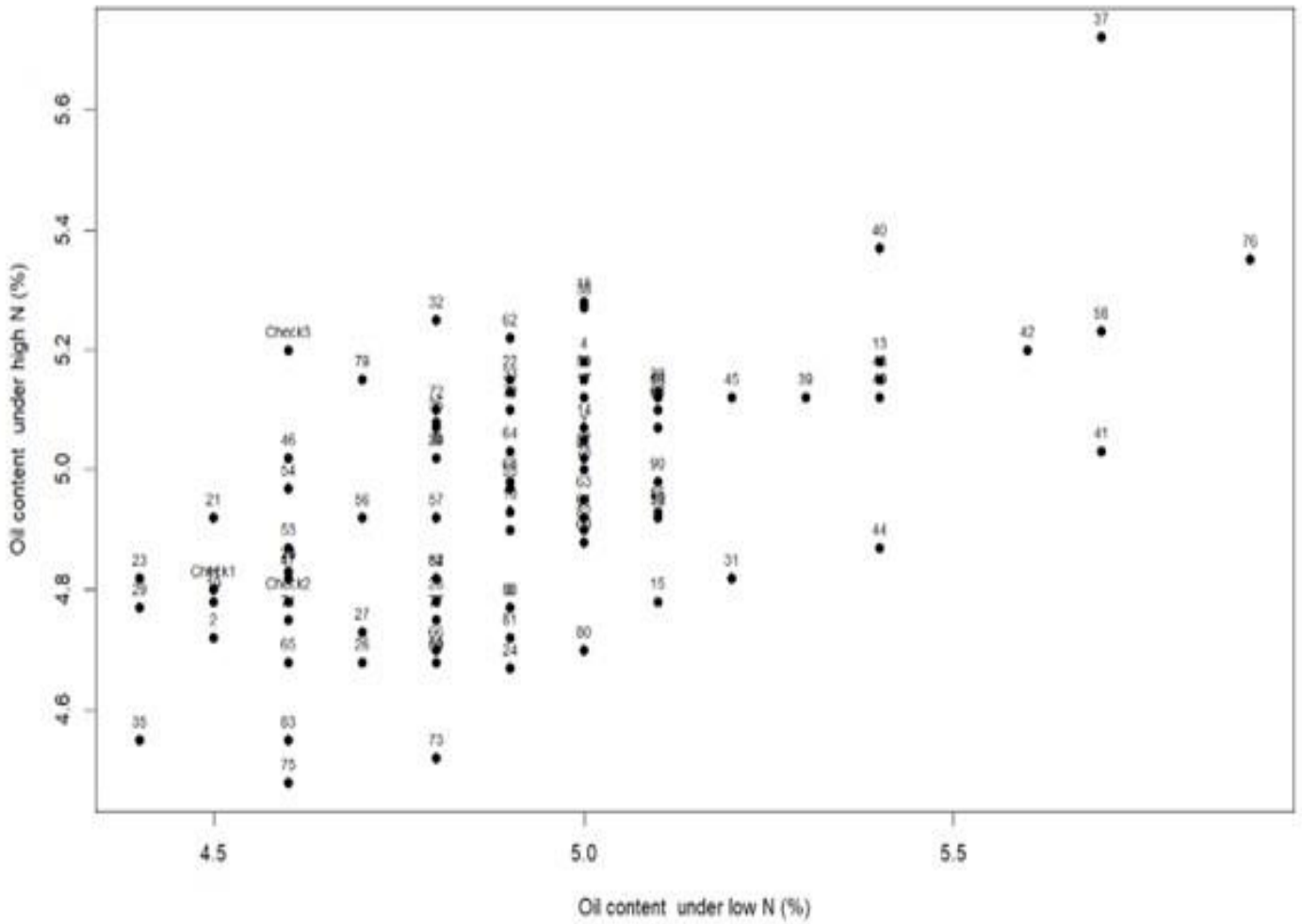


Figure 4.4 Scatterplot showing relations between genotype oil content under low and high N conditions.

Similarly, protein content exhibited a linear relationship between low and high nitrogen management conditions (Fig 4.5). Protein content is expected to increase by 0.18% under high nitrogen application compared to low nitrogen conditions. Figure 4.6 shows that protein content was high and stable in genotypes 39, 84, 44, 13 and 70.

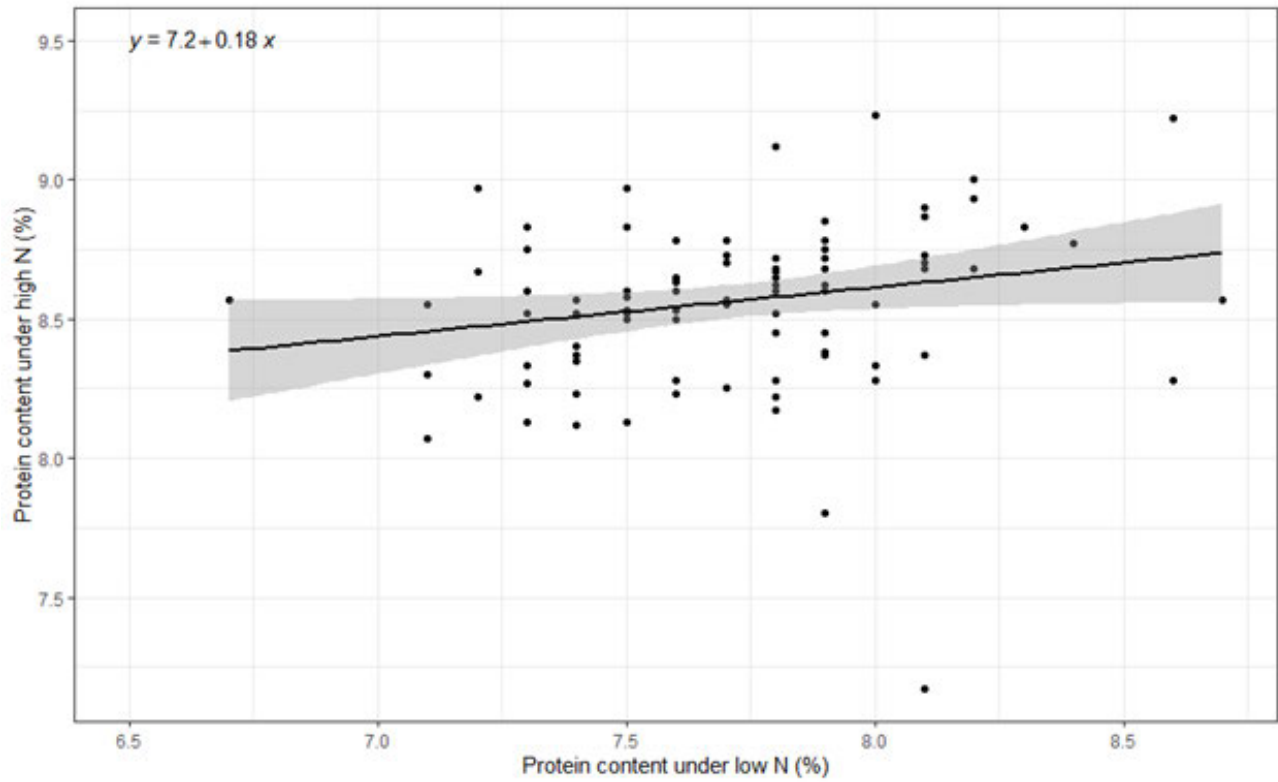


Figure 4.5 Scatterplot showing the linear relationship between genotype protein content under low and high N conditions.

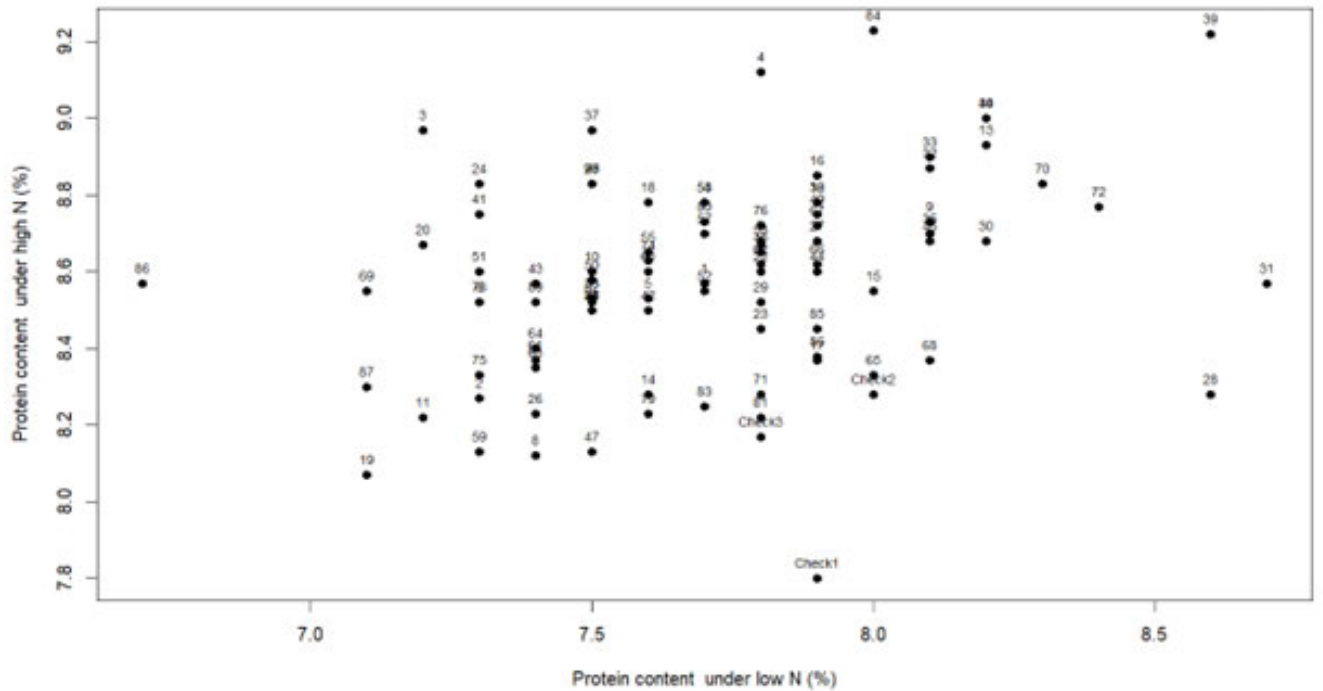


Figure 4.6 Scatterplot showing the genotype protein content under low and high N conditions. There was a strong linear relationship between starch content recorded under low nitrogen conditions compared to high nitrogen conditions (Fig.4.7). For every unit increase in starch content under low nitrogen conditions, a 0.44% increase would be expected in starch content under high nitrogen application rate. In Figure 4.8, the genotypes that had consistently high starch content under both nitrogen management conditions were 75, 2, 19, 29, 26, 52 and 23.

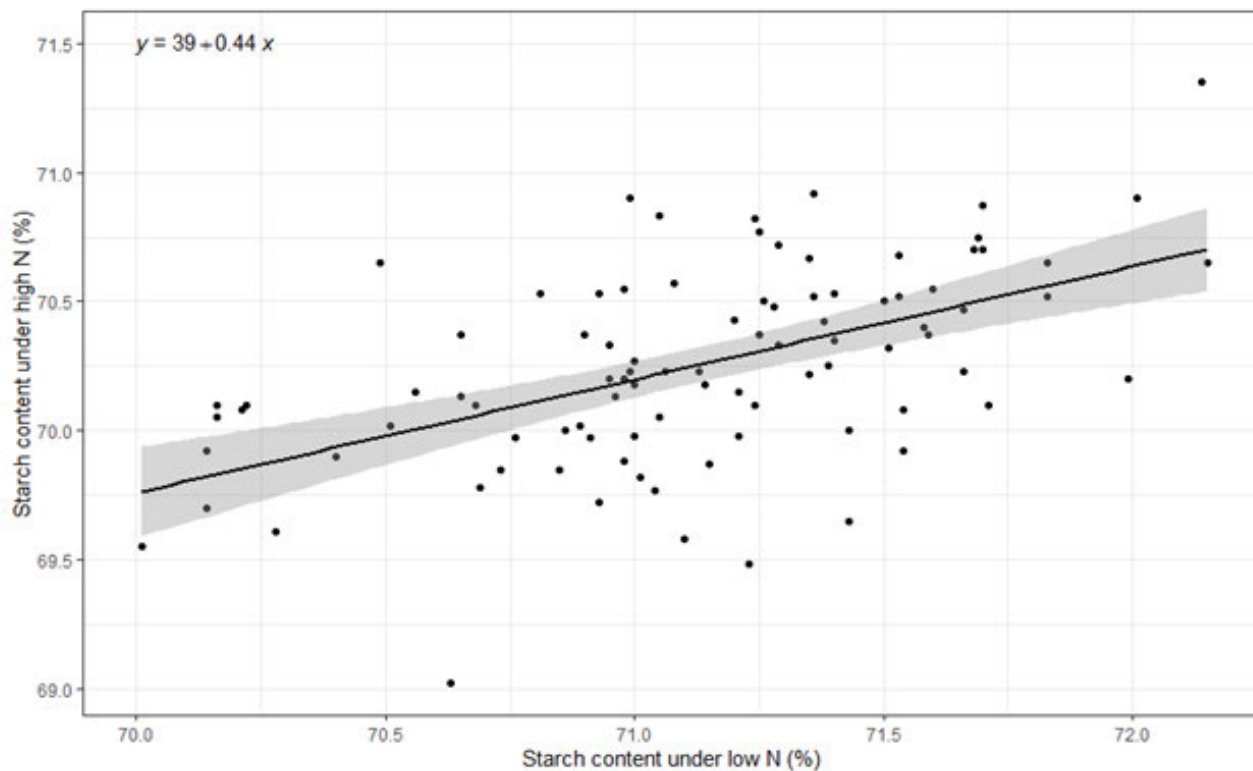


Figure 4.7 Scatterplot showing the linear relationship between starch content under low and high N conditions.

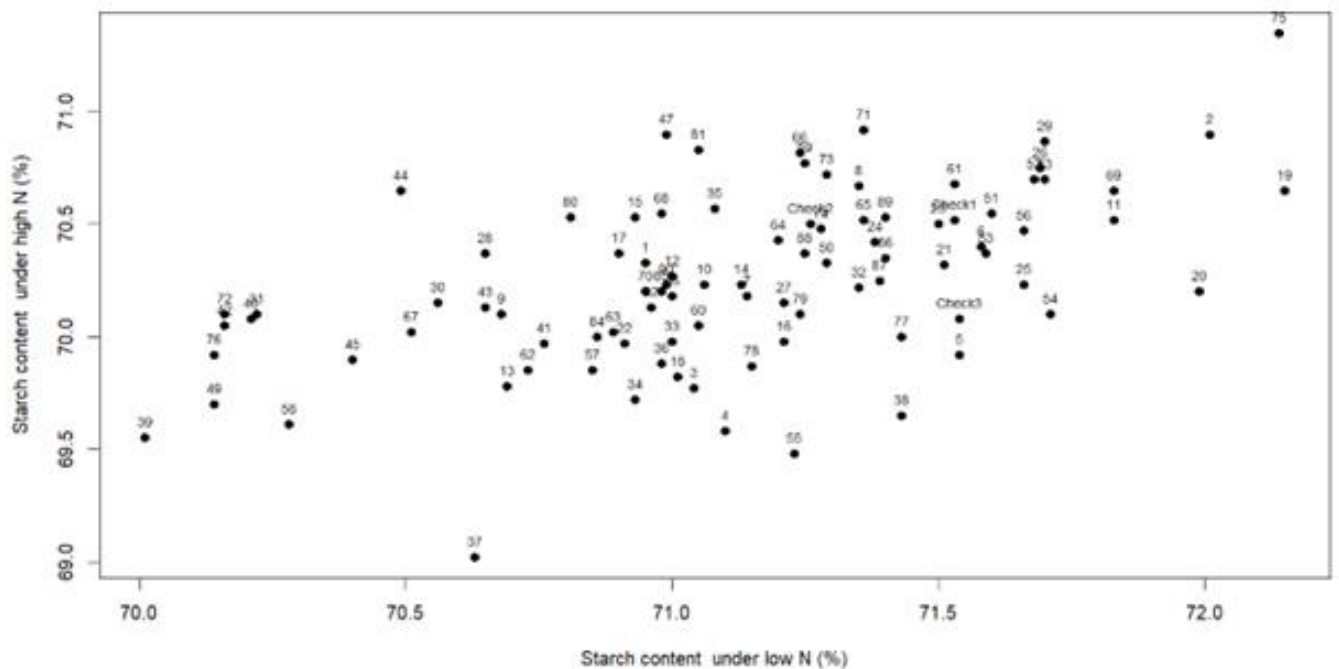


Figure 4.8 Scatterplot showing the genotype performance for starch content under low and high N conditions.

4.4 Combining ability effects.

A summary of mean squares and significant tests of combining ability effects for yield and secondary traits of genotypes evaluated across two nitrogen availability conditions in two locations is presented in Table 4.8. The environment main effects were significant ($p < 0.05$) for all traits including nutritional components. Similarly, grain yield, ear prolificacy, shelling percentage, days to anthesis, days to silking and plant height exhibited significant ($p < 0.05$) genotypic variation across the environments. Both GCA and SCA effects were significant ($p < 0.05$) for the grain yield, while only the GCA effects were significant for ear prolificacy, shelling percentage, days to anthesis, days to silking and plant height. There were significant ($p < 0.05$) reciprocal effects for

grain yield, ear prolificacy and days to anthesis only. Maternal effects were only significant ($p < 0.05$) for shelling percentage, grain moisture, days to anthesis and days to silking while nonmaternal effects affected grain yield, ear prolificacy and days to anthesis only. The environment x genotype interaction effects were significant ($p < 0.05$) for most traits including grain yield, shelling percentage, grain moisture content, days to anthesis, days to silking and anthesis to silking interval. However, the environment x GCA interaction effects were similarly significant ($p < 0.05$) for the same traits and, additionally, plant and ear height. In comparison, the environment x SCA interaction effects were only significant for days to anthesis and silking. With respect to nutritional traits, the environment, genotype and GCA effects were significant ($p < 0.05$) for starch, oil, and protein. Reciprocal, non-maternal, environment x genotype, environment x GCA, environment x SCA, environment x reciprocal and environment effects were significant ($p < 0.05$) for oil. The effects due to interaction of the environment with reciprocal, maternal and non-maternal effects were not significant for many traits.

Table

Table 4.8 Mean squares for combining ability effects of hybrid genotypes evaluated for agronomic performance and nutritional content across different nitrogen environments.

SOV	Df	GY	EPP	SP	GM	AD	SD	ASI	PH	EH	Starch	Oil	Protein
Environment	7	1166.***	0.96***	3892.6***	1268.7***	5453.0***	3810.7***	734.9***	339606.7***	213193.4***	227.5***	23.7***	302.3***
Replication (Environment)	7	9.02***	0,05	26,52	4.50*	243.07***	151.16***	30.60***	2441.74***	1995.94***	4,36	0,16	3.59***
Genotypes	89	5.38***	0.06***	109.09**	3,80	26.69***	32.35***	4,05	356.11**	197,66	6.21*	0.82***	1.00**
GCA	9	17.37*	0.23***	278.49**	11,32	120.09***	177.62***	8,51	869.08*	505,50	15.84**	6.07***	3.78***
SCA	35	4.58**	0,04	98,71	2,75	11,17	15,01	4,27	314,06	164,56	5,19	0,21	0,78
Reciprocal	45	3.61*	0.04*	83,28	3,11	20.08***	16,78	2,97	285,62	161,95	5,07	0.24*	0,61
Maternal	9	3,82	0,03	132.09**	6.84**	38.80*	34.62***	2,11	411,39	147,65	4,20	0,31	0,94
Non-Maternal	36	3.56*	0.05*	71,08	2,18	15.40*	12,32	3,19	254,17	165,53	5,29	0.23*	0,53
Genotype X Environment	534	2.84**	0,03	73.54*	3.06***	12.33***	14.10***	4.20*	244,86	161,22	4,59	0.20***	0,64
Environment X GCA	54	6.31***	0,03	86,20	9.00***	27.38***	34.02***	5,30	337.49*	254.52***	5,48	0.56***	0,82
Environment X SCA	210	2,45	0.03*	74,86	2,09	11.16*	11.40*	4.63**	223,50	129,85	4,64	0.16**	0,62
Environment X Reciprocal	270	2,46	0,03	69,98	2.63**	10,23	12.22**	3,64	243,62	166,97	4,38	0.15**	0,62
Environment X Maternal	54	2,90	0,03	51,25	2,83	11,42	9,93	4,56	307,10	104,78	4,81	0.21*	0,64
Environment non-maternal	216	2,35	0,03	74,67	2.59**	9,94	12.79**	3,41	227,75	182,52	4,27	0,14	0,61
Residual	623	2,30	0,03	62,91	1,94	8,92	9,43	3,49	216,72	156,89	4,42	0,12	0,65

SOV=Sources of variation, Env=environment, REP(Env)=replications within environment, Gen=genotype, Rec=reciprocal, Mat=maternal, GCA=general combining ability, SCA=specific combining ability, GY=grain yield, EPP=ears per plant, SP=shelling percentage, GM=grain moisture, AD=days to anthesis, SD=days to silking, ASI=anthesis silking interval, PH=plant height, EH=Ear height

4.4.1 General combining ability

Table 4.9 summarizes the GCA effects for grain yield and secondary traits of inbred lines evaluated across different environmental conditions. The parents that exhibited desirable GCA effects for anthesis days and silking days were parental lines L3 (CML181), L1 (CML144) and L4 (CML182), which tended to reduce the number of days to pollen shedding and silking. Parental line L6 (CML550) had a desirable GCA that reduced the anthesis silking interval but tended to increase anthesis days and silking days as suggested by its positive GCA for these two traits. The lines that could reduce plant height were lines L7 (CW14) and L9 (I-43), that had negative GCA effects for plant height of -2.81 and -2.20, respectively. Genotype L9 (I-43) had the highest negative GCA effects for ear height (-2.08) followed by parent L1 (CML44) -1.94. Positive and significant GCA effects for ears per plant were found in parental lines L2 (CML176) and L5 (CML511). Early dry down represented by grain moisture could be achieved by using parental lines L4 (CML182), L1 (CML144) and L10 (K64R) as they exhibited negative and significant GCA effects for grain moisture. The parental lines with high potential to increase oil content in their hybrids are parental lines L6 (CML550), L2 (CML176) and L8 (DT-SR-W) as they had positive and significant GCA effects for oil content. For protein content, parental lines L4 (CML182) and L6 (CML550) will be ideal for increasing the protein content in their offspring based on their positive and significant GCA for protein content. Only parental line L3 (CML181) exhibited positive and significant GCA effects for starch content. Overall, grain yield in the hybrids could be increased by using parental lines L2 (CML176) and L3 (CML181) in the developing hybrids due to their positive and significant GCA effects for grain yield.

Table**Table 4.9** General combining ability effects of parental lines used in generating hybrids that were evaluated across different nitrogen availability conditions in two locations.

Parent	GY	AD	SD	ASI	PH	EH	EPP	GM	Oil	Protein	Starch
L1	-0.18*	-0.58*	-0.63**	0.05	0.56	-1.94**	-0.05***	-0.26***	-0.03	-0.06	0.08
L2	0.55***	-0.10	0.03	-0.13	1.36	1.75*	0.06***	0.20**	0.11***	0.08	-0.00
L3	0.20*	-0.94***	-1.17***	0.24*	1.63	0.24	0.01	-0.04	-0.24***	-0.16**	0.45**
L4	-0.03	-0.56*	-0.53***	-0.03	-0.07	-1.06	-0.00	-0.35**	-0.10***	0.23***	-0.33*
L5	0.17	-0.11	-0.28	0.18	-0.06	0.18	0.03**	-0.01	-0.02	0.05	0.15
L6	-0.33***	1.62***	2.08***	-0.45***	3.81***	2.56**	0.02	0.20**	0.38***	0.18***	-0.48***
L7	-0.42***	0.63**	0.55*	0.08	-2.82***	-0.63	-0.03**	-0.01	-0.05*	-0.09	-0.14
L8	0.05	-0.36	-0.45**	0.09	-1.53	1.03	-0.02*	0.03	0.06**	-0.13**	0.06
L9	-0.08	0.33	0.43**	-0.09	-2.20**	-2.08**	0.00	0.40***	-0.09***	-0.09	0.21
L10	0.08	0.06	-0.01	0.07	-0.68	-0.06	-0.02	-0.17*	-0.02	-0.01	0.10
SE	0.10	0.19	0.19	0.12	0.93	0.79	0.01	0.09	0.02	0.05	0.13

GY=grain yield, EPP=ears per plant, SP=shelling percentage, GM=grain moisture, AD=days to anthesis, SD= days to silking, ASI=anthesis silking interval,

PH=plant height, EH=Ear height

Table 4.10 summarizes the GCA effects for grain yield and secondary traits of inbred lines evaluated across low nitrogen conditions. The parents that exhibited desirable GCA effects for Anthesis days and silking days were parental line, L1 (CML144), which tended to reduce the number of days to pollen shedding and silking. Parental line 6 (CML550) had a desirable GCA that reduced the anthesis silking interval, shelling percentage and starch but tended to increase all other measured traits as suggested by its positive GCA for these seven traits. The lines that could reduce plant height were lines L7 (CW14) and L9 (I-43), that had negative GCA effects for plant height of -3.24 and -4.56, respectively. Positive and significant GCA effects for ear height were found in parental line L6 (CML550) only. Early dry down represented by grain moisture could be achieved by using parental lines L4 (CML182), L1 (CML144) and L10 (K64R) as they exhibited negative and significant GCA effects for grain moisture. The parental lines with high potential to increase oil content in their hybrids are parental lines L6 (CML550), L2 (CML176) and L8 (DT-SR-W) as they had positive and significant GCA effects for oil content. For protein content, parental lines L4 (CML182) and L6 (CML550) will be ideal for increasing the protein content in their offspring based on their positive and significant GCA for protein content. Only parental line L3 (CML181) exhibited positive and significant GCA effects for starch content. Overall, grain yield in the hybrids could be increased by using parental line L2 (CML176) in the developing hybrids due to their positive and significant GCA effects for grain yield.

Table**Table 4.10** General combining ability effects of parental lines used in generating hybrids that were evaluated under low nitrogen availability conditions in two locations.

Parent	GY	SP	AD	SD	ASI	PH	EH	EPP	GM	Oil	Protein	Starch
L1	-0.17	-0.24	-0.48*	-0.56*	0.08	1.22	-1.19	-0.03*	-0.28*	-0.06	-0.10	0.10
L2	0.65***	0.09	-0.23	-0.21	-0.01	0.77	1.93	0.04***	0.14	0.11***	0.07	-0.09
L3	0.23	1.92**	-0.45	-0.56*	0.11	0.87	-0.17	-0.00	0.06	-0.33***	-0.17*	0.50***
L4	0.03	0.71	-0.45	-0.69**	0.24	0.91	-0.65	-0.00	-0.31*	-0.11***	0.33***	-0.13
L5	0.26	1.32*	0.22	0.08	0.14	0.60	0.71	0.03*	0.05	-0.05	0.08	0.06
L6	-0.29	-1.65*	1.10***	1.64***	-0.54***	4.72***	2.68*	0.01	0.31*	0.48***	0.18*	-0.64***
L7	-0.73***	-2.00**	0.63*	0.71**	-0.08	-3.34**	-1.13	-0.03*	0.02	-0.05*	-0.07	0.14
L8	0.03	0.35	-0.26	-0.32	0.10	-4.56***	-0.52	-0.02	0.10	0.10***	-0.19*	0.03
L9	-0.25	-0.23	0.11	0.29	-0.18	-0.77	-2.02	-0.10	0.19	-0.07**	-0.07	0.07
L10	0.24	-0.26	-0.22	-0.37	0.15	-0.41	0.35	0.01	-0.28*	-0.02	-0.05	-0.06
SE	0.15	0.62	0.23	0.24	0.14	1.13	1.05	0.01	0.13	0.02	0.08	0.07

Env=environment, REP(Env)=replications within environment, Gen=genotype, Rec=reciprocal, Mat=maternal, GCA=general combining ability, SCA=specific combining ability, GY=grain yield, EPP=ears per plant, SP=shelling percentage, GM=grain moisture, AD=days to anthesis, SD= days to silking, ASI=anthesis silking interval, PH=plant height, EH=Ear height

Table 4.11 summarizes the GCA effects for grain yield and secondary traits of inbred lines evaluated under high nitrogen conditions. Parent L2 (CML176) was the only parent to achieve a highly significant ($P < 0.001$) grain yield increase, while parent 6 registered a significant ($P < 0.01$) grain yield decrease. Line L2 (CML176) revealed positive and significant GCA for yield under high nitrogen, Line L6 (CML550) exhibited positive and significant GCA for oil content and protein. None of the lines showed significant GCA for starch but at least line L3 (CML181) had a positive but non-significant GCA effect for starch and grain yield. Line L7 (CW14) was not significant under high nitrogen for all traits. Parent L8 (DT-SR-W) was significant different for ear height and not significant for all other traits while Line L10 (K64R) were significant only for ears per plant and not for all other traits. The parents that exhibited desirable GCA effects for anthesis days and silking days were parental lines L3 (CML181) and L1 (CML144), which tended to reduce the number of days to pollen shedding and silking. Parental line L6 (CML550) had positive GCA that tend to increase anthesis days and silking days, but reduced grain yield and shelling percentage as suggested by its negative GCA for these two traits. The lines that could reduce plant height was line L9 (I-43), that had negative GCA effects for plant height of -4.11. Genotype L8 (DT-SR-W) had the highest negative GCA effects for ear height (-3.10) followed by genotype L1 (CML144) which also presented negative GCA effect for ear height (-2.94). Positive and significant GCA effects for oil were found in parental lines L2 (CML176) and L6 (CML550). Early dry down represented by grain moisture could be achieved by using parental lines L4 (CML182) as it exhibited negative and significant GCA effects for Grain moisture. The parental lines with high potential to increase oil content in their hybrids are parental lines L6 (CML550) and L2 (CML176) as they had positive and significant GCA effects for oil content. For protein content, parental line

L6 (CML550) will be ideal for increasing the protein content in its offspring based on its positive and significant GCA for protein content. There is no parental line that exhibited positive and significant GCA effects for starch content. Overall, grain yield in the hybrids could be increased by using parental line L2 (CML176) in the developing hybrids due to its positive and significant GCA effects for grain yield.

Table 4.11 General combining ability effects of parental lines used in generating hybrids that were evaluated under high nitrogen availability conditions in two locations.

Parent	GY	SP	AD	SD	ASI	PH	EH	EPP	GM	Oil	Protein	Starch
L1	-0.18	1.74*	-0.72*	-0.73*	0.02	-0.32	-2.94*	-0.08***	-0.23	0.01	-0.02	0.06
L2	0.41***	0.69	0.07	0.35	-0.29	2.16	1.50	0.09***	0.28*	0.12**	0.09	0.11
L3	0.15	1.82*	-1.58***	-1.99***	0.41	2.65	0.79	0.02	-0.16	-0.13**	-0.14*	0.38
L4	-0.12	-1.45	-0.71*	-0.32	-0.39	-1.38	-1.60	-0.00	-0.39**	-0.09*	0.09	-0.61
L5	0.05	0.80	-0.54	-0.77*	0.23	-0.94	-0.52	0.03	-0.09	0.01	0.00	0.26
L6	-0.37**	-2.69**	2.33***	2.66***	-0.34	2.59	2.39	0.03	0.05	0.25***	0.19**	-0.27
L7	-0.02	-0.03	0.64	0.34	0.30	-2.11	0.03	-0.02	-0.03	-0.04	-0.11	-0.51
L8	0.08	-1.52	-0.54	-0.62	0.08	2.51	3.10*	-0.04	-0.06	0.02	-0.04	0.08
L9	0.14	0.32	0.63	0.61	0.02	-4.11*	-2.14	0.02	0.67***	-0.13**	-0.10	0.40
L10	-0.14	0.31	0.43	0.46	-0.04	-1.06	-0.61	-0.05*	-0.04	-0.03	0.03	0.10
SE	0.10	0.83	0.31	0.32	0.20	1.58	1.22	0.02	0.12	0.04	0.06	0.30

GY=grain yield, EPP=ears per plant, SP=shelling percentage, GM=grain moisture, AD=days to anthesis, SD= days to silking, ASI=anthesis silking interval, PH=plant height, EH=Ear height

4.4.2 Specific combining ability of hybrids

Table 4.12 summarizes the SCA effects of hybrids evaluated across sites and nitrogen availability conditions. The crosses L5×L2 (CML511×CML176), and L6×L10 (CML550×K64R) combined well to reduce the anthesis days and silking days as exhibited by their negative SCA effects for these traits. For shorter hybrids, desirable hybrid combinations will be L5×L10 (CML511×K64R), L7×L10 (CW14×K64R), L8×L1 (DT-SR-W×CML144) and L9×L2 (I-43×CML176) as they had negative and significant SCA effects for plant height. The only cross that could result in lower ear height was L8×L1 (DT-SR-W×CML144) as shown by its highly significant and negative SCA effects for ear height. Only two crosses, L4×L1 (CML182×CML144) and L9×L4 (I-43×CML182) could potentially increase ear prolificacy based on their positive SCA effects for ears per plant. Early dry down in hybrids could be achieved by developing the following crosses, L5×L2 (CML511×CML176), L8×L10 (DT-SR-W×K64R), L9×L5 (I-43×CML511) and L9×L7 (I-43×CW14), which had negative and significant SCA effects for grain moisture. Potential increase in oil content would be possible from L3×L10 (CML181×K64R), L4×L1 (CML182×CML144) and L8×L7 (DT-SR-W×CW14) breeding populations that exhibited positive and significant SCA effects for oil content. There were four crosses, L4×L10 (CML182×K64R), L5×L3 (CML511×CML181), L6×L1 (CML550×CML144) and L9×L2 (I-43×CML176) that exhibited positive and significant SCA effects for protein content. Starch content could only be increased from the L8×L3 (DT-SR-W×CML181) cross. Overall, the population from L8×L3 (DT-SRW×CML181) had the highest potential for increasing grain yield with positive SCA effects of 0.70 followed by L6×L4 (CML550×CML182) with 0.54, L7×L1 (CW14×ML144) with 0.49 and L6×L10 (CML550×K64R) with 0.48.

Table 4.12 Specific combining ability of hybrids evaluated across sites under different nitrogen availability treatments.

F	M	GY	AD	SD	ASI	PH	EH	EPP	GM	Oil	Protein	Starch
L10	L1	-0.09	-0.21	-0.23	0.02	2.72	-1.01	-0.20	0.18	-0.4	-0.07	-0.07
L2	L1	0.09	-0.02	-0.35	0.33	-1.94	-0.58	0.03	0.02	-0.10	-0.24*	0.31
L2	L10	0.18	0.15	-0.19	0.33	3.68	0.77	0.04	0.06	-0.03	-0.26*	0.11
L3	L1	0.06	-0.82	-0.53	-0.29	-2.95	-1.78	-0.05*	-0.03	0.05	-0.04	0.076
L3	L10	-0.25	-0.55	-0.04	-0.50	-2.46	0.28	0.00	-0.26	0.12*	-0.05	0.19
L3	L2	-0.06	0.46	0.09	0.38	1.51	1.75	0.03	0.06	0.03	-0.13	0.37
L4	L1	0.13	-0.49	-0.31	-0.18	1.18	2.23	0.07**	0.03	0.10*	-0.04	-0.11
L4	L10	-0.45**	1.28**	1.24*	0.04	0.02	-0.99	-0.03	0.21	0.03	0.23*	-0.17
L4	L2	-0.29	0.22	0.48	-0.26	-0.57	-0.20	-0.01	0.06	-0.01	0.13	-0.25
L4	L3	-0.68***	0.02	0.16	-0.13	-2.83	-1.05	-0.06**	-0.34	0.02	0.03	0.24
L5	L1	-0.24	0.25	-0.38	0.63*	-2.11	-0.75	-0.02	0.27	0.11	0.04	-0.09
L5	L10	0.13	0.62	0.74	-0.12	-5.28*	-0.22	-0.01	0.67*	-0.091	0.20	0.03
L5	L2	0.05	-1.15**	-1.41***	0.27	1.14	-1.04	-0.01	-0.49*	-0.01	-0.06	-0.07
L5	L3	0.24	0.51	0.84	-0.32	5.80**	3.15	0.04	0.29	-0.10	0.28*	0.12
L5	L4	0.39	-0.37	-0.63	0.26	4.36*	-0.84	-1.90	0.40**	-0.10	-0.22	0.01
L6	L1	-0.22	0.92*	0.82	0.10	1.21	3.21	0.02	-0.27	-0.01	0.25*	0.12
L6	L10	0.49*	-0.99*	-0.80	-0.19	-0.90	-1.36	0.02	-0.10	0.04	-0.13	0.27
L6	L2	0.03	0.23	0.68	-0.45	1.51	0.47	0.01	0.04	-0.03	0.084	0.02

L6 L3	-0.64**	1.00*	0.47	0.53*	-3.18	-2.45	-0.04	-0.34	0.02	-0.16	-1.98
L6 L4	0.55**	-0.13	-0.14	0.01	-1.16	0.59	-0.01	-0.17	-0.00	0.10	0.34
L6 L5	-0.24	-0.32	0.33	-0.65	-1.24	-2.38	0.00	-0.32	0.08	-0.08	0.12
L7 L1	0.49**	-0.52	-0.57	0.05	3.76	2.70	-0.00	-0.06	-0.12**	0.04	-0.05
L7 L10	0.146	-0.04	-0.55	0.52*	-5.33**	-0.23	0.023	-0.22	-0.08	0.11	-0.05
L7 L2	0.02	-0.49	-0.25	-0.24	1.43	0.77	-0.06*	0.09	0.04	0.24*	-0.13
L7 L3	0.35	0.21	0.65	-0.44	0.82	-0.57	0.03	0.03	0.04	0.13	0.09
L7 L4	0.04	-0.03	-0.35	0.32	-1.80	0.01	-0.01	-0.17	-0.02	-0.25*	0.36
L7 L5	0.33	0.67	0.68	-0.02	1.40	2.74	0.01	-0.80	0.08	-0.06	-0.21
L7 L6	-0.70***	-0.41	-0.40	-0.02	0.06	-2.40	-0.01	0.72***	-0.06	-0.11	0.50
L8 L1	-0.32	0.72	1.38***	-0.66	-4.07**	-7.37***	0.01	-0.03	-0.06	-0.10	0.07
L8 L10	0.02	-0.09	-0.64	0.56	3.77	4.12*	0.01	-0.40**	-0.0	0.04	-0.21
L8 L2	-0.31	1.14**	1.56***	-0.42	-1.53	0.16	-0.04	0.06	0.09	0.05	-0.23
L8 L3	0.70***	-0.13	-0.83	0.71	0.74	0.43	0.02	0.33	-0.23***	-0.18	0.77**
L8 L4	-0.03	-0.51	-0.19	-0.32	-0.31	-0.78	-0.02	-0.29	-0.02	-0.08	-0.08
L8 L5	-0.50*	-0.77	-0.69	-0.08	-0.78	0.28	0.02	-0.26	0.18***	-0.01	-0.12
L8 L6	0.34	-0.32	-0.741	0.42	-1.69	0.61	-0.03	0.21	-0.06	0.20	0.18
L8 L7	0.26	-0.04	0.12	-0.16	5.02*	1.73	0.04	0.11	0.11*	0.12	-0.47
L9 L1	0.10	0.17	0.17	-0.00	2.19	3.36	-0.04	-0.11	0.03	0.15	-0.26
L9 L10	-0.18	-0.17	0.47	-0.65	3.79	-1.35	-0.04	-0.13	0.05	-0.06	-0.11

L9 L2	0.28	-0.55	-0.61	0.06	-5.23*	-2.10	0.00	0.10	-0.01	0.18	-0.13
L9 L3	0.30	-0.71	-0.79	0.08	2.55	0.23	0.04	0.26	0.04	0.13	0.14
L9 L4	0.35	0.01	-0.25	0.27	1.10	1.03	0.07**	0.28	0.00	0.11	-0.33
L9 L5	-0.15	0.57	0.53	0.04	-3.30	-0.95	-0.04	-0.47*	-0.15***	-0.10	0.20
L9 L6	0.39	0.02	-0.23	0.25	5.40**	3.70*	0.03	0.24	0.03	-0.15	0.43
L9 L7	-0.93***	0.66	0.67	-0.01	-5.36	-4.75	-0.02	-0.42*	0.02	-0.22*	-0.04
L9 L8	-0.16	0.00	0.04	-0.04	-1.15	0.82	-0.00	0.27	-0.02	-0.05	0.09
SE	0.25	0.50	0.51	0.31	2.45	2.09	0.03	0.23	0.06	0.13	0.35

SE=standard error, GY=grain yield, EPP=ears per plant, SP=shelling percentage, GM=grain moisture, AD=days to anthesis, SD= days to silking, ASI=anthesis silking interval, PH=plant height, EH=Ear height.

Table 4.13 summarizes the SCA effects of hybrids evaluated across sites and low nitrogen availability conditions. The crosses L5xL2 (CML511xCML176), and L6xL10 (CML550xK64R) combined well to reduce the anthesis days and silking days as exhibited by their negative SCA effects for these traits. For shorter hybrids, desirable hybrid combinations will be L5xL10 (CML511xK64R), L7xL10 (CW14xK64R), and L9xL2 (I-43xCML176) as they had negative and significant SCA effects for PH. The only cross that could result in lower ear height was L8xL1 (DT-SR-WxCML144) as shown by its highly significant and negative SCA effects for ear height. Only two crosses, L4xL1 (CML182xCML144) and L9xL4 (I-43xCML182) could potentially increase ear prolificacy based on their positive SCA effects for ears per plant. Early dry down in hybrids could be achieved by developing the following crosses, L5xL2 (CML511xCML176), L8xL10 (DT-SR-WxK64R), L9xL5 (I-43xCML511) and L9xL7 (I-43xCW14), which had negative SCA effects for grain moisture. Potential increase in oil content would be possible from

L3xL10 (CML181xK64R), L6xL5(CML550xCML511) and L8xL5 (DT-SR-WxCML511) breeding populations that exhibited positive and significant SCA effects for oil content. There was one cross, L5xL3 (CML511xCML181) that exhibited positive and significant SCA effects for protein content. Overall, the population from L8xL3 (DT-SR-WxCML181) had the highest potential for increasing grain yield with positive SCA effects of 1.00 followed by L6xL10 (CML550xK64R) and L6xL4 (CML550x CML182) 0.85, and L7xL1 (CW14xCML144) 0.82 populations.

Table 4.13 Specific combining ability of hybrids evaluated across sites under low nitrogen availability treatment.

F	M	GY	AD	SD	ASI	PH	EH	EPP	GM	Oil	Protein	Starch
L10	L1	-0.23	-0.39	-0.13	-0.26	0.56	-3.92	-0.01	0.21	-0.01	-0.07	-0.12
L2	L1	0.21	-0.54	-0.97	0.43	-0.86	0.18	0.00	-0.03	-0.07	-0.22	0.37*
L2	L10	0.15	0.71	0.56	0.15	2.10	1.62	0.00	-0.13	-0.04	-0.40	0.38*
L3	L1	0.09	-1.60*	-1.15	-0.45	-3.27	-1.16	-0.03	0.03	0.05	-0.06	-0.24
L3	L10	-0.26	-0.67	-0.43	-0.24	-0.57	0.98	-0.00	-0.51	0.17*	-0.08	-0.11
L3	L2	-0.03	0.68	0.48	0.21	-0.54	0.45	0.01	0.03	-0.02	-0.21	0.13
L4	L1	0.24	-0.15	-0.05	-0.10	1.91	5.49*	0.04	0.05	0.13	-0.06	-0.10
L4	L10	-0.70	1.10	1.36*	-0.26	0.74	-2.82	-0.05	0.42	0.03	0.27	0.00
L4	L2	-0.45	-0.18	0.45	-0.63	-1.12	-2.28	-0.04	0.07	0.03	0.12	-0.16
L4	L3	-0.80*	-0.12	-0.17	0.05	-3.34	0.76	-0.03	-0.39	0.05	-0.06	0.04
L5	L1	-0.62	0.79	0.96	-0.17	-2.46	-1.05	-0.02	0.29	0.01	-0.14	0.29
L5	L10	0.18	0.72	0.36	0.36	-4.69	-2.42	-0.03	0.69*	-0.12	0.27	0.07
L5	L2	0.59	-1.62*	-1.79**	0.18	1.96	2.62	0.06	-0.12	-0.13	-0.06	0.20
L5	L3	-0.20	0.82	0.66	0.17	5.60	0.60	0.03	-0.43	-0.07	0.47*	-0.23
L5	L4	0.08	-0.22	-0.43	0.21	3.72	-0.20	-0.01	0.38	-0.10	-0.28	0.05
L6	L1	-0.11	1.39*	0.95	0.43	0.60	1.57	0.03	-0.25	-0.10	0.33	-0.08
L6	L10	0.85*	-1.81**	-2.02**	0.21	2.62	-0.92	0.04	0.08	0.01	-0.13	0.05
L6	L2	-0.21	0.29	0.20	0.09	4.08	-0.38	0.03	-0.23	-0.08	0.17	-0.50**
L6	L3	-0.75	2.48***	1.77**	0.71	-2.71	-0.97	-0.11***	0.14	0.12	0.13	-0.05
L6	L4	0.85*	-0.76	-0.13	-0.63	-1.78	-2.39	-0.00	-0.06	0.00	0.18	0.02
L6	L5	-0.25	-0.32	0.44	-0.76*	-5.27	-3.05	-0.01	-0.41	0.21**	-0.21	-0.15
L7	L1	0.82*	-0.39	-0.46	0.07	-0.19	1.78	0.00	0.18	-0.12	0.03	0.16

L7	L10	0.31	0.60	-0.05	0.65	-4.67	0.72	0.04	-0.18	-0.0	0.24	-0.07
L7	L2	0.04	-0.23	0.11	-0.34	1.6	0.13	-0.03	0.09	0.09	0.27	-0.12
L7	L3	0.63	-0.48	0.24	-0.72	2.82	0.17	0.06	0.07	-0.04	0.10	-0.09
L7	L4	-0.03	-0.03	-0.5	0.50	-1.57	1.69	0.03	-0.50	0.01	-0.36	0.48**
L7	L5	0.282	-0.1	-0.15	-0.00	4.13	3.78	-0.01	-0.24	0.14*	-0.05	-0.28
L7	L6	-0.71	-0.81	-0.72	-0.09	-1.62	-0.23	-0.01	0.83	-0.02	-0.15	0.15
L8	L1	-0.65	0.84	1.25	-0.41	-2.34	-7.16*	-0.01	-0.09	0.04	-0.05	0.04
L8	L10	0.11	-1.23*	-1.22	-0.01	3.42	7.91**	0.03	-0.60	0.01	0.08	-0.24
L8	L2	-0.75	1.68**	1.56*	0.12	-2.62	-1.17	-0.02	0.01	0.11	0.02	-0.20
L8	L3	1.00*	-0.07	-0.75	0.68	-2.47	-2.13	0.03	0.41	-0.23***	-0.28	0.55**
L8	L4	0.4	-0.55	-0.52	-0.04	5.09	2.82	-0.01	-0.30	-0.13*	0.02	0.06
L8	L5	-0.09	-0.30	-0.01	-0.29	-1.40	0.04	-0.0	0.47	0.2***	-0.01	-0.23
L8	L6	0.04	-0.08	-0.14	0.06	-1.34	0.47	-0.02	-0.28	-0.12	0.08	0.1
L8	L7	-0.1	0.58	0.45	0.13	3.87	-1.52	0.01	0.21	-0.01	0.13	-0.28
L9	L1	0.24	0.04	-0.41	0.45	6.0	4.2	-0.02	-0.38	0.08	0.25	-0.33
L9	L10	-0.41	0.97	1.56*	-0.59	0.50	-1.15	-0.02	0.00	0.00	-0.18	0.04
L9	L2	0.45	-0.81	-0.60	-0.21	-4.61	-1.17	-0.20	0.31	0.10	0.32	-0.10
L9	L3	0.32	-1.0	-0.65	-0.40	4.48	1.30	0.05	0.56	-0.01	-0.0	-0.00
L9	L4	0.37	0.90	0.01	0.89*	-3.65	-3.06	0.08*	0.33	-0.00	0.18	-0.40
L9	L5	0.02	0.28	-0.04	0.32	-1.58	-0.34	-0.02	-0.63	-0.22***	0.02	0.28
L9	L6	0.28	-0.38	-0.36	-0.02	5.42	5.91*	0.03	0.17	-0.00	-0.39	0.37
L9	L7	-1.25**	0.91	1.11	-0.20	-4.37	-6.52*	-0.09**	-0.45	0.00	-0.20	0.05
L9	L8	-0.01	-0.87	-0.63	-0.24	-2.22	0.74	0.01	0.08	0.04	0.02	0.10
SE		0.39	0.62	0.64	0.37	2.96	2.76	0.03	0.34	0.06	0.21	0.18

SE=standard error, GY=grain yield, EPP=ears per plant, SP=shelling percentage, GM=grain moisture, AD=days to anthesis, SD= days to silking, ASI=anthesis silking interval, PH=plant height, EH=Ear height

Table 4.14 summarizes the SCA effects of hybrids evaluated across sites and high nitrogen availability conditions. The crosses L2xL10 (CML176xK64R) and L4xL1 (CML182xCML144) have positive and significant effect on ears per plant. The crosses L6xL2(CML550xCML176), and L8xL2 (DT-SR-WxCML176) combined well to reduce the anthesis silking interval as exhibited by their negative SCA effect for this trait. The only cross that could result in lower ear height was L8xL1 (DT-SR-WxCML144) as shown by its highly significant and negative SCA effects for ear height. Only two crosses, L4xL1 (CML182xCML144) and L9xL4 (I-43xCML182) could potentially increase ear prolificacy based on their positive SCA effects for ears per plant.

Early dry down in hybrids could be achieved by developing the following crosses, L5xL2 (CML511xCML176), L6xL3 (CML550xCML181) and L8xL5 (DT-SR-WxCML511), which had negative and significant SCA effects for grain moisture. Potential increase in oil content would be possible from L5xL1 (CML511xCML144) and L8xL7 (DT-SR-WxCW14) breeding populations that exhibited positive and significant SCA effects for oil content. There were one cross L8xL6 (DT-SR-WxCML550) that exhibited positive and significant SCA effects for protein content. Overall, the population from L5xL3 (CML511xCML181) had the highest potential for increasing grain yield with positive SCA effects of 0.82 followed by L5xL4 (CML511xCML182) 0.81, L8xL6 (DT-SR-WxCML550) 0.74, L8xL7 (DT-SR-WxCW14) 0.75 and L9xL6 (I-43xCML550) 0.55 populations.

Table 4.14 Specific combining ability effects of hybrids evaluated across sites under high nitrogen availability treatment.

F	M	GY	AD	SD	ASI	PH	EH	EPP	GM	Oil	Protein	Starch
L10	L1	0.11	0.03	-0.36	0.40	5.61	2.86	-0.04	0.13	-0.07	-0.07	0.00
L2	L1	-0.08	0.68	0.48	0.20	-3.38	-1.60	0.08	0.09	-0.08	-0.25	0.22
L2	L10	0.24	-0.60	-1.1	0.582	5.80	-0.37	0.10*	0.32	-0.02	-0.09	-0.25
L3	L1	0.01	0.22	0.31	-0.08	-2.52	-2.62	-0.09	-0.10	0.06	-0.03	0.49
L3	L10	-0.24	-0.40	0.47	-0.90	-5.00	-0.64	0.06	0.06	0.05	-0.02	0.59
L3	L2	-0.10	0.17	-0.43	0.60	4.26	3.49	0.06	0.10	0.11	-0.02	0.70
L4	L1	-0.0	-0.95	-0.66	-0.28	0.21	-2.12	0.12*	0.01	0.08	-0.02	-0.13
L4	L10	-0.13	1.52	1.09	0.44	-0.94	1.44	-0.0	-0.08	0.04	0.	-0.39
L4	L2	-0.08	0.7	0.51	0.24	0.16	2.57	0.02	0.05	-0.07	0.15	-0.38
L4	L3	-0.52	0.21	0.59	-0.38	-2.15	-3.45	-0.11*	-0.28	-0.01	0.14	0.49
L5	L1	0.26	-0.48	-2.1*	1.70**	-1.65	-0.36	-0.02	0.24	0.24*	0.21	-0.61
L5	L10	0.06	0.49	1.24	-0.75	-6.0	2.70	0.02	0.63*	-0.04	0.11	-0.03
L5	L2	-0.66*	-0.53	-0.91	0.3	0.04	-5.9	-0.10*	-1.00**	0.14	-0.06	-0.42
L5	L3	0.82**	0.09	1.08	-0.98	6.07	6.56*	0.06	1.25***	-0.15	0.04	0.58
L5	L4	0.81**	-0.57	-0.89	0.3	5.22	-1.70	0.01	0.44	-0.0	-0.13	-0.04
L6	L1	-0.37	0.29	0.65	-0.36	2.03	5.40	0.01	-0.29	0.10	0.15	0.38
L6	L10	0.00	0.0	0.82	-0.72	-5.60	-1.94	-0.00	-0.34	0.09	-0.13	0.56
L6	L2	0.35	0.16	1.33	-1.17*	-1.93	1.60	-0.03	0.40	0.04	-0.04	0.71
L6	L3	-0.48	-0.97	-1.27	0.30	-3.81	-4.42	0.05	-0.10**	-0.12	-0.54**	-4.55***
L6	L4	0.14	0.70	-0.15	0.85	-0.33	4.58	-0.01	-0.33	-0.01	-0.02	0.75
L6	L5	-0.24	-0.3	0.17	-0.50	4.14	-1.49	0.01	-0.21	-0.08	0.09	0.49
L7	L1	0.05	-0.70	-0.73	0.03	9.01*	3.94	-0.02	-0.38	-0.11	0.06	-0.32
L7	L10	-0.0	-0.89	-1.23	0.3	-6.22	-1.50	0.01	-0.28	-0.13	-0.06	-0.02
L7	L2	-0.02	-0.83	-0.72	-0.12	1.21	1.62	-0.09	0.11	-0.04	0.21	-0.14
L7	L3	-0.04	1.13	1.19	-0.06	-1.84	-1.57	-0.07	-0.02	0.15	0.17	0.32
L7	L4	0.12	-0.04	-0.11	0.07	-2.12	-2.2	-0.060	0.27	-0.07	-0.09	0.2
L7	L5	0.40	1.76*	1.80*	-0.03	-2.2	1.36	0.03	0.14	0.00	-0.09	-0.11
L7	L6	-0.69*	0.12	0.04	0.08	2.30	-5.28	-0.01	0.58	-0.12	-0.07	0.96
L8	L1	0.12	0.55	1.55	-0.99	-6.37	-7.66*	0.02	0.04	-0.19*	-0.16	0.12
L8	L10	-0.10	1.44	0.13	1.31*	4.23	-0.93	-0.01	-0.13	-0.03	-0.02	-0.17
L8	L2	0.29	0.42	1.56	-1.14*	-0.09	1.94	-0.07	0.13	0.07	0.10	-0.28
L8	L3	0.30	-0.21	-0.96	0.75	5.02	3.84	0.00	0.12	-0.22*	-0.05	1.05
L8	L4	-0.67*	-0.46	0.24	-0.70	-7.5	-5.57	-0.03	-0.30	0.12	-0.22	-0.27

L8	L5	-1.06***	-1.40	-1.60	0.20	0.05	0.60	0.06	-1.23***	0.04	-0.01	0.04
L8	L6	0.74**	-0.64	-1.53	0.90	-2.17	0.80	-0.04	0.87**	0.03	0.38*	0.18
L8	L7	0.75**	-0.87	-0.32	-0.55	6.55	6.06	0.08	-0.02	0.27**	0.12	-0.74
L9	L1	-0.10	0.34	0.94	-0.61	-2.93	2.14	-0.06	0.25	-0.03	0.03	-0.16
L9	L10	0.13	-1.70*	-0.98	-0.72	8.18	-1.63	-0.07	-0.32	0.10	0.11	-0.30
L9	L2	0.06	-0.22	-0.63	0.42	-6.06	-3.34	0.0	-0.18	-0.15	-0.00	-0.17
L9	L3	0.25	-0.26	-0.98	0.72	-0.03	-1.19	0.02	-0.14	0.12	0.31	0.33
L9	L4	0.33	-1.18	-0.61	-0.56	7.45	6.48*	0.07	0.22	0.01	0.02	-0.24
L9	L5	-0.38	0.96	1.30	-0.34	-5.58	-1.76	-0.07	-0.26	-0.07	-0.25	0.10
L9	L6	0.55*	0.57	-0.05	0.61	5.37	0.76	0.03	0.33	0.07	0.17	0.52
L9	L7	-0.49	0.33	0.08	0.25	-6.67	-2.39	0.07	-0.41	0.05	-0.25	-0.1
L9	L8	-0.36	1.16	0.93	0.23	0.2	0.93	-0.01	0.51	-0.09	-0.14	0.07
		0.28	0.82	0.83	0.54	4.16	3.20	0.05	0.31	0.10	0.17	0.78

4.3 Variance components

The variance components calculated across all the environments are presented in Table 4.15. The GCA variance exhibited a wide range of variability with estimates between 0.01 and 20.39. SCA was lowest for ears per plant while PH that had the highest SCA estimate. The GCA variance estimates for nutrients was between 0.10 for protein and 0.36 for starch. Grain yield had a GCA variance of 0.47. In comparison, SCA variance varied from 0.00 to 24.34 recorded for ears per plant and plant height, respectively. Starch had the highest SCA variance estimate of 0.19 among all the nutrients. The SCA variance for grain yield was 0.57. For all the traits except GM and protein, the non-maternal variance estimates were higher than the maternal variance estimates.

The GCA:SCA ratios ranged between 0.80 to 8.03. Among the agronomic traits, the highest GCA:SCA ratio was calculated for anthesis days (6.19) followed by ear height (5.68). Grain yield had a GCA:SCA ratio of 0.83. For nutrients, the ratios were 8.03, 2.95 and 1.84 for oil, protein, and starch contents, respectively. Plant height exhibited the highest phenotypic variance estimate

of 299.05 compared to 0.05 recorded for ears per plant. For grain yield, the phenotypic variance was about 4.14 while oil, protein and starch contents exhibited phenotypic variance estimates of 0.54, 0.90 and 5.55, respectively. The heritability estimates for all the traits were generally below 0.50 except for oil content that was highly heritable at 0.68 and 0.70 for narrow and broad heritability estimates, respectively. The highest heritability estimates among the agronomic traits were calculated for silking days with narrow and broad heritability estimates of 0.45 and 0.51, respectively. For grain yield, the narrow sense heritability estimate was 0.23 compared to 0.37 estimated for the broad sense heritability.

Table 4.15 Variance components calculated for 90 hybrids and their parents evaluated across two environments under different nitrogen availability conditions.

Component	GY	AD	SD	ASI	PH	EH	EPP	GM	Oil	Protein	Starch
GCA	0.47	3.47	5.26	0.16	20.39	10.89	0.01	0.29	0.19	0.10	0.36
SCA	0.57	0.56	1.40	0.20	24.34	1.92	0.00	0.20	0.02	0.03	0.19
Maternal	0.01	0.58	0.56	0.00	3.93	0.00	0.00	0.12	0.00	0.01	0.00
Non-Maternal	0.32	1.62	0.72	0.00	9.36	2.16	0.00	0.06	0.03	0.00	0.22
GCA-SCA ratio	0.83	6.19	3.77	0.80	0.84	5.68	3.61	1.44	8.03	2.95	1.84
Phenotypic Variance	4.14	19.22	23.17	4.00	299.05	182.75	0.05	3.02	0.54	0.90	5.55
Narrow Heritability	0.23	0.36	0.45	0.08	0.14	0.12	0.27	0.19	0.68	0.22	0.13
Broad Heritability	0.37	0.39	0.51	0.13	0.22	0.13	0.30	0.26	0.72	0.26	0.16

GCA=general combining ability, SCA=specific combining ability, GY=grain yield, EPP=ears per plant, SP=shelling percentage, GM=grain moisture, AD=days to anthesis, SD= days to silking, ASI=anthesis silking interval, PH=plant height, EH=Ear height

The GCA variance exhibited a wide range of variability with estimates between 0.17 and 20.58 under low nitrogen availability condition as presented in Table 4.16. GCA was lowest for ears per plant compared to plant height that had the highest GCA estimate. The GCA variance estimates for nutrients was between 0.08 for protein 0.30 for starch. Grain yield had a GCA variance of 0.48. In comparison, SCA variance varied from 0.00 to 6.36 recorded for ears per plant and plant height, respectively. Starch had the highest SCA variance estimate of 0.11 among all the nutrients. The SCA variance for grain yield was 0.45. For all the traits except plant height, grain moisture and protein, the non-maternal variance estimates were higher than the maternal variance estimates. The GCA:SCA ratios ranged between 0.41 to 11.69. Among the agronomic traits, the highest GCA:SCA ratio was calculated for grain moisture (4.67) followed by plant height (3.24). Grain yield had a GCA:SCA ratio of 1.08. For nutrients, the ratios were 5.02, 11.69 and 2.71 for oil, protein, and starch contents, respectively. Plant height exhibited the highest phenotypic variance estimate of 233.36 compared to 0.03 recorded for ears per plant. For grain yield, the phenotypic variance was about 4.89 while oil, protein and starch contents exhibited phenotypic variance estimates of 0.48, 1.36 and 1.36, respectively. The heritability estimates for all the traits were generally below 0.50 except for oil content that was highly heritable at 0.07 and 0.77 for narrow and broad heritability estimates, respectively. The highest heritability estimates among the agronomic traits were calculated for silking days with narrow and broad heritability estimates of 0.24 and 0.33, respectively. For grain yield, the narrow sense heritability estimate was 0.24 compared to 0.29 estimated for the broad sense heritability.

Table 4.16 Variance components calculated for 90 hybrids and their parents evaluated across two environments under low nitrogen availability conditions.

Component	GY	AD	SD	ASI	PH	EH	EPP	GM	Oil	Protein	Starch
GCA	0.48	0.84	1.81	0.12	20.58	3.57	0.00	0.11	0.17	0.08	0.30
SCA	0.45	2.03	1.44	0.09	6.36	1.96	0.00	0.02	0.03	0.01	0.11
Maternal	0.02	0.00	0.00	0.01	2.98	0.00	0.00	0.03	0.00	0.03	0.00
No Maternal	0.21	1.78	1.67	0.00	0.00	16.85	0.00	0.00	0.02	0.00	0.01
GCA-SCA ratio	1.08	0.41	1.26	1.38	3.24	1.82	1.27	4.76	5.02	11.69	2.71
Phenotypic Variance	4.80	13.29	15.18	3.12	233.36	182.30	0.03	2.63	0.48	1.03	1.36
Narrow Heritability	0.20	0.13	0.24	0.08	0.18	0.04	0.11	0.09	0.70	0.16	0.45
Broad Heritability	0.29	0.28	0.33	0.10	0.20	0.05	0.15	0.10	0.77	0.16	0.53

GCA=general combining ability, SCA=specific combining ability, GY=grain yield, EPP=ears per plant, SP=shelling percentage, GM=grain moisture, AD=days to anthesis, SD= days to silking, ASI=anthesis silking interval, PH=plant height, EH=Ear height

Table 4.17 reports the variance components for traits recorded under high nitrogen availability conditions. The GCA variance exhibited a wide range of variability with estimates between 0.01 and 8.37. GCA was lower for ears per plant compared to plant height that had the highest GCA estimate. The GCA variance estimates for nutrients were between 0.02 for protein and 0.07 for starch. Grain yield had a GCA variance estimate of 0.11. In comparison, SCA variance estimates varied from 0.00 recorded for anthesis days and ears per plant, and 11.09 recorded for plant height. Starch had the highest SCA variance estimate of 0.10 among all the nutrients. The SCA variance for grain yield was 0.34. For all the traits except anthesis days and silking days, the non-maternal variance estimates were higher than the maternal variance estimates. The GCA:SCA ratios ranged

between 0.31 to 16.0. Among the agronomic traits, the highest GCA:SCA ratio was calculated for silking days (4.46) followed by ears per plant (4.03). Grain yield had a GCA:SCA ratio of 0.31. For nutrients, the ratios were 16.00, 0 and 0.68 for oil, protein, and starch contents, respectively. Plant height exhibited the highest phenotypic variance estimate of 308.52 compared to 0.05 recorded for ears per plant. For grain yield, the phenotypic variance was about 1.88 while oil, protein and starch contents exhibited phenotypic variance estimates of 0.25, 0.48 and 9.72, respectively. The heritability estimates for all the traits were generally below 0.50. The highest heritability estimates among the agronomic traits were calculated for silking days with narrow and broad heritability estimates of 0.39 and 0.43, respectively. For grain yield, the narrow sense heritability estimate was 0.11 compared to 0.30 estimated for the broad sense heritability.

Table 4.17 Variance components calculated for 90 hybrids and their parents evaluated across two environments under high nitrogen availability conditions.

Component	GY	AD	SD	ASI	PH	EH	EPP	GM	Oil	Protein	Starch
GCA	0.11	3.17	4.16	0.08	8.37	6.61	0.01	0.22	0.04	0.02	0.07
SCA	0.34	0.00	0.93	0.50	11.09	3.32	0.00	0.40	0.00	0.00	0.10
Maternal	0.01	0.54	0.58	0.00	3.36	0.00	0.00	0.08	0.00	0.00	0.00
No Maternal	0.14	0.33	0.35	0.39	7.97	1.42	0.00	0.10	0.02	0.02	0.01
GCA-SCA ratio	0.31		4.46	0.17	0.75	1.99	4.03	0.53	16.0		0.68
Phenotypic Variance	1.88	18.21	21.48	5.48	308.52	175.54	0.05	2.53	0.25	0.48	9.72
Narrow Heritability	0.11	0.35	0.39	0.03	0.05	0.08	0.22	0.17	0.28	0.08	0.01
Broad Heritability	0.30	0.35	0.43	0.12	0.09	0.09	0.25	0.33	0.29	0.08	0.02

GCA=general combining ability, SCA=specific combining ability, GY=grain yield, EPP=ears per plant, SP=shelling percentage, GM=grain moisture, AD=days to anthesis, SD= days to silking, ASI=anthesis silking interval, PH=plant height, EH=Ear height

4.5 Summary

The ANOVA showed that the genotypes exhibited genetic variation which was further augmented by environmental influence on the expressed phenotype. The observed differences were influenced by location and nitrogen availability effects. Furthermore, superior genotypes with high yield, early maturity, favorable plant height and nutritional content were identified. The variance component showed that genotypic environmental variances were important in determining the trait heritability estimates. The parental lines showed differences in their combining ability. Parental lines with desirable GCA effects for yield, earliness, height and nutritional content were identified for selection. Similarly, there were superior crosses that exhibited desirable SCA effects for grain yield, earliness, height, and nutritional content.

Chapter 5: DISCUSSION

5.1 Introduction

5.2 Genotypic and environmental influence on agronomic traits and nutritional value under different nitrogen availability conditions

Overall, the environment main effects, genotypes main effects and their interaction effects affected agronomic performance of the hybrids tested in this study. This observation agrees with assertions that agronomic traits are quantitative traits that are influenced by environmental conditions and genetic constitution of the genotype (Dhariwal and Randhawa, 2022; Caballero, 2020). Quantitative traits are controlled by many genes and each genotype possess a different genetic make-up to other genotypes leading to the variation that is observed phenotypically (Kearsey and Pooni, 2020). Genotype performance is influenced by environmental conditions including soil nitrogen (Savolainen *et al.*, 2013).

Similarly, environment main effects and genotype main effects had significant impact on all the traits under low soil nitrogen conditions, while grain moisture content, anthesis to silking interval, plant height, and ear height did not exhibit significant genotypic variation which indicated that trait expression varied depending on the trait. Nitrogen availability is important for plant growth and development and its deficiency significantly impacts genotype performance (Plett *et al.*, 2020). The lack of genotypic differences for traits such as plant height, and anthesis to silking interval under poor nitrogen availability could be a result of the confounding effects of poor plant development due to low nitrogen availability. A severe environmental constraint could be so detrimental to plant growth such that inherent differences in agronomic performance can be

masked phenotypically leading to poor selection (Gavrilescu, 2021; Bhattacharya and Bhattacharya, 2021). The genotype by environment interaction mean squares were significant for anthesis and silk emergence dates, and starch and oil content under low soil nitrogen suggesting that plant growth and nutritional quality can be controlled by manipulating the growing environment and cultivating suitable cultivars. In some crops such as vegetables, soil nutrient content is manipulated to alter nutritional content, color, or flavor of vegetables (Sandhu *et al.*, 2021). Similarly, in field crops such as maize, the nutritional content would be expected to fluctuate with availability of soil nutrients such as nitrogen. Low nitrogen content in the soil reduces plant growth and ultimately agronomic performance while hindering biochemical process such as protein and oil synthesis (Sandhu *et al.*, 2021). Plant nutrients such as protein contain appreciable amounts of nitrogen and its deficiency in the soil can lead to skewed biochemical process or inadequate activation of the necessary biosynthesis pathways (Wang *et al.*, 2024).

Under high nitrogen availability, the environment effects were significant on all measured traits while genotype effects were only important for grain yield, anthesis days and silking days which can be attributed to the genotypes' ability to fully express their genetic potential and inherent differences. Significance of genotypic variation for grain yield and flowering indicates that there was opportunity for selecting hybrids which are highly productive, early, and late maturing under these full nitrogen fertilizer conditions. When soil nutrition is optimal, it allows genotypes to fully express their genetic potential in yield production, agronomic performance, and nutritional quality (Yahaya *et al.*, 2023). Optimal conditions enable effective selection of superior genotypes, but some genotypes could be superior under optimal conditions and have not dynamic stability to perform well under sub-optimal conditions (Liu *et al.*, 2022). However, the nutritional content did not vary significantly among the genotypes under high nitrogen availability, probably because all

the genotypes managed to accumulate high enough nutrients promoted by adequate soil nutrients availability. Nitrogen availability promotes availability of other nutrients such as phosphorus and ammonia which promote good agronomic performance and nutritional quality of maize (Zeng *et al.*, 2022). The significant variation among genotypes for yield production, agronomic performance and nutritional quality is important for breeding purposes. Successful breeding depends on availability of wide genetic variation for breeders to select from. The amount of phenotypic variability that passes from one generation to the next during breeding depends on the relative importance of these genotypic effects (Araus *et al.*, 2023.).

5.3 Genotypic variation in agronomic performance and nutritional quality across environments

The genotypes showed significant variation for agronomic performance and nutritional quality, which is vital for selection. The different hybrids had different parental combinations which means that they were genetically different, hence the variation in their agronomic performance. Agronomic traits are quantitative traits that are affected by genotype and environment effects and their interaction (Sjoberg *et al.*, 2020). Other studies have also reported differences in agronomic performances in maize (Amegbor *et al.*, 2022). Variation in agronomic performance and nutritional values provides opportunities for selection. Superior genotypes can be identified and selected for the broad or specific environments or for developing breeding populations.

Genotypes such as entry L27 can be used in developing early flowering hybrids. As drought and unpredictable seasons become more frequent, there is need for short season maize to fit in the shorter growing seasons (Simanjuntak *et al.*, 2023; Ayugi *et al.*, 2022). Ear prolificacy is important in drier areas of South Africa where maize is planted at low population densities and each plant is

expected to produce at least two ears. Genotype L18 will be important to increase ear prolificacy in hybrids that can be deployed in the low population density production areas.

Grain yield was highest in genotype L2, which means it can be selected for breeding high yield potential maize to enhance productivity of hybrids. Genotype L2 expressed positive and significant GCA for grain yield as well, showing its potential to pass additive gene effects for grain yield improvement in its offspring. In this study, there were some genotypes including entry L11 and L35 that were identified to be superior to commercial checks which means they have potential to replace these hybrids that are already on the market. The differences in mean performance across different environments shows that the environment is important and that some genotypes lack stability and there was opportunity to select hybrids with specific adaptation to certain target environments. In general, the average yield was higher under high nitrogen conditions which is expected given the importance of nitrogen in plants. Nitrogen is important for growth and development (Madan *et al.*, 2022; Ghadirnezhad *et al.*, 2024). Therefore, plants cannot attain their potential yield when nitrogen availability is limiting. Cedara and Potchefstroom stations represent different agroecological zones in South Africa. Cedara represents the higher potential area of the mist belt in KwaZulu-Natal province compared to Potchefstroom, which is in the drier Northwest province. Several studies have shown that the coastal region of KwaZulu-Natal has higher yield potential compared to the Northwest province (Modi and Mabhaudhi, 2020), which could explain the lower yield attained at Potchefstroom.

5.4 Crossover ranking of genotypes under different nitrogen management conditions.

In general, genotypes that performed had high grain yield productivity, and nutrients accumulation under low nitrogen conditions also performed well under high nitrogen conditions improve. This positive correlation between performance under the different nitrogen conditions is important for breeding because selection could be made in one environment to save breeding costs. However, the weaker coefficients of determination for grain yield and protein content shows that these traits were more influenced by nitrogen availability compared to oil and starch contents. Grain yield is a complex trait that is known to be hugely influenced by environmental conditions. Protein, oil and starch contents are also quantitative traits that have complex genetic (Wang et al., 2015; Zhang et al., 2015).

Genotypes that produced reasonably high yield under both conditions were genotypes 35, 11, 36, 60, 1 and 14. These hybrids exhibited more stable yield production. High oil content under both conditions was found in genotypes 37, 76, 58, and 40. High protein content across the two nitrogen regimes was found in genotypes 39, 84, 44, 13 and 70. The genotypes that had consistently high starch content under both nitrogen management conditions were 75, 2, 19, 29, 26, 52 and 23. Such genotypes that perform well under both nitrogen conditions have efficient nitrogen use, deep root systems, and robust growth, that is critical in both low and high nitrogen conditions (Buchaillet *et al.*, 2019). Furthermore, genomic studies have also identified genomic regions that are responsible for high yield and agronomic performance in both low and high nitrogen conditions (Kimutai *et al.*, 2023). Although there was a linear relationship between grain yield under low and high nitrogen conditions, the rankings of genotypes exhibited crossover ranking. Crossover ranking is when the rankings of genotypes are not consistent in time or space due to the confounding effects of the environment on trait expression (Happ *et al.*, 2021). Quantitative traits such as grain yield,

and nutritional content are subject to environment fluctuations that cause crossover ranking in performance (Qu *et al.*, 2021).

5.4 Variance and heritability of traits under different environmental conditions

The generally higher genotypic variance and heritability estimates for traits under non-stressed conditions signify that the genotypes had higher expression of their genetic potential under more favorable growing conditions. Water is important in maintaining cellular integrity, cell expansion (Seleiman *et al.*, 2021; Chaudhry *et al.*, 2022) and enzyme activity (Kapoor *et al.*, 2020). These processes are critical for plant growth and the expression of traits such as flowering and silking dates, plant height, and grain moisture (Khatibi *et al.*, 2022), which affect grain productivity. Grain production is dictated by the genetic variance but there is also a variable component determined by the external factors (Yadav *et al.*, 2023).

The GCA variance estimates exhibited a wide range showing that the traits were impacted differently by the genotype of the parental lines. Traits that exhibit high GCA variance can be estimated from the parental values more accurately compared to those traits that have lower GCA variance (Rogers *et al.*, 2021). The GCA component is the heritable component of variance that is important for breeding and can be exploited by selecting desirable parental lines (Mukri *et al.*, 2022). The SCA variance component also varied across the traits showing that traits are governed by different allele interactions. The SCA component arise from dominance, epistasis or over dominance when there is recombination between male and female alleles in the offspring (Asrat and Gojjam, 2022). While SCA can be beneficial in heterosis breeding, it is difficult to breed for because it happens by chance and the breeder has no control over allelic interactions (Muthoni and

Shimelis, 2020). High SCA variance arises when there is favorable allelic interaction between allele's derived from the male and female parents in the hybrid (Labroo *et al.*, 2021).

In addition, maternal and non-maternal variance components affected the traits differently. The traits that exhibited higher maternal variance estimates signify that they are controlled by genetic components located within the cytoplasm. Cytoplasmic genetic components are inherited from the maternal parent that contributes the cytoplasm after fusion of the male and female gametes (Camus *et al.*, 2022). From a breeding standpoint, traits that are affected by maternal effects require more attention to the crossing direction when designing crosses during breeding population development. Breeders should be careful when generating crosses on which parent to use as a female parent when considering traits that exhibited significant maternal effects. Most traits including grain yield did not exhibit significant maternal variance estimates showing that they are not affected by the crossing direction between two parental lines, either of the parental lines involved in the cross could be used as male or female parent. Reportedly, maternal effects were absent for grain yield in other studies on maize (Aboyousef *et al.*, 2022). However, John *et al.* (2024) found that both xenia and maternal effects were influential in conditioning kernel size and grain yield in maize. In this study, traits such as grain moisture content, plant height and anthesis to silking interval exhibited significant maternal variance estimates showing that they are affected by the choice of maternal parent. Similarly, it was found that silking in maize was influenced by maternal effects and depended more on the choice of lines used as female parents (Arunkumar *et al.* 2022; Ramadan and Muhammad, 2020).

The differences in variance component estimates for each trait among the different treatment conditions suggest that trait response is an aggregate of genetic, environmental and their interactive

effects. In general, this study found that stress conditions reduced genotypic variance, which means that environment conditions assume a more important role in conditioning trait expression under stress conditions. In contrast, the genotypic variance component was stronger under optimal condition showing that the genotypes expressed their genotypic potential more under optimal conditions. Stress conditions such as nitrogen deficiency can reduce the expression of growth and development. For instance, nitrogen stress has been implicated in reducing grain filling, cell expansion and multiplication resulting in higher environmental variance than genotypic variance (Anas *et al.*, 2020). Both stress and optimal conditions are important in breeding as they provide different approaches to identifying superior genotypes and quantifying heritability of traits. Optimal conditions allow the breeder to estimate the full genetic potential of the germplasm, while stress conditions provide a basis to understand reactive or dynamic adaptation (Nyoni *et al.*, 2023).

The narrow sense heritability estimates the additive genetic component while the broad sense heritability entails the additive, non-additive and epistatic genetic components (Coelho *et al.*, 2020). It is imperative to base breeding efforts on the narrow sense heritability estimates, which are related to GCA that can be influenced by parental line selection. In this study, narrow sense heritability estimates were generally higher under optimal nitrogen availability except for grain yield, anthesis silking interval, plant height and oil and protein contents. Optimal nitrogen conditions allow genotypes to express higher genetic variance and reduced environmental variance leading to higher heritability estimates (Tucker *et al.*, 2020). Some traits such anthesis and silking were enhanced by stress leading to higher heritability estimates under stress rather than optimal conditions, which contrasted with many assertions showing that heritability estimates are higher under optimal conditions (Ertiro *et al.*, 2020). However, environmental stress such as drought, heat and low soil nutrient availability are known to accelerate reproductive growth in plants (Dos Santos

et al., 2022). When plants encounter such stresses, they are stimulated into reproductive phase as a mechanism to produce seed for survival in the next generation. Thus, stress accelerated flowering and anthesis dates in this study possibly because the maize engaged in survival mode. The heritability estimates were moderate for anthesis days, silking days, and grain moisture showing that these traits are strongly controlled by the genetic make-up compared to the other traits indicating that selection would be effective to improve the base breeding populations for these traits. However, there remained a significant portion influenced by the environment. The other traits had weak heritability estimates that suggested that the environment was more influential in conditioning the phenotypic expression of those traits. In contrast to findings of this study, plant height has been reported to be strongly controlled by genes, with moderate to high heritability due to the major *Rht* allele (Liu *et al.*, 2020). However, in this study we found low heritability estimates for plant height which led to the contrasting results. The quantitative nature of plant height means that measurements and calculations of heritability estimates is influenced by the population under investigation, prevailing environmental conditions and the accuracy of measurement. These could have led to the observed contrasts from previous reports.

Across the environments and nitrogen conditions, the broad sense heritability estimate for ear height was 0.13 while it was 0.13 for anthesis silking interval. In comparison, the corresponding narrow sense heritability estimate for ear height and anthesis silking interval were 0.12 and 0.08, respectively. Under low nitrogen conditions, the broad sense heritability estimates for ear height and anthesis silking interval were lower. The recorded broad sense heritability estimates for ear height and anthesis silking interval were 0.05 and 0.10, respectively. In general, broad sense heritability estimates were lowest under low nitrogen conditions. Traits such as plant height, ear height and anthesis silking interval recorded broad sense heritability of 0.09, 0.09 and 0.12

respectively. This study has shown that quantitative traits including yield, plant height and ear prolificacy are strongly influenced by the environment by presenting highly significant and positive values. This have also been confirmed by Ross *et al.*, (2020). Traits with low heritability estimates indicate that they are controlled by several genes with small cumulative effects (Afolabi *et al.*, 2020). Quantitative traits are not easy to select for and their selection response is variable under different environments (Bocianowski *et al.*, 2021). Numerous selection cycles will be required to improve such traits with low heritability, which increases the cost of breeding for new cultivars. However, nutritional traits usually have high heritability estimates because they are qualitative traits with fewer genes influencing their expression (Sinha *et al.*, 2021). In this study, protein, a key component of QPM, exhibited low heritability estimates suggesting that the environment had higher influence compared to the genetic component. The QPM trait is primarily controlled by a few key genes although overall, a combination of factors affects its expression, which could reduce its heritability across environments (Amegbor *et al.*, 2022). The *Opaque 2* is the important gene for QPM but works in combination with some modifier genes and quantitative trait loci (QTL) to influence the QPM expression in maize (Maqbool *et al.*, 2021). Usually, the trait should express high levels of heritability due to the few genes in control, but the involvement of the modifier genes and QTLs makes its expression variable under different environments leading to high environmental variance and low heritability estimates. Heritability for QPM has been estimated between 11 and nearly 70% while the building blocks for QPM, lysine and tryptophan have shown moderate to high heritability values (Amegbor *et al.*, 2022).

5.5 Combining ability across nitrogen environments.

The significant genotype x environment interaction variance revealed in the analysis of variance is usual for quantitative traits, such as grain yield, grain moisture, anthesis days, silking days, anthesis

silking interval, shelling percentage and oil content. Genotype x environment interaction effects provide both challenges and opportunities in breeding. As a challenge, they make selection across environment to be difficult and less effective. However, it can be beneficial in identifying superior genotypes with specific adaptation to a niche environment or broad adaptation to several environments (Shandu *et al.*, 2022). Potential hybrids were identified for potential yield by presenting positive and significant SCA across nitrogen availability conditions were L8xL3 (DTSR-W x CML181), L5xL3 (CML511xCMI181) under high nitrogen availability conditions and L6xL4 (CML550xCML182) under low nitrogen availability conditions. The significant genotypic variance found in this study could be due to genotypic differences among the hybrids and parental lines and their response to environmental conditions. Gene action analysis can be conducted in circumstances where the genotypes have opportunities to express their genetic potential (Rai *et al.*, 2021). The environmental variance was significant for all traits showing that trait expression for all traits varied from one environment to another. This is consistent with the findings of Amegbor *et al.* (2023), who also identified the location as a highly significant factor, while investigating the combining ability of maize. Conversely, maternal and non-maternal effects did not have large effects on the measured traits, suggesting that the genetic factor of the traits was not harbored in the cytoplasm. For traits such as grain yield that were influenced by significant maternal effects, the crossing direction that determines which parent is used as a female during hybridization becomes more important. Maternal effects can be important source of phenotypic variance (Moore *et al.*, 2019).

The analysis of variance for yield and agronomic traits revealed that GCA variance was more important for most measured traits, especially silking days, grain moisture and oil content, compared to SCA. This suggested that the traits were mainly influenced by additive genetic effects.

The observed results are consistent with several previous studies (Magar *et al.*, 2021), yet differ from Amegbor *et al.* (2020), who reported that SCA was more important than GCA for conditioning grain yield. The knowledge of gene action conditioning traits is important as it helps to devise an appropriate breeding design (Muthoni *et al.*, 2020). The higher significance of GCA effects for most traits under low nitrogen compared to high nitrogen conditions could indicate that additive gene action is more important when plants are subjected to stress conditions (Wang *et al.*, 2021). The parents that exhibited desirable GCA effects for anthesis days and silking days were parental lines L3 (CML181), L1 (CML144) and L4 (CML182), which tended to reduce the number of days to pollen shedding and silking. Early dry down represented by grain moisture could be achieved by using parental lines L4 (CML182), L1 (CML144) and L10 as they exhibited negative and significant GCA effects for grain moisture. These parents with desirable GCA effects for anthesis days, anthesis silking interval and grain moisture can be used in developing early maturing hybrids, which are suitable for the short seasons especially in the eastern regions of South Africa.

Parents with negative GCA effects for days to flowering and silking and grain moisture content, which is desirable, contributed genes to that reduce the time to flowering and silking and dry down in hybrids. This contributes to early maturity in their hybrids. Parents with desirable GCA effects under a set of conditions show that they can transfer their heritable traits to their offspring. However, parental lines that exhibit desirable GCA effects across diverse conditions will be more useful for breeding as their resultant hybrids can be deployed across wider production regions (Amegbor *et al.*, 2022). In this study the following line exhibited desirable GCA across grain yield L2 (CML176) in developing hybrids due to their positive and significant GCA effects for grain yield. Similarly, genotypes with negative GCA effects for plant height could be useful in developing shorter hybrids with improved stalk or root lodging resistance.

The genotypes that could be useful in reducing plant height of hybrids were parental lines L7 (CW14) and L9 (I-43), that had negative GCA effects for plant height. Genotype L9 (I-43) had the highest negative GCA effects for ear height followed by parent L1 (CML144), which is also helpful in ensuring that ear insertion is reduced to avoid preponderance of stalk lodging. Semi-dwarfing genes *Rht1* and *Rht2* have been reported to be involved in controlling plant height and help in improving drought tolerance by increasing root volume in the topsoil horizons (Agarwal *et al.*, 2020). Positive and significant GCA effects for ears per plant were found in parental lines L2 (CML176) and L5 (CML511) showing that they can increase the number of ears per plant in the hybrids. Ear prolificacy is an important trait for hybrids that can be deployed in the western regions of South Africa where plant population density is low, and the plants should have the potential to compensate through production of secondary ears. The parental lines with high potential to increase oil content in their hybrids were parental lines L6 (CML550), L2 (CML176) and L8 (DTSR-W) as they had positive and significant GCA effects for oil content. For protein content, parental lines L4 (CML182) and L6 (CML550) will be ideal for increasing the protein content in their offspring based on their positive and significant GCA for protein content. Only parental line L3 (CML181) exhibited positive and significant GCA effects for starch content.

Overall, grain yield in the hybrids could be increased by using parental lines L2 (CML176) and L3 (CML181) in the developing hybrids due to their positive and significant GCA effects for grain yield. Grain yield is the primary goal of breeding programs in general but the advent of consumers that are becoming more informed about their diets has increased the need to integrate the improvement of nutritional value and grain yield. From the findings in this study, it is possible to improve both yield and nutritional quality using recurrent selection of elite parents. However, it

would be important to evaluate the correlations among nutrients and agronomic traits and yield. It will be ideal to understand such correlations as they can indicate possible linkage drag that needs to be broken during multi-trait improvement.

Proportionally, the GCA/SCA variance ratios were above 1 showing that additive gene effects were more important than non-additive gene effects for all traits under both nitrogen availability conditions. The preponderance of additive gene effects for traits in this population means that the improvement of the agronomic performance, yield productivity and nutritional content can be achieved by selecting superior parents under both conditions. This is consistent to suggestions by previous researcher such as Kamal *et al.* (2023). The differences in GCA variance of traits across the different sites and nitrogen conditions indicates that selection for specific environments could be helpful to achieve high genetic gains in subsequent generations and improve adaptation (Badu-Apraku *et al.*, 2022).

The SCA variance was also significant for starch although the SCA component was not higher than the corresponding GCA component. However, the presence of significant SCA variance indicates that the expression of traits such as grain yield, ears per plant, anthesis silking interval and plant height was partially controlled by non-additive gene effects to some extent. The presence of non-additive gene effects could help in transgressive selection at advanced generations after successive inbreeding (Dwivedi *et al.*, 2021). Higher performance of offspring compared to parents, represented by the SCA variance component, could arise from dominance, overdominance or epistatic gene effects that provide opportunities for selecting transgressive crosses (Roth *et al.*, 2022). The presence of some crosses that exhibited higher mean values compared to either of their parents could be due oligogenic or epistatic gene control of the traits (Zhang *et al.*, 2020).

Oligogenic control refers to the control of inheritance influenced by more than a single gene but usually less than 20 genes and the variation is discrete. However, the traits in this study did not exhibit discrete or discontinuous variation, which show that they were quantitative and could not have been influenced by oligogenic control. It points strongly to the presence of epistasis, which occurs when there is interaction between genes with masking or modifying effects on other genes resulting in unexpected phenotypic expression from what would be expected if the genes were not interacting (Ramstein *et al.*, 2020). Such SCA is important for developing specific hybrids for targeted market segments.

The higher mean performance in some hybrids, possibly caused by epistatic gene effects, over their parents shows there is possible genetic gains in agronomic performance and nutritional content. The crosses L5×L2(CML511x CML176), and L6×L10 (CML550xK64R) combined well to reduce the anthesis days and silking days as exhibited by their negative SCA effects for these traits showing that there was favorable interaction between the parental alleles to reduce maturity, which is critical for short season environments. For shorter hybrids, desirable hybrid combinations will be L5×L10 (CML511xK64R), L7×L10(CW14xK64R), L8×L1(DT-SR-W xCML144) and L9×L2(I-43 xCML176) as they had negative and significant SCA effects for plant height. The only cross that could result in lower ear height was L8×L1(DT-SR-W xCML144) as shown by its highly significant and negative SCA effects for ear height. Only two crosses, L4×L1(CML182 xCML144) and L9×L4(I-43 x CML182) could potentially increase ear prolificacy based on their positive SCA effects for ears per plant. Early dry down in hybrids could be achieved by developing the following crosses, L5×L2(CML511x CML176), L8×L10(DT-SR-W x K64R), L9×L5(I-43x

CML511) and L9×L7(I-43×CW14), which had negative and significant SCA effects for grain moisture. Potential increase in oil content would be possible from L3×L10(CML181×K64R), L4×L1(CML182 ×CML144) and L8×L7(DT-SR-W×CW14) breeding populations that exhibited positive and significant SCA effects for oil content. There were four crosses, L4×L10 (CML182×K64R), L5×L3(CML511×CML181), L6×L1(CML550×CML144) and L9×L2(I-43×CML176) that exhibited positive and significant SCA effects for protein content. Starch content could only be increased from the L8×L3 (DT-SR-W×CML181) cross. Overall, the population from L8×L3(DT-SR-W×CML181) had the highest potential for increasing grain yield with positive SCA effects of 0.69 followed by L6×L4 (CML550×CML182) 0.54, L7×L1(CW14×CML144) 0.49 and L6×L10 (CML550×K64R) 0.48 populations. Crosses that exhibit desirable SCA, even though they are derived from parental lines whose GCA is not desirable indicate the benefits of epistasis from the favorable interaction of genes involved in the control of the traits (Guimarães *et al.*, 2023).

Chapter 6: CONCLUSIONS AND RECOMMENDATIONS

6.1 Introduction

This chapter presents the general conclusions drawn from the study. In addition, overall recommendations are highlighted. Furthermore, the chapter outlines areas for further research to augment the current findings.

6.2 Conclusions

The following conclusions were derived based on the results from the experiments:

1. The wide genetic variation for agronomic traits among the hybrids and their parents was revealed by the study. It was concluded that the germplasm used in this study can be used for breeding by selecting superior parents for line maintenance and favorable crosses for population development and hybridization to improve agronomic performance, yield, and nutritional quality of maize.
2. The mean performance varied significantly allowing for selection to be conducted. The best and worst performing hybrids and parental lines were identified. The best and favorable hybrids and parental lines were selected giving an opportunity for germplasm improvement and hybrid development.
3. The variance analysis revealed that GCA was the more important component controlling inheritance of the traits. Thus, it was concluded that additive gene effects were the major determinant of trait inheritance. In that case, the most appropriate strategy for improving this germplasm and developing better hybrids will be through selection of superior parents for mating followed by recurrent selection. The SCA component was less preponderant showing that non-additive gene effects were minor. This was important for developing

- specific hybrids that were superior in agronomic performance and nutritional quality for targeted market segments by exploiting the non-additive gene effects to develop F₁ hybrids
4. There was significant genotype by environment interaction effects on the agronomic performance and nutritional content of maize inbred lines and their hybrid combinations evaluated under low and high soil nitrogen.
 5. General combining ability analysis revealed that the parental lines passed their traits to their offspring in different proportions. Some parental lines had higher ability to contribute to their offspring performance as shown by their favorable combining ability. Similarly, specific combining ability revealed that some hybrid combinations were more favorable than others. Favorable allelic combinations resulted in higher performance in specific hybrids leading to their ability to outperform either parent or expected performance. The higher performance of specific hybrids over their parents showed that genetic gains were achieved in some of the hybrids.
 6. Parental lines that include L2 (CML176), L3 (CML181) and L6 (CML550) that had positive and significant GCA effects for grain yield, protein, oil, and starch across the environments should be selected for inbred line maintenance. These can be used in generating crosses in diverse combinations. The other lines such as L7 (CW14), L9 (I-43) and L10 (K64R) that had negative GCA for Plant height, anthesis days, Anthesis silking interval, and grain moisture should be maintained for use in developing early maturity and shorter hybrids that fit in short season regions and reducing stalk and root lodging.
 7. Crosses such as L5xL2 (CML511xCML176) and L6xL10 (CML550xK64R) which had lower anthesis days, Anthesis silking interval and grain moisture, and L8xL3 (DT-

SRWxCML181), L6xL4 (CML550xCML182) with higher grain yield and L4xL1 (CML182xCML144), L4xL10 (CML182xK64R), and L8xL3 (DT-SR-WxCML181) which had higher protein, oil, and starch compared to their parents under low nitrogen conditions would be recommended for selection to developing suitable breeding populations. All the traits were predominantly controlled by additive gene effects. On the other hand, there was a proportion of non-additive gene effects that were significant in the inheritance of the traits indicating that a hybridization strategy would also be effective.

6.3 Recommendations

From the conclusions, the following recommendations are proposed:

1. Line CML176 (L2) had particularly good GCA for grain yield and other desirable traits including high ear per plant, grain moisture, and oil content. It is recommended to use this line in hybrid combinations to develop superior hybrids with good adaption to low soil nitrogen conditions.
2. The lines with good agronomic performance and nutritional quality should be maintained in inbred line management program to maintain their purity.
3. The hybrids with good SCA should be used in breeding population development and hybridization programs to develop superior hybrids.
4. Further research should investigate the molecular basis of agronomic traits and nutritional quality in this germplasm for marker assisted selection and to reduce environmental bias.
5. Furthermore, research on trait correlations and on subsequent generations is required to validate the present results and to fine tune the breeding strategy for maximum genetic gains.

Overall, this research found significant variations for grain yield, agronomic traits, and nutritional traits for the QPM and normal endosperm maize inbred lines and their hybrid progenies.

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