

Combining ability, Genetic Gains and Path Coefficient Analyses of Maize Hybrids developed from Maize Streak Virus and Downey Mildew Resistant Recombinant Inbred Lines

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



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GENERAL ABSTRACT

Farmers in SSA continue to obtain low yields (less than two tonnes per hectare) despite the high potential yield (about 14 tonnes per hectare) that can be achieved. The development of improved and high yielding hybrids can help to reduce this gap significantly. Characterisation of maize inbred lines is crucial for developing high yielding maize hybrids. A line x tester analysis involving 38 crosses generated by crossing 19 maize inbred lines with two tropical testers was conducted for different agronomic traits. The maize inbred lines used in this study were sampled from a bi-parental inbred population developed by a shuttle breeding program at University of KwaZulu Natal. The objectives of the study were to estimate combining ability of inbred lines and hybrids, to evaluate the performance of the hybrids in agronomic traits and grain yield, to calculate breeding gains achieved through selection and to deduce the relationship between secondary traits and grain yield. In total 50 hybrids, including control hybrids were evaluated in the trial. The hybrids were planted in the summer season of 2014/15 under rainfed conditions at three sites, Cedara, Dundee and Ukulinga in five metre row plots and replicated twice in 5X10 alpha lattice design under recommended agronomic practices for maize. Data was collected using a CIMMYT protocol and subjected to statistical analyses using ANOVA and REML packages in GENSTAT 14th edition and PATHSAS macros in SAS 9.3 computer software. The results showed varying performances between the lines, crosses and control hybrids at the different sites. Inbred lines DMSR-8, DMSR-13, DMSR-30 and DMSR-35-5 were shown to have good combining ability while DMSR-21 and DMSR-73 showed positive specific combining ability. Selection across sites improved grain yield by 9.32% over the population mean and by 10.22% and 12.73% at Cedara and Dundee, respectively over commercial hybrids. Ranking by mean yield identified hybrids 15XH16, 15XH20 and 15XH28 at Cedara, Dundee and Ukulinga respectively, as the highest yielding hybrids for that particular environment. GGE biplot and AMMI analyses revealed that

hybrids 15XH10, 15XH13, 15XH20, 15XH25, 15XH28, 15XH34 and 15XH39 were the most stable hybrids. Secondary traits were found to be associated with grain yield potential of hybrids. Ear prolificacy had the most important relationship with grain yield and was recommended for selection in grain yield improvement programs.

Keywords: Combining ability, genetic gains, genotype X environment interaction, line X tester, path coefficient analysis.

DECLARATION

I, **Isack MATHEW**, declare that:

1. The research presented in this dissertation, except where otherwise indicated, is my original research.
2. This dissertation has not been submitted for any degree or examination at any other university.
3. This dissertation does not contain other scientists' data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other scientists.
4. This dissertation does not contain other scientists' writing, unless specifically acknowledged as being sourced from other scientists. Where other written sources have been quoted, then:
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.....

Isack MATHEW (Candidate)

As supervisor I agree to submission of the dissertation

Professor John Derera

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Above all, I am grateful to God Almighty for everything that I am and ever will be.

DEDICATIONS

To God Almighty, who enables me. He is my Strength, Shield and Sanctuary.

To my late father, for seeing it first. My father taught me to rise against all odds and adversity.

To my family, for all your love. My mum, Julie Lyness, Elizabeth, Mary, Moses and Nastasia have always stood by me. I love you all

Table of Contents

GENERAL ABSTRACT	ii
DECLARATION	iv
ACKNOWLEDGEMENTS	v
DEDICATIONS	vi
Table of Contents	vii
List of Tables	xiii
List of Figures	xv
List of Acronyms and Abbreviations	xiii
Chapter 1 : General Introduction	1
1.1. Introduction	1
1.2. Importance of Maize	1
1.3. Overview of Production Constraints	2
1.4. Prospects of Crop Improvement	3
1.5. Problem Statement	4
1.6. Significance of the Study	4
1.7. Research Goals and Objectives	5
1.7.1. Goal of the Study	5
1.7.2. Specific Objectives	5
1.8. Research Hypotheses	6
1.9. Structure of Dissertation	6

Chapter 2 : Literature Review.....	8
2.1. Introduction.....	8
2.2. Importance of Superior Seed.....	8
2.3. Line X Tester Analysis	9
2.4. Combining Ability	10
2.4.1. General Combining Ability (GCA)	11
2.4.2. Specific Combining Ability (SCA)	11
2.5. Importance of Tester Lines	12
2.6. Application of Combining Ability	13
2.6.1. Prediction of Hybrid Performance.....	13
2.6.2. Evaluation of Inbred Lines	13
2.6.3. Determination of Gene Action.....	14
2.7. Genetic Gains.....	15
2.7.1. Genetic Gains Achieved in Grain Yield over the years.....	16
2.7.2. Some Genetic Gains Achieved in Secondary Traits over the years	17
2.8. Factors Influencing Genetic Gains Achieved through Selection.....	19
2.8.1. Selection Pressure.....	19
2.8.2. Heritability and Genetic Variance	19
2.8.3. Genetic Variability.....	20
2.8.4. Genotype X Environment (GXE) Interactions	20
2.8.5. Heterosis	23
2.8.6. Transgressive Segregation	23

2.9. Measuring Genetic Gains	24
2.10. Correlation, Regression and Path Coefficient Analyses	25
2.10.1. Grain Yield and its Relationship with Secondary Traits	26
2.10.2. Importance of Secondary Traits.....	28
2.10.3. Efficiency of Selecting Secondary Traits in Grain Yield Improvement.....	30
2.11. Summary and Conclusion	31
Chapter 3 : Materials and Methods.....	33
3.1. Introduction.....	33
3.2. Description of Germplasm	33
3.3. Description of Sites	37
3.4. Experimental Layout and Crop Management	39
3.5. Data Collection	40
3.6. Data Analyses	42
3.6.1. Mean Performance	42
3.6.1.1. Grain Yield	42
3.6.1.2. ANOVA and Mean Separation Test	43
3.6.1.3. Frequency Distribution and Mean Ranking.....	44
3.6.2. Line X Tester Analysis	44
3.6.2.1. ANOVA.....	44
3.6.2.2. General Combining Ability (GCA)	45
3.6.2.3. Specific combining ability (SCA)	45
3.6.3. Genetic Gains.....	46

3.6.3.1. Phenotypic and Genotypic Variances	46
3.6.3.2. Broad-sense Heritability	47
3.6.3.3. Coefficients of Variation	47
3.6.3.4. Predicted Genetic Gain	48
3.6.3.5. Estimation of Realised Genetic Gains	48
3.6.4. Relation between Grain Yield and Secondary Traits	50
3.6.4.1. Correlation Analysis	50
3.6.4.2. Regression Analysis	50
3.6.4.3. Path Analysis	51
3.6.5. Genotype X Environment Interaction	51
3.6.5.1. Additive Main Effects and Multiplicative Interaction Analysis (AMMI)	51
3.6.5.2. Genotype and Genotype X Environment Interaction Analysis (GGE)	52
3.6.5.3. Cultivar Superiority Index	52
3.6.5.4. Cultivar Stability and Mean Rank Analysis	53
Chapter 4 : Results	54
4.1. Analysis of Variance	54
4.2. Frequency Distribution	56
2.3. Mean Performance of the Hybrids	62
2.4. Line X Tester Analysis	64
2.5. Combining Ability	65
2.6. Genetic Gains	70
2.7. Relationship between Grain Yield and Secondary Traits	79

4.7.1.	Correlations.....	79
4.7.2.	Regression Analysis.....	85
4.7.3.	Path Coefficient Analysis	85
2.8.	Genotype X Environment Interactions	91
4.8.1.	Additive Main effects and Multiplicative Interactions	91
4.8.2.	Stability and Cultivar Superiority Analysis	92
4.8.3.	Genotype and Genotype X Environment (GGE) Biplot Analysis.....	93
Chapter 5 : Discussion of Results.....		96
5.1.	Analysis of Variance	96
5.2.	Frequency Distribution for Yield and Secondary Traits	98
5.3.	General Combining Ability.....	101
5.4.	Specific Combining Ability	102
5.5.	Gene Action	103
5.6.	Heritability estimates, Selection and Genetic Gains	105
5.7.	Correlations between Grain Yield and Secondary Traits.....	113
5.8.	Correlations among Secondary Traits.....	116
5.9.	Regression of Traits on Grain Yield	118
5.10.	Path Coefficient Analysis.....	118
5.11.	Genotype X Environmental Interaction Analysis	120
5.11.1.	Discriminating Ability and Representativeness of Test Environments.....	121
5.11.2.	Environmental Main Effects.....	122
5.11.3.	Genotype Performance	123

5.11.4. Crossing Over of Genotypes.....	125
5.11.5. AMMI Model Best Hybrid Selection	125
5.11.6. Stability and Cultivar Superiority Analysis	126
5.11.7. Genotype Adaptation	126
Chapter 6 : Conclusions and Recommendations	128
6.1. Findings.....	128
6.2. Recommendations	130
6.3. Overall Conclusion	131
References	132

List of Tables

Table 3.1: Description of inbred lines and testers and their origins	34
Table 3.2: Description of the experimental hybrids, pedigree and their origin	35
Table 3.3: The control hybrids, their pedigree and origin	36
Table 3.4: Average weather conditions at Cedara during Oct 2014 to May 2015	37
Table 3.5: Average weather conditions at Ukulinga during Sept. 2014 to Jun. 2015	38
Table 3.6: Average weather conditions for Newcastle during Sept. 2014 to May 2015	38
Table 3.7: Description of traits and the data collection methods	41
Table 4.1: Mean squares for yield and secondary traits across three sites	55
Table 4.2: Mean squares for secondary traits across two sites	55
Table 4.3: Descriptive statistics of yield and secondary traits across sites	56
Table 4.4: Mean yield and ranking of hybrids excluding control hybrids.....	63
Table 4.5: Mean yield and ranking of commercial and control hybrids.....	64
Table 4.6: Mean squares for grain yield and secondary traits across the three sites	65
Table 4.7: GCA effects for grain yield and secondary traits	67
Table 4.8: SCA for grain yield and secondary traits for crosses of tester LP19.....	68
Table 4.9: SCA for grain yield and secondary traits for crosses of tester LP21.....	69
Table 4.10: Means of selected hybrids and control hybrids across sites	72
Table 4.11: Estimates of variance components, heritability and genetic gains across sites	73
Table 4.12: Means of selected hybrids and control hybrids at Cedara.....	74
Table 4.13: Estimates of variance components, heritability and genetic gains at Cedara.....	75
Table 4.14: Means of selected hybrids and control hybrids at Dundee.....	76
Table 4.15: Estimates of variance components, heritability and genetic gains at Dundee.....	76
Table 4.16: Means of selected hybrids and control hybrids at Ukulinga	77
Table 4.17: Estimates of variance components, heritability and genetic gains at Ukulinga ...	78
Table 4.18: Correlations between grain yield and secondary traits at Cedara.....	80

Table 4.19: Correlation between grain yield and secondary traits at Ukulinga.....	82
Table 4.20: Correlations between grain yield and secondary traits across sites.....	84
Table 4.21: Regression of secondary traits on grain yield across sites	85
Table 4.22: Direct and indirect effects of secondary traits on grain yield across sites.....	88
Table 4.23: Direct and indirect effects of secondary traits on grain yield at Cedara	89
Table 4.24: Direct and indirect effects of secondary traits on grain yield at Ukulinga	90
Table 4.25: AMMI ANOVA for grain yield using predicted means.....	92
Table 4.26: The AMMI model best four hybrids selected in different environments	92
Table 4.27: Stability of maize hybrids based on superiority index and mean ranking.....	93

List of Figures

Figure 1.1: Global maize production levels from year 2003 to 2013	3
Figure 4.1: Histograms for grain yield for the three sites	58
Figure 4.2: Histograms for ear prolificacy for the three sites	58
Figure 4.3: Histograms for number of days to anthesis for two sites	59
Figure 4.4: Histograms for anthesis silking interval for two sites	59
Figure 4.5: Histogram for number of days to ear maturity for two sites	60
Figure 4.6: Histograms for grain moisture content for three sites	60
Figure 4.7: Histograms for plant height for two sites	61
Figure 4.8: Histogram for disease ratings at Cedara	61
Figure 4.9: GGE biplot showing hybrid performance in each environment	95
Figure 4.10: GGE biplot comparing environments	95

List of Acronyms and Abbreviations

AD	Anthesis date (days)
AMMI	Additive Main effects and Multiplicative Interaction
ANOVA	Analysis of Variance
ARC	Agricultural Research Council
ASI	Anthesis Silking Interval
°C	Degree Celsius
CC	Chlorophyll content
CED	Cedara Research Station
CIMMYT	International Maize and Wheat Improvement Centre
CML	CIMMYT Maize Line
CV	Coefficient of Variation
D.F	Degrees of Freedom
DUN	Dundee Research Station
E	East
EH	Ear height
EM	Ear maturity
EPO	Ear position
EPP	Number of ears per plant (also known as ear prolificacy)
F ₁ or F ₂	First or Second filial generation
FAO	Food and Agriculture Organization of the United Nations
GCA	General Combining Ability
GCV	Genotypic Coefficient of Variation
GGE	Genotype Main Effect plus Genotype-Environment Interaction
GLS	Grey Leaf Spot

GXE	Genotype by Environment interaction
GYG	Grain yield
HC	Husk cover
IIAM	Instituto de Investigação Agrária de Moçambique (IIAM) (Agricultural Research Institute of Mozambique)
(I)PCA	(Interaction) Principal Component Axis
KZNDARD	KwaZulu-Natal Department of Agriculture & Rural Development
LSD	Least Significant Difference
m	Metres (distance)
MAE	Mean of advanced experimental hybrids
MBC	Mean of best commercial hybrid
MBIO	Mean of hybrids of biological founder parents
MC	Mean of commercial hybrids
mm	Millimetres
MOI	Grain moisture content
MP	Mean of population
MS	Mean of selected hybrids
MSV	Maize Streak Virus
NLB	Northern Leaf Blight
NPK	Nitrogen: Phosphorous: Potassium
OPV	Open Pollinated Variety
P	Probability significance level
PAR	Photosynthetically active radiation
PCV	Phenotypic Coefficient of Variation
PG	Predicted gain
PH	Plant height

PLS	<i>Phaeosphaeria</i> Leaf Spot
RG	Realised gains
RL	Root lodging
S	South
SADC	Southern African Development Community
SCA	Specific Combining Ability
sd	Standard Deviation
SD	Silking date (days)
se	Standard Error
SL	Stem lodging
SOV	Source of Variation
SREG	Sites Regression
SSA	Sub-Saharan Africa
t/ha	Tonnes per hectare
UKU	Ukulinga Research Farm of UKZN
UKZN	University of KwaZulu Natal

Chapter 1 : General Introduction

1.1. Introduction

This chapter introduces maize as a staple crop of importance in Sub-Saharan Africa (SSA). Factors affecting maize production and prospects of crop improvement are briefly highlighted. The chapter also outlines the significance, problem statement, objectives and hypotheses of the study. The general structure of the dissertation is also outlined in this chapter. Finally, the chapter summarizes the above and highlights the focus of the study.

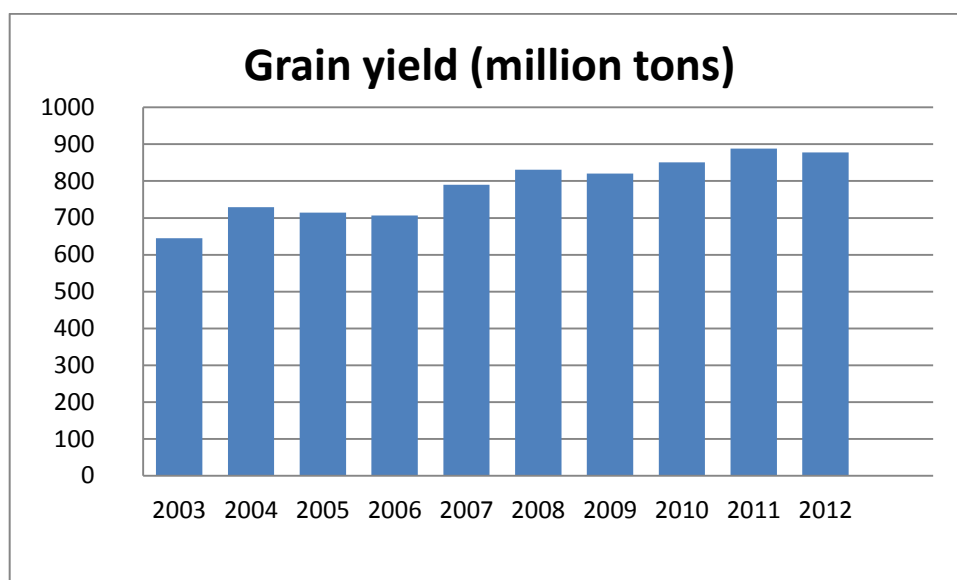
1.2. Importance of Maize

More than four billion people across the world depend on maize as a staple food Shiferaw et al. (2011). Maize is also important as animal feed; in South Africa about 50% of the maize produced is used for animal feed mostly in poultry production. It is one of the most globally traded cereals and is ranked above traditional cereals, such as sorghum and millet, in both utilization and production. South Africa produced nearly ten metric tonnes of maize every year over the last decade (FAOSTAT, 2014), making it a net exporter of maize and among the top three producing countries in Africa. It usually meets the shortfall in the Southern African Development Community (SADC) region (Shiferaw et al., 2011). The importance of maize in SADC is evidenced by a high per capita consumption which is estimated at over 150 kilograms per annum in most countries in this region (Langyintuo et al., 2008). Maize production is integral to the agriculture sector and economy as it contributes significantly to the gross domestic production of South Africa.

1.3. Overview of Production Constraints

Despite the importance of maize in South Africa, the yields of approximately 2.4 tonnes per hectare (Langyintuo et al., 2008) obtained by the majority of farmers are lower compared to those obtained in other countries such as Mexico, India or Brazil (3.18, 3.04 and 5.1 tonnes per hectare, respectively) (NUE-Web, 2016) due to a number of constraints. Limited access and low availability of improved varieties to most farmers rank among the most important constraints (Langyintuo et al., 2008). Pratt and Gordon (2006) estimated that more than a third of farmers grow unimproved varieties which may be adapted but are low yielding. Pixley and Banziger (2002) implicated capital constraints as the most common cause for farmers to retain hybrid seed or continue to plant old varieties instead of buying new seed each season.

Varieties which are high yielding are becoming increasingly compulsory to increase productivity amid challenges of changing weather patterns, increased pests and disease pressures and increasing global population and food demand. Global maize production has generally been on the increase (Figure 1.1) following the advent of hybrids (Duvick, 2005a). However, the current rate of increase in production is not adequate to meet population growth.



Adapted after FAOSTAT, 2014

Figure 1.1: Global maize production levels from year 2003 to 2013

1.4. Prospects of Crop Improvement

Crop improvement can complement agronomic practices such as fertilizer use to improve maize productivity. Maize yields have improved significantly wherever improved hybrids have been adopted (Duvick, 2005a). Edmeades et al. (1996) estimated that crop improvement can contribute between 15 and 20% improvement in yield. This estimate is lower than 50% estimated by Duvick (2005a) in the US, but nevertheless serves to show the importance of crop improvement. Maize breeding can be regarded as a step-wise process involving identification of maize lines with desirable traits, making crosses between identified lines and evaluating the progeny for breeding gains. Identifying maize lines with desirable traits is a prerequisite for successful breeding (Zaidi et al., 2007). The identified lines can be crossed according to the objectives of the breeder to generate progeny which may show improved characteristics compared to their parents or other hybrids. Those crosses which are economically important to the breeder are selected for further testing or development. The number of breeding cycles required to reach desired level of improvement depends on the genotype, trait heritability and environmental conditions (Pixley et al., 2006). Maize lines

suitable for use in hybrid development can be identified through various mating designs including line X tester mating design to evaluate the combining abilities of individual lines and the resultant progeny can then be assessed for improved yield.

1.5. Problem Statement

Farmers in South Africa continue to obtain low yields (less than two tonnes per hectare) despite the high potential yield (14 tonnes per hectare) that can be achieved. The wide gap between actual yields obtained and potential yields is partly due to growing of unimproved varieties by the majority of farmers. The development of improved and high yielding hybrids can help to reduce this gap significantly. However, hybrid development is a process that includes several intermediary steps such as trait identification, line development, progeny evaluation for breeding gains and analysis of grain yield and secondary traits. The process is constrained by lack of precise models for estimating genetic parameters and evaluation of hybrids (Longin et al., 2012) as a potential solution to low productivity.

1.6. Significance of the Study

The determination of combining ability helps to identify parental lines with high potential for use in developing hybrids. Measuring genetic gains shows the progress made by a breeding program and therefore provides vital information for breeders to take corrective action where needed. The study also deduced the relationship between yield and its related secondary traits by undertaking path coefficient analysis. Such knowledge is useful in maize improvement, particularly in hybrid development. Path coefficient analysis deduces the magnitude of the contribution of each secondary trait towards the ultimate yield. This will enable the breeder to target specific traits with a high potential to increase grain yield potential since selecting directly for yield is not always feasible or effective (Zaidi et al., 2007). Maize breeding has

been ongoing for many years, but nevertheless there is need to optimize the current breeding strategies (Longin et al., 2012) in order to improve productivity in the face of new challenges. The demand for food is set to increase in the coming years and development of high yielding hybrids will play a critical role in mitigating food shortages. Increasing maize productivity will depend on improving the yield potential through genetic improvement (Meng et al., 2013). Thus it is imperative to identify all possible lines with desirable traits that are important in improving grain yield.

1.7. Research Goals and Objectives

The goal and objectives of this study were as follow:

1.7.1.Goal of the Study

The goal of this study was to improve maize productivity in the maize growing areas of South Africa. The major objective was to evaluate the potential of the experimental maize inbred lines for use in developing new high yielding hybrids.

1.7.2. Specific Objectives

The specific objectives were as follows:

- To determine general combining ability of inbred lines and specific combining ability of hybrids.
- To determine genetic gains achieved by evaluating grain yield and yield components of hybrids developed at UKZN.
- To identify and deduce the nature of association between secondary traits and grain yield.

1.8. Research Hypotheses

The following hypotheses were tested:

- The experimental maize lines differ in their general and specific combining ability with the tester lines.
- Significant genetic gains were achieved by the breeding program at UKZN.
- There is a significant relationship between grain yield and secondary traits.

1.9. Structure of Dissertation

This dissertation is structured as follows;

Chapter 1 General Introduction

Maize is introduced as a crop of importance and shortage of superior varieties is highlighted as a challenge to its productivity. The problem statement, importance, objectives and hypotheses of the study are included in this chapter.

Chapter 2 Literature Review

This chapter reviews literature on previous related studies as a basis for this study. It first presents the lack of access to seeds of improved maize varieties by most farmers as a highly contributory factor to low productivity in SSA. The literature covers the concepts of specific combining ability, determination of breeding gains and deduction of association between yield and secondary traits. This chapter concludes by identifying the importance of hybrid development in improving productivity and also identifies the knowledge gap that this study attempts to fill.

Chapter 3 General Materials and Methods

This chapter presents the methodology and procedures followed by the researcher. It covers all the procedures and materials pertaining to crop management, experimental designs, description of sites and data collection and analyses. It is divided into sections accordingly.

Chapter 4 Results

The obtained results are presented in this chapter. They are presented in the form of tables and graphical presentations. Brief descriptions of trends shown in the tables and graphs are provided.

Chapter 5 Discussion

The results obtained are discussed in this chapter. The discussion includes description of observed trends, meaning and implications of such trends. The results are discussed in comparison to other researchers' findings.

Chapter 6 Conclusions and Recommendations

Conclusions and recommendations drawn from key results are presented in this chapter.

Chapter 2 : Literature Review

2.1. Introduction

This chapter reviews work by other researchers covering the importance of superior hybrid varieties, concept of combining ability, genetic gains achieved and relationship between grain yield and secondary traits. It also reviews the use of correlation and path coefficient analyses to determine the importance of selecting secondary traits for grain yield improvement. Finally, it identifies gaps in the literature and presents the focus of the study.

2.2. Importance of Superior Seed

Maize productivity in Sub-Saharan Africa (SSA) is hindered by growing of unimproved varieties as most farmers in this region cannot afford to buy superior hybrid seed (Pixley and Banziger, 2002). Hybrids have higher yield potential which can be attributed to heterosis resulting from crossing different parental lines with high yield potential and other desirable traits (Townsend et al., 2013). However, some modern hybrids have not performed satisfactorily under stress environments and low management practices that are common among smallholder farmers (Araus et al., 2002). This has warranted continuous efforts by breeders to develop adapted and high yielding hybrids.

The selection of parents to use in a hybridisation program is highly important. In most breeding programs high yielding lines are often selected as parents because the aim is to improve grain yield. Selection of parental lines is determined by availability of resources and the amount of information available on the traits of interest. Even after selecting high yielding parental lines, hybrids formed may not always perform as highly as expected. The performance of a hybrid is influenced by the interaction between the genotypes of the

parental lines used to develop it. It is essential that breeders understand these interactions in order to accurately predict hybrid performance. It is highly important that before developing a hybrid, breeders should obtain as much information on the genetics of the parental lines and identify hybrid combinations that may produce the highest yields. A method that rapidly and accurately provides useful information for preliminary identification of potential parents is required. Commonly, the performance of hybrids generated by crossing inbred lines with common testers is evaluated to provide such information (Yalçın, 2005).

2.3. Line X Tester Analysis

Characterisation of inbred lines is important in hybrid development. A line X tester analysis evaluates a set of parents by crossing each to a common tester which is normally treated as a male (Motamedi et al., 2014). The method helps in determining the ability of the parental lines to pass on heritable traits to the offspring. It was proposed by Kempthorne (1957) to investigate the interaction of genotypes of a tester with known performance and a line of unknown performance. It is based on the principles of a factorial experiment whereby the genotype of the tester is treated as one factor and the genotype of the line as the other factor. It has been adopted for studies on combining ability, especially in maize trials. It allows the deduction of effects attributed to lines, testers and their interaction (Kaushik et al., 1984). Many studies on maize have concluded that this mating design produces reliable information on combining ability, mechanisms of quantitative inheritance, gene action and heritability (Kaushik et al., 1984; Motamedi et al., 2014; Sanghera and Hussain, 2012). Since the testers are common to all the lines being tested, any observable variations in the offspring are due to the parental line and its interaction with the tester (Motamedi et al., 2014). Data on the phenotypic performance of the hybrids developed between the tester and the line can be used to estimate genetic components (Kempthorne and Curnow, 1961). This is important in informing the breeder to select parents based on genetic variances and their combining

ability. Genetic variances are the basis of heritability estimation (Zuk et al., 2012) which is important in hybrid development and inbred line maintenance.

2.4. Combining Ability

Combining ability measures the relative ability of a parental line to pass genetic information to its offspring (Aly, 2013). It helps in identifying parental lines to use in developing hybrids (Gowda et al., 2012). Suitable inbred lines are used in crosses to develop hybrids whose performance level depends on the heritability of the traits and the combining ability of the parental lines. Therefore, knowledge of combining ability and genetic variances is pivotal in the development of high yielding hybrids (Motamedi et al., 2014). Information on combining ability can be used to predict performance of a cross between different lines without necessarily making the cross (Makumbi et al., 2011). This greatly reduces time and resources spent on hybrid development. In addition, the information generated from the analysis of combining ability helps in devising the best strategy to fully exploit the genetic potential of inbred lines (Gowda et al., 2012). Breeding for higher genetic gains depends on the ability to predict line and hybrid performance and use of suitable breeding methods and favourable environments (Esmail, 2007).

While combining ability can be used as an indicator of breeding value of lines (Townsend et al., 2013), crossing lines with high combining ability does not always produce high yielding hybrids ((Bagheri and Jelodar, 2010; Jensen, 1959). The success rate is dependent on the accurate estimation of genetic components of each parent involved and the interaction of their genes (Mohammadi et al., 2010). It is therefore important to note that combining ability analysis attempts to partition genetic factors from any other factor that may influence the observed performance. It is composed of general combining ability (GCA) and specific combining ability (SCA) which are important in partitioning total observed phenotype into

parental genotype main effects and genotypic interaction effects respectively (Mohammadi et al., 2010). The potential value of a line in improving yield in maize depends on these components and their efficient utilisation.

2.4.1. General Combining Ability (GCA)

General combining ability (GCA) was defined as the deviation of mean performance of a parent genotype in all its hybrid combinations from the population mean (Griffing, 1956). It is used as an indicator of the potential performance of a line when it is crossed to different genotypes. GCA of a line emanates from additive gene effects exerted by the genotype of that line (Marinković et al., 2000). The gene effects of the lines involved in the cross should be neither dominant nor recessive to each other so that the observed phenotype in the offspring will be a sum total of parental effects. For a line to be selected it must have a positive and higher GCA for a particular trait. The application of GCA has been emphasized in a lot of studies although it is suggested to be more useful in yield estimates and in material that was not previously selected (Ceyhan et al., 2008). It is also important for developing synthetic varieties (Ali et al., 2014). In the current study GCA was determined by crossing test inbred lines derived from a bi-parental population to two tropical testers.

2.4.2. Specific Combining Ability (SCA)

Specific combining ability is the deviation of the mean performance of a particular hybrid from the expected performance based on the GCA of its parents and the overall mean of the population (Griffing, 1956). SCA differs from GCA in that it is focused on a particular combination of one line and a tester hence it is specific. Since SCA is a result of interaction between line and tester genotypes, it takes into account dominance or epistatic gene effects (Marinković et al., 2000). A desirable SCA means the genetic interactions between the

genotypes involved in a particular hybrid are favourable. Although SCA is specific to a hybrid combination it can also be used to give an indication of how a genotype may perform in other crosses (Ceyhan et al., 2008). It is expected that SCA will be positive when parents from distinctly different backgrounds are crossed and vice versa for related parents (Betrán et al., 2003) due to heterosis. In crosses involving more than two testers SCA provides useful information on the performance of individual lines. While both SCA and GCA are important components of combining ability, SCA is more important in previously selected material (Ceyhan et al., 2008; Jensen, 1959) and when the focus is on developing hybrids (Ali et al., 2014). Therefore in this study SCA was emphasised more than GCA because the inbred population was previously selected for maize streak virus (MSV) and Downey mildew resistance and the lines are targeted for hybridisation.

2.5. Importance of Tester Lines

Testers can be populations, inbred lines or single cross hybrids (Aguilar et al., 2008) but the most widely used are inbred lines (Hallauer and Miranda, 1988). As a result of self-pollination inbred lines are highly homozygous and of known characteristics. An expected mean can be calculated when a known tester line is crossed to an inbred line or hybrid. However, deviations from the expected mean often occur and they can be used to differentiate the combining abilities of the lines being tested (Makumbi et al., 2011).

Rawlings and Thompson (1962) challenged the proposal to strictly use homozygous testers. It was argued that there is no need to differentiate the nature of the testers since they will be common to all parents. It was further contested that if the homozygosity theory was true then the parent offspring regression would always show positive correlation and high combiners would always be expected to have low variance coefficient. It has been proved that this is not always true (Rawlings and Thompson, 1962). However, the importance of using a narrow

base tester is to reduce the variation due to the tester (Genter and Alexander, 1965). The basis of using a common tester is that all the variations expressed in the offspring will be due to the lines and not the tester (Genter and Alexander, 1965). Whether homozygous or heterozygous testers are used, line X tester analysis can differentiate lines based on their combining ability and it remains a very powerful tool for exploiting lines in a breeding program. In the current study tropical inbred testers were used to discriminate the lines on the basis of grain yield potential and SCA.

2.6. Application of Combining Ability

The concept of combining ability can be used for different purposes in breeding. Although most of its uses are predictive in nature, its application has tremendous benefits in maize improvement.

2.6.1. Prediction of Hybrid Performance

Field trials that rely on phenotypic evaluations are expensive and difficult to manage (Maenhout et al., 2010). It is envisaged that early identification and prediction of hybrid performance will reduce the cost of developing hybrids by reducing the number and size of field trials. The number of trial genotypes will be restricted to only those entries that exhibit the highest potential to produce economically important hybrids for selection. Combining ability analysis using the line X tester design can generate information useful in predicting performance. The information may also be used to predict performance of three way crosses.

2.6.2. Evaluation of Inbred Lines

Inbred lines are used as parents in the generation of hybrids. Identification of suitable parents for hybrid development is therefore important. A large amount of germplasm may

accumulate after every cycle of breeding leading to difficulty in maintenance. Therefore, there is need to identify and maintain only relevant and important inbred lines as parental stock.

The differentiation of inbred lines on the basis of their combining ability has long been identified as a fundamental step to crop improvement (Jensen, 1959). Researchers cited in Jensen (1959) presented conflicting data on the performance of lines and their hybrids. Some researchers found that lines were high yielding both as lines and in crosses. Other researchers found data which showed a difference in the performance of a line and its hybrid combinations (Jensen, 1959). These contradictions show that when lines are crossed in hybrid combinations there may be other factors related to genotypic interactions which may be difficult to explain. They need to be investigated. Bagheri and Jelodar (2010) asserted that the performance of an individual line may not necessarily correspond to its ability to combine with other lines in hybridisation. These variations necessitate the need to evaluate each line separately and in combination. Line X tester analysis helps in partitioning combining ability into GCA which is due to an individual line and SCA which is due to a combination of different genotypes in a particular cross. These components are then used as indicators of importance of each line. Studies on combining ability are still relevant as shown by several researchers using different populations (Ali et al., 2014; Beyene et al., 2013; Jacobson et al., 2014; Ruswandi et al., 2015).

2.6.3. Determination of Gene Action

It is known that the genetic make-up of an individual plant interacts with the environment under which it is grown and results in the observed phenotypic response which can be measured (Hazel and Lush, 1942; Mendel, 1997). Genotype, environment and their interaction determine the proportion of additive, non-additive or dominance gene effects

(Khotyleva and Trutina, 1973). Summation of additive effects of line and tester makes the GCA component while the SCA component is made up of dominance and epistatic effects of the interaction between the line and tester genotypes (Darbeshwar, 2000). Since GCA is the sum of line and tester genotype main effects and SCA is due to line X tester genotype interaction, it follows that additive and dominance gene action can be deduced from the estimates of GCA and SCA, respectively. A higher GCA or SCA estimate means that a trait will be under control of additive or dominance gene action, respectively (Aly et al., 2011).

2.7. Genetic Gains

Achieving breeding gains in maize yield is important for increased food production amid sharp population growth, climate change and increased land demand for urban and industrial expansion. Evaluating breeding gains allows breeders to understand the potential of a genotype and assess any unexploited genetic potential (Ci et al., 2011). Investigation of breeding gains also helps in evaluating progress of current breeding program, prediction of possible course of action in future and selection of a breeding strategy (Govindaraj et al., 2010; Jines, 2007). All these are necessary to improve maize yields and meet demand for consumption and industry.

Breeding gain is a positive (for desirable traits) change achieved in the mean of a trait observed in the progeny compared to the base population as a result of deliberate selection (Jines, 2007). Early maize varieties were mainly low yielding landraces and open pollinated varieties (OPVs) contributed to the early improvements in maize yields (Duvick, 2005b). Since the advent of hybrids significant gains have been realised. Many breeding programs now aim to improve the hybrids in one or more traits which contribute to yield increase. To achieve high breeding gain the hybrids developed must outperform the base population from which they are developed (Musundire, 2013). The improvement in performance can be measured by comparing sets of phenotypic data between parents and offspring (Septiningsih

et al., 2003) or against commercial hybrids. It may also be calculated by comparing the actual performance of a genotype and an expected performance (Callister et al., 2013). In many cases breeders have specific traits which they want to improve and a standard against which they compare. Commercial hybrids on the market or biological founder parents can be used as benchmarks for the expected performance. In this study both commercial and biological checks are used. The amount of breeding gain achieved is postulated to depend on the combining ability of the parental lines, heritability of the trait and environmental effects (Bello et al., 2012). Several researchers have reported different genetic gains in grain yield and secondary traits in maize (Almeida et al., 2013; Badu-Apraku et al., 2014; Beyene et al., 2015; Cairns et al., 2013). The differences reported show that genetic gains are variable under different conditions and with different maize populations.

2.7.1. Genetic Gains Achieved in Grain Yield over the years

Several researchers concur to that maize yields have changed over the years. About 50% of the yield increases realised in the US since the 1930s have been attributed to genetic improvement accompanied by morphological changes in yield related traits (Duvick, 2005a). The traits mostly targeted for change are those which contribute to efficient biomass accumulation and grain filling. These improvements have been enhanced by factors such as adequate genetic variability in the germplasm (Viana, 2007), high heritability coefficients in selected traits and advancement of breeding techniques (Sreckov et al., 2011). However, breeding gains achieved in any of the traits are only important if they are followed by breeding gains in grain yield (Sreckov et al., 2011) which is the main objective of many breeding programs. Since heritability of traits varies with environment and genotype (Shimelis and Shiringani, 2010), breeding gains should be measured under prevailing environmental conditions and against specific objectives of a breeding program. Grain yield improvement is a stepwise and indirect process through the selection of secondary traits.

Therefore, breeding gains or improvement in any of the secondary traits would be expected to contribute to final yield. However, the final gain in yield depends on the genotype and correlations between the trait and grain yield (Bello and Olaoye, 2009).

Bello et al. (2014) cited an estimated 20% yield increase in maize yields between 1985 and 1990. Since then, the yields have continued to increase to reach as high as 14 t/ha in favorable environments for hybrids developed between the 1970s and 1990s (Adebo and Olaoye, 2010). This concurs with Candido and da Costa Andrade (2008) who reported a 19.2% genetic gain in yield. However, these figures fall short of 82.11% reported by Souza et al. (2009). Despite the differences, there is general consensus that yield has improved over the years. This study aims at estimating and quantifying genetic gains in yield and some agronomic traits achieved by selecting for high yield potential in a bi-parental population at UKZN.

2.7.2. Some Genetic Gains Achieved in Secondary Traits over the years

Reduction in plant height and ear height in maize has been a target of many breeding programs for a number of reasons, such as reducing lodging (Candido and da Costa Andrade, 2008), improving standing ability of plants and reducing the amount of energy channeled towards maintenance of vegetative growth. These factors when combined lead to a higher efficiency in energy utilization resulting in higher reproductive capacity which is critical for yield increase (Duvick, 2005b). Duvick et al. (2004) noted a decrease in the number of branches and weight of the male flower. This has been identified as a way to reduce apical dominance and competition for assimilates between male and female parts. Reducing apical dominance reduces the amount of assimilates channeled towards the tassel while promoting ear development thereby contributing to yield improvement.

Phenology, which refers to the timing of biological events in the life cycle of an organism (Koch et al., 2007), has been exploited in plant improvement. Modern hybrids have longer periods of growth due to stay green genes. They also flower earlier with better anthesis-silking synchrony (Barker et al., 2005). The synchronization of male and female flowering period promotes efficient pollination that enhances grain filling and increases yield accumulation. Cob dry down period has also been noted to have decreased over time (Duvick, 2005b). Dry down is estimated in the field by the number of days taken by a plant to have 50% of the cobs to dry to harvestable moisture level. This is also confirmed by measuring moisture content at harvesting. The importance of quick dry down is the reduction of potential attack by diseases such as cob rots and the ease of fitting in cropping patterns such as rotation. Number of ears per plant has been enhanced for improved yield. Candido and da Costa Andrade (2008) reported 11.1% increase in ear prolificacy which together with reduced barrenness in modern hybrids (Duvick et al., 2004) resulted in more kernel numbers and weight. These are vital components for increasing productivity.

All these gains can be attributed to exploitation of genetic diversity (Bello et al., 2014; Duvick, 2005b) and breeding gains realised in these components may correlate with gains realised in yield (Khazaei et al., 2010). The complex heritability of grain yield requires the indirect selection of yield related traits with higher breeding gains which are strongly correlated with yield. However, Breseghello and Coelho (2013) cited that it is difficult to improve all the traits concurrently due to genetic correlations between the different traits which may be caused by pleiotropy, linkages or structural arrangements of the genes. This is in agreement with Jines (2007) who also considered genetic variance as a factor in achieving breeding gains. Therefore, genetic interactions should be well accounted for in genetic studies of heritability.

2.8. Factors Influencing Genetic Gains Achieved through Selection

The amount of genetic gains realised through breeding depends on several factors. The factors include but are not limited to the following.

2.8.1. Selection Pressure

Jines (2007) and Breseghello and Coelho (2013) concurred on the importance of selection which can cause desired or undesirable change in the traits under consideration. The intensity of selection determines how many genotypes and what level of phenotypic expression will be selected. Selection can lead to unpredicted outcomes, which can contribute to breeding gains when the observed mean is above normal range. Breeding gains are increased by selecting individuals with higher mean performance (De La Fuente et al., 2013). In this study selection intensity of 1.67 at 10% selection was used. Selection of more genotypes reduces selection intensity and may result in less genetic gains being realised. Secondary traits offer an easier but indirect way to select for yield (Mallikarjuna et al., 2011) and thus the number of selected traits and size of the selected population determine the amount of gains that can ultimately be achieved.

2.8.2. Heritability and Genetic Variance

Genetic variance is the proportion of heritable material that can potentially be transmitted to the progeny (De La Fuente et al., 2013) during mating. This is the portion of heritability that is important in transfer of a trait from parent to offspring. The amount of genetic variance will determine how much of the heritable material can be exploited. So a higher genetic variance indicates higher potential for breeding gains (Zuk et al., 2012). The coefficient of heritability will therefore depend largely on the amount of genotypic variance in observed

response by a genotype under prevailing conditions. Traits with higher heritability can help to increase genetic gains as they can easily be passed to the progeny.

2.8.3. Genetic Variability

In maize, genetic variability promotes heterosis which is the basis for genetic improvement (Dickert and Tracy, 2002). The information regarding genetic constitution of the populations will give estimates of possible genetic gain using introgression approaches. Narrow genetic variability can limit breeding gains since heterosis is low in less divergent populations (Ortiz et al., 2010). The differences in phenotypic expression among a population may be a sign of available variability for exploitation.

2.8.4. Genotype X Environment (GXE) Interactions

The observed performance of an individual plant is influenced by its genetic composition, environmental effects and the interaction of these two (Alberts, 2004; Ding et al., 2007). The interactions are important in conferring adaptation but their inconsistencies and unpredictability complicate the selection process (Akçura et al., 2011; Ding et al., 2007). GXE interactions cause genotypes to perform differently in different environments (Crossa, 1990). Environmental influence can affect the expression of a genotype leading to selection or non-selection of such a genotype (Hallauer and Miranda, 1988). This complicates selection of many traits since they have variable expression under different environments (Zaidi et al., 2007). In addition, GXE interactions reduce heritability of quantitative traits (Nzuve et al., 2013). It is therefore important to carry out multi-environment trials (Aly et al., 2011) to quantify genotype x environment interactions (Babić et al., 2011) in order to accurately account for the interactions before any effective selection can be carried out. Homogenous environment are expected to have similar GXE coefficients, but this is not easily attainable in

practice, especially in sub-Saharan Africa where environments vary in soil properties, rainfall and agronomic practices (Alberts, 2004). Genotype X environment interactions result in variable performance of a genotype over time and space such that in many cases GXE interactions are treated as undesirable and confounding effects (Yan and Tinker, 2006) although they can provide breeding opportunities. Multi-environment trials are expected to predict and estimate yield potential, identify stable genotypes and most adapted genotypes for a particular environment (Aly et al., 2011). The major concern for breeders is not only to quantify GXE interactions but also to match genotypes to their most suitable environments (Yan and Tinker, 2006) as GXE interactions can be an important way of separating adapted from non-adapted genotypes.

Quantification of GXE interactions can be carried out by several methods including combined ANOVA, stability and multivariate analyses (Kandus et al., 2010). The former method is most widely used despite its weaknesses of assuming homogeneity across the different sites and not accounting for non-additive terms (Kandus et al., 2010; Mitroviã et al., 2012). The additive main effects and multiplicative interaction (AMMI) model is a powerful tool for estimating genotype, environments and GXE interactions components (Babić et al., 2011). In addition, it breaks down the interaction component into its separate components for each environment (Bose et al., 2014). The AMMI compresses the interactions into principal components depending on the amount of interactions that are significant (Kandus et al., 2010). However, despite such usefulness the AMMI also has its own shortcomings such as failure to identify superior genotypes or suitable environments. This can be accounted for by incorporating the GGE biplot analysis.

GGE biplot analysis combines tools from several methods such as regression and AMMI (Ding et al., 2007). GGE biplot is a scatter plot that enables the simultaneous visualization of

row and column factors and their underlying interactions (Yan and Tinker, 2006). It is useful in genotype and environment evaluation and identifying adapted and stable genotypes (Ding et al., 2007). Adapted genotypes are those which perform best in respect of the trait under a given environment, while stable genotypes perform relatively well across several environments. Environment evaluation entails deduction of the discriminating ability of an environment and its representativeness of the ideal environment (Ding et al., 2007). This makes GGE such an important tool that its application in agriculture is on the increase (Yan and Tinker, 2006). In the current study both the AMMI and GGE biplot methods were used to identify the best hybrids and the lines with superior performance.

Selection of superior genotypes is confounded by GXE interactions. These interactions result in different performances by the same genotype across different environments. The effects of GXE interactions are not stable over time or across sites and resultantly lead to inefficient yield-based selections (Scapim et al., 2000). Therefore, assessing and evaluating the stability of a genotype is of paramount importance in identifying suitable hybrids for multiple environments (Kandus et al., 2010). There are several methods to evaluate genotype superiority and stability. One of the methods was proposed by Lin and Binns (1988). The method provides an easier way to identify specific adaptation and stability across environments based on the comparison of the mean of a genotype and the highest mean in each environment. A more superior genotype will have a smaller superiority index compared to less superior genotypes. Huehn (1990) proposed the stability concept whereby a stable genotype is identified by having a similar ranking across different environments. The similarity in the rankings is hypothesized to emanate from the ability of the genotype to stabilize its performance across the environments (Huehn, 1990). A cultivar with higher average ranking across the environments is then selected for stability. In instances where two environments have the same ranking for the same genotype, the environments can be

considered useful in selection even though the genotype shows different mean performances. These methods are better than parametric models such as regression as they do not require the fulfillment of assumptions of normality, homogeneity of variance and linearity of genotypic effects (Scapim et al., 2000). Huehn (1990) also highlighted that non-parametric methods reduce bias caused by outliers.

2.8.5. Heterosis

Heterosis was coined by Shull in 1914 as the superiority of the F_1 progeny over the parental lines (Melchinger et al., 2007). However, such heterosis where hybrids are compared to their parents is not useful since generally the mean yield of maize hybrids is higher than mean of the lines used to develop that particular hybrid (Gallais, 1988). Hence standard heterosis, where the F_1 progeny is compared against a standard check such as commercial variety, is used widely. This form of heterosis is important since it allows the breeder to determine whether the experimental testcrosses can be developed to replace the varieties already being grown for a particular agricultural zone. The most important heterosis in maize breeding is the grain yield heterosis which has received lots of reviews (Hosana et al., 2015; Jebaraj et al., 2010; Jiang and Reif, 2015; Ruswandi et al., 2015). However, the genetic basis of heterosis is still debated despite widespread studies. Dominance and epistasis hypotheses have been proposed in many studies (Melchinger et al., 2007). In this study heterosis was measured as the realised gains after selection over the control hybrids including commercial, advanced and hybrids of the founder parent (CML505).

2.8.6. Transgressive Segregation

Transgressive segregation is a term used to refer to a process whereby a group of progeny exhibits mean values that exceed parental phenotypic values (Rieseberg et al., 1999; Sleper

and Poehlman, 2006). Breseghello and Coelho (2013) stated that the selection of one of correlated traits can result in unanticipated changes in the dependent variable which may fall outside of the normal range. The offspring exhibiting superior transgressive traits are selected over the inferior genotypes. The superior performance by transgressive offspring can increase genetic gains. The reasons contributing to transgressive segregation are inconclusive but genetic recombination or expression of previously less dominant alleles or heterosis are likely to be involved (Rieseberg et al., 1999). Transgressive segregation would therefore be particularly important in a population derived from common ancestry such as a bi-parental population derived from LP23 and CML 505 in the current study. The superior performance of the segregants can be computed from field data to enhance selection. Hence the need for line X tester analysis to determine gene action and selection of suitable parents for hybridisation in order to produce desirable transgressive segregants (Shattuck et al., 1993). The current study aimed to identify lines that exceeded yield potential of their founder parents, among other factors.

2.9. Measuring Genetic Gains

The difference between the mean of selected genotypes and the breeding population can be expressed as genetic gain in different forms. The gains are calculated from phenotypic evaluations on grain yield and related traits. Genetic gains can be measured per cycle or per year (De La Fuente et al., 2013). The only difference in the methods is the period at which the evaluations take place. However, calculating gain per year is more useful in comparing different breeding programs than gain per cycle (De La Fuente et al., 2013). The mean of the selected genotypes is compared to the mean of the base population, control hybrids or any other set benchmark depending on the objectives of the program. In this study the breeding gains are measured against the performance of commercial standard hybrids, advanced

control hybrids and hybrids of the founder parents. In this method the genetic gains are calculated per one cycle.

2.10. Correlation, Regression and Path Coefficient Analyses

Crop breeding entails the improvement of a variety or line in one or more characteristics. Yield increase is the most important objective in many maize breeding programs. Due to GXE interactions yield expression is variable under different environments (Güler et al., 2001; Khazaei et al., 2010). The direct selection of yield may be ineffective and difficult due to the complex nature of yield heritability and its variability under different environmental conditions and selection pressures. Consequently, yield improvement in maize can be achieved through exploitation of the relationship between yield and its related traits (Machikowa and Laosuwan, 2011). The relationship has been used in several studies to overcome the complexity associated with grain yield heritability. Grain yield selection and evaluation should be carried out with relative precision using models that minimise environmental influence and which are able to differentiate and quantify the contributory factors.

Correlations estimate the nature of relationship that may exist between variables. Correlations are found where variables have a cause and effect relationship in which one variable is dependent on the other such that a change in the independent variable causes a change in the dependent variable (Bello et al., 2010). The relationship can either be positive or negative; strong or weak. Where variables are positively correlated both independent and dependent variables change in the same direction whereas in negatively correlated variables, the variables change in opposite directions. Information on correlations is important in maize where selection of yield is indirect and achieved through selection of secondary traits (Bello and Olaoye, 2009). However, correlations are inadequate in describing the importance of

each trait in contributing to final yield (Sreckov et al., 2011). The inadequacy can be misleading where observed variations are due to more than one indirect cause (Bizeti et al., 2004). Therefore there is need for a more in-depth analysis of the interactions to understand the importance of each trait and rank their importance for targeting in selection. One way to achieve this is by using the path coefficient analysis (Udensi and Ikpeme, 2012).

Path coefficient analysis is important in partitioning the observed change in the dependent variable into contributory effects by each independent variable (Beiragi et al., 2011). It is a useful way of examining direct and indirect relationships of complex traits (Manggoel et al., 2012). Understanding of the grain yield-secondary traits relationship will greatly improve selection methods (Rafiq et al., 2010) as it helps to rank the traits in order of their importance in yield improvement. The breeder will then target traits with highest contributory effects for selection. Therefore it was prudent to investigate the role of secondary traits in determining yield in the current study.

2.10.1. Grain Yield and its Relationship with Secondary Traits

Grain yield is the primary and most important trait targeted in maize improvement (Zaidi et al., 2007) except in a few cases where maize is bred for silage biomass or nutritional quality. Unfortunately, grain yield heritability is highly variable and its selection is confounded by inconsistencies under variable environments (Zaidi et al., 2007). Studies on hybrids and inbred lines have concluded that yield is a sum of contributions by several traits having different contributory effects (Mohammadi et al., 2003). It is therefore important to understand the nature of relationship that exists between grain yield and the secondary traits. The understanding of the relationship can help in devising an effective method to achieve high breeding gain in yield. The secondary traits are easier to select, highly heritable and less complex (Zaidi et al., 2007) but contribute differently to the final yield. Path analysis is used

to deduce the nature and magnitude of the contribution of each trait. Selection of secondary traits has been helped by statistical analyses which can compute genetic correlations and carry out path coefficient analysis (Kashiani and Saleh, 2010).

The relationship between yield and secondary traits has been exploited in breeding for increased yield in hybrids. It is difficult to select directly for yield despite its high heritability. Bello et al. (2012) and Ullah et al. (2013) reported between 37% and 98% heritability for grain yield in maize. Although heritability of economically important secondary traits is also complex and environmentally sensitive (Smalley et al., 2004), they have high heritability and are easier to select. Most of the important secondary traits such as ear prolificacy, plant height, flowering and anthesis days, ear length and grain moisture content have been reported to have high heritability and have been used in improving yield (Bello et al., 2012; Souza et al., 2009; Ullah et al., 2013).

Several studies have demonstrated the importance of secondary traits by evaluating their genetic correlations with grain yield (Betrán et al., 2003). Reports on phenotypic and genetic correlations of secondary components with grain yield evaluated on many inbred progenies in different trials and environments showed that grain yield was strongly correlated to anthesis silking interval (negative correlation) and the number of ears per plant (positive correlation), while it was low for number of tassel branches, leaf senescence and leaf chlorophyll (Betrán et al., 2003). Number of ears per plant, cob length and 100 grain weight have also been reported to be positively correlated with grain yield (Nzuve et al., 2014). However, Sreckov et al. (2011) reported a negative correlation between plant height and grain yield. The differences in the findings may be due to factors such as environments, unpredicted interaction between the traits or differences in germplasm used. As a result correlation measures may not sufficiently explain some observations in yield response due to interactions

which may inadvertently exist between the variables (Sreckov et al., 2011). It is therefore imperative to analyse the interaction between the secondary traits in order to deduce the contribution of each trait to final yield.

2.10.2. Importance of Secondary Traits

Selection of secondary traits is important in many programs. As a result it has been studied extensively in maize. The secondary traits which have been targeted mainly in maize are plant height, number of ears per plant, tassel branches, ear prolificacy, reduced anthesis-silking interval (Bekavac et al., 2007), delayed senescence and prolonged absorptance of photosynthetically active radiation. These traits are quantitative and have continuous distribution expressed as a result of minor effects from many gene loci (Septiningsih et al., 2003).

In breeding, reduction in plant height is considered a desirable trait (Johnson et al., 1986). Betrán et al. (2003) concluded that reduction in plant height leads to reduced strength of other sinks in order to partition assimilates for flower development. Shorter plant height is associated with reduced lodging due to wind, good ear placement height and higher yield due to more assimilates being partitioned to reproductive growth.

Ear prolificacy is measured as the number of ears per plant and is strongly linked to grain yield. Several studies cited by Betrán et al. (2003) found strong positive correlations between yield and ears per plant (EPP). The number of kernels, 100 grain weight and the number of rows per ear are characteristics of the ear which also contribute to yield (Betrán et al., 2003).

Early maturity predicted from days taken by 50% of the plants to flower and shed pollen plays a significant role in determining the final yield (Campos et al., 2004). A short anthesis silking interval (Bekavac et al., 2007) is considered a desirable trait in breeding for high

yield. Hybridisation can be hampered by low pollen viability and short period of receptivity by the female flowers (Longin et al., 2012). There is need to develop accurate phenotyping models that can precisely predict dates for pollen shedding and female silking (Longin et al., 2012) in order to be able to generate desirable hybrids.

Genotypes with many tassel branches are likely to have reduced grain yield due to suppression of ear development and high assimilate expenditure for head maintenance (Sangoi, 2001). Experiments involving the detasseling of modern hybrids have revealed that it has no effect on the final yield. This suggests that tassels in these hybrids already have reduced dominance over ear set. Their reduced rates of development and lower sink strength contribute to better synchronization of pollen shed and silking emergence (Sangoi, 2001) leading to increased kernel set, kernel number and kernel rows per ear.

Trials involving the simulation of northern leaf blight (NLB) showed that removal of leaves in the lower third of the plant had minimal effect on the final grain yield (Pataky, 1992). In another study removal or non-removal of the two leaves above the ear at grain filling stage was shown to account for between 70 and 90 % of yield differences in grain yield (Gates and Mortimore, 1972). This shows the strong positive correlations expected between yield and the number of leaves per plant and their position in relation to the ear.

Chlorophyll content is related to the health status and phenological stage of the plant. Under drought conditions delayed senescence of healthy green leaf and plant height have moderate correlations with total yield (Edmeades et al., 1996). However, in tropical maize low productivity could be attributed to the early onset of and rapid leaf senescence after anthesis (Osaki, 1995). During ear development and grain filling there is need to maintain a photosynthetically active canopy for continued photosynthesis and translocation of

photosynthates to the grains. Several authors cited in Bekavac et al. (1998) agree that stay green genes are important in improving maize productivity, but they also stress that its relationship with grain yield is governed by the vegetative length and genetic makeup of the variety. Generally, all plants with the ability to stay green for longer have higher yields than the non-stay green plants (Xu et al., 2000).

Plant height is strongly correlated with flowering date (Dickert and Tracy, 2002). This has been attributed to cessation of internode growth after flower initiation. As a result some early flowering varieties have significantly shorter height. However, this is also linked to reduced yield, which is speculated to result from reduced photosynthetic capacity (Dickert and Tracy, 2002).

2.10.3. Efficiency of Selecting Secondary Traits in Grain Yield Improvement

The selection for yield through indirect selection of a secondary trait is efficient provided the secondary trait has higher heritability than grain yield and their genetic correlation is sufficiently high (Zaidi et al., 2007). However, selection of traits under different environmental conditions can result in misleading conclusions. The major limitation is in holding environmental conditions constant as this may give rise to variations in the performance of a particular genotype. The importance of any particular trait will be influenced by its contribution to the final yield, its level of expression under the prevailing conditions and level of complexity in selection. In maize, traits such as early maturity, reduced lodging tendency, short stems, short ear height, and shorter anthesis silking interval have been identified as important in yield improvement. They have been subsequently introgressed into tropical germplasm (Acquaah, 2007). Improving a variety in one trait may be easy and straight forward but may not improve the overall performance of the variety (Bresaghella and Coelho, 2013). However, improving a variety in many traits may improve overall performance but it is complicated by the complex genetic correlations that may exist

between the traits. Selection is efficient where the traits are favourably correlated such that an increase in one will result in a desirable change in the other.

2.11. Summary and Conclusion

The literature shows that for high yields to be obtained there is need for farmers to access and grow superior varieties. Superior hybrids are developed from parental lines with desirable traits that are genetically inherited. A line X tester mating design is commonly used to identify the parental lines with high combining ability. One important use of combining ability is to predict hybrid performance which reduces the cost of carrying out trials involving large numbers of genotypes. After every cycle of breeding there is need to evaluate if the breeding process was successful. The amount of genetic gains achievable is largely influenced by GXE interactions which provide both opportunities and challenges to breeding. It is important to evaluate or quantify the extent to which such interactions affect breeding outcomes. The relationship between yield and secondary traits has been targeted widely in maize improvement. The correlations that exist between the primary and secondary traits also largely affect breeding strategies and genetic gains.

This literature review identified the following gaps that need to be filled by the objectives of this study:

- The relationship between yield and secondary traits varies from population to population and environment to environment. Therefore there is need to evaluate the local population under local environments.
- Likewise, genetic gains are also variable under different environments and with different populations and with different benchmarks.

- The combining ability of the inbred lines at UKZN has not been evaluated and would generally depend on the testers used and the environment under which they are tested.
- There is need to identify traits which would result in the highest yield improvement in this population and also to identify the traits which were successfully introgressed from parental lines

The next chapter describes the materials and methods used to gather and generate data which helps to meet the research objectives and fill the gaps which have been identified in the literature.

Chapter 3 : Materials and Methods

3.1. Introduction

A bi-parental maize inbred population was developed at University of KwaZulu-Natal for maize streak virus (MSV) and downey mildew resistance. MSV resistant genotypes were selected using marker assisted selection and greenhouse inoculation in Zimbabwe while downey mildew resistance was selected in the field in low altitude tropical environment in Mozambique in 2011. The parental lines used in developing this population were CML505 and LP23. These parental lines are discussed in detail in Mafu (2013). 19 lines (Table 3.1) were sampled from the population for use in this study.

3.2. Description of Germplasm

Thirty eight test-crosses were generated by crossing 19 maize inbred lines derived from a bi-parental population to two testers. Commercial hybrids and other advanced experimental hybrids in the program at UKZN were included in the analysis as controls for different agronomic traits. The testers and experimental inbred lines are listed in Table 3.1. A total of 50 entries consisting of the 38 experimental crosses and 12 control hybrids were evaluated for yield and agronomic traits (Tables 3.2 and 3.3).

Table 3.1: Description of inbred lines and testers and their origins

Parental lines			
Code name	Pedigree	Origin	Status
DMSR-1	(CML505/LP23-F2B-1-1-2-1)-B	UKZN	Test line
DMSR-2	(CML505/LP23-F2B-2-1-1-2)-B	UKZN	Test line
DMSR-4	(CML505/LP23-F2B-3-1-2-1)-B	UKZN	Test line
DMSR-8	(CML505/LP23-F2B-6-1-3-1)-B	UKZN	Test line
DMSR-10	(CML505/LP23-F2B-10-1-2-1)-B	UKZN	Test line
DMSR-12	(CML505/LP23-F2B-11-1-4-2)-B	UKZN	Test line
DMSR-13	(CML505/LP23-F2B-12-1-3-1)-B	UKZN	Test line
DMSR-18	(CML505/LP23-F2B-15-1-4-2)-B	UKZN	Test line
DMSR-21	(CML505/LP23-F2B-16-1-1-1)-B	UKZN	Test line
DMSR-23	(CML505/LP23-F2B-17-2-1-1)-B	UKZN	Test line
DMSR-26	(CML505/LP23-F2B-18-3-4-1)-B	UKZN	Test line
DMSR-30	(CML505/LP23-F2B-21-2-3-1)-B	UKZN	Test line
DMSR-35-1	(CML505/LP23-F2B-25-1-1-1)-B	UKZN	Test line
DMSR-35-2	(CML505/LP23-F2B-25-2-1-1)-B	UKZN	Test line
DMSR-35-3	(CML505/LP23-F2B-25-2-3-1)-B	UKZN	Test line
DMSR-35-4	(CML505/LP23-F2B-25-3-1-1)-B	UKZN	Test line
DMSR-35-5	(CML505/LP23-F2B-25-4-4-1)-B	UKZN	Test line
DMSR-73	(CML505/LP23-F2B-83-1-2-1)-B	UKZN	Test line
DMSR-80	(CML505-1-1-2)-B	CIMMYT	Founder Parent
Testers	Pedigree	Origin	Status
LP19	Not established	IIAM-Mozambique	Tester
LP21	Not established	IIAM-Mozambique	Tester

CIMMYT= International Maize and Wheat Improvement Centre

IIAM= Instituto de Investigação Agrária de Moçambique (Agricultural Research Institute of Mozambique)

UKZN=University of KwaZulu-Natal

Table 3.2: Description of the experimental hybrids, pedigree and their origin

Name	Pedigree	Origin
15XH01	LP19/(DMSR-1:CML505/LP23-F2B-1-1-2-1)-B	UKZN
15XH02	LP19/(DMSR-2:CML505/LP23-F2B-2-1-1-2)-B	UKZN
15XH03	LP19/(DMSR-4:CML505/LP23-F2B-3-1-2-1)-B	UKZN
15XH04	LP19/(DMSR-8:CML505/LP23-F2B-6-1-3-1)-B	UKZN
15XH05	LP19/(DMSR-10:CML505/LP23-F2B-10-1-2-1)-B	UKZN
15XH06	LP19/(DMSR-12:CML505/LP23-F2B-11-1-4-2)-B	UKZN
15XH07	LP19/(DMSR-13:CML505/LP23-F2B-12-1-3-1)-B	UKZN
15XH09	LP19/(DMSR-18:CML505/LP23-F2B-15-1-4-2)-B	UKZN
15XH10	LP19/(DMSR-21:CML505/LP23-F2B-16-1-1-1)-B	UKZN
15XH11	LP19/(DMSR-23:CML505/LP23-F2B-17-2-1-1)-B	UKZN
15XH12	LP19/(DMSR-26:CML505/LP23-F2B-18-3-4-1)-B	UKZN
15XH13	LP19/(DMSR-30:CML505/LP23-F2B-21-2-3-1)-B	UKZN
15XH14	LP19/(DMSR-35:CML505/LP23-F2B-25-1-1-1)-B	UKZN
15XH15	LP19/(DMSR-35:CML505/LP23-F2B-25-2-1-1)-B	UKZN
15XH16	LP19/(DMSR-35:CML505/LP23-F2B-25-2-3-1)-B	UKZN
15XH17	LP19/(DMSR-35:CML505/LP23-F2B-25-3-1-1)-B	UKZN
15XH18	LP19/(DMSR-35:CML505/LP23-F2B-25-4-4-1)-B	UKZN
15XH20	LP19/(DMSR-73:CML509/LP23-F2B-83-1-2-1)-B	UKZN
15XH22	LP21/(DMSR-1:CML505/LP23-F2B-1-1-2-1)-B	UKZN
15XH23	LP21/(DMSR-2:CML505/LP23-F2B-2-1-1-2)-B	UKZN
15XH24	LP21/(DMSR-4:CML505/LP23-F2B-3-1-2-1)-B	UKZN
15XH25	LP21/(DMSR-8:CML505/LP23-F2B-6-1-3-1)-B	UKZN
15XH26	LP21/(DMSR-10:CML505/LP23-F2B-10-1-2-1)-B	UKZN
15XH27	LP21/(DMSR-12:CML505/LP23-F2B-11-1-4-2)-B	UKZN
15XH28	LP21/(DMSR-13:CML505/LP23-F2B-12-1-3-1)-B	UKZN
15XH30	LP21/(DMSR-18:CML505/LP23-F2B-15-1-4-2)-B	UKZN
15XH31	LP21/(DMSR-21:CML505/LP23-F2B-16-1-1-1)-B	UKZN
15XH32	LP21/(DMSR-23:CML505/LP23-F2B-17-2-1-1)-B	UKZN
15XH33	LP21/(DMSR-26:CML505/LP23-F2B-18-3-4-1)-B	UKZN
15XH34	LP21/(DMSR-30:CML505/LP23-F2B-21-2-3-1)-B	UKZN
15XH35	LP21/(DMSR-35:CML505/LP23-F2B-25-1-1-1)-B	UKZN
15XH36	LP21/(DMSR-35:CML505/LP23-F2B-25-2-1-1)-B	UKZN
15XH37	LP21/(DMSR-35:CML505/LP23-F2B-25-2-3-1)-B	UKZN
15XH38	LP21/(DMSR-35:CML505/LP23-F2B-25-3-1-1)-B	UKZN
15XH39	LP21/(DMSR-35:CML505/LP23-F2B-25-4-4-1)-B	UKZN
15XH40	LP21/(DMSR-47:CML509/LP23-F2B-29-4-1-2)-B	UKZN
15XH41	LP21/(DMSR-73:CML509/LP23-F2B-83-1-2-1)-B	UKZN

UKZN=University of KwaZulu-Natal

Table 3.3: The control hybrids, their pedigree and origin

Name	Pedigree	Origin
Hybrids of Biological Parents		
15XH21	LP19/(DMSR-80:CML505-1-1-2)-B	UKZN
15XH42	LP21/(DMSR-80:CML505-1-1-2)-B	UKZN
Advanced control hybrids		
11C1774		Seedco
11C1579		Seedco
11C1566		Seedco
11C2245		Seedco
11C1350		Seedco
11C1511		Seedco
11C2242		Seedco
11C1483		Seedco
10HDTX11		UKZN
Commercial control hybrids		
PAN 6Q-345 CB		PANNAR
BG5285		PANNAR

UKZN=University of KwaZulu-Natal

*pedigrees of hybrids from private companies removed for proprietary reasons

CML505 and LP23 were the two founder parents used to develop DMSR lines. CML505 was used as a donor line for MSV resistance and early flowering. LP inbred lines have been reported to have suitable anthesis-silking interval (ASI) and high number of ears per plant (EPP) (Betrán et al., 2003). The maize inbred line LP23 was used as the principal donor of high productivity and downy mildew resistance genes. Therefore, DMSR inbred lines have genes for MSV and downy mildew resistance, early flowering and high yield potential. DMSR-80 is considered the biological founder parent of all the DMSR lines and its hybrids formed by crossing to LP19 and LP21 were therefore treated as biological control hybrids. The testers LP19 and LP23 have been used extensively in other studies where they have exhibited good discriminating ability. Advanced control hybrids were hybrids developed by a private seed company and were in their final stages of testing. Commercial hybrids were from a private company and are widely grown in South Africa.

Advanced controls were not related to the inbred lines. Advanced control hybrids were included in the trial since they had performed consistently well in previous trials and their

inclusion provided a check against environmental variations. They were selected since they were in their final stage of evaluation before potentially being released as commercial varieties for the selected sites.

3.3. Description of Sites

Field trials were set up at three sites, Ukulinga, Dundee and Cedara on 26 November, 27 November and 08 December 2014, respectively. All the sites are in the KwaZulu-Natal province of South Africa. Ukulinga Research Farm is located 809 m above sea level at latitude 29° 67'E and longitude 30° 41'S (ARC, 2015). Dundee Research Station is at latitude 28° 10'S and longitude 30°31'E, 1219 m above sea level and is characterised by low rainfall (Van Schalkwyk and Gertenbach, 2000). Cedara is located in the Natal Midlands mist belt at latitude 29°67'S and longitude 30°41'E and is 1076 m above sea level with high humidity, relatively higher rainfall and lower temperatures which promote high disease occurrence (Fairbanks and Benn, 2000). Ukulinga and Dundee are generally dry and have low disease incidences. The weather data for the growing season of the maize trials is shown in Tables 3.4, 3.5 and 3.6. Weather data for Dundee was not available and weather data for the nearest town (Newcastle which is 70 kilometres away) was presented as a guide (Table 3.6).

Table 3.4: Average weather conditions at Cedara during Oct 2014 to May 2015

Year	Month	Maximum Temperature °C	Minimum Temperature °C	Rainfall (mm)
2014	September	26.99	8.33	49.79
2014	October	21.67	10.22	87.88
2014	November	22.75	12.02	132.57
2014	December	25.14	14.24	124.46
2015	January	27.37	15.22	118.60
2015	February	25.44	14.70	72.37
2015	March	25.69	14.32	83.30
2015	April	22.67	10.04	58.16
2015	May	24.19	7.44	5.32

Compiled from data generated on-farm by ARC (2015)

Table 3.5: Average weather conditions at Ukulinga during Sept. 2014 to Jun. 2015

Year	Month	Maximum Temperature °C	Minimum Temperature °C	Rainfall (mm)
2014	September	27.18	12.36	11.94
2014	October	22.67	12.36	53.09
2014	November	23.43	13.92	81.79
2014	December	26.04	15.96	91.44
2015	January	27.76	17.10	69.6
2015	February	26.22	16.55	118.87
2015	March	27.08	16.76	78.99
2015	April	23.86	13.51	32.26
2015	May	25.81	12.81	4.57
2015	June	21.87	9.76	2.29

Compiled from data generated on-farm by ARC (2015)

Table 3.6: Average weather conditions for Newcastle during Sept. 2014 to May 2015

Year	Month	Maximum Temperature °C	Minimum Temperature °C	Rainfall (mm)
2014	September	11.00	34.00	10.00
2014	October	12.00	34.00	27.00
2014	November	14.00	32.00	28.20
2014	December	17.00	33.00	39.20
2015	January	17.00	34.00	78.80
2015	February	18.00	33.00	15.60
2015	March	16.00	31.00	38.40
2015	April	13.00	28.00	2.60
2015	May	10.00	29.00	0.00

Adapted after WeatherUnderground (2015)

The soil at Ukulinga farm is loamy clay which is fertile and friable with good drainage. However, it is susceptible to cracking and crusting under flooding. The previous crop was maize and the residues were ploughed under giving good organic matter content. Dundee falls under the Sour Sandveld (KZNDARD, 2015) and is made up of sandy soils with high leaching potential and low fertility. The field had a significant slope that heavily influenced drainage pattern. It was previously fallow for one season and the grass provided little organic matter content. At Cedara there are sandy clay soils which are reasonably fertile and well

drained. Chances of flooding were very low due to a good slope and ground cover. The fields at Ukulinga and Dundee were ploughed and disced prior to planting while at Cedara there was minimum tillage. The Cedara field had high organic matter from the stover of preceding maize crop. The ground cover also provided mulch and helped in moisture conservation.

3.4. Experimental Layout and Crop Management

The experiments were laid out as 5X10 alpha lattice designs with two replications at all sites. The row numbers at each site were randomized. Each row plot was five metres long. At Ukulinga and Cedara the rows were 0.75 m apart while at Dundee they were 0.90 m apart due to differences in equipment calibration. Two seeds were hand planted at 0.30 m spacing, giving 34 plant stations per row. The plants were later thinned at three weeks to one plant per station. At Cedara and Dundee there were two border rows at either end, while at Ukulinga there was one border row. The hybrid 11C1579 was used as a border at all the sites. Average plant population was 45 000 per hectare at Cedara and Ukulinga and 38 000 at Dundee.

Weeds and pests were controlled by chemical sprays. Weeds were controlled by a combination of Basagran, Gramoxone and Troopers for the control of annual grasses and broadleaf weeds. Herbicides were complemented by manual weed control where necessary. Particular attention was paid to the control of cutworms, white grubs and stalk borer. A combination of pesticides including Karate was applied at recommended rates both as preventative and curative measures. Stalk borer was controlled by application of Carbofuran granules (at 0.30kg active ingredient per hectare) into the whorls of each plant at six weeks after crop emergence. Fertilizer was applied as basal NPK (2:3:4) at a rate of 250 kg/ha. The basal fertilizer was applied pre-planting and covered to avoid seed burn. Top dressing was applied four weeks after crop emergence and supplied in the form of lime ammonium nitrate

(LAN) (28% nitrogen) at 150 kg/ha as a single application. The crop at all sites was rainfed although at Dundee supplementary irrigation was supplied to prevent excessive wilting.

3.5. Data Collection

Grain yield and other secondary traits were measured according to CIMMYT protocol (Magorokosho et al., 2009). The description of the traits and the data collection tools and methods used in this study are presented in Table 3.7. Disease rating and scoring was carried out at Cedara only because they did not occur at the other sites. At Dundee, only grain yield, ear prolificacy and moisture were evaluated due to logistical reasons. The dates at which the traits were measured differed due to logistical arrangements. However, chlorophyll content was measured at four weeks interval starting at 10 weeks after planting at Cedara and Ukulinga Research Stations. Harvesting was done on the 5th of May 2015 at Ukulinga, 4th of June 2015 at Dundee and 15th of June 2015 at Cedara.

Table 3.7: Description of traits and the data collection methods

Traits	Descriptions	Collection method and tools
Plant height (PH)	Measured between the base of the plant to the first tassel branch of the same plant.	Metre Ruler
Ear height (EH)	Measured between the base of the plant to the insertion of the top ear of the same plant.	Metre Ruler
Anthesis days (AD)	Number of days after planting when 50% of the plants shed pollen.	Visual assessment and recording date of anthesis. Number of days to be calculated from planting date
Silking days (SD)	Number of days when 50% of plants have silks	Visual assessment and recording date of silking. Number of days to be calculated from planting date
Anthesis-silking interval (ASI)	Difference between SD and AD. Small or negative values indicate stress tolerance.	Calculated from AD and SD
Ear prolificacy (EPP)	Ratio of number of ears in a row to number of plants in a row	Calculated by physical counting of ears and plants in a row
Ear maturity (EM)	The number of days for 50% of the ears in a plot to dry.	Visual assessment and scoring. Calculated from day of planting to drying
Root lodging (RL)	The percentage of plants that are inclining at more than 45°	Visual assessment and counting and expressed as % of plants in a row
Stem lodging (SL)	Percentage of the plants which are broken below the ear	Visual assessment and counting and expressed as % of plants in a row
Chlorophyll content (CC)	The average of five plants in the row as measured by a chlorophyll meter.	SPAD meter SPAD 502 Plus, Konica Minolta
Ear position (EPO)	The position of the ear in relation to plant height	Calculated as ratio of ear height: plant height
GLS rating (GLS)	Rating of extent of GLS occurrence on individual rows	Visual assessment using a scoring scale from 1 being resistant to 9 being susceptible
PLS rating (PLS)	Rating of extent of PLS occurrence on individual rows	Visual assessment using a scoring scale from 1 being resistant to 9 being susceptible
Husk cover (PHC)	The number of ears which are not completely covered and exposing the tip of the ear	Counting number of ears with exposed tips per row and recorded as a % of total number of ears.
Grain moisture content (MOI)	Percentage of water content in the grain measured at harvest	Moisture meter (Eaton, Model 500)
Grain yield (GYG)	Weight of ears adjusted to yield per ha	Calculated from field weight and adjusted to 12.5% moisture content, 80% shelling percentage and plot size

Chlorophyll content was measured by a chlorophyll meter (SPAD 502 Plus, Konica Minolta). Three leaves per plant, starting with the leaf subtending the ear (ear leaf), of a plant were measured. Each leaf was divided into three equal segments along the length and one reading was taken per each segment. The average of the three segments was recorded for that leaf and the procedure repeated for each leaf. Three randomly selected plants were measured per row and their mean was recorded as the row reading.

Disease development was visually assessed and scored on the scale of 1-9. For disease development the following scale was used 1=0 %, 2=1 %, 3=1–3 %, 4 =4–6 %, 5=7–12 %, 6=13–25 %, 7=26–50 %, 8=51–75 % and 9=76–100 % leaf area covered by the disease (Sibiya et al., 2013).

3.6. Data Analyses

All data analyses were carried out using Genstat 14th edition. Only correlations and path coefficient analyses were carried out in SAS 9.3 (SAS Institute) computer software.

3.6.1. Mean Performance

Performances of each hybrid in every trait were subjected to analysis in Genstat 14th edition to estimate the mean performance.

3.6.1.1. Grain Yield

Grain yield was calculated from the field weight measured as cob weight per plot adjusted to 12.50% moisture and 80% shelling percentage using the following formula adapted from Lauer (2002):

$$GYG = \frac{\text{Field weight (kg)} * 10000(\text{m}^2) * (100 - \text{MOI}) * \text{Shelling}\%}{1000(\text{kg}) * \text{Plot area (m}^2) * (100 - 12.50)\%}$$

GYG=calculated grain yield per ha

MOI=measured grain moisture content at harvest

Shelling%=average shelling % for normal ears is 80% when fields are ready for harvest

(Horrocks and Zuber, 1970; Lauer, 2002)

3.6.1.2. ANOVA and Mean Separation Test

Data was analysed using the following fixed model in (Singh and Chaudhary, 1979):

$$\beta_{ijk} = \mu + G_j + E_i + G_j * E_i + E_i(r_k)(b) + \epsilon_{ijk}$$

β_{ijk} =observed response

μ =grand mean

G_j =the effect of j^{th} genotype

E_i =effect of i^{th} environment

$G_j * E_i$ =genotype X environment interaction

$E_i(r_k)(b)$ =error associated with k^{th} replication in blocks in i^{th} environment

ϵ_{ijk} =random error

Hybrid means were separated by Fischers unprotected LSD at $p \leq 0.05$ significance level

3.6.1.3. Frequency Distribution and Mean Ranking

Entry means were generated using Genstat 14th (Ed.). Entries were ranked in descending order according to the mean grain yield. Frequency histograms were generated for a selected set of traits.

3.6.2. Line X Tester Analysis

3.6.2.1. ANOVA

The ANOVA for line X tester analysis across sites was performed using the following model suggested by Singh and Chaudhary (1979):

$$Y_{ijk} = \mu + L_i + T_j + E_k + L_i * T_j + L_i * E_k + T_j * E_k + L_i * T_j * E_k + E(r) + E(r)(b) + \epsilon_{ijk}$$

Y_{ij}, Y_{ijk} =hybrid response, in k^{th} environment

μ =grand mean

L_i = effects of i^{th} line

T_j = effects of j^{th} tester

E_k =effects of k^{th} environment

$L_i * T_j$ = effects of line X j^{th} tester interaction

$T_j * E_k$ = effects of j^{th} tester X k^{th} environment interaction

$L_i * T_j * E_k$ = effects of i^{th} line X j^{th} tester X k^{th} environment interaction

$E(r)$ =effects of replications within environments

$E(r)(b)$ = effects of blocks within replications within environments effects

ϵ_{ijk} =random error

3.6.2.2. General Combining Ability (GCA)

GCA was estimated by the following equation adapted from Shashidhara (2008):

$$GCA = x_i - \mu$$

GCA=general combining ability

χ_i =predicted mean of line or tester

μ = grand mean

Standard error for GCA effects were estimated as presented in Dabholkar (1999):

$$SE = \sqrt{\frac{MSE}{E * T}}$$

SE=standard error

MSE_l =mean square for Lines

T=number of testers

E=number of environments

3.6.2.3. Specific combining ability (SCA)

SCA was estimated by the following equation adapted from Shashidhara (2008):

$$SCA = x_i - (GCA_{Tj} + GCA_{Lk} + \mu)$$

χ_i =observed mean of line i

μ = grand mean

GCA_{Tj} =GCA of tester j

GCA_{Lk} =GCA of line k

$(GCA_{Tj} + GCA_{Lk} + \mu) = \text{expected response}$

Standard error for SCA effects were estimated following the procedure presented by Dabholkar (1999):

$$SE = \sqrt{\frac{MSE}{E * r}}$$

SE=standard error

MSE =mean square for line X tester

E=number of environments

r =number of replications per environment

3.6.3. Genetic Gains

A selection intensity of 10% was adopted for grain yield and secondary traits for estimation of genetic parameters. Four hybrids with the best mean performance for each trait were selected from the 38 test hybrids.

3.6.3.1. Phenotypic and Genotypic Variances

Variances were calculated using the models suggested by Burton and Devane (1953):

$$\text{Genotypic variance } (\delta_g^2) = \frac{[MSg - MSe]}{r}$$

$$\text{Phenotypic variance } (\delta_p^2) = \delta_g^2 + \delta_e^2$$

MS_g = Genotypic Mean Squares

MS_e = Residual Mean Squares

r = Number of replications

3.6.3.2. Broad-sense Heritability

Within environments $H^2 = \frac{\delta_g^2}{\delta_p^2}$

Across environments $H^2 = \left[\frac{\sigma^2_g}{\frac{\sigma^2}{r_e} + \frac{\sigma^2_{ge}}{e} + \sigma^2_g} \right] \times 100$

H^2 =broad sense heritability

δ_p^2 =phenotypic variance

δ_g^2 =genotypic variance

δ_{ge}^2 = genotype X environment variance

δ^2 =error variance

r =number of replications

e =number of environments

3.6.3.3. Coefficients of Variation

The phenotypic (PCV) and genotypic coefficients of variation (GCV) were calculated based on the formula in Singh and Chaudhary (1979):

$$PCV = \left[\frac{\sqrt{\sigma_p^2}}{\bar{x}} \right] * 100$$

$$GCV = \left[\frac{\sqrt{\sigma_g^2}}{\bar{x}} \right] * 100$$

σ_g^2 =genotypic variance

σ_p^2 =phenotypic variance

\bar{x} =overall mean

3.6.3.4. Predicted Genetic Gain

$$PG = \Delta S * \sqrt{\delta_p^2 * h^2}$$

PG = predicted genetic gain;

ΔS = differential of selection.

δ_p^2 =phenotypic variance

h^2 = broad-sense heritability

3.6.3.5. Estimation of Realised Genetic Gains

The best four hybrids were selected in each environment and across sites and their mean will be compared to means of different control hybrids for analysis of genetic gains. The following abbreviations were used for the different means used in calculation of realised genetic gains: MS= mean of selected hybrids, MP= population mean, MBC= mean of best commercial hybrid, MC= mean of commercial hybrids, MAE= mean of advanced experimental hybrids and MBIO= mean of hybrids of biological founder parents.

Realised gains were calculated according to the equations adapted from Singh and Chaudhary (1979):

- i. Realised gains (RG1): genetic gains relative to population mean (trial mean).

$$RG1 = \left(\frac{MS - MP}{MP} \right) * 100$$

- ii. Realised gain (RG2): genetic gains relative to mean of the best commercial control hybrid

$$RG2 = \left(\frac{MS - MBC}{MBC} \right) * 100$$

- iii. Realised gains (RG3): genetic gains relative to mean of all commercial control hybrids

$$RG3 = \left(\frac{MS - MC}{MC} \right) * 100$$

- iv. Realised gains (RG4): genetic gains relative to mean of advance experimental hybrids

$$RG3 = \left(\frac{MS - MAE}{MAE} \right) * 100$$

- v. Realised gains (RG5): genetic gains relative to mean of biological founder parent hybrids

$$RG3 = \left(\frac{MS - MBIO}{MBIO} \right) * 100$$

3.6.4. Relation between Grain Yield and Secondary Traits

The relationship between grain yield and secondary traits was deduced using three different approaches as follows:

3.6.4.1. Correlation Analysis

Correlations were performed in Genstat 14th edition following the method of Payne et al. (2007) based on Pearson's correlation analysis.

3.6.4.2. Regression Analysis

Yield and agronomic traits were treated as response and independent variates respectively using the following model:

$$Y = \alpha + \beta X + \varepsilon$$

Y=yield response of the genotype (dependent variable)

α =yield response when the independent variable X=0

β =rate of change for Y for each unit of X

X=value of the independent variable

ε = the error associated with prediction of Y from X

Regressions with a coefficient of determination less than 10% were considered negligible

3.6.4.3. Path Analysis

Path analysis was performed using PATHSAS (Cramer and Wehner, 2000) macros in SAS version 9.3 to deduce direct and indirect effects of secondary traits on grain yield of hybrids.

3.6.5. Genotype X Environment Interaction

Genotype X environment interaction analyses were carried using different approaches as follows:

3.6.5.1. Additive Main Effects and Multiplicative Interaction Analysis (AMMI)

AMMI-2 model that combines additive and multiplicative parameters into a single model as follows (Bose et al., 2014) was generated:

$$Y_{ij} = G_i + E_j + \sum_{k=1}^n \lambda_k + \alpha_{ik} + \gamma_{jk} + \varepsilon_{ij}$$

Y_{ij} = yield response of i^{th} genotype in j^{th} environment

G_i = the mean of i^{th} genotype minus grand mean

λ_k = square root of the Eigen value of PCA axis k

α_{ik} and γ_{jk} = principal component scores for PCA axis k of the i^{th} genotype and j^{th} environment respectively.

ε_{ij} = residual error

3.6.5.2. Genotype and Genotype X Environment Interaction Analysis (GGE)

GGE biplot analysis was carried out for grain yield across three environments based on the following SREG model (Setimela et al., 2007)

$$Y_{ij} = \mu_j + \sum_{k=1}^t w_k \alpha_{ik} \gamma_{jk} + \varepsilon_{ij}$$

Y_{ij} =yield response

μ_j =location mean

$w_k (w_1 \geq w_2, \dots, \geq w_t)$ are singular values (scale parameters) with singular vectors for genotypes, $\alpha_k = (\alpha_{ik}, \dots, \alpha_{gk})$ and sites, $\gamma_k = (\gamma_{ik}, \dots, \gamma_{jk})$ such that $\sum_i \alpha_{ik}^2 = \sum_j \gamma_{jk}^2 = 1$ and $\sum_i \alpha_{ik} \alpha_{ik'} = \sum_j \gamma_{jk} \gamma_{jk'} = 0$ for $k \neq k'$, α and γ_{jk}

3.6.5.3. Cultivar Superiority Index

The performance of genotypes was analysed according to the model (Lin and Binns, 1988):

$$P_i = \sum_{j=1}^n \frac{(X_{ij} - M_j)^2}{2n}$$

P_i =mean square between the cultivar's yield and maximum yield in each environment.

X_{ij} =the yield of i^{th} genotype in the j^{th} environment

M_j =the maximum yield in the j^{th} environment

n =number of environment

3.6.5.4. Cultivar Stability and Mean Rank Analysis

Cultivar stability and mean ranking was carried out using following the model (Huehn, 1990):

$$S^3 = \sum_{j=1}^n \frac{|r_{ij} - \bar{r}_i|}{\bar{r}_i}$$

S^3 =the non-parametric stability measure

r_{ij} =rank of i^{th} genotype in the j^{th} environment

\bar{r}_i =mean ranking of i^{th} genotype across all environments

Chapter 4 : Results

4.1. Analysis of Variance

At Dundee Research Station only grain yield, ear prolificacy and moisture were measured due to logistical reasons. Only grain yield and ear prolificacy were analyzed across all three sites, the other traits were analyzed across two sites only (Cedara and Ukulinga Research Stations). GLS and PLS ratings were only scored at Cedara Research Station and are not included in analysis across sites because they did not occur at the other sites.

Table 4.1 shows that entry main effects for grain yield were significantly different ($p \leq 0.01$) across all the sites. Grain moisture content was not significantly different among the entries. The mean squares of secondary traits showed significant differences for genotype effects. Means squares for all traits were significantly different ($p \leq 0.05$) except chlorophyll content, number of tassel branches, root lodging and stem lodging (Table 4.2). The coefficients of variation were not very high except for poor husk, root lodging and stem lodging. All three traits measured across three sites revealed significant site X entry interaction main effects (Table 4.1 and Table 4.2). Across Cedara and Ukulinga, only chlorophyll content, ear maturity, number of tassel branches, root lodging and stem lodging showed non-significant mean squares.

Table 4.1: Mean squares for yield and secondary traits across three sites

Source of variation	Degrees of freedom	Grain Yield	Ear Per Plant	Grain Moisture Content
Environment	2	1515.09***	4.93***	742.80***
Environment/replication	3	12.53***	0.07	2.1*
Environment/replication/block	24	5.35***	0.15***	1.62**
Genotype	49	1.94**	0.09**	1.05
Genotype X Environment	98	1.47*	0.07*	1.21**
Residual	123	1.05	0.05	0.75
Mean		7.57	1.42	17.62
LSD _{0.05}		1.35	0.27	1.00
CV %		13.53	17.11	5.41

LSD=least significant difference at 5%, CV=coefficient of variation

*, **, ***=level of significance at p≤0.05, p≤0.01 and p≤0.001 respectively

Table 4.2: Mean squares for secondary traits across two sites

Source of variation	Degrees of freedom	Anthesis Days	Anthesis Silking Interval	Chlorophyll Content	Ear Height	Ear Maturity	Ear Position	Husk Cover	Number of Leaves	Number of tassel branches	Plant Height	Root Lodging	Stem Lodging
Environment	1	3715.2***	73.21***	38.14*	10153***	13317***	0.01*	73520***	39.61***	70.81***	22071***	38454.5***	47031***
Environment/replication	2	0.98	3.83*	98.22***	1655.8***	95.21*	0.05***	1165.6**	0.205	8.43	811.2***	1331.7*	3257.80***
Environment/replication/block	16	2.18	1.67	29.64***	741.50***	96.84***	0.01***	1779.10***	1.59***	6.58	501.3***	556.20*	594.40**
Genotype	49	4.57***	1.6638*	5.5	303.6***	38.74*	0.00***	1045.9***	0.6347***	2.09	307.7***	384.8	254
Genotype X Environment	49	3.22*	1.55*	7.35	307.20***	23.85	0.00***	702.80***	0.68***	4.64	204.20**	380.4	302.8
Residual	82	1.85	0.97	6.41	134.7	26.61	0	206.6	0.28	3.86	109.7	311.2	251.4
Mean		81	1	53.2	123	142.03	0.54	34.62	6.2	10	228	20.9	18.2
LSD _{0.05}		0.38	0.29	0.7876	3.7	1.48	0.01	4.57	0.16	0.58	3.25	4.98	5.05
CV %		1.67	70.01	4.76	9.4	3.63	7.24	41.51	8.48	19.55	4.59	84.37	87.21

S.O.V=source of variation, D.F=degrees of freedom, LSD=least significant difference at 5%, CV=coefficient of variation

*, **, ***=level of significance at p≤0.05, p≤0.01 and p≤0.001 respectively

Table 4.3 presents the descriptive statistics of the entries across the sites. Grain yield showed a wide range from 5.71 to 14.00 tonnes per hectare. Many secondary traits also showed wide ranges. Ear prolificacy had a very low standard deviation.

Table 4.3: Descriptive statistics of yield and secondary traits across sites

Trait	Mean + se	Median	Maximum	Minimum	Range	sd
Grain yield[#]	9.79±0.104	9.68	14.00	5.71	8.29	1.48
Anthesis Days	81.45±0.328	81.00	98.00	73.00	25.00	4.64
Anthesis Silking Interval	1.41±0.093	1.00	8.00	-2.00	10.00	1.32
Chlorophyll Content	53.17±0.216	53.43	59.83	45.51	14.32	3.06
Ear height	123.4±1.291	123.50	166.00	70.00	96.00	18.25
Ear maturity	142.0±0.714	139.50	168.00	124.00	44.00	10.10
Ear position	0.54±0.00425	0.54	0.68	0.36	0.32	0.06
Ear prolificacy	1.42±0.0205	1.39	2.33	0.77	1.57	0.29
Husk cover	34.62±2.28	27.53	100.00	0.00	100.00	32.25
Grain moisture content	17.62±0.0845	17.50	22.60	14.20	8.40	1.20
Number of leaves	6.25±0.062	6.00	9.00	4.00	5.00	0.88
Number of tassel branches	10.04±0.145	10.00	16.00	6.00	10.00	2.05
Plant height	228.1±1.286	229.00	282.00	181.00	101.00	18.18
Root lodging	20.91±1.685	11.76	88.24	0.00	88.24	23.83
Stem lodging	18.18±1.67	5.88	100.00	0.00	100.00	23.61
Grey Leaf Spot*	3.13±0.156	3.00	8.00	1.00	7.00	1.56
<i>Phaeosphaeria</i> Leaf Spot*	2.76±0.146	2.00	7.00	1.00	6.00	1.46

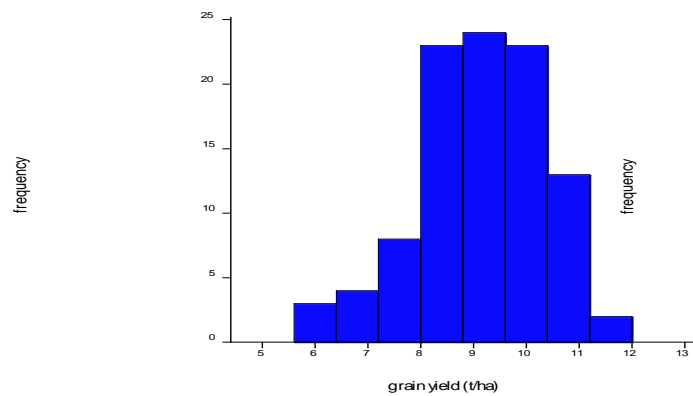
measured across three sites, *measured at Cedara only, sd=standard deviation, se=standard error

4.2. Frequency Distribution

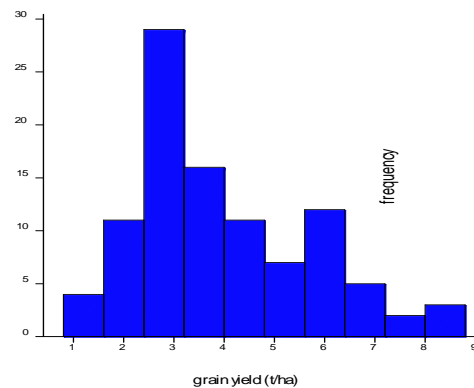
Grain yield was normally distributed at Cedara and Ukulinga Research Stations while at Dundee Research Station the distribution was discontinuous (Figure 4.1). It was negatively skewed at Cedara and positively skewed at Dundee. Dundee showed the least mean for grain yield whereas Ukulinga had the highest mean.

Figure 4.2 shows the frequency distribution of ear prolificacy at the three sites. At Ukulinga the distribution was bimodal and normal. The data at Cedara and Dundee were negatively skewed; however at Dundee the distribution was normal. At Ukulinga there was a higher

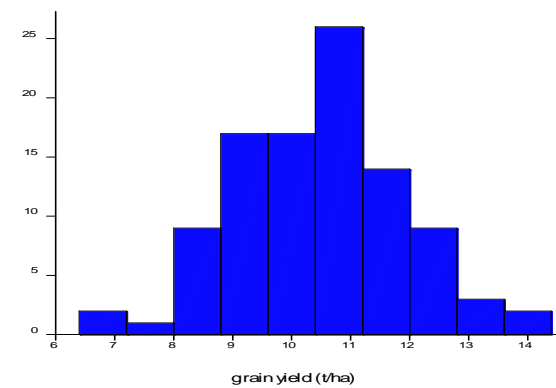
frequency for genotypes exhibiting high ear prolificacy than at the other two sites. Days to anthesis are presented in Figure 4.3. There were outliers at Cedara and the distribution was discontinuous. At Ukulinga there were no outliers and the entries took less number of days to shed pollen than at Cedara. The histogram for anthesis silking interval showed continuous distribution at Cedara and discontinuous distribution at Ukulinga (Figure 4.4). There were a few outliers at Cedara while 80% of the genotypes had anthesis silking interval of one day at Ukulinga. There were a few outliers regarding ear maturity at Cedara and Ukulinga (Figure 4.5) and the distributions at both sites were not normal. Like days to anthesis, ear maturity also took longer at Cedara than Ukulinga. The moisture content measured at harvesting was normally distributed at all sites (Figure 4.6). The frequency figures show that there were outliers at all sites and Ukulinga had the highest mean moisture content while the least mean moisture content was recorded at Dundee. The frequency of taller plants was higher at Cedara than at Ukulinga (Figure 4.7). Plant height distribution at Cedara was slightly positively skewed and normally distributed. At Ukulinga the distribution was also normally distributed but with a small negative skew. Disease ratings were not normally distributed (Figure 4.8). The highest frequency for GLS was between two and four rating scores while PLS highest frequency occurred between rating scores one and four. The maximum ratings for GLS and PLS were eight and seven, respectively.



CEDARA

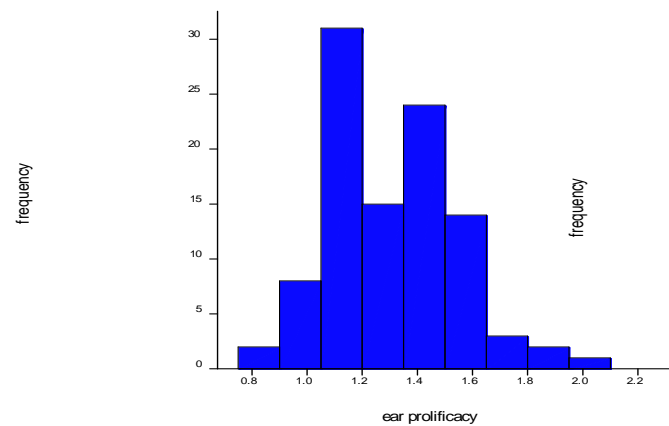


DUNDEE

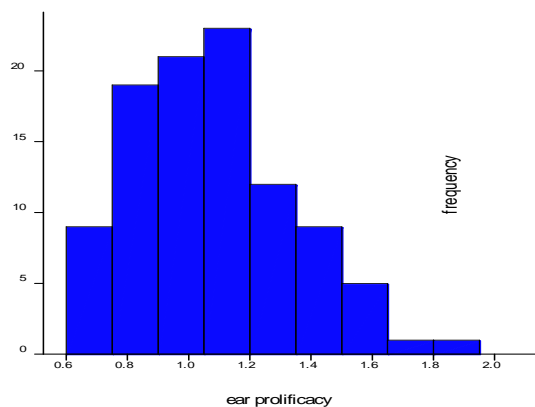


UKULINGA

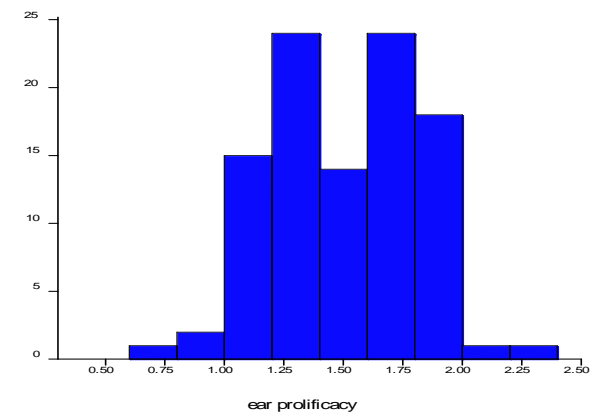
Figure 4.1: Histograms for grain yield for the three sites



CEDARA



DUNDEE



UKULINGA

Figure 4.2: Histograms for ear prolificacy for the three sites

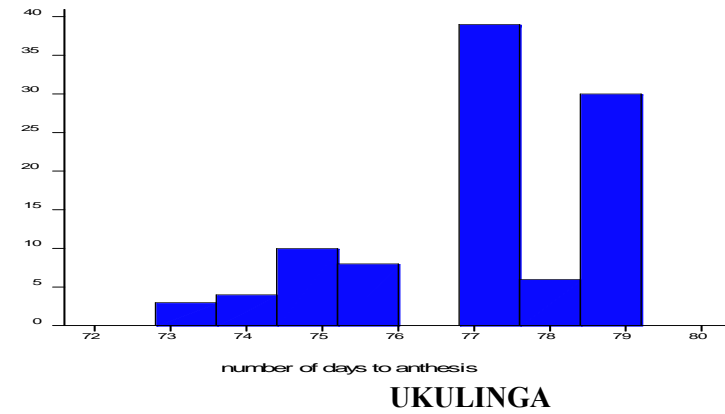
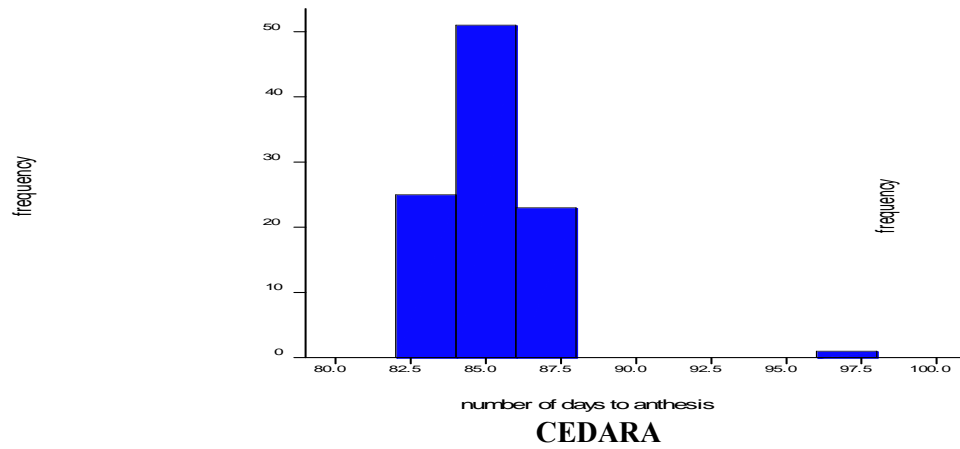


Figure 4.3: Histograms for number of days to anthesis for two sites

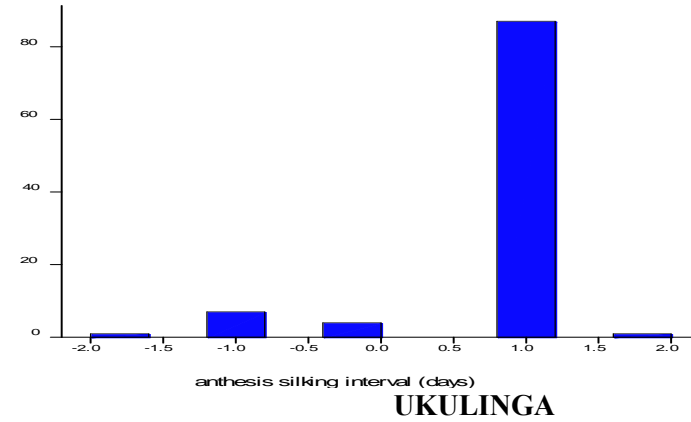
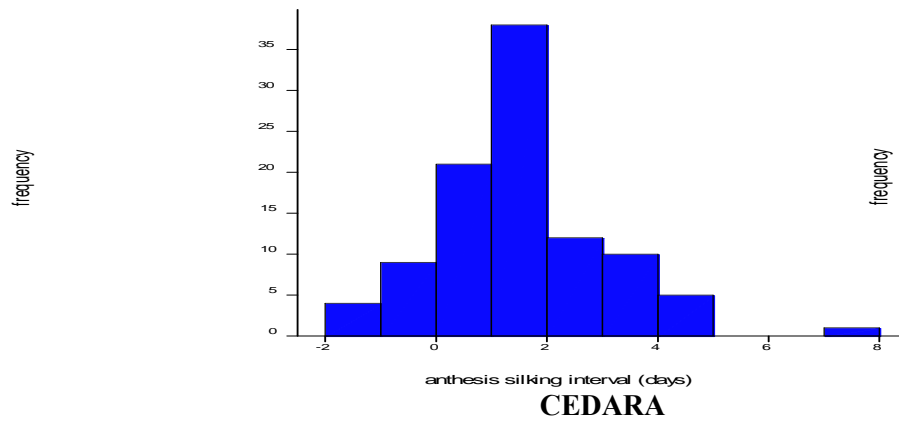
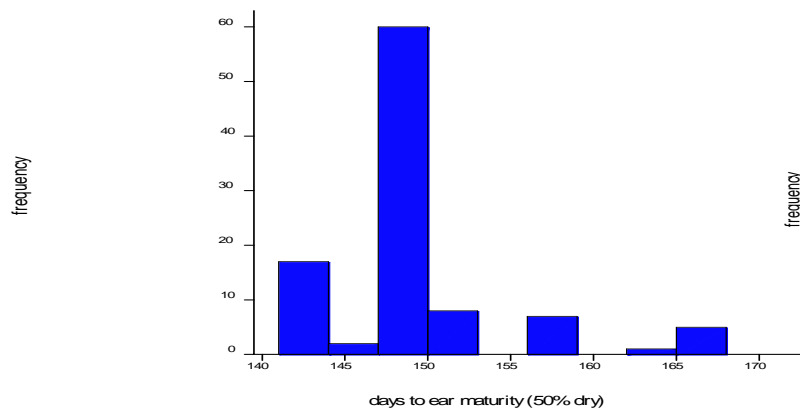
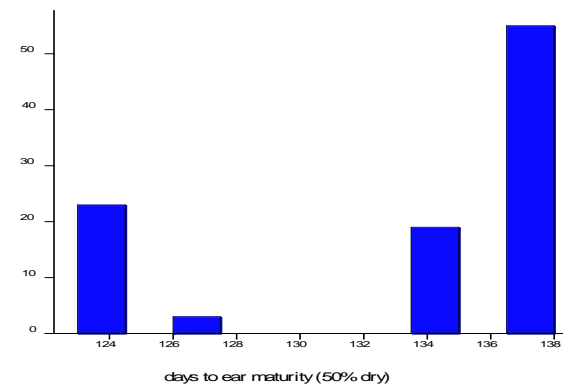


Figure 4.4: Histograms for anthesis silking interval for two sites

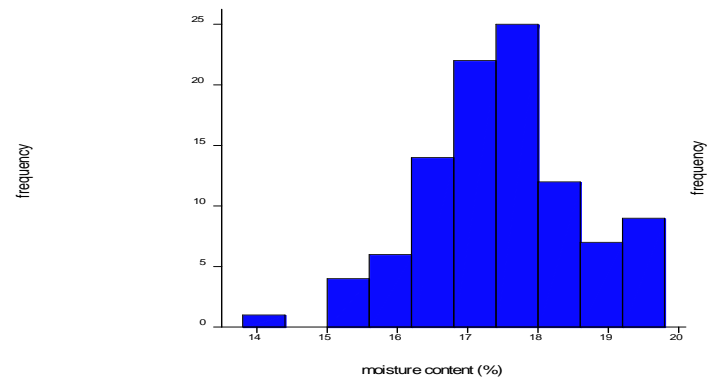


CEDARA

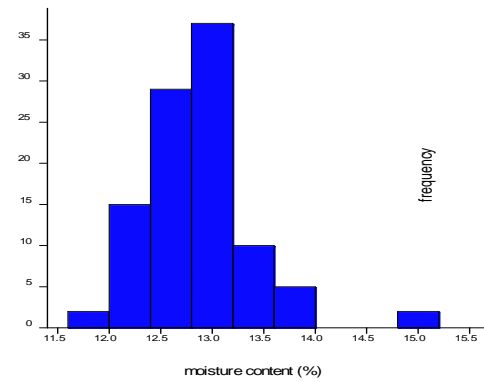


UKULINGA

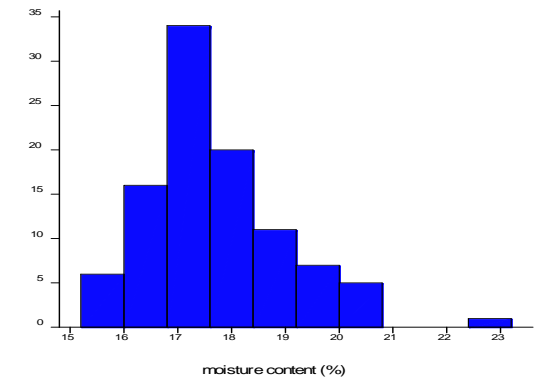
Figure 4.5: Histogram for number of days to ear maturity for two sites



CEDARA



DUNDEE



UKULINGA

Figure 4.6: Histograms for grain moisture content for three sites

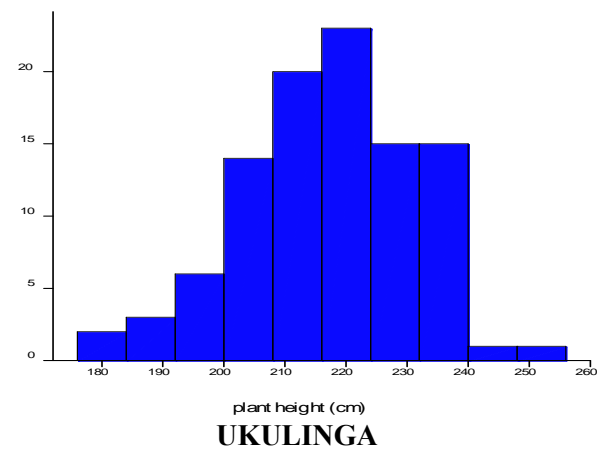
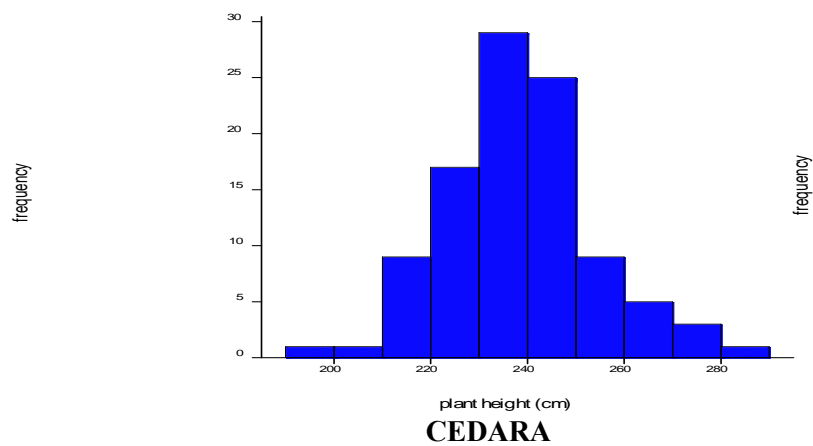


Figure 4.7: Histograms for plant height for two sites

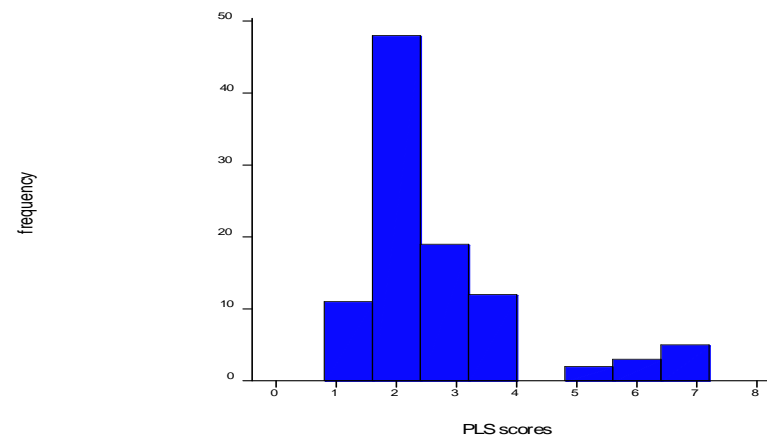
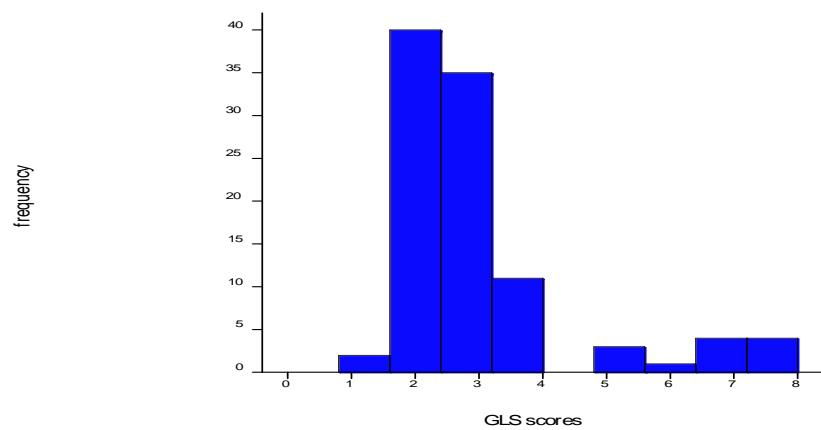


Figure 4.8: Histogram for disease ratings at Cedara

2.3. Mean Performance of the Hybrids

The genotypes were ranked differently according to grain yield across the three sites (Table 4.4). Hybrid 15XH16 was the highest yielding at Cedara Research Station. The top ten highest ranked genotypes at Cedara were all testcrosses. At Dundee Research Station the highest yielding testcross was 15XH39 which was ranked number 2. 15XH28 was ranked number 2 at Ukulinga Station. Overall 15XH10 was ranked second (Table 4.4).

Table 4.5 presents the means and ranking of the control checks. The rankings were also different across the sites. BG5285 yielded higher than PAN6Q-345 CB at Dundee and Ukulinga and across all environments. At Cedara, BG5285 had lower yield than PAN6Q-345 CB. PAN6Q-345 CB had the same ranking at Cedara and Dundee environments. At Ukulinga the commercial hybrids performed well as they were ranked in the top 10 performing genotypes. At Cedara they were not in the top 10 while at Dundee only BG5285 was in the top 10 where it was ranked third. Advanced hybrid checks were not in the top 10 at Cedara and Ukulinga, while four of the advanced hybrid checks were ranked in the top 10 at Dundee. Hybrids of biological parents performed poorly across all environments and were ranked in the bottom 10 at Ukulinga and overall. The hybrid of parent and tester LP21 (15XH42) was ranked 47 at both Cedara and Ukulinga Stations. The cross between founder parent and tester LP19 (15XH21) was always ranked above hybrid of parent and tester 21 (15XH42).

Table 4.4: Mean yield and ranking of hybrids excluding control hybrids

Cedara			Dundee			Ukulinga			Across sites		
Entry	Mean	Rank	Entry	Mean	Rank	Entry	Mean	Rank	Entry	Mean	Rank
15XH16	10.768	1	15XH39	4.875	2	15XH28	12.73	2	15XH10	8.437	2
15XH34	10.682	2	15XH20	4.528	4	15XH10	12.55	3	15XH39	8.23	5
15XH02	10.383	3	15XH13	4.482	6	15XH25	12.32	4	15XH13	8.229	6
15XH39	10.206	4	15XH05	4.369	7	15XH11	12.22	6	15XH28	8.226	7
15XH20	10.139	5	15XH27	3.98	10	15XH32	11.85	7	15XH20	8.185	10
15XH05	10.085	6	15XH15	3.889	11	15XH07	11.74	8	15XH25	8.178	11
15XH41	9.953	7	15XH30	3.798	12	15XH18	11.61	9	15XH24	8.168	12
15XH07	9.943	8	15XH18	3.63	13	15XH38	11.55	10	15XH34	8.107	14
15XH24	9.902	9	15XH04	3.601	14	15XH04	11.34	12	15XH04	8.089	15
15XH30	9.873	10	15XH06	3.527	15	15XH09	11.3	13	15XH38	8.042	16
15XH23	9.853	11	15XH31	3.451	16	15XH24	11.24	14	15XH07	8.023	17
15XH09	9.653	14	15XH24	3.359	20	15XH22	11.07	15	15XH30	8.011	18
15XH13	9.638	15	15XH10	3.266	21	15XH06	10.74	19	15XH27	7.966	19
15XH38	9.588	16	15XH16	3.263	22	15XH36	10.68	20	15XH18	7.861	21
15XH27	9.51	19	15XH33	3.194	23	15XH33	10.67	21	15XH32	7.712	22
15XH10	9.496	20	15XH25	3.187	24	15XH03	10.59	22	15XH16	7.706	23
15XH28	9.423	21	15XH34	3.093	25	15XH35	10.59	23	15XH09	7.638	24
15XH04	9.33	22	15XH38	2.983	26	15XH13	10.57	24	15XH11	7.603	25
15XH03	9.263	23	15XH36	2.975	27	15XH34	10.55	25	15XH05	7.518	26
15XH37	9.14	25	15XH02	2.921	28	15XH31	10.42	27	15XH31	7.491	27
15XH26	9.044	27	15XH41	2.852	29	15XH27	10.41	28	15XH23	7.49	28
15XH25	9.023	28	15XH35	2.844	30	15XH23	10.39	29	15XH41	7.451	29
15XH32	8.995	30	15XH37	2.84	31	15XH30	10.36	30	15XH33	7.445	30
15XH14	8.976	31	15XH01	2.736	33	15XH17	10.23	32	15XH02	7.431	31
15XH35	8.813	33	15XH12	2.671	34	15XH37	10.2	33	15XH35	7.415	32
15XH15	8.618	35	15XH26	2.658	35	15XH01	10.07	34	15XH36	7.394	33
15XH31	8.606	36	15XH28	2.526	37	15XH20	9.89	35	15XH37	7.392	34
15XH36	8.522	37	15XH07	2.383	38	15XH15	9.63	36	15XH15	7.379	35
15XH33	8.473	38	15XH11	2.381	39	15XH39	9.61	38	15XH03	7.328	36
15XH12	8.464	39	15XH32	2.289	41	15XH41	9.55	39	15XH06	7.199	37
15XH01	8.374	41	15XH23	2.223	42	15XH16	9.09	42	15XH22	7.119	38
15XH18	8.341	42	15XH14	2.215	43	15XH02	8.99	43	15XH01	7.06	39
15XH17	8.321	43	15XH22	2.215	44	15XH26	8.91	44	15XH26	6.869	42
15XH11	8.212	45	15XH03	2.129	45	15XH12	8.66	46	15XH17	6.713	43
15XH22	8.071	46	15XH09	1.956	47	15XH14	8.17	48	15XH12	6.598	45
15XH06	7.326	50	15XH17	1.589	50	15XH05	8.1	50	15XH14	6.453	49
P	0.05			0.05			0.05			0.05	
LSD_{0.05}	2.37			2.72			2.01			1.35	
CV (%)	12.57			29.31			9.49			13.53	

P=probability, LSD=least significant difference at 5%, CV=coefficient of variation

Table 4.5: Mean yield and ranking of commercial and control hybrids

	Cedara		Dundee		Ukulinga		Across all sites	
	Commercial hybrids							
Entry	Mean	Rank	Mean	Rank	Mean	Rank	Mean	Rank
BG 5285	9.12	26	4.71	3	12.89	1	8.91	1
PAN 6Q-345 CB	9.54	18	3.39	18	12.25	5	8.39	3
	Advanced experimental hybrids							
11C1774	9.20	24	4.51	5	10.89	18	8.20	9
11C1579	9.02	29	1.68	49	8.12	49	6.27	50
11C1566	8.25	44	1.78	48	9.48	40	6.50	48
11C2245	8.87	32	4.33	9	10.53	26	7.91	20
11C1350	7.65	49	2.83	32	9.63	37	6.70	44
11C1511	9.68	12	4.35	8	10.91	17	8.32	4
11C2242	8.66	34	5.03	1	10.98	16	8.22	8
11C1483	8.38	40	2.04	46	10.33	31	6.92	41
10HDTX11	9.56	17	3.38	19	11.55	11	8.16	13
	Hybrids of Biological Parents							
15XH21	9.67	13	2.57	36	8.74	45	6.99	40
15XH42	8.02	47	3.45	17	8.22	47	6.56	46

2.4. Line X Tester Analysis

The general ANOVA in Table 4.6 shows that line main effects were significant ($p \leq 0.05$) for grain yield and ear prolificacy across all environments. However, the line main effects for the grain moisture content were non-significant ($p > 0.05$). GXE interactions are revealed by the significance of the environment X line interaction effects. The environments are shown to be significantly different.

Table 4.6: Mean squares for grain yield and secondary traits across the three sites

S.O.V	Degrees of freedom	Grain yield	Ears per plant	Grain moisture content
Environment	2	1174.79***	4.33**	552.81***
Environment/replications	3	12.65***	0.11	1.03
Environment/replication/blocks	24	3.83***	0.11**	1.30
Line	18	2.04*	0.14**	1.17
Tester	1	0.01	0.00	1.02
Line X tester	18	1.27	0.03	0.74
Environment X line	36	1.80*	0.11**	1.07
Environment X tester	2	0.44	0.04	0.64
Environment X line X tester	36	1.30	0.04	0.97
Residual	87	1.02	0.06	0.80
Mean		7.57	1.42	17.62
LSD 5%		1.01	0.20	0.71
CV		13.53	17.11	5.41

LSD=least significant difference at 5%, CV=coefficient of variation, *, **, ***=level of significance at $p \leq 0.05$, $p \leq 0.01$ and $p \leq 0.001$ respectively

2.5. Combining Ability

Positive GCA effects for grain yield were significant ($p \leq 0.05$) for lines DMSR-8, DMSR-13, DMSR-30 and DMSR-35-5 while they were negative and significant ($p \leq 0.05$) for DMSR-26, DMSR-35-1 and DMSR-80 (Table 4.7). Some lines such as DMSR-18, DMSR-21 and DMSR-23 showed non-significant positive GCA effects for grain yield. Two lines DMSR-10 and DMSR-30 had corresponding significant ($p \leq 0.05$) negative GCA effects for both anthesis days and anthesis silking interval. DMSR-4, DMSR-18 and DMSR-73 showed undesirable positive and significant ($p \leq 0.05$) GCA effects for anthesis days and anthesis silking interval. Only line DMSR-35-3 showed significant ($p \leq 0.05$) positive GCA effects for chlorophyll content. Several lines exhibited significant ($p \leq 0.05$) GCA effects for ear maturity, ear position, husk cover, root lodging and stem lodging. Only four lines, DMSR-12, DMSR-18, DMSR-23 and DMSR-80, exhibited significant ($p \leq 0.05$) GCA effects for number of leaves. Several lines showed significant GCA effects for plant height. However, only four lines showed negative (desirable) GCA effects for plant height which were significant ($p \leq 0.05$).

Six lines (DMSR-2, DMSR-4, DMSR-21, DMSR-30, DMSR-35-1 and DMSR-35-3) showed significant ($p \leq 0.05$) negative GCA effects for GLS while four of these lines had significant ($p \leq 0.05$) negative GCA effects for PLS. DMSR-4 had significant ($p \leq 0.05$) positive GCA effects for PLS while DMSR-35-3 had negative but non-significant ($p > 0.05$) GCA effects for PLS.

Significant ($p \leq 0.05$) SCA effects for grain yield were obtained for DMSR-21 and DMSR-73 when crossed to tester LP19 (Table 4.8). Lines DMSR-10, DMSR-30, DMSR-35-3 and DMSR-80 showed relatively high positive SCA effects for grain yield with tester LP19. However, the SCA effects were not significant ($p > 0.05$). Similarly, lines DMSR-4, DMSR-12, DMSR-18, DMSR-26, DMSR-35-1 and DMSR-35-4 had substantially large negative SCA effects for grain yield which were non-significant ($p > 0.05$). Line DMSR-73 had the highest SCA effects for grain yield with tester LP19 compared to any other hybrid combination in this study. Lines DMSR-35-4 and DMSR-73 had significant ($p \leq 0.05$) SCA effects for grain yield when crossed to tester LP21 (Table 4.9). Lines DMSR-10, DMSR-23, DMSR-35-3 and DMSR-80 had positive SCA effects for grain yield with tester LP21 but the effects were not significant. Lines DMSR-4, DMSR-12, DMSR-26, DMSR-35-1 and DMSR-35-4 had the lowest SCA effects for grain yield with tester LP21 while DMSR-73 had the highest SCA effects for grain yield with tester LP21.

Table 4.7: GCA effects for grain yield and secondary traits

Lines	Grain Yield	Anthesis Days	Anthesis Silking Interval	Chlorophyll Content	Ear Height	Ear Maturity	Ear Position	Ears Per Plant	Husk Cover	Grain Moisture Content	Number of Leaves	Number of tassel branches	Plant Height	Root Lodging	Stem Lodging	Grey Leaf Spot	PLS
DMSR-1	-0.46	-0.13	-0.59*	0.33	5.66	2.24*	0.01	0.11	-2.21	-0.59*	0.25	0.60*	5.91	-4.81	10.12*	0.69*	-0.01
DMSR-2	-0.09	-0.39	0.23	-0.59	1.36	0.54	0.01	0.09	12.44*	-0.03	0.04	-0.41	-0.04	-4.67	7.04*	-0.56*	-0.51*
DMSR-4	0.20	0.97*	0.61*	-0.67	8.21*	3.29*	0.01	0.07	-4.77	0.01	-0.03	0.02	9.41*	2.86	0.39	-0.81**	0.24
DMSR-8	0.59*	0.27	0.16	0.70	6.91*	0.34	0.04**	0.13*	-9.06	-0.28	-0.17	-0.30	-2.44	0.63	-2.92	-0.06	-0.26
DMSR-10	-0.35	-2.46*	-0.56*	1.02	-12.14*	-5.51***	-0.02*	-0.24**	-10.55*	-0.41*	0.05	0.25	-15.39**	4.25	-3.36	0.69*	0.49*
DMSR-12	0.04	0.08	0.41*	0.95	-5.49	-3.96**	0.01	-0.08	-2.82	-0.17	-0.26	-0.39	-12.04**	-5.28	-5.37	-0.06	-0.26
DMSR-13	0.58*	0.91*	0.34	-0.40	4.16	1.54	0.02*	0.17*	-13.55*	0.40*	-0.54*	-0.22	-0.14	-3.44	-4.81	0.19	-0.51*
DMSR-18	0.28	1.42*	0.77*	0.03	-1.69	0.59	0.00	0.11	3.29	0.53*	0.16	-1.54**	-3.04	1.20	-9.84*	0.44*	-0.26
DMSR-21	0.42	0.18	-0.39	-0.08	-6.84*	1.64	-0.03*	-0.03	-7.45	0.68*	0.40*	-0.35	-1.24	23.76***	5.69	-0.56*	-1.01***
DMSR-23	0.11	0.11	-0.41	-1.49*	5.56	-2.06*	0.01	0.24**	-13.12*	-0.51*	-0.01	0.64*	7.46*	9.59*	-0.72	1.19**	0.74**
DMSR-26	-0.53*	-0.75	0.00	0.90	-13.14**	-3.56*	-0.04**	-0.24**	-4.15	-0.69*	0.31*	-0.27	-8.29*	-7.78	2.54	0.19	-0.26
DMSR-30	0.62*	-0.85*	-0.66*	-1.81*	5.01	-4.16**	0.00	0.21*	-4.79	-0.52*	0.07	-0.57	10.11*	-6.72	-8.02*	-1.31**	-0.51*
DMSR-35-1	-0.61*	-0.23	0.53*	-0.27	-2.19	2.84*	-0.02*	-0.20*	27.36**	0.46*	-0.02	-0.40	1.81	9.02*	17.84**	-0.81**	-0.51*
DMSR-35-2	-0.16	0.57	0.20	0.96	6.21*	0.29	0.03*	0.09	-0.13	0.25	-0.06	0.59*	-0.79	-4.10	8.64*	0.94**	0.24
DMSR-35-3	0.00	0.67	0.27	1.07*	4.46	1.49	0.02*	-0.26**	20.34**	0.82*	0.12	0.50	2.46	-6.54	-15.48**	-0.81**	-0.26
DMSR-35-4	-0.17	0.12	-0.36	-1.08*	-5.54	3.54*	-0.02*	-0.02	-2.28	-0.05	0.07	0.85*	-0.39	-5.38	2.39	0.19	0.74**
DMSR-35-5	0.50*	-0.18	-0.99*	0.35	5.31	2.54*	0.00	-0.03	14.51*	0.24	-0.11	-0.55	10.36*	2.59	3.44	-0.18	0.12
DMSR-73	-0.20	1.20*	0.60*	-0.79	6.61*	1.34	0.01	0.00	-9.21	0.43*	0.24	0.59*	8.81*	0.59	-4.45	0.44*	0.74**
DMSR-80	-0.77*	-1.49*	-0.15	0.87	-12.34**	-2.91*	-0.03*	-0.12*	6.17	-0.59*	-0.50*	0.92*	-12.49**	-5.73	-3.12	0.19	0.99***
SE	0.47	0.80	0.41	1.05	6.11	1.82	0.02	0.12	9.69	0.37	0.30	0.58	5.92	7.85	6.80	0.40	0.32

*, **, ***= 0.001, 0.01 and 0.05 level of significance, PLS=*Phaeosphaeria* Leaf Spot, SE=standard error

Table 4.8: SCA for grain yield and secondary traits for crosses of tester LP19

Line	Grain Yield	Anthesis Days	Anthesis Silking Interval	Chlorophyll Content	Ear Height	Ear Maturity	Ear Position	Ears Per Plant	Husk Cover	Grain Moisture Content	Number of Leaves	Number of tassel branches	Plant Height	Root Lodging	Stem Lodging	Grey Leaf Spot	PLS
DMSR-1	0.02	0.26	-0.24	0.43	5.71	0.76	0.00	0.02	-13.26*	-0.44*	0.22	0.71*	9.57*	-2.00	-9.84*	1.52**	0.19
DMSR-2	0.02	0.05	0.12	-0.34	-1.39	0.06	-0.01	0.12*	3.18	-0.98**	-0.01	-0.20	0.12	2.67	7.66	-0.23	0.19
DMSR-4	-0.37	-0.28	-0.49	-0.50	-3.74	-2.69*	-0.01	-0.01	9.08	0.06	0.07	-0.21	-4.23	-1.86	-6.75	0.02	-1.06**
DMSR-8	0.01	-0.08	-0.15	2.06**	-1.24	0.76	-0.01	-0.14*	6.89	0.07	0.06	0.80*	0.52	9.38	-4.31	0.77*	0.44
DMSR-10	0.37	0.26	0.28	-0.92	-5.39	-1.09	-0.02*	0.04	-15.59*	0.63*	0.62*	-0.05	-2.23	-7.28	4.21	-0.98*	-1.31**
DMSR-12	-0.33	-0.48	0.42	-0.43	-3.64	0.56	-0.01	0.03	-6.03	0.08	-0.37*	-0.99*	-3.78	8.47	10.83*	0.27	0.44
DMSR-13	-0.05	0.00	-0.48	0.37	3.21	0.76	0.02*	0.07	4.96	-0.07	-0.51*	0.18	-3.08	2.12	3.65	1.02*	0.69*
DMSR-18	-0.14	1.59*	0.92*	-0.61	1.56	0.91	0.01	-0.02	10.81	0.03	0.31	0.13	0.32	-2.02	-7.68	-0.73	-0.56*
DMSR-21	0.52*	-0.63	0.39	0.49	2.51	0.56	0.01	0.10*	-1.12	-0.84*	0.03	-0.36	1.32	6.07	-3.75	0.27	-0.31
DMSR-23	0.00	-0.23	-0.03	-0.18	1.11	-1.04	0.02*	-0.09*	9.94	0.46*	-0.30	0.16	-7.78	-22.01**	11.67*	-0.98*	-1.06**
DMSR-26	-0.37	-0.56	-0.43	-0.84	-0.99	-3.04*	0.01	-0.11	-18.95*	0.27	-0.38*	-0.70*	-2.83	3.26	5.54	-0.98*	-0.56*
DMSR-30	0.11	-0.10	-0.26	-0.01	-1.44	-0.44	-0.01	-0.07	-8.07	0.41	0.28	-0.47	2.77	-8.58	0.33	0.02	0.19
DMSR-35-1	-0.43	0.40	0.26	-0.33	3.16	-0.04	0.00	0.12*	-14.59*	-0.03	0.29	-0.57	4.17	3.09	-7.00	0.52	-0.31
DMSR-35-2	0.04	0.75*	0.47	-1.10*	9.06*	-0.29	0.02*	0.08	5.03	0.17	-0.22	0.18	7.37*	-0.84	7.22	-1.23*	-1.06**
DMSR-35-3	0.21	-0.14	-0.62*	1.10*	0.01	0.81	0.00	-0.06	7.43	0.18	0.02	-0.60	1.12	5.99	1.16	0.02	0.94*
DMSR-35-4	-0.61	0.11	0.12	-0.19	0.01	-0.54	0.00	-0.08	2.97	0.07	0.20	0.17	-1.23	5.24	-2.00	0.02	1.44**
DMSR-35-5	-0.13	-0.06	0.13	-0.47	-0.94	-0.14	0.00	0.00	0.69	0.50*	-0.13	0.58	-2.28	-5.97	-6.78	0.89*	1.07**
DMSR-73	0.89*	-0.11	0.33	1.93*	0.86	0.06	-0.01	0.00	5.07	0.39	-0.12	1.04*	4.07	-0.25	-4.12	0.27	0.94*
DMSR-80	0.27	-0.75*	-0.76*	-0.42	-8.49*	4.11**	-0.03*	0.00	11.53	-0.01	-0.05	0.21	-3.93	4.53	-0.09	-0.48	-0.31
SE	0.52	0.73	0.56	1.02	5.92	1.72	0.02	0.09	12.72	0.43	0.37	0.65	5.92	10.88	8.24	0.74	0.52

*, **, ***= 0.001, 0.01 and 0.05 level of significance, PLS=*Phaeosphaeria* Leaf Spot, SE=standard error

Table 4.9: SCA for grain yield and secondary traits for crosses of tester LP21

Line	Grain Yield	Anthesis Days	Anthesis Silking Interval	Chlorophyll Content	Ear Height	Ear Maturity	Ear Position	Ears Per Plant	Husk Cover	Grain Moisture Content	Number of Leaves	Number of tassel branches	Plant Height	Root Lodging	Stem Lodging	Grey Leaf Spot	PLS
DMSR-1	-0.08	0.12	-0.32	1.39*	13.59**	0.64	0.03*	0.03	-37.06**	-0.61*	-0.22	1.08*	10.93*	-0.33	-9.26*	0.98*	0.31
DMSR-2	-0.08	-0.09	0.04	0.63	6.49*	-0.06	0.03*	0.14*	-20.63*	-1.16**	-0.45*	0.17	1.48	4.34	8.25*	-0.77*	0.31
DMSR-4	-0.47	-0.43	-0.57*	0.47	4.14	-2.81*	0.02*	0.00	-14.73*	-0.12	-0.37*	0.16	-2.87	-0.19	-6.16	-0.52	-0.94*
DMSR-8	-0.09	-0.23	-0.24	3.03**	6.64*	0.64	0.03*	-0.12*	-16.91*	-0.11	-0.38*	1.18*	1.88	11.04*	-3.72	0.23	0.56*
DMSR-10	0.27	0.11	0.20	0.05	2.49	-1.21	0.02*	0.05	-39.39***	0.46*	0.18	0.32	-0.87	-5.61	4.79	-1.52**	-1.19**
DMSR-12	-0.43	-0.62	0.34	0.53	4.24	0.44	0.03*	0.04	-29.84**	-0.09	-0.81**	-0.62	-2.42	10.14	11.42*	-0.27	0.56*
DMSR-13	-0.15	-0.14	-0.56*	1.34*	11.09*	0.64	0.06***	0.08	-18.84*	-0.25	-0.95**	0.55	-1.72	3.79	4.23	0.48	0.81*
DMSR-18	-0.24	1.44*	0.84*	0.36	9.44*	0.79	0.05**	0.00	-13.00*	-0.14	-0.13	0.50	1.68	-0.35	-7.10	-1.27*	-0.44
DMSR-21	0.42	-0.77*	0.31	1.46*	10.39*	0.44	0.04**	0.12*	-24.92*	-1.02*	-0.41*	0.02	2.68	7.74	-3.16	-0.27	-0.19
DMSR-23	-0.10	-0.38	-0.11	0.78	8.99*	-1.16	0.06***	-0.07	-13.86*	-0.63*	-0.74**	0.54	-6.42*	-20.35*	12.25*	-1.52**	-0.94*
DMSR-26	-0.47	-0.71	-0.51	0.13	6.89*	-3.16*	0.04**	-0.09*	-42.75***	0.10	-0.82**	-0.33	-1.47	4.92	6.13	-1.52**	-0.44
DMSR-30	0.01	-0.24	-0.34	0.95	6.44*	-0.56	0.02*	-0.06	-31.88**	0.24	-0.16	-0.09	4.13	-6.92	0.92	-0.52	0.31
DMSR-35-1	-0.53	0.26	0.18	0.63	11.04*	-0.16	0.04**	0.14*	-38.39***	-0.21	-0.15	-0.20	5.53	4.76	-6.41	-0.02	-0.19
DMSR-35-2	-0.06	0.60*	0.39	-0.14	16.94**	-0.41	0.06***	0.10*	-18.77*	0.00	-0.66*	0.56	8.73*	0.82	7.81	-1.77**	-0.94*
DMSR-35-3	0.11	-0.29	-0.70*	2.06**	7.89*	0.69	0.03*	-0.04	-16.37*	0.00	-0.42*	-0.22	2.48	7.65	1.75	-0.52	1.06**
DMSR-35-4	-0.71*	-0.04	0.04	0.77	7.89*	-0.66	0.04**	-0.06	-20.84*	-0.11	-0.24	0.55	0.13	6.90	-1.41	-0.52	1.56**
DMSR-35-5	-0.23	-0.20	0.05	0.50	6.94*	-0.26	0.04**	0.02	-23.11*	0.32	-0.57*	0.96*	-0.92	-4.31	-6.20	0.36	1.18**
DMSR-73	0.79*	-0.25	0.25	2.89**	8.74*	-0.06	0.03*	0.01	-18.73*	0.22	-0.56*	1.42**	5.43	1.42	-3.54	-0.27	1.06**
DMSR-80	0.17	-0.89*	-0.84*	0.55	-0.61	3.99**	0.01	0.02	-12.27	-0.19	-0.49*	0.58	-2.57	6.19	0.50	-1.02*	-0.19
SE	0.56	0.73	0.56	1.02	5.92	1.72	0.02	0.09	12.72	0.43	0.37	0.65	5.92	10.88	8.24	0.74	0.52

*, **, ***= 0.001, 0.01 and 0.05 level of significance, PLS=*Phaeosphaeria* Leaf Spot, SE=standard error

2.6. Genetic Gains

The means of the best four selected hybrids across sites are presented together with population mean (MP), mean of the best commercial hybrid (MBC), mean of all the commercial hybrids (MC), mean of the advanced hybrid checks and the mean of the hybrids of biological founder parent (MBIO) in Table 4.10. Grain yield had low heritability across the sites (Table 4.11). The genotypic variance, genotypic coefficient of variance and phenotypic coefficient of variation were also low for grain yield. Realised gains were lower than predicted gains. However the highest realised gains were over the biological parents followed by gains over advanced hybrid checks. There was negative gain over the commercial checks. Some secondary traits showed considerably high heritability coefficients and significant gains were also realised over the commercial checks. Ear prolificacy had 52% heritability estimate and realised genetic gains over all checks.

The means of selected hybrids, population and control hybrids at Cedara are presented in Table 4.12. Heritability for grain yield was very low at Cedara (Table 4.13). However, there were significant genetic gains realised over all control checks. The testcrosses outperformed the commercial hybrids in yield performance and ear prolificacy. The testcrosses also showed significant genetic gains over the commercial hybrids in disease tolerance. However, disease tolerance for both diseases had zero heritability. Most of the secondary traits measured at Cedara had very low heritability estimates and genetic variances.

The grain yield mean of selected hybrids was lower than the mean of the best commercial check hybrid at Dundee although it was higher than overall means for commercial hybrids, advanced hybrid checks and the hybrids of the biological parents (Table 4.14). Grain yield heritability estimate at Dundee was low (Table 4.15). There was a large discrepancy between

GCV and PCV (4.67 versus 31.69) for grain yield. Positive realised gains were achieved over the mean of population, mean of commercial hybrids, advanced hybrid checks and biological parents. Ear prolificacy had zero heritability but achieved higher than predicted genetic gains over commercial hybrids. The selection reduced grain moisture content by 1% over the best commercial hybrid.

The mean of selected hybrids at Ukulinga was higher than the means of the whole population of hybrids tested, advanced hybrid checks and the hybrids of the biological parents. However, it was lower than the means of the best commercial and all commercial hybrids (Table 4.16). Heritability and predicted gains for grain yield were relatively high. There was a smaller difference between the coefficients of variance. Genetic gains were realised over population mean, advanced hybrid checks and biological parents (Table 4.17). Negative genetic gains were realised over the commercial hybrids although they were not very high. Ear prolificacy had higher heritability estimates and smaller difference between coefficients of variation. Selection achieved significant genetic gains over commercial hybrids and control checks. Realised gains over hybrids of the biological parents and advanced hybrid checks were higher than predicted. Most of the secondary traits had high heritability estimates of over 30% except ear maturity, grain moisture content, number of tassel branches and root lodging.

Table 4.10: Means of selected hybrids and control hybrids across sites

Trait	Grain Yield	Anthesis Days	Anthesis Silking Interval	Chlorophyll Content	Ear Height	Ear Maturity	Ear Position	Ear Per Plant	Husk Cover	Grain Moisture Content	Number of Leaves	Number of Tassel Branches	Plant Height	Root Lodging	Stem Lodging
MS	8.28	79.56	0.56	55.80	107.43	134.90	0.49	1.69	5.46	16.71	7.06	8.81	211.33	5.58	5.89
MP	7.57	81.45	1.41	53.17	123.38	142.04	0.54	1.42	34.62	17.62	6.25	10.05	228.11	20.91	18.18
MBC	8.91	80.50	0.75	55.27	113.00	140.50	0.50	1.62	16.63	16.65	7.00	8.50	215.30	25.00	12.99
MC	8.65	80.63	0.75	54.67	114.25	143.35	0.51	1.52	29.50	17.19	6.50	9.50	223.15	25.01	20.84
MAE	7.47	80.75	1.36	53.20	124.78	141.42	0.54	1.32	36.55	17.59	5.83	9.92	232.61	12.90	16.96
MBIO	6.78	80.13	1.25	53.28	109.20	139.00	0.51	1.30	39.44	17.08	5.75	10.50	215.90	14.60	20.84

MS=mean of selected entries, MP=mean of whole population, MBC=mean of best commercial check, MC=mean of all commercial checks, MAE=mean of advanced experimental hybrids, MBIO=mean of hybrids of biological parent

Table 4.11: Estimates of variance components, heritability and genetic gains across sites

Trait	δ^2_g	δ^2_p	H ² (%)	GCV (%)	PCV (%)	PG	PG%	RG1	RG2	RG3	RG4	RG5
Grain Yield [#]	0.21	1.26	16.67	2.77	16.64	32.93	4.35	9.32	-7.03	-4.25	10.90	22.18
Anthesis Days	2.71	4.57	59.43	3.35	5.64	223.48	2.74	-2.32	-1.16	-1.32	-1.47	-0.70
Anthesis Silking Interval	0.70	1.66	41.84	69.61	166.38	94.98	67.60	-59.96	-25.00	-25.00	-58.67	-55.00
Chlorophyll Content	0.00	6.41	0.00	0.00	12.05	0.00	0.00	4.95	0.96	2.08	4.89	4.73
Ear Height	169.00	303.60	55.63	137.32	246.83	1706.05	13.83	-12.93	-4.93	-5.97	-13.91	-1.63
Ear Maturity	12.13	38.74	31.31	8.54	27.28	343.00	2.41	-5.03	-3.99	-5.89	-4.61	-2.95
Ear Position	0.00	0.00	54.56	0.34	0.62	5.57	10.32	-9.58	-1.97	-4.23	-8.85	-3.77
Ear Per Plant	0.05	0.10	51.56	3.53	6.85	28.31	20.00	19.08	3.79	10.89	27.49	29.31
Husk Cover	839.00	1045.90	80.25	2424.32	3021.09	4567.57	131.94	-84.24	-67.20	-81.51	-85.08	-86.17
Grain Moisture Content	0.49	1.52	32.23	2.72	8.43	69.88	3.97	-5.20	0.33	-2.82	-5.06	-2.17
Number of Leaves	0.35	0.63	55.79	5.71	10.24	78.23	12.53	13.09	0.89	8.65	21.07	22.83
Number of Tassel Branches	0.00	3.86	0.00	0.00	38.55	0.00	0.00	-12.27	3.68	-7.24	-11.13	-16.07
Plant Height	198.00	307.70	64.35	86.84	134.96	1986.62	8.71	-7.36	-1.85	-5.30	-9.15	-2.12
Root Lodging	73.60	384.80	19.13	352.15	1841.15	660.35	31.58	-73.33	-77.69	-77.69	-56.75	-61.78
Stem Lodging	2.60	254.00	1.02	14.29	1395.60	28.71	1.58	-67.59	-54.64	-71.73	-65.26	-71.72

δ^2_g =genotypic variance, δ^2_p =phenotypic variance, H²=broad sense heritability, PCV=phenotypic coefficient of variance, GCV=genotypic coefficient of variance h²=narrow sense heritability, GYG[#]=grain yield measured across the three sites, all other traits are calculated for Cedara and Ukulinga, PG=predicted gain, RG1-5=realised gains, refer to Chapter 3

Table 4.12: Means of selected hybrids and control hybrids at Cedara

Trait	Grain Yield	Anthesis Days	Anthesis Silking Interval	Chlorophyll Content	Ear Height	Ear Maturity	Ear Position	Ears Per Plant	Husk Cover	Grain Moisture Content	Number of Leaves	Number of Tassel Branches	Plant Height	Root Lodging	Stem Lodging	Grey Leaf Spot	PLS
MS	10.51	84.25	0.25	57.11	114.88	144.00	0.49	1.63	0.00	16.44	6.63	8.88	221.38	0.00	9.97	1.88	1.56
MP	9.13	85.76	2.01	53.61	130.51	150.19	0.55	1.31	15.45	17.49	5.80	10.64	238.59	7.04	33.51	3.13	2.76
MBC	9.54	84.50	0.50	54.16	116.50	150.00	0.53	1.38	6.82	15.85	6.00	8.50	215.00	0.00	25.98	2.50	2.00
MC	9.33	84.50	1.00	53.08	124.00	153.75	0.54	1.24	14.62	17.15	6.00	9.25	230.25	7.35	41.69	3.25	2.25
MAE	8.81	85.61	2.00	54.00	132.22	149.94	0.55	1.27	15.74	17.49	5.78	11.50	241.67	8.17	31.13	3.39	2.72
MBIO	8.85	85.00	1.50	53.53	114.75	147.75	0.48	1.41	7.41	17.43	6.00	11.00	235.75	2.94	41.67	3.25	3.75

MS=mean of selected entries, MP=mean of whole population, MBC=mean of best commercial check, MC=mean of all commercial checks, MAE=mean of advanced experimental hybrids, MBIO=mean of hybrids of biological parent, PLS=*Phaeosphaeria* Leaf Spot

Table 4.13: Estimates of variance components, heritability and genetic gains at Cedara

Trait	δ^2_g	δ^2_p	H ² (%)	GCV (%)	PCV (%)	PG	PG%	RG1	RG2	RG3	RG4	RG5
Grain Yield	0.05	1.36	3.59	0.54	14.94	7.38	0.81	15.14	10.22	12.65	19.33	18.82
Anthesis Days	0.00	3.43	0.00	0.00	4.00	0.00	0.00	-1.76	-0.30	-0.30	-1.59	-0.88
Anthesis Silking Interval	0.54	2.19	24.50	26.74	109.13	63.87	31.78	-87.56	-50.00	-75.00	-87.50	-83.33
Chlorophyll Content	0.00	10.13	0.00	0.00	18.90	0.00	0.00	6.53	5.44	7.58	5.75	6.69
Ear Height	0.00	214.80	0.00	0.00	164.60	0.00	0.00	-11.98	-1.39	-7.36	-13.12	0.11
Ear Maturity	0.00	32.01	0.00	0.00	21.31	0.00	0.00	-4.12	-4.00	-6.34	-3.96	-2.54
Ear Position	0.00	0.00	0.00	0.00	0.35	0.00	0.00	-10.66	-8.69	-8.82	-10.63	0.75
Ears Per Plant	0.00	0.06	0.00	0.00	4.49	0.00	0.00	23.97	18.24	31.74	28.12	15.80
Husk Cover	109.45	384.05	28.50	708.41	2485.76	982.96	63.64	-100.00	-100.00	-100.00	-100.00	0.00
Grain Moisture Content	0.18	1.16	15.77	1.04	6.61	29.84	1.71	-6.03	3.71	-4.15	-6.01	-5.67
Number of Leaves	0.02	0.34	4.40	0.26	5.88	4.52	0.78	14.22	10.42	10.42	14.66	10.42
Number of Tassel Branches	0.00	3.85	0.00	0.00	36.17	0.00	0.00	-16.59	4.41	-4.05	-22.83	-19.32
Plant Height	0.00	184.20	0.00	0.00	77.20	0.00	0.00	-7.22	2.97	-3.85	-8.40	-6.10
Root Lodging	17.35	117.85	14.72	246.34	1673.29	281.29	39.94	-100.00	0.00	-100.00	-100.00	-100.00
Stem Lodging	20.95	509.85	4.11	62.52	1521.49	163.30	4.87	-70.25	-61.62	-76.08	-67.98	-76.07
Grey Leaf Spot	0.00	2.04	0.00	0.00	65.22	0.00	0.00	-40.00	-25.00	-42.31	-44.67	-42.31
<i>Phaeosphaeria</i> Leaf Spot	0.00	1.23	0.00	0.00	44.54	0.00	0.00	-43.28	-21.88	-30.56	-42.60	-58.33

δ^2_g =genotypic variance, δ^2_p =phenotypic variance, H²=broad sense heritability, PCV =phenotypic coefficient of variance, GCV =genotypic coefficient of variance h²=narrow sense heritability, PG=predicted gain, RG1-5=realised gains, refer to Chapter 3

Table 4.14: Means of selected hybrids and control hybrids at Dundee

Trait	Mean of selected hybrid	Mean of population	Mean of best commercial check	Mean of all commercial checks	Mean of advanced control hybrids	Mean of hybrids of biological parent
Grain yield	4.56	3.15	4.71	4.05	3.32	3.01
Ears Per Plant	1.39	1.07	1.37	1.12	1.11	1.20
Grain Moisture	12.38	12.90	12.25	12.48	12.79	16.73

Table 4.15: Estimates of variance components, heritability and genetic gains at Dundee

Trait	δ_g^2	δ_p^2	H ² (%)	GCV (%)	PCV (%)	PG	PG%	RG1	RG2	RG3	RG4	RG5
Grain yield	0.15	1.00	14.74	4.67	31.69	25.90	8.23	45.10	-3.09	12.73	37.28	51.64
Ears per plant	0.00	0.05	0.00	0.00	5.08	0.00	0.00	29.22	1.76	24.02	25.02	15.61
Grain moisture content	0.11	0.31	34.04	0.83	2.43	33.52	2.60	-4.10	1.02	-0.80	-3.28	26.01

δ_g^2 =genotypic variance, δ_p^2 =phenotypic variance, H²=broad sense heritability, PCV =phenotypic coefficient of variance, GCV =genotypic coefficient of variance
h²=narrow sense heritability, PG=predicted gain, RG1-5=realised gains, refer to Chapter 3

Table 4.16: Means of selected hybrids and control hybrids at Ukulinga

Trait	Grain Yield	Anthesis Days	Anthesis Silking Interval	Chlorophyll Content	Ear Height	Ear Maturity	Ear Position	Ears Per Plant	Husk Cover	Grain Moisture Content	Number of Leaves	Number of Tassel Branches	Plant Height	Root Lodging	Stem Lodging
MS	12.46	74.38	-0.38	56.15	84.50	124.00	0.42	1.97	3.61	16.33	8.00	7.50	189.88	5.51	0.00
MP	10.45	77.14	0.80	52.73	116.26	133.87	0.53	1.52	53.79	17.75	6.69	9.45	217.58	34.78	2.84
MBC	12.89	76.50	0.00	56.38	99.50	131.00	0.46	1.87	26.43	17.00	8.00	8.50	215.50	35.32	0.00
MC	12.57	76.75	0.50	56.26	104.50	133.00	0.48	1.81	44.38	17.23	7.00	9.75	216.00	42.66	0.00
MAE	10.27	75.89	0.72	52.40	117.33	132.83	0.52	1.37	57.36	17.69	5.89	8.33	223.50	17.62	2.79
MBIO	8.48	75.25	1.00	53.03	103.75	130.25	0.53	1.08	71.48	12.85	5.50	10.00	196.00	26.25	0.00

MS=mean of selected entries, MP=mean of whole population, MBC=mean of best commercial check, MC=mean of all commercial checks, MAE=mean of advanced experimental hhybrids, MBIO=mean of hybrids of biological parents

Table 4.17: Estimates of variance components, heritability and genetic gains at Ukulinga

Trait	δ^2_g	δ^2_p	H ² (%)	GCV (%)	PCV (%)	PG	PG%	RG1	RG2	RG3	RG4	RG5
Grain Yield	0.74	1.72	42.93	7.09	16.51	99.22	9.49	19.18	-3.37	-0.91	21.29	46.88
Anthesis Days	2.26	2.53	89.30	2.93	3.28	250.01	3.24	-3.58	-2.78	-3.09	-1.99	-1.16
Anthesis Silking Interval	0.10	0.38	26.44	12.56	47.49	28.68	35.85	-146.88	0.00	-175.00	-151.92	-137.50
Chlorophyll Content	2.43	5.13	47.43	4.61	9.72	189.01	3.58	6.48	-0.41	-0.19	7.15	5.88
Ear Height	207.88	262.38	79.23	178.74	225.60	2258.67	19.43	-27.32	-15.08	-19.14	-27.98	-18.55
Ear Maturity	5.23	26.44	19.77	3.90	19.74	178.86	1.34	-7.37	-5.34	-6.77	-6.65	-4.80
Ear Position	0.00	0.00	69.17	0.47	0.68	7.35	13.79	-20.43	-7.68	-12.32	-19.13	-19.92
Ears Per Plant	0.05	0.09	59.26	3.39	5.72	30.74	20.24	29.55	5.03	8.93	43.17	81.40
Husk Cover	558.35	696.85	80.12	1038.02	1295.50	3722.63	69.20	-93.30	-86.36	-91.88	-93.72	-94.96
Grain Moisture Content	0.37	1.45	25.28	2.06	8.17	53.58	3.02	-8.01	-3.97	-5.22	-7.74	27.04
Number of Leaves	0.36	0.60	60.62	5.42	8.94	82.49	12.33	19.58	0.00	14.29	35.85	45.45
Number of Tassel Branches	0.00	3.83	0.00	0.00	40.58	0.00	0.00	-20.63	-11.76	-23.08	-10.00	-25.00
Plant Height	148.27	183.48	80.81	68.14	84.32	1926.51	8.85	-12.73	-11.89	-12.09	-15.04	-3.13
Root Lodging	54.10	575.90	9.39	155.55	1655.84	396.77	11.41	-84.16	-84.40	-87.08	-68.72	-79.01
Stem Lodging	6.10	19.96	30.56	214.41	701.58	240.30	84.47	-100.00	0.00	0.00	-100.00	0.00

δ^2_g =genotype variance, δ^2_p =phenotypic variance, H²=broad sense heritability, PCV =phenotypic coefficient of variance, GCV =genotypic coefficient of variance, PG=predicted gain, RG1-5=realised gains, refer to Chapter 3

2.7. Relationship between Grain Yield and Secondary Traits

The associations between grain yield and secondary traits varied depending on the trait and environment. The association can be explained by correlation, regression and path coefficient analyses. These methods were interrelated.

4.7.1. Correlations

Table 4.18 presents the phenotypic correlations between traits measured at Cedara. Ear height, ear prolificacy and plant height were significantly correlated to grain yield ($p \leq 0.01$) while chlorophyll content and grain moisture content were correlated to grain yield ($p \leq 0.05$). These correlations were all positive but not very strong correlations as they were all less than 30%. *Phaeosphaeria* leaf spot (PLS) was positively correlated to ear prolificacy, grey leaf spot disease (GLS) and plant height. GLS and PLS were strongly correlated and the occurrence of one increased the chances of the other. GLS was also correlated to plant height ($p \leq 0.01$). PLS and GLS were both negatively correlated to grain yield although the correlations were not significant. Stem lodging and moisture were positively correlated ($p \leq 0.05$). Root lodging showed no significant ($p > 0.05$) correlations with any trait. However, root and stem lodging showed positive correlations to ear height, ear position and number of tassel branches. They showed negative correlations with grain yield, ear maturity, anthesis days, ear prolificacy and number of leaves. However, these correlations were not significant ($p > 0.05$).

Table 4.18: Correlations between grain yield and secondary traits at Cedara

	Anthesis Silking Interval	Grain Yield	Anthesis Days	Chlorophyll Content	Ear Height	Ear Maturity	Ear Position	Ears Per Plant	Grey Leaf Spot	Husk Cover	Grain Moisture Content	Number of Leaves	Number of Tassel Branches	Plant Height	PLS	Root Lodging	Stem Lodging
Anthesis Silking Interval	-																
Grain Yield	-0.17	-															
Anthesis Days	0.67**	-0.05	-														
Chlorophyll Content	-0.13	0.20*	-0.13	-													
Ear Height	-0.20	0.28**	0.12	0.37**	-												
Ear Maturity	0.08	0.03	0.12	0.29**	0.19*	-											
Ear Position	-0.21	0.16	0.03	0.47**	0.86**	0.10	-										
Ears Per Plant	-0.01	0.29**	0.09	-0.17	0.14	-0.12	-0.01	-									
Grey Leaf Spot	-0.06	-0.24	-0.03	-0.13	0.08	-0.06	-0.07	0.09	-								
Husk Cover	0.10	-0.11	0.03	-0.17	-0.18	0.15	-0.23	-0.07	0.00	-							
Grain Moisture Content	-0.02	0.21*	0.24**	0.05	0.15	-0.05	0.13	-0.03	-0.27	-0.12	-						
Number of Leaves	0.23*	0.10	0.25**	-0.10	-0.17	0.13	-0.21	0.03	-0.20	0.10	0.12	-					
Number of Tassel Branches	0.04	-0.07	0.11	0.27**	0.19*	-0.03	0.23	0.03	0.01	-0.12	0.08	0.10	-				
Plant Height	-0.06	0.29**	0.18*	-0.03	0.59**	0.20*	0.09	0.29**	0.30**	0.01	0.09	-0.03	0.00	-			
PLS	0.07	-0.21	-0.03	-0.28	-0.06	-0.07	-0.26	0.18*	0.60**	0.10	-0.19	-0.19	0.01	0.30**	-		
Root Lodging	-0.07	-0.04	-0.06	-0.04	0.11	-0.08	0.09	0.04	0.02	0.07	0.01	-0.03	0.09	0.08	0.00	-	
Stem Lodging	-0.08	-0.09	-0.06	0.02	0.02	-0.05	0.14	-0.11	-0.11	-0.07	0.09	-0.13	-0.05	-0.16	0.39	-0.01	-

PLS=*Phaeosphaeria* Leaf Spot

*, **= level of significance at $p \leq 0.05$ and $p \leq 0.01$ respectively

Correlations of traits measured at Ukulinga are presented in Table 4.19. Chlorophyll content, number of leaves and anthesis date were significantly ($p \leq 0.05$) correlated to grain yield. Ear maturity and ear prolificacy were highly significantly ($p \leq 0.01$) correlated to grain. Ear maturity was significantly ($p \leq 0.01$) and positively correlated to chlorophyll content, days to anthesis, root lodging, moisture content and number of leaves. Ear maturity showed non-significant ($p > 0.05$) negative correlations to ear height, anthesis silking interval and ear position. Ear height was significantly correlated to ear prolificacy and anthesis days ($p \leq 0.01$). The ear height: anthesis days correlations were significant ($p \leq 0.05$) and strong. Anthesis days were also highly significantly ($p \leq 0.01$) and strongly correlated to plant height. Moisture content, ear prolificacy and ear position correlated to anthesis ($p \leq 0.01$). Root lodging and stem lodging were positively correlated but the correlations were weak and insignificant ($p > 0.05$). However, root lodging was positively correlated to ear maturity and chlorophyll content ($p \leq 0.01$). Ear position was correlated with number of tassel branches and anthesis silking interval ($p \leq 0.01$). Grain moisture content showed a positive and significant ($p \leq 0.01$) correlation with plant height. Root lodging also was highly significantly ($p \leq 0.01$) correlated to moisture content.

Table 4.19: Correlation between grain yield and secondary traits at Ukulinga

	ASI	GYG	CC	EH	EM	EPO	AD	PH	RL	SL	EPP	HC	MOI	NP	NT	NL	GYG	ASI	EH	EPO	EM	CC
ASI	-																					
GYG	0.16	-																				
CC	-0.11	0.22*	-																			
EH	0.08	0.00	0.06	-																		
EM	-0.14	0.26**	0.37**	-0.07	-																	
EPO	0.19*	-0.02	0.11	0.91**	-0.11	-																
AD	0.02	0.17*	0.07	0.50*	0.29**	0.31**	-															
PH	-0.15	0.05	-0.05	0.66**	0.04	0.29**	0.57**	-														
RL	-0.16	0.04	0.42**	-0.06	0.37**	-0.04	0.15	-0.07	-													
SL	-0.20	0.04	-0.02	-0.09	0.07	-0.17	0.11	0.12	0.08	-												
EPP	0.13	0.61**	0.04	0.24**	0.08	0.17*	0.45**	0.26**	0.03	0.11	-											
HC	-0.15	-0.18	-0.15	-0.43	0.16	-0.47	-0.142	-0.14	-0.11	0.14	-0.25	-										
MOI	-0.06	-0.02	0.05	0.11	0.24**	-0.01	0.38**	0.28**	0.23**	0.03	0.06	-0.14	-									
NP	-0.02	0.31**	-0.14	-0.36	0.05	-0.29	-0.13	-0.29	-0.20	0.10	-0.25	0.31**	-0.04	-								
NT	0.02	-0.05	0.12	0.16	0.03	0.26**	0.02	-0.13	0.09	-0.27	0.03	-0.14	-0.03	-0.14	-							
NL	-0.04	0.17*	-0.09	-0.43	0.23*	-0.52	0.17*	-0.04	0.26**	0.24**	0.21*	0.17*	0.09	0.06	-0.01	-						
GYG	0.16	1**	0.22*	0.00	0.26**	-0.02	0.17*	0.05	0.04	0.04	0.61**	-0.18	-0.02	0.31**	-0.05	0.17*	-					
ASI	1**	0.16	-0.11	0.08	-0.14	0.19*	0.02	-0.15	-0.16	-0.20	0.13	-0.15	-0.06	-0.02	0.02	-0.04	0.16	-				
EH	0.08	0.00	0.06	1**	-0.07	0.91**	0.49**	0.66**	-0.06	-0.09	0.24**	-0.43	0.11	-0.36	0.16	-0.43	0.00	0.08	-			
EPO	0.19*	-0.02	0.11	0.91**	-0.11	1**	0.31**	0.29**	-0.04	-0.17	0.17*	-0.47	-0.01	-0.29	0.26**	-0.52	-0.02	0.19*	0.91**	-		
EM	-0.14	0.26**	0.37*	-0.07	1**	-0.11	0.29**	0.04	0.37**	0.07	0.08	0.16	0.24**	0.05	0.03	0.23*	0.26**	-0.14	-0.07	-0.11	-	
CC	-0.11	0.22*	1**	0.06	0.37**	0.11	0.07	-0.05	0.42**	-0.02	0.04	-0.15	0.05	-0.14	0.12	-0.09	0.22*	-0.11	0.06	0.11	0.37**	-

GYG=grain yield, AD=anthesis days, ASI=anthesis silking interval, CC=chlorophyll content, EH=ear height, NL=number of leaves, NT=number of tassel branches, PH=plant height, RL=root lodging, SL=stem lodging

*, **= level of significance at $p \leq 0.05$ and $p \leq 0.01$ respectively

EM=ear maturity, EPO=ear position, EPP=ears per plant, HC=husk cover, MOI=grain moisture content,

Grain yield was significantly correlated ($p \leq 0.01$) to ear prolificacy (Table 4.20). Grain yield showed negative correlation to anthesis silking days, plant height, ear height and ear maturity, although they were not significant ($p > 0.05$). Ear height, ear maturity, ear position and number of tassel branches were highly ($p \leq 0.01$) correlated to chlorophyll content. Days to anthesis were significantly but weakly correlated to chlorophyll content. Ear height showed strong positive correlations to ear maturity, ear position, anthesis days and plant height while it had weaker correlations to stem lodging and number of tassel branches. Ear maturity was observed to be strongly correlated with anthesis days, plant height, stem lodging and anthesis silking interval and weakly correlated to number of tassel branches. The correlations between ear position and anthesis days, plant height and number of tassel branches were highly significant ($p \leq 0.01$) but weak while ear position: stem lodging was also weak significant ($p \leq 0.05$). Anthesis days were strongly correlated to plant height, stem lodging and anthesis silking interval. Plant height was significantly correlated ($p \leq 0.05$) to stem length, anthesis silking interval and number of tassel branches. Root lodging increased with ear prolificacy, bad husk cover and numbers of leaves since their correlations were significant. Root lodging was strongly correlated to number of leaves. Stem lodging also positively correlated with number of tassel branches and anthesis silking interval. Ear prolificacy and bad husk cover showed strong correlation to number of leaves while number of leaves was weakly correlated to moisture content. Number of tassel branches also showed weak correlations to anthesis silking interval.

Table 4.20: Correlations between grain yield and secondary traits across sites

	ASI	GYG	CC	EH	EM	EPO	AD	PH	RL	SL	EPP	HC	MOI	NP	NT	NL	GYG	ASI	EH	EPO	EM	CC
ASI	-																					
GYG	-0.25	-																				
CC	-0.04	0.12	-																			
EH	0.10	-0.08	0.26**	-																		
EM	0.38**	-0.28	0.30**	0.35**	-																	
EPO	-0.01	0.00	0.30**	0.85**	0.09	-																
AD	0.58**	-0.40	0.12*	0.47**	0.80**	0.17**	-															
PH	0.21**	-0.15	0.05	0.69**	0.53**	0.22**	0.65**	-														
RL	-0.33	0.27**	0.10	-0.24	-0.37	-0.07	-0.52	-0.35	-													
SL	0.24**	-0.32	0.10	0.26**	0.51**	0.13*	0.60**	0.31**	-0.37	-												
EPP	-0.14	0.57**	-0.11	0.03	-0.29	0.05	-0.24	0.00	0.23**	-0.27	-											
HC	-0.30	0.20**	-0.13	-0.43	-0.46	-0.29	-0.58	-0.42	0.27**	-0.34	0.05	-										
MOI	-0.07	0.11	0.03	0.08	-0.03	0.04	0.01	0.09	0.19**	-0.02	0.06	0.02	-									
NP	-0.03	0.21**	-0.11	-0.19	0.05	-0.19	0.00	-0.10	-0.15	-0.04	-0.30	0.13*	-0.09	-								
NT	0.16*	-0.18	0.23**	0.27**	0.24**	0.27**	0.29**	0.12*	-0.10	0.14*	-0.08	-0.27	-0.01	-0.09	-							
NL	-0.15	0.34**	-0.15	-0.46	-0.32	-0.40	-0.41	-0.32	0.43**	-0.36	0.30**	0.38**	0.14*	-0.01	-0.12	-						
GYG	-0.25	1**	0.12	-0.08	-0.28	0.00	-0.40	-0.15	0.27**	-0.32	0.57**	0.20**	0.11	0.21**	-0.18	0.34**	-					
ASI	1**	-0.25	-0.04	0.10	0.38**	-0.01	0.58**	0.21**	-0.33	0.24**	-0.14	-0.30	-0.07	-0.03	0.17*	-0.15	-0.25	-				
EH	0.10	-0.08	0.26**	1**	0.35**	0.85**	0.47**	0.69**	-0.24	0.26**	0.03	-0.43	0.08	-0.19	0.27**	-0.46	-0.08	0.10	-			
EPO	-0.01	0.00	0.30**	0.85**	0.09	1**	0.17**	0.22**	-0.07	0.13*	0.05	-0.29	0.04	-0.19	0.27**	-0.40	0.00	-0.01	0.85**	-		
EM	0.38**	-0.28	0.30**	0.35**	1**	0.09	0.80**	0.53**	-0.37	0.51**	-0.29	-0.46	-0.03	0.05	0.24**	-0.32	-0.28	0.38**	0.35**	0.09	-	
CC	-0.04	0.12	1**	0.26**	0.30**	0.30**	0.12*	0.05	0.10	0.10	-0.11	-0.13	0.03	-0.11	0.23**	-0.15	0.12	-0.04	0.26**	0.30**	0.30**	-

GYG=grain yield, AD=anthesis days, ASI=anthesis silking interval, CC=chlorophyll content, EH=ear height, EM=ear maturity, EPO=ear position, EPP=ears per plant, HC=husk cover, MOI=grain moisture content, NL=number of leaves, NT=number of tassel branches, PH=plant height, RL=root lodging, SL=stem lodging

*, **= level of significance at $p \leq 0.05$ and $p \leq 0.01$ respectively

4.7.2. Regression Analysis

The regression data across Cedara and Ukulinga is presented in Table 4.21. The regression of ear prolificacy on grain yield was highly significant ($p < 0.01$). All traits except ear prolificacy were not important as they had very low coefficients of determination on grain yield regression. Only anthesis days and number of leaves had moderate regressions on yield as shown by their coefficients of determination. The other traits were either non-significant or their coefficients of determination were very low ($< 10\%$).

Table 4.21: Regression of secondary traits on grain yield across sites

Trait	Model	 β		
	F pr	R ² (%)	Estimate	SE	t pr
Anthesis Days	<.001***	15.200	20.050	1.700	<.001
Anthesis Silking Interval	<.001***	5.800	10.184	0.149	<.001
Chlorophyll Content	0.101	0.900	6.800	1.810	<.001
Ear height	0.278	0.100	10.558	0.715	<.001
Ear maturity	<.001***	7.500	15.670	1.420	<.001
Ear prolificacy	<.001***	31.700	5.701	0.432	<.001
Husk cover	0.004**	3.600	9.467	0.151	<.001
Grain Moisture Content	0.105	0.800	7.280	1.540	<.001
Number of leaves	<.001***	11.100	6.212	0.710	<.001
Number of Tassel Branches	0.01**	2.800	11.108	0.516	<.001
Plant height	0.039*	1.600	12.500	1.310	<.001
Root lodging	<.001***	7.000	9.434	0.134	<.001
Stem lodging	<.001***	10.100	10.158	0.125	<.001

R² (%) = coefficient of determination, β = regression coefficient, SE = standard error, t pr = t test probability

*, **, *** = $p \leq 0.05$, $p \leq 0.01$, $p \leq 0.001$ respectively

4.7.3. Path Coefficient Analysis

Ear height had the highest direct effects on grain yield on pooled data (Table 4.22). Ear prolificacy had the second highest direct contribution on grain yield. GLS had positive direct effects on grain yield. Ear position and plant height had the highest negative direct contributions to yield. Ear prolificacy confirmed its importance by having second highest

total effects on grain yield. Poor husk cover had the highest total effects on grain yield. GLS had lower than PLS total effects on yield. Days to anthesis negatively affected grain yield more than any other secondary trait.

Ear height had the highest positive direct effects on yield followed by ear prolificacy, grain moisture content and number of leaves at Cedara (Table 4.23). However, plant height, ear prolificacy, ear height, grain moisture content and ear position were the highest total contributors to yield as highlighted by their coefficients. The total contribution by grain moisture content was equal to its direct effect on grain yield. Total contribution by ear prolificacy and plant height was the same but ear prolificacy had higher positive direct effects than plant height which had negative direct effects. GLS and PLS had slightly different total contributions but had very different direct effects. Ear position had the highest negative direct effects followed by plant height, GLS, anthesis days and PLS. However, ear position and plant height had net positive effects on yield through interaction with other traits. Root and stem lodging had very low total negative effects on yield. However, stem lodging showed very small positive direct effects on yield.

At Ukulinga, ear prolificacy, ear height chlorophyll content and ear maturity had the highest positive direct effects on yield (Table 4.24). Ear prolificacy had the highest total contribution to yield followed by ear maturity, chlorophyll content, anthesis days and number of leaves. However, despite having the second highest direct contribution, ear height had zero net effect on yield. Anthesis silking interval and anthesis days had nearly the same total effects although anthesis days had higher negative effects while anthesis silking interval had lower and positive. Plant height, stem lodging and root lodging had very low positive total effects on yield. Ear position, anthesis days, stem lodging and plant height had negative direct

effects. The secondary traits which had the highest negative total effects on yield were number of leaves, grain moisture content and ear position. However, through interaction with other traits their net effects on yield were very small. Stem lodging and root lodging had similar total positive effects although their direct effects on yield were different and opposite.

Table 4.22: Direct and indirect effects of secondary traits on grain yield across sites

Traits	Anthesis Days	Anthesis Silking Interval	Plant Height	Ear Height	Ear Position	Root Lodging	Stem Lodging	Ears Per Plant	Husk Cover	Grain Moisture Content	Number of Plants	Ear Maturity	Chlorophyll Content	Number of Tassel Branches	Number of Leaves	Grey Leaf Spot	PLS	Total Effects
Anthesis Days	<u>-0.67</u>	0.05	-0.87	1.24	-0.27	0.07	0.00	-0.1	-0.11	0.01	0.00	0.09	0.01	-0.06	-0.01	0.02	-0.07	-0.67
Anthesis Silking Interval	-0.36	<u>0.08</u>	-0.22	0.27	-0.04	0.06	0.00	-0.09	-0.07	-0.02	0.00	0.04	0.00	-0.05	-0.01	-0.01	0.01	-0.39
Plant Height	-0.45	0.01	<u>-1.3</u>	1.97	-0.51	0.05	0.00	0.00	-0.08	0.03	-0.05	0.06	0.00	-0.03	-0.01	0.06	-0.15	-0.4
Ear Height	-0.3	0.01	-0.92	<u>2.79</u>	-1.7	0.03	0.00	0.04	-0.11	0.03	-0.09	0.03	0.01	-0.06	-0.01	0.02	-0.03	-0.25
Ear Position	-0.09	0.00	-0.33	2.41	<u>-1.97</u>	0.01	0.00	0.06	-0.09	0.02	-0.09	0.00	0.02	-0.06	-0.01	-0.01	0.06	-0.09
Root Lodging	0.28	-0.03	0.39	-0.52	0.06	<u>-0.17</u>	0.00	0.11	0.04	0.05	-0.07	-0.02	0.02	0.02	0.01	-0.02	0.08	0.23
Stem Lodging	-0.46	0.03	-0.5	0.65	-0.1	0.06	<u>0.01</u>	-0.13	-0.09	-0.02	0.01	0.07	0.00	-0.01	-0.01	0.00	0.1	-0.39
Ears Per Plant	0.13	-0.02	-0.01	0.23	-0.23	-0.04	0.00	<u>0.50</u>	0.00	0.02	-0.09	-0.03	0.00	0.01	0.01	0.03	-0.06	0.46
Husk Cover	0.35	-0.03	0.49	-1.41	0.85	-0.03	0.00	0.00	<u>0.21</u>	-0.02	0.08	-0.04	-0.01	0.06	0.01	-0.02	0.01	0.51
Grain Moisture Content	-0.02	-0.01	-0.15	0.35	-0.17	-0.04	0.00	0.04	-0.02	<u>0.22</u>	-0.03	0.00	0.01	0.00	0.00	-0.02	0.01	0.17
Ear Maturity	-0.52	0.03	-0.62	0.71	-0.02	0.03	0.00	-0.13	-0.07	0.01	0.03	<u>0.12</u>	0.02	-0.06	-0.01	0.01	0.04	-0.42
Chlorophyll Content	-0.06	0.00	0.02	0.35	-0.36	-0.04	0.00	-0.03	-0.03	0.02	-0.04	0.03	<u>0.08</u>	-0.05	0.00	0.00	0.06	-0.06
Number of Tassel Braches	-0.19	0.02	-0.19	0.78	-0.52	0.01	0.00	-0.03	-0.06	0.00	-0.04	0.03	0.02	<u>-0.22</u>	0.00	0.04	-0.11	-0.46
Number of Leaves	0.24	-0.02	0.37	-1.34	0.89	-0.07	0.00	0.15	0.08	0.02	0.00	-0.03	-0.01	0.03	<u>0.03</u>	-0.01	0.12	0.46
Grey Leaf Spot	-0.12	0.00	-0.54	0.39	0.16	0.03	0.00	0.12	-0.03	-0.03	0.04	0.01	0.00	-0.06	0.00	<u>0.13</u>	-0.27	-0.15
PLS	-0.13	0.00	-0.53	0.24	0.32	0.03	0.00	0.08	-0.01	0.00	0.02	-0.01	-0.01	-0.06	-0.01	0.10	<u>-0.37</u>	-0.36

*direct=underlined, total=bold
PLS=*Phaeosphaeria* Leaf Spot

Table 4.23: Direct and indirect effects of secondary traits on grain yield at Cedara

Traits	Anthesis Days	Anthesis Silking Interval	Plant Height	Ear Height	Ear Position	Root Lodging	Stem Lodging	Ears Per Plant	Husk Cover	Grain Moisture Content	Ear Maturity	Chlorophyll Content	Number of Tassel Branches	Number of Leaves	Grey Leaf Spot	PLS	Total Effects
Anthesis Days	<u>-0.20</u>	0.04	-0.05	0.14	-0.03	0.00	0.00	0.05	0.00	0.05	-0.01	-0.04	-0.02	0.03	0.01	0.00	-0.05
Anthesis Silking Interval	-0.13	<u>0.06</u>	0.02	-0.24	0.20	0.00	0.00	-0.01	0.00	0.00	-0.01	-0.04	-0.01	0.03	0.02	-0.01	-0.17
Plant Height	-0.04	0.00	<u>-0.31</u>	0.70	-0.09	0.00	0.00	0.14	0.00	0.02	-0.01	-0.01	0.00	0.00	-0.08	-0.03	0.29
Ear Height	-0.02	-0.01	-0.18	<u>1.20</u>	-0.82	-0.01	0.00	0.07	0.01	0.03	-0.01	0.11	-0.03	-0.02	-0.02	0.01	0.28
Ear Position	-0.01	-0.01	-0.03	1.03	<u>-0.95</u>	-0.01	0.00	-0.01	0.01	0.03	-0.01	0.14	-0.04	-0.02	0.02	0.03	0.15
Root Lodging	0.01	0.00	-0.02	0.14	-0.09	<u>-0.06</u>	0.00	0.02	0.00	0.00	0.01	-0.01	-0.02	0.00	0.00	0.00	-0.04
Stem Lodging	0.01	0.00	0.05	0.02	-0.14	0.00	<u>0.02</u>	-0.06	0.00	0.02	0.00	0.01	0.01	-0.01	0.03	0.04	-0.09
Ears Per Plant	-0.02	0.00	-0.09	0.17	0.02	0.00	0.00	<u>0.51</u>	0.00	-0.01	0.01	-0.05	-0.01	0.00	-0.03	-0.02	0.29
Husk Cover	-0.01	0.01	0.00	-0.22	0.22	0.00	0.00	-0.04	<u>-0.04</u>	-0.03	-0.01	-0.05	0.02	0.01	0.00	-0.01	-0.11
Grain Moisture Content	-0.05	0.00	-0.03	0.18	-0.13	0.00	0.00	-0.02	0.00	<u>0.21</u>	0.00	0.01	-0.01	0.01	0.08	0.02	0.21
Ear Maturity	-0.02	0.00	-0.06	0.22	-0.10	0.00	0.00	-0.06	-0.01	-0.01	<u>-0.07</u>	0.09	0.00	0.01	0.02	0.01	0.03
Chlorophyll Content	0.03	-0.01	0.01	0.44	-0.45	0.00	0.00	-0.09	0.01	0.01	-0.02	<u>0.30</u>	-0.04	-0.01	0.04	0.03	0.20
Number of Tassel Branches	-0.02	0.00	0.00	0.23	-0.21	-0.01	0.00	0.02	0.00	0.02	0.00	0.08	<u>-0.16</u>	0.01	0.00	0.00	-0.07
Number of Leaves	-0.05	0.01	0.01	-0.21	0.20	0.00	0.00	0.02	0.00	0.03	-0.01	-0.03	-0.02	<u>0.11</u>	0.06	0.02	0.10
Grey Leaf Spot	0.01	0.00	-0.09	0.10	0.07	0.00	0.00	0.05	0.00	-0.06	0.00	-0.04	0.00	-0.02	<u>-0.28</u>	-0.07	-0.24
PLS	0.01	0.00	-0.09	-0.07	0.24	0.00	-0.01	0.09	0.00	-0.04	0.00	-0.09	0.00	-0.02	-0.17	<u>-0.11</u>	-0.21

*direct=underlined, total=bold
 PLS=*Phaeosphaeria* Leaf Spot

Table 4.24: Direct and indirect effects of secondary traits on grain yield at Ukulinga

Traits	Anthesis Days	Anthesis Silking Interval	Plant Height	Ear Height	Ear Position	Root Lodging	Stem Lodging	Ears Per Plant	Grain Moisture Content	Number of Plants	Ear Maturity	Chlorophyll Content	Number of Tassel Branches	Number of Leaves	Total Effects
Anthesis Days	<u>-0.32</u>	0.00	-0.05	0.37	-0.17	0.01	-0.01	0.36	-0.01	-0.08	0.05	0.02	0.00	0.01	0.17
Anthesis Silking Interval	-0.01	<u>0.15</u>	0.01	0.06	-0.10	-0.01	0.02	0.10	0.00	-0.01	-0.02	-0.03	0.00	0.00	0.16
Plant Height	-0.18	-0.02	<u>-0.09</u>	0.49	-0.15	0.00	-0.01	0.20	-0.01	-0.17	0.01	-0.01	0.01	0.00	0.05
Ear Height	-0.16	0.01	-0.06	<u>0.74</u>	-0.49	0.00	0.01	0.19	0.00	-0.21	-0.01	0.01	-0.01	-0.03	0.00
Ear Position	-0.10	0.03	-0.02	0.67	<u>-0.54</u>	0.00	0.02	0.14	0.00	-0.17	-0.02	0.03	-0.01	-0.03	-0.01
Root Lodging	-0.05	-0.02	0.01	-0.05	0.02	<u>0.07</u>	-0.01	0.02	0.00	-0.12	0.06	0.10	0.00	0.02	0.04
Stem Lodging	-0.03	-0.03	-0.01	-0.07	0.09	0.01	<u>-0.10</u>	0.09	0.00	0.06	0.01	-0.01	0.01	0.02	0.04
Ears Per Plant	-0.14	0.02	-0.02	0.18	-0.09	0.00	-0.01	<u>0.79</u>	0.00	-0.15	0.01	0.01	0.00	0.01	0.61
Grain Moisture Content	-0.11	-0.01	-0.02	0.07	0.02	0.01	0.00	0.02	<u>-0.02</u>	-0.02	0.04	0.01	0.00	0.00	-0.01
Number of Plants	0.04	0.00	0.03	-0.26	0.15	-0.01	-0.01	-0.20	0.00	<u>0.60</u>	0.01	-0.03	0.01	0.00	0.31
Ear Maturity	-0.09	-0.02	0.00	-0.05	0.06	0.02	-0.01	0.07	-0.01	0.03	<u>0.16</u>	0.09	0.00	0.02	0.26
Chlorophyll Content	-0.02	-0.02	0.00	0.04	-0.06	0.03	0.00	0.04	0.00	-0.08	0.06	<u>0.24</u>	-0.01	-0.01	0.22
Number of Tassel Branches	-0.01	0.00	0.01	0.12	-0.14	0.01	0.03	0.02	0.00	-0.08	0.00	0.03	<u>-0.04</u>	0.00	-0.05
Number of Leaves	-0.05	-0.01	0.00	-0.32	0.27	0.02	-0.02	0.17	0.00	0.04	0.04	-0.02	0.00	<u>0.07</u>	0.17

*direct=underlined, total=bold

PLS=*Phaeosphaeria* Leaf Spot

2.8. Genotype X Environment Interactions

Genotypes performed differently under different environments. The different approaches used to evaluate environmental influence on hybrid performance managed to identify similar genotypes in the each environment.

4.8.1. Additive Main effects and Multiplicative Interactions

Genotype and environments main effects were highly significant ($p < 0.01$) for hybrid yield across the three sites as shown by the AMMI model (Table 4.25). The environmental main effects accounted for the largest part of all the observed variation in yield response. Genotype main effects were very small in comparison. Genotype X environment interactions were not significant and also contributed very little to the total variations observed. The interaction principal component axis (IPCA) 1 was highly significant and explained about 70% of the total interaction between environment and genotypes. IPCA2 was not significant and accounted for the remainder of the interactions. The model managed to explain all the variations by two IPCAs and therefore an AMMI-2 model was adopted.

The best four hybrids were selected based on the AMMI model and are presented in Table 4.26. Hybrids were ranked differently across the environments. Hybrid 15XH39 was ranked in top four at Cedara and Dundee, however the rankings were different.

Table 4.25: AMMI ANOVA for grain yield using predicted means

Source	Degree of Freedom	Mean Square	F	F prob	% Contribution
Total	299	11.90	0.000	0.00000	0.00
Treatments	149	22.3	15.84	0.00000	93.15
Genotypes	49	2.40	1.71	0.00750	3.31
Environments	2	1515.1	120.89	0.00000	85.02
Block	3	12.5	8.91	0.00002	1.07
Interactions	98	1.80	1.25	0.11383	4.83
IPCA	50	2.40	1.71	0.00756	3.37
IPCA	48	1.10	0.77	0.85654	1.46
Residuals	0	0.00	0.00	0.0000	0.00
Error	147	1.40	0.00	0.0000	0.00

Table 4.26: The AMMI model best four hybrids selected in different environments

Environment	Mean yield t/ha	IPCA score	Hybrid rank			
			1	2	3	4
Cedara	9.13	-1.21	15XH16	15XH34	15XH02	15XH39
Dundee	3.15	-1.06	15XH39	15XH20	15XH13	15XH05
Ukulunga	10.45	2.27	15XH28	15XH10	15XH25	15XH11

IPCA=Interaction Principal Component Axis

4.8.2. Stability and Cultivar Superiority Analysis

The genotypes were ranked according to their mean yield across the three sites and the top 10 and bottom five are presented below (Table 4.27). Hybrid 15XH10 had the highest mean yield and lowest superiority index and mean rank among the experimental hybrids. The commercial hybrid BG5285 was the highest performing between the two commercial checks.

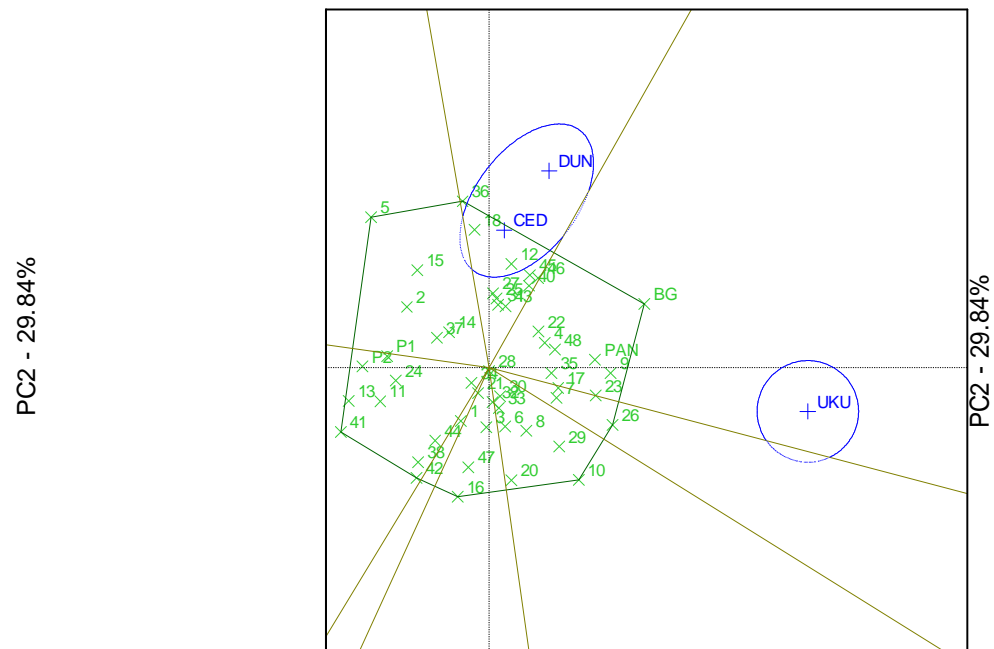
Table 4.27: Stability of maize hybrids based on superiority index and mean ranking

Hybrid	Mean	Superiority Index	Mean Rank
Top 10			
15XH 10	8.44	0.81	14.67
15XH39	8.23	1.85	14.67
15XH13	8.23	1.16	15.00
15XH28	8.23	1.35	20.00
15XH20	8.19	1.61	14.67
15XH25	8.18	1.13	18.67
15XH24	8.17	1.04	14.33
15XH34	8.11	1.54	17.33
15XH04	8.09	1.09	16.00
15XH38	8.04	1.23	17.33
Hybrids of Biological Parent			
15XH21	6.99	4.08	31.33
15XH42	6.56	5.31	37.00
Commercial Hybrids			
BG5285	8.91	0.47	10.00
PAN 6Q-345 CB	8.39	0.77	13.67
Bottom 5			
15XH26	6.87	4.08	35.33
15XH17	6.71	4.15	41.67
15XH12	6.6	4.80	39.67
15XH41	6.51	4.70	43.00
15XH14	6.45	5.57	41.00

4.8.3. Genotype and Genotype X Environment (GGE) Biplot Analysis

The commercial check BG5285 was found on the vertex of the polygon in the sector belonging to Ukulinga site (Figure 4.9). Cedara and Dundee were in the same mega environment where hybrid 15XH39 was the vertex entry. Hybrids such as 15XH24 (22), 10HDTX11 (48) and 15XH25 (23) were in the Ukulinga sector; while the family of 15XH20 (18), 15XH13 (12) and 11C2245 (43) was in the Cedara-Dundee sector. Entries such as 15XH05 (5), 11C1579 (41), 15XH17 (16), 15XH11 (10) and 15XH28 (26) did not show adaptation to a particular environment. Cedara and Dundee were separated by an acute angle

and were closer to each other (Figure 4.10). Cedara was closer to the average test environment (ATE) (depicted by small circle before the arrow on Figure 4.10). Ukulinga was the furthest from the ATE. The angle between vectors connecting Cedara and Ukulinga was obtuse while the Dundee-Ukulinga vectors were separated by an acute angle. The two principal components explained much of the variation as shown by a total of 82.83%.

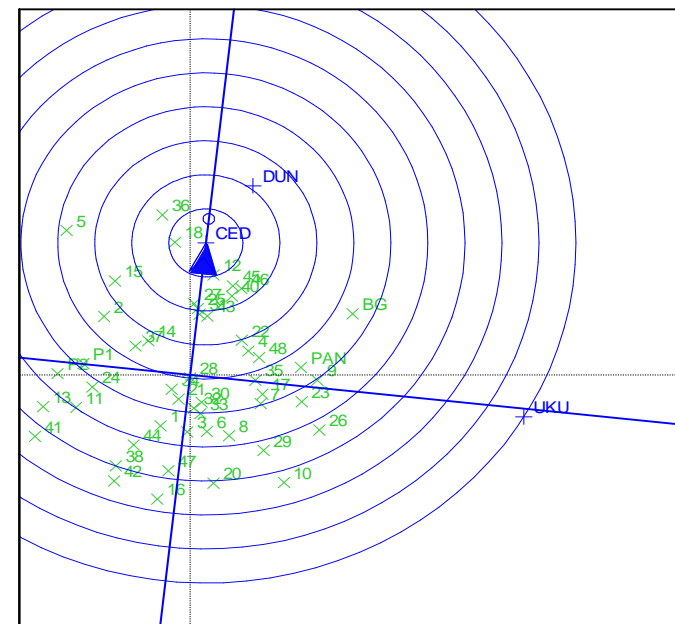


PC1 - 52.99%

PC2 - 29.84%

BG=BG5285
 PAN=PAN6Q-345 CB
 P1=Hybrid of founder parent/LP19
 P2=Hybrid of founder parent/LP21
 Numbers 1-48 represent hybrids, see Chapter 3
 CED=Cedara, Dun=Dundee, UKU=Ukulinga

Figure 4.9: GGE biplot showing hybrid performance in each environment



PC1 - 52.99%

PC2 - 29.84%

BG=BG5285
 PAN=PAN6Q-345 CB
 P1=Hybrid of founder parent/LP19
 P2=Hybrid of founder parent/LP21
 Numbers 1-48 represent hybrids, see Chapter 3
 CED=Cedara, Dun=Dundee, UKU=Ukulinga

Figure 4.10: GGE biplot comparing environments

Chapter 5 : Discussion of Results

5.1. Analysis of Variance

The mean square analysis of grain yield across sites revealed that hybrids differed significantly ($p \leq 0.05$). The wide range of grain yield signifies diverse responses by the genotypes. The genotypes differed also in secondary traits except grain moisture content, chlorophyll content, number of tassel branches, root lodging and stem lodging. The differences emanate from the transgressive segregation of the lines that were derived from a common parentage and also from the divergent testers that were used to generate the experimental hybrids. Several other authors reported differences in grain yield and secondary traits in maize inbred line populations (Abrha et al., 2013; Aly et al., 2011; Badu-Apraku and Akinwale, 2011; Betrán et al., 2003).

However, genotype main effects were not significantly ($p > 0.05$) different for grain yield and most secondary traits within environments, especially Cedara and Dundee Research stations. This lack of significant differences could be attributed to the lack of discriminating capacity by the prevailing conditions at these sites or less transgressive segregation. There were severe moisture stress and weed problems at Dundee, while Cedara experienced weather conditions which promoted disease development. Biotic or abiotic stresses reduce genotype performance (Araus et al., 2002) such that even the best genotypes fail to fully express their potential. Data from stress environments can be characterised by high error variances (Pidgeon et al., 2006), high coefficients of variation and very low genetic variances (Brancourt-Hulmel et al., 2005). These statistics reduce the probability of detecting significant differences among the genotypes evaluated under such environments (Bänziger et al., 1999). Thus, the

discriminating power of such test environments is reduced. A narrow genetic base may also be responsible for the findings of the analysis of variance. The hybrids were derived from related inbred lines which originated from an F₂ population. The common background may have resulted in some similarities in phenotypic response resulting in non-significant differences among the hybrids. Analysis of data from Ukulinga Research Station revealed that genotype effects were significantly different ($p \leq 0.05$). This means that the site provided a more discriminating environment where the adapted and high yielding genotypes could fully express their potential. These findings were in line with the concept that suitable environments achieve higher genetic response (Araus et al., 2002) and consequently genotype performance could be differentiated.

The observed phenotypes of traits varied across the sites and among the genotypes which indicates that there is ample variation especially at Ukulinga which represents a dry non-stress environment. This variability means that the studied population has potential for use in maize improvement (Alan et al., 2013; Badu-Apraku and Oyekunle, 2012). Plant height differed significantly at Ukulinga in a way similar to findings by Kage et al. (2013). Therefore, plant height could be directly selected or improved. Grain moisture content which can be used as an indicator of early physiological maturity showed a narrow range which means that there is limited opportunity for selection. However, it was significantly different between genotypes at Ukulinga in line with findings by Filipenco et al. (2013). Anthesis days were significantly different among entries at Ukulinga while anthesis silking interval showed variability among the genotypes at both Cedara and Ukulinga. The differences in anthesis period among the hybrids at Ukulinga can be targeted for possible yield improvement. Hefny (2011) observed similar variability for anthesis days and anthesis silking interval. Ear maturity was not different at both sites showing low genetic diversity in maturity. This could

be due to the fact that since the experimental lines which were used to make the test hybrids were introgressed with early maturity genes from the same biological founder parent (CML505), the diversity was reduced significantly. Similarly, there were no significant differences between the genotypes regarding number of tassel branches. According to Sangoi (2001) modern hybrids already have reduced tassel numbers and size, which could explain the observed low diversity. The genotypes also exhibited a wide range of root and stem lodging tendencies. These could only be explained by variations in environmental conditions such as storms and heavy rains at Cedara. Consequently, the study could not draw conclusive genotypic effects on these two traits.

5.2. Frequency Distribution for Yield and Secondary Traits

The different distributions exhibited by grain yield and secondary traits across environments exhibit significant genotype effects. More than 50% of the entries at all the sites had above average grain yield. Generally, most entries had higher grain yield at Ukulinga than the other sites. This shows that Ukulinga Research Station is a more favourable environment than Cedara or Dundee. Despite having higher rainfall for all months in comparison, Cedara gave lower yields than Ukulinga. Possible explanations include the later planting and low temperatures at Cedara (see Chapter 3). Tsimba (2011) provided that a planting interval of one to seven days could effectively reduce yield by five per cent. The author also noted that temperatures between 18 and 25°C during grain fill can substantially reduce yield. The low temperatures experienced at Cedara around January and February 2015 (six to eight weeks after planting) could have coincided with the grain filling stage which compromised yield.

In contrast, Dundee experienced higher temperature but there was soil moisture stress, low soil fertility (sandy soils) and weed pressure during the growing period. Begna et al. (2001) asserted that weed infestation can account for between 35-70% reduction in yield. These conditions may be responsible for the lower yields obtained at Dundee. Sandy soils are associated with low fertility status and low water holding capacity and may not be capable of supporting higher yields (Muoni et al., 2013). Several authors reported strong correlations between yield and soil water availability and around 50% yield losses can be incurred under water stress (Basnayake et al., 2012). Ear prolificacy was highest at Ukulinga. The strong correlation between ear prolificacy and grain yield explains the higher yields obtained at Ukulinga. The explanation for higher ear prolificacy could be the same as for grain yield observations across the sites. Genotypes flowered and matured earlier at Ukulinga than at Cedara. High temperatures and moderate heat stress increased rate of phenological development resulting in earliness at Ukulinga. The dependence of grain yield on anthesis and flowering is important in determination of final yield. The average anthesis silking interval at Cedara was higher than at Ukulinga. On average genotypes yielded 11% less at Cedara than at Ukulinga which corresponded to 1.21 days more in anthesis silking interval at Cedara than Ukulinga. This agreed with Bolaños and Edmeades (1993) who reported that 76% variation in maize grain yield could be explained by differences in anthesis silking interval and grain yield declines by 8.7% per day for every day increase in anthesis silking interval up to 10 days.

The few genotypes which had higher yields at Cedara than Ukulinga showed potential disease resistance as they had corresponding lower GLS scores. There were a few outliers for grain moisture content at each site. At Cedara, the outliers were below the average while at Dundee and Ukulinga the outliers had higher than average grain moisture content. Grain

moisture content can be used to explain maturity and the lower mean grain moisture content at Dundee could suggest that genotypes matured earlier at this site. This has an implication on the cropping system especially on rotation practices. The low temperatures and residual soil moisture at Cedara contributed to most genotypes having higher than average moisture. Plants were taller at Cedara than at Ukulinga. Soil moisture and low temperatures promoted vegetative growth more than reproductive growth at Cedara. Plants responded to organic matter from conservation farming by growing taller due to higher organic matter content and soil moisture retention (Linden et al., 2000). More plants suffered from GLS than PLS. GLS has been identified as more important foliar disease than PLS in lowland tropical environments (Sibiya et al., 2011). The prevalence of diseases at Cedara could also explain the lower performance of genotypes at Cedara than at Ukulinga for economically important traits such as ear prolificacy, ear maturity and grain yield.

The different rankings of genotypes across the sites suggest that each genotype responded differently to different environmental conditions. Top ranked hybrids such as 15XH16, 15XH34 and 15XH02 at Cedara could be considered to be tolerant to GLS and PLS. Genotypes which performed well at Dundee Research Station were adapted to low management and drier conditions. These can be considered to be heat and soil moisture stress tolerant. Genotypes which were adapted to Ukulinga Research Station are likely to be productive under high input and high management environments with moderate stress.

Commercial hybrids were not in the top ten ranked hybrids at Cedara which means the experimental hybrids can replace the commercial hybrids with no loss in productivity. Commercial hybrids were also outperformed by experimental hybrids at Dundee Research which means the commercial hybrids are not adapted to low management environments. The

performance of parent 15XH21 hybrids at Cedara shows that they possess some genes for disease tolerance but they are not adapted to drier conditions such as experienced at Dundee and Ukulinga Research stations. Consequently, the hybrids of founder parent 15XH21 cannot be recommended to smallholder farmers who often lack supplementary irrigation in cases of drought. Hybrids of founder parent 15XH42 performed poorly at Cedara and Ukulinga Research Stations. Its performance at Dundee could imply high tolerance to heat and moisture stress that occurred at that site.

5.3. General Combining Ability

Line main effects were significant ($p \leq 0.05$) for grain yield and ear prolificacy. It can therefore be concluded that grain yield was under additive gene control. Analysis of GCA effects of individual lines showed that most lines had non-significant ($p > 0.05$) GCA effects. The presence of GXE interactions might also be responsible for non-significance of line GCA effects. The presence of GXE effects show that the sites lacked homogeneity which could have contributed to lack of significant expression of GCA effects by some of the genotypes. Other researchers have also alluded to the weakness of pooled data analysis due to the assumption of homogenous variance across test sites (Bose et al., 2014; Sial et al., 2000). This assumption increases random variance which may contribute to lack of correlation between genotypes and expressed phenotypes. Nevertheless, lines DMSR-8, DMSR-13, DMSR-30 and DMSR-35-5 were identified as having significant positive GCA effects for grain yield. Positive GCA effects for grain yield are desirable and form the basis for crop grain improvement. These lines are recommended for further testing or development to determine whether the GCA effects are repeatable and stable. However, these lines need to be fixed in other traits in order to meet objectives of early maturity, higher yields, shorter plant

height and resistance to MSV, GLS, PLS and downey mildew diseases. For instance, line DMSR-8 was observed to have positive GCA for ear height and ear position which means it has an undesirable tendency to increase ear height and position when combined with other lines. In order to reduce the ear height and position it should be crossed with lines which showed negative GCA effects for ear height. Line DMSR-30 had significant GCA effects for both grain yield and ear prolificacy but however has a tendency to increase plant height as shown by a positive GCA effects for plant height. Line DMSR-35-5 increased the period to ear maturity, plant height and poor husk cover which are undesirable. Long ear maturity is suited to long season environments while poor husk cover may increase prevalence of secondary infection and damage by animals such as birds.

Negative GCA effects for grain yield are not desirable and lines which exhibit such GCA effects should be disregarded in advancement trials. However, before they are totally discarded they can be crossed with a different population to determine if they can have improved GCA effects or evaluated for other agronomic traits.

5.4. Specific Combining Ability

Two lines DMSR-21 and DMSR-73 showed significant ($p \leq 0.05$) SCA effects for grain yield when crossed to tester LP19. The high SCA effects exhibited by the cross between line DMSR-73 and tester LP19 is evidence that it is the best among the experimental hybrids to consider in grain yield improvement program. Although the cross between LP19 and DMSR-73 had the highest SCA for yield it had some few undesirable aspects such as positive SCA effects for longer anthesis silking interval, ear height, ear maturity, poor husk cover, grain moisture content, number of tassel branches and plant height and negative SCA for number

of leaves. However, the undesirable SCA effects were significant ($p \leq 0.05$) only for moisture, number of tassel branches and plant height.

Tester LP21 produced crosses with significant SCA with lines DMSR-35-4 and DMSR-73 only. However, SCA effects for grain for the hybrids LP21/DMSR-35-4 were undesirably negative. Cross LP21/DMSR-73 had the highest SCA effects for grain yield than all the hybrids involving LP21. However, this cross needs to be improved in other traits such as PLS tolerance, ear height or plant height in order to produce an ideal hybrid by crossing it to a line which has negative SCA for ear height and plant height.

Line DMSR-73 combined well with both testers to form hybrids with positive SCA for grain yield. It had higher SCA effects for grain yield with tester LP19 than tester LP21. Generally, all lines showed higher SCA effects for grain yield when crossed to LP19 than LP21. This shows that tester LP19 had more discriminating ability than tester LP21 since it allows lines to fully express themselves more than tester LP21. Tester LP21 had poor combining ability with 13 out of the 19 lines in contrast to tester LP19. It follows that tester LP19 can be more useful in hybridisation programs. However, since the margin of difference is not very large tester LP21 should not be completely discarded but rather be more carefully selected so that the gene pool is not narrowed. Lines DMSR-21 and DMSR-73 should be used for hybrid development to realise improved grain yield.

5.5. Gene Action

The positive SCA effects for crosses LP19/DMSR-10 and LP19/DMSR-73 were not expected since both lines showed negative GCA for grain yield. The interaction between the lines and

the tester show the importance of non-additive and dominance gene action involved in yield heritability. This supports the hypothesis that dominance is also partly responsible for heterosis in some crosses. Hoecker et al. (2008) asserted that heterosis is observed for adult stage traits such as biomass accumulation and dominance is responsible for heterosis as a result of complementarity between dominant alleles from both parents (Hoecker et al., 2008). It concurs with Amiruzzaman et al. (2011) who concluded that SCA does not reflect the GCA effects of the parents involved in the cross. Rather interactions can cause deviations from the expected GCA-based performance of individual parents. There are crosses whose parents showed positive GCA but had negative SCA effects (undesirable) for grain yield. LP21/DMSR-4 and LP21/ DMSR-18 had negative SCA effects for yield which shows that their parental genes were incompatible in improving grain yield. In contrast LP19/DMSR-80 and LP19/DMSR-73 had parents with negative GCA effects for grain yield but combined well to produce hybrids with positive SCA for grain yield. This shows that both SCA and GCA should be considered in selection of breeding material for advancement. Uddin et al. (2006) provided that GCA effects do not translate into high SCA and is supported by Amiruzzaman et al. (2011) who deduced that grain is under additive and non-additive gene action. Shashidhara (2008) implicated non-additive gene action while, on the contrary, Aly et al. (2011) found prominence of additive gene action. This study concluded that additive gene effects were more important and significant than non-additive action in grain yield heritability. Ojo et al. (2006) explained that the different findings could be attributed to different germplasm used in the studies, environmental conditions and statistical methods employed.

5.6. Heritability estimates, Selection and Genetic Gains

Heritability estimates for grain yield across the sites were low. Asghar and Mehdi (2010) and Abady et al. (2013) also found low heritability for grain yield. The low heritability estimates can be attributed to GXE interactions which are known to negatively affect heritability of quantitative traits (Nzuve et al., 2013) and affect genotype performance and phenotypic expression of traits. Heritability estimates of grain yield across the sites may be misleading as analysis of data pooled across sites has the weakness of assuming homogeneity of sites (Kandus et al., 2010). The three sites were clearly different in terms of soil properties, weather data and management practices and therefore, they were not homogenous. At Cedara and Dundee heritability estimates of grain yield were low but they were relatively higher at Ukulinga. The variation in grain yield heritability under different environments was also noted by Zaidi et al. (2007) who mentioned that variable heritability under different environments compounded selection and breeding progress.

Most secondary traits showed higher heritability when data was pooled across all the sites. The high heritability estimates exhibited by ear prolificacy was comparatively similar to findings by Dixit et al. (2013). Ear prolificacy is very important in yield determination and its high heritability provides an opportunity for yield improvement. However, at Cedara and Dundee heritability for ear prolificacy was zero and resultantly lower grain yield was achieved at these two sites than achieved at Ukulinga. In contrast, Ukulinga showed higher heritability for ear prolificacy than reported by Magorokosho and Tongoona (2004) and Aly et al. (2011). They reported 42% heritability for ear prolificacy under soil moisture stress. However, there was no notable water deficit at Ukulinga but high temperatures may have contributed to heat stress despite availability of soil moisture. The high heritability for ear

prolificacy and its positive correlation with grain yield helped the hybrids to yield higher at Ukulinga than the other sites. At Dundee there was high soil moisture stress but ear prolificacy heritability was zero. The low heritability could mean that ear prolificacy is not positively correlated to moisture stress. An alternative explanation may be that the soil moisture stress at Dundee exceeded minimum threshold level and caused irreversible damage to the genetic potential of the genotypes.

The low heritability estimates exhibited by root and stem lodging show that these traits were strongly related to environmental conditions such as storms, heavy rains or poor soil structure. Low heritability of stem lodging found at Cedara agreed with findings reported by Nzuve et al. (2014). The heritability of root lodging was comparatively similar at both sites which could be an indication of occurrence of environmental conditions which affected the genotypes in the same way. However, stem lodging was distinctly higher at Ukulinga despite having shorter plant height. Stem lodging may therefore not entirely be affected by plant height unlike root lodging but by the strength of the stem. Taller plants exert more strain on the support provided by the roots. If this occurs in combination with weak soil structure and windy environmental conditions the results can be more pronounced. At Cedara and Ukulinga the soil structure was relatively strong and this resulted in low root lodging despite occurrence of storm at both sites. Stem lodging can also be influenced by the age of the plant. As plants grow older the stem becomes weaker due to loss of turgidity and this makes them more susceptible (Zuber et al., 1999). However, this is more environmentally than genetically controlled, hence the lower heritability.

Anthesis days had the highest heritability estimates at Ukulinga in agreement with Mahmood et al. (2004) and Nadagoud and Jagadeesha (2008) who found above 89% heritability for

anthesis days. The period taken by a genotype to produce anthers with viable pollen is an important determinant of growing period. It also influences the anthesis silking interval and ear maturity which showed moderate heritability. These traits are important because they affect seed set, pollination and grain filling which determine kernel properties. They are also important in rain fed agriculture systems to escape drought (Abadassi, 2015).

Ear height, ear position and plant height showed zero heritability at Cedara but had higher heritability at Ukulinga and moderate heritability across sites. The results at Cedara may be due to large phenotypic variance which masked genetic effects. However, these three traits are related and show that their inheritance is not complex (Nzuve et al., 2014). Their importance is emphasized by selection for short plants with shorter ear height for higher yields such as those obtained at Ukulinga. Some authors reviewed literature that suggested that reduction in plant height resulted in increased grain yield (Duvick, 2005b) and reduced lodging (Candido and da Costa Andrade, 2008). This is in contrast to Nzuve et al. (2014) who proposed selection of taller ear and plant height for increased yield.

Husk cover showed high heritability and it can be a target of selection. Husk cover is important in conferring secondary infection and animal damage as it protects the ear from the environment (Abadassi, 2015). Its heritability provides an opportunity for improvement especially in areas where birds are a problem. However, husk cover can also affect the dry down period of the ear and should therefore be selected with careful consideration of cropping patterns and prevailing environmental conditions. Number of leaves, number of tassel branches, GLS, PLS, chlorophyll content and grain moisture content had very low to moderate heritability and variance components. These could be attributed to lack of diversity and changes in environmental conditions (Nzuve et al., 2014).

High heritability of traits cannot be used as the sole selection criteria. High heritability alone may not translate into yield improvement unless accompanied by favorable genetic advance (GA) (Ali et al., 2002; Johnson et al., 1955). High heritability and high GA show that a trait is be under more control of genetic effects and less of environmental influence and thus can successfully be selected for yield improvement (Akinwale et al., 2011). A trait with low heritability coupled with low genetic advance is not selected for improvement (Hefny, 2011). High GCV are indicators of less environmental influence and broader genetic base (Alan et al., 2013) and thus the trait can be selected for improvement. However, these may also be an indicator of static stability whereby the genotype may not respond to improvement in environmental conditions. Large difference between PCV and GCV indicate higher environmental influence while the GCV measures the variability in the trait (Akinwale et al., 2011).

Cedara had the highest environmental influence on grain yield heritability as shown by a higher margin between genetic variance and phenotypic variance than the other two sites. Cedara is a disease hotspot (Fairbanks and Benn, 2000) which could have contributed to other stresses already present at the site. Root lodging, stem lodging and bad husk cover showed high environmental variance suggesting these are not genetically controlled mostly. The higher PCV and GCV for root lodging and stem lodging at Cedara are disproportionate due to a storm that occurred a week prior to harvest. The low heritability exhibited by most traits at Cedara means that indirect selection may not be effective for yield improvement.

Higher GCV at Ukulinga for some traits means they can be effectively selected (Alan et al., 2013) while low heritability of some traits indicates that direct selection for that particular

trait may be ineffective. The small difference between genetic variance and phenotypic variance for anthesis days, ear position and ear prolificacy suggests that there is enough variability to exploit for hybrid development. The high heritability exhibited by ear prolificacy and its correlation with grain yield provide an opportunity that selecting hybrids with high ear prolificacy will inevitably increase grain yield. The response of ear prolificacy was found to be under more of genetic control than environmental influence as shown by the comparatively small difference between its PCV and GCV. Therefore indirect selection through ear prolificacy will be the most effective and efficient method to improve grain yield. However, some authors have concluded that increased ear prolificacy is a response to plant density, moisture or heat stress. Ear prolificacy was found to be negatively correlated with plant density (Tokatlidis et al., 2005) and moisture stress (Çakir, 2004; Munyiri et al., 2010). However, Sangoi (2001) stated that modern hybrids produce less number of ears at lower populations. This study used similar plant densities across the two sites so ear prolificacy cannot be explained by density. A possible explanation that needs further analysis and confirmation could lie in the C:N ratio. At Cedara there was minimum tillage and incorporation of maize stovers from preceding crop. This could have affected the N balance and caused deficit which reduces ears per row (Pandey et al., 2000). At Dundee, the moisture stress was severe and can explain the low number of ears and grain yield. Although maize can relatively tolerate moisture stress, its occurrence at critical growth stages and severity reduces leaf size, growth rate, plant height and grain yield by about 52% (Çakir, 2004) or cause complete abortion of ears (Munyiri et al., 2010).

At Cedara, all the top 10 performing genotypes were late maturing (more than 140 days to mature). Entries 15XH12 and 15XH41 and 15XH42 which were among the early maturing were in the bottom 10 yielding entries. At Ukulinga entries 15XH05, 15XH12, 15XH13,

15XH34 and 15XH06 were among early maturing entries but they performed poorly in yield. Earliness is undesirably linked to low grain yield. This negative correlation between yield and growth period complicates breeding for earliness as there is evidently a yield penalty paid by reduction in growth period. Therefore, selection for early ear maturity was not recommended in this study for yield improvement.

Planting date, prevailing temperatures (Bonaparte, 1975) and agronomic practices have been implicated in conditioning the number of leaves formed per plant (Rahmani et al., 2015). Significant gains were achieved over commercial checks at both Cedara and Ukulinga for number of leaves. The positive correlation between the numbers of leaves and grain yield coupled with high heritability makes it a potential target for selection in grain improvement. However, increase in the number of leaves was found to reduce the concentration of leaf chlorophyll which is important for photosynthesis. This study also found out that number of leaves had lower direct effects on grain yield than chlorophyll content. It is therefore concluded that it is more effective to breed for higher chlorophyll content in grain yield improvement than to select for higher number of leaves. Chlorophyll content is more important in determining yield (Peng et al., 2011).

In this study plant height, grain moisture content, husk covering, stem lodging, root lodging, number of tassel branches, ear position and ear height were found to have no considerable contribution towards final grain yield. However, shorter plants with lower ear position and lower grain moisture content were selected. In addition ears showing good husk cover on plants with less stem and root lodging scores and less profuse branching of the tassel are considered to be good for selection. Selection per individual site was more emphasized as it showed higher potential to improve yield than selection across all sites.

Across all sites realised genetic gains of selected entries over the population mean were positive. This shows that selection has the potential to improve grain yield. However, the genetic gains over commercial varieties were negative assuming that selection could not improve grain yield in comparison to the already grown varieties. There was significant improvement over the biological parents as shown by the positive realised gains. Heterosis over hybrids of biological founder parents was positive and highest showing that significant improvements were achieved by selection since the goal of the breeding program was to achieve higher yield than LP19 and LP21 which are highly productive in tropical low lying areas. Heterosis is a desirable aspect of breeding as it allows the deduction of potential of the testcross to perform better than a set benchmark. The ability by some of the testcrosses to exceed the performance of commercial varieties confirms there is enough variability among the testcrosses for possible exploitation.

At Cedara there were positive yield gains realised over commercial varieties. The high performance shown by the experimental hybrids in comparison to commercial hybrids means that under Cedara environmental conditions, they can be recommended in place of commercial and there is expected to be increased productivity. At Cedara all the top 10 yielding entries were experimental hybrids. This signifies considerable realised genetic advance and variability for further advancement of the experimental hybrids. The identified entries can be selected for possible development especially towards disease resistance. Similarly, at Dundee experimental testcross 15XH39 out yielded the commonly grown commercial variety BG5285. There were five experimental hybrids among the top 10 at Dundee, which also is a step in the positive direction for yield improvement under low management environments. The rankings at Ukulinga also showed tremendous potential of

the experimental hybrids. Although the commercial variety BG5285 had the highest yield, three experimental hybrids yielded better than the other commercial variety PAN6Q-345 CB and 80% of the top ten performing entries were experimental hybrids. Overall, 50% of the top performers were experimental hybrids. Experimental hybrid 15XH10 had the second highest average yield across the sites, performing better than one of the commercial varieties and several advanced experimental controls. However, there are still opportunities for further improvement regarding other traits.

Disease tolerance showed zero heritability, low genetic variance and low predicted gain. This means that phenotypic response of genotypes to disease pressure needs further investigation. The individuals which responded favorably against disease infection may have been escapees rather than tolerant or resistant. The lack of precise inoculation and recording of stage of infection may have compromised possible identification and selection of tolerant genotypes. Overall, heterosis highlighted potential improvement that can be made regarding traits measured at Cedara. Despite the low precision in disease ratings, the experimental hybrids performed better than the commercial and significant genetic gains were achieved.

The observation that genetic gains in more number of traits were achieved at Ukulinga agrees with the fact that genetic gains are higher under non-stress environments (Araus et al., 2002). When genotypes are evaluated under stress environments, the genetic gains achieved are proportional to the amount of stress that may be exerted. However, under extreme stress, genetic gains may be nearly zero or negative.

5.7. Correlations between Grain Yield and Secondary Traits

The presence of correlations between some of the secondary traits and grain yield shows that they can be exploited in yield improvement breeding. If the traits with positive correlations are fully expressed in the genotypes then yield can be improved. The genetic information involved in the expression of these traits in the parents can be exploited in line improvement. Correlations between grain yield and ear prolificacy is very important as shown by high significant correlations of about 57% across the sites. Several studies cited by Betrán et al. (2003) found strong positive correlations between yield and ears per plant (EPP). However, the correlations were lower at Cedara. This could be due to unfavourable conditions such as disease prevalence and low temperature unlike at Ukulinga. Svečnjak et al. (2006) stated that ear prolificacy is reduced under unfavourable conditions but when environmental conditions improve hybrids respond by producing one or several sub apical ears. This is in contrast to findings by Magorokosho and Tongoona (2004) and Aly et al. (2011) who asserted that ear prolificacy increases under soil moisture stress.

At Cedara and Ukulinga the correlation between plant height and grain yield and ear height and grain yield were similar to findings by Selvaraj and Nagarajan (2011). However, at Ukulinga the correlations were not significant ($p > 0.05$) and very weak unlike at Cedara where the correlations were significant ($p \leq 0.05$) and relatively more pronounced. The differences can be explained by environmental influence in genotype performance. The strong and positive correlations obtained at Cedara between plant height and grain yield can be explained by improved light interception and higher photosynthetic capacity. Light capture is a critical component of the process that converts chemical energy into grain yield (Peng et al., 2011) and breeding exploits this characteristic to develop high yielding hybrids. However,

the emphasis by current breeding for shorter hybrids is in contrast. Taller plants are claimed to have higher maintenance demands and lower sink capacity for grain filling which compromises yield (Duvick, 2005b). Chlorophyll content and ear prolificacy were positively correlated to yield at both sites. The correlations obtained between chlorophyll content and grain yield concur with conclusions by Edmeades et al. (1996) that chlorophyll content has moderate correlations with grain yield.

Ear maturity at Ukulinga was positively and significantly ($p \leq 0.05$) correlated to yield. At Cedara the correlation was weakly positive and insignificant ($p > 0.05$). The correlations imply that the lengthening of grain filling and maturity period of the ear contribute to yield improvement. The findings are substantiated by conclusions by Magorokosho et al. (2009) which reiterated that early maturing varieties yield 15-30% less than late maturing varieties; hence the positive correlation between maturity and grain yield. However, due to erratic and unreliable rainfall seasons in SSA, late maturing hybrids pose a huge risk to crop failure and as such early maturing varieties have been promoted widely to escape crop failure (Gasura et al., 2013).

Other aspects related to maturity are anthesis and flowering days. Anthesis silking interval exhibited negative correlations with yield although they were not significant at any of the sites. Rahmani et al. (2015) reported similar negative correlations between yield and flowering dates. However, it is an indication of the importance of synchronization of pollen shed and female flower receptivity. The synchrony allows for efficient pollination and subsequent increase in yield. Campos et al. (2004) highlighted the role of silking and pollen shed in the final yield while Bekavac et al. (2007) emphasised that the anthesis silking interval should be short. Failure to meet these conditions can result in failure to develop

successful hybrids (Longin et al., 2012) as longer anthesis silking interval may result in low grain fill due to inadequate pollination (Noor et al., 2013). The rationale behind reduced yield under late flowering and long anthesis silking interval is that the plants will channel more assimilates to vegetative growth stages rather than to reproductive growth.

Number of leaves was significantly and positively correlated to yield at Ukulinga and overall. At Cedara the correlation was positive though weak. Number of leaves is related to the number of photosynthetic components such as chloroplasts and therefore an increase in the number of leaves improves photosynthetic capacity. Experiments by Gates and Mortimore (1972) which involved removal of leaves concluded that number of leaves above the ear account for 70-90% yield fluctuations. However, there could be a limit to the number and size of leaves before there is competition for light interception among the plants in the stand and reduction in chlorophyll concentration in mature leaves. This could have happened at Cedara and resulted in lower grain yield and correlation between grain yield and the number of leaves.

The number of tassel branches was negatively correlated with grain yield as predicted by Sangoi (2001) and Duvick et al. (2004) who asserted that a large male inflorescence reduces yield potential by competing for assimilates with the ear. The average number of tassel branches at Cedara was higher than at Ukulinga and resultantly the average yield was also comparatively lower. The male inflorescence should therefore be reduced to a minimal size just big enough to produce adequate and viable pollen.

Disease progression was negatively correlated to yield. Both GLS and PLS had negative correlation indicating the role of disease proliferation in reducing yield. The hybrids should

be introgressed with disease resistance genes in order to improve yield especially at environments such as Cedara which are favourable for disease development. The correlations were not significant. Nonetheless they highlight the need for improvement in disease resistance in order to help the average farmer who may not afford chemical control.

5.8. Correlations among Secondary Traits

Correlations between root and stem lodging were insignificant ($p \leq 0.05$) at both sites which was in agreement with Sposaro et al. (2008) who provided that lodging can be environmentally influenced by events such as heavy rains and strong winds or by genetic factors such as disease and pest resistance or yield. Rajcan and Tollenaar (1999) cited several authors who stated that lodging can be attributed to the translocation of assimilates from the stem to yield components leaving the stems weak and susceptible to mechanical stress. The stems become weak and unable to support a high yield. This is agreement with the high root lodging observed at Ukulinga where the yield was higher. In overall data across the sites, stem lodging was positively and significantly correlated with ear position showing the effects of genetic constitution on stem lodging unlike root lodging.

The negative correlations between chlorophyll content and number of leaves at both sites signifies that although the number of leaves is important in improving photosynthetic capacity, it also has a negative impact on the concentration of photosynthetic organelles in the leaves. The mobilisation of nitrogen from older leaves to younger leaves could explain the reduction in the concentration of chlorophyll as the number of leaves increases. Therefore, the number of leaves should be increased under breeding programs with also a consideration of the chlorophyll content in the leaves. High number of leaves with lower

concentration of chlorophyll could be undesirable as they increase competition for light interception with reduced photosynthetic activity in the leaves. The positive and significant correlations between chlorophyll content and number of tassel branches at Cedara and across sites are of considerable concern to the breeder. This relationship complicates breeding efforts since chlorophyll is positively correlated with grain yield and in contrast number of tassel branches is negatively correlated to grain yield. High chlorophyll content improves photosynthetic capacity which in turn leads to high biomass accumulation. However, growth in number of tassel branches leads to reduced female flower growth due to apical dominance. Grain moisture content and plant height correlation are positive signifying that high dry matter prolongs dry down of the ear. Both these traits are not desirable in yield improvement and their positive association simplifies the breeding effort since reduction of one can lead to reduction of the other. The positive correlation between moisture and ear maturity at Ukulinga can be explained by the need for moisture to continue supporting biochemical activity in ear development until physiological maturity is attained. The negative correlations observed at Cedara are unusual and are difficult to explain. However, it can be speculated that since there were fewer plants with open tips (poor husk cover) the ear retain moisture due to a good and thick husk cover that prevented grain moisture content loss. This needs further investigation.

Days to anthesis define the earliness or lateness of a variety. Longer days to anthesis and silking resulted in late maturity of the ear. The correlations between anthesis days, anthesis silking interval and ear maturity were not different from reports by Augustina et al. (2013) and Pandey et al. (2009). Plant height was also correlated to anthesis days at Cedara and Ukulinga, in line with report by Dickert and Tracy (2002) who reported that early flowering varieties have been observed to be short. This could be affirmed by the shorter plant height

obtained at Ukulinga where plants flowered earlier than at Cedara. The partitioning of assimilates between vegetative and reproductive growth played a critical role in determining the final height of the plants. Interestingly, grain moisture content showed negative correlations with both diseases at Cedara. This may have resulted from a weakening defence mechanism by the plants as the ear matured. Alternatively, the disease proliferation may not be explained by the immune system of the plant due to maturity but rather by environmental conditions. Since these diseases have specific favourable weather conditions, their occurrence may not significantly reduce yield if the favourable conditions do not coincide with critical yield determining stages such as grain filling or flowering. The plants may only suffer from reduction in yield quality.

5.9. Regression of Traits on Grain Yield

Regression analysis helps the breeder to determine which correlations between the traits are of significant importance. A trait with a high coefficient of determination ($\geq 30\%$) is regarded as important in improving yield. Ear prolificacy was shown to be the most important trait for grain yield improvement according to the regression and correlation analyses. All other traits had relatively lower coefficients of determination than ear prolificacy. It is, therefore, concluded that only ear prolificacy had the most important correlation with grain yield.

5.10. Path Coefficient Analysis

The high direct effects shown by ear height are not considered important as the regression of ear height on grain yield was insignificant ($p > 0.05$). Path coefficient analysis also showed that ear prolificacy was the most important trait for grain yield improvement through its direct and indirect effects on grain yield. The high indirect contribution of ear prolificacy

through ear height can be used to infer to the importance of ear positioning and ear growth on grain yield.

At Cedara Research Station the contribution of ear prolificacy was second to the contribution of ear height. However, regression analysis revealed that ear height correlation with grain yield was not significant ($p>0.05$). These findings consolidate the importance of directly selecting genotypes with higher ear prolificacy in yield improvement programs. Its highest indirect contribution was through ear height suggesting the vitality of their relationship. The low indirect effect of ear prolificacy through number of plants may be related to genotype response to planting density. Some genotypes compensate low density by being more prolific. Studies on ear prolificacy and planting density by Al-Naggar et al. (2011) showed that prolificacy is reduced under higher plant density. Since the same planting density was used at both sites, it can be concluded that ear prolificacy in this study was not a result of planting density. The two diseases also had similar total contributions at Cedara Research Station. 80% of the total yields reducing effects of PLS were exerted through GLS. This means that in the absence of GLS, PLS may not be very problematic. These findings indicate that GLS might be more important than PLS which has been identified as less widespread in Africa (Sibiya et al., 2011). The analysis also revealed the significance of ear height in determining grain yield at Cedara Research Station. This significance could be due to the relationship between ear height and number of leaves above the ear. In a research by Gates and Mortimore (1972), it was concluded that the most important leaves were the ones starting at the ear leaf going up the plant. This means that higher ear height will limit the number of leaves on the upper part of the plant. This relationship is also confirmed by the negative correlations between ear height and number of leaves above the ear.

From data obtained at Ukulinga it can be concluded that selecting for shorter plants with a lower ear position, shorter anthesis silking interval, high ear prolificacy, longer days to maturity and with higher number of leaves will improve grain yield. However, the most emphasis is placed on ear prolificacy for exploitation in grain improvement at Ukulinga Research.

5.11. Genotype X Environmental Interaction Analysis

Genotype X environmental interaction effects were not significant for grain yield. However, more than 60% of the traits showed that they were significantly affected by GXE interactions. The complexity brought about by these interactions confounds the selection process by weakening the phenotypic response of a genotype (Farshadfar et al., 2012). Such confounding effects not only reduce the predictability of yield response given the genotypic potential of a hybrid or line but also cause imbalances in the genetic control of trait expression. These interactions are confirmed by the AMMI-2 model ANOVA which showed that interaction principal components axes (IPCA) were highly significant.

The interaction between environment and genotypes contributed more to the total variation than the genotypes themselves. This phenomenon can be explained by the narrow genetic base from which these hybrids were derived and therefore variation in environmental conditions assumed more importance. The significant differences in the AMMI can also be used to mean that different genotypes are adapted to different environments. These interactions affect the stability of secondary traits and result in rank changes from one site to the other as reported by Issa (2009) and Khalil et al. (2010).

Although GXE interaction effects were not significant for grain yield, they were exerted through secondary traits. The changes in expression of secondary traits under different environments are highly important as they affect selection for high yield. Direct selection for high yield may not always be possible due to factors such as climate, agronomy or pests such as experienced at Dundee and Cedara. Therefore the absence of GXE interaction effects on grain yield per se may not signify that direct selection for yield is the most appropriate method for yield improvement.

5.11.1. Discriminating Ability and Representativeness of Test Environments

Cedara and Dundee had shorter environmental representative vectors which correspond to low discriminating capacity (Kandus et al., 2010). Ukulinga had higher discriminating ability as evidenced by its long vector from the origin. The biplot revealed that Ukulinga allowed the genotypes to express themselves more and was therefore able to distinguish less performing genotypes from higher performing genotypes more than any other site. However, Cedara was more representative of the average test environment as shown by its proximity to the average test coordinates (ATC). This was based on the performance of the genotypes. However, a breeder will always target an environment where the genotypes express higher yield potential such as at Ukulinga. Cedara and Dundee environments were positively correlated since their vectors were separated by an acute angle (Yan and Tinker, 2006). This similarity gives the breeder room to drop one of the sites from test sites and reduce costs of testing without necessarily losing information (Xu et al., 2014). Ukulinga was negatively correlated to Cedara as shown by the obtuse angle between their vectors. However, Dundee and Ukulinga were positively correlated. The lack of correlation between sites means that they have different capacities in discriminating the genotypes and removal of one site results in loss of

valuable information. Therefore in future trials all the three sites are needed. If the pattern is repeatable then one of the sites can be dropped off the test sites list.

5.11.2. Environmental Main Effects

Variability in rainfall patterns, temperature and agronomic practices are some of the factors implicated in causing variable response of genotypes in different environments. Planting dates are very important and could have led to differences in the yield between sites particularly Cedara and Ukulinga. Cedara was planted 12 days later than Ukulinga. Tsimba et al. (2013) reported that late planting coincides with deterioration in environmental conditions such as temperature, radiation and moisture at grain filling stage resulting in lower yields. From the GGE biplot analysis Cedara and Dundee were grouped in the same mega environment. This, however, does not mean that genotypes responded similarly but rather shows that the sites were correlated in some way (Yan and Tinker, 2006) since they both experienced biotic and abiotic stresses. In terms of environmental conditions Ukulinga was on the average, while Cedara and Dundee were on the extreme ends. Cedara experienced low temperatures and had high water retention capacity (see Chapter 3). However, plant growth was challenged by disease proliferation. Dundee was very hot and experienced a mid-season drought and is characterised by low fertility sandy soils with high leaching potential. Ukulinga experienced high temperatures than Cedara but lower than Dundee and was more fertile than Dundee with higher water and nutrients holding capacity but lower than at Cedara (see Chapter 3). Therefore, Ukulinga had higher discriminating power as revealed by the GGE biplot. This is also supported by mean comparison of the sites.

5.11.3. Genotype Performance

The genotypes performed differently in different environments. Cedara and Dundee were in the same mega-environment sector characterised by similar top performers. Entries 5, 18 and 36 were among the top ten performing entries at both Cedara and Dundee. This is also consolidated by the GGE biplot analysis where hybrids 15XH05 and 15XH20 are found in the Cedara-Dundee sector. The ‘which-won-where’ biplot helps to identify adapted genotypes for a particular environment and from this analysis it can be concluded that hybrid 15XH39 was adapted to both Cedara and Dundee. The common high performing entries at Cedara and Dundee may possess disease resistance and heat stress tolerant genes. They should be further tested for these traits. Crossing over ranking of hybrids across sites complicates selection process as it becomes difficult to select the most adapted or stable hybrid for several environments. However, hybrids 15XH05, 15XH20 and 15XH39 could be considered for possible dynamic stability. Dynamic stability is whereby a genotype yields higher when there is an improvement in environmental conditions (Lin and Binns, 1988). They responded well to adverse conditions at Dundee and improved their performance at Cedara showing that they respond positively to improvement in environmental conditions. Similarly, hybrids 15XH04 and 15XH18 performed well under stress at Dundee and responded to improved conditions at Ukulinga. Entry 15XH07 was in the top performing entries at Cedara and Ukulinga.

Some entries were found to yield consistently lower than the average across sites. Such entries included hybrids 15XH17, 15XH22 and 11C1566 between Cedara and Dundee, hybrids 15XH41 and 15XH42 between Cedara and Ukulinga while between Dundee and Ukulinga hybrids 11C1579 and 15XH14 were identified. These were confirmed by both

AMMI plot of genotype and environment means and the table of means for low performing entries. These entries were not selected because they exhibited static stability. This is whereby a genotype consistently yields low despite improvements in the environments (Kandus et al., 2010). The AMMI plot also revealed entries which had low and high stability. Entry 46 had the lowest stability as depicted by high IPCA score followed by entries such as 15XH09, 15XH06, 15XH23 and 11C2245. The IPCA scores show the magnitude of variation between the mean yields for a genotype across the sites. Genotypes should preferably have IPCA scores closer to zero for high stability (Crossa, 1990). It can also be deduced that despite having the highest mean yield across all sites, the commercial check BG5285 showed a high level of instability.

All the commercial and advanced trial checks were out-yielded by the experimental hybrids at Cedara. At Dundee one experimental hybrid was second to advanced trial check but yielded better than the commercial variety BG5285. This is vital for genetic gains and breeding advance. However, at Ukulinga the commercial variety BG5285 was the top yielding entry. There were three experimental hybrids which performed better than the other commercial variety PAN6Q-345 CB. This means that these experimental hybrids have potential to be recommended in the agro-ecological zones represented by Ukulinga where variety PAN6Q-345 CB is currently grown. The entries which performed well at Cedara can be hypothesized to possessing some form of disease resistance or tolerance which needs to be investigated further. Those adapted to Dundee should be considered for low management environments with moisture challenges. Ukulinga represents a more favourable environment with good management and less disease and moisture stresses. Therefore, entries that performed well at Ukulinga can be recommended for agro-ecological zones with average environmental conditions.

5.11.4. Crossing Over of Genotypes

Environments with vectors separated by a more than 90° angle are negatively correlated (Yan and Tinker, 2006) and this means that most adapted genotypes in each environment will differ (Dawson et al., 2008). This is known as crossing over ranking. Crossing over complicates selection and identification of suitable genotypes in breeding. Similar findings have been reported by different authors who also bemoaned delay in achieving breeding gains due to these unwanted crossovers (Arulselvi and Selvi, 2010; Tonk et al., 2011). At least 50%, 40% and 70% of hybrids in the top 10 yielding groups at Cedara, Dundee and Ukulinga, respectively, performed well at that one particular site and were not in the top performing entries anywhere else. However, there were other hybrids which showed dynamic stability across two sites. These were hybrid 15XH18 at Dundee and Ukulinga, hybrid 15XH39 at Dundee and Cedara and hybrid 15XH07 at Cedara and Ukulinga. These genotypes showed response to changes in environmental conditions such as reduced disease pressure and improved soil moisture content. These hybrids can do well across a number of sites since they have shown to be stress tolerant but when conditions improve they also improved their productivity.

5.11.5. AMMI Model Best Hybrid Selection

The AMMI-2 model revealed ranks according to interaction principal component axes (IPCA) scores. From the analysis, four hybrids were identified for each environment. Hybrids 15XH16, 15XH34, 15XH02 and 15XH39 were identified to be suitable for Cedara, showing prospective disease resistance and low temperature tolerance in these genotypes. The study concluded that hybrids 15XH39, 15XH20, 15XH13 and 15XH05 were adapted to low management and soil moisture stress environment such as experienced at Dundee. These

hybrids can be recommended for drier and low fertility areas. For environments represented by Ukulinga, which had favourable environmental conditions, hybrids 15XH28, 15XH10, 15XH25 and 15XH11 were identified as being suitable. These hybrids, apart from hybrid 15XH39 showed static stability which makes them suitable for a single environment. Such stability is useful for recommendation of hybrids for specific sites but may be counterproductive when blanket recommendations are made.

5.11.6. Stability and Cultivar Superiority Analysis

Stability analysis shows that hybrid 15XH13 was more stable than 15XH39, and 15XH04 was second to 15XH10 in stability. Hybrid 15XH39 was the least stable among the top 10 performing hybrids. Lin and Binns (1988) provided that superior genotypes have smaller indices while Huehn (1990) asserted that the stability rank tended towards zero as a genotype attains its maximum stability. Mean ranking was premised on the same principle such that a lower mean rank showed that the hybrid was ranked high in more environments than a genotype with a higher mean rank. Selection of hybrids across environments should be based on their yield superiority, stability and mean ranking over the given test environments. Stability analysis provides a general solution for the response of the genotypes to environmental change.

5.11.7. Genotype Adaptation

The GGE analysis helps to identify genotypes which are adapted to specific environments. The genotype which occupies the vertex of a polygon connecting outermost genotypes and bound by a sector belonging to a particular environment or group of environments is regarded as the most adapted for that environments or environments (Ding et al., 2007). The biplot

grouped Cedara and Dundee in the same mega environment while Ukulinga was in its own sector. Hybrid 15XH39 was identified to be adapted to Cedara and Dundee Research Stations while the commercial hybrid BG5285 emerged as the most adapted at Ukulinga. Hybrid 15XH39 is therefore considered to be both disease and moisture stress tolerant while the commercial hybrid performed well under high management at Ukulinga. There are a number of entries which showed no adaptation to any particular environment and these are shown marked in unnamed sectors. The GGE biplot and AMMI analyses managed to show that different genotypes can be selected for different agro ecological environments.

Chapter 6 : Conclusions and Recommendations

6.1. Findings

In this study it was found that:

- Genotype x environment interactions influenced performance of experimental hybrids which were reflected by the differences in ranking and stability of genotypic mean performance. Ukulinga was identified as the most suitable site for discriminating genotypes.
- Yield was identified as having complex heritability consisting of mostly additive gene action and its heritability was lower than most yield related traits. GCA effects of the lines were significant for grain yield showing the importance of additive gene action. SCA effects were mostly insignificant for grain yield and most secondary traits. This shows that non-additive gene action was negligible indicating that hybridisation might not be a viable strategy for improving grain yield potential of this inbred population.
- Ranking by mean yield of the hybrids identified 15XH16, 15XH20, and 15XH28 at Cedara, Dundee and Ukulinga respectively as the highest yielding genotype for that particular environment. These hybrids were developed from DMSR-35-3, DMSR-73 and DMSR-13 inbred lines, respectively. These inbred lines are therefore considered suitable for grain yield improvement.

- The AMMI-2 best four model deduced that hybrids 15XH16, 15XH34, 15XH39 and 15XH02 were adapted to Cedara, hybrids 15XH39, 15XH20, 15XH13 and 15XH05 were adapted to Dundee while hybrids 15XH10, 15XH28, 15XH25 and 15XH11 were adapted to Ukulinga. These entries will be selected for further testing and would be deployed in the environments which were represented by these three sites.
- The GGE biplot analysis revealed that hybrids 15XH10, 15XH13, 15XH20, 15XH25, 15XH28, 15XH34 and 15XH39 were the most stable. These were also selected by the AMMI model confirming that they are the best genotypes with respect to stability of performance.
- Inbred lines DMSR-8, DMSR-13, DMSR-30 and DMSR-35-5 should be maintained as inbred lines since they show high GCA estimates which is potentially useful for use in developing synthetic varieties.
- Inbred line DMSR-73 showed positive SCA with both testers while DMSR-21 had positive SCA estimates with tester LP19 only. These lines should be considered for hybridisation.
- Significant breeding gains were made in grain yield and a number of yield related traits through selection based on the AMMI best four hybrids selection.
- The relationship between secondary traits and yield varied in magnitude and direction according to each environment. Traits were also revealed to have different pathways in effecting change in grain yield.

- Ear prolificacy was the most important trait to exploit in grain yield improvement program because it was highly associated with grain yield potential of the hybrids.

On the basis of these conclusions some recommendations were drawn to meet the objectives of this study. They are presented in the next section.

6.2. Recommendations

In light of the above conclusions, the following recommendations were drawn:

- The shuttle breeding program at UKZN should be continued as significant gains have been made in introgressing desirable traits and developing high yielding hybrids.
- It is recommended that there is need to repeat the experiments for another season before final selection can be made.
- The experiments should be repeated to confirm if the observed genotype X environment interaction are repeatable over different seasons.
- Selection through ear prolificacy should be emphasized to improve grain yield.
- Dundee and Cedara must not be discarded as test sites as they represent stress environment which can be useful in identifying stress tolerant genotypes.

6.3. Overall Conclusion

Overall, the study was successful at identifying the lines with potential for use in developing potentially high yielding hybrids. This was reflected by the combining ability data, gains over the benchmarks and commercial hybrids especially under disease stress at Cedara. Selection for ear prolificacy will be emphasized to improve grain yield of the hybrids that can be developed from this inbred population.

References

- Abadassi, J. (2015). Maize Agronomic Traits Needed in Tropical Zone. *International Journal of Science, Environment and Technology*, 4:2 371-392.
- Abady, S., Merkeb, F., Dilnesaw, Z. (2013). Heritability and path-coefficient analysis in soybean (*Glycine Max* L. Merrill) genotypes at Pawe, North Western Ethiopia. *Journal of Environmental Science and Water Resources*, 2:8 270-276.
- Abrha S.W., Zeleke H.Z., Gissa D.W. (2013). Line x tester analysis of maize inbred lines for grain yield and yield related traits. *Asian Journal of Plant Science Research* 3:5 12-19.
- Acquaah, G. (2007). *Principles of plant breeding and genetics*. Carlton, Australia: Blackwell, Malden, MA.
- Adebo, F. A., Olaoye, G. (2010). Growth indices and grain yield attributes in six maize cultivars representing two era of maize breeding in Nigeria. *Journal of Agricultural Science*, 2:3 218-228.
- Aguiar, C. G., Schuster, I., Amaral Júnior, A. T. d., Scapim, C. A., Vieira, E. S. N. (2008). Heterotic groups in tropical maize germplasm by test crosses and simple sequence repeat markers. *Genetics and Molecular Research*, 7:4 1233-1244.
- Akçura, M., Taner, S., Kaya, Y. (2011). Evaluation of bread wheat genotypes under irrigated multi-environment conditions using GGE biplot analyses. *Agriculture*, 98:1 35-40.
- Akinwale, M. G., Gregorio, G., Nwilene, F., Akinyele, B. O., Ogunbayo, S. A., Odiyi, A. C. (2011). Heritability and correlation coefficient analysis for yield and its components in rice (*Oryza sativa* L.). *African Journal of plant science*, 5:3 207-212.
- Al-Naggar, A. M. M., Shabana, R., Rabie, A. M. (2011). Per se performance and combining ability of 55 new maize inbred lines developed for tolerance to high plant density. *Egyptian Journal of Plant Breeding*, 15:5 59-84.

- Alan, Ö., Kinaci, G., Kinaci, E., Kutlu, I., Basciftci, Z. B., Sonmez, K., Evrenosoglu, Y. (2013). Genetic Variability and Association Analysis of Some Quantitative Characters in Sweet Corn. *Notulae Botanicae Horti Agrobotanici Cluj-Napoca*, 41:2 404-413.
- Alberts, M. J. A. (2004). A comparison of statistical methods to describe genotype x environment interaction and yield stability in multi-location maize trials. Doctoral Thesis, University of The Free State, Bloemfontein, South Africa.
- Ali, A., Khan, A. S., Assad, M. A. (2002). Drought tolerance in wheat: Genetic variation and heritability for growth and ion relations. *Asian Journal of Plant Science*, 1:4 420-422.
- Ali, Q., Ali, A., Awan, M. F., Tariq, M., Ali, S., Samiullah, T. R., Azam S., Din S., Ahmad M., Sharif, N. M. (2014). Combining ability analysis for various physiological, grain yield and quality traits of *Zea mays* L. *Life Science Journal*, 11:8 540-551.
- Almeida, G. D., Makumbi, D., Magorokosho, C., Nair, S., Borém, A., Ribaut, J. M., Bänziger M., Prasanna B.M., Crossa J., Babu, R. (2013). QTL mapping in three tropical maize populations reveals a set of constitutive and adaptive genomic regions for drought tolerance. *Theoretical and Applied Genetics*, 126:3 583-600.
- Aly, R. S., Metwali, E. M. R., Mousa, S. T. M. (2011). Combining ability of maize (*Zea mays* L.) inbred lines for grain yield and some agronomic traits using top cross mating design. *Global Journal of Molecular Science*, 6 01-08.
- Aly, R. S. H. (2013). Relationship between combining ability of grain yield and yield components for some newly yellow maize inbred lines via line x tester analysis. *Alexandria Journal Agriculture Research*, 58:2 115-124.
- Amiruzzaman, M., Islam, M. A., Pixley, K. V., Rohman, M. M. (2011). Heterosis and combining ability of CIMMYT's tropical × subtropical quality protein maize germplasm. *International Journal of Sustainable Agriculture*, 3:3 76-81.

- Araus, J. L., Slafer, G. A., Reynolds, M. P., Royo, C. (2002). Plant Breeding and Drought in C3 Cereals: What Should We Breed For? *Annals of Botany*, 89:7 925-940.
- Agricultural Research Council (ARC). (2015). Data generated from on-farm weather station at Cedara, KwaZulu Natal, South Africa.
- Arulselvi, S., Selvi, B. (2010). Grain yield stability of single cross maize (*Zea mays* L.) hybrids over three different environments. *Electronic Journal of Plant Breeding*, 1:4 577-584.
- Asghar, M. J., Mehdi, S. S. (2010). Selection indices for yield and quality traits in sweet corn. *Pakistan Journal of Botany*, 42:2 775-789.
- Augustina, U. A., Iwunor, O. P., Ijeoma, O. R. (2013). Heritability and character correlation among some rice genotypes for yield and yield components. *Journal of Plant Breeding and Genetics*, 1:2 73-84.
- Babić, V. B., Babić, M. M., Ivanović, M. R., Filipović, M. R. (2011). Pattern in interaction in the maize yield trial. *Journal of Agricultural Sciences, Belgrade*, 56:2 101-110.
- Badu-Apraku, B., Akinwale, R. O. (2011). Cultivar evaluation and trait analysis of tropical early maturing maize under *Striga*-infested and *Striga*-free environments. *Field Crops Research*, 121:1 186-194.
- Badu-Apraku, B., Fakorede, M. A., Oyekunle, M. (2014). Agronomic traits associated with genetic gains in maize yield during three breeding eras in West Africa. *Maydica*, 59:1 49-57.
- Badu-Apraku, B., Oyekunle, M. (2012). Genetic analysis of grain yield and other traits of extra-early yellow maize inbreds and hybrid performance under contrasting environments. *Field Crops Research*, 129 99-110.
- Bagheri, N., Jelodar, N. B. (2010). Heterosis and combining ability analysis for yield and related-yield traits in hybrid rice. *International Journal of Biology*, 2:2 222-232.

- Bänziger, M., Edmeades, G. O., Lafitte, H. R. (1999). Selection for drought tolerance increases maize yields across a range of nitrogen levels. *Crop Science*, 39:4 1035-1040.
- Barker, T., Campos, H., Cooper, M., Dolan, D., Edmeades, G., Habben, J., Schussler, J., Wright, D., Zinselmeier, C. (2005). Improving drought tolerance in maize. *Plant Breeding Reviews*, 25 173-253.
- Basnayake, J., Jackson, P. A., Inman-Bamber, N. G., Lakshmanan, P. (2012). Sugarcane for water-limited environments. Genetic variation in cane yield and sugar content in response to water stress. *Journal of Experimental Botany*, 63:16 6023-6033.
- Begna, S. H., Hamilton, R. I., Dwyer, L. M., Stewart, D. W., Cloutier, D., Assemat, L., Foroutan-Pour K., Smith, D. (2001). Morphology and yield response to weed pressure by corn hybrids differing in canopy architecture. *European Journal of Agronomy*, 14:4 293-302.
- Beiragi, M. A., Ebrahimi, M., Mostafavi, K., Golbashy, M., Khorasani, S. K. (2011). A study of morphological basis of corn (*Zea mays* L.) yield under drought stress condition using correlation and path coefficient analysis. *Journal of Cereals and Oilseeds*, 2:2 32-37.
- Bekavac, G., Purar, B., Stojaković, M., Jocković, D., Ivanović, M., Nastasić, A. (2007). Genetic analysis of stay-green trait in broad-based maize populations. *Cereal Research Communications*, 35:1 31-41.
- Bekavac, G., Stojaković, M., Jocković, D., Boćanski, J., Purar, B. (1998). Path analysis of stay-green trait in maize. *Cereal Research Communications*, 26:2 161-167.
- Bello, O. B., Abdulmalik, S. Y., Afolabi, M. S., Ige, S. A. (2010). Correlation and path coefficient analysis of yield and agronomic characters among open pollinated maize

- varieties and their F₁ hybrids in a diallel cross. *African Journal of Biotechnology*, 9:18 2633-2639.
- Bello, O. B., Ige, S. A., Azeez, M. A., Afolabi, M. S., Abdulmalik, S. Y., Mahamood, J. (2012). Heritability and genetic advance for grain yield and its component characters in maize (*Zea mays* L.). *International Journal of Plant Research*, 2:5 138-145.
- Bello, O. B., Olaoye, G. (2009). Combining ability for maize grain yield and other agronomic characters in a typical southern guinea savanna ecology of Nigeria. *African Journal of Biotechnology*, 8:11 2518-2522.
- Bello, O. B., Olawuyi, O. J., Lawal, M., Ige, S. A., Mahamood, J., Afolabi, M. S., Azeez M.A., Abdulmalik, S. Y. (2014). Genetic gains in three breeding eras of maize hybrids under low and optimum nitrogen fertilization. *Journal of Agricultural Sciences, Belgrade*, 59:3 227-242.
- Betrán, F. J., Beck, D., Bänziger, M., Edmeades, G. O. (2003). Secondary traits in parental inbreds and hybrids under stress and non-stress environments in tropical maize. *Field Crops Research*, 83:1 51-65.
- Beyene, Y., Mugo, S., Gakunga, J., Karaya, H., Mutinda, C., Tefera, T., Njoka S., Chepkesis D., Shuma J.M., Tende, R. (2013). Combining ability of maize (*Zea mays* L.) inbred lines resistant to stem borers. *African Journal of Biotechnology*, 10:23 4759-4766.
- Beyene, Y., Semagn, K., Mugo, S., Tarekegne, A., Babu, R., Meisel, B., Sehabiague P., Makumbi D., Magorokosho C., Oikeh, S. (2015). Genetic gains in grain yield through genomic selection in eight bi-parental maize populations under drought stress. *Crop Science*, 55:1 154-163.
- Bizeti, H. S., Carvalho, C. G. P., Souza, J. R. P., Destro, D. (2004). Path analysis under multicollinearity in soybean. *Brazilian Archives of Biology and Technology*, 47:5 669-676.

- Bolaños, J., Edmeades, G. O. (1993). Eight cycles of selection for drought tolerance in lowland tropical maize. II. Responses in reproductive behavior. *Field Crops Research*, 31:3 253-268.
- Bonaparte, E. E. N. A. (1975). The Effects of Temperature, Day length, Soil Fertility and Soil Moisture on Leaf Number and Duration to Tassel Emergence in *Zea mays* L. *Annals of Botany*, 39:4 853-861.
- Bose, L. K., Jambhulkar, N. N., Singh, O. N. (2014). Additive Main Effects and Multiplicative Interaction (AMMI) Analysis of Grain Yield Stability in Early Duration Rice. *Journal of Animal and Plant Sciences*, 24:6 1885-1897.
- Brancourt-Hulmel, M., Heumez, E., Pluchard, P., Beghin, D., Depatureaux, C., Giraud, A., Le Gouis, J. (2005). Indirect versus direct selection of winter wheat for low-input or high-input levels. *Crop Science*, 45:4 1427-1431.
- Breseghello, F., & Coelho, A. S. G. (2013). Traditional and modern plant breeding methods with examples in rice (*Oryza sativa* L.). *Journal of Agricultural and Food Chemistry*, 61:35 8277-8286.
- Burton, G. W., Devane, E. H. (1953). Estimating heritability in tall fescue (*Festuca arundinacea*) from replicated clonal material. *Agronomy Journal*, 45:10 478-481.
- Cairns, J. E., Hellin, J., Sonder, K., Araus, J. L., MacRobert, J. F., Thierfelder, C., Prasanna, B. M. (2013). Adapting maize production to climate change in sub-Saharan Africa. *Food Security*, 5:3 345-360.
- Çakir, R. (2004). Effect of water stress at different development stages on vegetative and reproductive growth of corn. *Field Crops Research*, 89:1 1-16.
- Callister, A. N., England, N., & Collins, S. (2013). Predicted genetic gain and realised gain in stand volume of *Eucalyptus globulus*. *Tree Genetics and Genomes*, 9:2 361-375.

- Campos, H., Cooper, M., Habben, J. E., Edmeades, G. O., Schussler, J. R. (2004). Improving drought tolerance in maize: a view from industry. *Field Crops Research*, 90:1 19-34.
- Candido, L. S., & da Costa Andrade, J. A. (2008). Breeding potential of maize composite Isanão VF1 in small spacing in the second growing season. *Crop Breeding and Applied Technology*, 8:1 56-64.
- Ceyhan, E., Avci, M. A., Karadas, S. (2008). Line X tester analysis in pea (*Pisum sativum* L.): Identification of superior parents for seed yield and its components. *African Journal of Biotechnology*, 7:16 2810-2817.
- Ci, X., Li, M., Liang, X., Xie, Z., Zhang, D., Li, Lu Z., Ru G., Bai L., Xie C., Hao Z., Zhang, S. (2011). Genetic Contribution to Advanced Yield for Maize Hybrids Released from 1970 to 2000 in China. *Crop Science*, 51:1 13-20.
- Cramer, C. S., & Wehner, T. C. (2000). Path analysis of the correlation between fruit number and plant traits of cucumber populations. *HortScience*, 35:4 708-711.
- Crossa, J. (1990). Statistical analyses of multilocation trials. *Advances in Agronomy*, 44 55-85.
- Dabholkar, A. R. (1999). *Elements of Bio Metrical Genetics* (Revised and Enlarged ed.) Concept publishing company, New Delhi, India.
- Darbeshwar, R. (2000). *Plant Breeding—Analysis and Exploitation of Variation*. Narosa, New Delhi.
- Dawson, J. C., Murphy, K. M., Jones, S. S. (2008). Decentralized selection and participatory approaches in plant breeding for low-input systems. *Euphytica*, 160:2 143-154.
- De La Fuente, G. N., Frei, U. K., Lübberstedt, T. (2013). Accelerating plant breeding. *Trends in Plant Science*, 18:12 667-672.

- Dickert, T. E., Tracy, W. F. (2002). Heterosis for flowering time and agronomic traits among early open-pollinated sweet corn cultivars. *Journal of the American Society for Horticultural Science*, 127:5 793-797.
- Ding, M., Tier, B., Yan, W., Wu, H. X., Powell, M. B., McRae, T. A. (2007). Application of GGE biplot analysis to evaluate Genotype (G), Environment (E) and GxE interaction on *P. radiata*: a case study. Paper presented at the Australasian Forest Genetics Conference –Breeding for Wood Quality”, 11–14 April 2007, Hobart, Australia
- Dixit, N., Sharma, S., Marker, S. (2013). Studies on heritability and genetic advance estimates in Maize genotypes. *Bioscience Discovery: An International Journal of Life Sciences*, 4:2 165-168.
- Duvick, D. N. (2005a). The Contribution of Breeding to Yield Advances in maize (*Zea mays* L.). In L. S. Donald (Ed.), *Advances in agronomy*. Academic Press. 86 83-145
- Duvick, D. N. (2005b). Genetic progress in yield of United States maize (*Zea mays* L.). *Maydica*, 50:3/4 193-202.
- Duvick, D. N., Smith, J. S. C., Cooper, M. (2004). Long-term selection in a commercial hybrid maize breeding program. *Plant Breeding Reviews*, 24:2 109-152.
- Edmeades, G. O., Banziger, M., Mickelson, H. R., Pena-Valdivia, C. B. (1996). Developing Drought and Low N-tolerant Maize: Proceedings of a Symposium, 25-29 March, CIMMYT, El Batán, Mexico.
- Esmail, R. M. (2007). Detection of genetic components through triple test cross and line X tester analysis in bread wheat. *World Journal of Agricultural Science* 3:2 184-190.
- Fairbanks, D. H. K., Benn, G. A. (2000). Identifying regional landscapes for conservation planning: a case study from KwaZulu-Natal, South Africa. *Landscape and Urban planning*, 50:4 237-257.

- Food and Agriculture Organisation Statistics (FAOSTAT). (2014). Production of commodity in selected country. FAO Statistics Division <http://faostat3.fao.org/browse/Q/QC/E> (Accessed 10 February 2016)
- Farshadfar, E., Mohammadi, R., Aghaee, M., Vaisi, Z. (2012). GGE biplot analysis of genotype x environment interaction in wheat-barley disomic addition lines. *Australian Journal of Crop Science* 6:6 1074-1079.
- Filipenco, A., Mandache, V., Valsan, G., Ivan, F., Ciocazanu, I. (2013). Efficiency of Utilization of A selection Index in Assessment of Drydown of Corn Genotypes (*Zea mays* L.). *Scientific Papers-Series A, Agronomy*, 56 249-252.
- Gallais, A. (1988). Heterosis: its genetic basis and its utilisation in plant breeding. *Euphytica*, 39:2 95-104.
- Gasura, E., Setimela, P., Edema, R., Gibson, P. T., Okori, P., Tarekegne, A. (2013). Exploiting grain-filling rate and effective grain-filling duration to improve grain yield of early-maturing maize. *Crop Science*, 53:6 2295-2303.
- Gates, L. F., Mortimore, C. G. (1972). Effects of removal of groups of leaves on stalk rot and yield in corn. *Canadian Journal of Plant Science*, 52:6 929-935.
- Genter, C. F., Alexander, M. W. (1965). Testcross Variability of Samples from a Broad Base Population of Maize (*Zea mays* L.). *Crop Science*, 5:4 355-358.
- Govindaraj, M., Shanmugasundaram, P., Muthiah, A. R. (2010). Estimates of genetic parameters for yield and yield attributes in elite lines and popular cultivars of India's pearl millet. *African Journal of Agricultural Research*, 5:22 3060-3064.
- Gowda, M., Longin, C. F. H., Lein, V., Reif, J. C. (2012). Relevance of specific versus general combining ability in winter wheat. *Crop Science*, 52:6 2494-2500.
- Griffing, B. (1956). Concept of general and specific combining ability in relation to diallel crossing systems. *Australian Journal of Biological Sciences*, 9:4 463-493.

- Güler, M., Adak, M. S., Ulukan, H. (2001). Determining relationships among yield and some yield components using path coefficient analysis in chickpea (*Cicer arietinum* L.). *European Journal of Agronomy*, 14:2 161-166.
- Hallauer, A. R., Miranda, J. B. (1988). *Quantitative genetics in maize breeding*. Springer-Verlag New York, New York, USA.
- Hazel, L. N., Lush, J. L. (1942). The efficiency of three methods of selection. *Journal of Heredity*, 33:11 393-399.
- Hefny, M. (2011). Genetic parameters and path analysis of yield and its components in corn inbred lines (*Zea mays* L.) at different sowing dates. *Asian Journal of Crop Science*, 3:3 106-117.
- Hoecker, N., Keller, B., Muthreich, N., Chollet, D., Descombes, P., Piepho, H. P., Hochholdinger, F. (2008). Comparison of maize (*Zea mays* L.) F₁-hybrid and parental inbred line primary root transcriptomes suggests organ-specific patterns of non-additive gene expression and conserved expression trends. *Genetics*, 179:3 1275-1283.
- Horrock, R. D., Zuber, M. S. (1970). Corn Shelling percentage studies. *Research Bulletin*, Agricultural Experiment Station, Missouri University, 35
- Hosana, C., Alamerew, S., Tadesse, B., Menamo, T. (2015). Test Cross Performance and Combining Ability of Maize (*Zea Mays* L.) Inbred Lines at Bako, Western Ethiopia. *Global Journal of Science Frontier Research*, 15:4 1-25.
- Huehn, M. (1990). Nonparametric measures of phenotypic stability. Part 1: Theory. *Euphytica*, 47:3 189-194.
- Issa, A. B. (2009). Genotype by Environment Interaction and yield stability of maize hybrids evaluated in Ethiopia. Doctoral Thesis, University of the Free State, Bloemfontein, South Africa.

- Jacobson, A., Lian, L., Zhong, S., Bernardo, R. (2014). General combining ability model for genomewide selection in a biparental cross. *Crop Science*, 54:3 895-905.
- Jebaraj, S., Selvakumar, A., Shanthi, P. (2010). Study of gene action in maize hybrids. *Indian Journal of Agricultural Research*, 44:2 136-140.
- Jensen, S. D. (1959). Combining ability of unselected inbred lines of corn from incomplete diallel and top-cross tests. Doctoral Thesis, Iowa State University, USA.
- Jiang, Y., Reif, J. C. (2015). Modeling epistasis in genomic selection. *Genetics*, 201:2 759-768.
- Jines, M. P. (2007). Enhancing genetic gain in maize with tropical germplasm, QTL mapping, and spatial methodologies. Doctoral Thesis, North Carolina University, USA.
- Johnson, E. C., Fischer, K. S., Edmeades, G. O., Palmer, A. F. E. (1986). Recurrent selection for reduced plant height in lowland tropical maize. *Crop Science*, 26:2 253-260
- Johnson, H. W., Robinson, H. F., Comstock, R. E. (1955). Estimates of genetic and environmental variability in soybeans. *Agronomy Journal*, 47:7 314-318.
- Kage, U., Wali, M. C., Madalageri, D., Natikar, P., Gangashetty, P. (2013). Gene action and heterosis study in hybrids derived from new inbred lines in maize (*Zea mays* L.). *Molecular Plant Breeding*, 4:18 146-149
- Kandus, M., Almorza, D., Boggio Ronceros, R., Salerno, J. C. (2010). Statistical models for evaluating the genotype-environment interaction in maize (*Zea mays* L.). *Phyton-Revista Internacional de Botanica Experimental*, 79 39-46
- Kashiani, P., Saleh, G. (2010). Estimation of genetic correlations on sweet corn inbred lines using SAS mixed model. *American Journal of Agricultural and Biological Sciences*, 5:3 309-314

- Kaushik, L. S., Singh, D. P., Paroda, R. S. (1984). Line x tester analysis for fixed effect model in cotton (*Gossypium hirsutum* L.). Theoretical and Applied Genetics, 68:6 487-491.
- Kempthorne, O. (1957). An introduction to genetic statistics. Wiley and Sons, Oxford, England
- Kempthorne, O., Curnow, R. N. (1961). The partial diallel cross. Biometrics, 17:2 229-250.
- Khalil, I. H., Shah, S. M. A., Ahmad, H. (2010). Stability analysis of maize hybrids across North West of Pakistan. Pakistan Journal of Botany, 42:2 1083-1091.
- Khazaei, F., Alikhani, M. A., Yari, L., Khandan, A. (2010). Study the correlation, regression and path coefficient analysis in sweet corn (*Zea mays* var. *saccharata*) under different levels of plant density and nitrogen rate. ARPN Journal of Agricultural Biological Science, 5:6 14-10.
- Khotyleva, L. V., Trutina, L. A. (1973). A study of comparative stability of additive and non-additive gene action in different environmental conditions. Plant Breeding Abstracts, 43 86
- Koch, E., Bruns, E., Chmielewski, F. M., Defila, C., Lipa, W., Menzel, A. (2007). Guidelines for plant phenological observations. World Climate Data and Monitoring Programme. file:///C:/Users/214550352/Downloads/guidelines-ges-fin_2%20(1).pdf (Accessed 10 February 2016)
- KwaZulu-Natal Department of Agriculture and Rural Development (KZNDARD). (2015). Dundee Research Station.
<http://www.kzndae.gov.za/en-za/agriculture/researchandtechnologydevelopment/researchstations/dundeeresearchstation/aboutus.aspx> (Accessed 23 October 2015)

- Langyintuo, A. S., Diallo, W. M., MacRobert, A. O., Dixon, J., J Banziger, M. (2008). An analysis of the bottlenecks affecting the production and deployment of maize seed in Eastern and Southern Africa: CIMMYT, Harare, Zimbabwe.
- Lauer, J. (2002). Methods for calculating corn yield. *Field Crops* 28 47-33.
<http://corn.agronomy.wisc.edu>
- Lin, C. S., Binns, M. R. (1988). A superiority measure of cultivar performance for cultivar \times location data. *Canadian Journal of Plant Science*, 68:1 193-198.
- Linden, D. R., Clapp, C. E., Dowdy, R. H. (2000). Long-term corn grain and stover yields as a function of tillage and residue removal in east central Minnesota. *Soil and Tillage Research*, 56:3 167-174.
- Longin, C. F. H., Mühleisen, J., Maurer, H. P., Zhang, H., Gowda, M., Reif, J. C. (2012). Hybrid breeding in autogamous cereals. *Theoretical and Applied Genetics*, 125:6 1087-1096.
- Machikowa, T., Laosuwan, P. (2011). Path coefficient analysis for yield of early maturing soybean. *Sonklanakarin Journal of Science and Technology*, 33:4 365-368.
- Maenhout, S., De Baets, B., Haesaert, G. (2010). Prediction of maize single-cross hybrid performance: support vector machine regression versus best linear prediction. *Theoretical and Applied Genetics*, 120:2 415-427.
- Mafu, N. F. (2013). Marker-assisted selection for maize streak virus resistance and concomitant conventional selection for downy mildew resistance in a maize population. Masters' Thesis, KwaZulu-Natal, Pietermaritzburg, South Africa.
- Magorokosho, C., Tongoona, P. (2004). Selection for drought tolerance in two tropical maize populations. *African Crop Science Journal*, 11:3 151-161.

- Magorokosho, C., Vivek, B., MacRobert, J. (2009). Characterization of maize germplasm grown in Eastern and Southern Africa: Results of the 2008 regional trials coordinated by CIMMYT. CIMMYT, Harare, Zimbabwe
- Mahmood, Z., Malik, S. R., Akhtar, R., Rafique, T. (2004). Heritability and genetic advance estimates from maize genotypes in Shishi Lusht a valley of Krakurm. International Journal of Agricultural Biology, 6:5 790-791.
- Makumbi, D., Betrán, J. F., Bänziger, M., Ribaut, J. M. (2011). Combining ability, heterosis and genetic diversity in tropical maize (*Zea mays* L.) under stress and non-stress conditions. Euphytica, 180:2 143-162.
- Mallikarjuna, N. M., Haradari, C., Shashibhaskar, M. S., Prahalada, G. D. (2011). Genetic variability and correlation studies for yield and related characters in single cross hybrids of maize (*Zea mays* L.). Current Biotica, 5:2 157-163.
- Manggoel, W., Uguru, M. I., Ndam, O. N., Dasbak, M. A. (2012). Genetic variability, correlation and path coefficient analysis of some yield components of ten cowpea (*Vigna unguiculata* L. Walp) accessions. Journal of Plant Breeding and Crop Science, 4:5 80-86.
- Marinković, R., Škorić, D., Dozet, B., Jovanović, D. (2000). Line x tester analysis of the combining ability in sunflower (*H. annuus* L.). Paper presented at the Proceedings of 15th International Sunflower Conference, 12-15 June, Toulouse, France.
- Melchinger, A. E., Piepho, H., Utz, H. F., Muminović, J., Wegenast, T., Törjék, O., Kusterer, B. (2007). Genetic basis of heterosis for growth-related traits in *Arabidopsis* investigated by testcross progenies of near-isogenic lines reveals a significant role of epistasis. Genetics, 177:3 1827-1837.

- Mendel, G. (1997). Father of Genetics. Great Minds of Science. Enslow Publishers, 128.
http://www.nkec.ednet.ns.ca/staffpages/JenniferOsmond/AP_Bio/chapter_notes/mendelian_web.pdf
- Meng, Q., Hou, P., Wu, L., Chen, X., Cui, Z., Zhang, F. (2013). Understanding production potentials and yield gaps in intensive maize production in China. *Field Crops Research*, 143 91-97.
- Mitroviã, B., Treski, S., Stojakoviã, M., Ivanoviã, M., Bekavac, G. (2012). Evaluation of experimental maize hybrids tested in multi-location trials using AMMI and GGE biplot analyses. *Turkish Journal of Field Crops*, 17:1 35-40.
- Mohammadi, A. A., Saeidi, G., Arzani, A. (2010). Genetic analysis of some agronomic traits in flax (*Linum usitatissimum* L.). *Australian Journal of Crop Science*, 4:5 343-352.
- Mohammadi, S. A., Prasanna, B. M., Singh, N. N. (2003). Sequential path model for determining interrelationships among grain yield and related characters in maize. *Crop Science*, 43:5 1690-1697.
- Motamedi, M., Choukan, R., Hervan, E. M., Bihamta, M. R., Kajouri, F. D. (2014). Investigation of genetic control for yield and related traits in maize (*Zea mays* L.) lines derived from temperate and sub-tropical germplasm. *International Journal of Biosciences*, 5:12 123-129.
- Munyiri, S. W., Pathak, R. S., Tabu, I. M., Gemenet, D. C. (2010). Effects of moisture stress at flowering on phenotypic characters of selected local maize landraces in Kenya. *Journal of Animal and Plant Sciences*, 8:1 892-899.
- Muoni, T., Rusinamhodzi, L., Thierfelder, C. (2013). Weed control in conservation agriculture systems of Zimbabwe: Identifying economical best strategies. *Crop Protection*, 53 23-28.

- Musundire, L. (2013). Genetic and economic value of a shuttle breeding programme for enhancing adaptability of tropical maize germplasm in South Africa. Doctoral Thesis, University of KwaZulu-Natal, Pietermaritzburg, South Africa.
- Nadagoud, V. K., Jagadeesha, R. C. (2008). Stability analysis of maize (*Zea mays* L.) inbred lines/introductions for yield parameters. Masters' Thesis, University of Agricultural Sciences, Dharwad, India.
- Noor, M., Durrishahwar, H., Ullah, H., Ali, F., Iqbal, M., Shah, I. A., Ullah, I. (2013). Change in heritability estimates due to half-sib family selection in the maize variety Pahari. *Genetics and Molecular Research*, 12:2 1872-1881.
- NUE-Web. (2016). World Wheat , Maize (Corn) and Rice. Oklahoma State University http://nue.okstate.edu/Crop_Information/World_Wheat_Production.htm (Accessed 10 February 2016).
- Nzuve, F., Githiri, S., Mukunya, D. M., Gethi, J. (2013). Analysis of genotype x environment interaction for grain yield in maize hybrids. *Journal of Agricultural Science*, 5:11 75-85.
- Nzuve, F., Githiri, S., Mukunya, D. M., & Gethi, J. (2014). Genetic variability and correlation studies of grain yield and related agronomic traits in maize. *Journal of Agricultural Science*, 6:9 166-176.
- Ojo, D. K., Omikunle, O. A., Oduwaye, O. A., Ajala, M. O., Ogunbayo, S. A. (2006). Heritability, character correlation and path coefficient analysis among six inbred-lines of maize (*Zea mays* L.). *World Journal of Agricultural Science*, 2:3 352-358.
- Ortiz, R., Taba, S., Tovar, V. H. C., Mezzalama, M., Xu, Y., Yan, J., Crouch, J. H. (2010). Conserving and enhancing maize genetic resources as global public goods—a perspective from CIMMYT. *Crop Science*, 50:1 13-28.

- Osaki, M. (1995). Comparison of productivity between tropical and temperate maize: I. Leaf senescence and productivity in relation to nitrogen nutrition. *Soil Science and Plant Nutrition*, 41:3 439-450.
- Pandey, P., Anurag, P. J., Tiwari, D. K., Yadav, S., Kumar, B. (2009). Genetic variability, diversity and association of quantitative traits with grain yield in rice (*Oryza sativa* L.). *Journal of Bio-Science*, 17 77-82.
- Pandey, R. K., Maranville, J. W., Admou, A. (2000). Deficit irrigation and nitrogen effects on maize in a Sahelian environment: I. Grain yield and yield components. *Agricultural Water Management*, 46:1 1-13.
- Pataky, J. K. (1992). Relationships between yield of sweet corn and northern leaf blight caused by *Exserohilum turcicum*. *Phytopathology*, 82:3 370-375.
- Payne, R. W., Murray, D. A., Harding, S. A., Baird, D. B., Soutar, D. M. (2007). GenStat for windows introduction. VSN International, Hemel Hempstead, UK.
- Peng, Y., Gitelson, A. A., Keydan, G., Rundquist, D. C., Moses, W. (2011). Remote estimation of gross primary production in maize and support for a new paradigm based on total crop chlorophyll content. *Remote sensing of environment*, 115:4 978-989.
- Pidgeon, J. D., Ober, E. S., Qi, A., Clark, C. J. A., Royal, A., Jaggard, K. W. (2006). Using multi-environment sugar beet variety trials to screen for drought tolerance. *Field Crops Research*, 95:2-3 268-279.
- Pixley, K., Dhliwayo, T., Tongoona, P. (2006). Improvement of a maize population by full-sib selection alone versus full-sib with selection during inbreeding. *Crop Science*, 46:3 1130-1136.
- Pixley, K. V., Banziger, M. (2002). Open-pollinated maize varieties: a backward step or valuable option for farmers? *Integrated Approaches to Higher Maize Productivity in*

- the New Millennium. Paper presented at the 7th Proceedings of the Eastern and Southern Africa Regional Maize Conference. 5-11 February, Nairobi, Kenya.
- Pratt, R. C., Gordon, S. G. (2006). Breeding for resistance to maize foliar pathogens. Plant Breeding Reviews, 27, (ed. Janick, J.), John Wiley & Sons, Inc., Oxford, UK.
- Rafiq, C. M., Rafique, M., Hussain, A., Altaf, M. (2010). Studies on heritability, correlation and path analysis in maize (*Zea mays* L.). Journal of Agricultural Research, 48:1 35-38.
- Rahmani, A., Alhossini, M. N., Kalat, S. M. N. (2015). Standard ear yield and some agronomic characteristics of baby corn var. ksc 403 su under influence of planting date and plant density. American Journal of Experimental Agriculture, 6:2 104-111.
- Rajcan, I., Tollenaar, M. (1999). Source: sink ratio and leaf senescence in maize: Dry matter accumulation and partitioning during grain filling. Field Crops Research, 60:3 245-253.
- Rawlings, J. O., Thompson, D. L. (1962). Performance level as criterion for the choice of maize testers. Crop Science, 2:3 217-220.
- Rieseberg, L. H., Archer, M. A., Wayne, R. K. (1999). Transgressive segregation, adaptation and speciation. Heredity, 83:4 363-372.
- Ruswandi, D., Supriatna, J., Waluyo, B., Makkulawu, A. T., Suryadi, E., Chindy, Z. U., Ruswandi, S. (2015). GGE biplot analysis for combining ability of grain yield and early maturity in maize mutant in Indonesia. Asian Journal of Crop Science 7:3 160-173.
- Sanghera, G. S., Hussain, W. (2012). Heterosis and combining ability estimates using line x tester analysis to develop rice hybrids for temperate conditions. Notulae Scientia Biologicae, 4:3 131-142.

- Sangoi, L. (2001). Understanding plant density effects on maize growth and development: an important issue to maximize grain yield. *Ciência Rural*, 31:1 159-168.
- Scapim, C. A., Oliveira, V. R., Cruz, C. D., Andrade, C. A. B., Vidigal, M. C. G. (2000). Yield stability in maize (*Zea mays* L.) and correlations among the parameters of the Eberhart and Russell, Lin and Binns and Huehn models. *Genetics and Molecular Biology*, 23:2 387-393.
- Selvaraj, C. I., Nagarajan, P. (2011). Interrelationship and path-coefficient studies for qualitative traits, grain yield and other yield attributes among maize (*Zea mays* L.). *International Journal of Plant Breeding and Genetics*, 5:3 209-223.
- Septiningsih, E., Prasetyono, J., Lubis, E., Tai, T., Tjubaryat, T., Moeljopawiro, S., McCouch, S. (2003). Identification of quantitative trait loci for yield and yield components in an advanced backcross population derived from the *Oryza sativa* variety IR64 and the wild relative *O. rufipogon*. *Theoretical and Applied Genetics*, 107:8 1419-1432.
- Setimela, P. S., Vivek, B., Bänziger, M., Crossa, J., Maiden, F. (2007). Evaluation of early to medium maturing open pollinated maize varieties in SADC region using GGE biplot based on the SREG model. *Field Crops Research*, 103:3 161-169.
- Shashidhara, C. K. (2008). Early generation testing for combining ability in maize (*Zea mays* L.). Masters' Thesis, University of Agricultural Sciences, Dharwad, India
- Shattuck, V. I., Christie, B., Corso, C. (1993). Principles for Griffing's combining ability analysis. *Genetica*, 90:1 73-77.
- Shiferaw, B., Prasanna, B. M., Hellin, J., Bänziger, M. (2011). Crops that feed the world 6. Past successes and future challenges to the role played by maize in global food security. *Food Security*, 3:3 307-327.

- Shimelis, H., Shiringani, R. (2010). Variance components and heritabilities of yield and agronomic traits among cowpea genotypes. *Euphytica*, 176:3 383-389.
- Sial, M. A., Arain, M. A., Ahmad, M. (2000). Genotype x environment interaction on bread wheat grown over multiple sites and years in Pakistan. *Pakistan Journal of Botany*, 32:1 85-92.
- Sibiya, J., Tongoona, P., Derera, J. (2013). Combining ability and GGE biplot analyses for resistance to northern leaf blight in tropical and subtropical elite maize inbred lines. *Euphytica*, 191:2 245-257.
- Sibiya, J., Tongoona, P., Derera, J., van Rij, N., Makanda, I. (2011). Combining ability analysis for *Phaeosphaeria* leaf spot resistance and grain yield in tropical advanced maize inbred lines. *Field Crops Research*, 120:1 86-93.
- Singh, R. K., & Chaudhary, B. D. (1979). Biometrical methods in quantitative genetic analysis. Kalyani, New Dehli, India
- Sleper, D. A., Poehlman, J. M. (2006). Breeding field crops. Blackwell publishing. Oxford, UK.
- Smalley, M. D., Daub, J. L., Hallauer, A. R. (2004). Estimation of heritability in maize by parent-offspring regression. *Maydica*, 49 221-229.
- Souza, A. R. R., Miranda, G. V., Pereira, M. G., Souza, L. V. d. (2009). Predicting the genetic gain in the Brazilian white maize landrace. *Ciência Rural*, 39:1 19-24.
- Sposaro, M. M., Chimenti, C. A., Hall, A. J. (2008). Root lodging in sunflower. Variations in anchorage strength across genotypes, soil types, crop population densities and crop developmental stages. *Field Crops Research*, 106:2 179-186.
- Sreckov, Z., Nastasic, A., Bocanski, J., Djalovic, I., Vukosavljev, M., Jockovic, B. (2011). Correlation and path analysis of grain yield and morphological traits in test-cross populations of maize. *Pakistan Journal of Botany*, 43:3 1729-1731.

- Svečnjak, Z., Varga, B., Butorac, J. (2006). Yield components of apical and sub-apical ear contributing to the grain yield responses of prolific maize at high and low plant populations. *Journal of Agronomy and Crop Science*, 192:1 37-42.
- Tokatlidis, I. S., Koutsika-Sotiriou, M., Tamoutsidis, E. (2005). Benefits from using maize density-independent hybrids. *Maydica*, 50:1 9-17.
- Tonk, F. A., Ilker, E., Tosun, M. (2011). Evaluation of genotype x environment interactions in maize hybrids using GGE biplot analysis. *Crop Breeding and Applied Biotechnology*, 11:1 01-09.
- Townsend, T., Segura, V., Chigeza, G., Penfield, T., Rae, A., Harvey, D., Bowles D., Graham, I. A. (2013). The use of combining ability analysis to identify elite parents for *Artemisia annua* F₁ hybrid production. *PloS one*, 8:4 1-11
- Tsimba, R. (2011). Development of a decision support system to determine the best maize (*Zea mays*. L) hybrid-planting date option under typical New Zealand management systems. Doctoral Thesis, Massey University, Palmerston North, New Zealand.
- Tsimba, R., Edmeades, G. O., Millner, J. P., Kemp, P. D. (2013). The effect of planting date on maize grain yields and yield components. *Field Crops Research*, 150 135-144.
- Uddin, M. S., Khatun, F., Ahmed, S., Ali, M. R., Bagum, S. A. (2006). Heterosis and combining ability in corn (*Zea mays* L.). *Bangladesh Journal of Botany*, 35:2 109-116.
- Udensi, O., Ikpeme, E. V. (2012). Correlation and path coefficient analyses of seed yield and its contributing traits in *Cajanus cajan* (L.) Millsp. *American Journal of Experimental Agriculture*, 2:3 351-358.
- Ullah, K., Noor, M., Iqbal, M. (2013). Heritability estimates and yield performance of half sib families derived from maize variety Sarhad White. *Sarhad Journal of Agriculture*, 29:1 29-32.

- Van Schalkwyk, A. P., Gertenbach, W. D. (2000). The effect of closing date on the performance of beef weaners grazing foggaged *Digitaria eriantha* and *Acroceras macrum*. South African Journal of Animal Science, 30:1 82-86.
- Viana, J. M. S. (2007). Breeding strategies for recurrent selection of maize. Pesquisa Agropecuária Brasileira, 42:10 1383-1391.
- WeatherUnderground (2015). Newcastle Historical Weather Data.
http://www.wunderground.com/history/wmo/68377/2015/6/3/MonthlyHistory.html?req_city=Newcastle&req_state=&req_statename=South+Africa&reqdb.zip
 (Accessed 3 November 2015).
- Xu, N., Fok, M., Zhang, G., Jian, L., Zhou, Z. (2014). The application of GGE biplot analysis for evaluating test locations and mega-environment investigation of cotton regional trials. Journal of Integrative Agriculture, 13:9 1921-1933.
- Xu, W., Subudhi, P. K., Crasta, O. R., Rosenow, D. T., Mullet, J. E., Nguyen, H. T. (2000). Molecular mapping of QTLs conferring stay-green in grain sorghum (*Sorghum bicolor* L. Moench). Genome, 43:3 461-469.
- Yalçın, K. (2005). Determining combining ability in sunflower (*Helianthus annuus* L.). Turkish Journal of Agriculture and Forestry, 29:4 243-250.
- Yan, W., Tinker, N. A. (2006). Biplot analysis of multi-environment trial data: Principles and applications. Canadian Journal of Plant Science, 86:3 623-645.
- Zaidi, P. H., Maniselvan, P., Sultana, R., Yadav, M., Singh, R. P., Singh, S. B., Dass S., Srinivasan, G. (2007). Importance of secondary traits in improvement of maize (*Zea mays* L.) for enhancing tolerance to excessive soil moisture stress. Cereal Research Communications, 35:3 1427-1435.

- Zuber, U., Winzeler, H., Messmer, M. M., Keller, M., Keller, B., Schmid, J. E., Stamp, P. (1999). Morphological traits associated with lodging resistance of spring wheat (*Triticum aestivum* L.). Journal of Agronomy and Crop Science, 182:1 17-24.
- Zuk, O., Hechter, E., Sunyaev, S. R., Lander, E. S. (2012). The mystery of missing heritability: Genetic interactions create phantom heritability. Proceedings of the National Academy of Sciences. 109:4 1193-1198.