

# **WHY SR52 IS SUCH A GREAT MAIZE HYBRID**

by

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**The Great maize hybrid SR52 and its inbred line parents SC and N3**

*The first single cross maize hybrid to be commercialized in the world represents Zimbabwe's contribution to global knowledge and food security*



## GENERAL ABSTRACT

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Maize is Africa's most important food crop. Unfortunately a yield gap currently exists in Africa which can be attributed to the use of inferior maize varieties such as open-pollinated varieties, double and three-way cross hybrids. Single cross maize hybrids, such as the world's first commercial hybrid, SR52, have a higher yield potential, which is reflected by the doubling of maize yields in southern and eastern Africa by SR52, within a decade of its release. The main objective of this study was to determine the genetic basis behind SR52's high yield potential and heterosis. This was established through a generation mean and path coefficient analysis of the SR52 maize hybrid.

Research to determine genetic basis of yield and secondary trait was conducted using a randomized complete block design at two sites during the 2012/13 season, in South Africa. Six derivative generations of SR52 namely, its two parents N3 and SC, F1 and F2, and F1 backcross progenies (BC1<sub>N3</sub> and BC1<sub>SC</sub>) were evaluated. A generation mean analysis was performed using PROC GLM procedures in SAS computer software program. High levels of mid-parent heterosis for grain yield potential was confirmed and ranged from 140% at Cedara to 311% at Ukulinga. The additive-dominance model was not adequate to explain the yield potential of SR52. Although negligible (less than 10%), epistatic gene effects were also influential ( $P < 0.01$ ) on grain yield and its components in SR52. The dominance and additive gene effects were highly significant ( $P < 0.01$ ), but dominance effects were the most influential. Correlation and path coefficient analysis of SR52's segregating F2 and BC1 populations was performed in SAS. Most secondary traits, such as ear mass, ear length, total number of kernels per ear and plant height, were significant ( $P < 0.05$ ) and positively correlated with yield. However, the ear length, number of kernel rows, kernels per row and 100-kernel mass displayed the largest direct effects on yield of SR52, while indirect effects of secondary traits were small. The presence of genetic variation, as well as transgressive segregants for the yield components indicates possibility for extracting new germplasm lines with the desired QTL's. It is concluded that SR52 is such an exceptional hybrid because of dominance gene action and direct contribution of superior cob length, number of kernel rows and mass of kernels to yield.

## DECLARATION

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I, Tatenda Rambli Musimwa, declare that:

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

.....  
Tatenda Rambli Musimwa

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

.....  
Professor John Derera

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## DEDICATION

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This work is dedicated to my parents, Herbert Musimwa and Catherine Musimwa nee Maboreke, my sisters Imelda, Mary, Mildred, Star and my brother Timothy. Not forgotten is my uncle Abel Maboreke whose passion to see me excel in whatever I did will forever drive me towards reaching my full potential.

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## LIST OF ABBREVIATIONS

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GYLD	grain yield
PHT	plant height
EHT	ear height
CHL	leaf chlorophyll concentration
DMP	days to initial pollen shed
DMS	days to silk emergence
LA	leaf area
NLV	number of leaves above primary ear
ELTH	ear length
EWT	ear mass
NRW	number of kernel rows on ear
MST	grain moisture content
HKWT	hundred kernel mass
TKRNL	total number of kernels on ear
KPRW	number of kernels on ear row
GRTH	ear girth
KDPTH	kernel depth
ASI	anthesis to silking interval

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## INTRODUCTION TO DISSERTATION

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### Importance of maize

Maize gives the highest total yield when compared to all cereal crops grown in the world (FAO, 2013). In terms of yield, maize is ranked as the number one cereal crop in the world, with the United States of America being the number one maize-producing country (Kynast, 2012). The crop is cultivated on 33.5 million hectares of land in Sub-Saharan Africa, with it accounting for 21% of the more than 116 million tons consumed in the world (FAO, 2013). Contrary to what happens in Sub-Saharan Africa 70% of maize in the developed world is utilised as stock feed (Dowsell *et al.*, 1996). In southern Africa where it is a staple food in most countries, maize contributes 30-70% of the total calorie consumption (FAO, 2013). Per capita consumption of maize is at its highest in southern Africa with levels of over 100kg/capita/year being realised in Lesotho, South Africa, Zambia and Zimbabwe (FAO, 2013). The importance of maize as a food crop in this region cannot be overstated (Smale *et al.*, 2013).

The popularity of maize as a food crop in Africa could be as a result of its ability to grow under varying conditions of temperature, altitude and fertility. Taking into consideration that maize gives one of the highest yields per man-hour of labour spent on it, it provides nutrients in a compact form and contains husks that give it protection against birds and rain. It explains why maize is one of Africa's top crop of choice (Pingali and Pandey, 2001; Purseglove, 1972). At a fluctuating average yield of 1.6  $\text{tha}^{-1}$ , maize yields in Sub-Saharan Africa remain low. Such yield is just enough for farmers to attain sufficiency in most areas in this part of the world (Cairns *et al.*, 2012). In Zimbabwe, where it is both a staple and cash crop, maize is the most important cereal crop. All the maize used for human consumption is white, with yellow maize only utilised as food during periods of drought (Rukuni *et al.*, 2006). Maize accounts for 80% of total cereal production in Zimbabwe and was grown on 0.96 million hectares in the 2011/2012 agricultural season, with a total yield of 1 million tons being realised (FAO, 2013).

The data in Figures 0.1 and 0.2 reveals that there is a gap between maize yields and population growth, worldwide. The rate at which the world's population was increasing prior to 2007 was greater than the rate at which maize production was rising. However, a fluctuating pattern is observed for maize yields, whereas the world's population keeps on rising steadily. In Zimbabwe, the discrepancies between population growth and maize production are huge, with Figure 0.2 indicating that maize yields are actually on the decline past the new millennium, as compared to the decade before. In order to close the yield gap that exist, plant breeders need to produce hybrid varieties that are high yielding, in order to improve food security particularly in developing countries such as Zimbabwe. The yield gap in Zimbabwe, as observed in Figure 0.2, could partly be explained by reversal of hybrid technology, as the country has shifted from growing single cross maize hybrids such as SR52 to three-way cross hybrids and even open pollinated varieties. From the late 1970s, Zimbabwe reversed the trend, while the USA moved up through extensive use of single crosses. In emphasising the importance of maize in the Zimbabwean economy, Figure 0.3 reveals that percentage GDP growth in the country is related to maize yield, as similar fluctuations take place between these two variables.

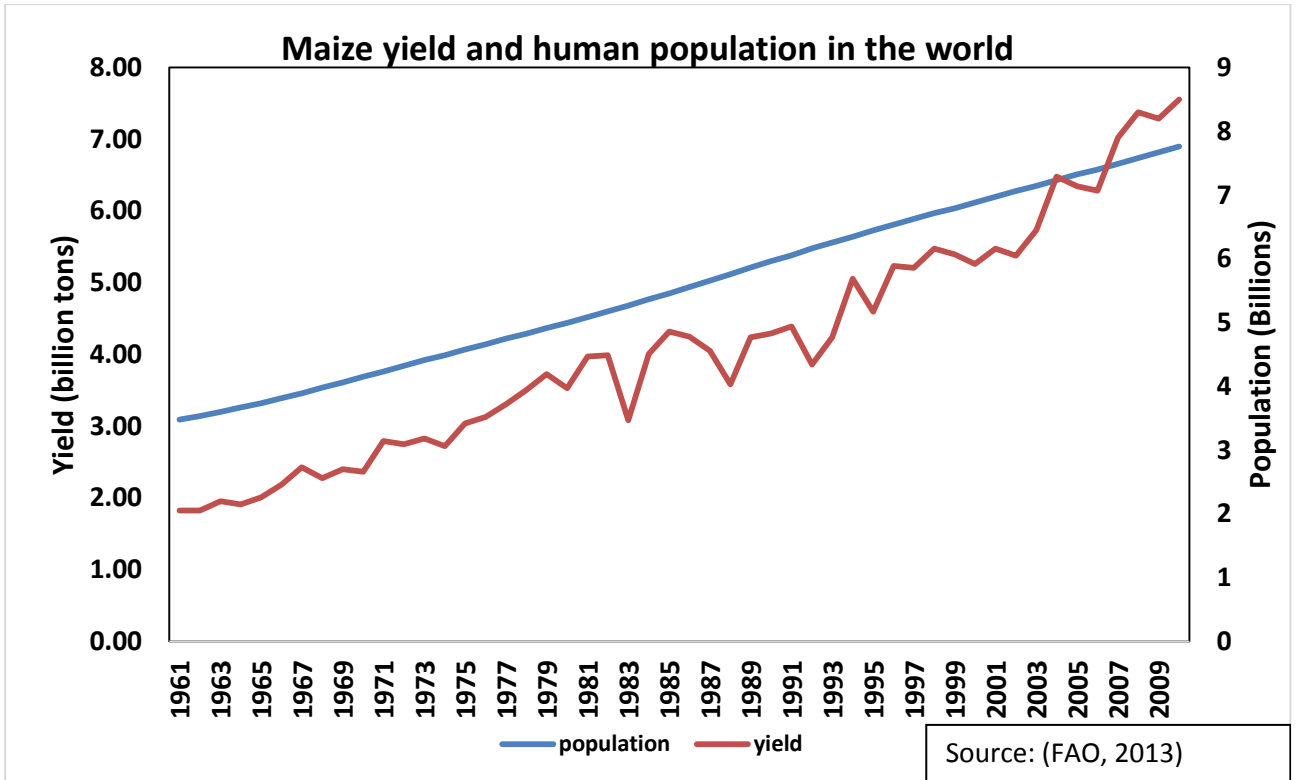


Figure 0.1: Total maize yield (tonnes) produced and human population in the world.

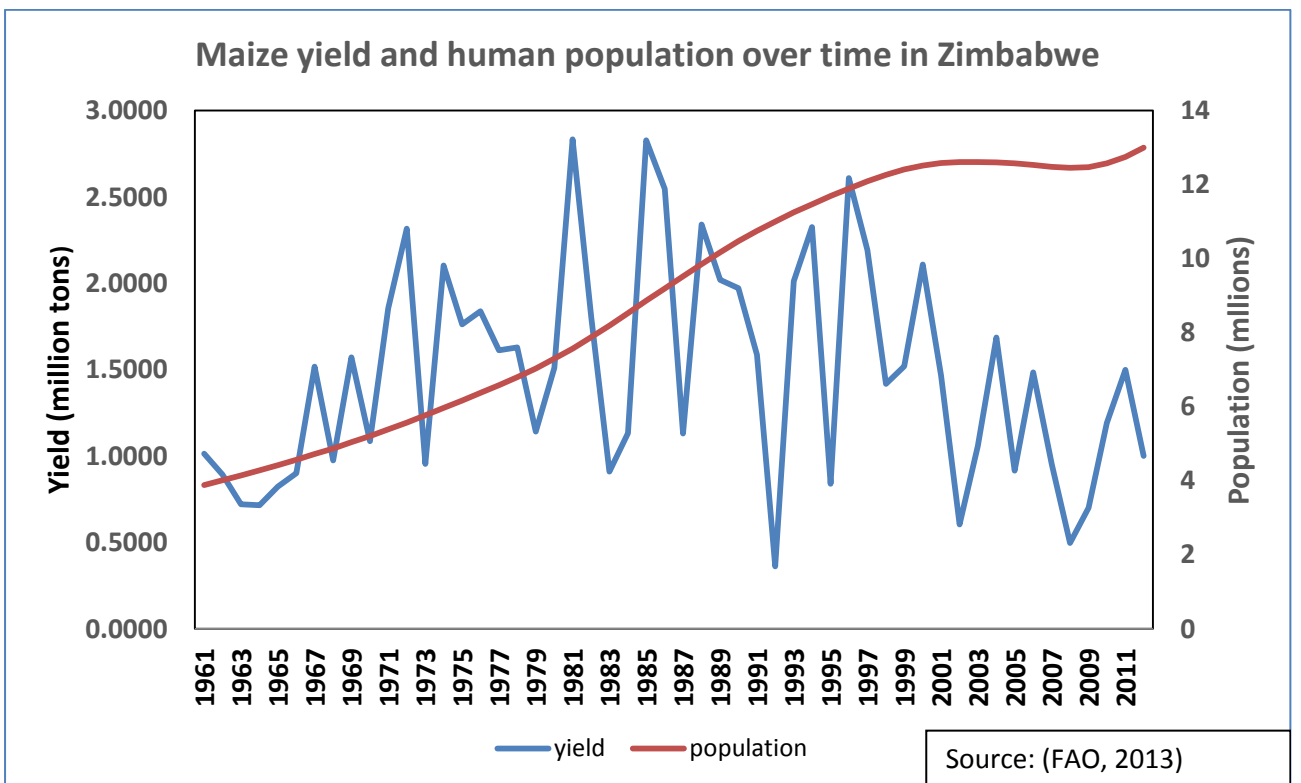


Figure 0.2: Total maize yield (tonnes) produced and human population over time in Zimbabwe



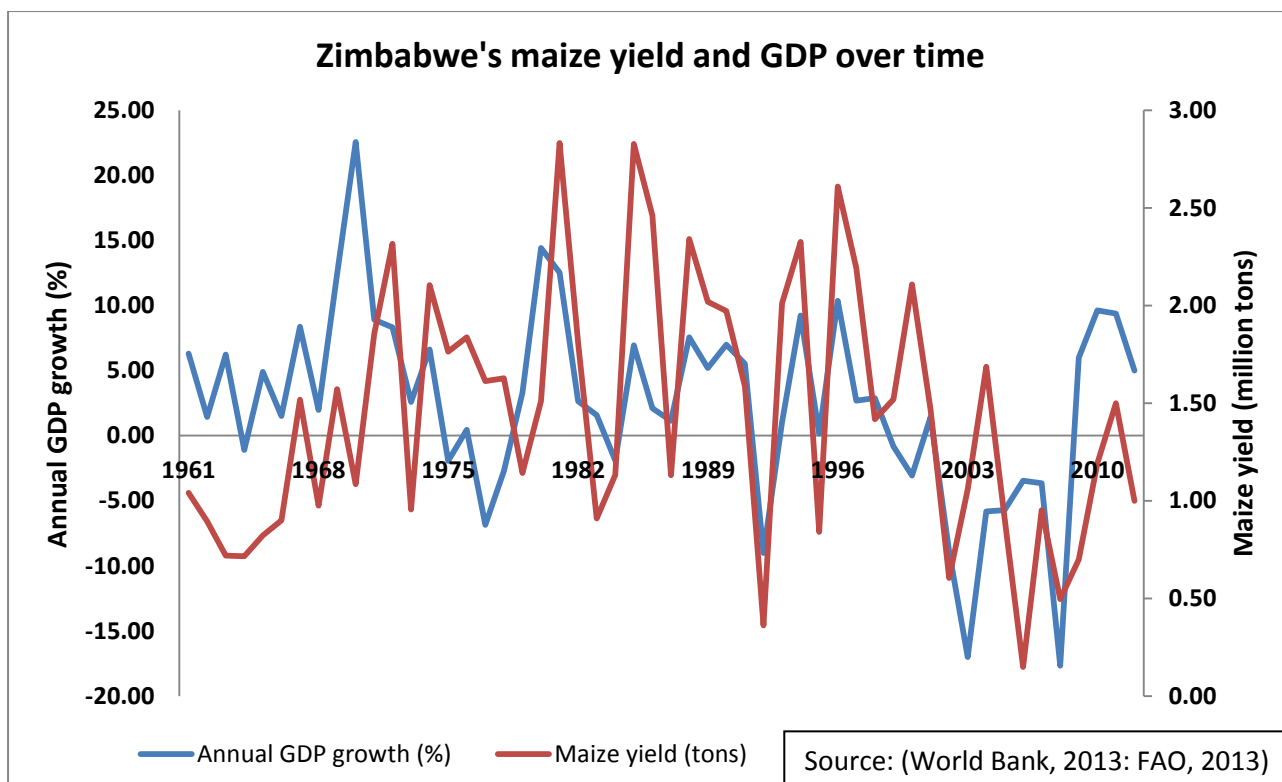


Figure 0.3: Zimbabwe's total maize yield (tonnes) and GDP growth (%).

### SR52 hybrid

The first commercial single cross maize hybrid variety in the world, SR52, was developed in Zimbabwe, then Southern Rhodesia, in 1960. This hybrid represents Zimbabwe's contribution to global knowledge and maize technology, in particular. Hybrids are obtained by crossing inbred lines obtained through several generations of selfing, until near homozygosity is achieved. SR52 was the product of government research in maize which had commenced in 1904 at the Salisbury Research Station, with a hybrid maize programme being initiated in 1932 (Alumira and Rusike, 2005). SR52 is a derivative of two late-maturing inbred lines, N3.2.3.3 and SC5522, which were developed from the OPVs Salisbury white and Southern Cross, adapted to Zimbabwean conditions (Dowsell *et al.*, 1996; Mhike *et al.*, 2011). Initially, as in the USA, double cross hybrids formed the backbone of Zimbabwe's maize breeding programme, as they were the only viable means of producing hybrid seed. A combination of good management practices and better yielding inbred lines led to economic production of single cross hybrid seed (Mashingaidze, 1994).

Table 1 shows how double cross hybrids SRH1, 8, 11 and 13 were out-yielded by SR52, showing the yielding nature of the single cross. By 1970, 98% of Zimbabwe’s maize area was planted to SR52, with neighbouring countries also adopting it as the variety of choice (Rusike, 1998). SR52 is credited with raising African maize yields three-fold a decade after its release (McCann, 2009). Through its adoption by farmers, coupled with the use of inorganic fertilizers, Zimbabwe became a net exporter of maize (Ratray, 1988). By virtue of it being a long-season variety, SR52 responded well to high moisture regimes and high levels of management giving good agronomic qualities (McCann, 2009). Overall, SR52 revolutionised single cross maize breeding in the USA and the world over. Indeed, the world learnt that productive inbred lines can be found that can be used to produce single crosses productively. Today, the world’s leading maize-producing countries, such as the USA, China and Brazil, use single cross hybrids.

Table 1.0 Yields of hybrids released in Zimbabwe between 1950-60 in comparison to open-pollinated variety - Hickory King

<b>Cultivar</b>	<b>Yield %</b>	<b>Year of release</b>
<b>Hickory King</b>	100	—
<b>SRH1</b>	118	1949
<b>SRH8</b>	123	----
<b>SRH11</b>	130	----
<b>SRH13</b>	144	1964
<b>SR52</b>	160	1960

(Ratray, 1988)

SR52’s major weakness was its susceptibility to grey leaf spot disease *Cercospora* spp. Poor standing ability, coupled with it being a long-season variety, led to its decline in use a decade after its release. Other undesirable qualities that SR52 possessed included the inability of its husks to fully cover the cob. The hybrid’s grain was soft, making it very susceptible to insect attack, pre and post-harvest (Derera *et al.*, 2001; McCann, 2009). However, to this day, SR52 is being grown for the green maize market in Swaziland, Zimbabwe and the northern KwaZulu-Natal region of South Africa.

## **Rationale of the study**

With Africa's population expected to rise from the current 1 billion to above 1.5 billion in 2030, it is essential that food production on the continent increases over the same period in order to meet the nutritional needs of the rising population. Maize yields need to increase, as maize is the continent's number one cereal crop and Zimbabwe's staple food. High-yielding hybrids are key in raising Africa's maize yields. Several studies have indicated the high-yielding nature of single cross hybrids, compared to three-way and double crosses.

The introduction of single cross hybrids from the early 1960s in the USA was met with improvements in yield. Despite the fact that single cross hybrids give better yields, when compared to double crosses, most maize breeding programs in Africa have shifted toward double and three-way crosses in an effort to reduce the cost of seed production. This has partly contributed to the yield gap on the continent. In a bid to shift focus toward single crosses, this study seeks to unravel what it is that made SR52 an exceptional hybrid. Numerous maize hybrids have been developed but a few have had such a positive impact on Zimbabwe and Africa's maize yields like SR52. Studying this hybrid in the hope of exploiting such knowledge in the development of other high yielding single crosses will aid in closing the yield gap in Africa. An understanding of the genetics and morphological traits that made SR52 an exceptional hybrid can be extended to other hybrids and used to improve Africa's yield, which is lagging behind that of the rest of the world. It is also worth mentioning that the major heterotic patterns in east and southern Africa are built upon SR52's parents SC and N3 and several successful hybrids have been developed from these two heterotic groups (Sibiya *et al.*, 2011). To emphasise the importance of this hybrid, SR52 has been used as a parent for several three-way hybrids, in Kenya and Malawi, in particular. Undoubtedly the hybrid forms the basis of productive hybrid programmes in tropical east and southern Africa.

The hypothesis that was being tested in this study is that additive genetic components inherited from both parents N3 and SC are responsible for SR52's yield. If this is the case,

then the hybrid's yield is fixable. If non-additive gene action (dominance and epistasis) are behind SR52's exceptional yield, then it would imply that SR52 was a hybrid created by mere chance and re-creating a similar hybrid is unlikely. Whilst still maintaining focus on the genetics of SR52, this study also seeks to identify yield components that make a significant contribution toward the yield of the hybrid. It is also a considered view that the current yield plateau and yield gap in Africa can be closed by shifting from three-way to single cross hybrids.

### **Research objectives**

The main objective of this study is to uncover the basis of SR52's yield potential by investigating the genetic basis of its exceptional yield, using a generation mean analysis. The results will be exploited to create hybrids that are high-yielding, including a modified improved version of SR52. The results will be crucial for devising the best hybrid breeding program for producing single cross hybrid products for Africa

The specific objectives of the study were:

- a) To estimate relative genetic effects that confer high yield in SR52
- b) To confirm the expression of heterosis in SR52 and the basis behind it
- c) To determine direct and indirect contribution of secondary traits to yield potential of SR52
- d) To determine the heritability of yield and its related traits in SR52.

### **Research hypotheses**

The following research hypotheses were tested:

- a) Additive genetic effects contribute toward SR52's high yield and, hence selection would be effective to derive new productive inbred lines

- b) Epistasis plays a significant role in the high levels of SR52's heterosis, and hence selection would not be effective in breeding new inbred lines
- c) There are high direct and indirect effects of secondary traits on yield, which can be exploited in breeding new inbred lines
- d) Yield and yield components of SR52 exhibit high levels of heritability, and therefore the population will respond to selection.

### **Dissertation outline**

The layout of the dissertation is as follows:

Chapter 1: Literature review

Chapter 2: Generation mean analysis for yield and secondary traits of SR52

Chapter 3: Correlation, path coefficient analysis and heritability in SR52.

Chapter 4: General overview of the study and future directions.

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## CHAPTER ONE

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### LITERATURE REVIEW

#### 1.1 Introduction

Contained in the literature review chapter are topics relevant to studying the genetic components responsible for the SR52 hybrid's yield. The review explores the relationship between the SR52 hybrid's grain yield and its secondary traits. Initially, the review provides background information to maize as a crop, as well as the significance and importance of hybrid maize in agriculture. Aspects on breeding for yield in maize, grain yield and yield potential, gene action and effects, generation mean analysis, heritability, heterosis and its causes are reviewed. Discussion of correlation and path coefficient analysis sum up the literature review.

#### 1.2 Importance of maize

Maize plays a key role in various aspects of human nutrition, animal feed and as an industrial raw material. Globally, maize utilisation is in the following proportions: 48% is used as poultry feed, 28% is used for human consumption, 11% for animal feed, 1% for seed production, with starch and oil production accounting for 12% (Hepziba *et al.*, 2013). When compared to other adapted African cereals such as pearl millet and sorghum, maize is a relatively "new" crop in Africa, having been introduced to the continent during the 1500s by Portuguese traders (McCann, 2009). Therefore its level of adaptation to the continent is not at a similar level as these other traditional cereals. However, despite being relatively "new", maize has been adopted as the staple crop in the majority of east and southern African countries such as Kenya, Malawi, South Africa, Zambia and Zimbabwe. In Zimbabwe and several eastern and southern African countries, hunger is usually synonymous with maize shortages. Improving the maize yield has thus been identified as being critical to improving food security in the region (Homann-kee *et al.*, 2013).



### **1.3 Impact and significance of hybrid maize**

The benefit of using hybrid maize was discovered at the beginning of the 20<sup>th</sup> century. It took until the mid-1900s for most farmers in the United States of America to fully adopt hybrid technology. From the 1920s to 1960, all hybrids grown commercially were double cross, with a shift to single crosses taking place after 1960 (Crow, 1998). The first commercial double cross maize hybrid released outside the USA was SR1, which was developed in Zimbabwe, then Southern Rhodesia, in 1949. Zimbabwe then went a step further in 1960 by being the first country in the world to develop and release the first commercial single cross hybrid (Alumira and Rusike, 2005). This represents Zimbabwe's contribution to global knowledge and maize technology, in particular. These advances must be sustained if Zimbabwe is to close its current yield gap and ensure its food security.

Hybrid maize seed offers yield advantages over open-pollinated varieties (OPVs). This was shown by the earliest maize hybrids in the USA, that yielded 15% more than the best-yielding OPVs (Duvick, 1999). Other than yield, maize hybrids possess desirable traits such as better resistance to lodging, offering efficient mechanical harvesting, with single cross hybrids offering excellent uniformity and hence improved management practices by the farmer (Duvick, 1999). In high maize production regions, the use of hybrid maize varieties has improved yield gains by over 40% (Mashingaidze, 1994). Under drought conditions, hybrid maize varieties maintain at least 30% yield advantage over OPVs (Mashingaidze, 1994).

#### 1.4 Superiority of single cross hybrids

The higher rate of increase in maize yield in the USA after 1960 (Figure 4) is mainly attributed to the adoption of single cross maize hybrids. Half of the yield gained since the introduction of hybrid maize is attributed to breeding. Total maize yield gain per year in the USA has been increasing at an average of 0.11 tonnes per hectare per year between 1960 and 2007, whereas the global rate of gain was pegged at 0.06 during the same period (Edgerton, 2009). The USA is the world's largest producer of maize and has one of the highest yields per ha (FAO, 2013). Considering that the USA has fully adopted single cross hybrids, there is little doubt that widespread use of single cross hybrids can improve Africa's maize yields that currently sit at the bottom of world production figures.

It is generally thought that the best single cross hybrids gave greater yield than the best double crosses. Kumara *et al.* (2013) reported that, apart from the fact that single crosses gave higher yield potential when compared to both double and three way hybrids, they have an added advantage in that they are simpler and faster to produce. However, the margin at which the best single crosses out-perform the double crosses is widely debated. Wricke and Weber (1986) indicated that the margin at which the highest yielding single crosses out-perform double crosses does not exceed 5%. Evaluations of the top-yielding double and single cross maize hybrids in Brazil by Sobrinho *et al.* (2010) also gave results that concurred with Wricke and Weber (1986). In one of the earlier studies to determine the performance of single, three-way and double crosses, Weatherspoon (1970) found that single crosses were the best yielding and three ways came in second. In assessing maize hybrids that would be ideal for the western high plains of the USA, single cross hybrids were observed to give an average yield advantage of 11.5% when compared to double crosses (Guillen-Portal *et al.*, 2003).

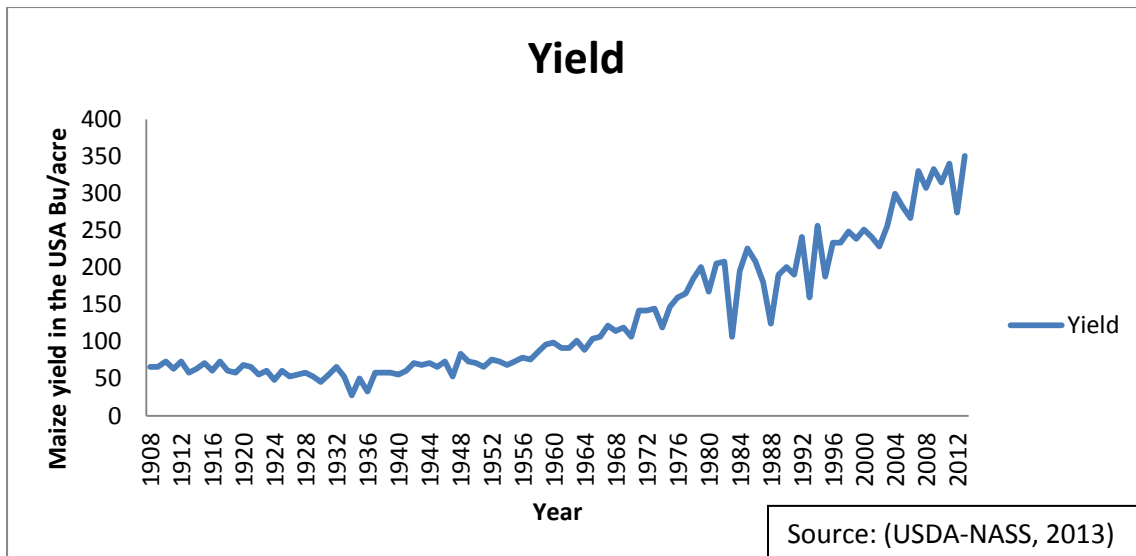


Figure 1.1:Maize yield (bu/acre) in the USA from 1908.

High levels of uniformity in single cross maize hybrids, as compared to both three-way and double crosses, are of much advantage to farmers as they simplify most agronomic practices such as spraying and harvesting. However, in most parts of the world, such as in the small scale farming areas in Africa, where machine harvesting is not employed, the uniformity factor of the single cross hybrids is of limited utility (Sobrinho *et al.*, 2010). The move from single to double and three way maize hybrids in Africa has been driven by the need to make seed production cheaper.

#### 1.4 Grain yield and yield potential

The definition of yield varies with respect to different crops. Several genetic and environmental processes determine yield. In cereals, grain yield is the summation of numerous growth processes taking place throughout the plant's entire growth period (Tollenaar and Lee, 2002). The complexity of grain yield inheritance is a result of the interdependence of various yield components (Stevanovic *et al.*, 2012). Fischer and Edmeades (2010) estimated that the difference between potential yield and farmers' yields (yield gap) in Africa was at least 200%. This is quite a large yield gap and one which necessitates breeding efforts aimed at reducing it.

Attainable yield was defined by Fischer and Edmeades (2010) as what a competent farmer should achieve as yield, taking into consideration sensible economic factors and risks. They emphasised the fact that attainable yield would not be consistent, as farmers differed, as did their ways of operating and budgeting. Definitions for yield potential do vary according to different authors, but the most commonly used one is by Evans (1993). He defines it as the yield of a crop when cultivated under optimum environments to which it is adapted with water and nutrients non-limiting and both biotic and abiotic stress under control. Taking into consideration that it is not practically possible to eliminate all biotic and abiotic stresses under field conditions, the yield potential definition can be modified to a more practical form (Duvick and Cassman, 1999). In this regard, yield potential could be expressed as the yield obtained when an adapted cultivar is grown under minimum possible stress, in the absence of natural hazards such lodging, heaving, frost and hail (Fischer and Edmeades, 2010). Crop yield potential differs by location. Within the same location it differs with regards to year and season.

### **1.5 Grain yield components**

The primary trait of focus in maize breeding is yield (Stevanovic *et al.*, 2012). This is because yield is the economic trait that represents harvestable dry matter. Maize yield can be analysed in terms of three components: number of ears  $\text{ha}^{-1}$ , number of grains  $\text{ear}^{-1}$  and the mean mass of the grain. Increases in maize yields by up to 50% have been attributed to plant breeding efforts (Duvick, 2005). Over the past few decades, breeding maize hybrids for tolerance to higher plant densities, weed interference, low soil nitrogen and low soil water has had positive influence on grain yield (Tollenaar and Lee, 2002). However, there is still need to identify adaptive traits that have contributed to yield under both stress and non-stress conditions.

In breeding for yield in maize, breeders target traits that indirectly influence yield, such as delaying leaf senescence, continued nitrogen uptake and increasing kernel mass and number (Moll *et al.*, 1994). Rajcan and Tollenaar (1999) reported that the 1.5% increase in

maize yields achieved in North America for the past five decades was a result of direct selection for yield *per se*. Of utmost importance is breeding for stress tolerance, as it has been shown to be an effective means of improving grain yield in maize (Tollenaar and Lee, 2002). According to Tollenaar and Lee (2002), selection for higher levels of yield stability, in part, could have resulted in indirect breeding for stress tolerance. They further defined stress as any factor that hinders the capture and exploitation of resources (water, light and nutrients). Stress tolerance was then defined as the ability of a cultivar to modulate the impact of both abiotic and biotic factors (Tollenaar and Lee, 2002). Maize yield components exhibit a systematic sequence of development, namely number of cobs per plant, number of kernel rows, number of kernels per row and kernel mass. This implies that searching for favourable yield components can be exploited as an indirect selection method (Viola *et al.*, 2003).

### **1.6 Generation mean analysis**

Gene action controlling quantitative traits can be determined by the use of genetic models. Generation mean analysis has been used to detect additive, dominance and epistasis gene effects involved in the inheritance of several quantitatively inherited traits (Shashikumar *et al.*, 2010). Epistasis effects can be partitioned into additive x additive, dominance x dominance and additive x dominance forms (Singh and Singh, 1992). Another advantage of using the generation mean analysis is that the populations used provide generations that can be used in a breeding programme (Coates and White, 1998). In the current study, the segregating generations will be used as base population for selection of new inbred lines. Considering the fact that generation mean analysis takes into account trait means and not variances, its sensitivity and accuracy could be of considerable use in maize breeding programmes (Zdunic *et al.*, 2008).

Generation mean analysis has been recently employed by several researchers in an effort to establish gene action responsible for several trait expressions. Mushongi *et al.* (2013) used generation mean analysis to identify genetic effects responsible for inheritance of leaf chlorophyll content, from mid-silking to physiological maturity, in maize. Results from the study revealed that all forms of gene effects were significant. In a study by Iqbal *et al.*

(2010), to determine if epistasis played a role in the inheritance of plant height and leaf area in maize both dominance and additive gene effects were found to be significant with dominance having a larger contribution for both traits. Epistasis, though in small proportions, was also detected for leaf area (Iqbal *et al.*, 2010).

### **1.7 Gene action**

Plant breeders are interested in the estimation of gene effects, with the aim of determining the most advantageous breeding procedures for improvement of the trait in question. The yield of maize is a quantitative trait which is characterised by continuous distribution. Genes which contribute to the inheritance of yield in maize have small, similar and cumulative effects (Dabholkar, 2006). Genes exist as additive, dominance and epistasis genes (Falconer, 1989). Additive gene effects will occur when the combined effects of alleles at different loci are equal to the sum of their individual effects (Falconer, 1989). Dominant gene action is a shift from the additive, as it results in a heterozygote that resembles one parent more than the other (Allard, 1999). Dominance can be partial, where the offspring's phenotype is placed closer to one parent than the other, complete where the offspring's phenotype resembles that of one of the parents, or over-dominance, in which the offspring's phenotype lies outside the range of both parents (Allard, 1999).

Epistasis occurs as a result of non-allelic gene interactions and can be taken as the failure of combined additive effects from two or more genes to explain the phenotype of an individual (Hinze and Lamkey, 2003). The two or more genes may have no effect individually on phenotype, but when they interact an effect on the phenotype is observed (Falconer, 1989). The non-allelic gene interactions may involve all combinations within additive or dominance gene effects, or between additive and dominance gene effects (Hallauer *et al.*, 2010a). Epistasis of the additive x additive form is fixable, whereas epistasis of the additive x dominance and dominance x dominance cannot be fixed; this implies that epistasis offers little to no breeding value, with its presence causing complications during selection.

### **1.7.1 Gene action conditioning grain yield and secondary traits in maize**

Gene effects that are responsible for the inheritance of grain yield vary from one variety to another and across environments. Dominance gene effects are thought to be the most significant, even though they are smaller in proportion compared to additive gene effects in the inheritance of maize grain yield (Sofi and Rather, 2007). Dominance gene effects were found to be the most important, with additive effects having a minor role in the inheritance of grain yield for two single cross hybrids with one parent in common (Todorović *et al.*, 2011). In another study on single cross maize hybrids, similar results indicating that dominance effects were more important than additive ones were obtained for grain yield, along with ear length, kernel number per row and total kernel number per ear (Shahrokhi and Khorasani, 2013).

Some studies indicate that additive gene effects are the most important in the inheritance of grain yield and secondary traits in maize (Swanson-Wagner *et al.*, 2006). Additive gene effects are generally amplified under conditions of stress in maize (Betrán *et al.*, 2003; Derera *et al.*, 2008). One of the earliest experiments to assess the role of epistasis in maize found that epistasis played a minor but significant role for grain and forage dry matter content in maize (Melchinger *et al.*, 1988). Even though the role of epistasis is widely debated, its contribution, none-the-less, is felt. However, the general consensus is that epistasis does not play a major role in maize grain yield (Larièpe *et al.*, 2012). Epistasis has generally been given the scapegoat role in explaining genetic non-linearity in phenomena such as heritability and heterosis (Wallace *et al.*, 2013). Just like additive effects, Wolf and Hallauer (1997) suggested that epistatic effects had been found to be more pronounced for maize grain yield in extreme environments that were either high or low yielding (Ceballos *et al.*, 1998). Despite the success of the hybrid SR52, the role of genetic effects has never been tested. It is therefore prudent to study this, as such information would be beneficial to an understanding of the success behind the hybrid SR52. In addition, such information could prove valuable to current and future breeding programmes.

### **1.7.2 Implications of gene effects on breeding**

Having dominance as the major form of gene action for important traits is not generally desired by breeders. This is because this type of gene action cannot be easily fixed, hence selection becomes difficult and a long-term process (Zdunic *et al.*, 2008). The main practical option when dominance is the main genetic mode of action is heterosis breeding (Sofi and Rather, 2007). When additive gene action is the main mode of inheritance for important traits, recurrent or any other type of cyclic selection could be the most effective breeding strategy, as such gene action is fixable (Mushongi *et al.*, 2013). Epistasis that involves additive effects is fixable and can be made use of in intra-population improvement, whereas those forms of epistasis where dominance effects are involved is not fixable and is made use of in hybrid breeding (Sofi and Rather, 2007). The current study seeks to investigate the role of various gene effects within the SR52 population. The information obtained would be useful in finding a viable breeding strategy for the programmes which aim at deriving new maize inbred lines from this elite cross.



## 1.8 Heritability

Heritability is the proportion of phenotypic variance that can be attributed to genotypic variance (Hallauer *et al.*, 2010). Positive correlation between genotypic and phenotypic variance is indicative of high heritability. Dominance and epistatic variances, along with environmental variance, weigh down breeding values (Hallauer *et al.*, 2010). Heritability can be partitioned into broad sense or narrow sense, with the former being synonymous with genotypic and the latter breeding value (Falconer, 1989).

The ratio of the genotypic variance to the total phenotypic variance is the broad sense heritability (Falconer, 1989):

$$H_B^2 = VG/VP \quad \text{Equation 1}$$

where  $H_B^2$  = Broad sense heritability,

VG = Genotypic variance and

VP = Phenotypic variance.

Narrow sense heritability:

$$H_N^2 = VA/VP \quad \text{Equation 2}$$

Where  $H_N^2$  = Narrow sense heritability and

VA = Additive genetic variance.

Narrow sense heritability is the proportion of additive genetic variance to the total phenotypic variance (Falconer, 1989). Narrow sense heritability or breeding value is of much utility to breeders, compared to the broad sense heritability, as it reflects the genotypic proportion that can be passed onto offspring from parents.

Heritability values differ among populations and also vary for different traits, as well as within a population. Robinson *et al.* (1949) categorised heritability as follows: low (0-30%), moderate (30-60%) and high (>60%). A study conducted by Saleh *et al.* (2002) on tropical maize hybrids found moderate broad sense heritability estimates for grain yield, moderate to low estimates for plant and ear height, with days to silk emergence being the least to low

estimates for plant and ear height, while days to silk emergence were the least heritable trait. Elsewhere, Flint-Garcia *et al.* (2005), while studying several traits on 101 maize inbred lines, found that broad sense heritability values for all traits were higher than narrow sense values.

Genotype x Environment interaction can also affect heritability, because it contributes to environmental variance. A lower environmental variance results in higher heritability values. Working on single crosses of maize derived from a 12x12 diallel, Sujiprihati *et al.* (2003) found varying estimates of broad sense heritability across locations for all traits with grain yield showing low heritability. Low overall heritability estimates are generally indicative of the major role being played by environmental factors, compared to genetic factors.

Working on half-sib maize families, Noor *et al.* (2013) obtained broad sense heritability values of 64% and 74% for grain yield. Zhao *et al.* (2013) reported average, narrow sense heritability values ranging from 12% to 67% among 11 segregating families of maize tested across six sites. A very high broad sense heritability value of 98% was obtained for grain yield in a study involving 10 open-pollinated maize varieties (Bello *et al.*, 2012a). A high narrow sense heritability value of 88% for grain yield was observed in crosses involving lines obtained from distinct heterotic groups (Schön *et al.*, 2010). Rafiq *et al.* (2010) reported a narrow sense heritability value of 91% for grain yield per plant, in a study to determine different parameters of genetic variability. High levels of additive gene action controlling a trait generally result in high heritability values. However, for traits whose preponderant mode of gene action is non-additive, high heritability values can still be obtained, though they are coupled with low genetic advance (Hallauer *et al.*, 2010).

### **1.9 Conceptualising heterosis**

The earliest recording of the phenomena that is heterosis was by Darwin in 1876. Later, a more detailed study was conducted by Shull in 1908 (Hoecker *et al.*, 2006). The definition of heterosis tends to vary according to the base of comparison used (Welsh, 1981). Heterosis can be taken as the superiority in performance exhibited by progeny over both their parents. This implies that offspring obtained as a result of hybridisation have more vigour

than their parents (Budak *et al.*, 2002). In the case of negative heterosis, the progeny will be performing poorer than the least performing parent. Mid-parent heterosis is generally viewed as the superiority of F1 progeny over the average of the two parents and is the most widely used for scientific purposes (Springer and Stupar, 2007). Better parent heterosis, which quantifies the performance of progeny over the better performing parent, is of greater economic importance (Springer and Stupar, 2007). It determines whether the F1 or progeny line should be deployed as a variety. This is very important in self-pollinated crops, where the end-product is a pure line variety. Hybrid vigour is the basis behind most maize hybrid breeding programs with heterosis manifested by hybrids contributing 15% toward yield increases per annum (Duvick, 1999).

The highest better parent heterosis value of 92% was obtained in a study conducted on 91 F1 crosses of maize from a diallel mating design involving 14 inbred lines (Hiremath *et al.*, 2013). Extremely high mid-parent heterosis values of up to 490% under stress conditions have been observed (Makumbi *et al.*, 2011). This can be a result of weak inbred lines failing to adapt to harsh environments, compared to their more vigorous hybrids. Negative mid-parent or better parent heterosis values for days to silk emergence or days to anthesis implies that an F1 hybrid matures earlier than either or both of its parental inbred lines (Wegary *et al.*, 2013). This highlights that, when interpreting heterosis data, direction is very important.

### **1.9.1 Causes of heterosis**

With the aid of various experimental designs, researchers have for long attributed the phenomena of heterosis to dominance and over-dominance theories. Budak *et al.* (2002) have indicated that epistatic effects have an important role in determining the levels of heterosis in maize hybrids. Supporters of the dominance theory assume that heterosis is a result of the masking of recessive alleles controlling deleterious effects by alleles that are dominant. Genotypes that contain higher numbers of dominant alleles would therefore be expected to perform better than those containing fewer dominant alleles (Lamkey and Edwards, 1999). However, the major weakness of this theory is that if heterosis is a result of accumulation of favourable dominant genes, then inbred lines containing all homozygous

dominant alleles should express as much vigour as single cross hybrids, but this is yet to be achieved (Hallauer *et al.*, 2010). This theory assumes that yield can be enhanced by stacking favourable dominant QTLs in a single variety.

The over-dominance theory is centred on the heterozygote progeny obtained by crossing two homozygous parents being a better performer than both parents. With this theory, heterozygosity itself causes heterosis (Hallauer *et al.*, 2010). Dominance and over-dominance have for long been seen as the theories explaining heterosis. However, of late, several studies have indicated that epistasis plays a significant role in heterosis (Lippman and Zamir, 2007; Melchinger *et al.*, 2007). Studies conducted using generation mean analysis have frequently indicated small, but significant, epistatic effects on heterosis in maize (Melchinger *et al.*, 2007).

#### **1.10 Correlation analysis**

Breeding for direct increase in maize yield is complicated, as yield is the end-product of interactions among contributing traits (Raghu *et al.*, 2011). An alteration in a particular trait results in changes in another trait as explained by Ahmad (2003). Knowledge of the association of yield components and their traits as well as association between the yield components themselves, can improve selection efficiency (Raghu *et al.*, 2011). Correlation refers to the association of variables that exhibit some related trends of change (Mohan, 2010). The correlation of characters can either be negative or positive (Mohan, 2010). The coefficient of correlation signifies the intensity of correlation between cause and effect (Sharma, 2006).

Correlation can be phenotypic as well as genotypic, which expresses the degree to which two characteristics are genetically associated (Yousuf and Saleem, 2001). Both genotypic and phenotypic correlation can be used as the basis of indirect selection (Yousuf and Saleem, 2001). Interpretation of the correlation between yield and its secondary traits should always be done with caution, as the results are generally confounded by genetic differences among genotypes for other traits, or by the presence of outliers (Bolanos and

Edmeades, 1996). For this reason, the current study will investigate correlation among traits in a population of SR52 where individuals have the same background.

### **1.10.1 Relationship among secondary traits**

Yusuf (2010) observed that several secondary traits, such as number of leaves per plant with plant height, days to silking with tasselling, and plant with ear height, were positively correlated and that these pairs of correlated traits could be simultaneously selected for. A positive correlation between silking and tasselling enables efficient breeding for early-maturing maize varieties. Highly positive correlation between 100 kernel mass and number of kernels per row was reported in eleven maize hybrids (Zarei *et al.*, 2012). This positive correlation is welcome, as these two traits contribute toward grain yield. Improving both traits at the same time will thus have a positive effect on grain yield. Total number of kernels and ear mass were significantly correlated (Bello *et al.*, 2010b), indicating that ear mass could be improved by selecting for many rows. Several studies conducted on maize have reported that plant and ear height were positively correlated (El-Shouny *et al.*, 2005; Bello *et al.*, 2010b; Rafiq *et al.*, 2010). This facilitates synchronised breeding for a desired plant stature.

### **1.10.2 Relationship between yield and secondary traits**

In order to improve gains from selection, it is desirable to have positive significant correlations between yield and agronomic characteristics that contribute towards higher yield. Ear mass and grain yield are highly and positively correlated (El-Shouny *et al.*, 2005), implying that selecting for heavier maize cobs will contribute toward higher grain yield. El-Shouny *et al.* (2005) indicated that primary selection for traits which are positively correlated with yield, such as plant and ear height, ear length and girth, contributes to high single plant yield potential in maize. However contradicting findings have been reported by other previous investigators (Kumar *et al.*, 2006; Jayakumar *et al.*, 2007). They found negative correlations between grain yield and days to silking. These differences in results obtained by several researchers can be explained by the use of different populations.

### **1.11 Conceptualising path coefficient analysis**

Path coefficient analysis is a statistical method capable of partitioning correlations into direct and indirect effects, as well as distinguishing between correlation and causation. Path coefficient estimates are useful in understanding the contribution and roles played by different plant traits in establishing growth pattern and behaviour of crop cultivars in a particular environment (Carpici and Celik, 2010). Path coefficient analysis enables breeders to test theoretical hypotheses about the cause and effect, without employing variables. It is an important tool when dealing with quantitative traits such as grain yield (Acquaah, 2007; Hepziba *et al.*, 2013).

Path coefficient analysis can be exploited in measuring the direct influence of a single variable upon another (Ojo *et al.*, 2006). The breeder sets knowledge on the relative contribution of yield-determining traits and thus aids in making a decision on whether to practise either indirect or direct selection (Makanda *et al.*, 2009). For this reason, path analysis has found wide application in maize (Rafiq *et al.*, 2010; Hepziba *et al.*, 2013), bambara groundnut (Makanda *et al.*, 2009) and many other crops. The existence of positive and significant associations between grain yield per plant and the majority of yield-related traits indicates that improvements in grain yield can be made through simultaneous selection of these traits (Ojo *et al.*, 2006).

### **1.12 Application of path coefficient analysis**

Research based on path analysis of five yield components on maize conducted by Agrama (1996) indicated that the number of grains per ear, along with grain size, could serve as potential traits in breeding for superior-yielding maize lines. Ear mass per plant had the highest positive direct effects on grain yield, as was days to 50% tasselling and 100 kernel mass (Hefny, 2011). It was concluded that ear mass and days to 50% tasselling could be used for indirect selection in the improvement of grain yield. Studies by Oktem (2008) revealed that single ear mass and ear length had highly positive effects on grain yield. The number of kernel rows had a positive direct effect on grain in single cross maize hybrids (Kumar *et al.*, 2011). Studies by Ahmad and Saleem (2003) revealed that the number of kernel rows had a direct effect on grain yield per plant.

The yield component with the highest direct effect on grain yield, out of several traits studied by Rafiq *et al.* (2010) in maize, was 100 seed mass. The other characteristics, such as the number of grain rows and ear length also have direct effects. Ear diameter, followed by ear height, were found to have the highest indirect effect on grain yield (Rafiq *et al.*, 2010). Maximum positive direct effect on grain yield has also been attributed to number of grains per row, with ear length, ear girth, days to tasselling, total sugars and plant height, respectively (Jayakumar *et al.*, 2007). Separate studies revealed that days to 50% silking had a negative direct effect on grain yield (Bello *et al.*, 2010b). In another study by Sofi and Rather (2007), path analysis indicated that 100 grain matched the highest positive direct effect on grain yield with kernels per row, with number of kernel rows per ear and ear length, respectively, having the least direct contribution. Contrary to most studies, Jayakumar *et al.* (2007) reported that negative direct effect on yield was attributable to kernel rows. The other characteristics that had a lower negative direct effect on yield were days to silking, days to maturity, shelling percentage and number of leaves above the ear.

## 1.14 Conclusion

Maize remains an important staple food crop for South Africa and the region at large. Efforts to improve maize yields have been on-going, dating as far back as the 1960s, to the present. In doing so, it is important to look back at the successes and use them to answer pertinent questions. The hybrid SR52, being the first single cross hybrid to be commercialised in the world continues to enjoy success among farmers and breeders, who aim to derive superior maize inbred lines for use in developing new hybrids. The pertinent question to be asked, therefore, is “why is the hybrid SR52 so successful?” The literature review showed that all forms of gene action play a role in the inheritance of grain yield, with dominance effects being more pronounced. Most maize hybrids exhibit high levels of heterosis, with vast number of traits such as ear length, 100 kernels mass and ear mass, being highly correlated with yield. Also, direct effects on yield by most ear related traits are common in maize. Heritability values are variable across sites and also from one population to the other for grain yield and secondary traits. The review confirmed the widely held opinion that single cross hybrids will generally perform better than both three-way and double cross hybrids. The margin of superiority of single crosses over both double and three-way crosses is, however, a contentious issue. The genetic basis of the exceptional heterosis of SR52 has never been reported in the literature. The question “why SR52 is such an exceptional maize hybrid” remains unanswered. The current study aims to investigate the genetic effects that govern grain yield and secondary traits in SR52. The contributions of secondary traits to grain yield in SR52 is not reported in the literature. Therefore the current study includes a path analysis for the exceptional yield of SR52.



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## CHAPTER TWO

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### GENERATION MEAN ANALYSIS FOR YIELD AND SECONDARY TRAITS OF MAIZE HYBRID SR52

#### Abstract

Although SR52 is such an exceptional hybrid, the basis of its outstanding yield and heterosis has never been explained. Therefore genetic components of yield and its secondary traits of one of the most successful and first single cross hybrid to be commercialised in the world, SR52, were studied, using generation mean analysis. The information would be crucial in designing an appropriate breeding strategy that could result in other high-yielding hybrids of SR52's calibre. The six populations comprising the two highly homozygous parents N3 and SC, F1, F2, BCP1 and BCP2 were evaluated in field trials at Cedara and Ukulinga Research Station, using a randomised complete blocks design, during the 2012/2013 season. High levels of heterosis, reaching up to 311% for yield, were confirmed. The lack of fit generation mean analysis model was significant for most traits, indicating the presence of additive and dominance effects. The role of epistasis was further investigated by partitioning it into additive x additive, additive x dominance and dominance x dominance gene effects. The full model confirmed the presence of epistasis of the additive x additive nature for grain yield. Both dominance and additive gene effects were highly significant for yield and the majority of the yield and secondary traits. With regards to relative importance, dominance gene action along with other non-fixable epistatic effects contributed over 80% to yield, as well as 70% to yield components such as ear length and ear mass. The results indicated that dominance gene action was the basis of the exceptional heterosis which is displayed by SR52, because additive gene effect played a significant but minor role for grain yield at both sites. Epistatic effects were non-significant, with the exception of the additive x additive form which was significant at  $P < 0.05$  and  $P < 0.01$  at Ukulinga and Cedara, respectively, though negligible in magnitude. Having dominance gene effects as the main mode of inheritance for grain yield has implications for breeding strategy and suggests that good inbred lines must be selected on the basis of their performance in crosses.

## 2.1 Introduction

The low maize yield potential explains the gap between production and consumption in Africa. With an average of two tonnes per hectare, African maize yields are much lower compared to those in other continents such as Asia and Europe (FAO, 2013). Unfortunately, adequate production of the staple maize cannot be enhanced by expanding the area under production. The acquisitions of land in Africa, mainly for biofuel projects, have reduced the land available for staple crop production (Borras and Franco, 2010). Therefore future increases in maize yields in Africa will be realised through improvement of yield, rather than expanding the production area. Schroeder *et al.* (2013) indicated that improvements in maize yield potential by small-scale farmers, particularly in marginal areas, has mainly been through adaptation of technologies, such as utilisation of hybrid maize and adequate fertilizer. Unfortunately, in Sub-Saharan Africa fertilizer is not easily available to resource-poor farmers. Therefore genetic improvement should be emphasised to boost the productivity of the staple maize. The current study investigated the basis of heterosis in SR52 in order to devise an appropriate breeding strategy for extracting inbred lines out of this hybrid.

The exploitation of heterosis in maize was identified long ago as one strategy for enhancing yield potential in maize. In 1908, H.D. Shull observed the phenomena of hybrid vigour. His work forms the basis for most studies on heterosis (Shull, 1908). Recently, Paschold *et al.* (2010) defined heterosis as the superiority of performance of highly heterozygous F1 hybrids in relation to the average performance of their inbred parents. Many studies of heterosis have been conducted on maize because the end-product is the F1 cross. The farmers grow the F1 hybrid. Therefore maximum heterosis is desired in the F1 generation. The hybrids are selected on the basis of high levels of heterosis for grain yield (Amiruzzaman *et al.*, 2010). The choice of heterotic groups and patterns has also been found to be of much importance in hybrid maize breeding. The levels of heterosis increase when maize inbred lines are genetically divergent (Mohammadi *et al.*, 2008). The level of divergence between the lines is therefore exploited to predict F1 performance. Among other factors, the current study aimed at determining the actual levels of mid-parent

heterosis in the hybrid SR52. Although its standard heterosis has been widely reported in the literature, the mid parent heterosis data has not been covered in the literature.

Zimbabwe's agricultural green revolution is based on exploitation of heterosis in the hybrid SR52. Farmers in Zimbabwe changed from growing land races and open-pollinated varieties to hybrids, which resulted in high levels of productivity. The adoption of the single cross hybrid maize variety SR52 in 1960, which out-yielded the commonly grown open-pollinated variety Hickory King by 46%, proved how the use of hybrid maize could greatly improve maize yield (Rattray, 1988). SR52, which was the world's first commercially grown single cross hybrid, revolutionised maize farming in Zimbabwe, but also had implications worldwide. Previously, single cross hybrids had not been exploited commercially because of the difficulty in producing seed at a viable price for farmers. This was due to the low levels of productivity of the inbred parents. However, in Zimbabwe it was widely accepted by commercial farmers because of its high yielding ability (McCann, 2009), which made it commercially viable. This hybrid raised maize yields threefold, compared to the decade prior to its release. It became the leading variety in south eastern Africa and the KwaZulu-Natal region of South Africa (McCann, 2009). SR52 was such an exceptional hybrid because its yield at some commercial farms in Zimbabwe (then Rhodesia) surpassed that of the USA corn belt material and its success led to its adoption by east and west Africa farmers (McCann, 2009). SR52 has also been used as a parent for several three-ways cross hybrids, particularly in Kenya. SR52 is, and should be, the basis of hybrid breeding programmes in central, eastern and southern Africa. Unfortunately, sufficient resources have not been invested to support further research and development of the SR52 heterotic pattern. As a result, hybrids that surpass the performance of SR52 have not been developed and today Zimbabwe is growing three-way cross hybrids and OPVs that are cheaper to produce, though lower yielding when compared to SR52. This partly explains the reduction in yield to a level that fails to match the increasing population growth.

As an elite maize cross, SR52 can be exploited as a potential source of productive maize inbred lines. However the genetic basis of the hybrid is not known. This has implications for

the breeding strategy. Knowledge of the nature of gene action that governs the grain yield can be exploited by maize breeders to maximise the efficiency of their breeding programmes (Mather and Jinks, 1982). The type of breeding method employed for any trait of interest is determined by the predominant type of gene action responsible for its inheritance. Despite it being of particular importance for most breeding programmes in eastern and southern Africa, no particular study has attempted to investigate SR52 and its populations in order to find out the gene action that is predominant for its yield and yield-related traits. This partly explains why breeders have not been successful at developing new heterotic patterns that can surpass the grain yield potential of SR52.

A survey of the literature indicates that there is no knowledge regarding the basis of the outstanding performance of the hybrid SR52. However, the observation that similar hybrids or those that can surpass its performance have not been developed suggests that its performance could be a result of non-fixable genetic effects such as dominance or epistasis. The current study aims to investigate the genetic basis of the high yield potential of the hybrid SR52. The information would be crucial for plant breeders who aim to extract productive inbred lines from this hybrid.

Generation mean analysis was appropriate for studying the genetic effects of the maize hybrid SR52. This is because the principal requirements for the generation mean analysis are fulfilled, as defined by Mather and Jinks (1971). SR52 was developed from two highly homozygous and divergent inbred lines, namely N3-2-3-3 (N3) and SC5522 (SC) cum heterotic groups (Rattray, 1988). Lines from these two heterotic groups combine well and have been modified to produce several other successful commercial hybrids (Dowswell *et al.*, 1996). Evidence for polymorphism between the two lines is built on estimates of genetic distance based on 1242 single nucleotide polymorphisms (SNPs). The SNPs genotyping showed the genetic distance between N3-2-3-3 and SC5522 to be 0.342. The lines were placed in different genetic clusters in the dendrogram (Ndhlela, 2012). The phenotypic data also placed the two lines into different clusters (Ndhlela, 2012).

To sum up the research focus, the genetic components that resulted in SR52 being a successful hybrid were investigated in this study, using generation mean analysis. Generation mean analysis is still commonly used to study genetic effects in maize and other crops, such as melon (Zalapa *et al.*, 2006); cucumber (Sun *et al.*, 2006); common bean (Checa *et al.*, 2006); Sorghum (Audilakshmi *et al.*, 2010). Besides the fact that SR52 has been one of the greatest success stories in maize breeding, no study has attempted to investigate the genetic basis of its yield and secondary traits or the heterosis it exhibits. By investigating the mode of inheritance of SR52's yield and yield components, the study aims to establish methods that breeders can employ to derive other high-yielding single crosses of SR52's calibre, given that most breeding programmes in southern Africa are based on parents of SR52 or their derivatives. Several genetic studies on hybrids have indicated both additive and dominance as the main mode of inheritance for grain yield. The role of epistasis for controlling grain yield is not well understood (Azizi *et al.*, 2006). It is possible that epistasis influences the yield potential of SR52, but this has never been established. Therefore the main objective of this study was to determine the genetic basis of yield and its component traits in SR52. This includes investigating the levels of mid parent heterosis for several traits of the hybrid SR52. Thus, although the levels of heterosis of SR52 over its open-pollinated predecessors, such as Hickory King, have been reported by Rattray (1988), there is no single citation of the levels of mid-parent heterosis. The current study will fill the missing information gaps for the genetic basis of the world class hybrid SR52. The knowledge will be used to improve breeding strategies of the maize programs in eastern and southern Africa.

## **2.2 Materials and methods**

### **2.2.1 Germplasm**

The heterotic groups N3 and SC were originally derived from southern African landraces. The inbred line SC was extracted from a landrace which was grown on a Mr Southey's farm was called Southern Cross. The N3 was derived from the landrace Salisbury white, which was widely grown in Salisbury (now Harare). It was designated as "Northern Cross" because it was heterotic (or supposed to be the opposite) to the SC inbred line. The landrace Salisbury White was widely grown in Zimbabwe (then Rhodesia) before the advent of hybrid

maize in 1960 (Rattray, 1988). The Southern Cross landrace was also grown extensively in Zimbabwe and South Africa prior to 1950 (Sibiya *et al.*, 2011). Therefore the two landraces were very adapted and formed the best populations for extracting good lines. Out of the many lines that were extracted from these populations, two late-maturing maize inbred lines, which represent an exceptional heterotic pattern for the maize programme in Zimbabwe, were selected and designated as N3-2-3-3 (coded as P1 in the current study) and SC5522 (coded as P2), at the Crop Breeding Institute (CBI). The two lines formed the basis of maize hybrid breeding in Zimbabwe since 1960 and were fitted into the heterotic groups N3 and SC (Mickelson *et al.*, 2001), which are currently used by the maize programme in Zimbabwe. The lines are maintained by the CBI, in the Department of Research and Specialist Services (DR & SS), in Zimbabwe. The lines have white grain, are tall, late in maturity and generally adapted to the subtropical and medium altitude (800 – 1500 m) environments, in east, central and southern Africa. They are not stress-tolerant, since they were derived from landraces that were adapted to high yield potential environments of Harare, which is 1300 to 1600 m above sea level, and enjoys high and well distributed rainfall (above 1000 mm per year).

The genetically pure inbred seed for these two lines and their F1 generation seed were obtained from CBI of Zimbabwe. The seed was sourced from the CBI because it was important to obtain genetically pure seed for the generation mean analysis. The F1 generation was advanced to the F2 in the winter of 2012 (May-October), at the Makhathini Research Station (latitude 27°39`S; longitude 32°10`E; and altitude 72 m), in South Africa. Concurrently, the two parents, N3-2-3-3 and SC5522, were backcrossed to the F1 during the same season, to generate BCP1 and BCP2, respectively, at the same site. The F1 was used as the mother parent in the backcrosses in order to exploit its vigour and obtain adequate seed for the study. This was necessary because previous experience indicated that the medium altitude-adapted inbred lines would yield few seeds at this low altitude station. Specifically, the inbred line SC generally fails to produce adequate silk to allow pollination in the low altitude (<800 m) areas, such as the Makhathini Research Station. Unfortunately there is limited literature about the seed production ability of this crucial inbred line. According to Caulfield (2013 personal communication), the SC5522 has poor silk emergence in most

environments, including the mid-altitude (800–1500 m) environments in Zimbabwe. Therefore it is used as the male parent in the hybrid SR52. Adequate seeds of the six generations, namely P1 (i.e.N3-2-3-3), P2 (SC5522), F1 (P1 x P2), F2, BCP1 and BCP2, was available for planting the trials for the generation mean analysis, in November and December of 2012.

The inbred lines, SC5522 and N3-2-3-3, have been maintained by self-pollination at the CBI since 1960. Therefore the lines are highly homozygous, because they have gone through at least 54 generations of self-pollination. This was confirmed by genotyping with 1242 single nucleotide polymorphism (SNP) markers, by the CBI (Ndlela, 2012). In a study by Ndlela (2012, p154), both N3.2.3.3 and SC5522, were found to be highly homozygous qualifying them as suitable parents for use in a generation mean analysis. Theoretically, inbred lines are considered fixed after only eight generations of self-pollination (Chahal and Gosal, 2002). In the same study, the two inbred lines were shown to be highly divergent because they were fitted into different clusters on the dendrogram, based on both genetic and phenotypic data (Ndlela, 2012). For these two reasons, the hybrid SR52 was found to be a suitable population for conducting the generation mean analysis. According to Mather and Jinks (1982), the parents for use in a generation mean analysis should be fully inbred and divergent. These conditions are fulfilled by the maize hybrid SR52.

### **2.2.2 Experimental design and management**

The seeds of the six generations were planted at the Ukulinga Research Station (latitude 29°66`S, longitude 30°40`E, altitude 808 m) on 11 of November 2012. According to the CIMMYT classification system, Ukulinga lies at the margin of a medium-altitude (>800m) and the lowland (<800m) environment (Magorokosho *et al.*, 2009). The planting was replicated at the Cedara Research Station (1066 m altitude) on 12 of December 2012. The Cedara Research Station represents a medium-altitude environment. The two environments were, therefore, considered to be different. The trials at Cedara were planted late, because the recommended last planting date for maize at Cedara Research Station, which is in the mist-belt of the Natal Midlands, is generally 15 of December (Smith, 2006).

The experiments were laid out as a randomised complete block design (RCBD), with two replications, in the field at both sites. The field layout of the experiment is indicated in Figure 2.1 for Ukulinga Research Farm. A similar layout, but different randomisation, was used at the Cedara Research Station. This design has been used by many previous researchers, such as Yeboah *et al.* (2008), Piepho and Mohring (2010) and Shahrokhi *et al.* (2011). Due care was taken by planting two border rows of inbred lines between the plots of the vigorous generations and those of the inbred lines, P1 and P2.

Plot 1	Plot 2	Plot 3	Plot 4	Plot 5	Plot 6	Block I
<b>P1</b>	<b>P2</b>	<b>F2</b>	<b>BCP1</b>	<b>BCP2</b>	<b>F1</b>	
Plot 7	Plot 8	Plot 9	Plot 10	Plot 11	Plot 12	Block II
<b>BCP1</b>	<b>BCP2</b>	<b>F1</b>	<b>F2</b>	<b>P2</b>	<b>P1</b>	

Figure 2.1: Field layout of the experiment at Ukulinga Research Farm.

Five rows per plot were planted for each of the non-segregating populations, P1, P2 and the F1. Ten rows were planted for each of the segregating generations, F2, BCP1 and BCP2. Each row was 5 m long, with spacing of 0.75 m between the rows and 0.3m within the rows. Three seeds were planted per station and thinned down to one plant at three weeks after seedling emergence. Each row had a maximum potential of 17 plants. This implies that a maximum of 85 plants could be obtained for each of the non-segregating generations and a maximum of 170 plants per plot for each of the segregating generations.

The experiments were rain-fed at both sites. The rainfall and temperature data are shown in Figure 2.2 and Figure 2.3. The rainfall was generally higher at Cedara than Ukulinga, except in February. The maximum temperature was similar, but the minimum temperature was consistently lower at Cedara than Ukulinga. However the minimum temperature was higher



than 10<sup>0</sup>C, which is the base temperature for the normal growth and development of maize during the season. Basal fertilizer (NPK) was applied (75 kg N, 50 kg P, 25 kg K per hectare) before planting. The top dressing of 120 kg per hectare in the form of LAN (28% N) was applied four weeks after crop emergence. Hand weeding and other cultural practices were conducted, as and when they were required. The cultural practices which are recommended for maize in South Africa were followed. They included regular chemical sprays to control stalk-borer, and application of herbicides, such as atrazine and gramoxone, to control the weeds. The crop was not subjected to stress at both sites. The season was considered to be normal for maize production with respect to all the weather variables, including rainfall. The crop was harvested by hand during May 2013.

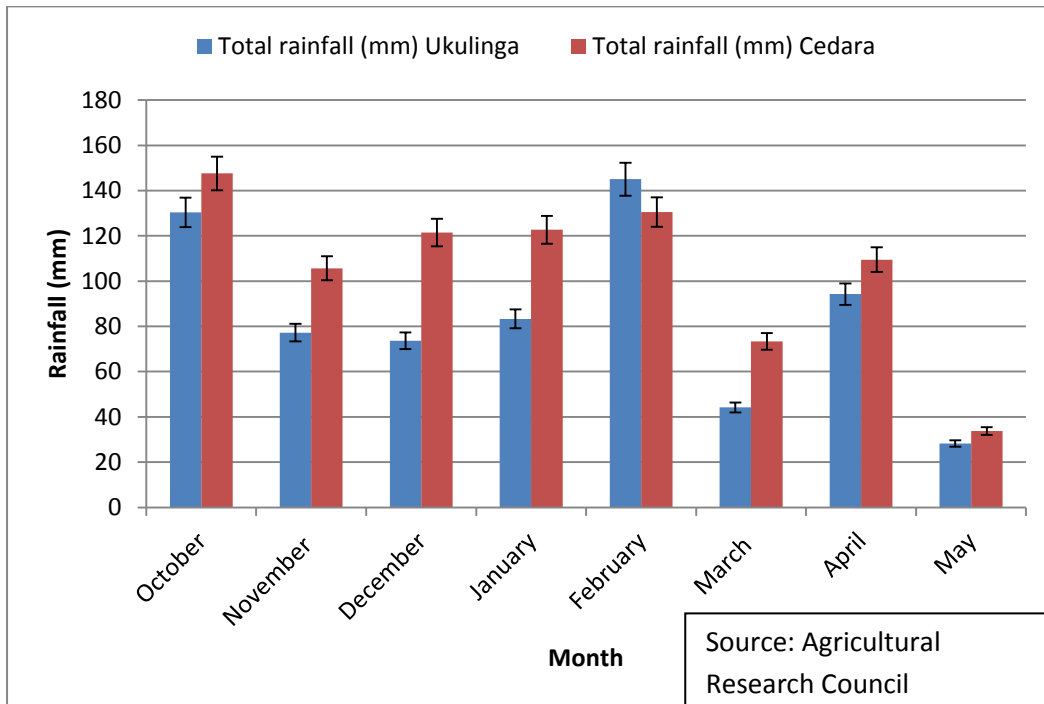


Figure 2.2: Total rainfall for Ukulinga and Cedara Research Station during the summer season, October 2012 to May 2013.

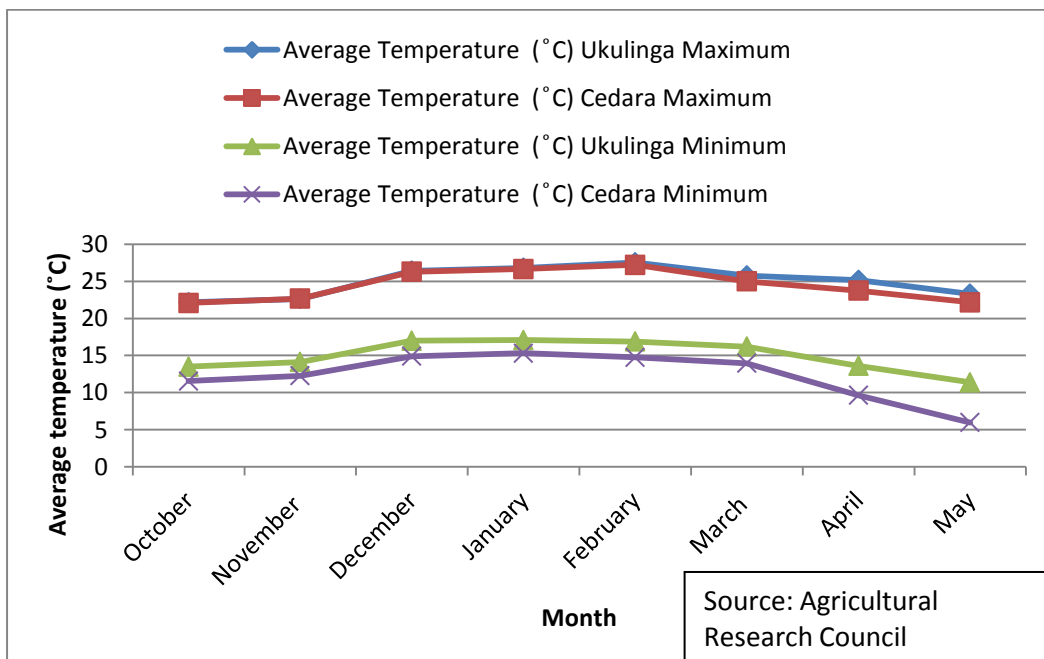


Figure 2.3: Average temperature of Ukulinga and Cedara October 2012 to May 2013.

### 2.2.3 Data collection

The data was collected on an individual plant basis, following standard protocols used at CIMMYT (Magorokosho *et al.*, 2009). The data was collected from all plants in each plot and each generation. The pooled number of plants was 85 per plot (170 plants pooled over the blocks) for the non-segregating generations, and 170 plants (total of 340 pooled over the blocks) for the segregating generations at each site. The traits measured were plant height (from the surface of the soil to the tip of the highest tassel branch, ear height (from the soil surface to the primary ear), number of days from planting to initial silk emergence, number of days from planting to the first pollen emergence, number of leaves above primary ear, leaf chlorophyll content, number of rows per ear, ear length (where there was prolificacy, the longest ear, generally the uppermost primary ear, was measured), leaf area (the first leaf above the primary ear), ear mass (which was taken as single plant yield, in the case of ear prolificacy, the combined mass of all the ears was taken as the yield), 100-kernel mass and grain moisture content. The grain moisture content was determined using the grain moisture meter MC-7825G (ONMI instruments, UK). The leaf chlorophyll content was measured using a chlorophyll content meter (OPTI-SCIENCES) CCM 200 plus. All efforts were made to try and measure at the same spot on every leaf (the furthest point from the midrib which is closest to the plant stem). The leaf area was measured using the portable area meter LI-300C (LI-COR, USA).

## 2.3 Data analysis

### 2.3.1 General analysis of variance

The data for all traits were analysed using the PROC Mixed procedures of SAS 9.2 (SAS Inc., 2012). The PROC Mixed procedure was used because the number of plants was different for each generation. This is consistent with recommendations by previous researchers (Yeboah *et al.*, 2008; Piepho and Mohring (2010). The following model was used for data analysis: Response = population mean + block effects + generation effects + random error effects.

$$Y_{ijk} = \mu_i + b_j + g_{ijk} + e_{ij}$$

$Y_{ijk}$  = response

$\mu_i$  = population mean

$e_{ij}$  = experimental error

$g_{ijk}$  = plant specific genetic errors

$b_j$  = effect of the  $j$ th block on the  $k^{\text{th}}$  plant

The blocks, and block x generation effects, were treated as random effects and the generations were considered fixed effects. The traits with significant data at  $P \leq 0.05$  were then subjected to the mean separation test.

### **2.3.2 Mean separation**

The t-test was used to separate means of generations at both  $P \leq 0.05$  and  $P \leq 0.01$  levels of significance. The mean separation test was necessary to determine whether or not there were significant differences at  $P \leq 0.05$  between P1 and P2 for the traits measured. The use of dissimilar parents is a precondition for performing the generation mean analysis (Mather and Jinks, 1982). Therefore, the generation mean analysis was only performed when the mean separation test indicated that the two parents were significantly different for the traits of interest. The use of the mean separation test as a tool for identifying the suitable traits for the generation mean analysis is consistent with many previous studies, such as those of Checa *et al.* (2006); Lyimo *et al.* (2011), Kere *et al.* (2013) and Mushongi *et al.* (2013).

### **2.3.4 Heterosis**

The levels of heterosis for each trait with regards to either of the two parents, N3-2-3-3 and SC5522, were calculated. Mid-parent heterosis (MPH), which is the average performance of

the parents relative to their F1 (Fehr, 1991), was also calculated. The equations used to calculate mid-parent and better parent heterosis are as follows:

$$\text{Mid-parent heterosis (MPH)\%} = 100 * ([M_{F1} - (M_{P1} + M_{P2})/2] / (M_{P1} + M_{P2})/2)$$

$$\text{Better parent heterosis for yield (BPH)\%} = 100 * ([M_{F1} - M_B] / M_B)$$

Where;

$M_{F1}$  = mean performance of F1 (i.e. SR52)

$M_{p1}$  = mean performance of parent 1 (i.e. N3-2-3-3)

$M_{p2}$  = mean performance of parent 2 (i.e. SC5522)

Because small-scale farmers, especially in Africa, are likely to plant the seed of the F2 generation, the heterosis was also estimated for the F2 generation relative to both parents and the mid-parent mean.

### 2.3.5 Genetic effects

The number of traits which were submitted for genetic analysis has been reduced from 11 to four traits. Only the four traits that show very large mean differences between the two parents lines have been selected for the generation mean analysis (Viana, 2000). Taking into consideration the fact that variances of the six generations were variable, weighting before submitting them for analysis in the generation mean analysis model was required. The weighting factor was calculated as the inverse of the variance for each generation (Mather and Jinks, 1982; Kang 1994).

### 2.3.6 The lack of fit test

The data that was significant in the ANOVA, showing significant differences between the parents, P1 and P2, was submitted to the lack of fit test, using the SAS macros for the PROC Mixed models, as indicated by Piepho and Mohring (2010). According to Piepho and Mohring (2010: p1675), the lack of fit test is equivalent to the Joint Scaling Test of Mather and Jinks (1971). Before the SAS analysis, the data was coded and arranged in an Excel

spreadsheet, as indicated by Piepho and Mohring (2010). An example of how the data was organised is shown in Figure 2.2.

The lack of fit test was performed to determine the adequacy of the additive-dominance model in explaining the dependent variables. The model used was as follows:

$$\mu_i = m + [a]x_{i1} + [d]x_{i2} + \lambda_i$$

where  $i = (1, \dots, G)$

$m$  = an intercept

$[a]$  = the additive effect

$[d]$  = the dominance effect

$x_{i1}$  and  $x_{i2}$  = the corresponding coefficients

$\lambda_i$  = a lack-of-fit effect

Block	Plot	Plant No.	Generatio	Depender	Lack of fit	a	d
1	1	1	P1	X1	P1	1	0
1	1	2	P1	X6	P1	1	0
1	1	3	P1	X8	P1	1	0
1	2	4	BCP1	X3	BCP1	0.5	0.5
1	2	5	BCP1	X6	BCP1	0.5	0.5
1	2	6	BCP1	X2	BCP1	0.5	0.5
1	2	7	BCP1	X9	BCP1	0.5	0.5
1	2	8	BCP1	X3	BCP1	0.5	0.5
1	3	9	F2	X7	F2	0	0.5
1	3	10	F2	X7	F2	0	0.5
1	3	11	F2	X4	F2	0	0.5
1	3	12	F2	X2	F2	0	0.5
1	3	13	F2	X6	F2	0	0.5
1	3	14	F2	X7	F2	0	0.5
1	3	15	F2	X8	F2	0	0.5
1	3	16	F2	X1	F2	0	0.5
1	3	17	F2	X5	F2	0	0.5
1	3	18	F2	X5	F2	0	0.5
1	4	19	BCP2	X12	BCP2	-0.5	0.5
1	4	20	BCP2	X8	BCP2	-0.5	0.5
1	4	21	BCP2	X11	BCP2	-0.5	0.5
1	4	22	BCP2	X7	BCP2	-0.5	0.5
1	4	23	BCP2	X4	BCP2	-0.5	0.5
1	5	24	P2	X7	P2	-1	0
1	5	25	P2	X8	P2	-1	0
1	5	26	P2	X10	P2	-1	0
1	6	27	F1	X16	F1	0	1
1	6	28	F1	X13	F1	0	1
1	6	29	F1	X11	F1	0	1

Figure 2.4: Spread-sheet giving an example of coded data before running it in SAS

### 2.3.7 Testing for epistasis

For the traits where the lack of fit test showed significant data at the  $P \leq 0.05$ , the genetics model was expanded to include the elements of epistasis, aa, ad and dd, as recommended by Mather and Jinks (1982) and many previous researchers, such as Zalapa *et al.* (2006) Lyimo *et al.* (2011) and Kere *et al.* (2013). The expanded model was analysed using the PROC GLM models, in accordance with the SAS macros developed by Kang (1994:p80). The PROC

GLM procedures were necessary because the data was collected on an individual plant basis. This model can detect epistasis and partition it into its different forms of aa, ad and dd. The data was organised in Excel as described above. This model is also in accordance with Mather and Jinks (1982):

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

Y = generation mean

m = mean of the F2 generation as the base population

$\alpha$  and  $\beta$  = coefficients of a and d as defined by Mather and Jinks (1982:p73; Table 2.1)

a = cumulative additive effect

d = dominance effect

aa = cumulative additive x additive effect

ad = cumulative additive x dominance effects

dd = cumulative dominance x dominance effects.

This model has been used by many previous researchers, such as Chungu *et al.* (1996), Sun *et al.* (2006) and Zalapa *et al.* (2006). In the current study the elements of the model were tested one at a time beginning with the additive effects and then in combination. Ultimately the full model which had the greatest R<sup>2</sup> values for all the traits was adopted.



Table 2.1: Coefficients of  $\alpha$  and  $\beta$  utilized for the construction of different models in generation mean analysis

Generation	Genetic effects					
	m	a	d	aa	ad	dd
P1 (N3-2-3-3)	1	1	-0.5	1	-1	0.25
P2 (SC5522)	1	-1	-0.5	1	1	0.25
F1	1	0	0.5	0	0	0.25
F2	1	0	0	0	0	0
BCP1	1	0.5	0	0.25	0	0
BCP2	1	-0.5	0	0.25	0	0

(source: Mather and Jinks, 1982; Kang, 1994)

Proportions of all the genetic effects relative to the sum of squares for the generations were calculated. Proportion of fixable (additive; additive x additive) to the non-fixable gene effects (dominance; additive x dominance; dominance x dominance) was estimated relative to the generation sum of squares. Previous researchers, such as Mushongi *et al.* (2013), have used the same approach to quantify the roles of each element of the model.

### Data transformation

Data that showed a lack of fit for the additive-dominance model was subjected to the square root transformation. Then the data that still showed the lack of fit was subjected to the full model analysis. The transformed data also showed lack of fit, and the un-transformed data was submitted for the full generation mean analysis model. It was found that the un-transformed data was normal and there was no gain (as reflected by the changes in the  $R^2$  values) that was achieved by transforming all the traits in the study. The lack of differences between transformed and un-transformed data was a result of the relatively large plant population when compared with previous studies on GMA.

### 2.3.8 Variance components

The additive variance component for the population was estimated, as described by Checa *et al.*, (2006), using a combination of formulas derived from Mather and Jinks (1971). Calculation of additive variance was conducted, as it is the genetic component that can be

effectively exploited by breeders and fixed into inbred lines. The formulae used are as follows:

$$\text{Environmental variance } V_e (F_2) = 0.25(VP_1 + VP_2 + (2VF_1))$$

$$\text{Genotypic variance } V_g (F_2) = VF_2 - V_e$$

$$\text{Additive variance } V_a (F_2) = 2VF_2 - VBCP_1 - VBCP_2$$

The narrow sense heritability, which was calculated in Chapter 3 using a formula by Fehr (1981), was also calculated in this chapter using the genetic variance obtained from the above formulae.

$$\text{Narrow sense heritability } h^2_n = 100(V_a/VF_2)$$

## **2.4 Results**

### **2.4.1 Analysis of variance**

The two sites were considered to be different with respect to altitude data, which is reflected by the behaviour of the hybrid SR52. The sites represented different mega-environments. Generally, Ukulinga tended to represent lowland areas, whereas Cedara represented medium altitude environments. There was no homogeneity of error variance for most of the traits, as tested by the F-max test. As an example the MSE for plant height was 32.5 at Ukulinga while it was 578 at Cedara. This gives a ratio of 17.78. The mean square error data is presented in Table 2.3. For these reasons the data could not be combined for the analysis of variance. Results were therefore presented and discussed separately, for each environment. The analysis of variance indicated that the data was highly significant ( $P < 0.0001$ ) for most of the quantitative traits at both sites (Table 2.2). The genetic and environment variance data is presented in Tables 2.3 and 2.4. Environmental variance was found to play a higher role for trait expression at Ukulinga, when compared to Cedara. The highest genotypic variance proportions were observed for quantitative traits such as yield and leaf area at Ukulinga and total kernel number and ear weight at Cedara. Yield components such as grain moisture and ear weight had the highest magnitude of additive variance at Cedara. Yield and days to silk emergence had a high proportion of additive variance at Ukulinga. The heritability values ranged from moderate for secondary traits to very high for grain yield at both sites (Tables 2.3 and 2.4).

Table 2.2: Results from ANOVA for selected traits of the maize hybrid SR52 at Ukulinga and Cedara Research Stations, during the 2012/13 summer season

Parameter (traits)	Ukulinga Research Farm		Cedara Research Station	
	F value		F value	
	Generation	replication	Generation	replication
Grain moisture	21.65***	1.88	97.47**	18.47**
Grain yield	42.02***	0.04	77.71***	0.02
Ear weight	45.34***	0.01	67.54***	0.11
100 kernel mass	18.32***	1.64	18.58***	2.37
Ear length	32.60***	0.31	49.71***	0.01
Ear height	191.70***	5.73*	115.93***	5.02*
Leaf chlorophyll content	40.20***	6.11*	19.71***	0.07
Leaf area	93.06***	5.19*	70.15***	6.89**
No. of leaves above ear	39.00***	0.63	47.35***	0.61
No. of kernel rows on ear	9.47***	1.88	12.65***	0.29
Silk emergence (days)	63.67***	23.98**	46.70***	0.08
Pollen shed (days)	75.48***	10.85**	40.95***	1.63
Number of kernels on ear row			86.84***	0.16
Kernel depth			27.24***	1.26
Total number of kernels on ear			69.76***	0.01

\*\*\* Data is significant at  $P < 0.0001$ , \*\* =  $P < 0.01$ , \* =  $P < 0.05$

#### 2.4.2 Mean separation

Tables 2.3 and 2.4 show the means of all traits at the two sites. Consistently, the F1 generation displayed the highest superiority of mean for most traits. There were also significant differences between the means of the inbred line parents and the F1 and segregating generations for most of the traits. The results indicate larger differences between P1 and P2 at Ukulinga. However the differences between the inbred lines were smaller at Cedara than at Ukulinga. Out of the 13 traits that were analysed at Ukulinga, two (plant height and number of rows on ear) had similar means ( $P > 0.05$ ) for the inbred lines P1 and P2. At the Cedara Research Station the data for 16 traits were analysed. The data for five traits (days to silk emergence, days to pollen shed, ear height, kernel depth, total number of kernels and ear mass) showed similar means for P1 and P2 at Cedara. The trait means that were similar for the two inbred lines were not subjected to the generation mean analysis. Also incorporated into Tables 2.3 and 2.4 are genetic variances of all the traits, as calculated by formulas given by Checa *et al.* (2006); Mather and Jinks (1971).

Table 2.3: Trait means for six generations of the maize hybrid SR52 at the Ukulinga Research Farm

Gen	n	Plant height	Ear height	Days to Pollen shed	Days to Silk emergence	Leaf area	chlorophyll	Grain moisture	No. of leaves above ear	Ear length	100-Kernel weight	No. of rows on ear	Ear weight	Yield
<b>P1</b>	160	215d	103d	78.8b	80.6b	603cd	31.01c	14.4d	4.9d	134e	48.7e	10.3c	113.4c	94.0.c
<b>P2</b>	160	219d	97e	85.1a	89.7a	411e	37.68b	18.4a	5.7b	146d	67.3a	10.0c	34.6d	21.7d
<b>F1</b>	172	306a	163a	73.2d	77.0c	934a	57.80a	16.6b	6.1a	203a	62.6b	12.1a	301.7a	238.0a
<b>F2</b>	246	248c	120c	76.7c	80.5b	644c	36.92b	15.4c	5.7b	158c	57.0c	11.6ab	127.2c	104.1c
<b>BCP1</b>	244	265b	130b	77.6c	80.3b	712b	38.21b	15.4c	5.2c	157cd	54.5cd	11.2b	174.9b	142.7b
<b>BCP2</b>	268	267b	132b	77.2c	80.9b	595d	39.29b	15.9c	5.7b	170b	53.6d	11.4ab	143.7bc	111.8c
<b>Mean</b>		256	125	77.8	81.1	660	39.99	15.7	5.6	162	56	11.3	150.4	150.4
<b>CV (%)</b>		12.7	12.4	5	5.7	23.8	32.71	11.3	11.3	21.5	19.8	15.8	80.2	80.2
<b>Ve</b>		968.88	183.03	17.65	21.23	22713.5	143.53	4.08	0.29	1110.4	123.65	1.27	16642	11606
<b>Va</b>		328.6	164.7	8	20.4	13223	1.9	2.1	0.47	526	15.5	4.27	20825	13866
<b>H<sup>2</sup>n</b>		28.34	48.05	55.94	82.59	41.056	0.97	57.065	77.049	33.65	11.78	86.44	91.75	91.24

Means with different letters are significantly different at  $P < 0.05$ .  $V_e$ =Environmental variance,  $V_g$ =genotypic variance of the F2,  $V_a$ =additive variance of the F2,  $V_d$ =dominance variance of the F2, as calculated using the variance analysis method described by Checa *et al.* (2006) and Mather and Jinks (1971).

Table 2.4: Trait means for six generations of SR52 at the Cedara Research Station

Gen	n	Plant height	Ear height	Days to pollen shed	Days to silk emergence	Leaf area	Chloro-phyll	Grain moisture	No. of leaves above ear	Ear length	100-kernel weight	No. of rows on ear	No. kernels on row	Tot. no. of kernels	Kernel depth	Ear weight	Yield
<b>P1</b>	162	243e	108e	85.1a	88.1a	607d	17.5d	15.9d	4.9a	140 e	35.0 c	10.1c	23.5d	238c	16.6d	90.6d	81e
<b>P2</b>	166	262d	97e	84.6a	89.3a	460e	29.1bc	18.4b	5.5c	158 d	41.5 b	10.8b	21.2e	230c	15.9d	98.7d	106d
<b>F1</b>	156	327a	164a	77.4d	80.1d	851a	38.7a	19.4a	6.2a	214 a	50.6 a	11.6a	43.4a	499a	25.4a	290.8a	227.6a
<b>F2</b>	284	281c	120c	79.7bc	83.2b	652c	29.7bc	17.5c	5.7b	165cd	41.0 b	11.5a	32.7c	378b	21.1bc	146.7c	138.8c
<b>BCP1</b>	260	291b	130b	78.9c	82.1c	691b	26.8c	17.2c	5.5c	172c	42.3 b	10.6bc	36.0b	387b	21.9b	173.b	145.5c
<b>BCP2</b>	312	292b	132b	80.9b	85.7b	588d	31.0b	18.4b	5.8b	182b	43.4 b	11.4a	35.3b	406b	20.4c	183.b	162.1b
<b>Mean</b>		284	126	80.7	84.5	642	29	17.7	5.6	170	41.9	11	32.5	363	20.2	150.4	142.8
<b>CV (%)</b>		8.43	11.9	5.41	5.79	20.2	48	9.6	10.5	16.7	21.1	13.8	21.8	27.3	18.4	43.8	30.2
<b>Ve</b>		192.8	162.5	9.85	14.68	14513	180.68	2.125	0.31	683.2	76.98	1.625	39.58	6342	8.48	4153	2129
<b>Va</b>		275	161.4	9.7	4.3	5542	22.7	2.2	0.03	432	47.4	1.4	5.6	1462	5.5	2243	3618
<b>H<sup>2</sup>n</b>		40.44	50.98	33.56	14.93	26.41	10.39	66.67	8.57	39.45	49.02	42.42	10.11	11.99	47.01	35.78	93.18

Means with different letters are significantly different at  $P < 0.05$ .  $V_e$ =Environmental variance,  $V_g$ =genotypic variance of the F2,  $V_a$ =additive variance of the F2,

$V_d$ =dominance variance of the F2, as calculated using the variance analysis method described by Checa *et al.* (2006) and Mather and Jinks (1971).

### 2.4.3 Heterosis

The high levels of heterosis of the F1 over its parents were observed for all traits (Tables 2.5 and 2.6). The mid-parent (MP) heterosis data with respect to N3 and SC are shown in Tables 2.5 and 2.6. The highest levels of heterosis at Ukulinga Research Farm were for ear mass and yield which gave mid-parent heterosis values of 311.2 and 307.7%, respectively. For both of these traits, heterosis with regards to SC was 996.3% for yield and 772% for ear mass. Other traits with high levels of heterosis at Ukulinga were leaf area, leaf chlorophyll content and ear height, with values of 84.1, 68.3, and 63.8%, respectively, for the mid-parent heterosis. On the other end of the scale, the number of leaves above the ear, 100-kernel mass, number of rows and grain moisture content exhibited the lowest mid-parent heterosis of 15.1, 8, 16.3 and 1.2%, respectively, at Ukulinga.

The highest mid-parent heterosis values at Cedara were 207.2% for ear mass and 143.4% for grain yield. The other high values for heterosis at Cedara were 113.3, 94.2, 66.1 and 61.5% for the total number of kernels per year, number of kernels per row, leaf chlorophyll content and leaf area, respectively. As at Ukulinga, the traits with the lowest levels of mid-parent heterosis at Cedara were the number of leaves above the ear, 100-kernel mass, number of rows and grain moisture content with values of 19.2, 32.6, 11 and 13.1%, respectively. Figure 2.3 shows the visual impression of the levels of heterosis for ear length and girth for the hybrid SR52, relative to its inbred parents.

With respect to yield the data showed the switch of better parent between the sites. The SR52 showed a higher level of heterosis for yield over P1 than P2 at Ukulinga. The reverse was observed at Cedara. The levels of heterosis declined in the F2 for all traits, at both sites.

Table 2.5: Heterosis of the maize hybrid SR52 for the different traits at Ukulinga

Parameter	F1 Heterosis (%)			F2 Heterosis (%)		
	MPH	N3	SC	MPH	N3	SC
Plant height	41	42	40	14	15	14
Ear height	64	59	69	21	17	25
Leaf area	84	55	127	27	7	57
Chlorophyll	68	87	53	7	19	-2
No. leaves above ear	15	25	7	7	16	0
Grain Moisture	1	15	-10	-6	7	-16
No. of kernel rows	16	18	15	12	13	10
Ear length	45	51	39	13	18	8
100 kernel weight	8	29	-7	-2	17	-15
Ear weight	307	166	772	72	12	268
Pollen shed (days)	10	-5	-14	-10	-5	-15
Silk emergence (days)	-11	-7	-14	-2	2	-5
Yield	311	153	996	80	11	379



Table 2.6: Heterosis of the maize hybrid SR52 for different traits at Cedara

Parameter	F1 Heterosis (%)			F2 Heterosis (%)		
	MPH	N3	SC	MPH	N3	SC
Plant height	30	34	25	11	15	7
Ear height	40	39	41	13	12	13
Leaf area	62	42	87	22	7	42
Chlorophyll content	66	121	33	27	69	2
No. of leaves above ear	19	27	13	10	17	4
Grain moisture	13	22	5	2	10	-5
No. of ear rows	11	15	7	10	14	7
Ear length	44	53	36	11	18	5
100 kernel weight	33	45	23	7	17	-1
Ear weight	207	221	195	55	62	49
Days to pollen shed	-9	-9	-8	-6	-6	-5
Days to silk emergence	-10	-9	-10	-6	-6	-7
Kernel depth	56	53	60	30	27	33
No. of kernels on ear row	94	85	105	46	39	54
Ear girth	27	29	26	-58	-59	-59
Tot. no. of kernels	113	110	117	61	59	64
Yield	143	181	115	48	71	31



Figure 2.5: Visual impression of heterosis for ear length of the maize hybrid SR52 (Source T. Musimwa, 2013)

## 2.4.4 Genetic analysis

### 2.4.4.1 Additive-dominance model

The study indicated lack of fit of the additive-dominance model for all traits at Ukulinga (Table 2.7). The same trend was observed for all traits at Cedara, except for the 100 kernel mass, which fitted the additive-dominance model (Table 2.8).

Table 2.7: Lack of fit GMA model showing F-values and their significance for different traits of the maize hybrid SR52 at Cedara

Parameter	Additive (a)		Dominance (d)		Lack of fit of the additive-dominance model	
	F-value	p-Value	F-value	p-Value	F-value	p-Value
<b>100-kernel weight</b>	35.02	<0.0001	10.81	0.00110	15	<0.0001
<b>Leaf area</b>	76.37	<0.0001	368.57	<0.0001	8.82	<0.0001
<b>Ear weight</b>	18.43	<0.0001	185.3	<0.0001	6.74	<0.0001
<b>Yield</b>	21.04	<0.0001	60.8	<0.0001	4.89	0.0002

Table 2.8: Lack of fit GMA model showing F-values and their significance for different traits of the maize hybrid SR52 at Cedara

Parameter	Additive (a)		Dominance (d)		Lack of fit of the additive-dominance model	
	F-value	p-Value	F-value	p-Value	F-value	p-Value
<b>100-kernel mass</b>	27.92	<0.0001	60.8	<0.0001	2.09	0.0649
<b>Leaf area</b>	87.29	<0.0001	304	<0.0001	11.39	<0.0001
<b>Yield</b>	0.28	0.7950	0.07	<0.0001	268.37	<0.0001

#### **2.4.4.2 Genetic effects**

Epistasis was tested for those traits where the lack of fit was significant ( $P \leq 0.05$ ). The ANOVA tables indicated that the generation mean analysis model was highly significant ( $P < 0.001$ ) for all traits submitted for generation mean analysis at both sites. At Ukulinga, additive effects were highly significant for all traits (Table 2.9). The data in Table 2.10 shows a similar trend at Cedara. With regard to the dominance effects, they were significant for most traits, with the exception of leaf area at Cedara (Table 2.10). The same trend was observed for these traits at Ukulinga. The epistasis effects were highly significant at Cedara for grain yield. At Ukulinga, epistatic effects were highly significant for the 100-kernel mass and the ear mass.

Table 2.9: Gene effects for different traits and their standard errors ( $\pm$ SE) for the maize hybrid SR52 at Ukulinga

Parameter	m	Additive	Dominance	Additive X Additive	Additive X Dominance	Dominance X Dominance	Type of non-allelic interaction
Leaf area	470.67 $\pm$ 79.61***	96.08 $\pm$ 13.42***	230.17 $\pm$ 188.87	36.51 $\pm$ 78.47	41.96 $\pm$ 50.46	233.06 $\pm$ 116.26*	_____
100 kernel weight	69.64 $\pm$ 4.42***	-9.29 $\pm$ 0.88***	-43.69 $\pm$ 10.36***	-11.64 $\pm$ 4.33**	20.29 $\pm$ 2.83***	36.64 $\pm$ 6.32***	Duplicate
Ear weight	-4.40 $\pm$ 2.85	-2.87 $\pm$ 9.46***	29.96 $\pm$ 6.86***	10.96 $\pm$ 2.81***	-1.44 $\pm$ 1.89	-9.68 $\pm$ 4.3*	_____
Yield	-38.18 $\pm$ 44.93	33.51 $\pm$ 7.90***	289.42 $\pm$ 107.81**	96.13 $\pm$ 44.21*	-5.11 $\pm$ 29.53	-13.29 $\pm$ 67.40	_____

Table 2.10: Gene effects for different traits and their standard errors ( $\pm$ SE) for the maize hybrid SR52 at Cedara

Parameter	m	Additive	Dominance	Additive X Additive	Additive X Dominance	Dominance X Dominance	Type of non-allelic interaction
Leaf area	481.32 $\pm$ 57.00***	63.89 $\pm$ 9.52***	224.06 $\pm$ 137.95	52.09 $\pm$ 56.08	103.05 $\pm$ 37.67**	156.30 $\pm$ 87.29	_____
100 kernel weight	34.76 $\pm$ 4.20***	-3.02 $\pm$ 0.71***	13.30 $\pm$ 9.99*	3.47 $\pm$ 4.11	3.85 $\pm$ 2.62	2.10 $\pm$ 6.39	_____
Yield	45.17 $\pm$ 20.32*	-9.73 $\pm$ 3.57**	204.16 $\pm$ 48.57** *	47.89 $\pm$ 19.82**	-13.85 $\pm$ 12.93	-21.71 $\pm$ 31.27	_____

#### **2.4.4.3 Relative contribution of genetic effects**

The relative proportion of fixable gene effects (additive and additive x additive effects) and the non-fixable effects (dominance, additive x dominance, and dominance x dominance) for the generation sum of squares varied, depending on the trait. At Ukulinga, the non-fixable genetic effects were predominant for most traits. However, there was an almost equal contribution of the fixable and non-fixable effects for 100-kernel mass (Table 2.11). The non-fixable effects had a larger contribution toward the generation sum of squares for 100-kernel mass.

Table 2.11: Percentage contribution of gene effects to the different traits of the maize hybrid SR52 at Ukulinga

Trait	Additive	Dominance	Additive x Additive	Additive x Dominance	Dominance x Dominance	Fixable	Non-Fixable
Leaf area	16	78.5	4.5	0.1	0.9	20.5	79.5
100 kernel mass	38.5	11.8	7.8	23.7	18.2	46.3	53.7
Ear mass	8.2	82.4	9.4	0	0	17.6	82.4
Yield	10.6	81.7	7.7	0	0	18.3	81.7

Table 2.12: Percentage contribution of gene effects to the different traits of the maize hybrid SR52 at Cedara

Trait	Additive	Dominance	Additive x Additive	Additive x Dominance	Dominance x Dominance	Fixable	Non-Fixable
Leaf area	21	70.3	6.1	1.8	0.8	27.1	72.9
100-kernel mass	24.5	68	5.1	2.3	0.1	29.6	70.4
Yield	8.4	88.5	2.7	0.3	0.1	11.1	88.9

## 2.5. Discussion

### 2.5.1 Analysis of variance

The data was significant for all the traits, indicating significant differences between the generations. This was expected, because the F1 hybrids exhibit hybrid vigour whereas the parents P1 and P2 displayed the effects of inbreeding depression for most of the traits. Theoretically, the F1 mean is expected to be superior to the mean of the F2 and the back-cross generations by at least 50%. According to Falconer (1989), heterosis declines by 50% in the F2 generation. The mean separation test indicated that the differences between the means for most traits, especially between the inbred lines P1 and P2, tended to become smaller as the conditions changed from the low-yielding environment (Ukulinga) to the higher yielding environment (Cedara). This can be explained by the genotype x environment interaction effects. The maize hybrid SR52 was developed at medium altitude (1500 m) from the landraces that were adapted to these high-yield potential conditions around Harare (then Salisbury). The genotype x environment interaction effects (GxE) on the quantitative traits, such as the grain yield of SR52, has been explained in the literature (Rattray, 1988; McCann 2009, Caulfield 2013, personal communications), and in other populations (Hallauer *et al.*, 2010).

The higher environmental variances at Ukulinga was reflected the variation in the population of the parental line P2 (SC5522), in which some plants failed to produce silks. The environmental variance was also reflected by the variation for all the quantitative traits in the other non-segregating populations, such as P1 and the F1 hybrid, at both sites (data not shown). Theoretically, the homozygous inbred lines would be more vulnerable to environmental influence due to the fixed genetic base (Falconer, 1989). In the current study, the additive genetic variance was estimated, because this is the variance that indicates whether or not selection for yield and secondary traits would be feasible in the hybrid SR52. Additive genotypic variance proportion to total genotypic variation was quite pronounced for the yield, but was in the range of medium to high for most of the traits (Bello *et al.*,



2012; Schön *et al.*, 2010). The large heritability for grain yield implies that the population would respond to selection. The heritability for yield was greater than the heritability for secondary traits, indicating that direct selection for yield would be effective. This is in sharp contrast to studies by Smalley *et al.* (2004); Asghar and Mehdi (2010) who reported that heritability was larger for secondary traits than yield. The results are however, consistent with other studies by (Allard, 1960; Mahmud and Kramer 1952; Mather and Jinks 1982; Akbar *et al.*, 2008; Bello *et al.*, 2012), who reported large heritability estimates, exceeding 80% for yield. The medium to large heritability estimates in the current study indicated that the study was generally repeatable, which is encouraging for plant breeders who wish to extract productive inbred lines from the segregating populations of the hybrid SR52. The heritability and phenotypic distribution of all the traits in segregating populations are presented and discussed in Chapter 3.

## **2.5.2 Mean separation**

### ***Flowering traits***

The flowering data of the SR52 hybrid confirmed the observation of significant GxE and reflected its adaptation ability. Under the high-yielding conditions at Cedara, the mean of the two inbred lines did not show any significant differences for the days to silk emergence and days to pollen shed. The generation mean analysis was, therefore, not performed for these traits. The means of the two inbred lines were, however, different at Ukulinga, the days to silk emergence and days to pollen shed. The anthesis to silking interval (ASI) was longer for P2 (4.6 days), compared to P1 (1.8) days. The long ASI explains the low yield potential that was obtained for P2, compared to P1 under the low altitude conditions (low yield potential), at Ukulinga Farm. Failure of the silks to emerge is one of the major weaknesses of the inbred P2 that account for the low yield potential of the inbred line under lowland areas and the stressful low input conditions. At the Makhathini Research Station, which is a lowland station, all the P2 plants failed to produce silks during the winter of 2012. This was also observed during the three preceding seasons. For this reason, the F1

hybrid was used as the maternal parent and the P2 as the male parent in making the backcross generations (i.e. BCP2).

At Cedara, which is generally considered to be a high-yielding environment, the anthesis to silking interval (ASI) for SR52 (F1) was shorter (2.6 days) compared to Ukulinga (3.8 days), further cementing the fact that SR52 is highly adapted to and will therefore give good yield under high potential environment as represented by the Cedara. With regard to SR52's ASI, there is room for improving the hybrid's adaptability particularly in drought-prone areas where farmers have failed to make use of this exceptional hybrid. Such improvements can be made by breeding for a lower ASI, as it is one of the traits which have been reported to be important for conferring drought-tolerance in maize hybrids (Bolanos and Edmeades, 1996). It is, however, possible to breed for a lower ASI in SR52 by introgressing the genes for early silk emergence into the SC parent. This has to be done without disrupting the greater part of the genome of SC, because yield potential can be compromised by the linkage drag. Effective biotechnology tools can be exploited to minimise the effects of linkage drag. Marker assisted backcross (MABC) has been proven to be successful in breeding for traits that improve drought adaptation in maize, such as ASI (Ribaut and Ragot, 2007). A set of DNA markers such as Single Nucleotide Polymorphism (SNPs) markers can be used for background selection.

### ***Plant traits***

The means for SC and N3 were not significantly ( $P>0.05$ ) different for plant height according to the mean separation test  $LSD_{0.05}$  at Cedara and ear height at Ukulinga. With an average plant height of 243.2 and 261.6 at Cedara, as well as 215 and 218.8 cm for N3 and SC respectively, the two inbred lines can be considered to be tall relative to most maize inbred lines. This height could be the main reason behind the high levels of lodging experienced by the taller inbred SC, particularly at Ukulinga. The high levels of lodging could have played a contributory role toward SC's low yield potential at Ukulinga. The tall plants are generally

susceptible to lodging which, in turn, leads to a reduction in yield output (Ji-hua *et al.*, 2007). The observation of extremely tall phenotype for the inbreds P1 and P2 in the current study is consistent with the phenotypic descriptions of these inbred lines (Ndlela, 2012, Personal communication).

### ***Leaf traits***

The means of the two inbred lines were significantly different for the number of leaves above the ear (NLV), at both sites. There was no consistent trend across the sites. SC had higher NLV at Ukulinga, with the opposite being true at Cedara. This is indicative of the presence of genotype by environment interaction effects for the NLV. This was previously reported by Tollenaar and Hunter (1983). There are different schools of thought on the effect of leaf number on grain yield in maize. In comparing two drought-resistant maize hybrids, Ackerson (1983) observed that the shorter hybrid, with a lower number of leaves was more resistant to the effects of drought. The genetic manipulation of leaf number and proportion of leaves, both above and below the ear, has been found to have implications for yield improvement (Shaver, 1983). Previous researchers have reported that a higher proportion of leaf area as a result of greater leaf numbers above the ear compromises the vegetative period, thereby prolonging the grain filling period (Pinter *et al.*, 2012; Shaver, 1983). The higher mean for the leaf area for the F1 hybrid at the two sites can be directly linked to a larger photosynthetic surface area. Consistent with theoretical expectations, the means for the backcrosses, BCP1 and BCP2s, tended to drift closer towards those of their respective parent, as they share a higher percentage of similar genes with the parents. The inferior means of the BCs to the F1 is due to the effects of one generation of inbreeding, which reduces yield due to the inbreeding depression.

### **Grain traits**

The inbred line SC had a high mean for grain moisture content at both sites, confirming the fact that it is a late-maturing inbred line. This high level of grain moisture content was directly proportional to the 100 kernel mass which was observed for the SC kernels at the two locations. At Ukulinga, the means of the inbred lines were the most contrasting for 100 kernel mass and grain moisture content, suggesting that heterosis might be a result of partial dominance. Such an assumption is in agreement with Lu *et al.* (2003) who identified 16 QTLs when working with an F2 population of elite maize for grain moisture content, with most of the QTLs showing partial to complete dominance.

### **Grain yield**

The inbred line N3 completely out-yielded the SC at Ukulinga, indicating its superior adaptation ability. The SC is very difficult to grow and only produces silks under a limited range of conditions, indicating its lower adaptation ability than the N3. At low-altitude areas, such as Makhathini, which is 72m above sea level, the SC does not produce silk. This was observed for three consecutive seasons at the research station. At Ukulinga, which is 809 m above sea level and lies between the low and mid-altitude environments, most plants of SC failed to produce silk. This contributed to its low yield potential and the difference with the N3. However, when grown in areas where it is adapted, the SC performs well. In the current study the SC out-yielded the N3 at Cedara, which is generally considered as a high yielding and higher altitude site (1027 m) than Ukulinga. This altitude makes Cedara fall within the mid-altitude environments, in accordance with the CIMMYT classification system. The mean of the F1 was the highest amongst all the generations, as was expected, because heterosis is highest in the F1 (Azizi *et al.*, 2006; Malvar *et al.*, 2008; Torodovic *et al.*, 2011). The mean yield of SR52 at the high yield potential environment of Cedara was expected to be higher than that of Ukulinga. However, the SR52 (F1) had a higher yield at Ukulinga as a result of the late planting at Cedara. Yield reductions as a result of late planting of maize hybrids have been reported in the literature (Tsimba *et al.*, 2013).

### 2.5.3 Heterosis

Exceptional heterosis of the hybrid SR52 was confirmed by the study. The degree of heterosis varied from trait to trait, as well as across sites, which is consistent with observations of the significant role that was played by the GxE. Even though mid-parent heterosis is generally investigated in many studies on maize, better-parent heterosis is of great importance to the plant breeder, as it is of more economic importance. It indicates whether or not the F1 or the parents should be deployed to the farmers. However, in maize it is generally known that the F1 is superior to the inbred parents. Therefore very few researchers have investigated the better-parent heterosis in maize. The values for better-parent heterosis exhibited by SR52 were quite high for grain yield, with Ukulinga recording 153.1% and Cedara having 114.7%. These values can be considered as exceptionally high, taking into consideration that the inbred lines SC and N3 are generally considered as high-yielding inbreds. This is not consistent with previous studies which indicated lower levels of heterosis in maize hybrids. Ninety-one maize hybrids derived from a diallel cross all had better parent heterosis values that were less than 95% (Hiremath *et al.*, 2013). The negative heterosis value with regards to SC grain moisture is mainly a consequence of higher grain moisture content at harvest in the inbred line, compared to the F1 generation, confirming the fact that the inbred is very late relative to its F1 progenies. Due to hybrid vigour, the F1 reaches physiological maturity earlier than the parents. This indicates that earlier-maturing varieties can be obtained through hybridisation in maize.

With respect to mid-parent heterosis, SR52 was also outstanding. Mid-parent heterosis value of 311.7% was obtained at Ukulinga. In a study on 140 F1 hybrids, Kustanto (2012) observed heritability values ranging from -1.7 to 212.4; this clearly shows that SR52's mid-parent heterosis values are very high. Mid-parent heterosis values of over 100% cannot be entirely explained by dominance gene action. With evidence obtained from the generation mean analysis conducted for SR52, epistasis could be playing a minor but highly significant

contributory role toward the high levels of mid-parent heterosis for grain yield in the hybrid at both sites, as a figure of 180% was also obtained at Cedara for mid-parent heterosis.

The high levels of better parent heterosis that were found in the current study are in contrast to the lower levels that have been reported in the literature. In an experiment involving the highly heterotic Mo17 and B73 lines, Springer and Stupar (2007) reported better-parent heterosis of 64.7% for yield. The results of the current study agree with the higher levels of mid-parent heterosis that exceeded 200%. In a study by Frascaroli *et al.* (2007), the single cross maize hybrid obtained from a cross of B73 and H99 had a mid-parent heterosis value of 239%. Heterosis levels were also different between the two sites, indicating that heterosis of SR52 depends on the environment under investigation. This is explained by the differences in adaptations of the inbred lines at the two sites. The inbred SC had fewer plants with silks emerged, which explains its lower yield potential at Ukulinga and also explains the higher levels of heterosis relative to this line. The line also experienced higher root lodging at Ukulinga than Cedara. These factors contributed to its yield potential. When comparing the two sites used for the experiment, Ukulinga can be considered as a higher stress environment, as it lies in a rain shadow and the soils are very heavy, with poor drainage. The ultimate result that there was higher mid-parent and better-parent heterosis at Ukulinga, compared to Cedara, is in agreement with the work done by Betran *et al.* (2003) and George *et al.* (2011). They found that these two forms of heterosis were higher under stress conditions than non-stress conditions.

This present study confirmed that the farmers would lose a great amount of yield and income by recycling the seed of SR52. At Ukulinga, the SR52 lost 52% of its yield when advanced to the F2 and at Cedara the hybrid lost 39% of its yield due to just one cycle of inbreeding. These findings are in line with the results obtained by Waddington *et al.* (1997). They reported that SR52 lost 41% under both high and low fertilizer application when farmers plant the F2 seed. The findings are in line with the theoretical expectations that heterosis declines by about 50% in the F2 generation (Falconer, 1989). This has great

implications for farmers who wish to recycle seed. The present study showed that farmers stand to lose heavily by recycling the SR52 seed and there are implications for smallholder farmers, who have a tendency to recycle hybrid seed on-farm.

#### **2.5.4 Genetic Effects**

The study indicated that many traits were significantly different between the P1 and P2 judging from the mean separation test results (Steel and Torrie, 1980). This high level of phenotypic differences between the parental lines indicates that there is a high level of genetic divergence between the inbred parents, qualifying SR52 as a suitable hybrid for conducting the generation mean analysis. The results are consistent with previous studies. Ndlela (2012) found that there were significant differences between P1 and P2 for eight of the 14 traits that were measured across four locations in Zimbabwe. The high level of phenotypic differences for many traits partly explains the exceptional levels of heterosis of SR52 that have been confirmed in the present study. Falconer (1989) indicated that heterosis is caused by the genetic divergence between the parents. Unfortunately the magnitude of the means of the parents depended on the sites and, in particular, GxE, as in many previous studies, which tend to affect the levels of difference between the means of the two parents. As a result, different researchers have used different number of traits for the generation mean analysis. Some researchers found only a few traits to be divergent between the inbred parents. This can be explained by the masking of genetic effects by the large GxE. Checa *et al.* (2006) used only three traits in beans, while Yeboah *et al.* (2008) used six traits in cucumber for the generation mean analysis (GMA). In the current study, 11 traits were significantly different between the parents of SR52 at each of the two sites. It was considered prudent to subject only four traits, whose progenitors showed sharp contrast in one or all the environments, to the GMA. This is, however, in contrast with previous researchers, who found significant differences for many traits between the hybrid parents and used all of them for the GMA. Shahrokhi *et al.* (2011) subjected 13 traits to generation mean analysis in maize in two populations. Shahrokhi *et al.* (2011) have reported

high heritability estimates for most of the traits under investigation. They have given a range of 82% to 90% for the hybrid KE72012 x K1263/1, and between 78% and 92% in the B73xMo17 based on five formulas. In the current study, heritability was large at both sites and approximated 91% for yield, which explains why the study managed to reveal large phenotypic differences for many traits between the two inbred parents of the SR52.

A survey of the literature indicates that the discretion regarding which traits should be, or should not be, subjected to GMA analysis can be based on the mean separation tests. In the current study, the trait mean data that did not show any significant differences at  $P=0.05$  between the P1 and P2 was rejected and therefore not submitted to GMA. This is in agreement with previous researchers such as Mushongi *et al.* (2013). Other previous researchers have submitted all the traits to GMA analysis regardless of the lack of significant differences between the parents. Kere *et al.* (2013) tested four traits and found that two were not significantly different but still submitted all the traits for GMA. Even though the mean separation test was initially conducted, Mihaljevic *et al.* (2005) went on to submit all traits including those whose data did not exhibit any differences between the inbred parents. The reason could be the challenges of obtaining the extreme phenotype for the quantitative traits, which are greatly influenced by the environment. The differences between the P1 and P2 are masked by the large GxE and large environmental effects, as reflected by low heritability in stress-prone lowland environments. However, it is recommended that sound experimental management should be implemented to maximise heritability and reveal phenotypic differences between the parents for GMA and that the mean separation test should be used to indicate the differences. It is also recommended that only the data that show significant differences between the inbred parents should be used for the GMA in all crops, because the GMA assumes that there is divergence between the two inbred parents.

Data from the two locations did not adequately fit a simple additive-dominance model. The study indicated the lack of fit of the additive-dominance model for explaining most of the



quantitative traits of the maize hybrid SR52. This implied that epistasis played a significant role in conditioning these traits, in addition to the additive and dominance gene effects. It was therefore prudent to test for epistasis for all the traits that showed a lack of fit for the additive-dominance model. This is consistent with the previous studies of (Zalapa *et al.* (2006) Lyimo *et al.* (2011) and Kere *et al.* (2013) and recommendations by Mather and Jinks (1982).

### ***Leaf area***

Gene effects in the form of dominance x dominance had a major role to play for the leaf area. Additive gene effects were highly significant for leaf area, indicating that this trait can be improved through many selection methods and the genes can be fixed into lines. Significantly high values of additive x dominance (ad) effects which are not fixable were observed at Cedara for leaf area, with Ukulinga having a high proportion of dominance x dominance. This is in agreement with previous studies (Iqbal *et al.*, 2010).

### ***100 kernel mass***

The 100-kernel mass was of particular interest, as dominance was the main genetic effect at both sites. However, the dominance effects were positive at Cedara and negative at Ukulinga. This would imply that the environment effect played a major role on the genes responsible for this trait. In spite of this, the fact is that having dominance as the main gene effect for a particular trait makes it difficult for breeders to select for that particular trait in the long term (Zdunic *et al.*, 2008). This indicates that kernel mass can be improved by the hybridisation strategy. The absence of significant epistatic gene effects at Cedara for 100 kernel mass implies that the value for both additive and dominance effects are unlikely to be biased, as all forms of epistasis tend to compromise such effects (Viana, 2005). Dominance and dominance x dominance gene effects indicated that no complementary type of interaction was present in the genetic control of this trait. This kind of interaction is

termed “duplicate epistasis” and is known to hinder improvement through selection (Azizi *et al.*, 2006).

### ***Ear weight and grain yield***

The gene effects trend for yield was similar for the two sites and indicated that dominance gene action is the basis for the exceptional grain yield of the hybrid SR52. The highest contribution toward yield was a result of dominance gene action and additive x additive epistasis. The importance of dominance as the basis of high grain yield potential of the hybrid SR52 is consistent with previous investigations of other hybrids in the USA. In a study by Azizi *et al.* (2006) on the elite and famous hybrid (just as famous as SR52 in Africa) of B73 and Mo17 at several planting densities, the dominance gene effects contributed the greatest magnitude of gene action for grain yield. Dominance gene effects have also been cited by several other researchers as being more important in comparison to additive gene effects, especially under high-yielding environments (Ceballos *et al.*, 1998; Malvar *et al.*, 2008). The presence of additive x additive gene effects is encouraging for breeders hoping to fix the SR52’s yield by extracting productive inbred lines. These additive x additive effects are fixable and exploitable in intra-population improvement (Sofi and Rather, 2007). Additive effects had a negative effect at Cedara, suggesting an opposite nature of interaction with additive x additive gene action for yield and as such could compromise yield. Contrary to findings in the current study, the additive component was reported to be two-to-four-fold larger than the dominance component (Sofi and Rather, 2007). Although epistasis was absent in studies by Sofi and Rather (2007), some studies detected the presence of epistasis effects for grain yield (Hinze and Lamkey, 2003). It is encouraging that for SR52 only additive x additive epistasis which has breeding value, is present. Breeding procedures, such as pedigree selection, can be exploited in an endeavour to fix yield in the presence of additive x additive epistasis. Overall, the high magnitude of dominance effects for yield indicates that a breeder stands to achieve more success by exploiting heterosis, compared to recurrent selection to develop a new population and to extract inbred lines. The additive x additive gene effects could suggest the presence of complementary QTL for grain yield in the hybrid. This was suggested by previous investigators (Lyimo *et al.*, 2011).

### **2.5.5 Relative contribution of fixable and non-fixable genetic effects**

The ratio of fixable and non-fixable genetic effects was estimated by taking additive and additive x additive genetic effects as the fixable component. Dominance, additive x dominance, and dominance x dominance effects are the non-fixable components (Gregorio, 2002; Mushongi *et al.*, 2013). Non-fixable gene action, mainly in the form of dominance, was the highest contributor for all traits at the two sites, with the exception of grain moisture at Ukulinga. Percentages of 81.7% and 88.9% for non-fixable gene action for yield at the two sites can, however, be taken as overwhelming evidence that the non-fixable component contributed toward the hybrids' yield. Dominance gene action contributed 100% of the non-fixable gene action for yield, implying that selection for yield in the SR52 population would prove to be a futile exercise; but that the hybridisation strategy would be the most effective to exploit the non-additive variation in the hybrid.

### **2.6 Conclusion and implications**

Analysis using the generation variances showed that additive genetic variation was significant and important for most traits in SR52, indicating that selection would be effective to derive new inbred lines. The generation mean analysis, which was the main experimental method in this study, revealed that dominance gene action is the basis of the exceptional heterosis, which is displayed by the maize hybrid SR52. Significant epistatic gene effects were negligible (less than 20%) for the yield and most of the secondary traits. This has implications for breeding strategy and suggests that good inbred lines must be selected on the basis of their performance in crosses. High levels of mid-parent heterosis of 311% and 143% for SR52 were confirmed at Ukulinga and Cedara, respectively. This is exceptional heterosis and explains why the SR52 is such a great hybrid. It can be concluded, therefore, that SR52 is such an exceptional hybrid due to dominance gene effects that confer exceptional heterosis.

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## CHAPTER THREE

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### CORRELATION AND PATH COEFFICIENT ANALYSIS IN SR52 MAIZE HYBRID

#### Abstract

Although exceptional heterosis for yield in SR52 has been confirmed, the role of secondary traits has not been established. The objectives of this study were to establish the relationship between grain yield and its secondary traits, as well as assessing the genotypic variation in SR52's segregating F2 and backcross populations. The knowledge of the associations between yield and secondary traits would be crucial for breeders who aim at extracting productive inbred lines from the population. Grain yield and other traits were subjected to correlation and path coefficient analysis in SAS computer program. The path analysis model accounted for more than 70% of the variation ( $R^2$ ) in all populations. High positive correlations amongst secondary traits were observed for days to pollen shed and days to silk emergence, leaf area and plant height, grain moisture content and 100-kernel mass. The traits that had a highly consistent positive correlation with grain yield were ear mass, ear length and number of kernel rows on ear. The same traits, with the addition of ear components such as ear girth, number of kernels per row and total number of kernels on ear, had a high direct effect on yield. A few major indirect effects were observed; plant height had total correlation with grain yield, boosted through indirect association with traits such as ear length at Ukulinga and number of kernel rows on ear at Cedara. Substantial phenotypic variation, particularly in the F2 and BCP2 populations was noted with the presence of transgressive segregants. Ear length and mass can be exploited for the indirect selection for grain yield in SR52's segregating generations. The 100-kernel mass, and number of kernel rows on ear can to a lesser extent be exploited in selecting for grain yield. The presence of phenotypic variability in the segregating generations of SR52 gives impetus for selecting productive inbred lines from the hybrid.

### 3.1 Introduction

Maize is the staple food in many Third World countries, including South Africa. The diversification of diets in developed countries coupled with health-related reasons such as gluten intolerance and diabetes, have increased the demand for maize human consumption (Malvar *et al.*, 2008). Among the three most important cereals in the world, maize is the cheapest to produce, making it the most appropriate carbohydrate source for the resource-poor and subsistence farmers in some of the poorest parts of the world, especially Africa (Fuglie, 2004). Southern Africa has the highest per capita maize grain consumption in the world (FAO, 2013). This prompts research on the crop to increase maize yield in order to match consumption. For the past four decades, maize production has been lagging behind population growth in the world (Jayne *et al.*, 2006). Therefore it is important to devise strategies that can be used to enhance the yield of maize in Africa.

With huge success in its country of origin, Zimbabwe, and throughout most of eastern and southern Africa, SR52's ability to give exceptional yield potential cannot be questioned. The single cross hybrid parents, N3 and SC, represent a heterotic pattern that has been exploited in main maize breeding programs across Africa. With this in mind, new inbred lines can be obtained from the SR52's segregating generations. The new lines could possibly be exploited in the development of several high yielding hybrids, with the potential of raising Africa's maize yield potential. However, selection for inbred progenies with high grain yield potential can be compromised if there are any significant negative associations between grain yield and its secondary traits.

The efficiency of a breeding programme is mainly determined by the direction and size of the association between yield and its associated traits, as well as the contribution of each trait towards grain yield potential. Taking into consideration that grain yield is quantitatively inherited, improvement in grain yield can only be effective when there is simultaneous

improvement in yield components as well (Bello and Olaoye, 2009). All yield-contributing traits require close analysis, with breeders placing more breeding effort on those that contribute the most towards yield (Abirami *et al.*, 2007). Ample knowledge of traits that are significantly associated with yield is crucial, as such characters can be used as an indirect selection criterion for yield enhancement (Ojo *et al.*, 2006). The existence of a significant positive or negative correlation between two traits implies that selection for either of the traits will result in a shift on the other, depending on the size of the correlation (El-Shouny *et al.*, 2005). Unfortunately, the relationship between grain yield potential and secondary traits is not known in SR52. This affects the designing of an optimum breeding strategy for deriving productive maize inbred lines.

The correlations are measures of mutual association with regards to cause. The implications of this are that most decisions based entirely on correlation coefficients may not be of much help, particularly for plant breeders (Basalma, 2008). The best possible scenario for a breeder is when major yield-contributing traits are positively correlated. Under such circumstances, breeding for those particular yield-contributing traits would be effective. A more complicated situation arises when negative associations are significant for yield-related components. Under such a scenario, simultaneous selection for those traits becomes extremely difficult (Bello *et al.*, 2010). It is therefore important to determine the direction of the correlations and the level of their contribution to grain yield potential.

The contribution of individual traits to the grain yield in SR52 can be established by path analysis. The path analysis partitions correlation coefficients into their direct effects on yield and indirect effects on yield through other independent variables (Toebe, 2013). Path coefficient analysis is of much utility to the plant breeder as it determines the exact correlation in terms of cause and effect (Hefny, 2011). Mohammadi *et al.* (2003) stated that during analysis of the actual contribution of each trait toward yield, challenges can be faced as the effects are confounded as a result of collinearity. Unfortunately the direct and

indirect effects of the secondary traits on the outstanding yield potential of SR52 have not been reported in the literature.

Another important concept of high utility in devising the breeding strategy is the heritability. Knowledge of heritability of a trait is key and also a prerequisite for improvement of the trait (Hepziba *et al.*, 2013). There are two types of heritability, namely broad and narrow sense heritability. Broad sense heritability is the proportion of the total genetic variance to the phenotypic variance. However, it is the narrow sense heritability, which is the ratio of additive genetic variance to the total phenotypic variance, which is of utility to plant breeders (Falconer *et al.*, 1996). This is because narrow sense heritability indicates the level of additive genetic variation which can be exploited by selection of productive individuals. Therefore, narrow sense heritability estimates are used to predict the expected gains from selection (Holland *et al.*, 2003). Heritability values can vary for different family structures obtained from the same base population, and between different populations. The study of heritability from the family structures is crucial in determining the family or generation which can be exploited in order to boost genetic gain over time (Burton and Carver, 1993; Holland *et al.*, 2003). The heritability of yield and secondary traits in the maize hybrid SR52 has never been reported in the literature.

The hybrid SR52 has been shown to exhibit high levels of heterosis for grain yield (see Chapter 2), but the traits that contribute towards these high levels of heterosis have not been unravelled. The main objective of the present investigation was to estimate heritability and to determine the relationships among traits of the hybrid SR52. Most importantly the study aimed at establishing the traits which make the highest direct and indirect contributions to the exceptional yield potential of the hybrid SR52.

## **3.2 Materials and methods**

### **3.2.1 Germplasm**

Six generations of the single cross hybrid SR52 were planted at Ukulinga and Cedara Research stations in South Africa on the 15 of November and 13 of December 2012, respectively. The generations were made up of the two parental lines N3 (P1), SC (P2), F1, F2, BC(N3) (BCP1) and BC(SC) (BCP2). The generations were developed as described in Chapter 2.

### **3.2.2 Trial design and management**

The experiment was laid out as a randomised complete blocks design, with two replications per site. Each of the non-segregating generations (P1, P2 and F1) were planted in five rows each. The segregating generations (F2, BCP1 and BCP2) were planted in 10 rows each. Each of the rows was 5m long with inter-row spacing of 0.75m and intra-row spacing of 0.3m. Three seeds were planted per station and thinned down to one, three weeks after emergence. Each row could accommodate 17 plants after thinning, giving a potential of 85 plants for the non-segregating generations and 170 for the segregating generations at each site. The experimental design and management are described in detail in Chapter 2.

### **3.2.3 Data collection**

Data was collected from all plants for each generation, following standard protocols used at CIMMYT (Magorokosho *et al.*, 2009). The following traits were measured as described in Chapter 2: grain yield, grain moisture content, ear mass, ear length, ear height, plant height, days to silk emergence, days to pollen shed, kernel rows on ear, number of kernels per row, total number of kernels on ear, number of leaves above primary ear, leaf chlorophyll concentration, leaf area, ear girth and kernel depth.

### 3.2.4 Data analysis

#### 3.2.4.1 Frequency distribution of phenotypic traits

For the traits measured, frequency distribution was plotted for the F2, BCP1 and BCP2 populations, using GenStat computer package. Variations within a phenotype were observed by creating groups for each trait with respect to differing values. Phenotypic variation of each of the segregating populations was detected from the distribution of phenotypic traits.

#### 3.2.4.2 Heritability

Narrow sense heritability ( $h^2$ ) was estimated using estimates of variances of segregating generations from the single cross (Warner *et al.*, 1952; Kere *et al.* 2013; Lyimo *et al.*, 2011; Roy, 2000; Fehr, 1991).

$$h^2 = \frac{2VF_2 - (VB_{CP1} + VB_{CP2})}{VF_2}$$

Where,

$h^2$  = narrow sense heritability

$VF_2$  = phenotypic variance of the F2 generation

$VB_{CP1}$  = phenotypic variance of backcross to parent 1

$VB_{CP2}$  = phenotypic variance of backcross to parent 2

### **3.2.4.3 Correlation and path coefficient analysis**

Data was analyzed using the Proc GLM procedures of the SAS statistical program (SAS institute, Cary N.C). Correlations were determined using Pathsas (Cramer, 1998). Grain yield and ear mass as the dependent variables were analyzed against other traits as independent variables.

## **3.3 Results**

### **3.3.1 Frequency distribution of phenotypic traits**

Frequency distributions of selected traits of the segregating generations are shown in Figures 3.1 to 3.9. A continuous distribution curve was observed for all traits. Generally the histograms showed positive or negative skewedness for most of the traits. With regards to yield, a high proportion of barren plants, particularly in the F2 (44%) and BCP2 (33%), were observed at Ukulinga. Though to a lesser proportion, the same two generations had 12% to 20% barren plants at Cedara. . The F2 population had a sizeable proportion of plants on the higher yield end bracket at Ukulinga, compared to the two backcross populations at the same site.

With regards to the traits such as ear length, hundred kernel mass, plant height, ear height, number of kernels on ear row and total number of kernels on ear, the backcross to SC population (BCP2) had a greater frequency of plants in the higher end values. Observations for the number of kernel rows on ear was of particular interest, because ears with 16 kernel rows were observed in the F2 generation at both sites, as well as in the BCP1 population at Ukulinga. For both parents and the F1 generation, the maximum number of kernel rows that was observed was 14 at both sites.



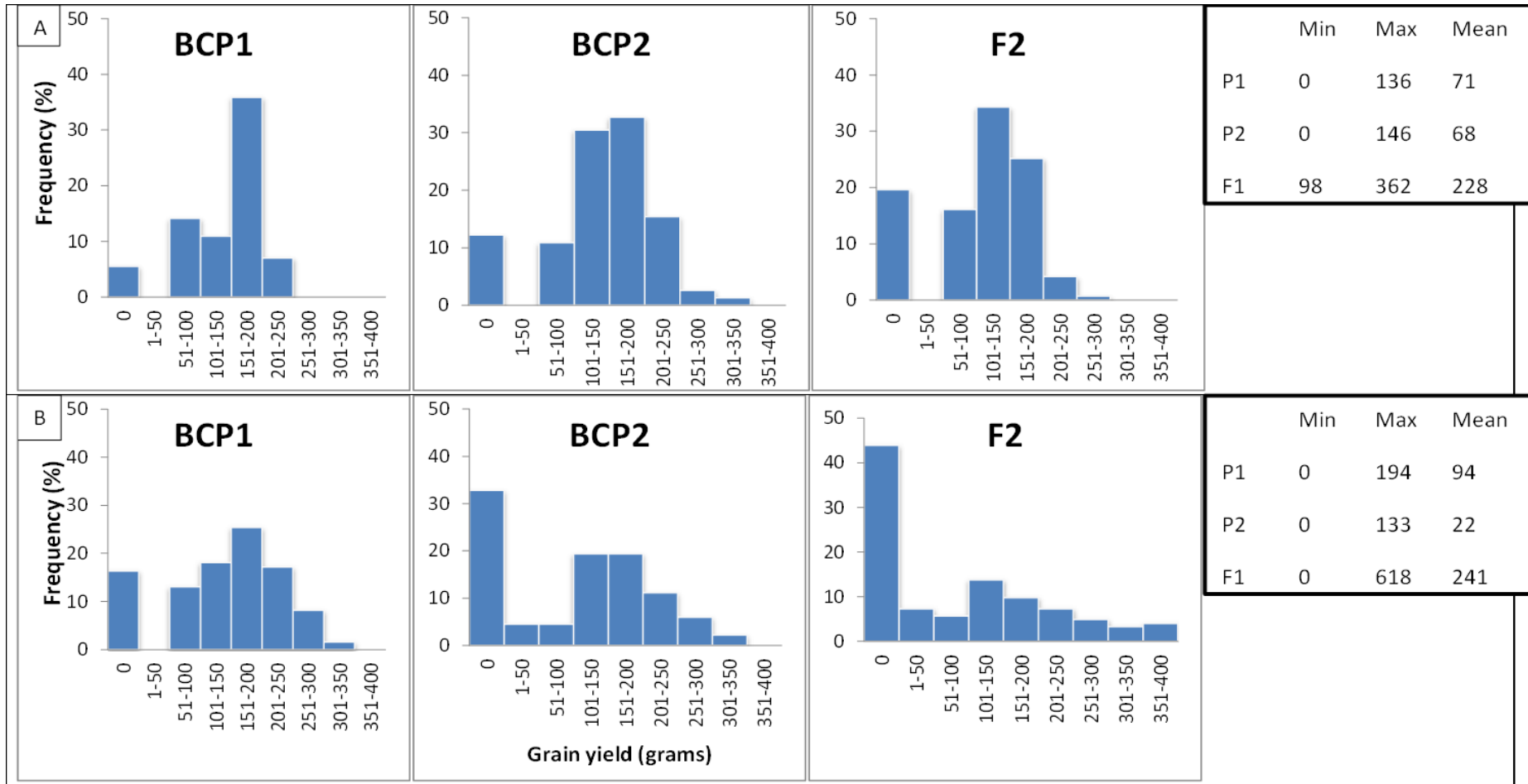


Figure 3.1: Frequency distribution of grain yield data of generations at A) Cedara and B) Ukulinga

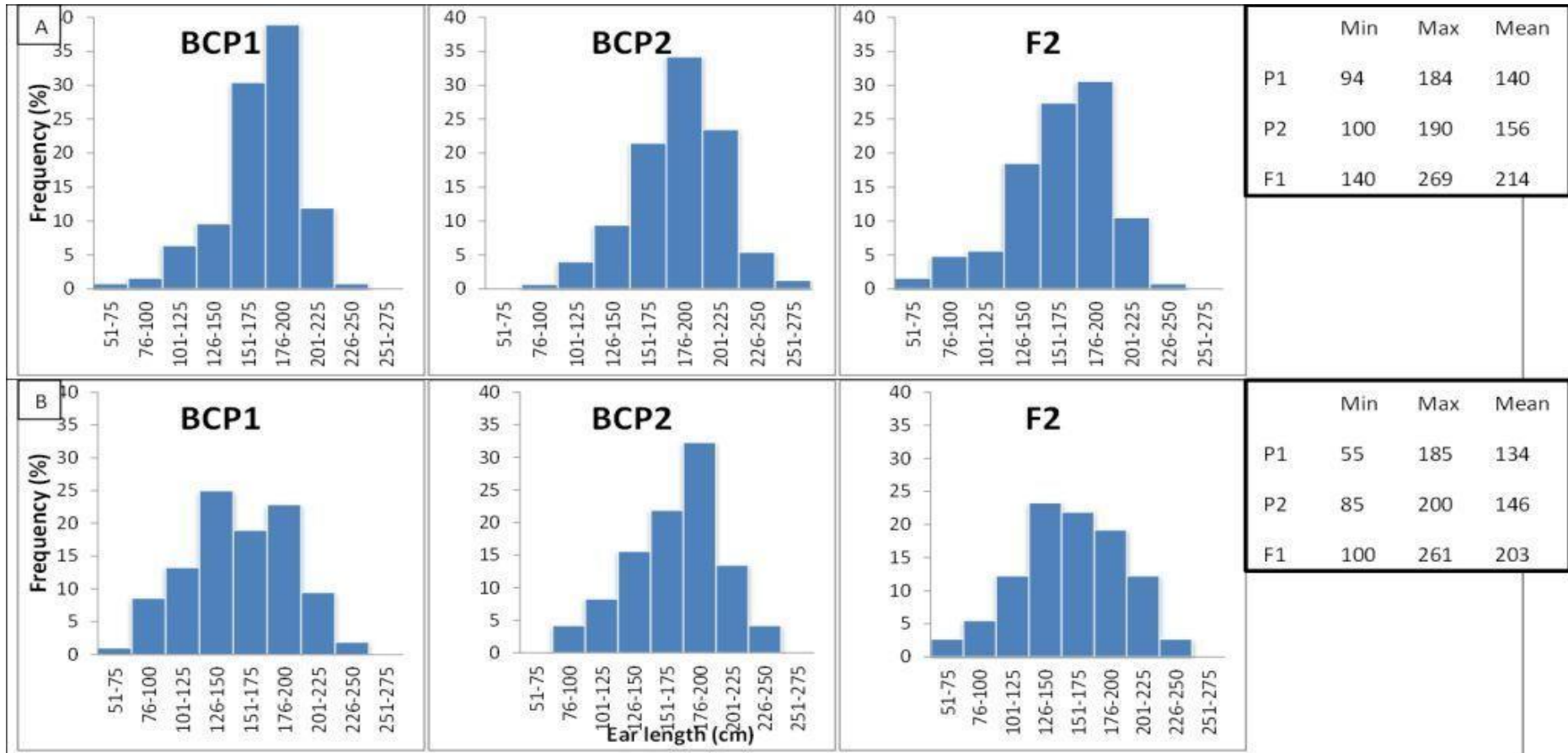


Figure 3.2: Frequency distribution of ear length data of generations at A) Cedara and B) Ukulinga

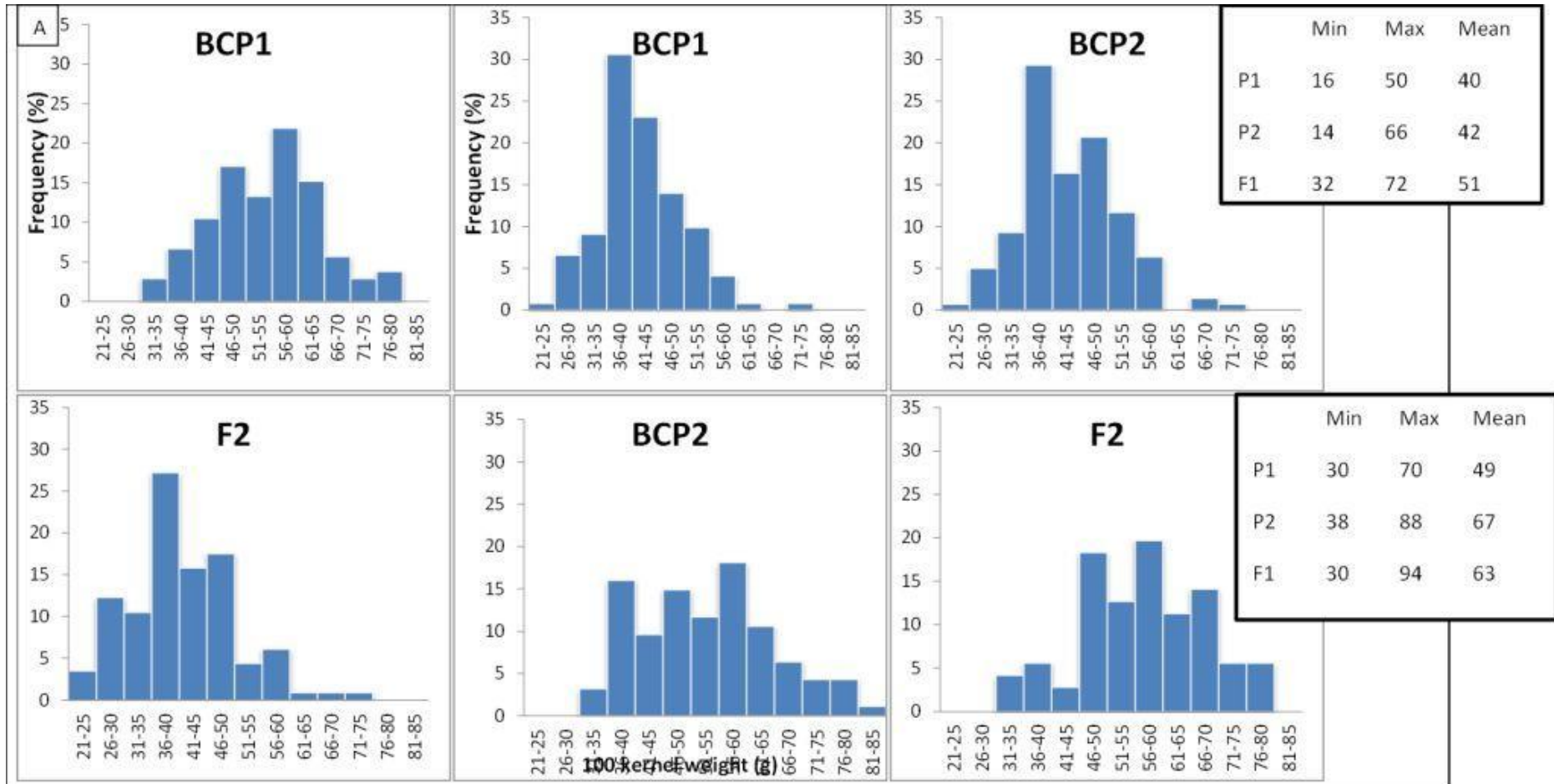


Figure 3.3: Frequency distribution of hundred kernel mass data of generations at A) Cedara and B) Ukulinga

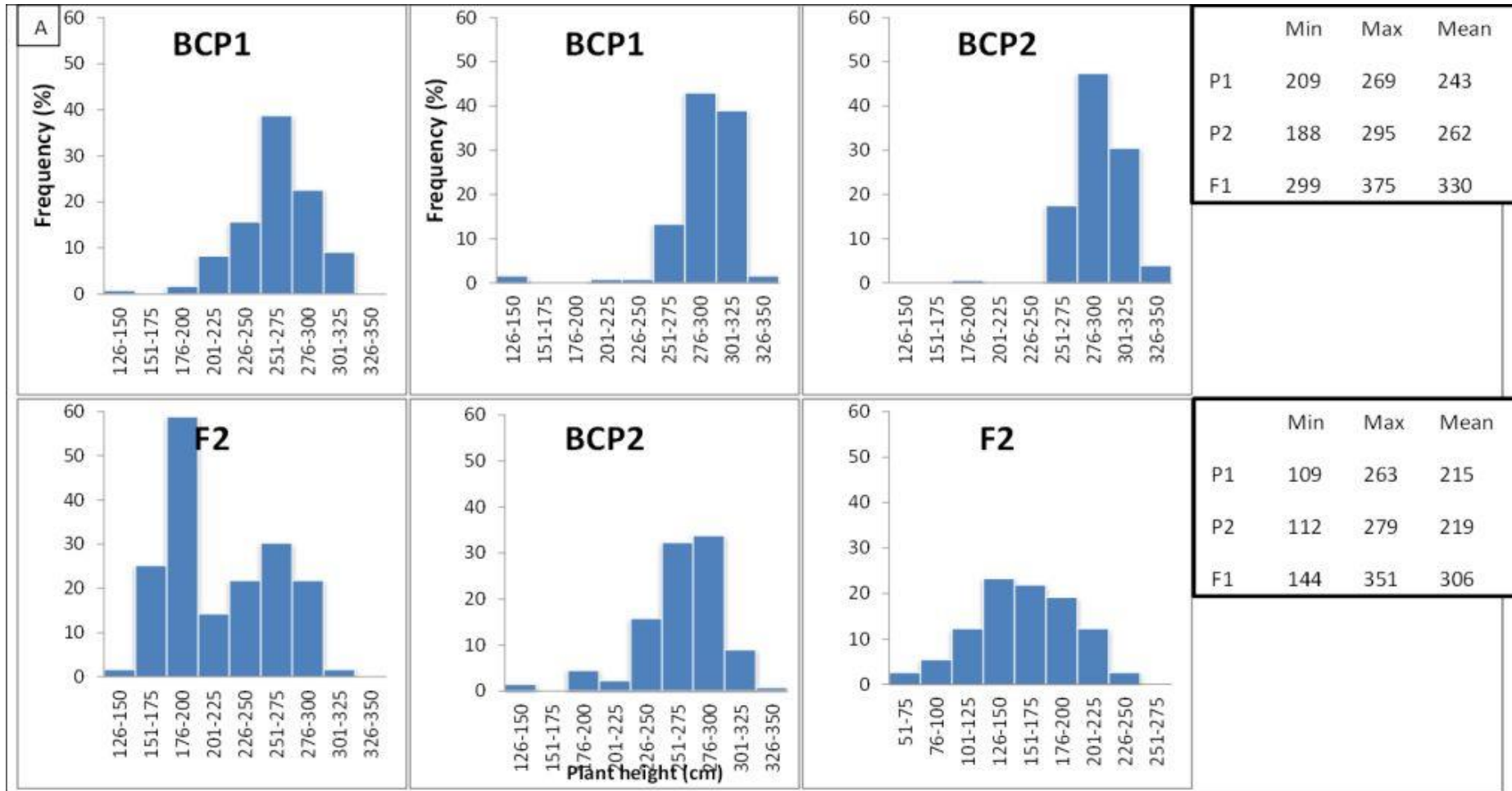


Figure 3.4: Frequency distribution of plant height data of generations at A) Cedara and B) Ukulinga

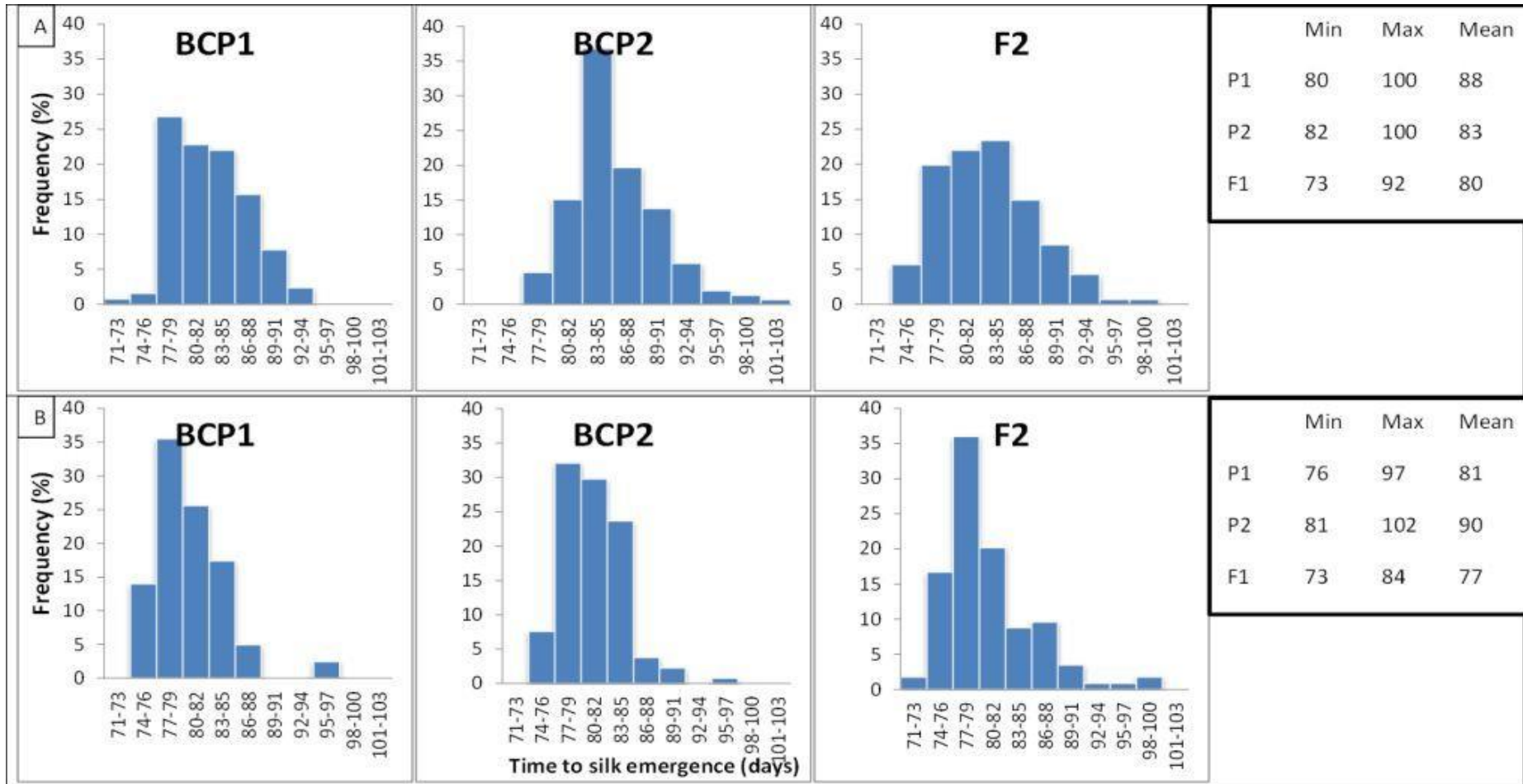


Figure 3.5: Frequency distribution of days to silk emergence data of generations at A) Cedara and B) Ukulinga.

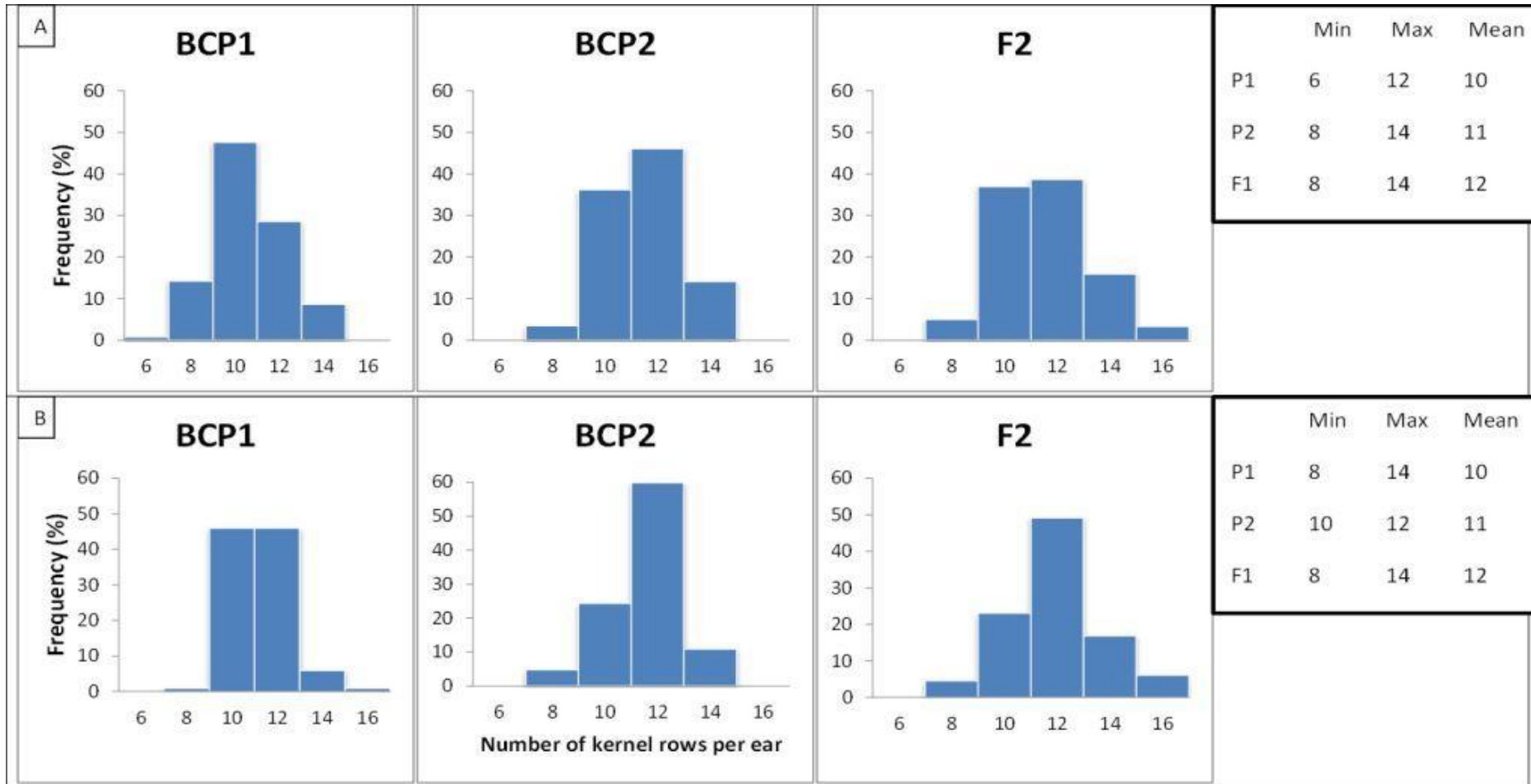


Figure 3.6: Frequency distribution of number of kernel rows per ear data of generations at A) Cedara and B) Ukulinga

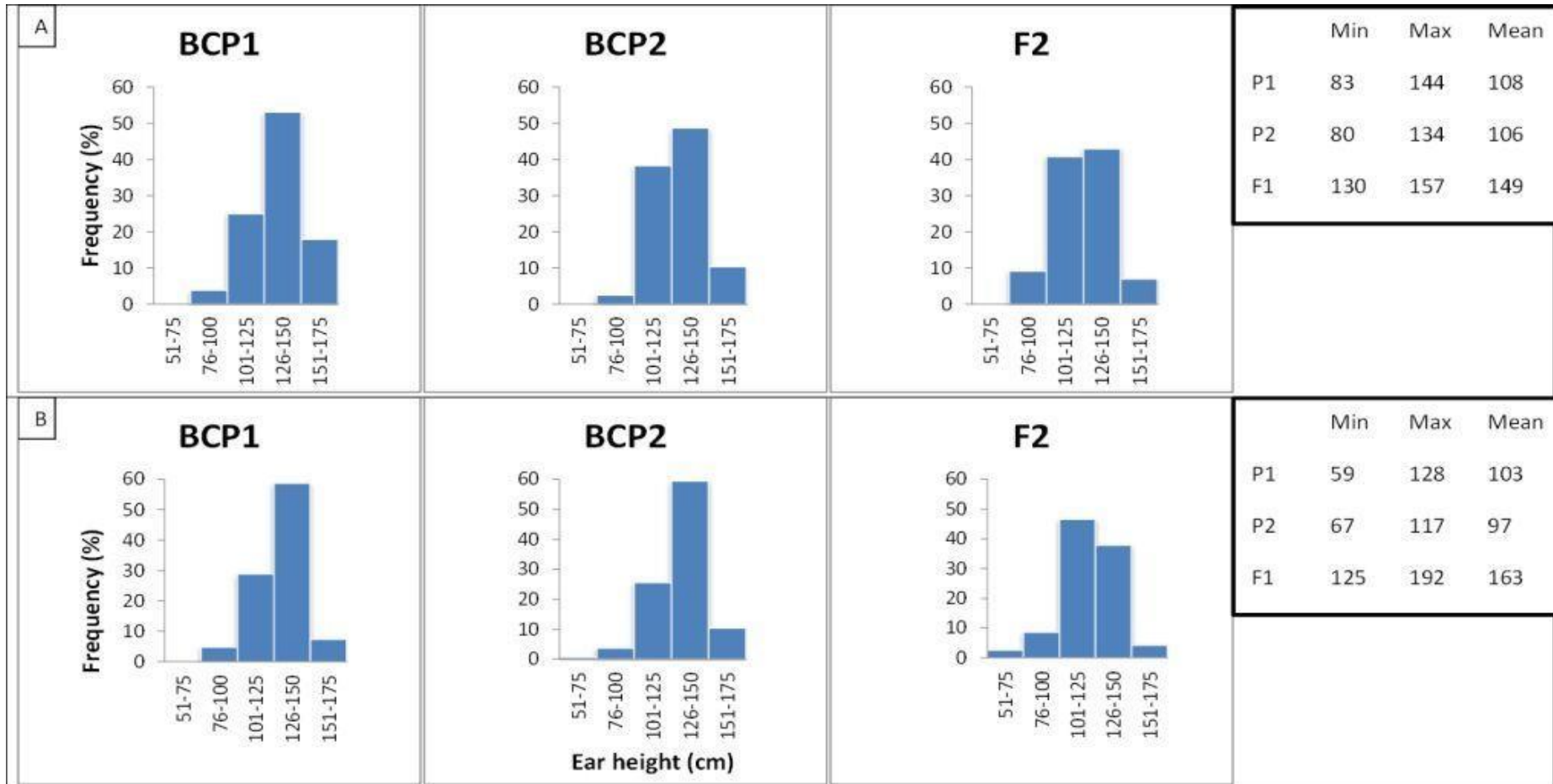


Figure 3.7: Frequency distribution of ear height data of generations at A) Cedara and B) Ukulinga

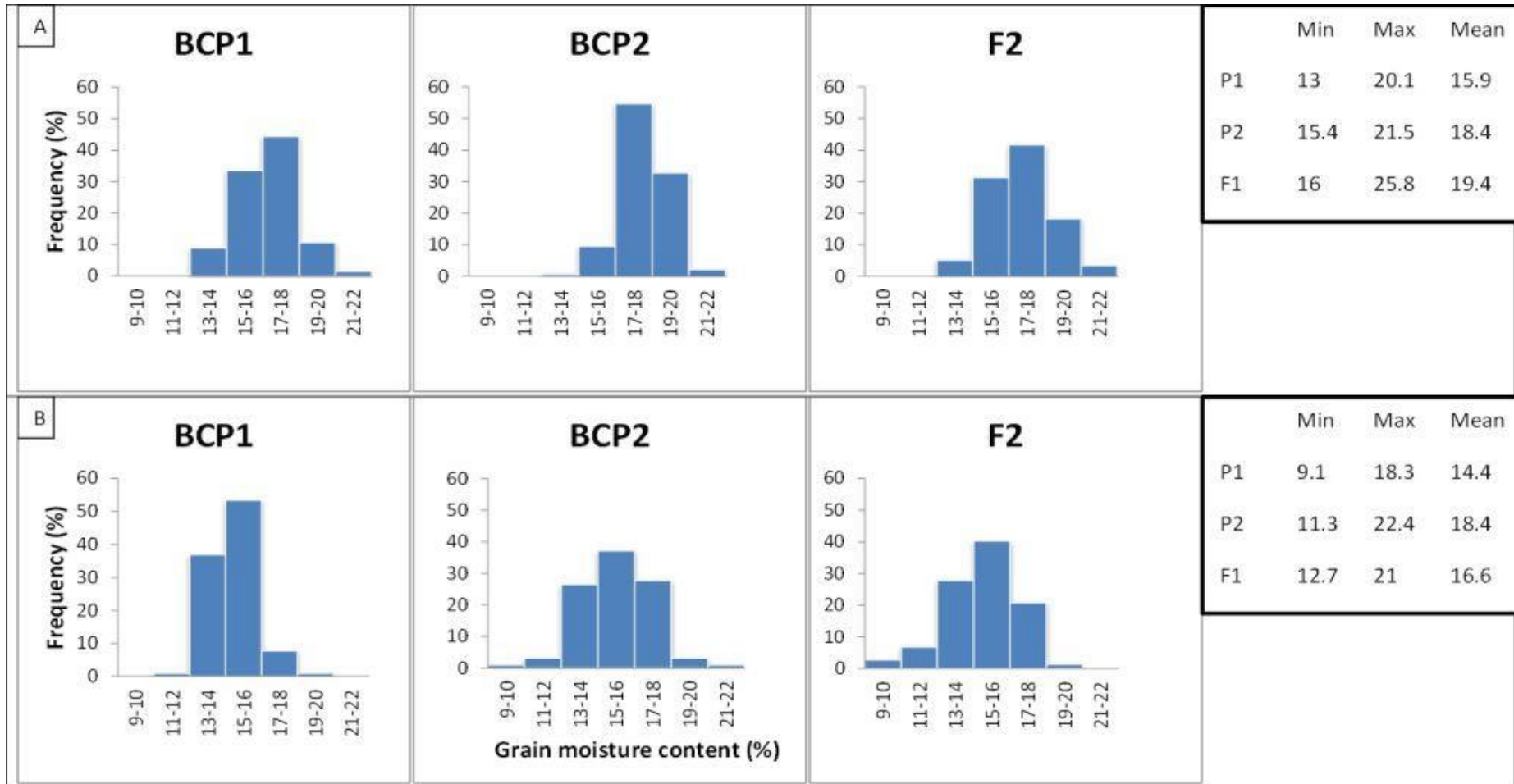


Figure 3.8: Frequency distribution of grain moisture content data of generations at A) Cedara and B) Ukulinga



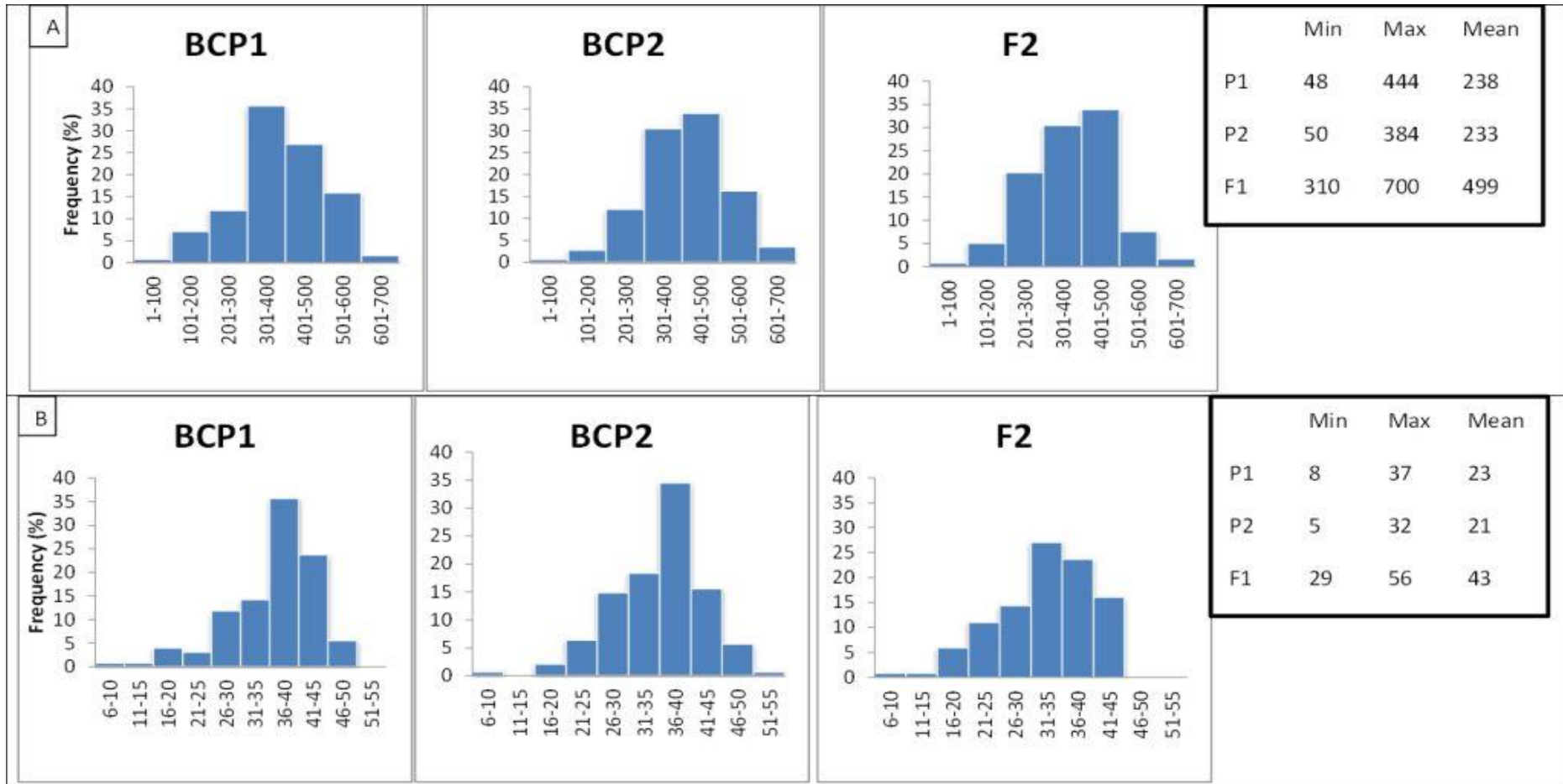


Figure 3.9: Frequency distribution of A) total number of kernels on ear and B) number of kernels on ear row at Cedara

### 3.3.2 Correlation

#### Ukulinga

Tables 3.1 and 3.2 indicate that ear mass had the highest positive correlation with yield at both sites. For the F2 generation the following traits were positively correlated with yield: plant height (0.49\*\*), leaf area (0.35\*\*), ear length (0.67\*\*) and number of kernel rows per ear (0.50\*\*). Days to silk emergence (DMS) had one of the highest significant negative correlations with yield in all the generations. Highly significant positive correlations of above 0.40 were observed for DMS and days to pollen shed (DMP) for all generations at the site. With the exception of DMP and DMS, all traits had a positive significant correlation with yield in the BCP1 generation. Significant positive correlations observed in the BCP2 generations were mainly for agronomic traits such as leaf area (0.50\*\*) and plant height. Days to silk emergence were negatively correlated to plant height (-0.26\*\*) and ear height (-0.21\*\*), respectively. The highest significant correlations observed in the BCP2 generations were for plant and ear height (0.68\*\*), plant height and leaf area (0.43\*\*), number of leaves above ear and leaf chlorophyll content (0.98\*\*), ear mass and ear length (0.70\*\*), grain moisture content and number of leaves above ear (0.70\*\*).

#### Cedara

Tables 3.3 and 3.4 show simple correlations between traits at Cedara. As was the trend at Ukulinga, ear mass (EWT) had the highest positive correlation with grain yield for all generations. Yield components such as 100 kernel mass (HKWT), total number of kernels per ear (TKRNL), ear length (ELTH) and number of kernels in a row (KPRW) were consistently positively correlated with yield in all the generations. The trend of high positive correlations that were observed at Ukulinga for DMS and DMP were also manifested at Cedara. As was the case at Ukulinga, plant and ear height data were positively correlated (0.69\*\*) in the F2, (0.68\*\*) in the BCP2 and (0.45\*\*) in the BCP1 generation. Hundred kernel mass was also significantly correlated with yield, correlation values of (0.32\*\*), (0.42\*\*) and (0.48\*\*) in the F2, BCP2 and BCP1, respectively were observed.

Table 3.1: Phenotypic correlation coefficients between SR52 traits in the F2 population at Ukulinga

Trait	DMP	DMS	PHT	EHT	CHL	LA	NLV	ELTH	EWT	NRW	MST	HKWT	GYLD
DMP	<b>1.00</b>	0.80**	-0.21	-0.06	-0.10	-0.25*	-0.16	-0.19	-0.23*	-0.19	0.11	0.02	-0.16
DMS		<b>1.00</b>	-0.52**	-0.20*	-0.10	-0.40	-0.26*	-0.25*	-0.40	-0.35	0.14	0.11	-0.43**
PHT			<b>1.00</b>	0.72**	0.06	0.57**	0.26**	0.47**	0.43**	0.37**	0.24*	0.22	0.49**
EHT				<b>1.00</b>	-0.06	0.29**	0.02	0.18	0.19	0.02	0.20	0.26**	0.11
CHL					<b>1.00</b>	0.06	0.10	0.05	0.20	0.07	-0.01	0.01	0.00
LA						<b>1.00</b>	0.18	0.25	0.44**	0.19	0.33*	0.36**	0.35**
NLV							<b>1.00</b>	0.17	0.32**	0.15	-0.12	-0.05	0.12
ELTH								<b>1.00</b>	0.68**	0.44**	0.37**	0.17	0.67**
EWT									<b>1.00</b>	0.46**	0.35**	0.19	0.99**
NRW										<b>1.00</b>	-0.11	-0.20	0.50**
MST											<b>1.00</b>	0.60**	0.21
HKWT												<b>1.00</b>	0.13
YIELD													<b>1.00</b>

† DMP=days to pollen shed; DMS=days to silk emergence; PHT=plant height; EHT=ear height, CHL=leaf chlorophyll concentration; LA=leaf area, NLV=number of leaves above primary ear; ELTH=ear length; EWT=ear mass; NRW=number of kernel rows per ear; MST=grain moisture; Hundred kernel mass; GYLD=grain yield. \*\*= significant at (P<0.01); \*=significant at (P<0.05)

Table 3.2: Correlation between SR52 traits in the BCP1 (below diagonal) and BCP2 (above diagonal) populations at Ukulinga

Trait	DMP	DMS	PHT	EHT	CHL	LA	NLV	ELTH	EWT	NRW	MST	HKWT	GYLD
DMP	<b>1.00</b>	0.76**	-0.18**	-0.19*	0.14	-0.22**	0.13	-0.20*	-0.28**	0.10	0.14	0.09	-0.10
DMS	0.89**	<b>1.00</b>	-0.26**	-0.21**	0.11	-0.22**	0.07	-0.34**	-0.44**	0.01	0.16*	0.13	-0.21**
PHT	-0.56**	-0.54**	<b>1.00</b>	0.68**	-0.13	0.43**	-0.11	0.39**	0.34**	0.16	-0.06	0.00	0.28**
EHT	-0.40**	-0.43**	0.66**	<b>1.00</b>	-0.21**	0.28**	-0.16**	0.16*	0.14	0.05	-0.07	-0.06	0.14
CHL	-0.50**	-0.47	0.36**	0.36**	<b>1.00</b>	-0.51**	0.98**	0.07	-0.18*	0.35**	0.72**	0.61**	-0.03
LA	-0.39**	-0.31**	0.36**	0.05	0.25*	<b>1.00</b>	-0.46**	0.35**	0.44**	-0.13	-0.36	-0.19	0.42**
NLV	-0.16	-0.16	0.31**	0.06	0.05	0.32**	<b>1.00</b>	0.07	-0.17*	0.33**	0.70**	0.57**	0.05
ELTH	-0.40**	-0.35**	0.49**	0.26*	0.25*	0.48**	0.34**	<b>1.00</b>	0.70**	0.18*	0.13	0.20**	0.60**
EWT	-0.56**	-0.56**	0.46**	0.28**	0.31**	0.47**	0.23*	0.76**	<b>1.00</b>	0.18*	-0.08	0.01	0.98**
NRW	-0.07	-0.09	0.16	0.25*	-0.08	-0.08	0.00	-0.07	0.04	<b>1.00</b>	0.35**	0.21*	0.26**
MST	-0.16	-0.02	0.19	0.14	0.10	0.16	0.12	0.42**	0.34**	-0.29**	<b>1.00</b>	0.90**	-0.31**
HKWT	-0.31**	-0.33**	0.14	0.01	0.10	0.22*	0.08	0.06	0.51**	-0.25*	0.32**	<b>1.00</b>	-0.32**
GYLD	-0.52**	-0.49**	0.44**	0.26**	0.17	0.41**	0.26*	0.64**	0.99**	0.10	0.29**	0.40**	<b>1.00</b>

† DMP=days to pollen shed; DMS=days to silk emergence; PHT=plant height; EHT=ear height, CHL=leaf chlorophyll concentration; LA=leaf area; NLV=number of leaves above primary ear; ELTH=ear length; EWT=ear mass; NRW=number of kernel rows per year; MST=grain moisture; Hundred Kernel mass; GYLD=grain yield. \*\*= significant at (P<0.01); \*=significant at (P<0.05)

Table 3.3: Correlation between SR52 traits in the F2 population at Cedara

Trait	EWT	DMS	DMP	EHT	PHT	LA	CHL	NLV	NRW	ELTH	HKWT	KPRW	KDPTH	GYLD	MST	GRTH	TKRNL
EWT	<b>1.00</b>	0.07	0.12	0.11	0.07	0.98**	0.02	0.01	-0.11	-0.18	0.72**	0.44**	0.68**	0.52**	-0.06	0.10	0.61**
DMS		<b>1.00</b>	0.73**	0.01	-0.04	0.09	-0.33**	-0.18*	0.08	0.27**	0.07	-0.08	-0.08	-0.01	0.21*	0.10	-0.03
DMP			<b>1.00</b>	0.09	-0.05	0.13	-0.16	-0.10	-0.01	0.07	0.04	-0.07	0.01	0.04	0.06	0.05	0.05
EHT				<b>1.00</b>	0.69**	0.13	0.00	0.00	-0.18*	-0.01	-0.02	-0.05	0.06	0.06	0.03	0.07	0.10
PHT					<b>1.00</b>	0.10	0.24**	0.13	0.12	-0.16	-0.02	0.12	0.04	0.08	-0.03	0.04	0.11
LA						<b>1.00</b>	0.05	0.00	-0.12	-0.19	0.71**	0.41**	0.69**	0.00	-0.11	0.10	0.60**
CHL							<b>1.00</b>	0.25**	0.07	-0.40**	0.10	0.06	0.14	0.00	-0.32**	-0.11	0.12
NLV								<b>1.00</b>	-0.01	-0.16	0.05	0.02	0.08	-0.09	-0.08	0.03	0.05
NRW									<b>1.00</b>	0.30**	-0.08	-0.09	-0.20*	0.15	0.10	-0.10	-0.20*
ELTH										<b>1.00</b>	-0.02	-0.40**	-0.20*	0.67**	0.52**	0.06	-0.05
HKWT											<b>1.00</b>	0.27**	0.73**	0.33**	-0.27**	-0.29**	0.57**
KPRW												<b>1.00</b>	-0.01	0.57**	0.03	0.03	-0.18
KDPTH													<b>1.00</b>	0.40**	-0.38**	-0.18	0.83**
GYLD														<b>1.00</b>	0.16	0.58**	0.52**
MST															<b>1.00</b>	0.71**	-0.40**
GRTH																<b>1.00</b>	-0.20**
TKRNL																	<b>1.00</b>

† PHT=plant height, EHT=ear height, LA= leaf area, CHL= leaf chlorophyll content, NLV=number of leaves above primary ear, MST=grain moisture, NRW=number of kernel rows per year, ELTH=ear length, HKWT=hundred kernel mass, EWT=ear mass, GYLD = grain yield, DMP=days to pollen shed, DMS=days to silk emergence, ,TKRNL=total number of kernels on ear, GRTH=ear girth, KDPTH=kernel depth, KPRW=number of kernels on ear row.. \*\*= significant at (P<0.01); \*=significant at (P<0.05)

Table 3.4 Correlation between SR52 traits in the BCP1 (below diagonal) and BCP2 (above diagonal) populations at Cedara

EWT	DMS	DMP	EHT	PHT	LA	CHL	NLV	NRW	CLTH	HKWT	KPRW	KDPTH	GYLD	MST	GRTH	TKRNL
<b>1.00</b>	-0.07	0.05	0.03	0.11	0.20*	0.12	0.00	0.39**	0.76**	0.48**	0.58**	0.46**	1.00**	0.08	0.70	0.65**
-0.19*	<b>1.00</b>	0.82**	0.19*	-0.08	-0.30**	-0.31**	-0.20*	-0.09	0.02	0.07	-0.11	-0.03	-0.05	0.07	-0.09	-0.13
-0.25	0.27**	<b>1.00</b>	0.27**	0.08	-0.14	-0.23	-0.23**	-0.10	0.05	0.21*	-0.14	-0.01	0.06	0.14	0.00	-0.15
0.05	0.04	0.02	<b>1.00</b>	0.68**	0.15	-0.12	-0.21*	0.00	-0.07	0.08	-0.11	0.07	0.04	0.14	0.00	-0.07
0.40**	-0.04	-0.06	0.45**	<b>1.00</b>	0.38**	0.06**	0.14	0.01	0.00	0.17*	-0.06	0.19*	0.10	0.20*	0.13	-0.03
0.24**	0.09	-0.03	-0.02	0.02	<b>1.00</b>	0.26**	0.14	0.00	0.13	0.25**	0.03	0.14	0.19*	0.14	0.16	0.02
0.18	-0.07	-0.09	0.16	0.15	0.07	<b>1.00</b>	0.10	0.17	0.19*	0.09	0.04	-0.07	0.11	0.03	0.16	0.10
0.02	-0.05	0.06	-0.15	0.19*	0.00	-0.01	<b>1.00</b>	0.01	0.01	-0.03	0.08	0.09	-0.01	0.10	0.04	0.06
0.42**	0.01	-0.12	0.13	0.27**	0.19	0.15	-0.01	<b>1.00</b>	0.24**	-0.03	0.16	0.36**	0.38**	-0.14	0.59**	0.66**
0.71**	-0.21	-0.23*	0.12	0.41**	0.26*	0.21*	0.18	0.29**	<b>1.00</b>	0.40**	0.67**	0.27**	0.78**	-0.05	0.51**	0.62**
0.41**	-0.01	0.03	-0.13	0.02	0.15	-0.03	-0.09	-0.10	0.11	<b>1.00</b>	-0.08	0.20*	0.47**	0.39**	0.48**	-0.08
0.69**	-0.36	-0.30	0.10	0.35**	0.15	0.27**	0.08	0.31**	0.81**	-0.12	<b>1.00</b>	0.25**	0.59**	-0.23**	0.31**	0.84**
0.41**	-0.13	-0.21*	-0.04	0.08	0.00	0.12	-0.12	0.22*	0.22**	0.18	0.23*	<b>1.00</b>	0.45**	0.02	0.72**	0.38**
1.00**	-0.19*	-0.25	0.06	0.40**	0.25*	0.19*	-0.01	0.41**	0.71**	0.42**	0.70**	0.40**	<b>1.00</b>	0.07	0.69**	0.65**
0.18	0.17	0.13	0.08	0.02	-0.10	-0.10	-0.04	0.01	-0.08	0.28**	-0.15	0.23*	0.19	<b>1.00</b>	0.04	-0.25
0.62**	-0.11	-0.22*	-0.08	0.16	0.11	0.20	-0.06	0.44**	0.34**	0.29**	0.32**	0.81**	0.61**	0.15	<b>1.00</b>	0.55**
0.70**	-0.22*	-0.27**	0.14	0.38**	0.19*	0.25*	0.05	0.79**	0.69**	-0.11	0.82**	0.29**	0.70**	-0.09	0.48**	<b>1.00</b>

‡ PHT=plant height, EHT=ear height, LA= leaf area, CHL= leaf chlorophyll content, NLV=number of leaves above primary ear, MST=grain moisture, NRW=number of kernel rows on ear, ELTH=ear length, HKWT=hundred kernel mass, EWT=ear mass, GYLD = grain yield, DMP=days to pollen shed, DMS=days to silk emergence, ,TKRNL=total number of kernels on ear, GRTH=ear girth, KDPTH=kernel depth, KPRW=number of kernels on ear row. \*\*= significant at (P<0.01); \*=significant at (P<0.05)

### **3.3.3 Path analysis**

#### **Ukulinga**

Results for path analysis between grain yield and its related components at Ukulinga are shown in Tables 3.5 to 3.7. Ear length had the highest direct effect on grain yield in all three segregating generations BC(N3), BC(SC) and F2. Its effects were further amplified, to some extent, through positive indirect interactions with hundred kernel mass and days to silk emergence. The greatest negative direct effects on grain yield were observed for days to silk emergence in all the SR52 segregating populations at the site. Days to silk emergence were also responsible for substantial negative indirect effects on grain yield, particularly through ear length. The number of rows per ear also had positive direct effects on grain yield for all the generations.

#### **Cedara**

Path coefficient analysis for independent traits with grain yield as the dependent variable at Cedara is shown in Tables 3.8 to 3.10. The number of kernels per row on the ear had the highest direct effect on grain yield in the F2 and BCP1 generations. The BCP2 generation had total number of kernels on ear (0.65) having the highest direct effect on grain yield. Unlike in the other two segregating populations of SR52, number of kernels in a row had a negative direct effect on grain yield in the BCP2 generation. However, positive indirect effects through other yield components such as ear length, total number of kernels on ear and girth, resulted in an overall positive association between kernels per row on ear and grain yield. The number of leaves above the primary ear had a negligible yet negative effect on yield for all generations. As was observed at Ukulinga, ear length and hundred kernels mass had a positive direct effect on yield in all of SR52's segregating generations at Cedara.

Table 3.5 Direct (underlined and bold) and indirect effects of grain yield components on grain yield in the F2 population at Ukulinga ( $R^2=0.73$ )

Trait	DMP	DMS	PHT	EHT	CHL	LA	NLV	ELTH	NRW	MST	HKWT	Total Correlation to Yield
DMP	<b><u>0.10</u></b>	-0.20	-0.01	0.01	0.01	-0.01	0.01	-0.01	-0.05	0.00	0.00	<b>-0.17</b>
DMS	0.07	<b><u>-0.28</u></b>	-0.03	0.02	0.01	-0.01	0.01	-0.11	-0.08	0.00	0.00	<b>-0.43</b>
PHT	-0.02	0.14	<b><u>0.06</u></b>	-0.07	0.00	0.02	-0.01	0.21	0.09	0.00	0.04	<b>0.49</b>
EHT	-0.01	0.05	0.04	<b><u>-0.10</u></b>	0.00	0.01	0.00	0.06	0.01	0.00	0.03	<b>0.10</b>
CHL	-0.01	0.03	0.00	0.01	<b><u>-0.08</u></b>	0.00	0.00	0.01	0.02	0.00	0.01	<b>-0.02</b>
LA	-0.02	0.11	0.03	-0.03	0.00	<b><u>0.04</u></b>	-0.01	0.11	0.04	0.00	0.04	<b>0.35</b>
NLV	-0.01	0.07	0.02	0.00	-0.01	0.01	<b><u>-0.04</u></b>	0.06	0.03	0.00	0.00	<b>0.12</b>
ELTH	0.00	0.08	0.03	-0.01	0.00	0.01	-0.01	<b><u>0.42</u></b>	0.10	0.00	0.02	<b>0.67</b>
NRW	-0.02	0.09	0.02	0.00	-0.01	0.01	-0.01	0.16	<b><u>0.25</u></b>	0.00	-0.03	<b>0.50</b>
MST	0.01	-0.02	0.02	-0.02	0.00	0.01	0.01	0.16	-0.03	<b><u>0.01</u></b>	0.07	<b>0.21</b>
HKWT	0.00	-0.01	0.02	-0.03	-0.01	0.01	0.00	0.07	-0.06	0.01	<b><u>0.12</u></b>	<b>0.13</b>

† DMP=days to pollen shed; DMS=days to pollen shed; PHT=plant height; EHT=ear height, CHL=leaf chlorophyll concentration; LA=leaf area; NLV=number of

Leaves above primary ear; ELTH=ear length; EWT=ear mass; NRW=number of ear rows; MST=grain moisture; Hundred Kernel mass; GYLD=grain yield.



Table 3.6: Direct (underlined and bold) and indirect effects of grain yield components on grain yield in the BCP1 population at Ukulinga ( $R^2=0.87$ )

Trait	DMP	DMS	PHT	EHT	CHL	LA	NLV	ELTH	NRW	MST	HKWT	Total correlation to Yield
DMP	<b><u>-0.12</u></b>	-0.15	0.04	-0.03	0.04	-0.01	0.00	-0.20	-0.01	-0.01	-0.06	<b>-0.52</b>
DMS	-0.11	<b><u>-0.16</u></b>	0.04	-0.04	0.04	-0.01	0.00	-0.19	-0.01	0.00	-0.05	<b>-0.50</b>
PHT	0.07	0.09	<b><u>-0.07</u></b>	0.06	-0.03	0.01	0.00	0.23	0.03	0.00	0.04	<b>0.43</b>
EHT	0.05	0.07	-0.05	<b><u>0.09</u></b>	-0.03	0.00	0.00	0.09	0.04	0.00	0.01	<b>0.26</b>
CHL	0.06	0.08	-0.03	0.03	<b><u>-0.08</u></b>	0.01	0.00	0.10	-0.01	0.00	0.01	<b>0.17</b>
LA	0.05	0.05	-0.03	0.00	-0.02	<b><u>0.04</u></b>	0.00	0.25	-0.01	0.01	0.05	<b>0.41</b>
NLV	0.02	0.03	-0.02	0.00	0.00	0.01	<b><u>0.01</u></b>	0.17	0.00	0.01	0.02	<b>0.26</b>
ELTH	0.05	0.06	-0.04	0.02	-0.02	0.02	0.01	<b><u>0.48</u></b>	-0.01	0.01	0.05	<b>0.64</b>
NRW	0.01	0.02	-0.01	0.02	0.01	0.00	0.00	-0.03	<b><u>0.15</u></b>	-0.01	-0.04	<b>0.10</b>
MST	0.02	0.01	-0.01	0.00	0.00	0.01	0.00	0.10	-0.04	<b><u>0.03</u></b>	0.16	<b>0.29</b>
HKWT	0.04	0.04	-0.01	0.00	0.00	0.01	0.00	0.13	-0.03	0.03	<b><u>0.19</u></b>	<b>0.40</b>

‡ DMP=days to pollen shed; DMS=days to pollen shed; PHT=plant height; EHT=ear height, CHL=leaf chlorophyll concentration; LA=leaf area; NLV=number of leaves above primary ear; ELTH=ear length; EWT=ear mass; NRW=number of ear rows; MST=grain moisture; Hundred Kernel mass; GYLD=grainyield. EWT and GYLD are the dependent variables

Table 3.7: Direct (underlined and bold) and indirect effects of grain yield components on grain yield in the BCP2 population at Ukulinga ( $R^2=0.83$ )

Trait	DMP	DMS	PHT	EHT	CHL	LA	NLV	ELTH	NRW	MST	HKWT	EWT	Total correlation to yield
DMP	<b><u>0.08</u></b>	-0.07	0.01	-0.01	0.00	-0.02	0.01	-0.10	0.00	0.00	0.00	<b>-0.10</b>	<b>-0.10</b>
DMS	0.06	<b><u>-0.09</u></b>	0.01	-0.01	-0.01	-0.02	0.00	-0.16	-0.01	0.01	0.00	<b>-0.21</b>	<b>-0.21</b>
PHT	-0.02	0.02	<b><u>-0.03</u></b>	0.02	0.00	0.05	0.02	0.17	0.05	-0.01	0.00	<b>0.28</b>	<b>0.28</b>
EHT	-0.02	0.02	-0.02	<b><u>0.03</u></b>	0.01	0.03	0.00	0.07	0.02	0.00	0.00	<b>0.14</b>	<b>0.14</b>
CHL	0.00	-0.01	0.00	0.00	<b><u>-0.05</u></b>	0.01	0.01	-0.05	0.01	0.02	0.03	<b>-0.04</b>	<b>-0.04</b>
LA	-0.01	0.02	-0.01	0.01	0.00	<b><u>0.12</u></b>	0.02	0.20	0.02	0.03	0.04	<b>0.42</b>	<b>0.42</b>
NLV	0.02	0.00	-0.01	0.00	-0.01	0.03	<b><u>0.07</u></b>	-0.03	0.02	-0.02	-0.02	<b>0.05</b>	<b>0.05</b>
ELTH	-0.02	0.03	-0.01	0.01	0.01	0.05	0.00	<b><u>0.44</u></b>	0.03	0.03	0.03	<b>0.60</b>	<b>0.60</b>
NRW	0.00	0.00	-0.01	0.00	0.00	0.01	0.01	0.07	<b><u>0.20</u></b>	-0.01	-0.02	<b>0.26</b>	<b>0.26</b>
MST	0.00	-0.01	0.00	0.00	-0.01	0.03	-0.01	0.11	-0.01	<b><u>0.12</u></b>	0.09	<b>0.31</b>	<b>0.31</b>
HKWT	0.00	0.00	0.00	0.00	-0.01	0.05	-0.01	0.14	-0.03	0.09	<b><u>0.11</u></b>	<b>0.32</b>	<b>0.32</b>

† DMP=days to pollen shed; DMS=days to pollen shed; PHT=plant height; EHT=ear height, CHL=leaf chlorophyll concentration; LA=leaf area;NLV=number of leaves above primary ear; ELTH=ear length; EWT=ear mass; NRW=number of ear rows; MST=grain moisture; Hundred Kernel mass; GYLD=grain yield. EWT and GYLD are the dependant variables

Table 3.8: Direct (underlined and bold) and indirect effects of grain yield components on grain yield in the F2 population at Cedara ( $R^2=0.85$ )

Trait	DMS	DMP	EHT	PHT	LA	CHL	NLV	NRW	ELTH	HKWT	KPRW	KDPTH	MST	GRTH	TKRNL	Total Correlation to Yield
DMS	<b><u>-0.02</u></b>	0.02	0.00	0.00	-0.01	0.00	0.00	0.01	0.00	0.00	-0.04	0.00	0.00	0.01	0.00	<b>-0.01</b>
DMP	-0.02	<b><u>0.03</u></b>	0.01	0.00	0.00	0.00	0.00	0.02	0.02	-0.02	0.02	0.00	0.00	0.01	-0.01	<b>0.04</b>
EHT	0.00	0.00	<b><u>0.09</u></b>	-0.04	0.00	0.00	0.00	0.02	0.00	-0.02	0.03	0.00	0.00	0.00	-0.02	<b>0.06</b>
PHT	0.00	0.00	0.06	<b><u>-0.06</u></b>	0.00	0.00	0.01	0.03	0.01	0.01	0.02	0.00	0.00	0.01	-0.02	<b>0.08</b>
LA	0.01	0.00	0.00	-0.01	<b><u>0.02</u></b>	-0.01	0.01	0.00	0.01	-0.01	0.00	-0.01	0.00	-0.01	0.00	<b>0.00</b>
CHL	0.00	0.00	0.00	-0.01	0.01	<b><u>-0.02</u></b>	0.00	-0.01	0.02	-0.01	0.05	-0.01	0.00	-0.01	-0.01	<b>0.00</b>
NLV	0.00	0.00	-0.02	-0.01	0.01	0.00	<b><u>0.03</u></b>	-0.01	-0.02	0.00	-0.07	-0.01	0.00	-0.01	0.02	<b>-0.08</b>
NRW	0.00	0.00	0.01	-0.01	0.00	0.00	0.00	<b><u>0.23</u></b>	0.00	-0.11	0.05	0.02	0.00	0.08	-0.11	<b>0.15</b>
ELTH	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	<b><u>0.23</u></b>	0.09	0.36	0.02	0.01	0.08	-0.10	<b>0.66</b>
HKWT	0.00	0.00	-0.01	0.00	0.00	0.00	0.00	-0.09	0.07	<b><u>0.30</u></b>	-0.05	0.00	0.02	0.04	0.05	<b>0.32</b>
KPRW	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.02	0.17	-0.03	<b><u>0.48</u></b>	0.01	-0.01	0.06	-0.15	<b>0.55</b>
KDPTH	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.07	0.02	0.10	<b><u>0.05</u></b>	0.01	0.13	-0.06	<b>0.39</b>
MST	0.00	0.00	0.00	-0.01	0.00	0.00	0.00	0.00	0.04	0.12	-0.08	0.01	<b><u>0.05</u></b>	0.02	0.02	<b>0.16</b>
GRTH	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.11	0.10	0.07	0.18	0.04	0.00	<b><u>0.17</u></b>	-0.10	<b>0.56</b>
TKRNL	0.00	0.00	0.01	-0.01	0.00	0.00	0.00	0.14	0.13	-0.08	0.40	0.02	-0.01	0.09	<b><u>-0.18</u></b>	<b>0.51</b>

† PHT=plant height, EHT=ear height, LA= leaf area, CHL= leaf chlorophyll content, NLV=number of leaves above primary ear, MST=grain moisture, NRW=number of kernel rows on ear, ELTH=ear length, HKWT=hundred kernel mass, EWT=ear mass, GYLD = grain yield, DMP=days to pollen shed, DMS=days to silk emergence ,TKRNL=total number of kernels on ear, GRTH=ear girth, KDPTH=kernel depth, KPRW=number of kernels on ear row.. \*\*= significant at  $P<0.01$ ; \*=significant at  $P<0.05$ .EWT

and GYLD are the dependent variables

Table 3.9: Direct (underlined and bold) and indirect effects of grain yield components on grain yield in the BCP1 population at Cedara ( $R^2=0.86$ )

Trait	DMS	DMP	EHT	PHT	LA	CHL	NLV	NRW	ELTH	HKWT	KPRW	KDPTH	MST	GRTH	TKRNL	Total correlation to yield
DMS	<b><u>0.04</u></b>	-0.01	0.00	-0.01	0.00	0.00	0.00	0.00	-0.01	0.00	-0.26	0.02	0.03	-0.03	0.04	<b>-0.19</b>
DMP	0.01	<b><u>-0.04</u></b>	0.00	-0.01	0.00	0.00	0.00	-0.02	-0.01	0.01	-0.21	0.03	0.02	-0.06	0.04	<b>-0.25</b>
EHT	0.00	0.00	<b><u>-0.04</u></b>	0.06	0.00	0.00	0.01	0.03	0.00	-0.05	0.07	0.00	0.01	-0.02	-0.02	<b>0.06</b>
PHT	0.00	0.00	-0.02	<b><u>0.13</u></b>	0.00	0.00	-0.01	0.06	0.02	0.01	0.25	-0.01	0.00	0.04	-0.06	<b>0.41</b>
LA	0.00	0.00	0.00	0.00	<b><u>0.04</u></b>	0.00	0.00	0.04	0.01	0.06	0.11	0.00	-0.02	0.03	-0.03	<b>0.24</b>
CHL	0.00	0.00	-0.01	0.02	0.00	<b><u>-0.01</u></b>	0.00	0.03	0.01	-0.01	0.17	-0.02	-0.02	0.06	-0.04	<b>0.19</b>
NLV	0.00	0.00	0.01	0.03	0.00	0.00	<b><u>-0.05</u></b>	0.00	0.01	-0.03	0.06	0.02	-0.01	-0.02	-0.01	<b>-0.01</b>
NRW	0.00	0.00	0.00	0.04	0.01	0.00	0.00	<b><u>0.21</u></b>	0.01	-0.04	0.22	-0.03	0.00	0.12	-0.13	<b>0.41</b>
ELTH	-0.01	0.01	0.00	0.05	0.01	0.00	-0.01	0.06	<b><u>0.04</u></b>	0.04	0.57	-0.03	-0.01	0.10	-0.11	<b>0.71</b>
HKWT	0.00	0.00	0.00	0.00	0.01	0.00	0.00	-0.02	0.00	<b><u>0.38</u></b>	-0.09	-0.02	0.04	0.08	0.02	<b>0.42</b>
KPRW	-0.02	0.01	0.00	0.05	0.01	0.00	0.00	0.06	0.03	-0.05	<b><u>0.71</u></b>	-0.03	-0.02	0.09	-0.13	<b>0.70</b>
KDPTH	-0.01	0.01	0.00	0.01	0.00	0.00	0.01	0.04	0.01	0.07	0.17	<b><u>-0.12</u></b>	0.04	0.23	-0.05	<b>0.40</b>
MST	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.11	-0.10	-0.03	<b><u>0.16</u></b>	0.04	0.01	<b>0.19</b>
GRTH	0.00	0.01	0.00	0.02	0.00	0.00	0.00	0.09	0.01	0.11	0.22	-0.10	0.02	<b><u>0.28</u></b>	-0.08	<b>0.60</b>
TKRNL	-0.01	0.01	-0.01	0.05	0.01	0.00	0.00	0.16	0.03	-0.04	0.58	-0.04	-0.01	0.13	<b><u>-0.16</u></b>	<b>0.70</b>

† PHT=plant height, EHT=ear height, LA= leaf area, CHL= leaf chlorophyll content, NLV=number of leaves above primary ear, MST=grain moisture, NRW=number of kernel rows on ear, ELTH=ear length, HKWT=hundred kernel mass, EWT=ear mass, GYLD = grain yield, DMP=days to pollen shed, DMS=days to silk emergence, ,TKRNL=total number of kernels on ear, GRTH=ear girth, KDPTH=kernel depth, KPRW=number of kernels on ear row.. \*\*= significant at  $P<0.01$ ; \*=significant at  $P<0.05$ . EWT and GYLD are the dependent variables

Table 3.10: Direct (underlined and bold) and indirect effects of grain yield components on grain yield in the BCP2 population at Cedara ( $R^2=0.74$ )

Trait	DMS	DMP	EHT	PHT	LA	CHL	NLV	NRW	ELTH	HKWT	KPRW	KDPTH	MST	GRTH	TKRNL	Total Correlation to yield
DMS	<b><u>-0.16</u></b>	0.12	0.01	0.00	-0.01	0.01	0.01	0.02	0.01	0.01	0.02	0.00	0.01	-0.02	-0.08	<b>-0.05</b>
DMP	-0.13	<b><u>0.15</u></b>	0.02	0.00	0.00	0.01	0.01	0.02	0.02	0.04	0.03	0.00	0.01	0.00	-0.10	<b>0.06</b>
EHT	-0.03	0.04	<b><u>0.06</u></b>	-0.03	0.00	0.00	0.01	0.00	-0.02	0.02	0.02	0.00	0.01	0.00	-0.05	<b>0.04</b>
PHT	0.01	0.01	0.04	<b><u>-0.04</u></b>	0.01	0.00	0.00	0.00	0.00	0.03	0.01	0.01	0.02	0.02	-0.02	<b>0.10</b>
LA	0.05	-0.02	0.01	-0.01	<b><u>0.02</u></b>	-0.01	0.00	0.00	0.05	0.05	-0.01	0.01	0.01	0.03	0.02	<b>0.19</b>
CHL	0.05	-0.03	-0.01	0.00	0.01	<b><u>-0.04</u></b>	0.00	-0.04	0.07	0.02	-0.01	0.00	0.00	0.03	0.07	<b>0.11</b>
NLV	0.03	-0.03	-0.01	-0.01	0.00	0.00	<b><u>-0.03</u></b>	0.00	0.00	-0.01	-0.02	0.00	0.01	0.01	0.04	<b>-0.01</b>
NRW	0.01	-0.01	0.00	0.00	0.00	-0.01	0.00	<b><u>-0.22</u></b>	0.09	-0.01	-0.03	0.01	-0.01	0.11	0.43	<b>0.38</b>
ELTH	0.00	0.01	0.00	0.00	0.00	-0.01	0.00	-0.05	<b><u>0.37</u></b>	0.08	-0.13	0.01	0.00	0.10	0.41	<b>0.78</b>
HKWT	-0.01	0.03	0.00	-0.01	0.01	0.00	0.00	0.01	0.15	<b><u>0.20</u></b>	0.02	0.01	0.03	0.09	-0.05	<b>0.48</b>
KPRW	0.02	-0.02	-0.01	0.00	0.00	0.00	0.00	-0.04	0.25	-0.02	<b><u>-0.20</u></b>	0.01	-0.02	0.06	0.55	<b>0.59</b>
KDPTH	0.00	0.00	0.00	-0.01	0.00	0.00	0.00	-0.08	0.10	0.04	-0.05	<b><u>0.04</u></b>	0.00	0.14	0.25	<b>0.45</b>
MST	-0.01	0.02	0.01	-0.01	0.00	0.00	0.00	0.03	-0.02	0.08	0.05	0.00	<b><u>0.08</u></b>	0.01	-0.16	<b>0.07</b>
GRTH	0.01	0.00	0.00	0.00	0.00	-0.01	0.00	-0.13	0.19	0.10	-0.06	0.03	0.00	<b><u>0.19</u></b>	0.36	<b>0.69</b>
TKRNL	0.02	-0.02	0.00	0.00	0.00	0.00	0.00	-0.15	0.23	-0.02	-0.16	0.02	-0.02	0.11	<b><u>0.65</u></b>	<b>0.65</b>

† PHT=plant height, EHT=ear height, LA= leaf area, CHL= leaf chlorophyll content, NLV=number of leaves above primary ear, MST=grain moisture, NRW=number of kernel rows on ear, ELTH=ear length, HKWT=hundred kernel mass, EWT=ear mass, GYLD = grain yield, DMP=days to pollen shed, DMS=days to silk emergence, ,TKRNL=total number of kernels on ear, GRTH=ear girth, KDPTH=kernel depth, KPRW=number of kernels on ear row.. \*\*= significant at  $P<0.01$ ; \*=significant at  $P<0.05$ . EWT

and GYLD are the dependent variables

### **3.3.4 Heritability of SR52's yield components**

Narrow sense heritability values of all traits measured are shown in Tables 3.11 and 3.12. The contribution and significance of epistatic gene effects was included in the Tables (see Chapter 2 for estimation of epistasis). High narrow sense heritability for yield was observed at both locations. The traits with the lowest contribution toward narrow sense heritability were leaf chlorophyll content at both sites and hundred kernel mass at Ukulinga. The number of leaves above primary ear, days to silk emergence, number of kernels per ear row and the total number of kernels on ear had low narrow sense heritability values of below 15% at Cedara. No observable trend was detected between contribution or significance of epistasis and heritability across the two sites. Hundred kernel mass at Ukulinga had the highest epistatic contributions, which were followed by a low narrow sense heritability value of 12%. Values on heritability did not remain constant across sites for most of the traits.

Table 3.11: Heritability for traits of SR52 at Ukulinga

Trait	$h^2n$ (%)	% epistasis	Significance of epistasis
Plant height	28	-	x
Ear height	48	5.5	***(aa; dd); *(ad)
Leaf area	41	5.5	*(dd)
Chlorophyll content	1	9.8	*(dd)
No. of leaves above ear	77	24.6	***(dd); **(aa)
Grain moisture content	57	5.5	***(ad)
No. of kernel rows on ear	89	-	x
Ear length	34	6.8	ns
100 kernel mass	12	49.7	***(ad; dd); **(aa)
Ear weight	92	9.4	***(aa); *(dd)
Grain yield	91	7.7	*(aa)
Days to silk emergence	83	10.4	***(ad)
Days to pollen shed	56	9.8	***(ad)

ns=not significant;\*=significant at (P<0.05); \*\*=P<0.01; \*\*\*=P<0.0001 ; aa=additive x additive gene action; ad=additive x dominance gene action; dd= dominance x dominance gene action,

Table 3.12: Heritability for traits of SR52 at Cedara

Trait	$h^2_n$ (%)	% epistasis	Significance of epistasis
Plant height	40	3	** (aa; ad); *(dd)
Ear height	51	-	x
Leaf area	26	8.7	** (ad)
Chlorophyll content	10	4.3	*(dd)
Number of leaves above ear	9	4	** (aa); *(dd)
Grain moisture	67	3.8	** (dd)
Number of kernel rows on ear	42	20.1	** (aa); *(ad; dd)
Ear length	39	7.6	** (aa)
100 kernel weight	49	7.5	ns
Ear weight	36	-	x
Grain yield	92	3.1	** (aa)
Days to silk emergence	15	-	x
Days to pollen shed	34	-	x
Ear girth	19	3.8	** (dd)
Number of kernels on ear row	10	5.9	*** (aa; dd)
Tot. No. of kernels on ear	12	-	x
Kernel depth	47	-	x

† ns=not significant; \*=significant at ( $P < 0.05$ ); \*\*= $P < 0.01$ ; \*\*\* $P < 0.0001$ ; aa=additive x additive gene action; ad=additive x dominance gene action; dd= dominance x dominance gene action



### **3.4 Discussion**

#### **3.4.1 Frequency distribution of phenotypic traits**

For most traits, a continuous distribution was observed. This indicates the presence of phenotypic variation in the segregating populations of SR52. Considering the fact that the sample population used was very large and heritability was also high for the economic traits, such as grain yield, the phenotypic variations observed in the current study can be taken as a reflection of the genotypic variance. Continuous distribution observed for traits such as grain yield and hundred kernel mass is indicative of the quantitative nature of inheritance and the presence of several QTLs cannot be overlooked. For traits such as number of kernel rows, two major classes 10-12 and 14-16 kernel rows seemed to dominate indicating the possibility that few genes or major QTLs could be responsible for the inheritance of such a trait. The observation of the few classes could also be attributed to a narrow genetic base for the number of kernel rows per ear. With the exception of number of kernel rows per ear, all the other traits in Figures 3.1-3.6 showed presence of large phenotypic variation amongst SR52's segregating generations, implying that improvement of the population through selection would be possible.

#### **3.4.2 Correlations studies**

In a bid to decide on the relative importance of the contribution of secondary traits to the yield potential of SR52, correlation coefficient analysis was employed. Grain yield in all of the segregating populations of SR52 showed a highly significant positive correlation with ear mass indicating that this trait makes a major contribution to the hybrid's exceptional heterosis. Such a positive and significant correlation between these traits has been recorded by other researchers on hybrids (Abirami *et al.*, 2007; Bello *et al.*, 2010; Hepziba *et al.*, 2013). The present study revealed that ear length had a positive significant correlation with yield, indicating that this component can be emphasised during selection for productive inbred lines. This positive correlation has been alluded to in a number of studies (Alvi *et al.*, 2003; Kumar *et al.*, 2006; Kumar *et al.*, 2011). Positive correlations observed between ear

length and kernels per row on ear can be attributed to the assumption that a longer ear can accommodate more kernels indicating that selection for this combination will enhance grain yield potential of inbred lines. Such a positive correlation between ear length and kernels per row was reported by Alvi *et al.* (2003).

The high positive correlation between ear length and most yield-related traits, such as hundred kernel mass, kernel depth, ear girth and grain moisture, is encouraging for breeders who intend to derive new maize inbred lines from the hybrid SR52. These traits can be simultaneously selected for, in order to push for yield enhancement in the population. Positive correlations among all yield-related components are however, difficult to achieve regularly as yield is a constant capacity system which normally sees one yield-related trait being compromised as another one is increased (Yan and Wallace, 1995) .

Days to silk emergence is one trait which was negatively correlated to yield and its components, in all the generations. Most studies conducted on maize do concur that days to silk emergence is negatively correlated to grain yield and its components (Hefny, 2011; Hepziba *et al.*, 2013). Implications of this negative correlation are that low yields are obtained if silks fail to emerge on time in order to synchronise with pollen. Silks that emerge late will not be pollinated. This is why SC gave lower yield than N3 at Ukulinga.

Monneveux *et al.* (2008) found significant positive correlations between plant height and grain yield. Such findings are similar to those obtained in the present study. The highly significant correlation between plant height and grain yield can be exploited by using plant height for the indirect selection for grain yield. For agronomic purposes, the selection of tall plants might not be desirable. With SR52 in mind, its massive height means that the hybrid cannot be grown under high plant densities, as it would be prone to serious lodging. The lack of significant correlation between ear height and yield is encouraging for breeders. The trait ear height is important as high ear placement leads to yield losses due to increased risk of lodging, especially when machine harvesting is done. Results from this study show that breeders can manipulate ear height in SR52's segregating populations without compromising on yield.

### 3.4.3 Path analysis

Relationships between single plant grain yield and secondary traits were studied using path coefficient analysis to determine direct and indirect contributions of secondary traits to yield. Ear length had the largest direct effect on yield at Ukulinga for all generations. A large positive direct effect exerted on grain yield by ear length was also observed in previous studies (El-Shouny *et al.*, 2005). Along with ear length, the number of kernel rows and hundred kernel mass were key in boosting grain yield of SR52 at Ukulinga, as these three traits had a marked high direct effect on yield. These traits were found to have a positive direct effect in many previous studies conducted on maize (Hefny, 2011; Kumar *et al.*, 2006; Mohammadi *et al.*, 2003). Contrary to the findings of the present research, Hepziba *et al.* (2013) found negative direct effects between hundred kernel mass and grain yield. At Ukulinga, the direct effects on yield expressed by ear length, number of kernel rows and hundred kernel mass were also found at Cedara, indicating consistency of findings.

Direct effect on yield by leaf chlorophyll content was found to be negligible and oriented toward the negative spectrum of values for all generations, at both sites. Shandu (2013) did find a low positive direct effect of 0.19 for the chlorophyll content on grain yield, with an overall positive association of 0.44 with grain yield in popcorn. In this study on SR52, despite its slight negative direct effect on yield, positive association of chlorophyll content with grain yield in the BCP2 generation were a result of positive indirect effects through days to silk emergence and days to pollen shed at Ukulinga, as well as number of kernels per ear row and ear girth at Cedara. Of particular interest was the total number of kernels per ear, which had a negative direct effect on yield for the F2 and BCP1 generations, whilst having a high positive direct effect on grain yield in the BCP2 generation. This is because BCP2 has two dosages of SC, where the number of kernels can be compromised by bareness of SC. Such discrepancies are common across populations or environments when working with path analysis, as several studies give contrasting values, depending on populations or generations studied. Mohammadi *et al.* (2003) found high direct effects between total

number of kernels on ear and grain yield at one of his sites, whilst at another site they shrunk considerably. In this study, high indirect effects between total number of kernels on ear with number of kernels per row and number of kernel rows resulted in a high positive association between total number of kernels on ear and grain yield, in all generations.

### **3.4.3 Heritability**

The interpretation of heritability data is based on Robinson *et al* (1949). They categorised heritability as low (0-30%), moderate (30-60%) and high (>60%). Moderate to high levels of heritability for number of kernel rows on ear is encouraging as this trait has been found in the present study to have a positive direct effect on grain yield. Rebourg *et al.* (2001) also obtained high narrow sense heritability value of 87% for this trait. Selecting for the number of kernel rows on ear as a secondary trait can be exploited by breeders in SR52's segregating populations in order to enhance the grain yield potential. High to moderate levels of heritability for grain yield components such as ear mass, total number of kernels on ear and ear length implies that higher gain in selection for grain yield potential is achievable by using these traits for indirect yield selection.

The contribution of epistasis toward grain yield and its components as well as on its components, is not quite understood. Ma *et al.* (2007), alluded to the fact that traits with low heritabilities were affected more by inter-allelic interactions. This may hold true for traits such as hundred kernel mass in this study, which had epistasis contributing 49.7% of its gene action sum of squares. However, at Ukulinga, the trend of having high epistatic interactions coupled with low heritability did not hold for some of the traits such as number of leaves above the primary ear.

Inconsistencies on narrow sense heritability values across sites for traits such as plant height, ear mass, days to silk emergence and days to pollen shed is generally expected, because heritability is not constant and can be affected by variations caused by environmental factors and interaction between the environment and genotypes (Wray and

Visscher, 2008). Ear length, which had a high positive correlation, plus positive direct effects with grain yield, had moderately low narrow sense heritability values of 34% and 39% at the two sites. This did not agree with work done by Wolf *et al.* (2000), who found high narrow sense heritability values of 89% for ear length in the S1 population of a high-yielding single cross maize hybrid. The quest to improve yielding ability of SR52 seems achievable through selection, as high heritability values for grain yield were obtained. High heritability values for grain yield would ultimately be expected to increase the response to selection, because it is directly proportional to heritability.

### **3.5 Conclusion**

The main objective of this investigation was to estimate heritability and determine relationships among traits of the hybrid SR52, in order to identify traits that can be exploited indirectly in breeding for yield advance and adaptability of the hybrid. The positive correlation and high direct effects between ear length and yield, coupled with moderate heritability values and high phenotypic variance for this trait, indicates that this trait can be used for indirect selection, as a cheaper and faster breeding method whilst conducting selections, as there would not be a need to wait for the plants to reach physiological maturity for selections to be made at harvest in SR52's segregating populations. High levels of indirect effects on yield and positive associations with yield by its components, such as total number of kernels on ear and number of kernels on ear, enables simultaneous selection of these traits, which can ultimately enhance yield potential of SR52. Lack of adequate phenotypic variation for the number of kernel rows on ear may reduce progress in breeding for a higher number of kernel rows. Low heritabilities of several traits may reduce the utility of these traits for the indirect selection for yield of SR52's populations. Together with ear length, the number of kernel rows per ear and hundred kernel mass are key to enhancing grain yield potential of SR52, because they exhibited large contribution to yield potential. However, direct selection for the grain yield potential would be recommended

because heritability was very large at both sites. It can be concluded that SR52 is such a great hybrid because of the large direct effects these traits have on grain yield potential.

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## CHAPTER FOUR

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### GENERAL OVERVIEW OF RESEARCH

#### 4.1 Introduction

Previous chapters have emphasised the impact SR52 has had on maize yields in Sub-Saharan Africa. The aim of Chapter Four is to provide an overview of the findings obtained in this study, with the intention of mapping out recommendations. The implications for breeding from the results obtained will also be discussed.

The aim of the study was to give reasons “Why SR52 is such a great hybrid”.

Specific objectives of the study were to:

- Determine the genetic basis of the exceptional yield potential of the hybrid SR52.
- To confirm the levels of heterosis expressed for yield and several traits of the hybrid SR52.
- To determine phenotypic variation of SR52 traits in its segregating generations.
- To establish contributions of different secondary traits to the exceptional yield potential of SR52.

The objectives were dealt with by evaluating several generations derived from the SR52 hybrid and its parents at two test environments, in South Africa.

#### 4.2 Summary of the major findings

##### 4.2.1 Genetic basis of SR52's yield and secondary traits

Dominance gene effects were the main mode of gene action in the inheritance of grain yield and secondary traits in the SR52 maize hybrid:

- Dominance and additive gene effects were significant ( $P < 0.01$ ) for grain yield, with additive x additive epistasis also showing significance for the trait.
- Dominance gene effects were predominant for yield and secondary traits (>80%), indicating that most orthodox selection strategies would not achieve much success in fixing SR52's yield.
- Even though it had a low contribution in terms of gene action sum of squares (<10%), high levels of significance for epistasis would complicate breeding.
- Epistasis of the additive x additive was significant and can be fixed.
- The non-fixable genetic components comprising dominance and epistasis in the additive x dominance and dominance x dominance had a higher proportion, compared to the fixable components. The implication of this is that hybridisation would be a more effective breeding strategy compared to selection.

#### **4.2.2 Heterosis for yield and several traits in SR52**

The study confirmed high levels of heterosis at the two sites.

- Mid-parent heterosis was 311% at Ukulinga, indicating SR52's exceptional grain yield when compared to the average of its parents.
- A much lower hybrid vigour (heterosis) value in the F<sub>2</sub>, compared to F<sub>1</sub>, has implications for farmers who recycle seed, as they stand to lose a substantial amount of yield. This is consistent with theoretical expectations for the hybrid technology.
- Very low yield for SR52's pollen parents (SC) under lowland conditions where it is not adapted, indicates that the inbred has narrow adaptability. Also genes for standing ability and silk emergence also need to be introgressed into the line to improve SR52's performance.
- SC performed poorly at Ukulinga and therefore breeders need to select inbred lines based on their performance in crosses rather than on their individual performance.

- The role of epistasis in SR52's high levels of heterosis cannot be overlooked as it was shown to be significant though negligible when generation mean analysis was conducted.

#### **4.2.3 Phenotypic variation of SR52's traits in its segregating populations**

Wide phenotypic variation was found to exist in SR52's segregating population in the completed study. Because a large sample was used this variation tends to approximate the genetic variation, which is also reflected by the large heritability estimate for yield.

- Results showed high and continuous phenotypic variation in SR52's F2, BCP1 and BCP2, indicating the quantitative nature of inheritance for most of the traits measured.
- Transgressive segregants were observed for traits in the segregating populations; creating opportunity for traits to be selected that can improve SR52's yield, standing ability and earliness.
- Transgressive segregants with 16 kernels per ear were obtained in the F2 and BCP2 populations, which can be selected for, and greatly aid in, the creation of a much improved high-yielding SR52.
- An SR52 ideotype was modelled using the best possible combination of trait values including transgressive segregants from the hybrid's segregating populations.

#### **4.2.3 Relationship between secondary traits and yield**

Most traits had a positive correlation with grain yield at both sites.

- Highly significant ( $P > 0.001$ ) positive correlations were observed for grain yield with secondary traits such as ear mass and ear length, at both sites.
- Ear length and number of kernel rows per ear had the highest positive direct effect on yield in all three segregating generations at Ukulinga. At Cedara, the number of kernels per row and hundred kernel mass had the largest positive direct effects in

the F2 and BCP1 generation. In the BCP2 generation, ear length and total number of kernels on ear had the highest direct effects on yield at Cedara.

- Direct selection for ear length, number of kernel rows per ear, total number of kernels per ear and number of kernels per ear row can be effective for improving the grain yield potential of SR52.
- As well as having negative correlations with grain yield in most of the segregating generations across the sites, days to silk emergence had negative direct effects on grain yield. This implies that selecting for early silk emergence in segregating populations would enhance yield and adaptability of SR52.
- Indirect effects on grain yield were more pronounced at Cedara, where the highest indirect interactions were observed for number of kernels on ear row with ear length, and number of kernels on ear row with total number of kernels in the BCP1 population. The small number of secondary traits with large indirect effects suggests that general selection of secondary traits would not be effective for improving yield of SR52.
- High heritability values for grain yield indicate that a direct selection strategy for yield enhancement could be highly effective in SR52's segregating generations.
- Although it had high positive direct effects on grain yield, using ear length as an indirect trait in selection could be deterred by the fact that it had moderately low heritability values. The same applies for the number of kernels per ear row and hundred kernel mass.
- This leaves ear mass as the most effective reliable trait for the indirect selection for grain yield courtesy of its high levels of correlation with grain yield potential, coupled with its high heritability.

#### **4.3 General outlook and way forward**

With maize breeding programmes that have been in existence for well over 70 years, it is shocking that African countries, such as Zimbabwe, are still not producing enough maize to feed their ever-growing populations. The question is, where are these African countries

getting it wrong? Adoption of three way and double cross maize hybrids at the expense of higher yielding single crosses seems to play a part in the low yields currently being attained in Africa. The solution to Africa's food security could lie in the adoption of single cross hybrid varieties of SR52's merit by farmers, both commercial and small-scale. However, such single crosses must be developed from higher-yielding inbred lines in order to make their cost of production relatively cheap. Appropriate agronomic practices, such as adequate fertilizer application, weed control and irrigation, should be practised along with the adoption of single cross hybrids. This combination could result in higher yields being realised in Zimbabwe, and in Sub-Saharan Africa as a whole.

Results from this study confirmed SR52's high levels of heterosis and the genetic basis of its exceptional yield. With such high yield per plant achieved by this great hybrid, the improvement of SR52 has the capacity to raise Africa's yield the way it did five decades ago. Through detection and rectification of its weaknesses, an improved version of this single cross can ignite Zimbabwe's second green revolution. What then remains to be answered is how this hybrid can be improved, so that it can go back on the market as the variety of choice. The answer lies in the completed study, poor standing ability, poor and late silk emergence coupled with a long growing season are the hybrids' weaknesses, which it inherits from its parents. Improvement of the male parent SC for silk emergence would go a long way towards achieving dream yields for Africa.

#### **4.4 Recommendations**

The following steps can be employed in developing new productive inbred lines that can be crossed in order to come up with better versions of SR52:

- I. SR52's segregating populations will be advanced to F3 and other proceeding generations through selfing. SNP markers will be used to identify QTL for standing ability, yield and good silk emergence in those plants that are predominantly SC (genetically) and such genes will be stacked through crossing such lines and selfing

them. The same procedure will be done with N3, but with QTLs for earliness and yield being stacked. This will be done up until the F7. SNP markers would also be employed for background selection of progenies. Inbred lines containing predominantly SC background with stacked QTL are then crossed with those with predominantly N3 background, in the hope of establishing an improved SR52. The lines will be crossed to other complementary heterotic groups such as K64r.

- II. Alternatively, two backcross schemes running concurrently can be initiated in order to introgress genes for standing ability and early silking in SC, as well as earliness in N3. Donor plants with high yield potential and good silk emergence, standing ability and earliness, from within the same heterotic pattern with either of the inbred lines are identified and backcrossed to N3 and SC. Plants with required genes donated from the selected donor lines are selected at each backcross to recover both N3 and SC genetic background. Background selection can be facilitated by the use of SNP markers. Once their genetic background has been recovered, improved N3 and SC lines are then crossed to give single cross hybrids with exceptional yield.

#### **4.5 Conclusion**

The major objective of this study was to determine the genetic basis behind SR52's yield and secondary traits. Correlation and path coefficient analysis was performed to establish the relationship between secondary traits and yield. The study established that dominance gene action was highly significant and contributed the largest proportion of genetic sum of squares for grain yield and most secondary traits in SR52. Overall, the study was successful in answering the question "Why SR52 is such a great maize hybrid". It is due to dominance gene action and large direct contributions of ear length, number of kernel rows per ear, hundred kernel mass and total number of kernels per ear row on yield, among other traits.