INTRODUCTION OF DESIRABLE TRAITS FROM TEMPERATE MAIZE (*Zea mays L.*) INTO TROPICAL MAIZE FOR LOW PHOSPHORUS SOILS

BY

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DECLARATION

I Lovemore Daka declare that this dissertation, prepared for the Master of Science in Plant Breeding and Seed Systems Degree, which was submitted by me at the University of Zambia (UNZA) is my own work. This work has not been submitted for any degree to any other University.

SIGNATURE: ……………………………. DATE: ………………………

APPROVAL

This dissertation of Lovemore Daka has been approved by the University of Zambia as partial fulfillment of the requirements for the award of the Degree of Master of Science in Plant breeding and Seed Systems.

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ABSTRACT

Maize (*Zea mays L.*) is one of the most important cereal crops in the world after wheat and rice. It is the staple food crop of people in Zambia, but phosphorus (P) deficiency in soils has been limiting grain yield. The objective of this study was to introgress desirable yield enhancing alleles from temperate genotypes of maize into tropical maize to increase grain yield on phosphorus deficient soils in Zambia. Twenty-four (24) single-cross hybrids and 9 local checks were evaluated in a 3 × 11 α-lattice design with 2 replications at Mutanda station under low P soil condition.

Highly significant differences ($P \leq 0.01$) among genotypes were found for grain yield (GY), harvest index (HI), 100 grain weight (100GW), shelling %, root biomass (RB), plant height (PH), plant biomass (PB), plant-tissue phosphorus (PTP) and purpling symptom suggesting the presence of genetic variation in maize under low phosphorus soil conditions. Temperate inbred parents gave highly significant ($P \leq 0.01$) GCA variances for GY (27.3**), 100GW (0.00005**) and significant ($P \leq 0.05$) GCA variance for HI (0.016*), implying the presence of additive gene action. Similarly, tropical inbred parents gave highly significant ($P \leq 0.01$) GCA variances for; GY (36.19**), HI (0.06**), 100GW (0.00006**), shelling % (171.73**), PH (331.3*), PTP (42543**) and RB (1.01**), implying the presence of sufficient additive gene action. As such, breeding progress under low phosphorus could be achieved through selection of parental genotypes based on the fore-mentioned traits.

The single-cross hybrids gave highly significant ($P \leq 0.01$) SCA variances for; GY (13.89**), HI (0.03**), 100GW (0.00007**), RB (0.37**) PTP (140491**) and significant ($P \leq 0.05$) SCA variance for PH (246.22*), implying the presence of dominance gene action for effective hybridization under low phosphorus soils. The Baker's ratio was low for GY, HI, PH, RB, 100GW and PTP indicating the preponderance of dominance gene action over additive, hence justifying the vigour realized in hybrids. However, there was a predominance of additive gene action over dominance gene action for shelling percentage only.

There was highly significant positive ($P \leq 0.01$) correlations for GY with; PH (r = 0.40**), HI (r = a0.76**), shelling % (r = 0.60**) and PB (r = 0.43**) and highly significant negative ($P \leq 0.01$) correlation with purpling of leaves (r = -0.50**). The coefficient of multiple determinations (R^2) revealed that harvest index had highly significant ($P \leq 0.01$) influence on grain yield explaining 65.7% of the total variation. Purpling symptom and plant height gave little contribution to grain yield, explaining only 3.3% and 2.9% of the total variation respectively.

Temperate inbreds J187 and Mo17 were identified as good sources of desirable yield enhancing alleles for introgression to improve tropical maize on phosphorus deficient soils. Inbred-line J185 was the best general combiner and source of desirable alleles followed by Mo17. Hybrids L151×J185, L151×Mo17, L152×J185, L1212×Mo17, 152×Mo17, L1212×J185 and L5527×J185 that produced high grain yield ranging from 8.28 tons/ha to 12.77 tons/ha were identified as potential good materials for extracting inbred-lines and developing 3-way cross or double-cross hybrids that are efficient in utilizing phosphorus in soils.

DEDICATION

Sincere gratitude goes to; my mother Betty, my wife Adraida, our beloved children; Sharon, Patience, Chisomo and Dalitso that generously encouraged me during studies at the University of Zambia. I will always appreciate your genuine love, care and support. We should always remember that every moment we walk with the almighty God, we are helped to improve our lives. To late grandmother Atalia, I will always miss you for great sacrifices you made in raising the family.

Lastly, I dedicate this piece of work to my mentor, Uncle Felix. He nurtured me into a productive man, without compromising the “Golden Rule”.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF APPENDICES

CHAPTER 1

INTRODUCTION

Maize (*Zea mays L.*) is one of the most important cereal crops in the world after wheat and rice (IITA, 2007). It is the most important crop in Sub-Saharan Africa and it provides the dietary nutrients for humans and livestock. In Zambia, maize is also the most important food and cash crop. It accounts for 60 % of the national calorie consumption and serves as the staple diet of people (Dorosh et al., 2010). Maize remains a cornerstone of the Zambian agricultural economy and government agricultural policy. Currently, maize is Zambia's number one commodity in terms of value, second after sugarcane in production and fourth in exports after sugar, cotton, and tobacco (FAO, 2011).

Industrialization coupled with rapid population growth has increased the demand for maize in Zambia. However, according to MACO/CSO (2010), the average yields of maize in Zambia are as low as 2.5 tons/ha on most arable lands. Yields are even less than 1.5 tons/ha in agro-ecological region III where soils have low available phosphorous due to soil acidity, while climate change has been limiting productivity on fertile arable land in agro-ecological regions I and II. In order to meet the rising demand for maize (food) in Zambia, there are some options, such as further exploration of planting during the dry seasons, increasing productivity per unit area and expansion of cultivation areas. Within this context, a significant fraction of cultivation can be performed in marginal areas that have low fertility (Giaveno et al., 2007). Although tropical maize germplasm is adapted to tropical environments, it inherently shows undesirable traits such as; low grain yield on P deficiency soils, low harvest index, excessive plant height and poor husk cover, (Abadassi1 and Herv´e, 2000). The potential yield enhancing alleles present in temperate maize genotypes such as J185, Mo17 and B73 have not adequately been exploited through introgression to develop cultivars that can produce high grain yield on marginalized phosphorus deficient soils in agro-ecological region III of Zambia.

As Ozanne (1980) reported, phosphorus is one of the yield limiting abiotic factors in many tropical and subtropical soils. To mitigate this problem, the application of commercial fertilizers is the most common recommendation. But there are various concerns associated with the use of commercial fertilizers in general and phosphorus fertilizers in particular. These concerns are:

1) The resource-poor farmers in tropical and subtropical regions are unable to use phosphorus based fertilizers due to lack of money and/or unavailability of fertilizers.
2) Phosphorus is rapidly transformed to hardly available form even after fertilizer application due to the prevailing adverse chemical properties (acidity and alkalinity) of tropical and sub-tropical soils.
3) The increase of legislative regulations that restrict the use of commercial inorganic fertilizers, so as to minimize environmental hazards after run-off (Sattelmacher et al., 2007).

The fore-mentioned limitations of inorganic fertilizers on one hand and increased population on the other hand necessitated the look for sustainable solutions to low grain yield on phosphorus deficient soils in Zambia. Development of phosphorus use efficient genotypes with a great ability to grow and yield in P deficient soil is therefore an important goal in plant breeding (Hash et al., 2002; Wissuwa et al., 2002; Yan et al., 2004). The release of efficient genotypes in both high and low-input farming systems would reduce the production costs associated with phosphorus fertilizer applications, minimize environmental pollution and contribute to the maintenance of P resources globally (Cakmak, 2002; Vance et al., 2003; Good et al., 2004).

Zambia is divided into three agro-ecological regions namely; Region I, Region II and Region III, defined according to climatic characteristics with rainfall as the main factor (Bunyolo et al., 1997). Region I cover major valleys of Zambia and lies 300 - 900 m above sea level. It receives rainfall not exceeding 800 mm per annum over a period of 80 - 120 rain-days. Frequent drought has rendered region I unsuitable for production of rain-fed crops. Region II lies 900 - 1300 m above sea level. It receives 800 - 1000 mm over a period of about 100 - 140 rain-days and experiences drought of about 1 - 3 ten-day periods. The region represents plateau of the country and generally contains inherent fertile soils. Region III lies about 1100 - 1700 m above sea level. It receives above 1000 mm of rain per year, over a period of 120 - 150 rain-days and drought days are very rare.

Of the above mentioned regions, Region III is the wettest part of the country and is characterized by very acidic ($pH<4.5$) soils. The soils have low reserves of primary minerals like available phosphorus including nitrogen but have high levels of Aluminium and manganese (SCRB, 2001). This region has potential for production of millet, cassava, sorghum and maize when soils are limed.

1.1 Objectives

The overall objective of the study was to introgress desirable yield enhancing alleles from temperate genotypes of maize into tropical maize in order to increase grain yield on phosphorus deficient soils, particularly agro-ecological region III in Zambia.

The specific objectives were to:

1) Identify temperate maize inbreds that could contribute yield enhancing alleles to tropical genotypes on phosphorus deficient soils.
2) Develop phosphorus-use-efficient single-cross hybrids that could be used as source of genetic materials for extracting improved tropical inbred-lines and 3-way cross or double-cross hybrids.

CHAPTER 2

LITERATURE REVIEW

2.1 Origin and description of maize

A phylogeny study of maize (*Zea mays L.*) domestication showed that maize originated from a wild ancestor, teosinte (*Euchleana Mexican schrand*) in southern Mexico about 9,000 years ago (Matsuoka et al., 2002a). It belongs to *Plantae* kingdom, *Poaceae* family and genus being *Zea*. Selection soon followed, favourable alleles at loci controlling plant morphology and kernel nutritional quality were fixed at least 4,400 years ago, and further selection by Native Americans facilitated maize adaptations to varied environments. Initially, the large phenotypic differences between maize and teosinte obscured the identity of the wild progenitor of maize for centuries. Recent genetic analyses coupled with precision phenotyping (Doebley, 2004) confirmed earlier genetic studies showing that the defining differences between maize and teosinte reside at relatively few loci. Together with sorghum and sugarcane, maize uses C_4 photosynthesis to fix atmospheric carbon dioxide. The crop has high rate of photosynthetic activity leading to high grain and biomass yield potential.

Maize was brought to Africa via plant introduction by the European explorers during the 16th century. It is a diploid, cross pollinated annual plant with 20 chromosomes ($2n = 20$). The maize plant has an erect, solid stem, rather than the hollow one of most other grasses. The leaves, which grow alternately, are long and narrow. Maize is a monoecious plant, with separate male and female flowers on the same plant. The main stalk terminates in a male inflorescence (tassel). The ear (cob) is enclosed in modified leaves called husks. The maize kernel (grain) consists of an endosperm, embryo, a pericarp and tip cap. The endosperm contains the main carbohydrates. The endosperm contains approximately 80 % of the carbohydrates, 20 % of the fat and 25 % of the minerals, while the embryo contains about 80 % of the fat, 75 % of the minerals and 20 % of the protein found in the kernel (Du Plessis, 2003). Kernels can be of the dent or flint (round) types. Maize with a high percentage of translucent of hard endosperm is preferred by the dry-milling industry, because it produces more of the popular high-quality and high-value products sought for than soft maize.

2.2 Adaptation and climatic requirements

Maize is grown all over the world from about latitudes 55° north to 40° south and from the sea level to 3,800 m altitude. It has adapted to a wide range of environments with its growing period ranging from 65 days in the lowland tropics to approximately 12 months in the tropical highlands (Fischer and Palmer, 1984). It performs well on well-drained fertile soils in areas with moderately high temperatures and adequate, but not excessive rainfall (Mungoma and Mwambula, 1997). Maize is a warm weather crop and is not grown in areas where the mean daily temperature is less than 19 ºC or where the mean of the summer months is less than 23 ºC. Although the minimum temperature for germination is 10 ºC, germination will be faster and less variable at soil temperatures of 16 ºC - 18 ºC. Under warm and moist conditions, seedlings emerge after about six to ten days, but under cool and dry conditions this may take two weeks or longer. Frost damages maize crop at all growth stages and a frost-free period of 120 - 140 days is required to prevent the damage (Du Plessis, 2003). Maize needs 450 - 600 mm of water per season, which is mainly acquired from the soil moisture reserves. With average rainfall of about 600 mm per season, Zambia receives enough rain to support maize production and achieve high yields.

The most suitable soil for maize is one with a good effective depth, favourable morphological properties, good internal drainage, optimal moisture regime, sufficient and balanced quantities of plant nutrients and chemical properties that are favourable specifically for maize production. For normal growth, maize requires essential elements, of which nitrogen (N), phosphorous (P) and potassium (K) are the most important. The assimilation of N, P and K reaches a peak during flowering. At maturity, the total nutrient uptake of a single maize plant is 8.7 g of N, 5.1 g of P, and 4.0 g of K. Each ton of grain produced removes 15.0 - 18.0 kg of N, 2.5 - 3.0 kg of P and 3.0 - 4.0 kg of K from the soil. No other crop utilises sunlight more effectively than maize, and its yield per hectare is the highest of all grain crops (Du Plessis, 2003).

2.3 Importance of maize in global agriculture

The world population doubled within 40 years after 1960. Despite some efforts to slow the growth rate, the global population will be about 7,500 million in 2020 according to a forecast by the United Nations using a medium-fertility model. In the more distant future, there may be 9,000 million people by 2050, and the number may stabilize at slightly more than 10,000 million after 2100 (IFPRI, 1997, 1999). The population increase during the next two decades will occur almost entirely in 93 developing countries. With a growth rate of 1.5 percent/year, there will be 1,500 million more people by 2020.

Compared with global food prospects, the challenge for the developing countries is much greater. The large increase in cereal demand will not only result from population growth but also from an increasing demand for meat, which will almost double to 30 kg/capita/year by 2020. As a consequence, the cereal demand for livestock feed will double, and the area of maize grown for animal feed is likely to exceed that of rice and wheat grown for human consumption. The cereal demand for 6,300 million people including both food and feed has been estimated at about 1,700 million tons (IFPRI, 1999).

2.4 Importance of maize in Zambia

Zambia covers about 752,600 square kilometres area. A large part of Zambia is on the central African plateau between 1,000 m and 1,600 m above sea level. Although Zambia is tropical, temperatures are modified by altitude. Maize is the most important food crop in Zambia and is produced in all provinces of the country (Figure 1). Approximately 65 % of the households in Zambia are agriculture-based and of these households, an estimate of 84 % is located in rural areas. Over 90 % of agricultural households are small-scale farmers and of these, 69 % cultivate only up to 2.0 ha land (MACO/CSO, 2006b). Further, approximately 86 % of the agricultural households grow maize while only 9 % grow millet, the second most widely cultivated cereal in the country (MACO/CSO, 2005). For an estimated population of 13.4 million people, the food balance sheet showed that maize required for human consumption was 1,396,341 tons per year (MACO/CSO, 2011). While the estimated maize requirement for industrial use, specifically stock-feed and breweries were 175,000 tons and 95,000 tons respectively.

Between 1997 and 2007, the area under maize production increased from 510,372 hectares during the 1997/98 season to 872,812 hectares during the 2006/07 season, while the average grain yield ranged from 1.25 ton/ha to 1.93 ton/ha over the same period (MACO/CSO, 2007). During the 2010/11 agricultural season, the production of Maize increased compared to the 2009/10 season. Total maize production in the 2010/11 season was estimated to be 3,020,380 tons. The total area planted with maize by small and medium scale farmers increased by 10.9 percent. Large scale farmers achieved an average maize yield of 5.27 tons/ha in the 2010/11 season compared to 5.13 tons/ha recorded in the 2009/2010 season. Small and medium scale farmers achieved an average yield of 2.13 tons/ha in the 2010/11 season, compared to 2.10 tons/ha during the 2009/2010 season (MACO/CSO, 2011). These yields obtained by farmers in Zambia are far much less than the one reported by Zambezi and Mwambula. According to Zambezi and Mwambula (1997) the yields of improved varieties of maize are over 10.0 tons/ha under research station conditions in southern Africa but less than 1.0 ton/ha under farmer conditions. Thus the wide gap between grain yield of maize at research stations and that obtained by small-scale farmers is a matter of concern in Zambia. The area under maize cultivation has continued to increase in Zambia, implying that maize will continue to be grown under sub-optimal conditions. Therefore, breeding for stress tolerance should take centre stage.

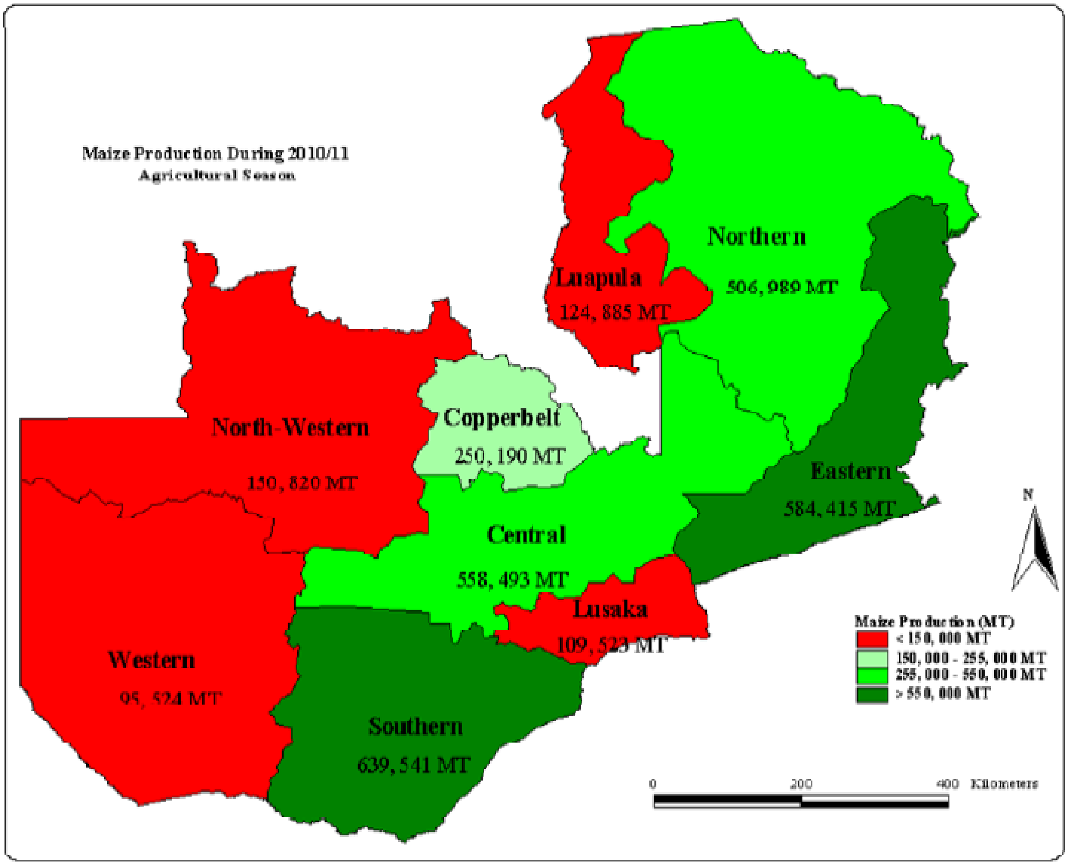

Figure 1: Tonnage of Maize production in Zambia. Source: MACO/CSO 2010/2011.

2.5 Maize production amidst climate change

Resource poor farmers grow maize under sub-optimal conditions rendering it being predisposed to biotic and abiotic stresses that reduce productivity. This has further been exacerbated by climate change. Climate change predictions indicate that most parts of Africa will experience higher temperatures and unstable rainfall, resulting in crop yield depression (Yesuf et al., 2008). The negative impact of climate change in Africa has been estimated to be highest on maize crop. Anticipated loss in crop yields is 22 %, 17 %, 17 %, 18 %, and 8 % for maize, sorghum, millet, groundnut, and cassava, respectively, by the mid of 21st century (Schlenker and Lobell, 2010). There is therefore need to develop maize cultivars that produce satisfactory yield when subjected to biotic/abiotic stress but that also have high productivity under ideal growing conditions.

2.6 Efforts to enhance maize production

Increasing maize production has been of economic importance in Zambia. In this vein, the Fertilizer Support Programme (FSP), currently known as the Farmer Input Support Programme (FISP) was launched by the Government of the Republic of Zambia (GRZ) in 2002. The objectives of FISP were to provide subsidized hybrid maize seed and fertilizer packages to small-scale farmers and to promote the participation of private traders in supply. The Government of Zambia and some non-governmental organizations (NGOs) distributed maize seed and inorganic fertilizers (D-compound and urea) to small-scale farmers across the country (MACO, 2005). However, the farm input support fell short of reaching all the farmers and the intervention was largely unsustainable.

The GRZ and some NGOs also promoted conservation farming (CF) among the farmers. According to Mulenga (2001), conservation farming practices, such as crop rotation, contour farming, mulching, use of cover crops, zero tillage and green manure are promoted in Zambia to enrich and protect the soil from further degradation, and increase farm productivity. However, the practices are often labour intensive and are rarely practised on a large scale (Mitti, 2007).

2.7 Factors limiting maize yields in Zambia

In plant nutrition, there is a law known as Liebig’s law of the minimum. It states that the growth of a plant is limited by the nutrient that is in shortest supply in relation to the optimal needs of a plant. Once its supply is improved, the next limiting nutrient controls the growth of the plant (FAO/FPN, 2006). Phosphorus is naturally available only in very small quantities in soil solutions. Not surprisingly, the amount of P available to plants is often the predominant limiting factor for agricultural production in large part of the world. Most soils in sub-Saharan Africa are generally deficient in available phosphorus (Bekunda et al., 1997). Insufficient P-fertilization and high P-fixation by Aluminium and Iron oxides in the soil have been identified as the key causes of phosphorus deficiency (Kochian, 1995).

Franzluebbers et al. (1998) have reported that small-scale farmers in Africa rarely apply sufficient P and N fertilizer for optimum crop growth. This happens against the background of serious soil nutrient depletion and limited resources. Soil fertility depletion is the major cause of declining food security on small-scale farms of Sub-Saharan Africa and phosphorus is among the nutrients that severely limit crop production (Sanchez et al., 1997). An average of 660 kg N/ha, 75 kg P/ha and 450 kg K/ha are reported lost during the last 30 years from about 200 million hectares of land in 37 African countries (Sanchez et al., 1997). Sanchez (2002) suggested average annual depletion of about 22 kg N/ha, 2.5 kg P/ha, and 15 kg K/ha on African land, yet farmers grow cultivars that are susceptible to low soil nutrients.

In Zambia, phosphorus has been reported as the second most limiting nutrient to crop production after nitrogen. As such, efforts to increase maize-grain yield beyond the 2.5 ton/ha in most small-scale farming systems are being undermined by nitrogen and phosphorus deficiencies. Drought has also been reported to cause yield losses in maize of up to 60 % in southern Africa (Edmeades et al., 1999). Some farmers fail to irrigate during the drought periods to mitigate the effects of water deficiencies while others fail to apply fertilizers to support plant growth due to lack of financial resources and non-availability of the product (Mungoma and Mwambula, 1997).

The causes of low P reserves in soils of tropical regions are long periods of intensive leaching, weathering and low P status of the underlying rocks. Phosphorus in the soils has also been widely depleted through continuous removal of nutrients through agricultural practices such as residue removal as well as harvest. Soil pH may also contribute to phosphorus deficiency. Soil pH less than 5.5 may reduce the availability of phosphorus in the soil solution by 30 % or more. Soil pH range below 4.4 (i.e. very acidic soils) yield response to basal application by just 2.1 incremental kg of maize per kg of fertilizer in Zambia (Burke et al., 2012). Treating phosphorus deficiency takes time because phosphorus is immobile in the soil. Therefore, roots of maize must grow into the zone where fertilizer was applied before they can absorb the phosphorus (Eric and Larry, 2008). Close placement of phosphorus to crops is very important especially for young plants have small root systems. The map of Zambia in figure 2 presents portions of land that classifies the soils based on soil reaction (pH). The areas coloured purple have low available phosphorus in soils.

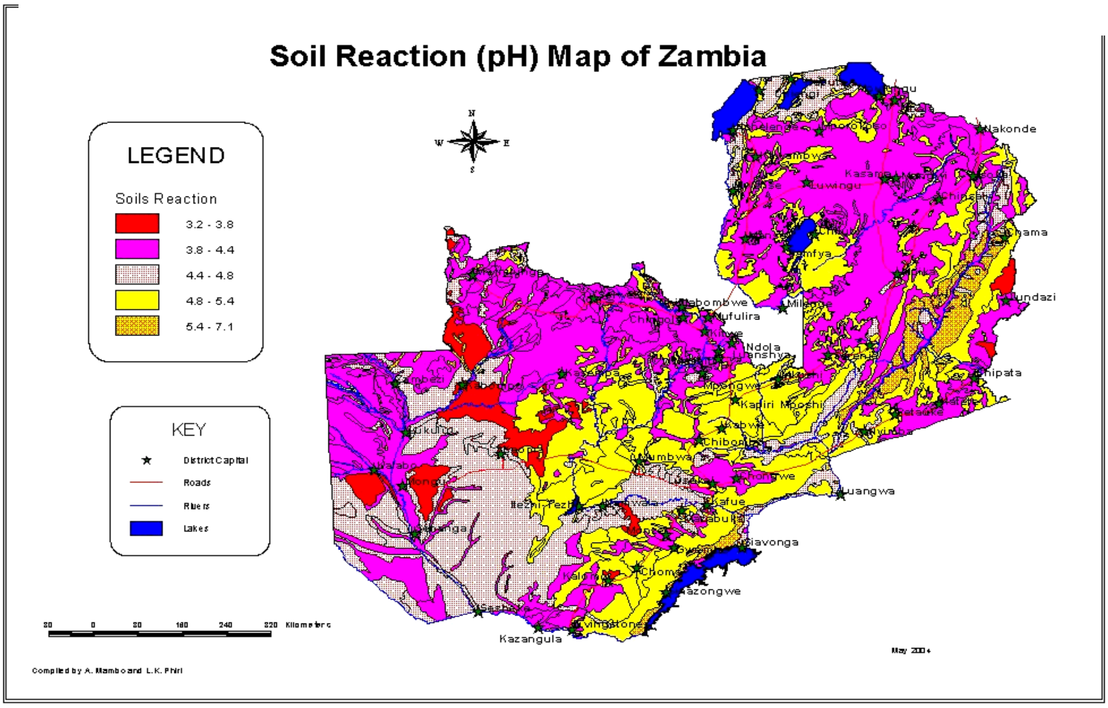

Figure 2: Soil reaction (pH) map of Zambia

2.8 Effects of phosphorous on maize

Phosphorus is a necessary element in the processes of storing the sun’s energy and plant growth (Griffiths, 2010). It is a crucial building block in ribonucleic acid (RNA) and deoxyribonucleic acid (DNA) of maize plant. It helps to strengthen the skeletal structure of the plant thereby preventing lodging. Phosphorus is essential for growth, cell division, root lengthening, seed and fruit development, and early ripening. It is a part of several compounds including oils, amino acids and the phosphorus based compounds adenosinediphosphate and adenosinetriphosphate which act as energy carriers within maize (FAO/FPN, 2006).

Phosphorus is readily mobile only within the plant (unlike in the soil) both in the xylem and phloem tissues. When maize plant faces phosphorus shortage (stress), phosphorus from the old leaves is readily translocated to young tissue. With such a mobile element in plants, the pattern of re-distribution seems to be determined by the properties of the source (old leaves, and stems) and the sink (shoot tip, root tip, expanding leaves and later the developing seed). Phosphorus deficiency retards growth, root development and delays maturity of the maize crop (FAO/FPN, 2006). The deficiency symptoms usually start on older leaves. Shortage of inorganic phosphate in the chloroplast reduces photosynthesis. Decreased shoot to root ratio is a feature of P deficiency, as is the overall reduced growth rate of the crop. Maize crops with P-deficiency symptoms are encountered frequently on inherently P deficient soils and in agricultural systems where nutrients are removed and not sufficiently replenished. Visual signs of P deficiencies are; stunted growth, restricted root development, delayed maturity and poor seed/fruit development. In acute cases of P deficiency, maize show purpling of leaves and stems (Van Straaten, 2002).

2.9 Sources of phosphorus

In order to replenish the removed phosphorus, farmers are forced to use inorganic fertilizers or manure and other P-bearing materials. Phosphate rocks (PR) have been defined as the naturally occurring materials containing one or more phosphate minerals as well as possessing chemical characteristics that make it acceptable for commercial use as a source of phosphorus (Notholt, 1980). Phosphate rock is insoluble and cannot be taken up by maize plant. Acidulation using sulphuric acid or phosphoric acid and even hydrochloric acid transforms the material into soluble form for plant uptake. While the resultant products are in general effective for crop production, the production of single/triple superphosphates (SSP or TSP) as well as mono/di ammonium phosphates (MAP or DAP) require high capital investments (Van Straaten, 2007). In much of sub-Saharan Africa industries, acidulation or even partial acidulation to break down the phosphate minerals and making phosphorus more available is constrained by lack of local sulphur or inadequate infrastructure to allow for economical transportation of sulphur or sulphuric acid and lack of capital.

According to Van Straaten (2002), various innovative techniques to enhance PR solubility have been investigated, including modification techniques like partial acidulation, heap leaching, thermal treatment, mechanical activation, as well as modification through biological processes. Although there are several options open to process PR into a form that is more plant available, the options for small-scale farmers are limited. Practical alternative methods and technologies of PR modification have to be developed for the farm level. Alternative processing techniques of PR need to be screened as to their suitability and acceptance in the local environment. The use of organic resources (compost) plays an important role in the dissolution of phosphate rocks. Microbes help in the solubilisation of phosphorus from PR by secreting organic acids, and in the process decreasing their particle size, reducing it to nearly amorphous forms (FAO/FPN, 2006). Making compost is generally laborious to farmers and the decomposition of crop residues takes longer time, usually not less than two months.

Phosphorus is absorbed as the orthophosphate ion (either as $H_2PO_4^-$ or HPO_4^{2-}) depending on soil pH. As the soil pH increases (>7.2), the relative proportion of $H_2PO_4^-$ decreases and that of HPO_4^{2-} increases. When working with phosphorus, it is necessary to distinguish between elemental phosphorus (P) and phosphate (P_2O_5) since soil test results may be reported as elemental phosphorus whereas commercial fertilizers are formulated on the basis of phosphate. Fertilizer recommendations and animal manure analysis are typically given as the amount of phosphate (Mullins, 2009).

2.10 Phosphorus use efficiency (PUE)

In cases of tolerance and efficiency, plants use physiological mechanisms, and sometimes, anatomic mechanisms to avoid the effect of stress and rapidly recover (Zheng et al., 2000). As a result, three main strategies have been recognized that plants use to cope with stress:

1) Specialization, the genotype is adapted to the specific environment.
2) Generalization, the genotype has moderate suitability in most environments.
3) Phenotypic plasticity, signals from the environment interacts with the genotype and stimulates the production of alternative phenotypes.

The farmer wants cultivars that produce a satisfactory yield when subjected to stress conditions but that have a high productivity under ideal growing conditions. The genetic control of stress tolerance and resource-use efficiency is quantitative and involves many loci distributed in different regions of the genome in cultivated species (Wu et al., 2011).

Tolerance to soil stress is the ability of plants to produce relatively more biomass or grain yield with sub-optimal soil conditions. High yield stability is not always a desirable characteristic because tolerant genotypes generally have moderate productivity, even under ideal growing conditions (Cruz et al., 2004). Genotypes with high yield stability are only important in marginal areas and under cultivation with permanent stress. Such genotypes exhibit superior productivity under phosphorus deficient environments. However, when the environmental conditions are not limiting, there is no significant increase in productivity. Given this fact, most of the crop improvement programs are aimed at increasing the resource use efficiency (RUE) or in obtaining genotypes with high phenotypic plasticity.

Phosphorus use efficiency (PUE) can be generally defined as the ability of a crop plant to produce high yield or dry matter in a soil (media) that is limiting in phosphorus supply (Gourley et al., 1994). Thus, when the plants are subjected to limiting conditions, they would use fewer resources to produce satisfactory results but show high yields when the conditions are ideal. Differences in phosphorus utilization efficiency may occur among plant species or genotypes of the same species due to differences in amounts of shoot dry matter produced per unit of phosphorus acquired (Rao et al., 1997).

Given this scenario, plant genotypes of a given species develop adaptive responses to phosphorus deficiency. Maize also differs greatly in adaptive mechanisms to phosphorus deficiency. To improve growth under phosphorus deficient conditions, P efficient plants have evolved two major adaptation mechanisms:

1) Enhancing phosphorus utilization efficiency.
2) Increasing phosphorus acquisition (phosphorus uptake mechanisms).

Phosphorus use efficiency in this case is the amount of phosphorus needed in the plant to produce one unit of dry matter. This is often known as internal phosphorus requirement (Bates and Lynch, 2001; Vance et al., 2003). Phosphorus internal utilization efficiency can be divided into two components: the P harvest index (capacity of the plant to redistributed P from shoot to grain) and the quotient of P utilization (grain produced per unit of P in the grain). The majority of the phenotypic variation for PUE in tropical maize (80.8%) has been explained by the latter (Parentoni and Souza, 2008).

On the other hand, phosphorus uptake efficiency of plants is the ability of the root system to acquire phosphorus from the soil and accumulate it in the shoots (Bhadoria et al., 2002). Plants have evolved an array of adaptation to enhance phosphorus acquisition from soils (Vance, 2001). One set of adaptive responses is the alteration of root architecture to increase phosphorus acquisition from the soil at minimum metabolic cost (Lynch and Brown, 2001). Among the possibly beneficial root traits for phosphorus acquisition, root hairs are particularly important.

2.11 Breeding for improved maize yield in phosphorus deficient soils

Maize is generally considered to have a high fertility requirement, but variation has been known to exist among maize genotypes for phosphorus efficiency for more than a century (Gaume et al., 2001). Temperate inbred-lines Mo17 has been previously shown to be more phosphorus efficient followed by B73. Jinming et al. (2004) discovered that root biomass of the phosphorus efficient genotype Mo17 was not negatively affected by low phosphorus, whereas phosphorus stress significantly reduced root biomass for B73. The main precondition for designing model hybrids for phosphorus deficient soils is to obtain parental inbred-lines possessing desirable genes to be paired up as parental lines that produce superior F_1 progeny over the existing hybrids for a number of agronomic traits. In United States of America, small but significant reduction of genetic diversity has been caused by recycling public inbreds in maize breeding programs (Lu and Bernardo, 2001). Maize breeders in temperate regions have advocated breeding with tropical germplasm (Goodman, 1992), which is the most logical source of additional genetic diversity.

Further, maize breeders have tried to incorporate exotic germplasm into adapted cultivars to increase genetic variability and to improve the derived populations for grain yield. Introgression of exotic germplasm to improve adapted maize populations has also been attempted by various authors; for example Tracy (1990) and Beck et al. (1991) for temperate populations, Sauvaire and Sanou (1989) for tropical populations. The rate of genetic gain must be increased to meet demand for food, feed and industrial raw materials in a fashion that also helps protect the environment. To achieve this, it requires improved efficiencies by breeders to identify associations of alleles that provide the genotypes with greater performance potentials in target agricultural environments.

In order to increase maize production among the predominantly small-scale farmers in Zambia, high yielding varieties that are efficient in utilizing phosphorus should be developed. Maize varieties with high grain yield under low phosphorus could reduce environmental pollution and increase the economic efficiency of phosphorus use. The selection of inbred parents of the existing maize hybrids, through pedigree selection (Bernardo, 1990a), is the common method used in commercial maize breeding programs. Selection of donors is crucial to the success of such breeding programs (Hallauer and Miranda, 1988). The largest number of favourable alleles is usually accumulated in the best hybrids, grown in a certain area (Dudley, 1984a, b). The identification of additional favourable alleles for quantitative traits not present in elite hybrids enhances crop improvement.

Knowledge of heritability (h^2) influences the choice of selection procedures used by the plant breeder to decide which selection methods would be most useful to improve the trait. The most important function of heritability in genetic studies of quantitative traits is its predictive role to indicate the reliability of phenotypic value as a guide to breeding value. Traits with high heritability can easily be fixed with simple selection resulting in quick progress (Bello et al., 2012). Although primary traits such as grain yield is an important criterion in selecting genotypes for stress tolerance, there is wide agreement that selection under stress is less efficient than under optimal conditions, mainly because heritability of grain yield declines under the stress (Banziger and Cooper, 2001).

Similarly, selecting under optimal conditions (high inputs) increases genetic variance relative to environmental variance and thus increases heritability. This increases the chances of selecting superior genotypes and enhances the breeding progress. Therefore, when selecting for grain yield under stress conditions (low P or low N), additional information on secondary traits of maize such as ear-per-plant and plant height should also be used to supplement the primary traits. The heritability of secondary traits may be optimized by low competition, enhancing gene fixation and conducting multiple-environment screening (Fasoulas and Fasoulas, 1997). Under low competition, the single plant phenotypic expression and differentiation increases; the coefficient of variation (CV) is reduced; and the share of genetic variance increases at the expense of the environmental variance and the genotype corresponds more closely to the phenotype. Heritability estimates in crops were classified as high (>0.50), medium (0.30 - 0.50), and low (<0.30) according to Bhateria et al. (2006).

2.12 Hybrid vigour

Hybrid vigour is the increase in size or productivity of the F_1 hybrid plant over the mean performance of its parents (David and John, 2006). An alternative term heterosis was proposed by Shull (1952) to denote the increase in productivity (size) of hybrids compared with corresponding inbreds (parents) as an expression of hybrid vigour. The two terms, hybrid vigour and heterosis are synonymous and may be used interchangeably in this paper. Hybrid vigour is generally greatest following crosses among diverse genotypes of maize. The principle in hybrid maize breeding is to cross homozygous parental genotypes (inbreds) that combines to produce superior F_1 hybrids. Experiences have shown that inbreds derived from unrelated populations combines well to produce high-yielding single-cross hybrids more frequently than inbreds derived from related parent material (David and John, 2006). Although hybrid plants are heterozygous at many loci, uniformity is attained like in a pure-line cultivar of self-pollinated crops because they have identical genotypes. Breeding hybrids depends on the generation of inbred-lines, such that when crossed to form a hybrid, heterosis is fully exploited. Thus, parental selection is an important step that results in the development of high yielding and stress tolerant hybrids.

In tropical maize breeding, research and development of the germplasm that belongs to different heterotic groups is fundamental for breeding high-yielding maize hybrids. As such, incorporating temperate inbred-lines which have unique alleles into tropically adapted lines could be beneficial for enhancing heterosis in grain yields (Weiwei et al., 2011). Exotic germplasm can provide new desirable alleles for line and population improvement. In order to enhance heterosis in grain yields of tropical maize, it is suggested that wider resources for introgression of exotic germplasm are needed to increase the genetic distances between opposite heterotic lines and populations (Reif et al., 2003).

2.13 Gene action conditioning grain yield under low phosphorus

To develop an appropriate breeding strategy in selecting genotypes that produces high grain yield under low P soil conditions, information on gene action is important. Tolerance to low P is a quantitatively inherited trait controlled largely by additive gene effects, although dominance and epistatic effects have also been shown to be important (Chaubey et al., 1994). Betran et al., (2003) also reported that dominance (no-additive) gene action in tropical maize was important. The information on General Combining Ability (GCA) and Specific Combining Ability (SCA) effects may be used to estimate gene action of traits.

In statistical terms, GCA effects are main effects and indicate primarily additive gene action (Falconer, 1981). Effects of GCA can also be used to select superior genotypes under low P conditions. High GCA effects under low P reflect the presence of the desired fixable low P alleles being sought. The SCA effects indicate primarily dominance (non-additive) gene action of traits and they are non-fixable. Thus, the GCA effects are useful for selection programs in crop improvement whereas, SCA effects are important for hybrid crop development. Genotypic variation for tolerance to P-deficiency exists in maize and this has allowed selection and development of efficient genotypes in phosphorus deficiency soils (Reiter et al., 1991, Da Silva and Gabelman, 1993).

CHAPTER 3

MATERIALS AND METHODS

3.1 Germplasm

Germplasm that was used in the research study was obtained from U.S.A, Zambia and Zimbabwe (CIMMYT). It included 9 tropical inbreds, 3 temperate inbreds and 9 commercial hybrids that were used as checks during evaluation (Table 1). These check hybrids were ideal for the study because they are commonly cultivated by farmers in agro-ecological region III of Zambia.

Table 1: Genotypes used in the study

Genotype	Type	Designation	Source
L1212	Inbred line	Female	Tropical
L913	Inbred line	Female	Tropical
L5527	Inbred line	Female	Tropical
L151	Inbred line	Female	Tropical
L911	Inbred line	Female	Tropical
L12	Inbred line	Female	Tropical
L917	Inbred line	Female	Tropical
L152	Inbred line	Female	Tropical
L1214	Inbred line	Female	Tropical
J185	Inbred line	Male	Temperate
Mo17	Inbred line	Male	Temperate
B73	Inbred line	Male	Temperate
MM752	Hybrid	Check	Tropical
MM603	Hybrid	Check	Tropical
ZMS638	Hybrid	Check	Tropical
GV704	Hybrid	Check	Tropical
MRI694	Hybrid	Check	Tropical
SC513	Hybrid	Check	Tropical
SC627	Hybrid	Check	Tropical
SC701	Hybrid	Check	Tropical
SC721	Hybrid	Check	Tropical

3.2 Study locations

The crossing block was set up at the field station of Seed Control and Certification Institute (SCCI) in July 2012, under an irrigation system. SCCI is located within agro-ecological region II, in Chilanga district of Lusaka province. The institute lies on longitude 26.26° east, latitude 15.55° south and altitude 1,227 m above sea level. The long term annual rainfall at SCCI is estimated at 800 to 1000mm (Bunyolo et al., 1997).

The evaluation trial was carried out on one site at Mutanda Research Station during the 2012/13 rain season. Mutanda research station is a government institution under the Zambia Agricultural Research Institute (ZARI). It is located within agro-ecological region III in Solwezi district of Zambia. The station lies on longitude 12° 11' east, latitude 26° 24' south and altitude 1386 m above sea level. It receives 1000 mm to 1500 mm of rainfall annually. In 2011/12 rain season, the site received annual rainfall of 1250 mm, with temperature in the range of 16-30 ºC, and average relative humidity of 74 %. The site is characterized by red to brown clayey to loamy soils with very strong acidity (pH<4.5), highly weathered and leached soils, low reserves of primary minerals, with high levels of Aluminium and Manganese (SCRB 2001).

3.3 Nursery management and hybridization

In July 2012, a crossing block (nursery) was established at SCCI station under irrigated optimal field conditions. Maize genotypes were planted in 3 meters long single-row plots, spaced at 0.75 m between rows and 0.30 m between plants within the row. All the 9 tropical inbred females were sown on 7th July 2012 while the 3 temperate males, were sown one week later. On the day of sowing maize, D-compound (N10:P20:K10) fertilizer was also applied at the rate of 200 kg/ha as basal dressing. Top-dressing fertilizer (Urea 46 % N) was applied at the rate of 200 kg/ha (thus 92 kg N/ha) 21 days after planting. Other agronomic practices like irrigation, weed management, pest and disease control were done optimally in accordance with recommendations for seed production. The North Carolina Design II (NCD II) mating design was used. Only 24 crosses produced successful single-cross hybrids while 3 crosses (i.e. L12×J185, L1214×B73 and L5527×B73) did not, due to poor synchronization of anthesis and silking.

At physiological maturity, the ears from successful crosses were hand-harvested, shelled and the F_1 (single-cross hybrid) seed was stored for evaluation during the 2012/2013 rain season. The successful F_1 single-crosses were designated by (✓) symbol and unsuccessful ones by (x) symbol (Table 2).

Table 2: Single crosses made

Tropical females	Temperate males		
	Mo17	B73	J185
L1212	(✓)	(✓)	(✓)
L913	(✓)	(✓)	(✓)
L5527	(✓)	(x)	(✓)
L151	(✓)	(✓)	(✓)
L911	(✓)	(✓)	(✓)
L12	(✓)	(✓)	(x)
L917	(✓)	(✓)	(✓)
L152	(✓)	(✓)	(✓)
L1214	(✓)	(x)	(✓)

3.4 Experimental design and trial management

The resultant 24 single-cross hybrids and nine (9) check hybrids were considered for evaluation under low phosphorus soil conditions at Mutanda Research Station. Initial fertility status of the site was determined prior to planting maize (Table 3). Available P in soil was determined using the Bray-I method (Bray and Kurtz, 1945). The results from 0 - 20 cm soil depth gave 7.0 ppm available phosphorus and pH ($CaCl_2$) of 4.8. Phosphorus level of 7.0 ppm in soil was far below the optimal range of 10 ppm to 15 ppm that is required for high crop productivity (Kisinyo et al., 2009). This constituted the basis of choosing Mutanda Research Station as the appropriate site for the study.

Table 3: Soil characteristics of research site

Name	Quantity
Phosphorus	7.0 ppm
Potassium	8.0 ppm
Nitrogen	0.01 %
Exchangeable Aluminium	0.0 me%
Magnesium	10.0 ppm
pH ($CaCl_2$)	4.8

The trial was planted in December 2013, on 3 m long single-row plots. Plants were spaced 0.75 m between rows and 0.30 m between plants. The experiment was laid out in a 3 × 11 alpha lattice design with 2 replications. Two seeds were initially planted per hill but were subsequently thinned to one plant per hill 4 weeks after germination. Two border rows were placed at either ends of the experimental field. Phosphorus fertilizer was not applied to the trial at any time. However, the recommended quantities of potassium (30 kg K/ha) and nitrogen (20 kg N/ha) were supplied to maize by applying potassium nitrate (47% K, 13% N) and urea (46 % N) fertilizers at the rates of 64 kg/ha and 25 kg/ha respectively as basal dress. Urea fertilizer was also applied 21 days after planting at the rate of 200 kg/ha (92 kg N/ha) as top dress. As the crop was growing, a dry spell occurred from mid-March lasting for 4 weeks. Water was supplemented through irrigation. Other agronomic practices such as weed management, pest and disease control were carried out according to the recommended practices of seed production.

3.5 Data collection

Data was collected from all plants in 3 m long single-row plots, except two plants at either end of the plots. Plants in border rows were not considered for data collection. Plants were harvested at physiological maturity, ears (cobs) separated from the stalk, and fresh weight of both parts recorded. The following parameters were measured:

1) **Grain yield (GY) –** Was determined as the total weight of shelled grain harvested from 3 m long rows adjusted to 12 % grain moisture in tons/ha.
2) **100 grain weight (100GW) –** Was measured as the weight of 100 grains shelled from the ear (cob) from a plot in kilograms.
3) **Plant biomass (PB) -** The weight of the above ground total dry matter including stalk and ears harvested from the plots in tons/ha.
4) **Purpling symptom on leaves –** It was done by scoring, where; 1 = No purpling, 2 = slight purpling, 3 = moderate purpling, 4 = partial purpling and 5 = complete purpling.
5) **Harvest index (HI) –** Was computed as the ratio between maize grain yield and the total above ground plant biomass harvested from a plot.
6) **Shelling percentage (shelling %) –** Was calculated as the weight of grains divided by the total weight of the ear (cob) with grains and expressed as percentage.
7) **Plant height (PH) -** Measured using a tape the average height of matured plants in each plot from ground level to flag leaf in centimeters.

8) **Plant-tissue phosphorus (PTP) -** Three plants were randomly collected per plot from the trial, milled and sub-samples were drawn for laboratory analysis of phosphorus in mg/kg using the Dry Ashing method.
9) **Root biomass (RB) -** Was determined by harvesting roots at physiological maturity using a bucket-auger from the soil depth of 0-20 cm. Dimensions of the bucket on the auger were 20 cm height and 4 cm radius. Roots were oven-dried to constant mass for 24 hours at 75 ºC, average dry-mass of roots was taken per plot and the root biomass was finally calculated as the mass of dry roots per volume of soil held by the auger in kg/m^3.

3.6 Statistical analysis

Data that was collected on various traits was compiled and analysed using the GenStat 13th edition software (Payne et al., 2010) and IBM SPSS statistics version 20.0. The number of plants per plot was considered as a covariate in the analysis. General analysis of variance (ANOVA) for primary traits (yield) and secondary traits of single-crosses and check hybrids was done. The Fisher Least Significant Differences (LSD) at 5 % was used to separate means of traits that had significant differences.

On genetic analysis, the mode of gene action conditioning traits under low P was assessed using the line × tester analysis. Only 18 single-cross hybrids were considered for this analysis, after removing 3 missing crosses (L12×J185, L1214×B73 and L5527×B73) and 6 more crosses that shared common parents with the missing crosses (L12×B73, L12×Mo17, L1214×J185, L1214×Mo17, L5527×J185 and L5527×Mo17). Check hybrids were also excluded from the genetic analysis. The expected mean squares were estimated using the methodology explained by Singh and Choudhary (1985). Main effects due to females and males were independent estimates of general combining ability (GCA) variances while male × female interaction effects represent specific combining ability (SCA) variance. According to Singh and Choudhary (1985), the generic ANOVA for a line × tester analysis is similar to that of the NCD II mating design (Table 4).

Table 4: Generic line × tester analysis of variance

Source	df	Mean square	Expected mean square
Replication	r-1		
Male	m-1	MS_m	$\sigma_e^2 + r\sigma_{fm}^2 + rf\sigma_m^2$
Female	f-1	MS_f	$\sigma_e^2 + r\sigma_{fm}^2 + rm\sigma_f^2$
Male × Female	(f-1)(r-1)	MS_{fm}	$\sigma_e^2 + r\sigma_{fm}^2$
Error	fm(r-1)	MS_e	σ_e^2

The general combining ability of parental inbreds and the specific combining ability of hybrids were estimated following the methodology by Hallauer and Miranda (1988). Thus, SCA is important for hybrid crop development whereas, GCA is useful for selection programs.

1) $GCA_f = X_f - \mu$, and $GCA_m = X_m - \mu$
2) $SCA_X = X_X - E\ (X_X) = X_X - [GCA_f + GCA_m + \mu]$

Where: GCA_f = GCA for female parent, GCA_m = GCA for male parent, X_f and X_m are means of male and female parents respectively, X_X = observed mean value of the cross, E (X_X) = expected value of the cross based on the two GCAs of its parents and μ = overall mean of all crosses made.

The relative contributions of GCA and SCA were estimated using the Baker's ratio $(\sigma^2gca_f + \sigma^2gca_m)/(\sigma^2gca_f + \sigma^2gca_m + \sigma^2sca)$, where σ^2gca_f and σ^2gca_m are the variance components of female GCA and male GCA respectively while σ^2sca is the variance component of SCA (Baker, 1978). The ratio shows how much of the observed variance can be explained by additive and dominance gene actions. The ratio values near a unit (1.0) indicated the preponderance of additive (fixable) gene action over dominance (non-fixable) gene action. The additive genetic variance ($\hat{\sigma}_A^2$) and dominance genetic variance ($\hat{\sigma}_D^2$) were determined using the equations; $\sigma_m^2 = 1/4\hat{\sigma}_A^2$, $\sigma_f^2 = 1/4\hat{\sigma}_A^2$ and $\sigma_{fm}^2 = 1/4\hat{\sigma}_D^2$.

Heritability (h^2) is a measure of the phenotypic variance attributable to genetic causes and has predictive function in plant breeding. It provides information on the extent to which a particular morphogenetic trait can be transmitted to successive generations. Information on heritability of secondary traits and their correlation with primary traits such as GY is important in predicting the breeding progress for environments of low available phosphorus. Therefore, narrow sense heritability was estimated using the formula $h^2 = \hat{\sigma}_A^2 / (\hat{\sigma}^2 + \hat{\sigma}_A^2 + \hat{\sigma}_D^2)$. The ratio of MS_f to MS_m was used to ascertain the presence of maternal effects, where MS_f = mean square for female and MS_m = mean square for male. The significance of ratio values was tested using an F-test at $P < 0.05$.

The simple correlation analysis was done to establish the associations among; grain yield, harvest index, 100 grain weight, shelling %, plant height, purpling symptom, root biomass, plant biomass and plant-tissue phosphorus in the study. Further, stepwise multiple regression was also done to determine the strength of cause and effect relationship between the grain yield and other independent variables (traits) basing on the coefficient of multiple determination (R^2). The R^2 is interpreted as the goodness of fit of a regression. It gives an overall measure of the usefulness of a regression. The higher the R^2 value, the better the variance that the dependent variable is explained by the independent variable.

CHAPTER 4

RESULTS

Results of the general analysis of variance for important primary and secondary traits were presented in table 5. Under phosphorus deficient soils, there were highly significant differences ($P \leq 0.01$) among the genotypes for; grain yield, harvest index, 100 grain weight, shelling %, plant-tissue phosphorus, root biomass, plant height, plant biomass and purpling symptom.

4.1 Mean performance of the genotypes for various parameters

Table 6 presents a summary of means for the traits under consideration.

4.1.1 Grain yield (GY)

Seven high yielding hybrids L5527×J185, L151×Mo17, L151×J185, L152×J185, L152×Mo17, L1212×J185 and L1212×Mo17 gave yields of 12.77 tons/ha, 12.69 tons/ha, 12.56 tons/ha, 12.41 tons/ha, 11.39 tons/ha, 8.47 tons/ha and 8.28 tons/ha respectively compared to the best check (SC721) which only produced 7.43 tons/ha. Grain yield of the above listed hybrids was much higher than the average grain yield of checks which was 3.79 tons/ha. The high grain yield obtained by hybrids; L152×Mo17, L151×Mo17 and L5527×J185 could partially be attributed to their relatively bigger sized cobs/ears compared to the low yielding hybrids (MM752 and SC721) as exhibited in Figure 3.

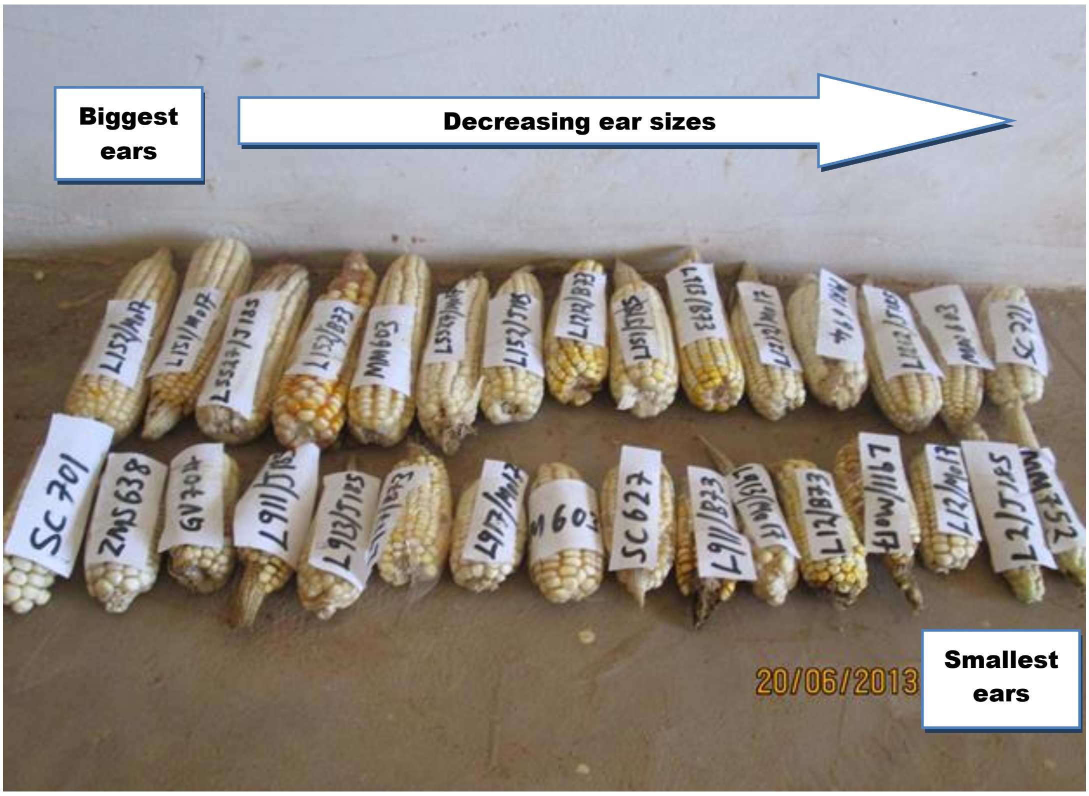

Figure 3: Ear/cob sizes

4.1.2 100 grain weight (100GW)

Only hybrid L5527×Mo17 had a 100GW of 0.12 kg, which was 50 % higher than 0.06 kg of the best check MM603. The average 100GW of all checks was 0.03 kg.

4.1.3 Harvest index (HI)

Seven hybrids that produced high grain yield also gave high harvest index. The HI of hybrids; L5527×J185, L151×J185, L151×Mo17, L152×J185, L152×Mo17, L1212×J185 and L1212×Mo17 ranged from 0.22 to 0.69 while that of the best check was 0.36. The average harvest index of these high yielding hybrids was 0.41, thus twice higher than 0.20 obtained from the checks.

4.1.4 Shelling percentage

Two hybrids L5527×J185 and L152×B73 gave highest shelling percentage of 80.3 % and 85.4 % respectively, compared to 79.0 % obtained by the best check SC627. Then hybrid L1212×Mo17 gave shelling percent of 77.2 % which was higher than

76.5 % obtained by the second best check SC721. Further, eleven hybrids L152×Mo17, L151×J185, L152×J185, L1212×B73, L917×Mo17, L911×B73, L12×B73, L151×Mo17, L12×Mo17, L917×B73 and L917×J185 gave higher shelling percentages ranging from 71.4 % to 76.0 %, than 69.3 % obtained by the third best check GV704.

4.1.5 Plant height (PH)

Seven hybrids that produced high grain yield; L5527×J185, L1212×J185, L152×J185, L151×J185, L151×Mo17, L1212×Mo17 and L152×Mo17 had tall stature with height ranging from 75.8 cm to 110 cm compared to the checks (SC513, SC627 and ZMS638) that had short stature with heights of 56.3 cm, 61.3 cm and 66.8 cm respectively.

4.1.6 Plant-tissue phosphorus (PTP)

Six of the high yielding hybrids; L1212×Mo17, L152×J185, L5527×J185, L151×J185, L1212×J185 and L151×Mo17 that produced high grain yield ranging from 8.28 tons/ha to 12.77 tons/ha accumulated 1326.9 mg/kg (P), 1445.5 mg/kg (P), 1520.9 mg/kg (P), 1606.7 mg/kg (P), 1803.1 mg/kg (P) and 1928.7 mg/kg (P) respectively in tissues. Whereas the best check SC721 produced low grain yield of 7.43 tons/ha despite accumulating a large quantity of phosphorus 1955.6 mg/kg (P) in tissues. In addition, checks such as SC701 and GV704 accumulated very large amount of phosphorus in tissues 2058.4 mg/kg and 2055.3 mg/kg, but they produced very low grain yield of 2.94 tons/ha and 3.06 tons/ha respectively.

4.1.7 Root biomass (RB)

Among the genotypes, hybrids; L5527×J185, L1212×Mo17, L151×J185, L151×Mo17 and L152×J185 that produce high grain yield ranging from 8.28 tons/ha to 12.77 tons/ha gave high root biomass at 0 - 20 cm soil depth. Their root biomass ranged from 1.22 kg/m^3 to 1.84 kg/m^3.

4.1.8 Purpling symptom

Scoring for purpling symptom on the leaves of maize was done at grain filling stage (Figure 4). High yielding hybrids had low scores while susceptible ones such as MM603, MRI694**,** SC627 and SC721 had high scores. Based on purpling scores, hybrids; L1212×Mo17, L913×J185, L152×Mo17, L151×Mo17, L911×Mo17, L151×J185, L152×B73 and L913×Mo17 had no purpling symptoms on leaves (had green leaves) hence were not susceptible to phosphorus deficiency compared to the best check MRI694 which exhibited partial purpling on leaves due to P deficiency.

Figure 4: Purpling symptom in maize

Table 5: General analysis of variance for parameters

Source	GY	100GW	HI	Shelling %	Purpling score	PH	PB	PTP	RB
Replication	0.125	0.000003	0.003	29.73	0.242	885.9	0.08	40429	0.002
Genotype	47.172**	0.0006**	0.046**	727.38**	3.802**	413.2*	191.73**	87734**	0.88**
Covariate	0.022	0.000043	0.019*	0.46	0.005	573.2	3.68*	-	0.04
Error	0.0773	0.00002	0.0034	14.23	0.1533	188	0.38	2039	0.070
CV (5%)	4.5	15.5	21.7	5.6	14	17	2.7	2.6	19.5

KEY: Grain yield (GY), harvest index (HI), 100 grain weight (100GW), plant biomass (PB), plant height (PH), plant tissue phosphorus (PTP) and root biomass (RB) at 0-20cm soil depth.

*Significant ($P \leq 0.05$), **Highly significant ($P \leq 0.01$), ns = Non-significant ($P > 0.05$).

Table 6: Mean performance of genotypes for various traits

Genotype	GY (ton/ha)	HI	100GW (kg)	Shelling %	Purpling score	PH (cm)	PTP (mg/kg)	RB (kg/m^3)
Single cross hybrids								
L5527×J185	12.77	0.52	0.03	80.3	2	110.0	1520.9	1.84
L151×Mo17	12.69	0.31	0.02	72.1	1	79.2	1928.7	1.37
L151×J185	12.56	0.47	0.03	74.8	1	85.6	1606.7	1.64
L152×J185	12.41	0.69	0.02	74.3	2	86.0	1445.5	1.22
L152×Mo17	11.39	0.40	0.02	76.0	1	75.8	2102.3	0.48
L1212×J185	8.47	0.22	0.02	67.1	2	86.4	1803.1	0.49
L1212×Mo17	8.28	0.25	0.02	77.2	1	77.4	1326.9	1.71
L917×B73	7.55	0.38	0.02	71.5	3	93.4	1629.7	0.48
L12×B73	7.49	0.29	0.02	72.7	4	104.0	1728.6	2.14
L911×Mo17	6.95	0.32	0.03	68.7	1	85.9	1639.1	0.88
L152×B73	6.71	0.40	0.03	85.4	1	85.1	1796.2	1.42
L911×B73	6.59	0.48	0.03	73.2	1	95.3	1801.2	1.53
L911×J185	6.42	0.33	0.03	66.0	3	83.6	1373.9	1.85
L5527×Mo17	6.38	0.28	0.12	35.0	4	70.5	1781.0	1.41
L913×J185	5.14	0.24	0.04	62.6	1	72.4	1914.8	0.47
L917×Mo17	4.96	0.29	0.02	73.6	2	83.4	1426.4	0.48
L917×J185	4.63	0.16	0.02	71.4	5	53.2	1904.9	0.51
L913×B73	4.28	0.30	0.01	69.6	5	65.1	1535.4	0.51
L151×B73	3.92	0.25	0.02	69.9	3	76.3	1646.3	1.59
L1212×B73	3.49	0.22	0.02	73.7	2	71.9	1506.9	1.24
L913×Mo17	1.60	0.10	0.03	53.0	1	60.0	1511.1	0.97
L12×Mo17	1.40	0.12	0.03	71.8	4	58.3	1956.0	1.26
L1214×Mo17	0.21	0.02	0.05	11.7	4	75.8	1679.6	1.79
L1214×J185	0.07	0.01	0.01	23.0	4	73.2	1891.0	1.99
Local check hybrids								
SC721©	7.43	0.36	0.03	76.5	2	93.6	1955.6	2.24
MM603©	6.64	0.21	0.06	66.7	2	107.1	1589.3	1.36
MM752©	4.13	0.36	0.02	66.4	4	82.2	1931.4	1.26
MRI694©	3.40	0.07	0.03	64.9	2	90.5	1605.1	1.97
GV704©	3.06	0.14	0.02	69.3	4	95.6	2055.3	0.86
SC701©	2.94	0.09	0.04	62.8	5	93.7	2058.4	3.39
SC627©	2.80	0.27	0.03	79.0	2	61.3	1720.4	0.57
ZMS638©	2.05	0.141	0.02	51.5	5	56.3	1749.7	1.24
SC513©	1.71	0.156	0.03	47.8	5	66.8	1932.0	2.04
LSD (5%)	0.56	0.12	0.01	7.8	0.81	28.82	91.97	0.54

KEY: Grain yield (GY), harvest index (HI), 100 grain weight (100GW), plant height (PH), plant tissue phosphorus (PTP) and root biomass (RB) at 0-20cm soil depth.

4.2 Combining ability effects

Temperate inbreds had significant ($P \leq 0.05$) GCA variances for; grain yield, harvest index and 100 grain weight (Table 7), implying the presence of additive gene action controlling the traits. Similarly, highly significant ($P \leq 0.01$) GCA variances for; grain yield, harvest index, 100 grain weight, shelling %, plant height, plant-tissue phosphorus and root biomass were observed in tropical inbreds, implying the presence of additive gene action controlling the traits. The single-cross hybrids had highly significant ($P \leq 0.01$) SCA variances for; grain yield, harvest index, 100 grain weight, shelling %, root biomass, plant height and plant tissue phosphorus (Table 7), implying the presence of dominant gene action controlling the traits.

Baker's ratio for shelling percent was high (near a unit) indicating the preponderance of additive gene action over dominance gene action. On the contrary, the Baker's ratios for; grain yield, harvest index, root biomass, plant height and plant-tissue phosphorus were low indicating the preponderance of dominance gene action over additive gene action. Further, the ratio MS_f/MS_m (maternal effect) was greater than one for grain yield, harvest index, 100 grain weight, root biomass and plant height suggesting greater contribution of females than males on these traits but, the ratios were non-significant (Table 7).

Table 7: Mean squares of various traits

Source	df	GY	100GW	HI	Shelling %	PH	PTP	RB
GCA_f	5	36.198**	0.00006**	0.064**	171.73**	331.3*	42543**	1.01**
GCA_m	2	27.3**	0.00005**	0.016*	49.98ns	64.16ns	1735ns	0.07ns
SCA	10	13.8969**	0.00007**	0.025**	42.68ns	246.22*	140491**	0.37**
Maternal effect		1.33ns	1.131ns	3.876ns	3.436ns	5.164ns	19.0ns	14.75ns
Baker's ratio		0.411	0.016	0.346	0.643	0.277	0.287	0.342

KEY: Grain yield (GY), harvest index (HI), 100 grain weight (100GW), plant height (PH), plant tissue phosphorus (PTP) and root biomass (RB) at 0-20cm soil depth.

*Significant ($P \le 0.05$), **Highly significant ($P \le 0.01$), ns = Non-significant ($P > 0.05$)

4.3 General combining ability effects

Table 8 presents the general combining ability effects of parental tropical and temperate inbred-lines for parameters that were considered in the study.

4.3.1 Grain yield (GY)

Temperate inbred-lines J185 and Mo17 exhibited highly significant positive ($P \leq 0.01$) GCA effects (1.17** and 0.54**) respectively while B73 exhibited highly significant negative ($P \leq 0.01$) GCA effect (-1.68**) for grain yield. Similarly, tropical inbred-lines L151 and L152 exhibited highly significant positive ($P \leq 0.01$) GCA effects (2.62** and 3.07**) respectively while L1212, L911, L913, L917 exhibited highly significant negative ($P \leq 0.01$) GCA effects (-0.36**, -0.94**, -3.43** and -1.39**) respectively.

4.3.2 100 grain weight (100GW)

Temperate inbred-lines J185 and Mo17 exhibited significant positive ($P \leq 0.05$) GCA effects (0.001* and 0.001*) respectively while B73 exhibited significant negative ($P \leq 0.05$) GCA effect (-0.002*) for grain yield. Tropical inbred-lines L911 and L152 exhibited significant positive ($P \leq 0.05$) GCA effects (0.003* and 0.003*) respectively while L1212 and L917 exhibited highly significant negative ($P \leq 0.01$) GCA effects (-0.005** and -0.003**) for 100 grain weight.

4.3.3 Harvest index (HI)

Temperate inbred-lines J185 and Mo17 exhibited significant positive ($P \leq 0.05$) GCA effects (0.03* and 0.04*) respectively while B73 exhibited significant negative ($P \leq 0.05$) GCA effect (-0.01*) for grain yield. Tropical inbred-line L152 and L911 exhibited highly significant positive ($P \leq 0.01$) GCA effects (0.17** and 0.05**) while L1212, L913 and L917 exhibited highly significant negative ($P \leq 0.01$) GCA effects (-0.09**, -0.11** and -0.05**) for harvest index.

4.3.4 Plant height (PH)

Tropical inbred-line L911 exhibited highly significant positive ($P \leq 0.01$) GCA effect (8.8**) while L913 exhibited highly significant negative ($P \leq 0.01$) GCA effect (-12.1**) for plant height.

4.3.5 Plant-tissue phosphorus (PTP)

Tropical inbred-line L151 and L152 exhibited highly significant positive ($P \leq 0.01$) GCA effects (66.1** and 120.2**) while L1212 and L911 exhibited highly significant negative ($P \leq 0.01$) GCA effects (-115.5** and -56.4**) for plant-tissue phosphorus.

4.3.6 Root biomass

Tropical inbred-line L151 and L911 exhibited highly significant positive ($P \leq 0.01$) GCA effects (0.49** and 0.36**) while L913 and L917 exhibited highly significant negative ($P \leq 0.01$) GCA effects (-0.39** and -0.56**) for root biomass.

Table 8: General combining ability effects of parental inbred-lines for various traits

Parents	GY	100GW	HI	Shelling %	PH	PTP	RB
Tropical inbreds (females)							
L1212	-0.36**	-0.005**	-0.09**	0.02ns	1.0ns	-115.5**	0.11ns
L151	2.62**	0.001ns	0.02ns	0.01ns	3.0ns	66.1**	0.49**
L152	3.07**	0.003*	0.17**	0.07ns	2.6ns	120.2**	-0.02ns
L911	-0.45**	0.003**	0.05**	-0.02ns	8.8**	-56.4**	0.36**
L913	-3.43**	0.001ns	-0.11**	-0.09ns	-12.1**	-7.3ns	-0.39**
L917	-1.39**	-0.003**	-0.05*	0.01ns	-3.6ns	-7.4ns	-0.56**
S.E.	0.05	0.001	0.02	1.23	2.78	12.47	0.07
Temperate inbreds (males)							
B73	-1.68**	-0.002*	-0.01*	0.03ns	2.3ns	-8.5ns	0.07ns
J185	1.17**	0.001*	0.03*	-0.02ns	-1.5ns	13.7ns	-0.01ns
Mo17	0.54**	0.001*	0.04*	-0.01ns	-0.9ns	-5.4ns	-0.05ns
S.E.	0.07	0.001	0.004	1.74	3.93	17.63	0.10

KEY: Standard error (S.E.), grain yield (GY), harvest index (HI), 100 grain weight (100GW), plant height (PH), plant tissue phosphorus (PTP) and root biomass (RB) at 0-20cm soil depth.

*Significant ($P \leq 0.05$), **Highly significant ($P \leq 0.01$), ns = Non-significant ($P > 0.05$).

4.4. Specific combining ability effects

Table 9 presents the specific combining ability effects of single-cross hybrids for parameters that were considered in the study.

4.4.1 Grain yield (GY)

The hybrids L911×B73, L913×B73, L917×B73, L1212×J185, L151×J185, L152×J185, L1212×Mo17, L151×Mo17, L152×Mo17 and L911×Mo17 exhibited highly significant positive (P ≤ 0.01) SCA effects (1.62**, 2.29**, 3.51**, 0.56**, 1.68**, 1.06**, 0.99**, 2.43**, 0.68** and 0.24**) respectively while hybrids L1212×B73, L151×B73, L152×B73, L911×J185, L913×J185, L917×J185, L913×Mo17 and L917×Mo17 exhibited highly significant negative (P ≤ 0.01) SCA effects (-1.57**, -4.14**, -1.76**, -8.52**, -0.29**, -2.28**, -2.62** and -1.29**) respectively for grain yield.

4.4.2 100 grain weight (100GW)

The hybrids L152×B73 and L913×J185exhibited highly significant positive (P ≤ 0.01) SCA effects (0.009**, 0.008**) while hybrids L913×B73, L152×J185 and L911×J185 exhibited highly significant negative (P ≤ 0.01) SCA effects (-0.01**, -0.005** and -0.027**) respectively for 100 grain weight.

4.4.3 Harvest index (HI)

The hybrids L911×B73, L917×B73, L151×J185 and L152×J185 exhibited significant positive (P ≤ 0.05) SCA effects (0.09*, 0.09*, 0.09*, 0.17*) respectively, while hybrids L151×B73, L152×B73, L911×J185 and L917×J185 exhibited highly significant negative (P ≤ 0.01) SCA effects (-0.10**, -0.12**, -0.39**, -0.15**) respectively for harvest index.

4.4.4 Plant height (PH)

Hybrid L917×B73 exhibited significant positive ($P \leq 0.05$) SCA effect (16.7*) while, hybrids L911×J185 and L917×J185 exhibited highly significant negative ($P \leq 0.01$) SCA effects (-80.6**, -26**) respectively for plant height.

4.4.5 Plant-tissue phosphorus (PTP)

The hybrid L911×B73, L1212×J185, L913×J185, L917×J185, L151×Mo17 and L152×Mo17 exhibited highly significant positive ($P \leq 0.01$) SCA effects (205.0**, 243.8**, 247.3**, 237.5**, 206.9**, 326.4**) respectively while, hybrids L151×B73, L913×B73, L151×J185, L152×J185, L911×J185, L1212×Mo17, L913×Mo17 and L917×Mo17 exhibited highly significant negative ($P \leq 0.01$) SCA effects (-72.4**, -109.9**, -134.2**, -349.5**, -1906**, -213.3**, -137.3**, -221.9**) respectively for plant-tissue phosphorus.

4.4.6 Root biomass

Hybrids L1212×Mo17 and L913×Mo17 exhibited significant positive ($P \leq 0.05$) SCA effects (0.64*, 0.39*) respectively while, hybrids L1212×J185, L911×J185, L152×Mo17 and L911×Mo17 exhibited significant negative ($P \leq 0.05$) SCA effects (-0.66*, -0.58*, -0.49*,-0.49*) respectively for root biomass.

Table 9: Specific combining ability effects of hybrids for various traits

F_1 Hybrid	GY	100GW	HI	Shelling %	PH	PTP	RB
L1212×B73	-1.57**	0.001ns	-0.02ns	-0.02ns	-8.7ns	-30.2ns	0.01ns
L151×B73	-4.14**	-0.001ns	-0.10*	-0.05ns	-4.4ns	-72.4*	0.02ns
L152×B73	-1.76**	0.009**	-0.12**	0.04ns	-1.5ns	23.4ns	0.26ns
L911×B73	1.62**	0.002ns	0.09*	0.01ns	2.4ns	205.0**	0.01ns
L913×B73	2.29**	-0.01**	0.07ns	0.05ns	-4.3ns	-109.9**	-0.24ns
L917×B73	3.51**	-0.001ns	0.09*	-0.03ns	16.7*	-15.5ns	-0.06ns
L1212×J185	0.56**	-0.003ns	-0.04ns	-0.04ns	8.3ns	243.8**	-0.66**
L151×J185	1.68**	0.004ns	0.09*	0.04ns	4.8ns	-134.2**	0.09ns
L152×J185	1.06**	-0.005*	0.17**	-0.03ns	5.6ns	-349.5**	0.23ns
L911×J185	-8.52**	-0.027**	-0.39**	-0.73ns	-80.6**	-1906**	-0.58**
L913×J185	-0.29*	0.008**	-0.00ns	0.03ns	8.7ns	247.3**	-0.15ns
L917×J185	-2.28**	0.000ns	-0.15**	0.01ns	-26**	237.5**	0.01ns
L1212×Mo17	0.99**	0.002ns	0.06ns	0.06ns	0.6ns	-213.3**	0.64**
L151×Mo17	2.43**	-0.003ns	0.01ns	0.01ns	-0.2ns	206.9**	-0.11ns
L152×Mo17	0.68**	-0.004ns	-0.05ns	-0.02ns	-3.8ns	326.4**	-0.49*
L911×Mo17	0.24*	0.001ns	-0.01ns	0.00ns	-1.3ns	39.8ns	-0.49*
L913×Mo17	-2.62**	0.002ns	-0.07ns	-0.08ns	-4.3ns	-137.3**	0.39*
L917×Mo17	-1.29**	0.001ns	0.06ns	0.02ns	9.3ns	-221.9**	0.06ns
S.E.	0.12	0.002	0.042	3.01	6.81	30.54	0.18

KEY: Standard error (S.E.), grain yield (GY), harvest index (HI), 100 grain weight (100GW), plant height (PH) plant tissue phosphorus (PTP) and root biomass (RB) at 0-20cm soil depth.

*Significant ($P \leq 0.05$), **Highly significant ($P \leq 0.01$), ns = Non-significant ($P > 0.05$).

4.5 Associations among traits

Simple correlation analyses were conducted among various components to determine the strength of association of the traits and also to estimate the inter-component correlations among them (Table 10). The results showed highly significant positive ($P \leq 0.01$) correlations for grain yield with; harvest index ($r = 0.76^{**}$), shelling % ($r = 0.60^{**}$), plant biomass ($r = 0.43^{**}$), plant height ($r = 0.40^{**}$) and a highly significant negative ($P \leq 0.01$) correlation with purpling of leaves ($r = -0.50^{**}$). However, purpling of leaves due to phosphorus deficiency showed significant negative ($P \leq 0.05$) correlations with; harvest index ($r = -0.36^{**}$), shelling % ($r = -0.29^{*}$), plant height ($r = -0.24^{*}$) and plant biomass ($r = -24^{*}$). The root biomass showed significant positive ($P \leq 0.05$) correlations with above ground plant biomass (0.29^{*}) and plant height ($r = 0.32^{**}$).

4.6 Stepwise multiple regression

Simple correlations measure character associations only. In order to determine the strength of cause and effect relationship between the grain yield and other traits, the stepwise multiple regression analysis was done. Grain yield (dependent variable) was regressed on independent variables such as; harvest index, shelling %, plant biomass, plant height, root biomass, 100 grain weight, plant-tissue phosphorus and purpling symptom of leaves. The harvest index gave highly significant ($P \leq 0.01$) influence on grain yield explaining 65.7 % of the total variation. Purpling symptom and plant height showed little contribution with 69.0 % and 71.9 % respectively according to the total variation in grain yield, which was 3.3 % and 2.9 % when expressed as R^2 (Table 11). Other variables showed non-significant ($P > 0.05$) differences according to the total variation in grain yield and were excluded in the model.

Table 10: Correlations of various parameters

Parameter	100GW	PB	GY	HI	PH	PTP	Purpling	RB	Shelling %
100GW	1	0.00ns	-0.02ns	-0.01ns	-0.01ns	0.07ns	0.07ns	0.12ns	-0.29*
PB		1	0.43**	-0.09ns	0.46**	-0.08ns	-0.24*	0.29*	0.25*
GY			1	0.76**	0.40**	-0.17ns	-0.50**	-0.08ns	0.60**
HI				1	0.21ns	-0.20ns	-0.36**	-0.17ns	0.62**
PH					1	-0.12ns	-0.24*	0.32**	0.33**
PTP						1	0.20ns	0.06ns	-0.16ns
Purpling							1	0.23ns	-0.29*
RB								1	-0.11ns
Shelling%									1

KEY: Grain yield (GY), harvest index (HI), 100 grain weight (100GW), plant biomass (PB), plant height (PH), plant tissue phosphorus (PTP) and root biomass (RB) at 0-20cm soil depth.

*Significant ($P \leq 0.05$), **Highly significant ($P \leq 0.01$), ns = Non-significant ($P > 0.05$)

Table 11: Stepwise multiple regressions of grain yield on various traits

Variable	Partial Square	R-Model Square	R-F-Value	Pr.>F
Harvest index	0.657	0.657	59.325	0.000
Purpling	0.690	0.033	3.198	0.084
Plant height	0.719	0.029	2.998	0.094

*Significant ($P \leq 0.05$), **Highly significant ($P \leq 0.01$), ns = Non-significant ($P > 0.05$)

4.7 Heritability

Parameters that were measured showed varying narrow sense heritability estimates under low phosphorus soil condition. Table 12 presents narrow sense heritability estimates of traits ranging from 1 % to 40 %. Shelling percentage, a component of yield gave medium heritability estimate of 40 %. Grain yield, plant-tissue phosphorus, harvest index, root biomass, 100 grain yield and plant height gave low heritability estimates of 26 %, 25 %, 20 %, 19 %, 6 % and 1 % respectively.

Table 12: Narrow sense heritability estimates

Parameter	Heritability (h^2)
Shelling percentage	40 %
Grain yield	26 %
Plant-tissue phosphorus	25 %
Harvest index	20 %
Root biomass	19 %
100 grain weight	6 %
Plant height	1 %

CHAPTER 5

DISCUSSION

Temperate maize inbred-lines were crossed to tropical inbred-lines at Mutanda station in Zambia. The objective was to introgress desirable yield enhancing alleles from temperate genotypes of maize into tropical maize under low phosphorus soil conditions. Genotypes showed highly significant differences in grain yield, harvest index, 100 grain weight, shelling %, root biomass, plant height, plant biomass and purpling symptom on phosphorus deficient soils. These differences meant that there was enough genetic variation in phosphorus use efficiency among the hybrids. Such variations among maize genotypes have also been reported by Da Silva and Gableman (1993).

5.1 Grain yield

The hybrids; L5527×J185, L151×J185, L151×Mo17, L152×J185, L152×Mo17, L1212×J185 and L1212×Mo17 produced higher grain yield ranging from 8.28 tons/ha to 12.77 tons/ha under low phosphorus soils than the best check (SC721) which only produced 7.43 tons/ha. The grain yield of these hybrids was much higher than the average of all checks which was 3.79 tons/ha. Crossing temperate inbreds to tropical inbreds increased grain yield by 33.76 % on phosphorus deficiency soils contrary to the findings of Parentoni et al. (2006) who recorded yield reductions from high to low P levels of approximately 45 %. These high yielding hybrids could be selected for extracting inbred-lines and varieties that are efficient in utilizing phosphorus. The use of grain yield under stress conditions as selection criteria for nutrient efficiency have been proposed in other studies by Osborne and Rengel (2002). These hybrids also had high harvest index ranging from 0.22 to 0.69 while the best checks gave low harvest index of 0.36. The average harvest index of the fore-listed high yielding hybrids was 0.41, thus twice higher than 0.20 obtained from all checks.

5.2 Phosphorus use efficiency

Six of the high yielding hybrids; L1212×Mo17, L152×J185, L5527×J185, L151×J185, L1212×J185 and L151×Mo17 were efficient in utilizing phosphorus because they mobilised and accumulated; 1326.9 mg/kg (P), 1445.5 mg/kg (P), 1520.9 mg/kg (P), 1606.7 mg/kg (P), 1803.1 mg/kg (P) and 1928.7 mg/kg (P) respectively in plant-tissues to produce grain yields ranging from 8.28 tons/ha to 12.77 tons/ha whereas the best check (SC721) mobilised/accumulated as high as 1955.6 mg/kg phosphorus in tissues but, produced lower grain yield of 7.43 tons/ha. Therefore, introgression of temperate alleles into tropical genotypes has potential to improve phosphorus use efficiency. On one hand, the fore-listed hybrids that produced higher grain yield could have been efficient in accumulating phosphorus in plant-tissues and utilizing it to produce grains, hence agreeing with Parentoni et al. (2010) that significant positive correlation between grain yield and PUE under low phosphorus conditions is an adequate selection criterion for phosphorus efficient genotypes. On the other hand, the best check (SC721) accumulated a lot of phosphorus in plant-tissues (1955.6 mg/kg), but was inefficient in utilising phosphorus to produce grains.

5.3 Plant height

Hybrids that produced high grain yield were tall in stature with heights ranging from 75.8 cm to 110 cm compared to checks (SC513, SC627 and ZMS638) that were short with heights of 56.3 cm, 61.3 cm and 66.8 cm respectively. In this study, all hybrid-plants with short stature could have succumbed to phosphorus deficiency in soil because apart from producing low grain yield, they also exhibited purple coloration on leaves.

5.4 Root biomass

Phosphorus is a primary nutrient required for good root development of maize. Hybrids L5527×J185, L1212×Mo17, L151×J185, L151×Mo17 and L152×J185 that produced high grain yield also produced high root biomass ranging from 1.22 kg/m^3 to 1.84 kg/m^3 hence, in agreement with the findings of Jinming et al. (2004). A dense and well-developed root system could have enabled these hybrids optimize nutrient absorption from the soil for growth and development. As such, these hybrids experienced increased growth and development as evidenced by their tall stature and a high above ground plant-biomass.

5.5 Combining ability effects

Temperate parental inbreds gave significant GCA variances for grain yield, harvest index and 100 grain weight, implying that additive gene action controlled the expression of the three traits in temperate inbreds. Similarly, tropical parental inbreds gave significant GCA variances for grain yield, harvest index, 100 grain weight, shelling %, plant height, plant-tissue phosphorus and root biomass. This implied that there was sufficient additive gene action controlling the expression of the seven traits in tropical inbreds. As such, significant breeding progress under low phosphorus could be achieved through cyclic selection of parental genotypes based on the fore-mentioned traits then exploit additive genes.

The hybrids exhibited highly significant SCA variances for; grain yield, harvest index, 100 grain weight, root biomass, plant height and plant-tissue phosphorus, implying that there was sufficient dominance gene action that controlled the expression of these traits. Significant gains in breeding could be achieved through hybridization to capitalize on the dominance gene action under low phosphorus. Therefore, if one parent has high GCA for yield related traits while the other does not, the dominance gene action could be exploited through hybridization to increase grain yield. Higher grain yields ranging from 8.28 tons/ha to 12.77 tons/ha were obtained by single-cross hybrids such as L5527×J185, L151×J185, L151×Mo17, L152×J185, L152×Mo17, L1212×J185 and L1212×Mo17. The production of such higher grain yields under phosphorus deficient soils could also be attributed to heterosis because temperate inbreds and tropical inbreds belonged to two different heterotic groups.

The Baker's ratio for shelling percent was high (near a unit) indicating the preponderance of additive genes over non-additive genes on this trait. Additive gene action largely influenced shelling percentage and cyclic selection based on this trait could bring genetic improvement under low phosphorus. On the other hand, the Baker's ratio for grain yield, harvest index, root biomass, plant height and plant-tissue phosphorus was low indicating the preponderance of dominance gene action over additive gene action, thus justifying the vigour realized in hybrids. This was in agreement with the findings of Parentoni et al. (2006) and Chen et al. (2009) that dominance genes were more important than additive genes under low P. As such, crossing temperate inbreds with tropical inbreds exploited the dominant genes in fore-mentioned traits thereby improving grain yield on phosphorus deficient soils.

Grain yield is an important quantitative trait in maize. Temperate inbred-lines J185 and Mo17 exhibited highly significant positive GCA effects for grain yield and equally the tropical inbred-lines L151 and L152. These four inbreds contributed alleles towards increasing grain yield. The temperate inbred-line J185 gave maximum GCA effects whereas among the tropical inbreds, L152 manifested maximum GCA effects indicating these two parents contained sufficient additive genes, and could be utilized in breeding programs for improving grain yield under low soil phosphorus. As such, inbreds J185 and L152 were the best general combiners for grain yield under low phosphorus soil conditions.

Harvest index is also an important trait in breeding programs focusing on phosphorus use efficiency of maize. Temperate inbreds J185 and Mo17 exhibited significant positive GCA effects for harvest index and equally tropical inbreds L911 and L152. These four inbreds contributed alleles towards increasing the expression of a trait. The temperate inbred-line Mo17 gave maximum GCA effects whereas among the tropical inbreds, L152 manifested maximum GCA effects indicating that both parents contained sufficient additive genes, and could be utilized in breeding programs for improving harvest index under low soil phosphorus. The GCA effects revealed that Mo17 and L152 were the best general combiners for harvest index under low phosphorus soil conditions.

The 100 grain weight is an important component of grain yield in maize. Temperate inbred-lines J185 and Mo17 exhibited significant positive GCA effects for 100 grain weight and equally tropical inbreds L911 and L152. These four inbreds contributed alleles towards increasing the expression of a trait. The temperate inbred-line J185 gave maximum GCA effects whereas among the tropical inbreds, L911 manifested maximum GCA effects indicating that both parents contained sufficient additive genes, and could be utilized in breeding programs for improving 100 grain weight under low soil phosphorus. The GCA effects revealed that J185 and L911 were the best general combiners for 100 grain weight under low phosphorus soil conditions.

The hybrids L911×B73, L913×B73, L917×B73, L1212×J185, L151×J185, L152×J185, L1212×Mo17, L151×Mo17, L152×Mo17 and L911×Mo17 exhibited highly significant positive SCA effects for grain yield. This implied that these hybrids combined well specifically and heterosis was optimized to increase grain yield. Hybrids L152×B73 and L913×J185 exhibited highly significant positive SCA effects for 100 grain weight, implying that these hybrids combined well specifically and heterosis was optimized in 100 grain weight.

The hybrids L911×B73, L917×B73, L151×J185 and L152×J185 exhibited significant positive SCA effects for harvest index. This meant that these hybrids combined well specifically and heterosis was optimized in harvest index. The hybrid L917×B73 exhibited significant positive SCA effect for plant height, implying that this hybrid combined well specifically and heterosis was optimized in plant height. The hybrids L911×B73, L1212×J185, L913×J185, L917×J185, L151×Mo17 and L152×Mo17 exhibited highly significant positive SCA effects for plant-tissue phosphorus, implying that these hybrids combined well specifically and heterosis was optimized in plant-tissue phosphorus. Similarly, hybrids L913×Mo17 and L1212×Mo17 exhibited significant positive SCA effect for root biomass, implying that these hybrids combined well specifically and heterosis was optimized in root biomass.

The fore-mentioned hybrids that exhibited positive significant SCA effects in grain yield, 100 grain weight, harvest index, plant height, plant-tissue P and root biomass optimized heterosis because their parental inbred-lines belonged to diverse heterotic groups hence in agreement with the ideas of David et al. (2006) and Weiwei et al. (2011). Furthermore, the single-cross hybrids that gave positive significant SCA effects with respect to grain yield, harvest index and plant height were potential materials that could be used for extracting inbred-lines and developing 3-way crosses or double-cross hybrids that are efficient at utilizing phosphorus in soils. This agreed with Dudley (1984a) that a largest number of favorable alleles are usually accumulated in the best hybrids.

5.6 Maternal effects

The ratios of MS_f/MS_m (maternal effects) were high for grain yield, harvest index, 100 grain weight, shelling %, root biomass, plant height, plant biomass and purpling symptom on leaves. The predominance of MS_f over MS_m on the fore-mentioned traits suggested the importance of maternal effects in modifying these traits under low phosphorus. However, the ratios were non-significant implying maternal effects had no influence on the traits. This agreed with Singh (1993) that except for some quality traits like seed size, maternal effects have generally not been reported to be very important in maize.

5.7 Association of traits

Simple correlation analyses showed highly significant positive correlation of grain yield with; plant height, harvest index, shelling percent and plant biomass. This meant that grain yield was dependent on plant height, harvest index, shelling % and plant biomass. The significant negative correlation between purpling symptom with; grain yield, harvest index, shelling percent, plant height and plant biomass meant that an increase in purpling of plants due to phosphorus deficiency resulted into reductions of; grain yield, harvest index, shelling percent, plant height and plant biomass. Genotypes that were efficient in utilizing phosphorus to produce grains grew vigorously without symptoms of purpling on leaves. Therefore, plant height and purpling of leaves could be used as indirect selection criteria for genotypes that are efficient in utilizing phosphorus.

The coefficient of multiple determinations (R^2) showed that harvest index had significant influence on grain yield explaining 65.7 % of the total variation, implying that the grain yield was strongly dependent on the harvest index in phosphorus deficient soils. Purpling and plant height had little contributions to the total variation in grain yield, explaining 3.3 % and 2.9 % respectively expressed as R^2. Therefore, harvest index gave strong influence on grain yield under phosphorus deficient soils. It could be deduced that harvest index could be used as an indirect selection criterion in breeding for phosphorus use efficiency followed by purpling symptom on leaves and then plant height.

5.8 Heritability

According to the classification by Bhateria et al. (2006), shelling percentage exhibited medium (40 %) narrow sense heritability under phosphorus stress and selection based on shelling % could be moderately effective. On the contrary, narrow sense heritability estimate of grain yield was low (29 %) under phosphorus stress. This agreed with the findings of Banziger and Cooper (2001) that heritability of grain yield declines under stress conditions hence reducing the effectiveness of selection basing on grain yield. Further, plant-tissue phosphorus, harvest index, root biomass, 100 grain weight and plant height were severely affected by phosphorus stress in soil and very low narrow sense heritability estimates of less than 29 % were obtained. Therefore, the fore-listed traits could further reduce the effectiveness of selection under low phosphorus soils.

CHAPTER 6

CONCLUSIONS

The study was undertaken to investigate possibilities of increasing grain yield of maize on phosphorus deficient soils in Zambia. Temperate inbreds J187 and Mo17 were identified as good sources of desirable yield enhancing alleles for introgression to improve maize on phosphorus deficient soils. Inbred J185 was the best general combiner followed by Mo17.

Crossing temperate inbred-lines J187 and Mo17 with tropical inbred-lines of maize significantly increased grain yield of single-cross hybrids. The resultant single-cross hybrids L151×J185, L151×Mo17, L152×J185, L152×Mo17, L1212×Mo17, L1212×J185 and L5527×J185 produced high grain yield of 8.28 tons/ha to 12.77 tons/ha. These hybrids were potential good materials that could be used for extracting improved inbred-lines and developing 3-way cross or double-cross hybrids that are efficient in utilizing the limited phosphorus in soils of Zambia.

The low Baker's ratios obtained for grain yield, harvest index, root biomass, plant height and plant-tissue phosphorus justified the vigour in hybrids, more especially that their parental inbreds belonged to two different heterotic groups. The coefficient of multiple determinations (R^2) revealed that harvest index strongly influenced grain yield on phosphorus deficient soils. Purpling symptom on leaves and plant height also gave little influence on grain yield. Therefore, harvest index, purpling symptom and plant height could define the selection index for genotypes that are efficient in utilizing phosphorus.

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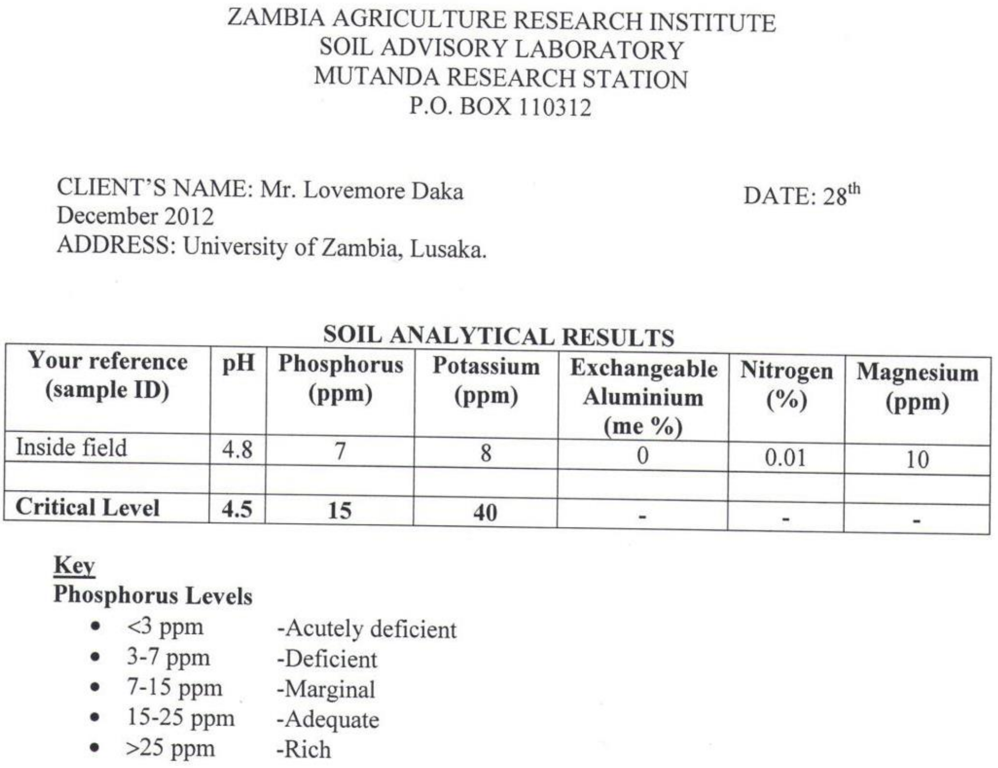
APPENDICES

Appendix 1: Soil characteristics of research site



ZAMBIA AGRICULTURE RESEARCH INSTITUTE
SOIL ADVISORY LABORATORY
MUTANDA RESEARCH STATION
P.O. BOX 110312

CLIENT'S NAME: Mr. Lovemore Daka DATE: 28th
December 2012
ADDRESS: University of Zambia, Lusaka.

SOIL ANALYTICAL RESULTS

Your reference (sample ID)	**pH**	**Phosphorus (ppm)**	**Potassium (ppm)**	**Exchangeable Aluminium (me %)**	**Nitrogen (%)**	**Magnesium (ppm)**
Inside field	4.8	7	8	0	0.01	10
Critical Level	**4.5**	**15**	**40**	-	-	-

Key

Phosphorus Levels

- <3 ppm -Acutely deficient
- 3-7 ppm -Deficient
- 7-15 ppm -Marginal
- 15-25 ppm -Adequate
- >25 ppm -Rich

Appendix 2: General analysis of variance for purpling symptom

Source of variation	d.f.	s.s.	m.s.	v.r.	cov.ef.	F pr.
Replications	1	0.2424	0.2424			
Genotypes	32	121.6680	3.8021	24.80	0.97	<.001
Covariate	1	0.0048	0.0048	0.03		0.860
Error	31	4.7527	0.1533		0.97	
Total	65	129.0303				
CV %	14.0					
LSD (5%)	0.8123					

Appendix 3: General analysis of variance for Grain Yield

Source of variation	d.f.	s.s.	m.s.	v.r.	cov.ef.	F pr.
Replications	1	0.11589	0.11589			
Genotypes	32	833.81347	26.05667	353.58	0.97	<.001
Covariate	1	0.01779	0.01779	0.24		0.627
Error	31	2.28452	0.07369		0.98	
Total	65	846.32957				
CV%	4.7					
LSD (5%)	0.5632					

Appendix 4: Line× Tester analysis of variance for Grain Yield

Source of variation	d.f.	s.s.	m.s.	v.r.	cov.ef.	F pr.
Replications	1	0.34540	0.34540			
Female parent	5	180.98940	36.19788	388.34	0.98	<.001
Male parent	2	54.60193	27.30096	292.89	0.94	<.001
Female parent × M. parent	10	138.96944	13.89694	149.09	0.94	<.001
Covariate	1	0.02624	0.02624	0.28		0.603
Error	16	1.49139	0.09321		0.96	
Total	35	377.26513				
CV%	4.3					

Appendix 5: General analysis of variance for Harvest Index

Source of variation	d.f.	s.s.	m.s.	v.r.	cov.ef.	F pr.
Replications	1	0.002886	0.002886			
Genotypes	32	1.468095	0.045878	13.61	0.97	<.001
Covariate	1	0.018716	0.018716	5.55		0.025
Error	31	0.104509	0.003371		1.14	
Total	65	1.625302				
CV%	21.7					
LSD (5%)	0.12046					

Appendix 6: Line × Tester analysis of variance for Harvest Index

Source of variation	d.f.	s.s.	m.s.	v.r.	cov.ef.	F pr.
Replications	1	0.000586	0.000586			
Female parent	5	0.318457	0.063691	17.87	0.98	<.001
Male parent	2	0.032862	0.016431	4.61	0.94	0.026
Female parent × M. Parent	10	0.251006	0.025101	7.04	0.94	<.001
Covariate	1	0.015567	0.015567	4.37		0.053
Error	16	0.057027	0.003564		1.20	
Total	35	0.745298				
CV%	18.9					

Appendix 7: General analysis of variance for 100 Grain Weight

Source of variation	d.f.	s.s.	m.s.	v.r.	cov.ef.	F pr.
Replications	1	0.00000304	0.00000304			
Genotypes	32	0.01991526	0.00062235	29.94	0.97	<.001
Covariate	1	0.00004353	0.00004353	2.09		0.158
Error	31	0.00064444	0.00002079		1.03	
Total	65	0.02217131				
CV %	15.5					
LSD (5%)	0.009459					

Appendix 8: Line × Tester analysis of variance for 100 Grain Weight

Source of variation	d.f.	s.s.	m.s.	v.r.	cov.ef.	F pr.
Replications	1	0.00000029	0.00000029			
Female parent	5	0.00027650	0.00005531	5.63	0.98	0.004
Male parent	2	0.00009784	0.00004892	4.98	0.94	0.021
Female parent × M. Parent	10	0.00006715	0.00006715	6.83	0.94	<.001
Covariate	1	0.00000707	0.00000707	0.72		0.409
Error	16	0.00000983	0.00000983		0.98	
Total	35	0.001302				
CV %	13.0					

Appendix 9: General analysis of variance for shelling percentage

Source of variation	d.f.	s.s.	m.s.	v.r.	cov.ef.	F pr.
Replications	1	29.73	29.73			
Genotypes	32	23276.22	727.38	51.10	0.97	<.001
Covariate	1	0.46	0.46	0.03		0.859
Error	31	441.24	14.23		0.97	
Total	65	23756.32				
CV%	5.6					
LSD (5%)	7.827					

Appendix 10: Line × Tester analysis of variance for shelling percentage

Source of variation	d.f.	s.s.	m.s.	v.r.	cov.ef.	F pr.
Replications	1	21.99	21.99			
Female parent	5	858.67	171.73	9.50	0.98	<.001
Male parent	2	99.96	49.98	2.77	0.94	0.093
Female parent × M. Parent	10	426.82	42.68	2.36	0.94	0.061
Covariate	1	0.02	0.02	0.00		0.976
Error	16	289.16	18.07		0.94	
Total	35	1844.33				
CV %	6.0					

Appendix 11: General analysis of variance for Plant Height

Source of variation	d.f.	s.s.	m.s.	v.r.	cov.ef.	F pr.
Replications	1	885.9	885.9			
Genotypes	32	13223.3	413.2	2.20	0.94	0.015
Covariate	1	573.2	573.2	3.05		0.091
Error	31	5828.8	188.0		1.06	
Total	65	23299.3				
CV %	17.0					
LSD (5%)	28.82					

Appendix 12: Line × Tester analysis of variance for Plant Height

Source of variation	d.f.	s.s.	m.s.	v.r.	cov.ef.	F pr.
Replications	1	265.01	265.01			
Female parent	5	1656.48	331.30	3.58	0.92	0.023
Male parent	2	128.32	64.16	0.69	0.94	0.515
Female parent × M. Parent	10	2462.23	246.22	2.66	0.92	0.039
Covariate	1	70.73	70.73	0.76		0.395
Error	16	1482.00	92.62		0.99	
Total	35	6688.62				
CV %	12.1					

Appendix 13: General analysis of variance for Root Biomass

Source of variation	d.f.	s.s.	m.s.	v.r.	cov.ef.	F pr.
Replications	1	0.00213	0.00213			
Genotypes	32	28.31080	0.88471	12.93	0.97	<.001
Covariate	1	0.04136	0.04136	0.60		0.443
Error	31	2.12058	0.06841		0.99	
Total	65	30.49266				
CV %	19.5					
LSD (5%)	0.54					

Appendix 14: Line × Tester analysis of variance for Root Biomass

Source of variation	d.f.	s.s.	m.s.	v.r.	cov.ef.	F pr.
Replications	1	0.00694	0.00694			
Female parent	5	5.06077	1.01215	15.36	0.98	<.001
Male parent	2	0.13728	0.06864	1.04	0.94	0.376
Female parent × M. Parent	10	3.75222	0.37522	5.69	0.94	0.001
Covariate	1	0.00117	0.00117	0.02		0.896
Error	16	1.05438	0.06590		0.94	
Total	35	10.01389				
CV %	24.3					

Appendix 15: General analysis of variance for plant-tissue phosphorus

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Replications	1	40429	40429	19.83	
Genotypes	32	2807487	87734	43.03	<.001
Error	32	65243	2039		
Total	65	2913159			
CV %	2.6				
LSD (5%)	91.97				

Appendix 16: Line × Tester analysis of variance for plant-tissue phosphorus

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Replications	1	28676	28676	15.38	
Female parent	5	212715	42543	22.81	<.001
Male parent	2	3470	1735	0.93	0.414
Female parent × M. Parent	10	1404909	140491	75.34	<.001
Error	17	31703	1865		
Total	35	1681472			
CV %	2.6				

Appendix 17: General analysis of variance for plant biomass

Source of variation	d.f.	s.s.	m.s.	v.r.	cov.ef.	F pr.
Replications	1	0.0847	0.0847			
Genotypes	32	6135.4327	191.7323	508.12	0.97	<.001
Covariate	1	3.6767	3.6767	9.74		0.004
Error	31	11.6974	0.3773		1.27	
Total	65	6718.1587				
CV %	2.7					
LSD (5%)	1.2744					

Appendix 18: Heritability and Variances

Parameter	σ_f^2	σ_m^2	σ_{fm}^2	σ_{Af}^2	σ_{Am}^2	σ_D^2	h^2
Shelling %	0.0022	0.0001	0.0012	0.0086	0.0002	0.0049	40%
Grain yield	3.72	1.12	6.94	14.87	4.47	27.74	26%
Plant-tissue Phosphorus	16325	11563	69313	65299	46252	277252	25%
Harvest Index	0.01	0.01	0.01	0.03	0.01	0.04	20%
Root biomass	0.11	0.03	0.15	0.42	0.10	0.62	19%
100Grain weight	0.00000	0.00000	0.00003	0.00001	0.00001	0.00011	6%
Plant height	14.18	15.17	76.80	56.72	60.69	307.20	1%

KEY: σ_f^2 =Variance due to females, σ_m^2 = Variance due to males, σ_{fm}^2 = Variance due to female and male interaction, σ_{Af}^2 = Additive genetic variance due to females, σ_{Am}^2 = Additive genetic variance due to males, σ_D^2 = Dominance genetic variance and h^2 = heritability.