Genotypic variability and combining ability of quality protein maize inbred lines under stress and optimal conditions

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By

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DECLARATION

I declare that the thesis hereby submitted by me for the degree of Philosophiae Doctor in Agriculture at the University of the Free State is my own independent work and has not previously been submitted by me at another university/faculty. I further cede copyright of the thesis in favour of the University of the Free State.

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Dagne Wegary Gissa Date

DEDICATION

This piece of work is dedicated to my father Wegary Gissa, my mother Tejitu Ayana and my son Begna.

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ABBREVIATION AND SYMBOLS

ACALL	Across all environments
ACDRT	Across drought stress environments
ACLN	Across low N stress environments
ACOPT	Across optimum N environments
DA	Days to anthesis
DS	Days to silking
AFLP	Amplified fragment length polymorphisms
AMMI	Additive main effect and multiplicative interaction
ANOVA	Analysis of variance
ARC	Agricultural Research Council of South Africa
ASI	Anthesis-silking interval
ASV	AMMI stability value
AWOM	Awassa optimum management
b	Base
b_i	Regression coefficient
BKLN	Bako Low N stress
BKOM	Bako optimum management
bp	Base pair
CHDS	Chiredzi drought stress
CIMMYT	International Maize and Wheat Improvement Centre
cm	Centimetres
cm^2	Square centimetres
CML	CIMMYT maize line
CTAB	Hexadecyltrimethylammonium bromide
CV	Coefficient of variation
d	Days
Df	Degrees of freedom
DNA	Deoxyribonucleic acid
dNTP	2'-deoxynucleoside 5'-triphosphate
ED	Ear diameter
EDTA	Ethylene-diamintetra acetic acid
EH	Ear height
EL	Ear length
F1	First filial generation
F2	Second filial generation
FAO	Food and Agriculture Organization
fl2	*Floury-2 allele*
FR	Foliage rating
g	Grams
G x E	Genotype by environment interaction
GA	Genetic advance
GAM	Genetic advance as percent of mean
GCA	General combining ability
GCV	Genotypic coefficient of variation
g_i	GCA effect of inbred line i
GLM	General linear model
GY	Grain yield

H^2	Broad sense heritability
h^2	Narrow sense heritability
ha	Hectare
HALN	Harare low N stress
HAOM	Harare optimum management
HCl	Hydrochloric acid
HPH	High-parent heterosis
HPV	High-parent value
IBPGR	International Board for Plant Genetic Resource
IITA	International Institute for Tropical Agriculture
IPCA	Interaction principal component axes
IRRI	International Rice Research Institute
JMOM	Jimma optimum management
KBDS	Kiboko drought stress
KBOM	Kiboko optimum management
Kg	Kilo gram
KPR	Number of kernels per row
kV	Kilo volt
l	Litre
LA	Leaf area
LL	Leaf length
LO	Leaf orientation
LR	Linear regression
LW	Leaf width
Max	Maximum
MD	Morphological distance
MET	Multi-environment trial
mg	Milligram
$MgCl_2$	Magnesium chloride
Min	Minimum
ml	Milliliter
MLOM	Melkasa optimum management
mM	Millimolar
MOD	Endosperm modification
MPH	Mid-parent heterosis
MPOM	Mpongwe optimum management
MPV	Mid-parent value
MS	Mean square
MSE	Managed stress environment
N	Nitrogen
NARS	National Agricultural Research Systems
ng	Nanogram
o2	*Opaque-2 allele*
^oC	Degree Celsius
OPV	Open pollinated variety
P_2O_5	Phosphate
PA	Plant aspect
PCA	Principal component analysis
PCV	Phenotypic coefficient of variation
PH	Plant height

PIC	Polymorphism information content
PR	Predictability ratio
PWOM	Pawe optimum management
QI	Protein quality index
QPM	Quality protein maize
R^2	Coefficient of determination
RAOM	Rattray Arnold Research Station optimum management
RAPD	Random amplified polymorphic DNA
r_{cop}	Cophenetic correlation
RFLP	Restriction fragment length polymorphisms
RPE	Number of rows per ear
rpm	Revolution per minute
s^2d_i	Deviation from regression
SADC	Southern African Development Community
SCA	Specific combining ability
SE	Standard error
S_{ii}	SCA effect of hybrid ij
SNP	Single nucleotide polymorphism
SSLP	Simple sequence length polymorphisms
SSR	Simple sequence repeat
SSRD	SSR distance
t	Ton
Taq	Thermus aquaticus
TE	Tris EDTA
TKW	Thousand kernel weight
TRP	Tryptophan concentration in grain
TS	Tassel size
UN	United Nations
UPGMA	Unweighted pair group method with arithmetic averages
v/v	Volume per volume
σ_p	Phenotypic standard deviation
σ_p^2	Phenotypic variance
σ_e^2	Environmental or error variance
σ_g^2	Genetic variance
σ_A^2	Additive genetic variance
σ_D^2	Dominance genetic variance
σ_I^2	Epistatic genetic variance
$\sum$	Summation
%	Percent
µl	Micro litre

Chapter 1

General introduction

Maize (*Zea mays* L.) is one of the three most important cereal crops in the world together with wheat and rice. Data from the United Nations (UN) Food and Agriculture Organization (FAO) showed that for 2006 world maize production was 144 million hectares while that for wheat was 216 million and for rice it was 154 million hectares (FAOSTAT, 2008). In terms of production, however, maize surpasses wheat and rice. World maize production for 2006 was 695 million metric ton, while that of wheat was 606 and rice was 635 million ton. Although 70% of the world maize area was in developing countries, only 49% of the world's maize was produced there (FAOSTAT, 2008). Africa's share of maize production for 2006 was 46 million metric ton or just about 7% of world production. In the developed world, maize is mostly used as a feed for livestock (70%) and only a small percentage (5%) as food. In contrast, developing countries consume about 34% as food and the remaining 62% as feed. The remaining quantity is used for varied industrial uses and as seed. With 43 kg per capita per year as food, maize contributes about 34% of Africa's protein and 35% of the calories derived from cereal crops. In eastern and southern Africa, maize accounts for over 25% and 31% of the total calories consumed with per capita annual consumption of 58 and 84 kg, respectively (FAOSTAT, 2008). Maize also occupies an important position in world economy and trades as a food, feed and industrial grain crop (Vasal, 2000).

In eastern and southern Africa, maize is by far the dominant staple crop grown by the vast majority of rural households. Consumption of maize is high throughout most of the region, reflecting its role as the primary food staple (Hassan et al., 2001; Smalberger and Toit, 2004; Diallo et al., 2004; Banziger and Diallo, 2004). In southern Africa, per capita annual consumption of maize averages more than 100 kg in several countries (Lesotho, 149 kg; Malawi, 181 kg; South Africa, 195 kg; Swaziland, 138 kg; Zambia, 168 kg; and Zimbabwe, 153 kg) (CIMMYT, 1999). In eastern Africa, per capita annual consumption ranges from 40 kg in Burundi to 105 kg in Kenya (Hassan et al., 2001). The predominant grain color of maize grown in eastern and southern Africa is white, since white maize is the dominant food

staple in the region. Maize in Africa is grown by small- and medium-scale farmers who cultivate 10 ha or less (DeVries and Toenniessen, 2001) under extremely low-input/low risk systems where average maize yields are 1.3 ton per ha (Banziger and Diallo, 2004). Sub-Saharan African countries do not produce enough maize to meet their needs and must therefore import approximately three million tonnes of maize annually (Pingali and Pandey, 2001; FAOSTAT, 2008). Use of improved cultivars and management practices should help increase maize yields and reduce imports in these countries (Heisey and Edmeades, 1999; Reeves et al., 1999; Pingali and Pandey, 2001).

From a nutritional perspective, however, the protein of maize and of most cereals is deficient in essential amino acids such as lysine and tryptophan (Bhatia and Rabson, 1987). Normal maize protein, as a point of comparison, has a biological value of 40% of that of milk (Bressani, 1991) and therefore needs to be eaten with complementary protein sources such as legumes or animal products. The need to improve this deficiency in maize has been recognized for a long time (Osborne and Mendel, 1914). In normal maize, the endosperm contains a high proportion of zein (seed storage protein of maize) fraction which is completely devoid of lysine and tryptophan. The high proportion of this particular fraction, then, is the primary cause of poor protein quality in maize. A reduction in the zein fraction thus results in a proportional elevation of other fractions rich in lysine and an elevation of these two amino acids in protein (Vasal, 2000).

Mutant alleles, *opaque-2* (*o2*) (Mertz et al., 1964) and *floury-2* (fl_2) (Nelson et al., 1965), discovered by Purdue University researchers were found to alter the amino acid profile and composition of maize endosperm protein and result in twofold increase in the levels of lysine and tryptophan compared to what is encountered in normal maize genotypes. The mutants derive their name from soft, floury opaque endosperm, respectively. The International Maize and Wheat Improvement Centre (CIMMYT) maize program has made extensive use of the *o2* gene in developing quality protein maize (QPM) germplasm in the past three decades. The *o2* gene enhances the quality of endosperm protein, but is associated with many undesirable traits, such as slow drying, low grain yield, opaque endosperm phenotype, greater vulnerability to ear rots and storage pests (Bjarnason and Vasal, 1992; Prasanna et al., 2001;

Vasal, 2001). Using innovative breeding methodologies, CIMMYT scientists overcame the problems associated with *o2* maize and developed source QPM germplasm with normal-looking kernel phenotype and with grain yield comparable to normal endosperm materials, with protein quality as an added bonus (CIMMYT, 1972; Vasal et al., 1980).

Many breeding programs in developed and developing countries have used CIMMYT QPM germplasm in developing source breeding populations and lines adapted for their specific conditions. QPM inbred lines have been developed by CIMMYT and national breeding programs and evaluated for combining ability effects (Bjarnason and Vasal, 1992; Hohls et al., 1995; Vasal, 2001; Hadji, 2004; Xingming et al., 2004). A number of QPM inbreds were released by CIMMYT and are available to national programs and to other private and public research organizations (Vasal, 2001). These lines will help QPM hybrid development efforts in those countries interested in hybrid development. Many African countries used QPM materials from CIMMYT as source germplasm in conjuction with their own materials and have developed well adapted inbred progenitors and hybrid combinations (Krivanek et al., 2007).

Inbred lines developed at CIMMYT are with known pedigree data and have also been tested in hybrid combinations with selected lines and testers. However, further systematic studies aimed at classifying these lines into different heterotic groups would be useful in the development of inbred lines and the generation and evaluation of maize hybrids and open-pollinated synthetic varieties (Menkir et al., 2004). Considering the mixed genetic composition and the broad genetic base of the source populations for the tropical inbred lines, Menkir et al. (2004) pointed out the difficulty of classifying these lines into distinct heterotic groups based only on the results of combining ability studies. Therefore, the combined use of molecular markers that allow direct comparison of the similarity of inbred lines at the DNA level with testcross evaluation should facilitate the separation of inbred lines into well-defined heterotic groups (Menkir et al., 2004; Xia et al., 2004). Molecular genetic markers are a powerful tool to delimit heterotic groups and to assign inbred lines in to existing heterotic groups (Melchinger, 1999).

Several DNA marker technologies have been developed and are available to study genetic diversity. The characteristics of good DNA markers are highly polymorphic, co-dominant, and abundant in the genome, display even distribution throughout the genome, easy and fast assay, high reproducibility and easy exchange of data between laboratories (Weising et al., 1998). No DNA marker technology fulfils all of these criteria. However, microsatellite or simple sequence repeat (SSR) fulfills most of these requirements. The SSR markers offer advantages in reliability, reproducibility, discrimination, standardization, and cost effectiveness over other marker types (Melchinger, 1999). In maize, SSRs have proved to be a valuable tool for diversity measurements (Warburton et al., 2002; Pinto et al., 2003; Legesse et al., 2007) and designation of lines in to heterotic groups (Enoki et al., 2002).

Farmers in sub-Saharan Africa, especially eastern, central and southern Africa regions, grow maize under conditions that differ from those used by many researchers during crop improvement. Several biotic and abiotic factors limit maize production and productivity across countries in sub-Saharan Africa (Badu-Apraku et al., 2003). Biotic factors limiting maize production in the region include insect pests, diseases, and parasitic weeds. The most important abiotic stresses limiting maize production in eastern and southern Africa are low soil fertility and drought, and these two are among the most important stresses threatening maize production, food security and economic growth in eastern and southern Africa (CIMMYT, 2003a; Banziger and Diallo, 2004). Banziger and Lafitte (1997) reported that low N availability in soils is an important yield limiting factor frequently found in farmers' fields in the tropics where fertilization is not commonly used and organic matter is rapidly mineralized. Most tropical maize is produced under rain-fed conditions and many of the maize-growing environments are susceptible to drought. Drought at any stage of crop development affects production, but maximum damage is inflicted when it occurs around flowering (Edmeades et al., 1992). The incidence of stress may increase, due partly to global climate changes, displacement of maize to marginal environments by high value crops, and decline in soil organic matter, reducing soil fertility and water holding capacity (Banziger et al., 2000). Maize productivity in maize-based cropping systems could be greatly improved by using cultivars that utilize nitrogen from fertilizers and other sources more efficiently as well as tolerating the periodic droughts facing the region (Diallo et al., 2003).

According to Banziger and Diallo (2004), a close relationship exists between rainfall and maize yields across the eastern and southern African region. In areas where the probability of drought stress is high, farmers often respond by reducing the application of nitrogen fertilizer (McCown et al., 1992). In seasons when rainfall is plentiful, maize crops are often severely N deficient (Banziger et al., 2000). Use of fertilizers is constrained by high cost and lack of credit faced by small holders even in the high potential moist mid altitude eco-zones (Diallo et al., 2004). Sub-Saharan Africa has by far the largest variability in maize yields in the developing world, mainly due to variation in rainfall. As average yields are lower and the agricultural sector is of greater importance, this yield variability is of greater socio-economic importance than in any other part of the world (Heisey and Edmeades, 1999).

CIMMYT approached breeding for stress tolerance by simulating abiotic stress factors that are important in the target environment and exposing breeding experiments to a clearly defined abiotic factor in environments termed 'managed stress environments' (MSEs) (Banziger and Cooper, 2001). MSEs were established under experiment station conditions by growing maize in the dry season and managing drought through omission of irrigation to assess drought tolerance at the seedling, flowering, and grain filling stages (Bolaños and Edmeades, 1996), and by using fields that were depleted of mineral nitrogen for assessing nitrogen stress tolerance (Banziger et al., 1997). In an effort to expand the range of technology choices available to farmers in the eastern and southern African regions, CIMMYT initiated the Southern Africa Drought and Low Fertility Project in 1996 and the Africa Maize Stress Project in 1998, for southern and eastern African regions (Banziger and Diallo, 2004). These projects, which are being carried out in collaboration with National Agricultural Research Systems (NARS) and private seed companies, aim to develop materials showing increased drought tolerance and enhanced nitrogen use efficiency. Improved germplasm developed through the project is rapidly making its way into breeding programs throughout the region (Banziger and Diallo, 2004).

The current effort on QPM is to increase its cultivation in the region, especially in sub-Saharan Africa, experiencing problems of malnutrition and where maize is the staple. In these regions, however, maize is frequently produced under environmental stress, among

which low soil nitrogen and drought are the most important. Impacts of low nitrogen and drought on grain yield of normal maize have been extensively studied (Banziger and Cooper, 2001; Edmeades et al., 2006; Banziger et al., 2006; Gezahegn et al., 2008). However, those impacts on protein quality and quantity of QPM germplasm have not yet been sufficiently addressed. Environment can differentially affect the performance of hybrids and combining ability of inbred lines. Since breeding programs in sub-Saharan Africa are targeting the low input farming conditions, germplasm to be developed for these environments need to be evaluated and selected under representative stress conditions before release for production.

In this study, genotypic and phenotypic variability of elite tropical and sub tropical white QPM inbred lines widely adapted in eastern and southern African regions was investigated using morpho-agronomic traits. Simple sequence repeat (SSR) markers were employed for genetic diversity analysis among the inbred lines at molecular level. A diallel study involving 15 tropical and sub-tropical white QPM inbred lines was conducted under low N and drought stress, and non-stress conditions to estimate general (GCA) and specific (SCA) combining ability of the inbred lines, analyze genotype-environment (G x E) interaction of the resulting hybrids across testing locations, and investigate the effects of stress on endosperm modification, protein quantity and quality of QPM. Association of parental genetic distance with F_1 performance, heterosis and specific combining ability of the hybrids under stress and optimal environments were studied. The study was conducted with the following objectives:

(i) To assess variability among elite QPM inbred lines adapted to the eastern and southern African region using morpho-agronomic traits.
(ii) To examine genetic diversity among the inbred lines using SSR analysis.
(iii) To estimate heterosis and combining ability of QPM inbred lines for grain yield, and agronomic traits under abiotic stress and optimal conditions.
(iv) To assess the relationship of genetic diversity of QPM parental inbred lines with F_1 performance, heterosis and SCA effects of hybrid progeny under stress and optimal conditions.
(v) To analyze G x E interaction and stability of QPM hybrids for grain yield.

(vi) To investigate the impact of low nitrogen stress on QPM hybrids and combining ability of inbred parents for endosperm modification, protein quantity and quality and identify good donor parents under low N stress and non-stress conditions.

Chapter 2

Literature review

2.1 Quality Protein Maize (QPM): Historical account

Poor nutritional value of maize grain is well known and the need to improve it has been recognized for a long time (Osborne and Mendel, 1914). Most of the protein in a mature maize kernel is contained in the endosperm and the germ. The endosperm protein is low in quality whereas the germ protein is superior. However, the endosperm constitutes the bulk of the grain and contributes as much as 80% of the total kernel protein (Zuber and Helm, 1972). Thus, any major improvements for quality protein need to target the endosperm.

The discovery of the biochemical effects of mutant alleles *o2* (Mertz et al., 1964) and *floury-2* (*fl2*) (Nelson et al., 1965) by the Purdue University researchers opened an exciting opportunity for improving the quality of maize endosperm protein. These mutants alter amino acid profile and composition of maize endosperm protein and result in two-fold increase in the levels of lysine and tryptophan compared to what is encountered in normal maize genotypes. The mutants derive their name from soft, floury opaque endosperm, respectively (Vasal et al., 1984b; Mertz, 1992; Villegas et al., 1992).

In the initial stages, both *o2* and *fl2* genes were used separately or in combination. Though *fl2* was used initially, eventually its use was discontinued (Bjarnason and Vasal, 1992; Vasal, 2000). The investigations and research conducted do not offer any better alternative to the *o2* gene (Vasal, 2001). Later some undesirable effects of the genes were discovered. Major emphasis in most breeding programs for protein quality is, therefore, placed on the utilization of the *o2* mutant (NRC, 1988; Glover, 1992; Villegas et al., 1992). Maize homogenous for the recessive *o2* allele (with two copies of the mutation) has substantially higher lysine (+69%) in grain endosperm compared to normal maize (Mertz et al., 1964). It was further determined that this genotype also shows a corresponding increase in tryptophan content, and

that the increased concentration of these two essential amino acids (normally deficient in the maize endosperm) effectively doubles the biological value of maize protein (Bressani, 1992).

Soon after the discovery of the nutritional benefits of the *o2* mutation, it was being incorporated into many breeding programs worldwide, with a major emphasis on conversion of normal endosperm populations and inbred lines to *o2* versions through a direct backcross approach (Gevers, 1995; Prasanna et al., 2001). However, enthusiasm over the direct use of the *o2* mutation in the breeding programs soon subsided after the discovery of serious negative secondary (pleiotropic) effects of this mutation (Bjarnason and Vasal, 1992; Prasanna et al., 2001). These effects are reduced grain yield (as compared to normal maize), low kernel density, soft and chalky kernel phenotype, greater vulnerability to ear rot, greater moisture content during dry-down of kernels following physiological maturity, lower rate of germination and greater kernel breakage (Lambert et al., 1969; Sreeramulu and Baumann, 1970; Wessel-Beaver and Lambert, 1982; Vasal et al., 1984a; Bjarnason and Vasal, 1992; Villegas et al., 1992; Glover, 1992; Moro et al., 1995; Lin et al., 1997; Vasal, 2001; Prasanna et al., 2001). The soft endosperm texture is not acceptable to many in the developing world who are accustomed to harder grain types (Krivanek et al., 2007). Such negative secondary effects severely limited practical use of the mutation in the field.

Selection for hard endosperm modification was rapidly incorporated into *o2* breeding schemes. Initial QPM breeding efforts at CIMMYT focused on conversion of a range of sub-tropical and tropical lowland adapted, normal endosperm populations to *o2* versions through a backcross-cum-recurrent selection procedure, with a focus of accumulating the hard endosperm phenotype, maintaining protein quality and increasing yield and resistance to ear rot (NRC, 1988; Villegas et al., 1992; Bjarnason and Vasal, 1992; Vasal, 2001; Prasanna et al., 2001). The number of genes involved in modifying the opaque phenotype of *o2* endosperm to translucent and similar to that of normal maize is not known, but most reports indicate that inheritance is complex (Bjarnason and Vasal, 1992; Lopes and Larkins, 1996).

The resulting genotypes with elevated lysine and tryptophan content relative to normal maize but without the negative soft endosperm phenotype were termed by CIMMYT as Quality

Protein Maize (QPM) (Vasal et al., 1984b; Bjarnason and Vasal, 1992). The term QPM now refers to maize homozygous for the *o2* allele, with increased lysine and tryptophan content but without the negative secondary effects of a soft endosperm (Vasal, 2001). QPM looks and performs like normal maize and can be reliably differentiated only through laboratory tests (Villegas et al., 1992). It should be highlighted that QPM is the product of conventional breeding and no genetic engineering was used during its development (Pixley and Bjarnason, 1993).

In addition to CIMMYT, other institutions that continued vigorously and persistently to improve the protein quality were the University of Kwazulu-Natal (previously University of Natal), South Africa and the Crow's Hybrid Seed Company at Milford, Illinois, USA (Vasal, 2000; Prasanna et al., 2001). The maize breeding program in South Africa has developed soft endosperm and hard endosperm, white and yellow high-lysine maize inbred lines, hybrid and OPVs with excellent agronomic quality (Gevers and Lake, 1992; Hohls et al., 1996; Bhatnagar et al., 2004). Crow's Hybrid Seed Company developed an *o2* hybrid with good yield characteristics and a thick protective husk for animal feed (Mertz, 1995). In the USA, Texas A&M has also maintained a breeding program to develop QPM inbreds and hybrids with normal seed appearance, competitive yield, and adaptation to the southern USA (Betran et al., 2003a;b;c). As a result of these efforts, many cultivars (both OPV's and hybrids) with improved protein quality were developed for temperate, tropical highland, and for subtropical and tropical lowland growing conditions.

The improved populations developed by CIMMYT were released for direct use in the field as open pollinated varieties (OPV's), or individual plants were self-pollinated to form inbred lines used in hybrid formation (Vasal et al., 1980; 1984b; Villegas et al., 1992). The CIMMYT QPM populations, pools, inbreds and hybrids adapted to subtropical and tropical environments are widely used in the development of high-lysine maize in many developing and developed countries (Bjarnason and Vasal, 1992; Villegas et al., 1992; Vasal, 2001).

CIMMYT started a QPM hybrid program in 1985, in response to growing interest in hybrids among national programs especially in developing countries (Bjarnason and Vasal, 1992;

Vasal et al., 1993b; Vasal, 2001). Several advantages were advocated for QPM hybrids over the open pollinated varieties including i) improving yield performance through exploitation of heterosis; ii) facilitating maintenance of the seed purity of inbred progenitors with respect to agronomic traits, the genetic modifiers and the protein quality; iii) reduce dependence on laboratory facilities for monitoring the protein quality provided the lines are fixed and kept genetically pure; iv) the hybrids will exhibit more uniformity and stability with respect to kernel modification and; v) attracting involvement of the private seed industry in the QPM effort (Gevers and Lake, 1992; Pixley and Bjarnason, 1993; Vasal et al., 1993a; 1993b; CIMMYT, 2000; Vasal, 2001; Hadji, 2004). Inbred line development efforts have been strengthened at CIMMYT and national breeding programs and evaluated for combining ability (Vasal, 2001; Prasanna et al., 2001; Bhatnagar et al., 2004; Hadji, 2004; Xingming et al., 2004).

In sub-Saharan Africa, commercial QPM seed is currently available in 17 countries and based on average seed production, approximately 200 000 hectare of land is being planted to QPM cultivars (Krivanek et al., 2007). Breeding efforts have led to the release of one or more OPV's and/or hybrids in these countries although the total number of different genotypes is more limited since many releases share the same pedigree. For example, Across 8363SR was released in 14 sub-Saharan countries with different cultivar names. A three-way cross CML144/CML159//CML176 was released in Ethiopia with the name BHQP542 (Gabissa) and in Tanzania as Lishe-H1 (CIMMYT, 2005b; Krivanek et al., 2007).

2.2 Biochemical characteristics

The maize genome is richly endowed with a whole array of endospermic mutants that can modify protein, starch, and oil characteristics of the mature corn kernel, particularly the endosperm (Vasal, 2001). The variants already known that affect endosperm characteristics are numerous. However, of particular interest in this review is an *o2* mutant that affects protein quality.

Cereal proteins are classified into the following four groups based on their solubility (Singh, 2005): (1) albumins (water soluble), (2) globulins (salt soluble), (3) prolamins (relatively highly alcohol soluble) (4) glutelins (dilute alkali soluble). Cereals can be divided into three groups on the basis of their prolamine content. Rice and oats have the lowest prolamine content (5 - 15%) and an excellent balance of amino acids in their proteins. Barley and wheat form the second group with 30 – 40% prolamines, while maize and sorghum have the highest prolamine content (50 - 60%) (Singh, 2005). In normal maize endosperm, the proportions of various protein fractions on average are albumins 3%, globulins 3%, prolamines 60%, and glutelin 34% (Schnieder, 1955). Prolamines are poor in basic amino acids, including lysine (Singh, 2005) and therefore, they have very poor nutritional value (Glover, 1992; Villegas et al., 1992). In each genus, the major seed storage protein is named on the basis of the genus name; thus, the major seed storage proteins in maize are called the zeins for the genus *Zea* and belong to the prolamin class of proteins (Darrigues et al., 2006).

The zeins can account for 40-60% of the total protein in the maize endosperm, and, because of their abundance, they are the primary determinants of the amino acid composition in maize kernels (Larkins et al., 1993; Singh, 2005). Osborne and Clapp (1908) first characterized the amino acid composition of the zein proteins and reported that they lack two essential amino acids, lysine and tryptophan. Zeins contain 0.1g/100g lysine while glutelins are considerably richer in lysine with 2g/100g or more (Misra et al., 1975; Lin et al., 1997). Darrigues et al. (2006) illustrated that in the amino acid balance of maize, lysine and tryptophan are the most deficient; histidine and leucine are surplus amino acids as compared to the egg protein which is a nearly balanced source of protein.

The introduction of high quality protein maize mutants alters the relative amounts of four major protein fractions present in maize (Mertz et al., 1964; Lopes et al., 1995; Darrigues et al., 2006). Kernels carrying homozygous *o2* mutant have elevated levels of lysine and tryptophan by suppressing or reducing the synthesis of the lysine-deficient zein fraction (Mertz et al., 1964; Habben et al., 1993). Since fractions other than zein are higher in lysine and tryptophan, zein reduction causes proportional elevation of other fractions high in lysine (Mertz et al., 1964; Habben et al., 1993; Vasal, 2000). The result is that the levels of lysine

and tryptophan become elevated in protein, but not on absolute basis of per unit endosperm (Vasal, 2001). Therefore, increasing the levels of lysine and tryptophan should be important goals for maize breeding efforts directed to improving grain amino acid balance.

2.3 QPM genetics and breeding strategies

The breeding of QPM involves the manipulation of three distinct genetic systems (Krivanek et al., 2007). The recessive mutant allele of the *o2* gene is the first and central component (Villegas et al., 1992; Vasal, 2001). Characterization of this gene has identified it as encoding a transcription factor (a gene regulator) of zein synthesis (Schmidt et al., 1990). Zeins, and particularly alpha-zeins are the most abundant proteins in the grain endosperm (Villegas et al., 1980; Lending et al., 1988; Prasanna et al., 2001; Gibbon and Larkins, 2005) but are also characteristically poor in the amino acids lysine and tryptophan (Vasal, 2000). As discussed above, the homozygous *o2* mutant causes a decrease of the production of these zeins resulting in a corresponding increase in non-zein proteins, which naturally contain higher levels of lysine and tryptophan (Vasal, 2002; Gibbon and Larkins, 2005).

The second distinct genetic system managed within QPM breeding is comprised of the alleles of endosperm hardness modifier genes which convert the soft/opaque mutant endosperm to a hard/vitreous endosperm with little loss of protein quality (Hohls et al., 1996; Vasal, 2002). Paez et al. (1969) were the first to report on endosperm modification in *o2* kernels (50% translucent and 50% opaque). Subsequently, modified *o2* kernels with varying proportions of translucent and opaque fractions have been observed and studied by a number of workers (Annapurna and Reddy, 1971; Bjarnason et al., 1976; Lodha et al., 1976). These endosperm modifiers along with the *o2* mutant allele can be used as a rapid and low cost method of selection (Hohls et al., 1996), whereby light is projected through the vitreous grains or blocked by the opaque grains, respectively (Vasal et al., 1980; Vasal, 2001; Krivanek et al., 2007). Grain endosperm opaqueness is rated on a scale from 1 (completely hard/vitreous) to 5 (soft/opaque) (Vasal et al., 1980; Lopes et al., 1995; Hohls et al., 1996; Vasal et al., 1997a). All grains with a score of 2 - 5 are homozygous for the *o2* allele, but only grains with score 2 - 3 have sufficient modified hard endosperm to be selected as QPM grains (Krivanek et al.,

2007). Hohls et al. (1996) reported that this visual screening method makes the more laborious measurements of kernel density and kernel hardness unnecessary.

The third genetic system critical to a QPM breeding program comprises of a distinct set of amino acid modifier genes which affect the relative levels of lysine and tryptophan content in the grain endosperm (Mertz et al., 1964; Villegas et al., 1992; Krivanek et al., 2007). The lysine levels in normal and QPM maize average 2% and 4%, and tryptophan average 0.4% and 0.8% of total protein in whole grain flour, respectively (Moro et al., 1996). However, lysine ranges across genetic backgrounds from 1.6 - 2.6% in normal maize and 2.7 - 4.5% in their *o2* converted counterparts, and tryptophan ranges from 0.2 - 0.5% in normal maize and 0.5 - 1.1% in QPM counterparts (Villegas et al., 1992; Moro et al., 1996; Vasal, 2001; CIMMYT, 2002). Lysine and tryptophan levels are highly correlated (Hernandez and Bates, 1969) and as such an assay for either amino acid can be used for analysing protein quality, although in practice the latter is most often chosen due to lower laboratory costs (Krivanek et al., 2007). Multigenes have been identified in controlling amino acid content (Wang et al., 2001; Wu et al., 2002). As a result, it becomes apparent that the simple genetic nature of *o2* maize is transferred into a classic polygenic trait in reference to QPM and must be manipulated as such in breeding programs. If lysine or tryptophan levels are not continuously measured during the breeding process the additional gains in protein quality may be lost even though the *o2o2* genotype is maintained (Krivanek et al., 2007).

Through recurrent selection for genetic modifiers in *o2* backgrounds (Lonnquist, 1964; Bjarnason and Vasal, 1992) and recombination of superior hard endosperm *o2* families, CIMMYT have successfully developed new cultivars, mainly for tropical and subtropical regions. These materials are similar in yield and other agronomic properties to normal maize (Villegas et al., 1980; Ortega et al., 1991; Bjarnason and Vasal, 1992; Villegas et al., 1992) and used as QPM donor stocks as well as QPM populations for further improvement (Vasal, 2000; Prasanna et al., 2001). The development of QPM donor stocks then led to large-scale QPM germplasm development in different genetic backgrounds using an innovative breeding procedure, termed a “modified backcrossing-cum-recurrent selection”. As a result, several

QPM populations and pools possessing different ecological adaptation, maturity, grain colour and texture were developed (Vasal et al., 1984b; CIMMYT, 1985; Vasal, 2001).

Current QPM breeding strategies at CIMMYT and national breeding programs in sub-Saharan countries focus on introducing and testing QPM developed elsewhere, conversion of existing adapted genotypes to QPM and pedigree breeding (CIMMYT, 2004b; Krivanek et al., 2007). Inbred lines, hybrids, and OPVs are acquired primarily from CIMMYT-Mexico (which has a wealth of QPM germplasm), as well as other breeding programs in Mexico, Ghana and South Africa to identify the most adapted cultivars for direct release.

Adapted normal maize genotypes that resist major biotic and abiotic stresses of the region are converted to QPM. Considerable effort has been dedicated to the formation of maize streak virus resistant varieties by converting resistant genotypes (CIMMYT, 2004b). Pedigree breeding is commonly used, whereby the best performing inbred lines, complementary in different traits, are crossed to establish new segregating families. Three types of crosses provide a choice of breeding strategies (Krivanek et al., 2007): QPM x QPM, QPM x normal, and QPM x normal backcross conversion (of the normal genotype to QPM using at least three backcross generations). Within each of these methods, successive inbreeding of the material is made in parallel with continual selection on the three important QPM genetic systems (recessive mutant allele of *o2*, endosperm and amino acid modification).

2.4 Nutritional and economic benefits

The QPM offers tremendous benefits in the nutrition of monogastric animals including humans; because essential amino acids such as lysine and tryptophan can not be synthesized through metabolism of these groups of animals. The nutritional and biological superiority of QPM to normal maize has been amply demonstrated in rats (Bressani et al., 1969; Gupta et al., 1970), pigs (Lopez-Pereira, 1992; Osei et al., 1994a), infants and small children (Bressani, 1995) as well as adults (Clark et al., 1977; Bressani, 1991; 1992), broiler chickens (Osei et al., 1994b; c), and dairy cattle (Glover, 1992).

Because of the 60 to 100% increase in concentrations of lysine and tryptophan, increased digestibility, and increased nitrogen uptake relative to normal-endosperm maize, the biological value (the amount of N that is retained in the body) of QPM is about 80%, whereas that of normal maize is 40 to 57% (Bressani, 1992). Bressani (1995) reported that protein quality of *o2* maize is 43% higher than that of normal maize and 95% of the value of casein. QPM is almost 50% more effective than normal maize at fostering growth in recovering malnourished children (Graham et al., 1980; NRC, 1988). Protein quality of *o2* maize is 90% of the value of milk (Bressani, 1992; 1995). In Ethiopia, QPM is much preferred to normal maize because of its suitability in making *injera*, the country's universal food (CIMMYT, 2004a).

Osei et al. (1994a) reported that pigs fed on QPM grew 2.3 times faster than pigs of the same age fed on the same quantity of normal maize. Carcasses of pigs fed on a QPM variety were as good as those fed the normal commercial variety (Osei et al., 1994a). A diet solely based on QPM is regarded as adequate in meeting the energy and protein needs of infants and children (Graham et al., 1980; 1990). Children suffering from a severe protein deficiency disease (Kwashiorkor) were brought back to normal health on a diet containing only *o2* maize as the source of protein (Clark et al., 1977). Recovering malnourished children fed QPM further showed the same growth as those fed modified cow milk formula (Graham et al., 1990). It has been seen both as a preventer of deficiency diseases such as kwashiorkor and as a remedy for serious cases of malnutrition (Bressani, 1992). QPM has a potential impact on certain disadvantaged populations whose maize consumption is high and access to complementary sources of protein are limited (Rahmanfer and Hamaker, 1999). Gupta et al. (1970) found modified texture *o2* maize to be nutritionally superior to normal maize in rat (*Rattus norvegicus*) feeding experiments. According to Glover (1992), US farmers who fed *o2* maize silage to dairy cattle benefited from increased milk production of their dairy cows. QPM silage may hold distinct nutritional and economic advantages in the feeding of dairy animals (Gevers, 1995). Substituting normal maize with high-lysine maize on an equal weight basis for growing pigs and sows can diminish the use of synthetic lysine in animal feeds to maintain proper amino acid balance (Asche et al., 1985; Burgoon et al., 1992; Knabe et al., 1992).

In animal nutrition, QPM can provide a cheaper way of obtaining a balanced animal feed and that effect can easily be calculated in monetary terms (Krivanek et al., 2007). In the USA, doubling lysine content in maize alone can add an estimated annual gross value of $360 million per year and can go up to $480 million per year if protein also is increased (Johnson et al., 2001). These findings indicate that QPM has the added advantage of being superior in protein quality and higher in food and feed efficiency.

2.5 Variability, correlation and heritability

2.5.1 Variability

Genetic variation is a prerequisite for any improvement. Knowledge of genetic variation and relationships between accessions or genotypes is important to understand the genetic variability available and its potential use in breeding programs (Thormann et al., 1994; Yoseph et al., 2005). An insight into the magnitude of variability is of utmost importance as it provides the basis for effective selection (Singh, 2005). The composition of the phenotype (the observable properties of an organism), is simply expressed as the outcome of three major sources of variation: the genotype, the environment which includes all factors external to the plant that affect development and growth, and interactions of all kinds (Lee, 2006). Falconer (1989), and Banziger and Cooper (2001) described genetic variance as a measure of the extent of genetic differences among the germplasm units (individuals or families) evaluated. The partitioning of variance into its components allows the breeders to estimate the relative importance of the various determinants of the phenotype, in particular the role of heredity versus environment. Genetic gains from phenotypic selection have been assessed for many plant species and environments, and the progress has been varied (Duvick, 1986; Volenec et al., 2002). Despite instances of spectacular success, phenotypic selection has revealed little about the fundamental basis of progress achieved by plant breeding (Lee, 2006).

The most important factor influencing selection gains is the amount of available genetic variation for general adaptation and traits necessary for improved production under specific constraints (Blum, 1988; Ceccarelli, 1989; Vasal et al., 1997b). In agreement with this report, others also indicated that selection cannot create variability but can act on heritable variability already existing in the population (Singh and Chaudhary, 1985; Hallauer and Miranda, 1988). Genetic variation can be created by domestication, germpasm collection, plant introduction, hybridization (intervarietal, distant, somatic), mutation, polyploidy, somaclonal variation and genetic engineering (Singh, 2005). It is considered best to start selection on high performing and agronomically desirable germplasm exhibiting large variation for stress tolerant traits (Vasal et al., 1997b). The choice of breeding methods for genetic improvement of a crop depends upon the nature and magnitude of genetic variability present (Singh and Chaudhary, 1985; Hallauer and Miranda, 1988). Different mating designs are used in the estimation of genetic variability and other components of variance. On the contrary, there is a method without mating design for estimation of genetic variances in a population that tests the unselected inbred lines themselves (Hallauer and Miranda, 1988). They pointed out that although no mating is used, variability among inbred lines can be used as an estimation of genetic variability of a reference population.

The total variance of a given character is its phenotypic variance (σ_p^2) and environmental variance (σ_e^2) which is that part of the phenotypic variance attributed to environmental conditions (Falconer and Mackay, 1996). The total genetic variance (σ_g^2) also known as variance of genotypic value, is the part of phenotypic value which can be attributed to genotypic differences among the phenotypes (Dudley and Moll, 1969). Total genetic variance is further portioned into additive genetic variance (σ_A^2), dominance genetic variance (σ_D^2) and epistatic genetic variance (σ_I^2). The additive genetic variance, which is the variance of breeding values, is the important component. It determines the observable genetic properties of the population and the response of the population to selection.

A primary goal of any plant breeding program is to develop and identify high yielding transgressive segregants. Kisha et al. (1997) indicated that populations with greater genetic

variance are expected to produce higher yielding transgressive segregants than populations having lower genetic variance.

Currently, there are QPM research activities in sub-Saharan Africa region led by CIMMYT and the International Institute for Tropical Agriculture (IITA) in collaboration with National Agricultural Research Systems (NARS). In the region, activities are highly integrated and coordinated enabling joint development, exchange and broad testing of promising genotypes for all agro-ecological niches (CIMMYT, 2005b). The long-term goals of all breeding programs are focused on broadening the genetic base of adapted QPM germplasm to suite their particular biotic and abiotic constraints (Krivanek et al., 2007). So far, a large number of elite QPM inbred lines adapted to the sub-Saharan African region have been developed and there is a need to morphologically characterize them and study their association and variability.

2.5.2 Correlation

Estimation of genotypic and phenotypic correlation among characters is useful for the formulation of a breeding program. Correlation measures the degree of association, genetic or non-genetic, between two or more characters and is measured by a correlation coefficient (Hallauer and Miranda, 1988). The cause of correlation in crop plants can be genetic or environmental (Hallauer and Miranda, 1988; Falconer, 1989). Two types of correlations, phenotypic and genetic, are commonly discussed in plant breeding. Phenotypic correlation (r_P) involves both genetic and environmental effects. It can be directly observed from measurements of the two characters in a number of individuals in a population (Hallauer and Miranda, 1988). Genetic correlation is the association of breeding values (i.e., additive genetic variance) of the two characters (Falconer, 1989). Both measure the extent to which degree the same genes or closely linked genes cause co-variation in two different characters (Hallauer and Miranda, 1988). Genetic correlations inherently have large errors because of difficulties to avoid the directional effects of confounding factors on additive correlation estimates (Falconer, 1989).

Betran et al. (2003d) observed negative phenotypic correlations between grain yield and anthesis date. Pixley and Bjarnason (2002) reported positive and significant correlation between ear height and grain yield for QPM cultivars. Genetic correlations for grain yield measured in stress and non-stress environments have been sufficiently low to make direct selection under stress, and more effectively in maize, than indirect selection under optimal conditions (Brun and Dudley, 1989; Byrne et al., 1995; Banziger et al., 1997). Moreover, the genetic correlation for grain yield between stress and optimal environments seems to decrease as stress intensity increases (Fukai and Cooper, 1995; Banziger et al., 1997; Cooper et al., 1997). This suggests that selection in optimal environments could not be effective in identifying superior genotypes for stress environments. Correlation analysis between grain yield and secondary traits must be interpreted with care, because results are often confounded by genetic differences among genotypes for other traits or by the presence of outliers (Blum, 1988; Bolaños and Edmeades, 1996).

Monneveux et al. (2005) studied the correlation of grain yield with ears per plant, grains per ear, grain weight, anthesis-silking interval, and plant and ear heights and reported a significant correlation of grain yield with grain weight under optimum N, and with anthesis-silking interval and grains per ear under low N conditions. In the course of recurrent selection for drought tolerance in six tropical populations, Bolaños and Edmeades (1996) evaluated a total of 3509 inbred progenies (S_1 to S_3 level) under 50 separate yield trials. Across all trials, phenotypic correlations ($P< 0.01$) of grain yield under drought with ears per plant, kernels per plant, kernel weight, anthesis-silking interval, and leaf senescence, in order listed, were 0.77, 0.90, 0.46, -0.53, and -0.11. Genetic correlations were generally similar in size and sign. Genetic correlations between grain yield and anthesis-silking interval or ears per plant were weak under well-watered conditions, but approached -0.6 and 0.9, respectively, under severe moisture stress (Bolaños and Edmeades, 1996). Low correlations of secondary traits with grain yield may indicate that variation in grain yield under moisture stress is dominated by variation in ear-setting processes related to biomass partitioning at flowering, and much less by factors putatively linked to crop water status (Bolaños and Edmeades, 1996).

A significant negative correlation was observed between grain weight and number of grains per ear under low N (Monneveux et al., 2005) confirming a resource limitation for grain filling. Significant positive correlations were found between plant and ear height, and days to anthesis while a significant negative correlation was found between anthesis-silking interval and days to anthesis (Monneveux et al., 2005) under low N conditions. High grain yields were associated with short anthesis-silking interval, increased number of ears per plant, and delayed leaf senescence (Banziger and Lafitte, 1997). They reported that absolute values for genetic correlations with grain yield were the highest for ears per plant, followed by leaf senescence, and anthesis-silking interval. Lafitte and Edmeades (1994b) measured significant genetic correlations between grain yield under low N and ear leaf area, plant height, antheisis-silking interval, and leaf senescence among full-sib progenies, indicating the potential value of these traits in a low N selection program.

Bolaños and Edmeades (1996) determined genotypic correlations between a range of secondary traits and grain yield under drought stress for a large number of S_1 - S_3 progeny from several populations. The results indicated that traits indicative of reproductive success (e.g., kernel number per plant, ears per plant and anthesis-silking interval) explained much more of the variation in grain yield than traits indicative of plant water status and water use efficiency (e.g., leaf extension rate, canopy temperature, leaf chlorophyll concentration, leaf senescence). These authors reported an average genetic correlation of -0.48 between grain yield and anthesis-silking interval. In the diallel cross progeny of 10 QPM inbred lines, Hadji (2004) observed positive and significant correlations between grain yield and ear height, plant height, ears per plant, ear length, ear diameter, kernels per row and kernel weight. The same trend was observed for genotypic correlation of grain yield with these traits but with larger magnitude than the corresponding phenotypic correlation.

Where G x E interaction between stressed and unstressed environment is high, genetic correlations between the two environments are usually low (Itoh and Yamada, 1990). Banziger et al. (1997) observed positive genetic correlation between grain yields under low and high N. It is likely that a selection environment more similar to the target environment would result in larger selection gain (Banziger et al., 1997). If the genetic correlation

between grain yields under both N levels is positive, it is possible to simultaneously select for a wide range of N stress levels (Kamprath et al., 1982; Carlone and Russel, 1987; Lafitte and Edmeades, 1994a; c; Banziger et al., 1997). As stress intensity increases, and hence relative yield reduction under low N increases, genetic correlation between grain yields under low and high N decreases (Banziger et al., 1997; Cooper et al., 1997; Fukai et al., 1999).

In addition to improved endosperm texture, protein quality must be maintained during the process of QPM improvement. Wessel-Beaver et al. (1985) suggested a study of relationships between endosperm texture, protein quality and traits associated with endosperm texture to increase endosperm modification in a breeding program. Previous findings indicated that percent protein increased with increased endosperm modification (Lodha et al., 1976; Bjarnason et al., 1977; Vasal et al., 1980). However, Wessel-Beaver et al. (1985) reported a negative relationship between kernel modification or vitreousness and protein quality, so selection must be accompanied by chemical analysis of the endosperm to maintain high levels of lysine and tryptophan (Vasal et al., 1984a; Glover, 1992). Pixley and Bjarnason (2002) observed non-significant correlation between endosperm hardness and grain yield. According to Pradilla et al. (1973), no relationship was found between endosperm modification and protein percentage. Perhaps in some materials one may have to accept a slight decrease (Vasal et al., 1980; 1984a; Vasal, 2001).

Concentrations of protein in grain and tryptophan in grain were positively correlated, and concentrations of protein in grain and tryptophan in protein were negatively correlated (Bjarnason et al., 1977; Wessel-Beaver et al., 1985; Pixley and Bjarnason, 1993). QPM grain yield is not associated with any of the protein quality measures (Pixley and Bjarnason, 1993), thereby indicating the possibility of simultaneous improvement of protein quality and grain yield. However, grain yield and protein content are negatively correlated in maize (Bhatia and Rabson, 1987). This is especially true when N is limiting to the crop, as may often be the case in low-input farming scenarios where QPM may have the greatest impact on human nutrition (Pixley and Bjarnason, 1993). Motto et al. (1978) found a positive genetic correlation between endosperm modification and percent protein. The whole grain protein content and quality are generally negatively correlated (Pixley and Bjarnason, 1993; 2002).

2.5.3 Heritability

Success of breeders in changing the characteristics of a population depends on the degree of correspondence between phenotypic and genotypic values (Dabholkar, 1992; Singh and Ceccarelli, 1995). In crop improvement, only the genetic component of variation is important since only this component is transmitted to the next generation. A quantitative measure, which provides information about the correspondence between genotypic and phenotypic variance, is heritability (Dabholkar, 1992). According to Falconer and Mackay (1996), the relative importance of heredity in determining phenotypic values is called the heritability of the character. The extent of contribution of genotype to the phenotypic variation for a trait in a population is ordinarily expressed as the ratio of genetic variance to the total variance, i.e., phenotypic variance, for the trait; this ratio is known as heritability (Singh, 2005). Thus heritability denotes the proportion of phenotypic variance that is due to genotype, i.e, heritable.

The term heritability has been further divided into broad sense and narrow sense, depending whether it refers to the genotypic value or breeding value, respectively (Falconer, 1989; Holland et al., 2003). The ratio of genetic variance to phenotypic variance (σ_g^2 / σ_p^2) is called heritability in the broad sense or genetic determination. It expresses the extent to which individual phenotypes are determined by the genotypes. A large percentage for a character is regarded as highly heritable whereas if it is smaller, some environmental agency is considered responsible for phenotypic manifestation of the character (Dabholkar, 1992). On the other hand, the ratio of additive variance to phenotypic variance (σ_A^2 / σ_p^2) is called heritability in the narrow sense. The ratio of additive variance to phenotypic variance expresses the extent to which phenotypes are determined by the genes transmitted from the parents. The ratio also expresses the magnitude of genotypic variance in the population, which is mainly responsible for changing the genetic composition of a population through selection (Falconer, 1989; Dabholkar, 1992; Holland et al., 2003).

Estimates of heritability serve as a useful guide to breeders. The knowledge of the relative heritability of the various traits and their genotypic and phenotypic correlation can aid in the

design of efficient breeding systems where many traits need to be improved simultaneously (Jones, 1986). The breeder is able to appreciate the proportion of variation that is due to genotypic (broad sense heritability) or additive (narrow sense heritability) effects, that is, the heritable proportion of variation in the first case, and the proportion of genetic variation that is fixed in pure lines in the latter case (Singh, 2005). A broad sense heritability estimate based on various components of variance provides information on the relative magnitudes of genetic and environmental variation in the germplasm (Dudley and Moll, 1969). However, the type of gene action involved in the expression of a character has a significant role in determining heritability values. Characters that are controlled largely by genes acting in an additive fashion have higher heritability than characters governed by genes with large non-additive effects (Hanson, 1963; Falconer, 1989; Dabholkar, 1992). According to Dabholkar (1992), it is important to note that heritability is a property not only of the character being studied, but also the population being sampled and the environmental circumstances to which individuals have been subjected. More variable environmental conditions also reduce the magnitude of heritability while more uniform conditions increase it (Rosielle and Hamblin, 1981; Blum, 1988). If heritability of a character is very high, for example, 0.8 or more, selection for the character should be fairly easy (Singh, 2005). This is because there would be a close correspondence between the genotype and the phenotype due to a relatively smaller contribution of the environment to the phenotype. A high heritability implies that the genetic variation for a trait can be precisely assessed from phenotypic observations (broad-sense) and that the trait can be easily transmitted to the offspring of the selected genotypes (narrow-sense) (Falconer, 1989; Banziger and Cooper, 2001). But for a character with low heritability, say less than 0.4, selection may be difficult or impractical due to the masking effect of the environment on genotypic effects (Singh, 2005). Even the unit used in reporting, influences the magnitude of heritability (Hanson, 1963). Furthermore, predicting response to selection, heritability estimates are used to identify optimum environments for selection (Singh and Ceccarelli, 1995).

A large number of studies have been conducted on maize to estimate both broad sense (H^2) and narrow sense (h^2) heritability. According to Hallauer and Miranda (1988), plant and ear height, and oil content had the highest estimates of heritability (H^2 >70%). The H^2 value for

number of ears, kernel weight, ear length and ear diameter ranged from 30 to 50%, while yield and kernel depth showed less than 30%. However, Sidwell et al. (1976) indicated that estimates of heritability depend on the method used to estimate them, the material from which the estimates are derived and the environmental conditions encountered during the test.

2.6 Genetic diversity and its relationship with heterosis/hybrid performance

Assessment of genetic diversity is important in plant breeding if there is to be improvement by selection. Genetic diversity among and within genera, species, subspecies, populations, and elite breeding materials is equally of interest in plant genetics and breeding. While plant taxonomists and germplasm banks are primarily interested in the higher levels of this hierarchy, plant breeders are mainly concerned with diversity among and within breeding populations and elite germplasm, because it largely determines the future prospects of success in breeding programs (Melchinger, 1999). One consequence of modern agricultural practices, which generally emphasizes maximum productivity with acceptable quality and uniformity, has been a reduction in genetic diversity (Lee, 1995). However, maize by virtue of its outcrossing nature and heterozygosity, posses broad genetic diversity. Detailed knowledge regarding genetic diversity and relationship among breeding materials is indispensable for the development of new maize inbred lines, establishment and assignment of maize inbred lines to heterotic groups, choice of testers and identification of promising combinations for exploitation of heterosis (Smith and Smith, 1992; Melchinger, 1999; Xia et al., 2005; Legesse et al., 2007). This applies particularly to hybrid breeding, where recognition and exploitation of heterotic patterns between different sources of germplasm are important for success.

Before 1970, established methods for measuring genetic diversity between taxonomic units have relied on pedigree analysis and morphological, physiological or cytological markers as well as biometric analysis of quantitative and qualitative traits, heterosis or segregation variance in crosses (Lee, 1995; Melchinger, 1999). Nevertheless, estimates of distance measures based on pedigree have several shortcomings. Some of the assumptions made in the

calculation of pedigree relatedness may not be valid, particularly the assumptions of equal contribution from parents and lack of selection in derivation of new lines (Smith and Smith, 1989a). Pedigree relationships often serve as standards to test the effectiveness of morphological and biochemical markers in determining relationships among breeding lines and predicting heterosis (Gerdes and Tracy, 1994). Morphological traits have long been used to estimate systematic relationships in maize. Although morphology has proved useful for classifying maize races and populations (Goodman and Brown, 1988), these markers have shortcomings in detecting differences among closely related genotypes (Bernardo, 1992) and elite breeding germplasm (Smith and Smith, 1989b). In addition, morphological characteristics can be affected by environmental conditions (Bernardo, 1992). Therefore, comparisons should be made between material measured in different years and/or different locations (Gerdes and Tracy, 1994). For example, Gerdes and Tracy (1994) grouped only closely related sweet maize inbred lines by morphological data in agreement with pedigree data, but morphological clustering did not provide an accurate assessment of the relationships present in these lines.

In the following two decades, isozymes were successfully used in numerous taxonomic and evolutionary studies (Hamrick and Godt, 1997); however, they often failed in the classification of elite breeding materials due to the limited number of marker loci available and the low level of polymorphism. The development of DNA-based molecular markers such as restriction fragment length polymorphisms (RFLP), random amplified polymorphic DNA (RAPD), amplified fragment length polymorphisms (AFLP), microsatellites or simple sequence repeats (SSR), single nucleotide polymorphism (SNP) and many others in the latter years has removed most of the limitations associated with isozymes (Melchinger, 1999).

For assessment of genetic diversity, molecular markers have been generally superior to morphological, pedigree, heterosis and biochemical data (isozymes and chromatography) (Melchinger et al., 1991; Melchinger, 1993). Molecular markers are a powerful complement to help define heterotic groups and to examine the relationships among inbred lines at the DNA level (Smith et al., 1997; Senior et al., 1998; Melchinger, 1999). Genetic diversity studies using DNA finger printing techniques have become simple and efficient to detect

sufficient polymorphisms in various crop species including maize (Smith and Smith, 1992; Pejic et al., 1998). Molecular markers are not influenced by environmental factors and are also fast, efficient and more sensitive than field testing to detect large numbers of distinct differences between genotypes at DNA level (Smith and Smith, 1992; Westmann and Kresovich, 1997; Melchinger, 1999).

Various molecular marker types have been used to investigate relationships among inbred maize lines from different heterotic groups (Dubreuil et al., 1996; Smith et al., 1997; Lu and Bernardo, 2001; Xia et al., 2004; 2005). The most commonly used marker methods in maize are RFLP, RAPD, AFLP, SSR and SNPs. However, with the development of many DNA marker technologies, the question raised which of them are most suitable for various applications in plant genetics and breeding. Molecular markers differ in efficiency, complexity and cost effectiveness (Yang et al., 1996; Pejic et al., 1998). PCR-based markers (RAPD, AFLP, SSR and SNP) are designed to amplify fragments that contain a microsatellite using primers complementary to unique sequences surrounding the repeat motif (Weber and May, 1989).

Among the genetic diversity estimates, the SSR markers offer advantages in reliability, reproducibility, discrimination, standardization, and cost effectiveness over other marker types (Melchinger, 1999). SSRs are DNA markers with short stretches of tandemly repeated di-, tri or tetra-nucleotide motif (Weber, 1990). They are also known as short tandem repeats (STRs) or simple sequence length polymorphisms (SSLPs) (Tanya et al., 2001). SSRs are characterized by a great abundance (Matsouka et al., 2002), high variability (Tautz, 1989; Schug et al., 1998) and even distribution throughout a wide range of genomic regions (Liu et al., 1996; Senior et al., 1996). These markers are co-dominant, highly polymorphic, multi-allelic, and have become the marker of choice for genetic analysis in crops (Gupta and Varshney, 2000).

In maize, microsatellites have proved to be a valuable tool for genome mapping (Taramino and Tingey, 1996), population and conservation genetics studies (Powell et al., 1996), property right protection (Kubik et al., 2001), marker assisted selection (Weising et al., 1998)

and diversity measurements (Warburton et al., 2002; Pinto et al., 2003; Xia et al., 2004; Vigouroux et al., 2005; Xia et al., 2005; Legesse et al., 2007). SSRs can provide greater power of discrimination than RFLP markers and can reveal genetic associations that are reflective of the pedigree of the inbred lines (Smith et al., 1997; Pejic et al., 1998). SSR markers have the power of distinguishing between closely related inbred lines (Smith et al., 1997; Legesse et al., 2007). In QPM breeding programs, the use of an *o2*-specific SSR marker can facilitate the differentiation of *o2*-carrying QPM genotypes from the non-opaque genotypes (Bantte and Prasanna, 2003).

Differences in the number of tandem repeats are readily assayed by measuring the molecular weight of the resulting PCR fragments. As the differences may be as small as two base pairs, the fragments are separated by electrophoresis on polyacrylamide gels or using capillary DNA sequencers that provide sufficient resolution. Microsatellites have also proved useful for designation of lines into heterotic groups (Enoki et al., 2002).

Genetic diversity in relation to hybrid performance and heterosis has been studied extensively in maize. Moll et al. (1965) reported positive correlations between morphological marker based genetic diversity of the parents with heterosis in maize hybrids. However, morphological markers have shortcomings in detecting differences among closely related genotypes and are influenced by prevailing environmental conditions (Smith and Smith, 1992). Genetic distance based on molecular markers has been suggested as a tool for grouping of similar germplasm as a first step in identifying promising heterotic patterns (Melchinger, 1999). Several reports have demonstrated the high correlation between genetic distance and hybrid performance in maize (Lee et al., 1989; Smith et al., 1990; Lanza et al., 1997; Ajmone-Marsan et al., 1998; Betran et al., 2003; Xu et al., 2004; Makumbi, 2005; Kiula et al., 2008). Contrary to these reports; many other workers reported that genetic distance measures are of limited use in predicting hybrid performance, heterosis and SCA of single crosses (Melchinger et al., 1990; Parentoni et al., 2001; Makumbi, 2005; Legesse et al., 2008). Drinic et al. (2002) reported that SSR markers provide an effective method for predicting hybrid performance and heterosis. Generally, it is concluded that genetic distance

estimate is more efficient for the prediction of hybrid performance between closely related inbred lines than in crosses between distantly related inbred lines (Melchinger, 1999).

2.7 Effects of low nitrogen and drought stress on maize production

The production of adequate food in the tropics is being challenged by rapid population growth (80 million people/year) and declining availability of water resources and arable fertile land (Beck et al., 1997). A decline in soil fertility, particularly in nitrogen levels, and recurrent droughts are widespread in sub-Saharan Africa, especially as agricultural populations increase. In consequence, crop yields are falling to very low levels and food insecurity is widespread amongst agricultural communities (Kamara et al., 2004).

According to Edmeades et al. (2006), empirical yield gap estimates for maize suggests that more than 50% of potential yield is lost to abiotic constraints. Improvements in agronomic practices and in genetic stress tolerance may each reduce this yield gap by 20 - 30%, but the balance will depend on additional inputs such as water and nitrogen (Edmeades et al., 2006). Improved maize varieties that tolerate drought, heat, and low soil fertility will help maize farmers in stress-prone areas to obtain better harvests under dry conditions and higher temperatures (Zaidi et al., 2003; CIMMYT, 2007). The effects of low N and drought on maize production make cultivars desirable that are able to perform well under such stresses and also when conditions are optimal (Betran et al., 2003d). Zaidi et al. (2003) also suggested that utilization of drought-tolerant and N-efficient cultivars in maize production of the tropics could lead to better stability of grain yield across the environments. Breeding maize for tolerance to drought and low nitrogen conditions has been ongoing at CIMMYT, and germplasm with tolerance to both stresses has been developed (Edmeades et al., 1992; Bolaños et al., 1993; Bolaños and Edmeades, 1993a; b; Lafitte and Edmeades, 1994a;b;c; Banziger and Lafitte, 1997; Banziger et al., 1999a; Banziger and Diallo, 2004; Banziger et al., 2006).

Maize genotypes perform differently under drought and low N conditions due to the existence of genetic variability for tolerance to these stresses (Bolaños and Edmeades, 1993b;

Lafitte and Edmeades, 1994c; Vasal et al., 1997b; Link et al., 1999; Edmeades et al., 1999; Banziger et al., 2000; Dencic et al., 2000; Diallo et al., 2004). Duvick and Cassman (1999) concluded that modern maize hybrids have increased stress tolerance rather than a higher yield potential. Other physiologists pointed out that increased yield and yield stability of some recent tropical and temperate maize genotypes have been related to increased abiotic stress tolerance (Byrne et al., 1995; Tollenaar and Wu, 1999). Betran et al. (2003e) observed hybrids performing well across stress levels and suggested the possibility of combining stress tolerance and yield potential in tropical maize hybrids. One approach to reducing the impact of N deficiency and water stress on maize production may be to select cultivars that are superior in their capacity to take up N and water from the soil and utilize them efficiently (Kamara et al., 2004). Tolerance of maize to stress from low N and drought is partly related to the development of the root system, which in turn influences water and nutrient uptake by crop plants (Moll et al., 1982; Kamara et al., 2004). In general, however, the amount of grain yield recorded from maize genotypes fall with the severity of low N and moisture stress (Betran et al., 2003e). As recommended by Edmeades et al. (2006), it is more efficient to select for improved yield under stress when stressed yields are less than 50 to 60% of the potential.

Secondary traits are valuable adjuncts in increasing the efficiency of selection for grain yield under stress (Banziger and Lafitte, 1997). Improvement in drought tolerance of maize for better anthesis-silking synchrony was found to be closely associated with improved N use efficiency (Banziger et al., 1999c; Muza et al., 2004). The highest grain yielding genotypes under low N and drought tend to show lower anthesis-silking interval, delayed senescence, and a higher number of ears per plant (Jacobs and Pearson, 1991; Bolaños and Edmeades, 1993b; Moll et al., 1994; Banziger and Lafitte, 1997; Banziger et al., 1999b; Diallo et al., 2004). An increase in anthesis-silking interval in maize indicates that pollen shed is essentially over by the time silks emerge (Banziger and Lafitte, 1997; Edmeades et al., 2006). Edmeades et al. (1993) found that delayed silking is related to less assimilate being partitioned to growing ears around anthesis, which results in lower ear growth rates, increased ear abortion, and more barren plants.

In most crops, kernel number per plant is proportional to plant growth rate around flowering, and any stress that lowers photosynthesis per plant at flowering will reduce kernel set (Edmeades et al., 2006). In maize, kernel number per plant is associated with ear growth that is inhibited by stress more than tassel growth, leading to anthesis-silking interval that increases under stress (Edmeades et al., 2006). The coincidence of pollen and emerged silks has been used to successfully model kernel set at low pollen concentrations typical of stressed fields (Lizaso et al., 2003). Increasing kernel set does not, however, guarantee an increase in yield unless they can be successfully filled (Edmeades et al., 2006).

CIMMYT (2003a) reported the negative effects of drought and low N stress on endosperm modification of QPM germplasm. Severe drought stress can significantly increase the frequency of soft or poorly modified grains relative to the same genotypes under optimal moisture growing conditions (Ngaboyisonga et al., 2006). Percent protein and trypthophan are lower under low N compared to optimum N and are not affected under drought (CIMMYT, 2003b). However, the tryptophan level of QPM under both low N and optimum conditions is higher than the tryptophan level of normal maize under optimum conditions (CIMMYT, 2003b; Mosisa, 2005). Similary, Pixley and Bjarnason (2002) reported that protein quality is very stable, whereas protein content and endosperm modification of QPM varieties are less stable across environments. Feil et al. (2005) evaluated the effect of pre-anthesis drought and different rates of N fertilization on mineral composition of grains of tropical maize varieties and the results showed that N, P, K, Mg, Ca, Mn, Zn, and Cu are fairly stable across the levels of N and pre-anthesis water supply.

2.7.1 Low nitrogen stress

Nitrogen is the most limiting nutrient in maize production in the humid and sub-humid tropics. It is the mineral element required in the greatest quantity by maize, thus efficient N uptake and use by maize plants is of fundamental importance to maize production systems in Africa (Muza et al., 2004). Ma and Dwyer (1998) identified N fertilizer as the most energy-consuming component of maize grain production. N is the most limiting nutrient as it is the most mobile in the soil and the nutrient needed in the largest quantities by the crop (Laegreid

et al., 1999). As the economic and environmental costs of excessive N rise, there should be more emphasis on the selection of varieties with greater N use efficiency (Ma and Dwyer, 1998). In low-input agriculture N-efficient cultivars, cultivars with better grain yield under low-N conditions, are recommended as one of the key elements for sustainable agriculture (Sattelmacher et al., 1994).

The performance of most commercial maize hybrids and varieties under low N, small holder conditions, is limited because they were developed under very high N levels on good soils found on research stations (Muza et al., 2004). Inorganic fertilizer use in sub-Saharan Africa is constrained by high cost, inaccessibility and lack of credit faced by small holders even in the high potential moist mid-altitude eco-zones (Kamara et al., 2004; Diallo et al., 2004; Banziger and Diallo, 2004; Banziger et al., 2006). Where there is a high risk of crop failure, especially due to drought, recommended N fertilizer rates are often lower than N rates that give maximum yields under optimum conditions (McCown et al., 1992). Poor weed control additionally increases the incidence of N stress in many instances. Together, these constraints result in low N being a frequent characteristic of maize-growing environments in the tropics (Banziger and Lafitte, 1997).

Variation in N supply affects both growth and development of maize plants (McCullough et al., 1994). The onset of grain filling is a critical phase of N supply within the maize plant (Christensen et al., 1981). As a consequence of grain filling, transport of carbohydrates to the roots is reduced and N uptake decreases (Monneveux et al., 2005). N affects photosynthetic rate, leaf area, size of the sink and thus yield (Dass et al., 1997). When N supply is limiting, leaves become the main source of mobilized N to the ear (Below, 1997). Chlorophyll concentration reduction and leaf yellowing are good indicators of N remobilization (Dwyer et al., 1995). N deficiency accelerates leaf senescence by reducing chlorophyll concentration (Monneveux et al., 2005). Stay green can reflect N balance in cereals during grain filling (Borrell et al., 2001), but greenness can also be cosmetic rather than functional (Thomas and Howarth, 2000). Lack of N enhances kernel abortion (Pearson and Jacob, 1987) and reduces final grain number (Lemcoff and Loomis, 1986; Uhart and Andrade, 1995; Monneveux et al., 2005) and grain yield (Monneveux et al., 2005). Reduction of grain weight under low N

condition is more attributable to reduction in grain filling period than in growth rate (Monneveux et al., 2005).

Cultivars yield differently in different N environments due to genetic differences (Smalberger and Toit, 2004). Relative grain yield reduction due to N stress also depends on the type of progeny and N-stress intensity (Banziger and Lafitte, 1997). Smalberger and du Toit (2004) recorded a grain yield ranging from 0.65 - 3.85 t ha^{-1} under low N and 4.17 - 6.93 t ha^{-1} under optimum N for South African cultivars. They observed that the cultivar that gave the best yield (6.93 t ha^{-1}) under optimum N gave as low a yield as 0.98 t ha^{-1} under low N. Betran et al. (2003e) compared maize hybrid yield under low and high N environments and found that grain yield for hybrids in the low N environment was 33% of grain yield in the high N environment. This indicates the need for developing cultivars that will give good yield under both optimum and low N conditions.

Diallo et al. (2004) evaluated 63 single crosses along with seven local checks under low N and optimal conditions and observed grain yields ranging from 1.2 - 3.5 t ha^{-1} under low N and from 3.1 - 7.4 t ha^{-1} under optimal conditions. Banziger et al. (1997) observed a relative grain yield reduction of 37 to 78% in different experiments conducted under low N in tropical maize. Similarly, Banziger and Lafitte (1997), and Banziger et al. (1999b) reported a relative grain yield reduction ranging from 37 to 89% and from 20 to 50%, respectively. Monneveux et al. (2005) noted an average yield reduction of 67.4% for maize hybrids under low N conditions as compared to optimum management. Experiments under low N, yielding on average 25 – 35% (1.5 – 3.5 t ha^{-1}) of the yields obtained under recommended agronomic management/high rainfall conditions (6.0 – 9.0 t ha^{-1}) is regarded as optimal for expressing N stress tolerance in tropical maize (Banziger et al., 1997).

Banziger and Lafitte (1997) observed a significant reduction in plant height (27.1%), ear height (42.2%), ears per plant (11.2%), grains per ear (47.8%) and grain weight (30.7%) under low N. The authors also observed an average of less than one ear per plant, which reflects bareness rather than prolificacy. Monneveux et al. (2005) reported that on average ASI increased from 0.33 days under optimal to 2.42 days under low N conditions, which is

more than seven fold that of the optimal conditions. Low N stress also increases the incidence of ear rot disease (Banziger et al., 2006).

Consideration of secondary traits could improve selection efficiency under low N stress conditions. Banziger and Lafitte (1997) noted that the use of secondary traits increased selection efficiency for grain yield when broad-sense heritability of grain yield was low under low N. Moll et al. (1987) found that selection for ears per plant improved the identification of superior genotypes under low N. Banziger and Lafitte (1997) used ears per plant and leaf senescence to discriminate superior genotypes under low N. A higher number of ears per plant under low N indicates the ability of a plant or genotype to produce a grain bearing ear under N stress (Wolfe et al., 1988).

2.7.2 Drought stress

Drought stress resulting from insufficient rainfall is one of the most important maize production constraints in Africa. Edmeades et al. (1994) reported that 50% of the losses in maize grain yield in the developing world are due to pre-anthesis drought stress. Possible climate change due to global warming further increase the chances of drought (Betran et al., 2003e). Yield losses can occur when drought coincides with establishment, flowering or grain filling. However, the maximum reduction in productivity is inflicted when it occurs at or around flowering, more than at any other time in the crop cycle (Bolaños and Edmeades, 1993a; 1996). Therefore, selection under managed drought stress at flowering is suggested as an effective means of increasing tolerance to a number of stresses occurring during near flowering (Chapman et al., 1997). According to Denmead and Shaw (1960), the reduction in grain yield due to drought stress during the vegetative, silking and ear stages were 25%, 50%, and 21%, respectively. Drought lasting for one to two days at pollination can reduce grain yield by up to 22% (Fischer et al., 1983).

Elite tropical maize germplasm contains considerable genetic variability for drought tolerance. By carefully managing drought stress levels, it is possible to observe genetic variation in grain yield and drought adaptive secondary traits and exploit this variability

(Manda and Mwambula, 1999). Drought tolerant maize germplasm can be developed through deliberate improvement for higher drought tolerance. Commercial hybrids developed using multilocation testing that supposedly included results from randomly drought stressed sites showed inferior performance under managed drought experiments (Banziger et al., 1999c). Commercial hybrids yielded on average 23% better than drought tolerant test-crosses under optimal conditions but 27% less than those test-crosses under severe drought stress. Diallo et al. (2004) reported that an average grain yield for the hybrids under drought was only 45% of average grain yield under optimal conditions. Manda and Mwambula (1999) screened 96 maize genotypes for drought tolerance and observed significant genotypic differences for grain yield, with a range of 0.5 - 5.7 t ha^{-1}.

Selection for improved performance under drought, based on grain yield alone has often been considered inefficient, but the use of secondary traits of adaptive value whose genetic variability increases and whose heritability remains high under drought can increase selection efficiency (Bolaños and Edmeades, 1996; Edmeades et al., 1997; Banziger and Lafitte, 1997; Banziger et al., 1999a). Many secondary traits have been proposed for a drought breeding program, all putatively related to improved survival or improved production in water stressed environments, but few traits have proven to contribute to increasing grain yield under stress (Fukai and Cooper, 1995).

Manda and Mwambula (1999) reported that anthesis-silking interval and ears per plant were the most useful secondary traits for selecting for better yields under drought stress conditions. The highest yielding genotypes under drought stress tended to have lower anthesis-silking interval and a higher number of ears per plant (Bolaños and Edmeades, 1993b; Diallo et al., 2004). Bolaños and Edmeades (1993a, 1996) reported a strong dependence of grain yield on anthesis-silking interval. Bolaños and Edmeades (1996) noted that grain yield decreased to less than 20% of its well-watered levels as anthesis-silking interval increased from 0 to 5 days, and then declined asymptotically to almost zero yields as ASI increased. Materials with longer anthesis-silking interval and more barren plants had inferior performance for grain yield (Banziger et al., 1999c). Anthesis-silking interval and ears per plant had stable or

increasing heritability as drought stress at flowering intensified, even as heritability for grain yield declined (Edmeades et al., 2006).

2.7.3 Managed stress environments

Although crop breeding is conducted under high-yielding conditions, a considerable proportion of maize in the tropics is grown under low nitrogen and drought conditions (Simmonds, 1991; Banziger et al., 1997; Banziger and Cooper, 2001). Thus, breeding under optimally managed agronomic conditions does not do justice to the type of conditions under which the majority of African farmers grow their crops (Bolaños et al., 1993; Banziger and Diallo, 2004; Muza et al., 2004). This indicates that success in breeding programs requires evaluation environments that are representative of the target population of environments (Allen et al., 1978). The unpredictable nature of weather-related stresses and the limited number of multi-environment trials (METs) that are possible, have led to the development and use of managed stress environments (MSEs) (Edmeades et al., 2006)

MSEs are selection environments for low input conditions established by simulating abiotic stress factors that are important in the target environment (Banziger and Cooper, 2001). Edmeades et al. (2006) described MSEs as specialized testing sites that allow stringent control of the nature, timing and intensity of stresses imposed on the target crop. The use of MSEs permits controlled and quantifiable consideration of the factors that affect breeding progress (Rosielle and Hamblin, 1981; Banziger and Cooper, 2001). MSEs seek to impose a repeatable stress representative of farmers' fields, yet efficiently severe that genetic variation for tolerance can clearly be distinguished (Edmeades et al., 2006). For stresses such as drought or low nitrogen, managed stress usually depends on rain-free natural environments equipped with irrigation systems, or they comprise spatially uniform, nitrogen depleted fields (Edmeades et al., 2006) and breeding experiments are exposed to these clearly defined abiotic stress factors (Banziger and Cooper, 2001).

In fact, when productivity is extremely low, it is not even possible to discriminate selectively among genotypes (Guillen-Portal et al., 2004). Because of this, and the often observed

moderate-to-high correlation of genotypic yield performance across a wide range of seasonal water amounts, some researchers have recommended that breeding for stress tolerance should be performed under optimal conditions (Byrne et al., 1995; Rajaram et al., 1996; Guillen-Portal et al., 2004). It has also been asserted that breeding for stress tolerance under optimal conditions permits an efficient allocation of the resources available (Allen et al., 1978; Glaz et al., 1985). Guillen-Portal et al. (2004) concluded that environments that allow maximum expression of genetic variability among genotypes and minimum interference of variations in the environmental conditions can be used as selection environments.

In contrast, other researchers found that even though heritability for grain yield usually decreases as stress intensifies, breeding progress may be increased if abiotic stresses in the target environment are included during selection (Atlin and Frey, 1990; Ceccarelli et al., 1992; Ud-Din et al., 1992; Zavala-Garcia et al., 1992; Banziger et al., 1997). Van Oosterom et al. (1993) asserted that breeding for stress should be performed under conditions that are representative of the target environment. Compared to genotypes selected under METs using conventional breeding approaches, genotypes selected under drought or N stress significantly increased grain yield across all stress levels (Bolaños and Edmeades, 1993b, 1993a; Granados et al., 1993; Lafitte and Edmeades, 1994a; b; c; Byrne et al., 1995; Edmeades et al., 1999). Byrne et al. (1995) demonstrated a greater yield stability of one drought tolerant population as compared to its conventionally selected counterpart across international testing locations. Improvements under drought were also associated with selection gains across a wide range of nitrogen supply levels (Banziger et al., 1999b; 2002), indicating that a screening approach using managed stress environments may have wider merit.

Edmeades et al. (2006) pointed out that simultaneous selection under stressed and unstressed conditions serves to combine high yield with stability. Rather than selecting exclusively under well-fertilized, well-irrigated conditions, as was done previously worldwide, CIMMYT and national breeders in sub-Saharan Africa prioritized the major stresses found in farmers' fields (drought, low soil fertility, insect pests, acid soils) and duplicated them on breeding stations (Banziger and Cooper, 2001; Banziger et al., 2006). To develop low N and drought tolerant genotypes for the region, selection is done using three types of environments: (i)

recommended agronomic management/high rainfall conditions, (ii) low N stress, and (iii) managed drought (Banziger et al., 2006).

Experiments conducted under low-yielding conditions have a higher frequency of producing statistically non-significant differences or having a large coefficient of error variation for grain yield than experiments conducted under high-yielding conditions (Banziger and Cooper, 2001). This is because the error variance of grain yield usually does not decrease as much as the genetic variance when moving from high- to low-yielding conditions (Banziger et al., 1997). With careful management, MSEs should decrease environmental variance and increase heritability (or repeatability) for stress tolerant plant attributes, thereby improving expected genetic gains (Banziger et al., 1997; 2006).

Bolaños and Edmeades (1996), and Banziger et al. (1997) mentioned that there should be an appropriate window of yield reduction targeted in MSEs, and if stress is too intense, genetic variance declines and heritability falls (Bolaños and Edmeades, 1996; Banziger et al., 1997). Banziger et al. (1997) reported that direct selection under low N is more efficient than indirect selection under high N when relative yield reductions under low N exceed 23%. This indicates that selection gains can be increased if low N selection environments are included in maize breeding programs targeting such areas. Even though there is extensive evidence that selection under target stresses may accelerate breeding gains for stress environments (Pederson and Rathjen, 1981; Atlin and Frey, 1990; Ceccarelli et al., 1992; Ud-Din et al., 1992; Banziger et al., 1997), the difficulty of choosing appropriate selection environments, given a highly variable target environment, may limit the identification of superior genotypes (Blum, 1979).

2.8 Hybrid performance, heterosis, combining ability and genotype-environment (G x E) interaction

2.8.1 Hybrid performance and heterosis

Hybrid varieties are the first filial generations (F_1) from crosses between two or more pure lines, inbreds, open-pollinated varieties, clones or other populations that are genetically dissimilar (Singh, 2005). Maize hybrid development began in the early 1900s (Hallauer et al., 1988). In maize, hybrid breeding remains the method of choice for attaining maximum genetic gain from the effect of heterosis. Food and feed supplies would undoubtedly be greatly reduced if only non-hybrids were available to the producer (Stuber, 1994b). According to Singh (2005), most of the commercial hybrid varieties are F_1's from two or more inbreds. An inbred is a nearly homozygous line obtained through continuous inbreeding of cross pollinated species with selection accompanying inbreeding (Singh, 2005). The success of hybrid maize development depends on the ability of the breeding program to rapidly isolate lines that combine well in hybrid combinations and to identify appropriate heterotic combinations to maximize the vigour of the hybrid (Kim and Ajala, 1996). The general process to develop maize hybrids starts with the creation of a source segregating breeding population that is used to develop inbred lines through inbreeding and selection (Betran et al., 2004). Selected inbred lines are then evaluated in hybrid combinations across locations to select superior hybrids and to estimate their combining ability.

With the decision to embark on the QPM hybrid breeding program, several diallel studies were conducted and information on hybrid combinations has been documented (Gupta et al., 1975; Pixley and Bjarnason, 1993; Vasal et al., 1993a;b; Hohls et al., 1995; Cordova et al., 2003; Hadji, 2004; Xingming et al., 2004; Bhatnagar et al., 2004). QPM hybrids yield more grain than open pollinated QPM cultivars, but mean grain yield does not differ for single-, three-way-, and double-cross QPM hybrids in multilocation trials (Pixley and Bjarnason, 2002). They suggested that failure of the single cross to yield more than three-way or double cross progeny is due to lack of heterosis among at least some of the parent lines used. They

further explained that broader genetic constitution of three-way and double cross hybrids buffer them better than single crosses against the extreme environmental diversity of the trial sites.

In a trial, Pixley and Bjarnason (1993) observed a QPM hybrid exceeding a normal-endosperm hybrid check on average by 14% for grain yield, 48% for tryptophan concentration in grain, and 60% for tryptophan concentration in protein. Bhatnagar et al. (2004) evaluated diallel crosses of white and yellow QPM inbred lines and reported higher grain yield for some crosses among white QPM inbreds but lower grain yield for all crosses among the yellow QPM inbreds as compared to normal maize checks used.

The term heterosis was coined by Shull (1952). It is defined as the difference between the hybrid value for one trait and the mean value of the two parents for the same trait (Falconer and Mackay, 1996). According to Miranda (1999), heterosis is the genetic expression of the superiority of a hybrid in relation to its parents. Two major types of estimation of heterosis are reported in literature; namely, mid-parent or average heterosis, which is the increased vigor of the F_1 over the mean of two parents; and high-parent or better parent heterosis, which is the increased vigor of the F_1 over the better parent (Sinha and Khanna, 1975; Jinks, 1983). Heterosis (usually considered to be synonymous with hybrid vigor) is one of the primary reasons for the success of the commercial maize industry (Stuber, 1994b). Although several economically important crops benefit from the manifestation of heterosis, both the genetic and physiological mechanisms underlying this phenomenon are still unexplained (Hallauer and Miranda, 1988; Tollenaar et al., 2004). Three major theories, such as dominance, over-dominance and epistasis, have been proposed as the main theories to explain mechanisms underlying the phenomena of heterosis (Hallauer and Miranda, 1988; Singh, 2005). However, it is generally accepted that heterosis, to a large extent, is due to dominance gene action (Singh, 2005). To overcome many of the difficulties that are encountered in the interpretation of heterosis for complex traits, component analysis approaches have been used to study the effect of heterosis on grain yield (Sinha and Khanna, 1975). Grain yield has been subdivided, for instance, into ear number, kernel number, and weight in an attempt to understand how heterosis influences grain yield (Sinha and Khanna,

1975). These grain yield components, however, are static attributes that do not lend themselves to a process-based analysis of grain yield formation (Tollenaar et al., 2004).

Heterosis is important in maize breeding and is dependent on level of dominance and differences in gene frequency. The manifestation of heterosis depends on genetic divergence of the two parental varieties (Moll et al., 1965; Hallauer and Miranda, 1988). Low grain yield heterosis is observed for crosses among genetically similar germplasm and for crosses among broad genetic base germplasm (Hallauer and Miranda, 1981; Beck et al., 1990; Crossa, 1990; Beck et al., 1991; Vasal et al., 1992a; b; 1993a; b). Higher levels of heterosis were seen with increased divergence within a certain range, but that heterosis declined in extremely divergent crosses (Moll et al., 1965; Prasad and Singh, 1986). Genetic divergence of the parents is inferred from the heterotic patterns manifested in a series of crosses (Moll et al., 1965; Hallauer and Miranda, 1988; Miranda, 1999).

Heterosis in maize has been investigated extensively. Hallauer and Miranda (1988) summarized results from studies on heterosis for grain yield in maize up to 1979. They reported that mid-parent heterosis ranged from -3.6% to 72.0% while high-parent heterosis ranged from -9.9% to 43.0%. Surprisingly, the magnitude of heterosis has not been changed during the hybrid era (Duvick, 1999), even though mean commercial maize grain yield has substantially increased during this time (Troyer, 1990; Tollenaar and Wu, 1999). Crossa et al. (1987) reported estimates of heterosis as percentage of the high yielding parent ranging from 0 to 47.7 in maize population crosses. In crosses among CIMMYT's subtropical and temperate maize germplasm, Beck et al. (1991) observed high-parent heterosis for grain yield ranging from -14.8 to 9.9%. Vasal et al. (1992a) reported a maximum high parent heterosis of 13% in diallel crosses among seven CIMMYT sub-tropical and temperate early-maturity maize germplasm lines. Glover et al. (2005) found high parent heterosis as high as 46% in crosses among 10 Chinese and US lines and concluded that the populations used in these crosses were more narrowly based than those used in other exotic maize diallel studies. In a study by Vasal et al. (1992b), high-parent heterosis ranged from -3.1% to 12.7% for grain yield, -7.7% to 4.5% for plant height, -4.7% to -0.1 for days to silk in pools and populations. Tollenaar et al. (2004) reported an average heterosis of 167% for grain yield, 109% for

number of kernels per plant and 12% for thousand kernel weight. In diallel crosses among CIMMYT's subtropical QPM germplasm, Vasal et al. (1993a) reported estimates of high-parent heterosis ranging from -14.8 to 11.5% for gain yield. Similarly, Vasal et al. (1993b) observed high-parent grain yield heterosis ranging from -10.8 to 15.6 for CIMMYT's lowland tropical QPM germplasm.

2.8.2 Combining ability

Sprague and Tatum (1942) introduced the concepts of general combining ability (GCA) and specific combining ability (SCA) to distinguish between the average performances of parents in cross combinations (GCA) and the deviation of individual crosses from the average performance of the parents involved (SCA) (Hallauer and Miranda, 1988). The diallel mating design is used as a method to analyze crosses, or parents and crosses, for GCA and SCA (Griffing, 1956), providing an assessment of their relative merits to guide selection and testing schemes. The term 'diallel' is a Greek word and implies all possible crosses among a collection of male and female animals (Dabholkar, 1992). Hayman (1954) and Stoskopf et al. (1993) defined "diallel cross" as the set of all possible matings between several genotypes.

Diallel cross mating schemes have been extensively used in breeding programs for the evaluation of the genetic potential of parents that range from inbred lines to wide genetic base varieties (Hallauer and Miranda, 1988; Stoskopf et al., 1993; Bernardo, 2002). Diallel analysis provides inferences on genetic control of the traits under investigation. As noted by Hallauer and Miranda (1988), the diallel mating design has been used and abused more extensively than any other in maize and other plant species. The diallel mating design, however, can be very useful if properly analyzed and interpreted (Hallauer and Miranda, 1988). Much of the abuse of diallel is due to the presence of two models for diallel analysis: a random model and a fixed model (Bernardo, 2002). The main problem seems to arise from interpretations and inferences that can be made about estimates obtained from analysis of the diallel crosses (Hallauer and Miranda, 1988). A random model is useful for estimating GCA and SCA variances; but a fixed model aims to measure the GCA effects for each parent and the SCA effects for each pair of parents (Bernardo, 2002).

Information on the combining ability of maize germplasm is of great value to maize breeders. GCA and SCA effects are important indicators of the potential value of inbred lines in hybrid combinations (Sprague and Tatum, 1942). Combining ability of inbred lines is the ultimate factor determining future usefulness of the lines for hybrid development (Hallauer and Miranda, 1988). Using the concept of combining ability, genetic variance is partitioned into two components: variance due to GCA and variance due to SCA (Hallauer and Miranda, 1988; Sughroue and Hallauer, 1997). GCA is recognized primarily as a measure of additive gene action and SCA as an estimate of non-additive gene action such as dominance and epistasis (Sprague and Tatum, 1942; Rojas and Sprague, 1952; Gowen, 1964; Kambal and Webster, 1965). The relative importance of additive versus non-additive effects in diallel crosses is an indication of the type of gene action (Baker, 1978). Besides, combining ability studies allow classification of selected parental materials with respect to breeding behaviour (Sprague and Tatum, 1942; Hallauer and Miranda, 1988; Poehlman and Sleper, 1995).

According to Hallauer and Miranda (1988), characterization of genetic variance and type of gene action operative in crosses of inbreds are interpreted relative to GCA and SCA of inbred lines. The proportion of additive and non-additive components of genetic variance depends on the genetic structure of the crosses analyzed and the environmental conditions in which they were grown (Khotyleva and Trutina, 1973). Kebede (1989) reported that additive gene effects were more important in determining traits in the populations while non-additive gene actions were important in inbred line crosses. Younes and Andrew (1978) reported that additive gene action is more important than non-additive components for most traits in previously unselected material. GCA is predominant for parents that have been developed through selection for GCA and for parents that have not been separated into heterotically complementary groups during their development (Pixley and Bjarnason, 1993).

On the other hand, Kambal and Webster (1965) reported the importance of non-additive gene action for some traits, including grain yield, in materials that were previously selected for GCA. Betran et al. (2003d) found negative SCA for hybrids involving inbred lines with the same germplasm origin or related by pedigree and greater SCA for hybrids involving inbred lines of different source germplasm origin. Kim and Ajala (1996) studied combining ability

among tropical and temperate maize inbred lines and reported that a major proportion of crosses sum of squares for grain yield was explained by GCA. San Vincente et al. (1998) reported greater relative importance of non-additive than additive genetic effects for grain yield in diallel crosses among improved tropical white endosperm populations. In crosses among subtropical and temperate CIMMYT germplasm, Beck et al. (1991) observed highly significant GCA effects for grain yield, time to silk and plant height. Vasal et al. (1992a) reported significant GCA and GCA x environment interaction effects for grain yield and days to silking. Similarly, results from combining ability studies of CIMMYT's tropical early and intermediate maize germplasm (Beck et al., 1990) showed highly significant GCA effects for grain yield. In a diallel cross among Mexican races of maize, Crossa et al. (1990) reported highly significant GCA and SCA mean squares for grain yield, days to anthesis and ears per plant. They further reported that GCA effect was the most important component of variation among the entries for grain yield. In population diallel crosses, Glover et al. (2005) observed significant GCA and SCA mean squares for grain yield, stalk lodging, ear height and days to silking.

The choice of the most effective breeding scheme and the rate of the genetic improvement are dependent upon the relative magnitude of various gene effects (Dhillon and Pollmer, 1978). Lee et al. (2005) reported that although both additive and non-additive genetic effects influence grain yield in inbred line crosses, 74% of the total genetic variance is attributed to the additive genetic component. The average of nearly 100 estimates indicate that, assuming no epistasis and no linkage, additive genetic effects on average account for 61.2% and dominance count for 38.8% of total genetic effects (Hallauer and Miranda, 1988).

The relative importance of GCA increases with drought stress level when comparing trials grown at the same location and during the same season (Betran et al., 2003e). Betran et al. (1999) analyzed the genetics of abiotic stress tolerance in 17 tropical inbred lines and reported that as drought stress increased so did the importance of GCA and additive genetic effects. Non-additive gene effects were more important under low-N stress and a significant number of cross-overs were observed between the GCA of lines under low and high N levels (Betran et al., 1999). Betran et al. (2003d) reported that additive genetic effects accounted for

84% of the genetic variance under severe drought, 60% under well-watered conditions and 61% across drought and low N stress, and unstressed environments. Under low N the non-additive gene effects were more important than the additive genetic effects and a significant number of crossovers were observed between the GCA of lines under low and high N. Results of evaluations of tropical maize progenies indicated that when low N stress became more severe, the correlation of grain yields between low and high N decreased and changes in genotype ranks increased when compared with high N environments (Banziger et al., 1997).

Makumbi et al. (2004) estimated GCA and SCA effects of 15 tropical maize inbred lines for anthesis date, silking date, plant height, anthesis-silking interval, ears per plant and grain yield under stressed and optimal conditions. The results indicated that both GCA and SCA effects across locations were significant for all traits and GCA x environment and SCA x environment interaction effects were significant for grain yield and ears per plant. They further reported that additive genetic effects were more important for grain yield under drought and well-watered conditions and non-additive genetic effects were found to be more important under low N stress conditions for ears per plant in these inbred lines.

In a diallel study of CIMMYT's QPM germplasm, Vassal et al. (1993a;b) observed significant GCA effects for grain yield, time to silk, ear height, plant height and endosperm hardness. Results of a combining ability study of CIMMYT's subtropical QPM germplasm showed highly significant GCA mean squares for all and non-significant SCA mean square for most of these traits. Based on these results, they suggested that additive gene actions are more important in controlling grain yield and kernel modification. Cordova et al. (2003) reported the importance of GCA effects for grain yield in a factorial crosses between QPM inbred lines from two heterotic groups. Fan et al. (2004) analyzed the combining ability of 10 yellow QPM indreds from CIMMYT and China, and reported significant GCA and SCA effects for grain yield.

Bhatnagar et al. (2004) studied combining ability of white and yellow QPM inbreds for grain yield, days to silk, plant and ear heights, lodging and grain moisture and reported presence of

significant GCA effects for all traits except for grain yield in both diallel sets across locations. Xingming et al. (2004) evaluated combining ability and heterotic groups of yellow QPM inbreds and observed significant differences among the crosses and GCA of lines for grain yield, plant height, rows per ear, kernels per row and thousand seed weight; and non-significant difference in SCA mean squares for all traits. Hadji (2004) evaluated the combining ability of 10 white QPM inbred lines and reported significant GCA mean squares for days to anthesis, ear and plan height, ears per plant, ear length, ear diameter, rows per ear, kernels per rows, kernel weight, endosperm hardness and grain yield and significant SCA mean squares for all these traits except endosperm hardness. He reported the dominance of GCA effects for most of the traits studied except for ear length, kernels per row and grain yield.

Several investigators reported the greater importance of additive genetic variance relative to dominance genetic variance for percent protein in grain, percent tryptophan or lysine in grain, and percent tryptophan or lysine in protein for different *o2* germplasm (Sreeramulu and Baumann, 1970; Bjarnason et al., 1977; Motto et al., 1978; Wessel-Beaver et al., 1985; Pixley and Bjarnason, 1993; De-quan and Shi-huang, 1995). The absence of SCA effects for protein quality traits is undesirable because heterosis cannot be exploited to directly contribute gains for these traits (Pixley and Bjarnason, 1993). However, Ngaboyisonga et al. (2008) reported the significance of both additive and non-additive gene action in conferring protein and tryptophan concentrations in QPM kernels. Pixley and Bjarnason (1993) conducted four diallel studies involving 34 tropical QPM lines and concluded that grain protein content, tryptophan in grain and tryptophan in protein are controlled largely by additive gene action. They reported the predominance of additive gene effect in a diallel cross of tropical QPM inbred lines for these traits.

The inheritance of *o2* modifier genes for endosperm texture is complex (Annapurna and Reddy, 1971; Vasal et al., 1980; Wessel-Beaver and Lambert, 1982). Several researchers reported that additive genetic effects are more important than non-additive effects for endosperm hardness in the *o2* background of QPM (Annapurna and Reddy, 1971; Sriwatanapongse et al., 1974; Bjarnason et al., 1976; Motto et al., 1978; Motto, 1979; Vasal

et al., 1980; Ortega and Bates, 1983; Wessel-Beaver et al., 1985; Pixley and Bjarnason, 1993; Vasal et al., 1993a; b; De-quan and Shi-huang, 1995). Non-additive genetic components also contribute to the expression of kernel vitreousness (Sriwatanapongse et al., 1974; Wessel-Beaver and Lambert, 1982). The genetic variance associated with protein and lysine concentrations in modified *o2* material was mostly additive (Bjarnason et al., 1977; Motto et al., 1978). Wessel-Beaver et al. (1985) suggested effective selection in increasing the frequency of the favourable alleles for endosperm modification.

Environmental conditions affect the gene action governing protein and tryptophan concentration. Ngaboyisonga et al. (2008) evaluated factorial crosses of QPM inbred lines under optimal, low N and drought conditions for protein and tryptophan concentrations in grain. The results showed that protein concentration is predominantly governed by additive gene action under optimum and drought, and by non-additive gene action under low N conditions. Tryptophan concentration is predominantly controlled by non-additive gene action under optimum, and by additive gene action under low N and drought conditions.

2.8.3 Genotype-environment (G x E) interaction

Cultivar performance is a function of the genotype and the nature of the production environment (Cooper and Byth, 1996). Environmental factors have a greater effect on quantitative traits than on qualitative traits, as a result of which performance tests of potential cultivars are conducted in multiple years and locations (Bernardo, 2002). In addition to genotype and environment main effects, performance of cultivars is also determined by the G x E interactions, which is the differential response of cultivars to environmental changes (Hallauer et al., 1988; Crossa et al., 1990; Vargas et al., 1999). Various biotic and abiotic stresses have been implicated as causes of G x E interaction. G x E interactions in African maize growing environments, for example, result from factors related to temperature, season rainfall, season length, within-season drought, sub-soil pH and socio-economic factors that result in sub-optimal input application (Banziger et al., 2006). Multi-environment trials (METs) are systematic approaches exploited to increase yield stability of new crop varieties in stress prone environments (Shakhatreh et al., 2001). Naturally, G x E interactions are

complex, when poorly understood, they represent a significant impediment to genetic improvement (Basford and Cooper, 1998).

The relative magnitude of G x E provides information concerning the likely area of adaptation of a given genotype. It is also useful in determining efficient methods of using time and resources in a breeding program (Ceccarelli, 1989; Kang, 1998). Consequently, improving genotype resistance/tolerance to different stresses to which they would likely be exposed might minimize G x E interaction (Kang, 1998). Mid season drought tolerant genotypes that perform well under variable moisture regimes (Chapman et al., 1997; Gezahegn et al., 2008) and N levels (Banziger et al., 1999b) are expected to give a better yield with increased stability across variable growing conditions compared to conventionally developed genotypes. Large G x E interaction is expected when genotypes are grown under a wide range of environments and outside their normal zone of adaptation (Beck et al., 1991). Selection of multi-environment sites to sample stresses adequately where G x E and genotype-by-year interaction are major sources of variation, is a critical step in a successful breeding program (Edmeades et al., 2006). The extent of performance testing depends on the magnitude of G x E, which occurs when genotypes differ in their relative performance across environments (Bernardo, 2002). Yield trials frequently have both significant main effects and a significant G x E interaction (Zobel et al., 1988). The existence of G x E interaction necessitates that breeders evaluate genotypes in more than one environment to obtain repeatable rankings of genotypes (Hallauer et al., 1988). However, G x E becomes of practical significance only when crossover interactions occur (Baker, 1988; Crossa and Cornelius, 1997). Crossover interactions occur in evaluation trials when ranks of cultivars change across environments (Russell et al., 2003).

Under conditions of varying environments, genotypes that provide high average yields with minimum G x E interaction have been gaining importance over increased yields (Ceccarelli, 1989; Gauch and Zobel, 1997; Kang, 1998). The definition of a stable cultivar varies with the type of stability analysis used, but generally breeders want cultivars with high mean yield that respond to improved environments (Hallauer et al., 1988). The predominant type of stability analysis used has been regression of cultivar means on environmental means, which

has been referred to as joint regression analysis (Freeman, 1973). Joint regression analysis of G x E interaction provides an estimate of the linear response of individual genotypes to environments (b_i) and an estimate of the deviations of the observed values from the predicted values (deviation mean square) (Eberhart and Russel, 1966; Perkins and Jinks, 1968; Freeman and Perkins, 1971; Wright, 1971; Shukla, 1972; Lin et al., 1986).

The conventional method of partitioning total variation into components due to genotype, environment, and G x E conveys little information on the individual patterns of response (Zobel et al., 1988). To optimize growers' yields, despite G x E interactions that cause no one genotype to win everywhere and always, the growing region must be subdivided into relatively homogeneous mega-environments and appropriate genotypes must be targeted for each of these mega-environments (Gauch and Zobel, 1997). The additive main effect and multiplicative interaction (AMMI) model meets these criteria effectively (Zobel et al., 1988; Crossa et al., 1990; Gauch and Zobel, 1997). The usual analysis of variance (ANOVA) fails to detect a significant interaction component, principal component analysis (PCA) fails to identify and separate the significant genotype and environment main effects, and linear regression (LR) accounts for only a small portion of the interaction sum of squares (Zobel et al., 1988). Since ANOVA, PCA, and LR are sub-cases of the more complete AMMI model (Zobel et al., 1988), AMMI offers a more appropriate first model of choice when main effects and interaction are both important (Zobel et al., 1988; Crossa et al., 1990; Gauch and Zobel, 1997). AMMI increases the precision of yield estimation and selection of higher yielding genotypes than treatment means (Crossa et al., 1990). AMMI has no specific experimental design requirements, except for a two-way data structure (Zobel et al., 1988).

Maideni et al. (2004) characterized maize testing environments in the Southern African Development Community (SADC) region and identified six groups based on consistent G x E interactions based across years and trials. They reported that drought and low N managed environments were each located in different categories. Long term climatic conditions and crop management affect site similarity but not national boundaries, demonstrating a scientific rationale for regional development and deployment of maize varieties (Maideni et al., 2004). Mosisa and Habtamu (2008) studied the G x E interaction and stability of 20 genotypes at

nine locations in Ethiopia for two years and identified cultivars with stable and specific adaptation. Gezahegn et al. (2008) analyzed G x E interaction of 28 drought tolerant maize hybrids along with two standard checks across 12 drought stressed and non-stressed environments. Based on specific adaptation, they successfully categorized the hybrids into four groups using the AMMI model.

Vasal et al (1993a) evaluated diallel crosses of 10 QPM populations across locations and reported highly significant G x E interaction for grain yield, time to silk, plant height, and endosperm hardness. Pixley and Bjarnason (2002) evaluated stability of grain yield, endosperm modification and protein quality of hybrid and open pollinated QPM cultivars and reported high stability of open pollinated cultivars followed by double crosses, three-way- and single cross progeny, successively. They observed the reverse trend for endosperm modification score and suggested that more homogenous cultivars have greater stability for this trait. Glover et al. (2005) evaluated diallel crosses among Chinese and US germplasm and observed significant G x E interaction effects for grain yield, stalk lodging, ear height and days to silking.

Chapter 3

Variability of QPM inbred lines as measured by morphological data and simple sequence repeat (SSR) markers

3.1 Abstract

Information on the extent of variability in quality protein maize (QPM) lines would help to design appropriate breeding strategies for development of nutritionally enhanced maize varieties. The objectives of this study were to assess the extent of phenotypic and genotypic variability, and from this to assess genetic diversity and relationships among elite QPM inbred lines, and to classify and identify groups of similar inbred lines by means of cluster analysis based on morpho-agronomic data and SSR markers. Thirty-five maize inbred lines (32 QPM and three normal maize line checks) were evaluated for 17 morpho-agronomic traits at Harare, Zimbabwe and Bako, Ethiopia. The lines varied significantly for all of the measured traits. Grain yield was positively and highly significantly correlated with most traits. Phenotypic and genotypic coefficients of variation were the highest for grain yield and anthesis-silking interval. Estimates of broad sense heritability were the highest for days to anthesis and thousand kernel weight. Unweighted paired group method using arithmetic averages (UPGMA) cluster analysis based on morpho-agronomic data grouped the inbred lines into four clusters mainly based on grain yield, days to anthesis, plant height and leaf area. In most cases, the clustering pattern did not follow the pedigree relationship among the inbred lines. Molecular analysis of the inbred lines using 40 SSR markers yielded a total of 217 alleles, averaging 5.4 and ranging from two to 10 alleles per locus. UPGMA cluster analysis based on SSR marker genetic distances revealed six clusters among the inbred lines. The clustering pattern was largely consistent with the available pedigree information of the inbred lines. The correlation between the two distance measures was significant but of very low value (r= 0.09*). SSR markers were more effective in discriminating maize inbred lines than morpho-agronomic data. Information from the current study can be used for better understanding of the genetic relationships among the QPM inbred lines, effective utilization of these lines in breeding programs for the development of varieties, the formation of heterotic populations and exploitation of heterosis.

3.2 Introduction

QPM breeding began with the objective of improving the nutritional value of maize grain protein. Normal maize is deficient in two essential amino acids: lysine and tryptophan (Bhatia and Rabson, 1987). Unfortunately, millions of people worldwide are overly dependent on maize as a staple food. This nutritional deficiency is of concern, particularly for people with high protein requirements, e.g. young children, pregnant or lactating women, and the ill, in countries where maize is a staple food and often a significant source of protein. QPM contains the *o2* mutation, which alters protein composition of the maize endosperm, resulting in increased concentrations of lysine and tryptophan (Mertz et al., 1964). Consumption of QPM may help alleviate human malnutrition problems in regions with maize based diets (NRC, 1988; Bressani, 1992; Mertz, 1992) because of the 60 to 100% increase in concentration of the two essential amino acids (Bressani, 1992). In Africa, where malnutrition is a common phenomenon, emphasis has been given to the development of elite QPM germplasm, and consequently, to increase its cultivation in several countries on the continent. Elite QPM inbred lines well adapted to eastern and southern African regions are being developed by CIMMYT-Zimbabwe. These inbred lines are available to national programs and to other private and public research organizations to help QPM hybrid development efforts.

Knowledge on the genetic diversity and relationships among maize inbred lines is indispensable to identify promising combinations for exploitation of heterosis and establishment of heterotic groups for use as source materials in a breeding program. The efficiency of a hybrid breeding program could be increased if the inbred lines *per se* could be screened for genetic diversity. Phenotypic descriptors and molecular markers have been widely used in crop diversity studies to measure genetic distances. Molecular markers are a powerful tool to delimit heterotic groups and to assign inbred lines into existing heterotic groups (Melchinger, 1999; Menkir et al., 2004). Unlike morphological markers, molecular markers are not influenced by environmental factors and are also fast, efficient and more sensitive than field testing to detect large numbers of distinct differences between genotypes at the DNA level (Melchinger, 1999). Molecular markers can usually be identified from any

plant tissue, even from young seedlings or kernels, while morphological markers frequently require the observation of whole, mature plants. Selection can therefore occur earlier in the plant's cycle when using molecular markers than when using morphological markers (Ragot and Lee, 2007).

Simple sequence repeats (SSRs) or microsatellites have become the marker of choice in maize, almost entirely displacing restriction fragment length polymorphisms (RFLPs) and previously developed polymerase chain reaction (PCR) based marker systems (Ragot and Lee, 2007). SSR markers have several advantages (Edwards and McCouch, 2007). SSR markers are co-dominant; the heterozygous state can be discerned from the homozygous state. The markers are easily automated using florescent primers on an automated sequencer and it is possible to multiplex (combine) several markers with non-overlapping size ranges on a single electrophoresis run. SSR loci have proven to be highly polymorphic and useful as genetic markers in many plant species (Smith et al., 1997). The SSR markers offer advantages in reliability, reproducibility, discrimination, standardization, and cost effectiveness over other marker types (Smith et al., 1997; Melchinger, 1999).

In maize, SSRs have proved to be a valuable tool for genome mapping (Taramino and Tingey, 1996), population and conservation genetics studies (Powell et al., 1996), property right protection (Kubik et al., 2001), marker assisted selection (Weising et al., 1998; Edwards and McCouch, 2007) and diversity measurements (Warburton et al., 2002; Pinto et al., 2003; Bantte and Prasanna, 2003; Legesse et al., 2007). SSRs can provide greater power of discrimination than other marker types and can reveal genetic associations that are reflective of the pedigree of the inbred lines (Smith et al., 1997; Pejic et al., 1998). SSR markers have the power of distinguishing between closely related inbred lines (Smith et al., 1997; Legesse et al., 2007). They have also proved useful for designation of lines into heterotic groups (Enoki et al., 2002). Using SSR markers, Warburton et al. (2002) and Xia et al. (2004; 2005) observed a very large amount of genetic diversity within a group of CIMMYT maize inbred lines, indicating that each heterotic group assigned on the basis of testcross data would contain very diverse materials.

Although currently available elite QPM inbred lines have been tested in hybrid combinations with selected lines and testers, a systematic study aimed at classifying the lines into different heterotic groups has not been done. Such information would be useful in the development of inbred lines and the generation and evaluation of maize hybrids and open-pollinated synthetic varieties (Menkir et al., 2004). Therefore, the objectives of this study were to (i) assess the extent of phenotypic and genotypic variability, phenotypic correlation, heritability (broad sense) and expected genetic advance, (ii) assess genetic diversity and relationships among elite QPM inbred lines using morphological data and SSR markers, and (iii) classify and identify groups of similar inbred lines by means of cluster analysis based on morphological data and SSR markers.

3.3 Materials and methods

Description of the experimental sites and field procedures

The field experiments were conducted at CIMMYT-Harare Research Station (here after referred to as Harare), Zimbabwe during the 2006/07 cropping season and at Bako Agricultural Research Center (here after referred to as Bako), Ethiopia in 2007. The locations represent sub-humid mid-altitude maize growing mega-environments of sub-Saharan Africa (Hartkamp et al., 2000). Harare lies at 17°8'S latitude, 31°05'E longitude at an altitude of 1489 m above sea level (masl). The soil is reddish brown clay (nitosol) with a pH ($CaCl_2$) of 5.2 and 5.4 for top soil (0 - 30) and sub-soil (30 - 60), respectively. The location received a total precipitation of 630 mm, and an average maximum and minimum temperature of 27.7°C and 16.1°C, respectively, during the growing season (November 2006 to March 2007). However, the long-term total annual rainfall is 890 mm, and average minimum and maximum temperatures are 26.8°C and 14.2°C, respectively. The site at Bako lies between 9°06' N latitude and 37°09' E longitude at an altitude of 1650 masl. The soil of the centre is reddish brown clay (nitosol) with pH (H_2O) of 6.0 and 5.9 for top soil (0 - 30) and sub-soil (30 - 60), respectively. The total precipitation during the growing season (May to November 2007) was 975 mm, and the mean minimum and maximum temperatures were 28.1°C and 14.0°C, respectively. The long term total annual rainfall is 1245 mm, with mean, minimum and maximum temperatures of 13.5 °C and 28°C, respectively.

The experiments were planted in an alpha-lattice design (Patterson and Williams, 1976) with two replicates at each location. Though the number of replications used was small, the efficiency of alpha-lattice design increases precision of the experiment. The plots were over sown with two seeds per hill every 25 cm at Harare and every 30 cm at Bako in one row of 4.0 m (Harare) and 4.8 m (Bako) in length spaced 75 cm apart. The plots were later thinned to the desired plant densities of 53 333 and 44 444 plants ha^{-1} at Harare and Bako, respectively. At Harare, nitrogen (N), phosphate (P_2O_5) and potassium (K) were basal applied before planting at rates of 28, 56 and 24 kg ha^{-1}. Additional N was applied at 28 and 56 days after emergence each at a rate of 69 kg ha^{-1}. Pre-emergence herbicides, Atrazine (4.0 l ha^{-1}) and Dual (1.8 l ha^{-1}), were applied at planting to control the weeds. Then, the weeds were controlled by hand weeding. At six weeks after emergence, Dipterex granules (3.5 kg ha^{-1}) were applied to control stalk borer (*Busseola fusca*). The experiment at Bako received 100 kg ha $^{-1}$ P_2O_5 at planting and 100 kg ha^{-1} N in two splits, half at planting and the rest 37 days after emergence. Pre-emergence herbicide, Lasso-Atrazin (5.0 l ha^{-1}) was applied at planting to control weeds; and then the weeds were controlled by hand weeding. The experiment at Harare was irrigated to field capacity at planting using sprinkler irrigation. Thereafter, the trial was irrigated to field capacity whenever soil moisture was less than 40% of field capacity as analysed gravimetrically. However, at Bako the experiment was grown exclusively under rain fed conditions.

Plant materials

Thirty-two white grained tropical mid-altitude QPM inbred lines and three white grained normal maize inbred line checks (CML395, CML444 and CML197) were obtained from CIMMYT-Zimbabwe (Table 3.1). The lines were developed by pedigree breeding with evaluation of top-cross performances under stress and non-stress conditions of eastern, central and southern African regions and are adapted to tropical and subtropical environments. The lines also showed good combining ability and agronomic performance across a range of environments.

Morphological characterization

Seventeen morphological and agronomic traits were recorded in each plot based on maize descriptors of IBPGR (International Board for Plant Genetic Resource) and CIMMYT (1991) (Table 3.2).

DNA extraction

Seedlings of the 35 inbred lines were raised in the greenhouse at the ARC-Grain Crops Institute, Potchefstroom, South Africa. Leaves of each of the 35 inbred lines were harvested from 15 three-week old plants and freeze-dried. Equal amounts of freeze-dried leaf material from 15 plants of the same inbred line were bulked and ground to a fine powder using a Tissue-lyzer (QIAGEN, GmbH, Hilden, Germany). Genomic DNA was isolated using the CTAB (hexadecyltrimethylammonium bromide) procedure according to the Applied Biotechnology Center's Manual of Laboratory Protocols (CIMMYT, 2005a). Briefly, about 50 mg of leaf tissue was sampled into a 2 ml screw-cap micro-centrifuge tube and 750 µl pre-warmed (65^{o}C) CTAB extraction buffer was added. The leaf tissue and extraction buffer were thoroughly mixed by gently inverting the tube and then incubated at 65^{o}C for 60 min, with continuous gentle rocking. After incubation, 500 µl chloroform-isoamyl alcohol (24:1 v/v) was added followed by centrifugation for 10 min at 1300 rpm. Thereafter the DNA was precipitated by adding cold absolute ethanol. The precipitate was spooled and washed twice in 70% ethanol. The pellets were air dried and re-suspended in 100 µl TE (10 mM Tris-HCl, pH 8.0 and 0.2 mM EDTA). The concentrations were determined using a NanoDrop spectrophotometer (NanoDrop Technologies, Wilmington, Delaware, USA) and the DNA was diluted to working concentrations of 25 ng/µl.

Table 3.1 List of maize inbred lines used for morpho-agronomic characterization

Line No.	Name	Pedigree	Adaptation
1	VL06386	(CLQRCWQ50/CLQRCWQ26)-B-47-B-B-1-B	Tropical
2	VL06375	(CLQRCWQ50/CML312SR)-2-2-1-B-1-B	Subtropical
3	VL052	[CML141/[CML141/CML395]F2-1sx]-4-2-1-B*4-1-B	Tropical/Subtropical
4	VL058	[CML144/[CML144/CML395]F2-8sx]-1-1-1-B*4-1-B	Tropical/Subtropical
5	VL05200	[CML144/[CML144/CML395]F2-8sx]-1-2-3-2-B*4-1-B	Tropical/Subtropical
6	VL05206	[CML144/[CML144/CML395]F2-9sx]-3-1-2-2-B*4-1-B	Tropical/Subtropical
7	VL05466	[CML144/SNSYNF2[N3/TUX-A-90]-102-1-2-2-BSR-B*4]-B-2-6-B*4-1-B	Tropical
8	VL05468	[CML144/SNSYNF2[N3/TUX-A-90]-102-1-2-2-BSR-B*4]-B-4-3-B*4-1-B	Tropical
9	VL05575	[CML150/CML373]-B-2-2-B*4-1-B	Tropical/Subtropical
10	VL054178	[CML159/[CML159/[MSRXPOOL9]C1F2-205-1(OSU23i)-5-3-X-X-1-BB]F2-3sx]-8-1-1-B-B-B-4-B	Tropical
11	VL052887	[CML181/[CML181/[MSRXPOOL9]C1F2-174-1(OSU31ss)-1-7(I)-X-X-1-B]F2-2sx]-1-3-3-1-B-B	Subtropical
12	VL05482	[CML182/TZMI703]-B-9-1-BB-#-B-2-B	Subtropical
13	VL0523	[CML202/CML144]F2-1-1-3-B-1-B*5-2-B	Tropical/Subtropical
14	VL0524	[CML205/CML176]-B-2-1-1-2-B*4-1-B	Tropical/Subtropical
15	CML511	[CML389/CML176]-B-29-2-2-B*5	Subtropical
16	VL0512464	[CML445/CML176]-B-22-2-1-B-1-B	Subtropical
17	VL05561	[GQL5/[GQL5/[MSRXPOOL9]C1F2-205-1(OSU23i)-5-3-X-X-1-BB]F2-4sx]-11-3-1-1-B*4-1-B	Tropical
18	VL0556	[GQL5/[GQL5/CML202]F2-3sx]-11-4-1-1-B-B-B	Tropical/Subtropical
19	VL0557	[GQL5/[GQL5/CML202]F2-3sx]-11-4-2-2-B*4	Tropical/Subtropical
20	VL05483	[TZMI703/CML176]-B-3-2-B*4-1-B	Subtropical
21	CML502	CLQRCWQ50-B-B-2-B	Tropical
22	CML144	Pob62c5HC182-2-1-2-B-B-3-1-#-#	Tropical
23	CML159	Pob63c2HC5-1-3-1-B-2-1-1-B-#-#	Tropical
24	CML176	(P63-12-2-1/P67-5-1-1)-1-2-B-B	Subtropical
25	CML181	UWO417-B-2-1-1-B-B	Subtropical
26	CML182	WOMTA1-B-1-1-1-B-B	Subtropical
27	CML503	(CML176*CML264)-BxCML264)-7-1xCML264]xCML264-F2(65)-B*4	Tropical
28	CML491	(6207QB/6207QA)-1-4-#-2-2-B-B	Tropical
29	CML492	P62C3HC163-3-3-3-2-#-1-1-2-B-B	Tropical
30	VL05119	GQL5	Tropical
31	VL05101	S99TLWQ-B-8-1-B*4-3-B	Tropical/Subtropical
32	VL05128	WWO1408-1-1-2-B*4-#	Tropical/Subtropical
33[a]	CML395	90323(B)-1-B-1-B*4	Subtropical
34[a]	CML444	P43C9-1-1-1-1-1-B*4	Subtropical
35[a]	CML197	MSR270-2S3-5-1-B-B	Subtropical

[a]Inbred lines no. 33 to 35 are normal maize (non-QPM)

Table 3.2 List of morpho-agronomic traits, abbreviations used and trait description

No	Abbre-viation	Trait	Units	Trait description
1	GY	Grain yield	Tons per Hectare (t ha^{-1})	The total grain yield from all the ears of each experimental unit; moisture level was adjusted to 12.5% to estimate grain yield per hectare
2	AD	Days to anthesis	Days (d)	The number of days from planting to when 50% of the plants in a plot shed pollen
4	ASI	Anthesis-silking interval	d	Number of days between anthesis and silking dates; where, silking date is number of days from planting to when 50% of the plants had emerged silks
5	PH	Plant height	Centimetres (cm)	The height from the soil surface to the base of the tassel branching; the measurement was made two weeks after pollen shedding has ceased
5	EH	Ear height	(cm)	The height from the ground level to the upper most ear-bearing node; like ear height, it was measured two weeks after pollen shedding ceased
6	PA	Plant aspect	1-5	Overall phenotypic appearance of the plant; where 1= excellent and 5= poor
7	ED	Ear diameter	cm	Measured at the mid-way along ear length, as the average diameter of 10 randomly taken ears
8	EL	Ear length	cm	Length of the ear from the base to tip; it was measured as the average length of ten randomly sampled ears from each experimental unit
9	TKW	Thousand kernel weight	Grams (g)	After shelling, random kernels from the bulk of each experimental unit was counted using a photoelectric seed counter and weighed in grams after the moisture was adjusted to 12.5%.
10	RPE	Number of rows per ear	Number (No.)	This was recorded as the average number of kernel rows per ear from the 10 randomly sampled ears
11	KPR	Number of kernels per row	No.	Recorded as the average number of kernels per row from the 10 randomly taken ears
12	LL	Leaf length	cm	Length of the leaf from ligule to apex; the measurement was taken after flowering from the leaf that subtends the uppermost ear
13	LW	Leaf width	cm	Measurement was taken from the same leaf as leaf length at mid-way along its length
14	LA	Leaf area	Square cm (cm^2)	Area of the upper most ear leaf computed as maximum width x length x 0.75 (Montgomery, 1911)
15	TS	Tassel size	3, 5 or 7	Recorded after milk stage as 3 (small), 5 (medium) and 7 (large)
16	LO	Leaf orientation	1-3	Recorded after flowering as 1 (erect), 2 (intermediate) and 3 (pendant)
17	FR	Foliage rating	3, 5 or 7	Rating of total leaf surface after milk stage as 3 (small), 5 (intermediate) and 7 (large); and the observation was made on 10 randomly selected plants in a plot.

SSR analysis and data collection

The 40 SSR markers used in this study were selected from previous studies (Smith et al., 1997; Senior et al., 1998; Warburton et al., 2002) and from the public maizeGDB database (http://www.agron.missouri.edu/ssr_probes/ssr.htm) based on repeat unit and bin location to provide a uniform coverage of the entire maize genome. Fluorescently labelled SSR primers were multiplexed in polymerase chain reactions (PCRs) for maximum efficiency. PCR reactions were set up in a total volume of 10 µl containing 25 ng template DNA, 0.05 - 0.2 µM each of forward and reverse primers (amount varied according to activity of the primer), and 2x Taq Mastermix (Promega Corporation). The 2x Taq Master Mix is a premixed, ready-to-use solution containing Taq DNA polymerase, dNTPs, $MgCl_2$ and reaction buffers at optimal concentrations for efficient amplification of DNA templates by PCR. The PCR Master Mix has been optimized for use in routine PCR for amplifying DNA templates.

The PCR amplification was performed in a MBS 384-well thermal cycler (Thermo Electron Corporation, Somerset, NJ). The amplification protocol consisted of an initial denaturation cycle at 94°C for 1 min, followed by 10 cycles at 94°C for 1 min, at 65°C to 55°C by decreasing 1°C each cycle for 1 min, and at 72°C for 90 sec. This was followed by 30 cycles of 1 min at 94°C, 1 min at 55°C and 72°C for 90 sec. A final extension of 72°C for 5 min was followed by a hold step at 4°C. The PCR products were diluted in sterile water at a ratio of 1:25 and 1 µl of diluted PCR products were added to a mix of 9 µl Hi-Di Formamide and 0.15 µl size standard (Genescan LIZ 500) in the wells of a 384-well microtitre plate. The samples were denatured at 94°C for 3 min in a PCR machine, and then immediately cooled on ice. PCR products were subsequently fractionated on an ABI 3130xl Genetic Analyser (PE Applied Biosystems, Foster City, Calif.). Capillary electrophoresis was carried out at an oven temperature of 60°C in POP-7 polymer using dye set G5. Samples were injected at 1.2 kV for 23 sec and run at 15 kV for 20 min.

The electropherograms were analysed with Genemapper 4.0 software (PE Applied Biosystems, Foster City, Calif.). Bands were coded as present (1) or absent (0) for all the genotypes. A matrix of binary data was constructed with rows equal to number of inbred

lines and columns equal to SSR marker alleles. The body of the matrix was filled in with zeros and ones, for absence and presence of the fragments for each inbred line, respectively.

Statistical analysis

Data of morpho-agronomic traits were analyzed using the PROC MIXED procedure of SAS (SAS, 2003) with inbred lines being considered as fixed effects and replications and blocks within replications as random effects. Lattice-adjusted inbred line means, for statistically significant traits, were used to conduct across location analysis of variance using PROC GLM procedure of SAS (SAS, 2003) using a RANDOM statement with TEST option. The F test for environment and line main effect mean squares were tested against line x location interaction mean squares. Mean squares attributable to environment x line interaction were tested using pooled error mean squares. Pearson phenotypic correlation coefficients were calculated among all traits to determine the relationships between the traits. Phenotypic similarity of genotypes was estimated using cluster analysis.

Variance components were estimated to identify genetic variability among genotypes and determine genetic and environmental effects on various characters. Error (σ_e^2), genotypic (σ_g^2) and phenotypic (σ_p^2) variances were calculated from expected mean squares of analysis of variance by adapting the formula suggested by Hallauer and Miranda (1988), and Singh and Chaudhary (1985). The standard errors of estimates of error and genotypic variance components were estimated following the methods given by Hallauer and Miranda (1988), and Wricke and Weber (1986).

- Error variance, $\sigma_e^2 = MS_e$, where MS_e= mean square of error
- Genotypic variance, $\sigma_g^2 = (MS_g - MS_e)/r$, where MSg= mean square of genotype (in this case genotype represent the inbred line used), MS_e= mean square of error, and r= number of replications
- Phenotypic variance, $\sigma_p^2 = \sigma_e^2 + \sigma_g^2$, where σ_e^2 = error variance and σ_g^2 = genotypic variance

- Genotypic coefficient of variation, GCV= $\left(\sqrt{\sigma_g^2}/X\right)\times 100$, where σ_g^2= genotypic variance and *X*= mean of the trait
- Phenotypic coefficient of variation, PCV= $\left(\sqrt{\sigma_p^2}/X\right)\times 100$, where σ_p^2= phenotypic variance and *X*= mean of the trait
- Heritability (broad sense), H^2= σ_g^2/σ_p^2, where σ_g^2= genotypic variance and σ_p^2= phenotypic variance
- Genetic advance (GA) and genetic advance as percent of mean (GAM) were estimated as devised by Johnson (1955), that is, GA = $k\sigma_p H^2$, where σ_p= the phenotypic standard deviation of the character, H^2= heritability estimate and k = the standardized selection differential at 5 % selection intensity (2.063); and GAM= (GA/*X*) × 100, GA = genetic advance, and *X*= mean for the trait
- Standard error (SE) of estimates of error variance= $\sqrt{2(MS_e)^2/df_e+2}$, MS_e= mean square of error and df_e= error degrees of freedom
- Standard error (SE) of estimates of genotypic variance component= $\sqrt{\frac{2}{r^2}\left[(MSg^2/df_g+2)+(MS_e{}^2/df_e+2)\right]}$, where MS_g= mean square of genotype, df_g= genotype degrees of freedom, MS_e= mean square of error and df_e= error degrees of freedom

The importance of different traits in explaining multivariate variation was assessed using principal component analysis (PCA) (Upadhyaya et al., 2004; Yoseph et al., 2005). In order to reduce the influence of outliers and scale the differences during cluster and PC analysis, the mean observations for each line were standardized by subtracting from each observation the mean value of the trait and subsequently dividing by its respective standard deviation (Hamza et al., 2004; Upadhyaya et al., 2004; Liu et al., 2007). This resulted in standardised values for each trait with average zero and standard deviation of one or less. The standardised values were used to perform PC and cluster analysis.

During PC and cluster analyses, 35 lines were used as rows and 17 morpho-agronomic traits were taken as variables by column. PC and cluster analyses were performed using Number Cruncher Statistical System, NCSS 2000 (Hintze, 1998). The unweighted pair group method with arithmetic averages (UPGMA) of cluster analysis was used to construct the dendrogram of inbred lines based on the Euclidean distance matrix.

For SSR markers, Euclidean distances were calculated between each pair of inbred lines using the Number Cruncher Statistical System, NCSS 2000 (Hintze, 1998). A dendrogram was constructed from the distance matrix using the unweighted pair group method with the arithmetic averages (UPGMA) method of cluster analysis. The goodness of fit of the dendrogram was confirmed by cophenetic correlation. To estimate the discriminatory power of each SSR primer, the polymorphic information content (PIC) was calculated according to Smith et al. (1997) as:

$$\text{PIC}= 1-\sum_{1}^{n} f_i^2$$

where f_i is the frequency of the i^{th} allele in the set of inbred lines analyzed. PIC values provide an estimate of the discriminatory power of a locus by taking into account, not only the number of alleles that are expressed, but also the relative frequencies of those alleles (Smith et al., 1997). PIC values can range from 0 (monomorphic) to 1 (highly discriminative). Correlations between genetic distance values generated from morphological and SSR marker data were determined using statistical package for social scientists (SPSS, 2002).

3.4 Results

Analysis of variance showed significant differences among the lines for all 17 morpho-agronomic traits at each location (Table 3.3). Considerable variability exists among the lines as was revealed by big differences between minimum and maximum values (Figure 3.1 and Table 3.3). A large proportion of the inbred lines gave higher yield and had earlier anthesis at Harare than at Bako (Figure 3.2). On average, the inbred lines yielded about 47% higher and 10 days earlier in anthesis at Harare compared to Bako.

Figure 3.1 Partial views of QPM inbed lines studied for morpho-agronomic variability

Table 3.3 Mean, standard error of the mean [SE(m)], range, F-test and coefficient of variation (CV) of 17 morpho-agronomic traits of maize inbred lines evaluated at Harare and Bako, 2006 and 2007

Trait†	Harare				Bako			
	Mean ± SE(m)	Range	F test	CV(%)	Mean ± SE(m)	Range	F test	CV(%)
GY	3.6 ± 0.70	1.6 - 7.8	**	27.5	2.46 ± 0.44	1.6 - 4.5	*	25.1
DA	77.6 ± 1.44	69.0 - 84.0	**	2.6	87.5 ± 1.94	80.0 - 99.6	**	3.1
ASI	0.0 ± 1.17	-3.5 - 7.5	**	-	2.1 ± 0.56	0.0 - 5.0	**	38.8
PH	174.9± 15.22	130.0 - 242.5	**	12.3	153.2± 8.04	118.9 - 192.2	**	7.4
EH	83.4± 9.73	53.2 - 106.6	*	17.3	70.6± 6.07	41.0 - 103.6	**	12.2
PA	2.5± 0.27	1.3 - 3.7	**	15.0	2.6 ± 0.23	2.0 - 4.3	**	12.6
ED	4.0± 0.14	3.6 - 4.6	**	5.1	3.7 ± 0.11	2.9 - 4.7	**	4.1
EL	12.9± 0.44	10.0 - 15.3	**	4.8	10.9 ± 0.95	7.3 - 13.9	*	12.3
TKW	217.0± 13.48	134.1 - 302.9	**	8.8	222.3± 23.71	112.0 - 359.3	**	15.1
RPE	14.0± 0.48	11.2 - 17.0	**	4.9	13.3 ± 0.81	6.6 - 15.9	**	8.6
KPR	26.7± 1.22	19.1 - 33.2	**	6.5	23.7 ± 1.39	15.1 - 30.0	**	8.3
LL	78.5± 2.19	90.8 - 1.0	**	3.9	76.3 ± 1.92	61.5 - 99.5	**	3.6
LW	9.7± 0.42	7.8 - 12.2	**	6.2	10.2 ± 0.27	8.5 - 12.7	**	3.7
LA	574.5± 36.75	401.7 - 831.7	**	9.0	584.6 ± 26.07	398.9 - 923.4	**	6.3
TS	5.0± 0.41	3.0 - 6.4	**	11.7	4.5 ± 0.36	3.1 - 6.6	**	11.2
LO	1.8± 0.34	1.0 - 3.0	**	27.0	1.9 ± 0.34	1.0 - 3.0	**	25.2
FR	4.9± 0.41	3.1 - 6.5	**	11.8	4.9 ± 0.40	3.5 - 6.5	**	11.6

† Abbreviations as explained in Table 3.2; * $P \leq 0.05$; ** $P \leq 0.01$

Combined analysis of variance over the two locations indicated effects of location and line to be significant for almost all traits whereas environment x line interaction was significant only for a few traits, namely, days to anthesis, number of kernels per row, leaf length, width and area and foliage rating (Table 3.4). Table 3.5 shows the mean performance of the studied lines over two locations (Harare and Bako). The highest grain yield (5.9 t ha^{-1}) was observed for the normal maize inbred line check, CML444 followed by QPM inbred lines, VL06375 (4.5 t ha^{-1}) and VL06386 (4.3 t ha^{-1}). CML444 is a vigorous line released by CIMMYT and it is characterized by good general combing ability, and tolerance to drought and low nitrogen stress. CML444 also showed higher yield components such as ear diameter and length, thousand kernel weight, number of rows per ear and number of kernels per row but later in anthesis and taller in plant stature. Generally, QPM inbred lines were lower in yield and yield components, earlier in anthesis, and shorter in stature as compared to the normal maize line checks (CML395, CML444 and CML197). All the lines evaluated in this experiment showed acceptable levels of anthesis-silking interval except CML197, which surprisingly exhibited the highest value of 6.2 days. Lines with closely related pedigree records, VL05206, CML144 and VL05200, exhibited larger leaf area. CML182, CML492 and CML176 had small tassel size while CML197 showed the largest.

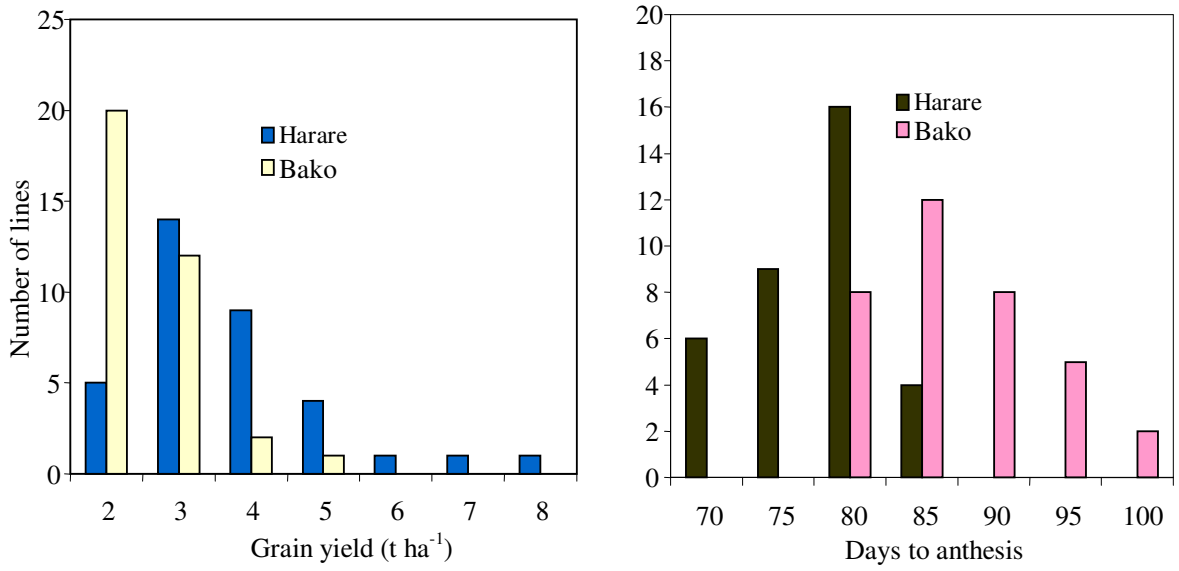

Figure 3.2 Frequency distribution of 35 maize inbred lines for grain yield and days to anthesis at Harare and Bako, 2006 and 2007

Table 3.4 Combined analysis of variance for 17 morpho-agronomic traits of maize inbred lines evaluated at Harare and Bako, 2006 and 2007

Trait†	Environment (df=1)	Line (df=34)	Environment x Line (df=34)	Error (df=44)
GY	23.6**	1.7*	0.8	0.68
DA	1732.0**	35.0**	12.0*	5.85
ASI	74.7**	3.6*	1.9	1.69
PH	8221.1**	774.6**	317.2	296.43
EH	3802.2**	256.4*	131.2	209.83
PA	0.1	0.4**	0.1	0.13
ED	1.1**	0.2**	0.0	0.03
EL	64.5**	3.1**	0.9	1.10
TKW	480.5	3283.8**	1089.6	743.73
RPE	8.6**	3.7**	1.1	0.89
KPR	156.0**	16.1*	7.2**	3.42
LL	84.5*	112.4**	16.0*	8.49
LW	3.2*	1.7**	0.7**	0.25
LA	1800.4	14159.0**	5183.8**	2029.94
TS	3.3**	0.9**	0.3	0.30
LO	0.5	0.5**	0.2	0.23
FR	0.0ns	1.1*	0.5*	0.33

† Abbreviations are as explained in Table 3.2; * $P \leq 0.05$; ** $P \leq 0.01$

Grain yield had positive and significant correlations with plant and ear height, ear diameter and ear length, thousand kernel weight, number of kernels per row, leaf length, area and orientation, and foliage rating (Table 3.6). On the contrary, grain yield had a negative and highly significant association with plant aspect. Days to anthesis had highly significant positive correlation with leaf width and area, and foliage rating. Ear height showed strong positive correlation with plant height, ear diameter, thousand kernel weight, leaf area, tassel size and foliage rating. Plant aspect had negative and significant correlation with plant and ear height, and ear diameter and length but positive and strong correlation with number of kernels per row. Ear diameter had positive and significant correlation with thousand kernel weight and number of rows per ear. Ear length showed positive and significant correlation with thousand kernel weight and number of kernels per row. Leaf area had positive and significant correlations with leaf length and width. Foliage rating had strong positive correlations with leaf length, width and area.

Table 3.5 Mean performance of maize inbred lines for 17 morpho-agronomic traits evaluated at Bako and Harare, 2006 and 2007

Line no	Traits[†]																
	GY	DA	ASI	PH	EH	PA	ED	EL	TKW	RPE	KPR	LL	LW	LA	TS	LO	FR
1	4.3	76.1	1.8	189.7	75.0	2.5	3.8	12.0	218.7	14.6	26.1	70.3	9.6	506.7	4.6	1.5	4.7
2	4.5	79.5	1.2	198.3	77.7	2.2	3.5	13.3	258.7	12.9	26.4	90.9	9.5	647.7	4.7	2.3	5.2
3	2.5	87.9	1.3	184.8	87.5	2.6	4.1	12.7	251.7	13.6	25.2	77.1	11.2	645.4	4.2	1.3	5.2
4	3.3	87.0	-0.5	139.5	76.3	2.8	3.9	12.1	244.4	13.1	22.4	75.0	11.6	651.2	5.7	1.0	5.8
5	3.5	84.0	0.5	133.9	76.5	2.7	4.2	10.9	279.7	14.6	22.9	78.7	11.9	702.3	5.0	2.0	6.0
6	2.6	89.5	0.5	151.6	80.6	3.0	3.7	12.0	238.3	11.5	23.0	94.8	11.3	804.1	4.8	2.3	5.6
7	2.1	84.8	2.0	169.5	79.2	2.2	3.8	11.4	215.6	13.9	27.3	65.6	10.2	500.9	4.8	1.0	4.8
8	2.7	86.4	2.0	173.3	86.0	2.3	4.0	11.9	154.9	16.2	28.7	70.5	10.7	565.8	5.5	1.3	5.2
9	2.4	80.7	0.0	149.2	72.8	3.0	3.6	10.6	210.8	13.9	22.7	84.6	9.2	587.7	4.2	1.3	4.1
10	2.3	75.8	1.7	146.0	71.1	3.5	3.3	12.4	237.6	11.2	22.2	63.7	8.6	411.6	4.9	2.0	4.2
11	4.0	85.4	-0.4	177.4	84.5	2.7	3.8	9.1	157.1	10.2	19.6	84.3	10.8	701.6	4.8	2.6	5.6
12	2.7	76.8	1.0	131.3	54.9	2.6	3.6	12.6	192.6	11.1	27.7	70.8	9.7	512.8	3.9	1.5	3.9
13	3.1	86.6	0.5	174.1	94.8	2.0	3.6	11.9	213.8	11.9	27.8	68.6	11.0	568.8	5.6	2.0	5.2
14	2.3	87.3	1.7	174.5	85.0	2.3	3.7	11.7	238.2	11.5	24.8	70.0	10.8	566.9	4.7	1.8	5.1
15	3.2	78.3	0.0	185.5	80.3	2.9	4.1	10.5	212.2	13.9	26.3	74.7	9.8	549.4	4.9	1.8	4.3
16	2.3	85.0	1.3	189.6	77.7	2.0	3.7	13.0	217.8	13.2	26.2	75.1	9.2	517.1	4.8	1.5	4.5
17	3.9	82.6	-0.8	140.2	76.5	2.3	3.7	13.6	220.3	13.6	28.4	79.3	9.5	563.4	4.9	2.3	5.2
18	2.8	83.8	-0.7	146.4	80.8	2.6	3.7	11.3	167.6	14.0	28.7	82.1	9.7	600.1	5.2	1.5	5.3
19	3.1	83.5	0.0	140.8	68.5	2.9	3.8	11.6	185.6	14.1	27.8	74.5	9.5	527.5	5.1	2.0	5.2
20	4.1	77.1	0.8	184.3	83.8	1.7	4.2	11.4	206.8	15.3	27.0	75.0	8.7	489.6	4.1	2.0	4.8
21	2.1	82.2	2.2	189.9	78.5	2.7	3.6	11.2	170.1	14.2	21.6	74.0	8.8	489.5	5.8	1.0	4.0
22	3.9	85.4	-1.3	152.4	72.6	2.2	4.1	11.9	181.6	14.6	27.1	83.0	11.7	726.6	5.0	2.0	5.4
23	3.2	80.3	1.2	156.0	70.0	2.3	4.0	13.9	249.2	13.9	24.1	78.5	9.6	570.9	4.3	2.5	4.8
24	1.6	81.6	3.3	163.8	67.8	2.4	4.1	11.2	200.1	14.7	25.3	67.2	8.9	450.9	3.8	1.3	3.6
25	3.7	74.7	0.8	179.4	81.7	2.5	4.0	14.3	271.2	12.0	26.9	82.7	10.5	649.4	5.5	2.0	4.9
26	2.3	76.5	1.0	152.9	72.8	2.8	3.8	10.0	154.9	14.2	26.9	76.6	9.0	516.7	3.2	1.8	4.4
27	2.3	83.2	0.5	148.8	61.4	2.6	3.9	10.5	203.6	14.7	23.1	81.6	9.7	591.1	5.2	1.8	4.3
28	3.3	89.3	2.0	179.6	78.7	2.6	3.8	13.1	238.9	13.9	28.0	84.3	10.6	674.4	4.0	3.0	5.3
29	2.1	85.1	1.0	143.2	61.9	4.0	3.6	10.1	174.4	13.6	19.0	70.9	9.9	525.8	3.4	1.3	5.1
30	1.9	78.8	1.3	137.0	64.2	3.0	3.9	11.7	181.7	14.7	25.2	77.4	8.8	511.9	4.4	2.0	4.6
31	2.1	81.6	1.2	162.9	61.7	2.5	3.8	11.8	213.0	15.7	23.3	80.0	9.1	547.7	4.4	2.3	4.8
32	2.8	78.7	0.8	152.6	77.5	2.7	4.2	11.1	255.4	13.4	22.9	66.7	10.4	522.5	5.5	2.5	4.6
33	4.1	89.1	2.0	178.3	85.0	2.4	4.4	13.9	331.1	13.4	27.4	86.2	9.8	636.9	5.4	2.3	5.3
34	5.9	82.7	-0.5	194.1	100.8	1.8	4.5	14.4	268.6	14.8	30.4	87.5	10.0	655.1	4.0	2.0	5.4
35	3.5	82.2	6.2	171.0	91.2	2.6	4.3	11.2	271.7	14.9	20.1	86.3	9.2	593.7	6.0	2.8	5.4
Mean	3.0	82.6	1.0	164.0	77.0	2.6	3.9	11.9	219.7	13.6	25.2	77.4	10.0	579.5	4.7	1.9	4.9
Min	1.6	74.7	-1.3	131.3	54.9	1.7	3.3	9.1	154.9	10.2	19.0	63.7	8.6	411.6	3.2	1.0	3.6
Max	5.9	89.5	6.2	198.3	100.8	4.0	4.5	14.4	331.1	16.2	30.4	94.8	11.9	804.1	6.0	3.0	6.0
$LSD_{0.05}$	1.2	3.4	1.9	24.5	21.2	0.5	0.3	1.5	38.9	1.3	2.6	4.2	0.7	64.2	0.8	0.7	0.8
CV(%)	27.3	2.9	127.6	10.5	18.8	13.9	4.6	8.8	12.4	6.9	7.3	3.8	5.0	7.8	11.5	26.1	11.7

[†] Abbreviations are explained in Table 3.2; Names of the lines are given in Table 3.1; CV(%)= coefficient of variation; LSD= least significant difference; Min= minimum; Max= maximum

In most cases, error variances (σ_e^2) were higher for Harare whereas genotypic variances (σ_g^2) were higher for Bako (Table 3.7). All variance components were significantly greater than the respective standard errors for most traits, except for ear diameter. Most of the traits showed higher values of σ_g^2 than σ_e^2 for both locations. Traits with higher data values had larger values of variance components.

The levels of variability apparent among the lines were assessed based on the genetic and phenotypic coefficient of variation (Table 3.8). The highest genotypic coefficient of variation (GCV) was determined for grain yield (33.6%) and the lowest for days to anthesis (5.2%) at Harare. At Bako, genotypic coefficient of variation was highest (46.8%) for anthesis-silking interval and lowest (4.1%) for ear diameter. The phenotypic coefficient of variation (PVC) ranged from 5.8% for days to anthesis to 43.4% for grain yield at Harare, and from 5.8% for ear diameter to 60.9% for anthesis-silking interval at Bako. In general, traits with higher phenotypic coefficients of variation showed higher genetic coefficients of variation.

Broad sense heritability (h^2) for 17 morpho-agronomic traits calculated using 35 maize inbred lines ranged from 0.26 for ear height to 0.84 for leaf length at Harare and from 0.39 for ear length to 0.89 for leaf length at Bako (Table 3.8). Results indicated that most characters were highly heritable. At both locations, most traits showed heritability greater than 0.50, except plant (0.48) and ear (0.26) height, and leaf orientation at Harare and grain yield, ear diameter and length. Traits with high heritability (>0.60) at both locations were days to anthesis, thousand kernel weight, number of rows per ear, number of kernels per row, leaf length, width and area.

Genetic advance (GA) as percent of the mean that could be expected from selecting the top 5% of the lines, varied from 8.1% for ear diameter to 53.5% for grain yield at Harare (Table 3.9). At Bako, expected genetic advance ranged from 5.8% for ear diameter to 74.4% for anthesis silking interval (Table 3.8). Traits with high expected genetic advance values were grain yield, anthesis silking interval, plant aspect, thousand kernel weight, leaf area and leaf

orientation. On the other hand, days to anthesis, ear diameter and length had lower values of genetic advance expressed as percent of the mean.

The principal component analysis computed using the correlation matrix grouped the 17 traits into 17 components, which accounted for 100% of the variability existing among the lines evaluated. It was also shown that the first 10 principal components (PC) explained 93.3% of the total variation. Six of the eigenvectors which had eigenvalues greater than one accounted to a cumulative of 78% of the entire variability available among the inbred lines (Table 3.9). The first PC which explained about 29.0% of the variation among genotypes was mainly attributed to variation in leaf area, grain yield, foliage rating, ear height, thousand kernel weight, leaf length and width. In the second PC (16.0%), plant aspect, leaf area and width, plant height and number of kernels per row were the most important traits. The third PC, which accounted for 9.9% of the total variation, was dominated by traits such as anthesis-silking interval, thousand kernel weight, tassel size, number of kernel per row. Leaf orientation, days to anthesis, ear height, leaf length and width were important delineating traits associated with the fourth PC, which accounted for 9.2% of the total variation. The fifth PC which explained 7.9% of the total variation was associated with variation due to tassel size, number of rows per ear, leaf length, ear length and diameter. Each trait was found to be an important source of variation in the PCA. Traits such as thousand kernel weight, leaf length and width contributed to variation in three of the first five PC's. Similarly, ear height, number of kernels per row, leaf area and tassel size contributed to two of the first five PCs.

Table 3.6 Phenotypic correlation coefficients among 17 morpho-agronomic traits of maize inbred lines evaluated at Bako and Harare, 2006 and 2007

Trait†	AD	ASI	PH	EH	PA	ED	EL	TKW	RPE	KPR	LL	LW	LA	TS	LO	FR
GY	-0.05	-0.27	0.38*	0.53**	-0.47**	0.40*	0.44**	0.42*	0.00	0.35*	0.47**	0.22	0.45**	0.13	0.42*	0.50**
AD		-0.04	0.05	0.33	-0.09	0.12	0.03	0.11	-0.06	-0.02	0.25	0.58**	0.54**	0.19	0.00	0.59**
ASI			0.27	0.08	0.04	0.15	0.00	0.24	0.18	-0.26	-0.15	-0.35*	-0.33	0.09	0.08	-0.23
PH				0.62**	-0.51**	0.21	0.25	0.22	0.06	0.22	0.15	-0.08	0.05	0.07	0.05	-0.01
EH					-0.48**	0.39*	0.23	0.36*	-0.06	0.25	0.23	0.33	0.35*	0.35*	0.17	0.48**
PA						-0.38*	-0.43*	-0.18	-0.21	0.61**	-0.11	-0.09	-0.12	-0.13	-0.10	-0.11
ED							0.14	0.43*	0.47**	0.15	0.21	0.21	0.26	0.09	0.20	0.23
EL								0.60**	-0.05	0.54**	0.23	0.03	0.16	0.08	0.21	0.15
TKW									-0.12	0.02	0.30	0.22	0.32	0.25	0.36*	0.32
RPE										0.20	0.01	-0.24	-0.18	-0.07	-0.14	-0.06
KPR											0.01	0.01	-0.02	-0.11	-0.03	0.01
LL												0.16	0.78**	0.04	0.47**	0.46**
LW													0.74**	0.26	0.05	0.68**
LA														0.17	0.36*	0.74**
TS															0.07	0.30
LO																0.36*

† Abbreviations are as explained in Table 3.2; * $P \leq 0.05$; ** $P \leq 0.01$

Table 3.7 Estimates of components of variances and their standard errors of 17 morpho-agronomic traits of maize inbred lines evaluated at Harare and Bako, 2006 and 2007

	Harare			Bako		
Trait[†]	$\sigma_e^2 \pm$ SE	$\sigma_g^2 \pm$ SE	$\sigma_p^2 \pm$ SE	$\sigma_e^2 \pm$ SE	$\sigma_g^2 \pm$ SE	$\sigma_p^2 \pm$ SE
GY	0.99 ± 0.29	1.47 ± 0.48	2.46 ± 0.72	0.38 ± 0.11	0.26 ± 0.12	0.64 ± 0.12
DA	4.14 ± 1.19	16.17 ± 4.34	20.31 ± 4.48	7.56 ± 2.18	20.64 ± 5.86	28.20 ± 5.86
ASI	2.74 ± 0.79	2.89 ± 1.08	5.63 ± 1.40	0.63 ± 0.18	0.92 ± 0.31	1.56 ± 0.31
PH	463.49 ± 133.80	421.77 ± 167.93	885.26 ± 168.33	129.37 ± 37.35	351.90 ± 99.95	481.27 ± 99.95
EH	345.92 ± 99.86	119.34 ± 85.09	465.27 ± 85.67	73.73 ± 21.28	124.23 ± 39.43	197.96 ± 39.43
PA	0.15 ± 0.01	0.17 ± 0.02	0.32 ± 0.11	0.11 ± 0.01	0.20 ± 0.01	0.30 ± 0.01
ED	0.04 ± 0.04	0.05 ± 0.06	0.09 ± 0.21	0.02 ± 0.03	0.02 ± 0.06	0.05 ± 0.06
EL	0.38 ± 0.11	1.41 ± 0.38	1.80 ± 0.51	1.81 ± 0.52	1.18 ± 0.56	2.99 ± 0.56
TKW	363.47 ± 104.93	1482.96 ± 395.87	1846.44 ± 396.00	1123.99 ± 324.47	1950.12 ± 613.93	3074.11 ± 613.93
RPE	0.47 ± 0.14	1.81 ± 0.49	2.28 ± 0.61	1.31 ± 0.38	2.15 ± 0.69	3.45 ± 0.69
KPR	2.99 ± 0.86	9.58 ± 2.65	12.57 ± 2.80	3.86 ± 1.12	8.77 ± 2.58	12.63 ± 2.58
LL	9.58 ± 2.77	49.82 ± 12.95	59.40 ± 13.05	7.39 ± 2.13	62.63 ± 15.67	70.02 ± 15.67
LW	0.36 ± 0.10	0.74 ± 0.22	1.10 ± 0.39	0.14 ± 0.04	1.08 ± 0.27	1.22 ± 0.27
LA	2700.53 ± 779.58	7183.42 ± 2048.83	9883.95 ± 2049.02	1359.34 ± 392.41	8258.01 ± 2115.75	9617.36 ± 2115.75
TS	0.34 ± 0.10	0.47 ± 0.16	0.80 ± 0.35	0.26 ± 0.07	0.45 ± 0.14	0.71 ± 0.14
LO	0.23 ± 0.07	0.21 ± 0.08	0.44 ± 0.27	0.24 ± 0.07	0.29 ± 0.10	0.53 ± 0.10
FR	0.33 ± 0.10	0.42 ± 0.15	0.75 ± 0.34	0.32 ± 0.09	0.37 ± 0.13	0.70 ± 0.13

[†] Abbreviations are as explained in Table 3.2; σ_e^2 = error variance; σ_g^2 = genotypic variance; σ_p^2 = phenotypic variance; SE= standard error

Table 3.8 Estimates of phenotypic (PCV) and genotypic (GCV) coefficients of variation, broad sense heritability (H^2) and genetic advance (GA) for 17 morpho-agronomic traits of maize inbred lines evaluated at Harare and Bako, 2006 and 2007

	Harare					Bako				
Trait†	GCV (%)	PCV (%)	H^2	GA	GA (% of mean)	GCV (%)	PCV (%)	H^2	GA	GA (% of mean)
GY	33.6	43.4	0.60	1.9	53.5	20.8	32.6	0.41	0.7	27.3
DA	5.2	5.8	0.80	7.4	9.5	5.2	6.1	0.73	8.0	9.2
ASI	–	–	0.51	2.5	–	46.8	60.9	0.59	1.5	74.4
PH	11.7	17.0	0.48	29.2	16.7	12.2	14.3	0.73	33.1	21.6
EH	13.1	25.9	0.26	11.4	13.7	15.8	19.9	0.63	18.2	25.8
PA	16.3	22.2	0.54	0.6	24.8	17.1	21.2	0.65	0.7	28.3
ED	5.4	7.4	0.53	0.3	8.1	4.1	5.8	0.49	0.2	5.8
EL	9.3	10.4	0.79	2.2	16.9	9.9	15.8	0.39	1.4	12.9
TKW	17.7	19.8	0.80	71.2	32.8	19.9	25.0	0.63	72.6	32.7
RPE	9.6	10.8	0.79	2.5	17.7	11.1	14.0	0.62	2.4	18.0
KPR	11.6	13.3	0.76	5.6	20.9	12.5	15.0	0.69	5.1	21.5
LL	9.0	9.8	0.84	13.3	17.0	10.4	11.0	0.89	15.4	20.2
LW	8.8	10.8	0.67	1.5	14.9	10.2	10.8	0.88	2.0	19.8
LA	14.8	17.3	0.73	149.1	26.0	15.5	16.8	0.86	173.7	29.7
TS	13.8	18.1	0.58	1.1	21.6	14.8	18.5	0.64	1.1	24.4
LO	26.1	37.5	0.48	0.7	37.4	27.8	37.6	0.55	0.8	42.6
FR	13.1	17.6	0.55	1.0	20.1	12.5	17.0	0.54	0.9	18.8

† Abbreviations are as explained in Table 3.2

Table 3.9 Eigenvectors, eigenvalues, individual and cumulative percentage of variation explained by the first five principal components (PC) for 17 morpho-agronomic traits of maize inbred lines evaluated at Harare and Bako, 2006 and 2007

Variables	Eigenvectors					
	PC1	PC2	PC3	PC4	PC5	PC6
Grain yield (t ha^{-1})	-0.34	-0.15	0.14	-0.22	0.03	-0.14
Days to anthesis	-0.21	0.27	-0.04	0.38	0.00	0.03
Anthesis-silking interval (d)	0.07	-0.21	-0.62	0.08	-0.01	0.01
Plant height (cm)	-0.17	-0.34	-0.14	0.15	-0.21	-0.52
Ear height (cm)	-0.32	-0.14	-0.12	0.27	-0.20	-0.28
Plant aspect (1-5)	0.23	0.37	-0.20	-0.19	0.04	0.06
Ear diameter (cm)	-0.23	-0.19	-0.18	0.16	0.47	0.20
Ear length (cm)	-0.22	-0.26	0.11	-0.25	-0.25	0.43
Thousand kernel weight (g)	-0.27	-0.10	-0.32	-0.22	-0.14	0.43
Number of rows per ear	0.02	-0.25	-0.02	0.25	0.65	0.13
Number of kernels per row	-0.13	-0.33	0.49	0.06	-0.05	0.16
Leaf length (cm)	-0.28	0.12	-0.02	-0.33	0.27	-0.28
Leaf width (cm)	-0.27	0.34	0.12	0.27	-0.07	0.18
Leaf area (cm^2)	-0.35	0.31	0.06	-0.07	0.13	-0.10
Tassel size (3,5 or 7)	-0.15	0.07	-0.27	0.23	-0.28	0.22
Leaf orientation (1-3)	-0.21	0.02	-0.20	-0.48	0.10	-0.10
Foliage rating (3,5 or 7)	-0.34	0.27	0.00	0.08	0.07	0.04
Eigenvalue	4.92	2.72	1.68	1.57	1.35	1.03
Individual percent variation explained	29.0	16.0	9.9	9.2	7.9	6.0
Cumulative percent variation explained	29.0	44.9	54.8	64.1	72.0	78.0

Estimates of genetic distance based on morphological data for all 595 pairwise comparisons among the 35 maize inbred lines averaged 1.37 and ranged from 0.58 (VL0556 vs VL0557) to 2.67 (CML492 vs CML444) (Table 3.10). Low morphological distances were observed between inbred lines VL0556 and VL0557 (0.58), VL05119 and VL05101 (0.60), CML503 and VL05101 (0.64), and VL0523 and VL0524 (0.64). Inbred lines with the smallest morphological distance (VL0556 and VL0557) are also closely related by pedigree. High genetic distance estimates were observed between CML492 and CML444 (2.67), VL054178 and CML444 (2.62), VL05482 and CML444 (2.30), and VL05482 and CML197 (2.30).

The dendrogram obtained from UPGMA cluster analysis of the inbred lines on the basis of combined morpho-agronomic data from two locations (Bako and Harare) classified the inbred lines into four clusters and two outlier inbred lines (Figure 3.3). The estimated cophenetic correlation value observed was significant (r_{cop}= 0.69). The first outlier inbred line, CML197, is a normal maize line and it was characterized by longer anthesis-silking interval, taller plant and ear height, larger grain size, smaller number of kernels per row, larger tassel size and pendent leaves. The second outlier, CML492, had lower grain yield, poor overall phenotypic appearance of the plant, low thousand kernel weight, smaller number of kernels per row, smaller tassel size and erect leaves. Among the four clusters, cluster I contained 60% of the lines. These lines had low to medium values of all the traits measured. In few cases inbred lines with closer pedigrees were clustered together; for example, VL0556, VL0557 and VL05561 are closely related by pedigree. Cluster II involved two lines (VL054178 and VL05482) with short plant and ear heights, smaller ear diameter and number of rows per ear and leaf area. Cluster III consisted of five lines, among which three are QPM and two are normal maize lines. These groups of lines were characterised by medium to high values of all the measured traits. Cluster IV comprised five lines most of which are closely related by pedigree. The lines were characterized by late anthesis, smaller anthesis-silking interval, shorter plant height, larger leaf area and tassel size.

Table 3.10 Estimates of genetic distance based on morphological (above diagonal) and SSR markers (below diagonal) for all pair-wise comparisons of 35 maize inbred lines

Line No†	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
1		1.09	1.20	1.48	1.53	1.85	0.91	1.11	1.15	1.38	1.72	1.26	1.25	1.15	0.72	0.88	1.11	1.18	1.03	0.80	1.06	1.41	0.97	1.14	1.10	1.08	1.15	1.38	1.62	1.10	1.01	1.07	1.52	1.61	1.64
2	0.70		1.29	1.57	1.55	1.36	1.49	1.58	1.42	1.78	1.52	1.64	1.29	1.26	1.26	1.10	1.02	1.30	1.34	1.28	1.59	1.35	1.02	1.86	0.88	1.60	1.45	1.02	2.04	1.53	1.27	1.51	1.22	1.36	1.64
3	0.67	0.49		1.02	1.11	1.19	0.93	1.03	1.28	1.87	1.54	1.67	1.05	0.76	1.08	0.98	1.26	1.16	1.26	1.37	1.42	1.12	1.11	1.45	1.16	1.51	1.27	1.01	1.62	1.43	1.27	1.24	1.11	1.46	1.64
4	0.66	0.55	0.40		0.81	1.16	1.25	1.30	1.35	1.82	1.45	1.69	1.19	1.09	1.34	1.42	1.22	1.06	1.12	1.78	1.59	1.02	1.36	1.87	1.34	1.77	1.20	1.50	1.55	1.50	1.46	1.24	1.46	1.92	1.85
5	0.63	0.62	0.49	0.41		1.14	1.47	1.43	1.48	2.05	1.45	1.87	1.40	1.28	1.38	1.64	1.30	1.28	1.25	1.65	1.89	0.93	1.23	1.91	1.37	1.74	1.25	1.29	1.71	1.51	1.39	1.12	1.31	1.75	1.58
6	0.68	0.56	0.40	0.41	0.55		1.72	1.74	1.45	2.05	1.14	1.90	1.43	1.24	1.61	1.60	1.40	1.30	1.45	2.02	1.91	1.17	1.42	2.15	1.41	1.85	1.41	1.09	1.76	1.67	1.55	1.61	1.44	1.95	1.80
7	0.67	0.55	0.51	0.53	0.62	0.52		0.78	1.15	1.46	1.78	1.26	0.96	0.74	0.95	0.68	1.21	1.01	0.98	1.17	0.97	1.39	1.18	0.93	1.39	1.17	1.06	1.41	1.49	1.11	1.08	1.11	1.57	1.90	1.77
8	0.66	0.53	0.47	0.54	0.62	0.52	0.34		1.45	1.95	1.82	1.72	1.06	1.14	1.11	1.04	1.28	0.96	1.07	1.23	1.20	1.16	1.36	1.36	1.50	1.43	1.22	1.37	1.80	1.32	1.25	1.33	1.55	1.73	1.70
9	0.61	0.62	0.59	0.62	0.64	0.60	0.61	0.56		1.30	1.54	1.13	1.54	1.26	0.90	1.12	1.24	0.98	0.99	1.40	1.06	1.40	1.16	1.17	1.45	0.84	0.68	1.51	1.07	0.80	0.88	1.23	1.80	2.08	1.87
10	0.62	0.59	0.64	0.60	0.62	0.63	0.62	0.61	0.61		2.01	1.15	1.72	1.47	1.42	1.44	1.55	1.64	1.33	1.85	1.34	2.15	1.44	1.49	1.65	1.41	1.47	1.93	1.40	1.19	1.42	1.32	2.15	2.62	2.07
11	0.65	0.53	0.42	0.46	0.56	0.44	0.47	0.48	0.59	0.59		1.96	1.39	1.31	1.44	1.69	1.60	1.42	1.51	1.82	1.79	1.36	1.64	2.16	1.65	1.72	1.50	1.49	1.73	1.77	1.68	1.52	1.87	2.09	1.88
12	0.63	0.66	0.64	0.64	0.68	0.66	0.65	0.64	0.66	0.62	0.61		1.63	1.40	1.31	1.25	1.26	1.37	1.13	1.58	1.50	1.67	1.20	1.20	1.50	1.07	1.21	1.73	1.50	1.00	1.26	1.39	2.05	2.30	2.30
13	0.67	0.52	0.46	0.51	0.59	0.49	0.56	0.52	0.60	0.64	0.51	0.67		0.64	1.17	0.97	1.06	1.03	1.15	1.40	1.43	1.21	1.31	1.73	1.21	1.64	1.43	1.24	1.95	1.58	1.48	1.19	1.42	1.67	1.80
14	0.68	0.57	0.50	0.50	0.57	0.53	0.58	0.55	0.61	0.64	0.55	0.69	0.29		1.07	0.80	1.16	1.10	1.10	1.39	1.25	1.30	1.11	1.38	1.21	1.41	1.20	1.10	1.53	1.34	1.23	1.06	1.35	1.81	1.64
15	0.68	0.63	0.60	0.64	0.67	0.66	0.68	0.65	0.63	0.69	0.66	0.62	0.61	0.60		0.95	1.15	0.96	0.91	0.95	1.02	1.23	1.05	1.16	1.09	0.96	0.88	1.34	1.49	0.99	1.00	0.82	1.49	1.67	1.65
16	0.68	0.69	0.67	0.65	0.62	0.68	0.67	0.69	0.68	0.66	0.69	0.71	0.66	0.62	0.64		1.03	1.05	1.03	1.04	0.91	1.39	0.94	1.08	1.16	1.25	1.07	1.22	1.69	1.14	0.94	1.20	1.37	1.68	1.72
17	0.67	0.65	0.65	0.66	0.70	0.65	0.65	0.64	0.68	0.66	0.65	0.65	0.65	0.64	0.66	0.65		0.78	0.69	1.18	1.56	0.99	0.79	1.64	1.03	1.35	1.15	1.09	1.78	1.10	1.06	1.18	1.30	1.46	1.84
18	0.68	0.69	0.66	0.68	0.70	0.67	0.66	0.65	0.63	0.63	0.66	0.60	0.65	0.66	0.55	0.67	0.62		0.58	1.29	1.28	0.91	1.20	1.54	1.30	1.13	0.92	1.28	1.52	1.01	1.08	1.26	1.57	1.75	1.87
19	0.69	0.71	0.69	0.68	0.68	0.68	0.70	0.69	0.66	0.66	0.70	0.66	0.68	0.64	0.55	0.63	0.62	0.40		1.24	1.25	1.06	0.96	1.34	1.30	1.03	0.78	1.23	1.32	0.70	0.84	0.99	1.53	1.87	1.77
20	0.60	0.69	0.65	0.66	0.65	0.64	0.63	0.66	0.65	0.68	0.65	0.65	0.61	0.63	0.55	0.59	0.69	0.64	0.64		1.41	1.43	1.04	1.26	1.35	1.16	1.33	1.45	1.99	1.27	1.12	1.23	1.52	1.33	1.69
21	0.59	0.67	0.64	0.66	0.64	0.66	0.68	0.66	0.65	0.64	0.64	0.62	0.66	0.68	0.61	0.62	0.68	0.67	0.67	0.51		1.77	1.44	1.10	1.58	1.32	1.04	1.78	1.50	1.18	1.14	1.32	1.89	2.27	1.70
22	0.70	0.66	0.60	0.57	0.59	0.63	0.62	0.62	0.69	0.68	0.63	0.69	0.67	0.63	0.65	0.62	0.65	0.68	0.63	0.68	0.68		1.19	1.86	1.29	1.56	1.14	1.14	1.85	1.43	1.30	1.34	1.44	1.50	1.94
23	0.64	0.64	0.67	0.64	0.62	0.68	0.65	0.64	0.63	0.45	0.63	0.59	0.67	0.67	0.69	0.69	0.68	0.67	0.67	0.68	0.67	0.67		1.28	0.93	1.24	1.01	0.97	1.64	0.92	0.75	0.91	1.15	1.51	1.48
24	0.64	0.68	0.65	0.65	0.66	0.65	0.66	0.65	0.64	0.68	0.64	0.67	0.62	0.62	0.49	0.58	0.70	0.65	0.64	0.36	0.48	0.69	0.67		1.77	0.99	1.14	1.74	1.48	0.98	1.06	1.31	1.94	2.25	1.89
25	0.63	0.65	0.68	0.68	0.68	0.71	0.68	0.66	0.68	0.62	0.67	0.61	0.67	0.66	0.71	0.69	0.61	0.66	0.68	0.74	0.69	0.64	0.62	0.75		1.66	1.40	1.26	2.07	1.46	1.39	1.15	1.10	1.39	1.62
26	0.69	0.64	0.67	0.66	0.69	0.69	0.69	0.67	0.69	0.64	0.65	0.54	0.67	0.66	0.61	0.68	0.63	0.64	0.61	0.67	0.67	0.62	0.63	0.66	0.60		1.05	1.56	1.21	0.71	0.97	1.33	2.04	2.10	2.01
27	0.61	0.66	0.65	0.66	0.66	0.66	0.63	0.64	0.63	0.64	0.62	0.63	0.67	0.70	0.65	0.66	0.68	0.66	0.70	0.61	0.47	0.70	0.69	0.62	0.67	0.70		1.39	1.25	0.71	0.64	0.97	1.62	2.07	1.65
28	0.66	0.49	0.44	0.51	0.56	0.50	0.54	0.49	0.59	0.64	0.44	0.60	0.53	0.56	0.61	0.68	0.65	0.63	0.67	0.65	0.64	0.62	0.67	0.67	0.67	0.65	0.62		1.84	1.43	1.18	1.40	1.07	1.46	1.56
29	0.60	0.67	0.65	0.66	0.68	0.64	0.59	0.61	0.65	0.66	0.62	0.69	0.64	0.65	0.68	0.63	0.65	0.67	0.66	0.62	0.68	0.63	0.66	0.66	0.67	0.64	0.67	0.64		1.15	1.32	1.58	2.29	2.67	2.19
30	0.65	0.69	0.69	0.69	0.71	0.69	0.67	0.67	0.68	0.65	0.67	0.65	0.70	0.72	0.66	0.66	0.59	0.46	0.50	0.63	0.67	0.67	0.69	0.67	0.66	0.62	0.69	0.67	0.62		0.60	1.06	1.78	2.12	1.74
31	0.71	0.69	0.63	0.63	0.63	0.59	0.68	0.69	0.68	0.70	0.65	0.73	0.66	0.66	0.70	0.68	0.64	0.65	0.61	0.72	0.70	0.61	0.69	0.71	0.69	0.69	0.73	0.65	0.66	0.66		1.06	1.57	1.95	1.57
32	0.68	0.71	0.72	0.67	0.70	0.71	0.66	0.69	0.70	0.67	0.69	0.69	0.74	0.72	0.71	0.62	0.65	0.66	0.64	0.70	0.69	0.57	0.70	0.74	0.63	0.65	0.71	0.70	0.61	0.64	0.67		1.43	1.90	1.44
33	0.67	0.63	0.58	0.57	0.59	0.57	0.59	0.59	0.64	0.61	0.64	0.69	0.62	0.62	0.71	0.68	0.63	0.68	0.67	0.69	0.68	0.67	0.66	0.71	0.64	0.67	0.66	0.63	0.69	0.68	0.66	0.68		1.20	1.35
34	0.70	0.58	0.57	0.59	0.64	0.54	0.60	0.56	0.63	0.65	0.58	0.67	0.59	0.63	0.64	0.68	0.66	0.62	0.63	0.65	0.61	0.64	0.67	0.65	0.71	0.68	0.64	0.55	0.65	0.64	0.64	0.68	0.66		2.04

†The names and pedigrees of the lines are given in Table 3.1

The 40 SSR markers used for the current study were dispersed on all 10 chromosomes, with at least three markers per chromosome except chromosome 1, which had two SSR markers. A total of 217 alleles were detected among 35 maize inbred lines using 40 SSR primers (Table 3.11). The number of amplified alleles per primer varied from two for *phi050* to 10 for *phi064*, *umc1019* and *phi041*, with a mean value of 5.43. Sizes of alleles amplified by the primers ranged from 60 to 297 bp. Primers *phi96100*, *phi093* and *phi032* amplified larger size alleles as compared to other primers. The PIC per primer ranged from 0.00 for *umc1256* to 0.77 for *umc1019* with a mean value of 0.44 (Table 3.11). SSR markers *phi064*, *phi233376*, *umc1143*, *phi96100* and *umc1019* showed PIC values equal to or greater than 0.70. All of these markers, except *phi233376*, amplified a higher number of alleles (range 9-10). Positive correlation (r= 0.60) was observed between PIC values and number of alleles amplified per primer. A total of 36 unique/rare alleles (alleles found in one inbred line out of 35 or less than 0.03 allele frequency) were detected in 25 SSR markers across 17 of the 35 inbred lines analyzed (Table 3.12). Seven of these alleles were found in normal maize inbred lines, CML395 (4 alleles) and CML444 (3 alleles). QPM inbred lines VL05575, VL0512464, VL05119 and VL05101 had three to four unique alleles each.

Genetic distance estimates based on SSR markers expressed as Euclidean distance for all 595 pairwise comparisons among the 35 maize inbred lines ranged from 0.29 (VL0523 vs VL0524) to 0.75 (CML175 vs CML181) (Table 3.12). The mean genetic distance for all pairwise comparisons was 0.64. Low genetic distance estimates were observed between inbred lines VL0523 and VL0524 (0.29), VL05466 and VL05468 (0.34), VL05483 and CML176 (0.36), and VL05561 and CML197 (0.39). High genetic distance estimates were observed between CML176 and CML181 (0.75), VL05483 and CML181 (0.74), VL0523 and VL05128 (0.74), and CML176 and VL05128 (0.74).

The dendrogram obtained from the UPGMA cluster analysis of 35 inbred lines on the basis of SSR marker based genetic distance estimates resulted in distinct separation of the lines into different groups (Figure 3.4). Six main clusters were observed with a high cophenetic correlation value of r_{cop}= 0.88. The number of inbred lines in a cluster ranged from two for cluster I to 14 for cluster III. Among the three normal maize inbred lines, CML197 was

grouped in cluster V with QPM inbred lines. Even though CML395 and CML444 were grouped in cluster III (larger cluster), they appeared as outliers separated from the other inbred lines. In the case of adaptation to mega-environments, the inbred lines did not follow clear trends of clustering in that inbred lines from tropical and subtropical environments were mixed. The correlation coefficient between morphological and molecular distance measures was significant but of very low value (r= 0.09*).

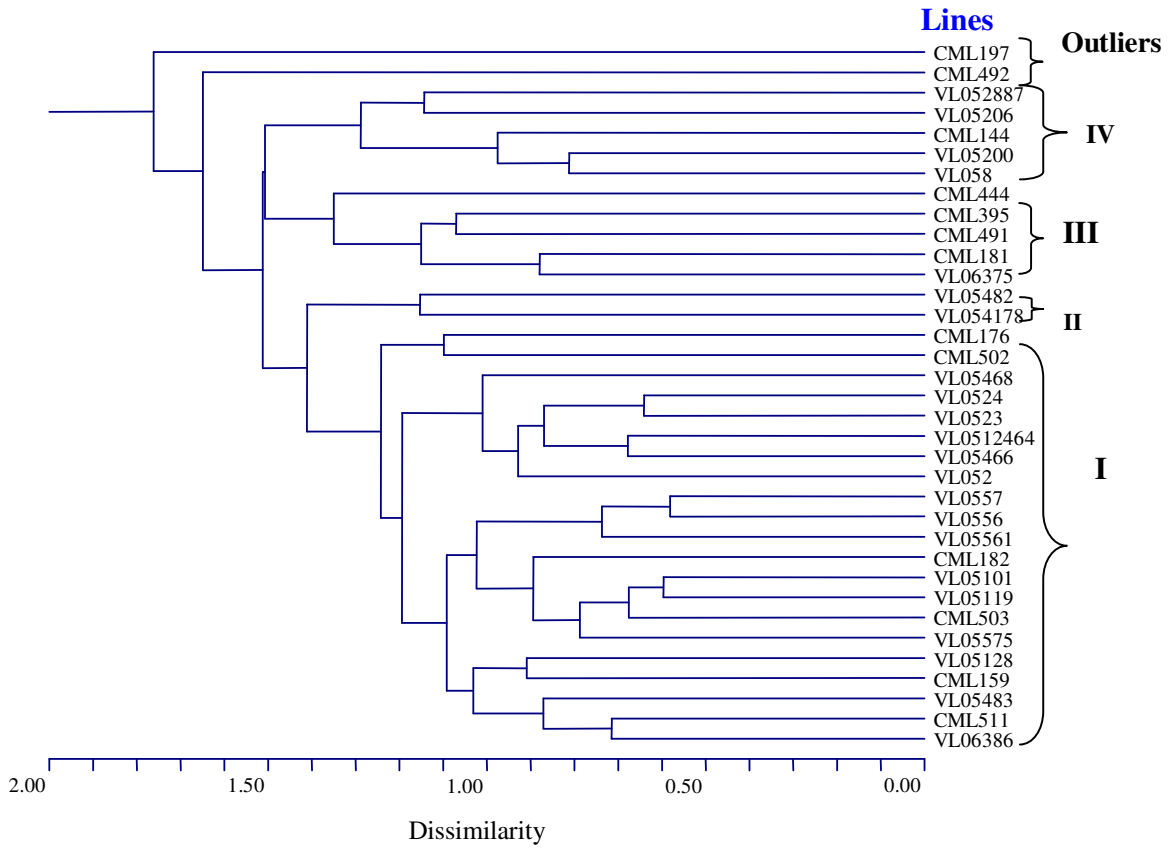

Figure 3.3 Dendrogram of 35 maize inbred lines revealed by UPGMA cluster analysis based on morpho-agronomic data combined over two locations

Table 3.11 SSR markers used and levels of genetic information generated for 35 QPM and normal maize inbred lines

SSR marker	Bin† No.	Repeat unit	Sizes (bp)	No. alleles	PIC
bnlg1057	1.00	-	240-291	8	0.51
phi064	1.11	ATCC	72-108	10	0.70
phi109642	2.00	ACGG	129-143	4	0.02
phi96100	2.00	ACCT	235-297	9	0.74
phi083	2.04	AGCT	126-139	6	0.60
phi127	2.08	AGAC	114-130	4	0.49
umc1256	2.09	-	117-180	7	0.00
phi104127	3.00	ACCG	152-172	7	0.59
phi029	3.04	AG/AGCG	150-162	5	0.47
phi053	3.05	ATAC	157-193	9	0.56
umc1644	3.06	-	153-162	4	0.35
phi046	3.08	ACGC	60-65	3	0.26
phi072	4.00	AAAC	141-155	5	0.52
umc1757	4.01	(TCC)7	135-157	7	0.59
phi079	4.05	AGATG	179-193	5	0.61
phi093	4.08	AGCT	283-290	4	0.45
phi006	4.11	CCT	83-94	4	0.27
phi076	4.11	AGCGGG	160-171	4	0.51
nc130	5.00	AGC	60-142	5	0.45
phi087	5.06	ACC	147-172	5	0.57
umc1019	5.06	-	65-101	10	0.77
phi070	6.00	-	74-81	4	0.38
umc1143	6.00	AAAAT	70-93	9	0.72
phi089	6.08	ATGC	84-92	3	0.21
umc1295	7.00	-	78-92	4	0.55
umc1407	7.00	-	82-97	6	0.12
umc1545	7.00	(AAGA)4	70-85	5	0.38
phi034	7.02	CCT	121-143	7	0.64
phi114	7.03	GCCT	134-167	5	0.47
umc1777	8.00	AGCC	113-119	3	0.28
umc1304	8.02	-	119-138	5	0.33
phi233376	8.03	CCG	137-156	5	0.71
umc1657	9.00	-	149-163	5	0.53
phi065	9.03	CACTT	108-153	4	0.29
phi032	9.04	AAAG	233-240	3	0.32
phi041	10.00	(CAT)5	186-226	10	0.56
phi050	10.03	AAGC	82-86	2	0.19
phi084	10.04	GAA	152-160	3	0.27
umc1993	10.06	-	75-94	3	0.35
umc1196	10.07	CACACG	138-158	6	0.43
Total				217	
Mean				5.43	0.44

†The bin number contains linkage group and genetic interval information. Each of the 10 maize linkage groups is divided into approximately 10 bins (MaizeGDB http://www.agron.missouri.edu/ssr_probes/ssr.htm.). At least two SSR loci were sampled in each maize chromosome

Table 3.12 Summary of number of unique alleles detected for specific inbred lines

Line	No. of alleles	SSR marker[†]
VL06386	2	*phi041*, *umc1019*
VL06375	2	*phi034*, *umc1019*
VL058	1	*phi104127*
VL05575	3	*phi029*, *phi041*, *umc1019*
VL052887	1	*phi065*
VL05482	2	*phi072*, *phi233376*
VL0512464	4	*phi029* (2), *phi053*, *umc1304*
VL0556	1	*phi087*
CML159	1	*phi104127*
CML182	2	*phi032*, *umc1545*
CML503	1	*phi114*
CML492	1	*phi064*
VL05119	3	*phi041*, *phi070*, *phi96100*
VL05101	3	*bnlg1057*, *phi083* (2)
VL05128	2	*nc130*, *umc1196*
CML395	4	*bnlg1057*, *phi064*, *phi089*, *umc1143*
CML444	3	*phi064*, *phi076*, *phi079*
Total	36	

[†] SSR loci *phi029* and *phi083* detected two unique alleles in inbred lines VL0512464 and VL05101, respectively. Numbers in the bracket are alleles of a given marker unique to a specific inbred line

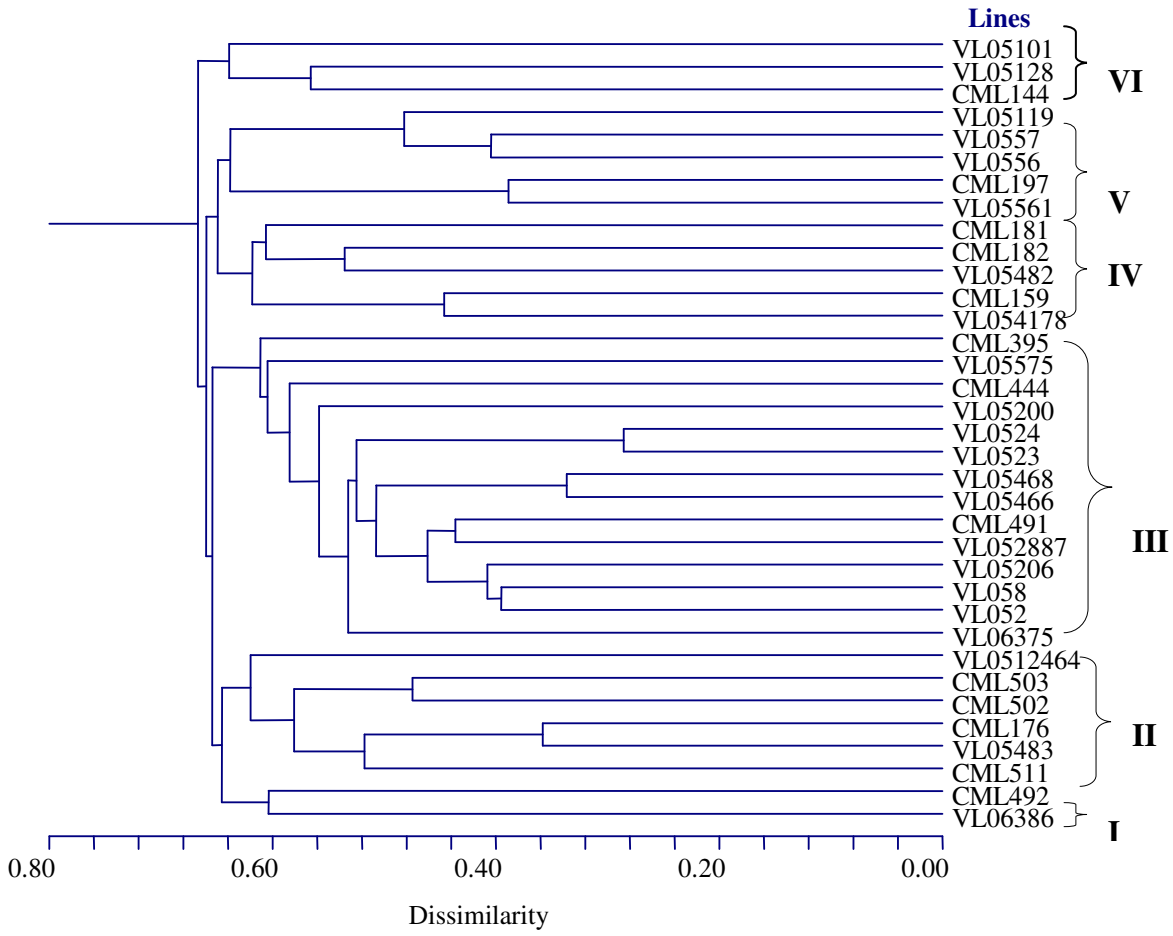

Figure 3.4 Dendrogram of 35 maize inbred lines revealed by UPGMA cluster analysis based on SSR markers

3.5 Discussion

Significant differences observed among the lines for all the traits evaluated (Tables 3.3, 3.4 and 3.5) indicate the presence of a high level of genetic variability in the inbred lines. Morpho-agronomic trait variations among CIMMYT's QPM genotypes have been previously reported by several investigators (Vasal et al., 1993a; b; Hadji, 2004; Akande and Lamidi, 2006). Furthermore, Prasanna et al. (2001) noted that genetic variability for most traits in maize is very high and amenable to enhancements. The existence of a wide range between minimum and maximum values of each trait further confirms the presence of substantial variation among the lines studied. The presence of such variation is an opportunity for maize breeders to improve traits of interest through selection, hybridization and recombination of

desirable genotypes. Higher grain yield observed at Harare than Bako, as indicated in Figure 3.2, can be attributed to the differences in management level and plot sizes used (see section 3.3). The experiment at Harare was irrigated to field capacity at planting and whenever soil moisture dropped to the minimum while the experiment at Bako was grown exclusively under rain fed conditions. One-row plots were used at Harare whereas two-row plots were used at Bako; which might have increased the experimental error and resulted in an inflated estimate of yield ha^{-1} at Harare. Bolaños and Edmeades (1996) pointed out that the use of single row plots for evaluation, favours tall progenies to capture additional radiation when surrounded by shorter neighbours.

Significant location effect in combined analysis of variance (Table 3.4) has been observed as the result of differences in the growing conditions between Harare and Bako. In maize production, higher grain yield and yield components, early maturity, short anthesis-silking interval, short plant stature and erect leaf orientation are desirable. Most of these features were observed at Harare. This indicated that the lines evaluated were more suitable for Harare compared to Bako. Most of the lines were developed by CIMMYT-Zimbabwe at Harare Research Station. Non-significant environment x line interaction for most traits (Table 3.4) is desirable as it indicates similar ranks of the lines in performance over the two locations. This makes the selection decision easier. QPM lines had lower yield than the normal maize line checks, especially CML444 (5.9 t ha^{-1}), indicating that more breeding efforts should be devoted to the development of QPM lines competent to the normal ones. QPM adoption in Africa could be facilitated if it is agronomically better than the normal maize cultivars to compete in open markets (Krivanek et al., 2007)

Knowledge of the level of relationship among traits is important in designing effective selection programs for crop improvement. Positive and significant correlations of grain yield with plant and ear height indicate that tall plants are high yielding. This phenomenon is undesirable and very important for maize breeders because they complicate simultaneous improvement for high yield and short plant statured lodging resistant lines. Lack of correlation between grain yield and anthesis-silking interval indicates the lack of functional relationship between these traits. Bolaños and Edmeades (1996) noted that correlations

between grain yield and anthesis-silking interval is weak under optimal management conditions but very strong under stress. The positive correlation of grain yield with its components such as ear diameter and length, thousand kernel weight and number of kernel per row (Table 3.7) has also been reported by other workers (Bolaños and Edmeades, 1996; Edmeades et al., 1997). Positive and significant correlation of grain yield with foliar traits such as leaf length and area, and foliar rating indicates that larger canopy can better intercept light that can photosynthetically be converted into dry matter, that is, grain yield. Similar results have been reported by Tollenaar et al. (2004). The correlation coefficient values observed in this experiment agrees with the range of values reported by Hallauer and Miranda (1988). The traits which showed positive and significant correlation with grain yield can be improved simultaneous during selection for higher grain yield. These traits can also be used as secondary traits during indirect selection for grain yield.

Genetic traits such as variance components, coefficients of variability, heritability and genetic advance provide estimates of genetic variation of quantitative traits. Higher error variance was observed at Harare than at Bako (Tables 3.8) as a result of smaller plot size used which increases experimental error. Significantly higher genetic variability observed for most traits indicates potential of the lines that can be exploited through selection. This phenomenon is also evident from the fact that σ_g^2 is greater than σ_e^2 for most traits. Grain yield, anthesis-silking interval and leaf orientation showed high values of phenotypic coefficient of variation and genotypic coefficient of variation. In most cases, traits with higher phenotypic coefficients of variation showed higher genetic coefficient of variation, indicating minimum effect of environment on the phenotypic expression of the traits.

Broad sense heritability (H^2) estimates were high (> 0.50) for most traits evaluated indicating that these traits are highly heritable. Therefore, further selection would be effective in the set of lines evaluated in this experiment. Selection for a character is fairly easy if its heritability is high but for a character with low heritability selection may be difficult or impractical due to the masking effect of the environment on genotypic effects (Singh, 2005). Hallauer and Miranda (1988) summarized numerous estimates of heritability in maize, and reported values ranging from 0.3 to 0.7, which is consistent with the results of this study.

According to Johnson et al. (1955) heritability by itself provides no indication of the amount of genetic progress that would result from selecting the best individuals. He suggested that the estimate of heritability and genetic advance should always be considered simultaneously. In addition, Assefa et al. (1999) suggested that genetic coefficients of variation together with heritability estimates would give the best picture of genetic advance to be expected from selection. Therefore, traits that exhibited a high genotypic coefficient of variation, heritability and genetic advance as percent of the mean would be useful as a base for selection. In this study, traits such as thousand kernel weight and leaf area (Table 3.9) had larger values of these three parameters. Simple selection of plants having higher thousand kernel weight, for example, may lead to success in improving the trait up to 37.8%. Therefore QPM line development should focus on thousand kernel weight as selection criteria to increase grain yield. Moreover, this trait had positive correlation with grain yield.

The existence of broad morphological variation among genotypes was further substantiated by PC analysis (Table 3.6), which indicated that the overall diversity observed could not be explained by a few eigenvectors. The variations in all traits were dissected into 17 PCs which accounted for 100% of the variability existing among the lines. However, some traits such as ear height, number of kernels per row, thousand kernel weight, tassel size, leaf length, width and area were the major contributors. Yoseph et al. (2006) reported that 71.8% of the total variation in 62 traditional Ethiopian highland maize accessions was explained by the first four PCs. These authors reported that ear height, number of kernels per row, thousand kernel weight, tassel size, leaf length and width are the traits predominantly contributing to the total variation, which is in line with the finding in this finding. The major role of morphological traits in phenotypic variation observed in this study is also consistent with the work of Alika et al. (1993).

Genetic distances estimated based on morpho-agronomic data revealed the existence of considerable variability among the inbred lines. Cluster analysis also confirmed the presence of variation among the lines. The dendrogram showed the resolution power of morphological and agronomic traits for grouping maize inbred lines. In some cases, lines tightly clustered together are closely related by pedigree. The high estimated cophenetic correlation value

(r_{cop}= 0.69) observed, indicated good fit of the dendrograms with the distance values. In line with this finding, Lucchin et al. (2003) clustered 20 Italian flint maize landraces into groups using morphological and agronomic traits. Yoseph et al. (2006) classified 62 traditional highland maize accessions into three groups using 15 morphological traits. In diversity analysis of 45 maize inbreds, Gerdes and Tracy (1994) successfully grouped closely related inbred lines by morphological data in agreement with pedigree data. However, reports consistently indicate that morphological markers have shortcomings in that they are highly influenced by prevailing environmental conditions (Bernardo, 1992; Gerdes and Tracy, 1994; Yoseph et al., 2005).

All 40 SSR marker loci analyzed were polymorphic across the 35 inbred lines evaluated. The range (2 – 10) and mean (5.43) alleles amplified per primer were similar to the results of previous studies using SSRs on maize inbred lines (Pejic et al., 1998; Senior et al., 1998; Lu and Bernardo, 2001; Warburton et al., 2002; Vaz Patto et al., 2004). These authors reported a mean number of alleles ranging from 4.9 to 5.3. However, the mean number of alleles observed in the current study were higher than that of Bantte and Prasanna (2003) and Legesse et al. (2007), who reported 3.25 and 3.85 alleles per primer, respectively; and lower than that of Pejic et al. (1998) and Xia et al. (2004, 2005), who reported 6.8, 7.4 and 7.2 alleles per primer, respectively. Differences in numbers of alleles between studies could be explained mainly due to the size of the studied samples; expected diversity or uniformity based on pedigrees, and most importantly, repeat type of SSR used. Dinucleotide SSR primers show higher numbers of alleles (Smith et al., 1997; Senior et al., 1998; Enoki et al., 2002; Legesse et al., 2007), but were not used in the current study. Generally, the use of dinucleotide SSR primers is not recommended because of the difficulty in accurately sizing alleles (Warburton et al., 2002; Choukan et al., 2006).

PIC demonstrates the informativeness of the SSR loci and their potential to detect differences among the inbred lines based on their genetic relationships. The mean PIC value (0.44) observed in this study was lower than the values reported by other researchers for maize inbred lines using SSR markers (Vaz Patto et al., 2004; Xia et al., 2004, 2005; Choukan et al., 2006; Legesse et al., 2007). Markers with very low PIC values, *umc1256* (0.00),

phi109642 (0.02), *umc1407* (0.12) and *phi050* (0.19), significantly affected the mean PIC value of this study. Since the markers used for this study have been selected for routine screening in many laboratories, preliminary exclusion of SSR primers with low discriminatory power was not done, unlike other studies (Enoki et al., 2002; Legesse et al., 2007). On the other hand, some markers with high PIC values and hence high discriminatory power were identified; *umc1019* (0.77), *umc1143* (0.72), *phi233376* (0.71) and *phi064* (0.70). According to Bantte and Prasanna (2003), the overall PIC value could be influenced by the type of germplasm used, number and distribution of SSR loci assayed, type of marker used and methodology employed for allele detection (electrophoresis).

The SSR markers with a high number of alleles subsequently produced high PIC estimates. The positive relationship between number of alleles per primer and PIC value was also reported by other researchers (Bantte and Prasanna, 2003; Vaz Patto et al., 2004). The detection of unique alleles in the inbred lines analyzed shows the usefulness of SSR markers in germplasm identification. Two (CML395 and CML44) of the three normal maize inbred lines included in the study as a check were distinguished from QPM inbred lines. Presence of unique alleles that are specific to single accessions were reported in previous studies (Bantte and Prasanna, 2003; Choukan et al., 2006).

The average genetic distance among all the inbred lines was relatively high (0.64), indicating high levels of polymorphism in the inbreds. The value is in agreement with the range reported by others (Vaz Patto et al., 2004; Legesse et al., 2007). The value observed in the current study, however, was lower than reported by Xia et al. (2004, 2005) who observed mean genetic distances of 0.76 and 0.78, respectively. Minimum genetic distance of 0.29 was recorded between inbred lines VL0523 and VL0524. These lines are not related by pedigree but they belong to the same heterotic group (B.S. Vivek, CIMMYT-Zimbabwe, personal communication, 2008). The other inbred lines with minimum genetic distances of 0.34 (VL05466 and VL05466) and 0.36 (VL05483 and CML176) are closely related by pedigree. This indicates the power of SSR markers to distinguish between closely related inbred lines (Smith et al., 1997). The ability to provide distance measures between the inbred lines that

reflect pedigree relatedness ensures a more stringent evaluation of the adequacy of marker profile data (Legesse et al., 2007).

The dendrogram obtained from the UPMGA clustering algorithm based on SSR markers showed that almost all of the inbreds could be distinguished from each other. The cophenetic correlation was high (r = 0.88), indicating a good fit of the genetic distance matrix with the dendrogram. The six clusters indicated that inbreds were grouped mostly in a manner that was consistent with pedigree information. This is in agreement with earlier studies (Smith et al., 1997; Vaz Patto et al., 2004; Legesse et al., 2007) that demonstrated the correspondence of SSR marker distance with pedigree information in maize inbred lines. Clusters containing most closely related inbred lines were cluster II, III, IV and V. Cluster II contained predominantly inbred lines recycled from CML176 or converted to QPM using CML176 as a donor parent. Cluster III contained mostly inbred lines recycled from CML144 and CML395. Cluster IV was constituted from inbred lines related to CML182 and CML159. All inbred lines in cluster V, except CML197, were related to GQL5 which was originally obtained from the Ghanaian QPM breeding program. Inbred lines CML197 and CML492 which were identified as outliers in cluster analysis based on morpho-agronomic data were grouped with VL05561 and VL06386, respectively in cluster analysis based on SSR data. This indicates a dramatic shift in grouping inbred lines based on the two distance measures. Generally, however, SSR markers grouped the inbred lines based on pedigree data more efficiently than the morphological data.

Inbred lines VL05575, VL0512464, VL05119, VL05101, CML395 and CML444 which had more than two unique/rare alleles were positioned separately within their respective clusters. No clear clustering was observed based on the mega-environments for which the lines were bred, indicating that CIMMYT tropical and subtropical inbred lines are not genetically distinct. Similarly, using SSR markers, Xia et al. (2005) failed to clearly cluster CIMMYT subtropical, tropical midaltitude and highland maize inbred lines based on mega environments; and explained that maize populations and pools used to extract the inbred lines are of mixed genetic composition. The two distance measures grouped the inbred lines differently. The low correlation coefficients observed between the two distance measures

reveals that morphological distances may not necessarily indicate molecular distances among maize inbred lines. SSR markers were relatively more reliable and efficient for precise discrimination of maize inbred lines into groups based on their genetic relationships.

3.6 Conclusions

Information on genetic diversity and relationships among breeding materials is important in choosing parents for variety development. The results of this study have identified QPM inbred lines for desirable traits. However, QPM lines performed poorer than the normal maize line checks for some traits. Hence, QPM line development effort in Africa should be devoted to increasing grain yield and yield components such as ear length, ear diameter, thousand kernel weight, number of rows per ear and number of kernel per row, and decreasing plant height. The lines displayed a substantial amount of variability for studied morpho-agronomic traits. The broad trait diversity evident among the inbred lines suggests ample opportunity for development of desirable QPM single-cross hybrids, three-way cross hybrids, or synthetic varieties from these lines. Selected lines can also be recombined to develop desirable recycled inbred lines. Based on morpho-agronomic data, some inbred lines related by pedigree were grouped together, indicating that the morpho-agronomic traits can be used at least for primary characterization of maize inbred lines. The 40 SSR primers used in the current study differed in number of alleles amplified and PIC; hence in discriminative power. Generally, positive association was observed between number of alleles and PIC of SSR locus. Genetic distance estimates based on SSR markers also showed the presence of genetic variation among QPM inbred lines, which creates opportunity for the development of improved QPM varieties. The UPGMA clustering algorithm grouped the inbred lines into six clusters, which generally agreed with their pedigree records. Results of this study indicated the robustness of SSR markers for diversity analysis and heterotic groupings more efficiently than morphological data. The information generated can be used for better understanding of the genetic relationships among the QPM inbred lines, more effective utilization of the inbred lines in the breeding programs for the development of varieties, and formation of heterotic populations used to derive promising inbred lines.

Chapter 4

Heterosis and combining ability of quality protein maize inbred lines under low nitrogen stress and optimal environments

4.1 Abstract

Low soil nitrogen is among the most important abiotic stresses limiting maize production in sub-Saharan Africa. Information on hybrid performance, heterosis and combining ability of quality protein maize (QPM) inbreds for grain yield and agronomic traits under low N stress is crucial to design appropriate breeding strategies for the development of nutritionally enhanced maize cultivars. In this experiment, a 15-parent diallel (Griffing's Method 4, Model 1) was evaluated at Harare, Zimbabwe and Bako, Ethiopia under low nitrogen (N) stress and optimal conditions. The objectives were to estimate heterosis and combining ability of QPM inbred lines for yield and agronomic traits under low N stress and non-stress conditions. The mean squares for general (GCA) and specific (SCA) combining ability were significant for most measured traits at each and across environments with the exception of SCA mean squares across low N environments. This indicates the importance of both additive and non-additive gene effects in most cases, while non-additive gene effects are less important under low N stress. Inbred lines VL054178, VL05561, VL05483, CML511, CML144, CML159, CML491 and VL06375 showed desirable GCA effects for most traits under both low and optimal N conditions. Crosses with good SCA effects for grain yield had one of these lines as a parent. Mean mid-parent heterosis (MPH) ranged from -9.1% for days to silking to 112.7% for grain yield and high-parent heterosis (HPH) from -12.0% for days to silking to 89.8% for grain yield. All the crosses showed negative MPH and HPH for days to anthesis and silking, and all the crosses showed positive MPH for plant and ear height, number of kernels per row and kernels per ear. This study identified QPM inbred lines and hybrid combinations that had desirable expression of important traits. This will be useful for the development of high yielding QPM hybrids for low N stress and optimal environments.

4.2 Introduction

Maize is the dominant staple crop grown by the vast majority of rural households in most parts of Africa. The protein of maize endosperm, however, is deficient in two amino acids, lysine and tryptophan; therefore maize is a poor source of protein for both humans and mono gastric animals. The *opaque-2* (*o2*) mutation alters protein composition of the maize endosperm resulting in increased concentrations of lysine and tryptophan (Mertz et al., 1964). Quality protein maize (QPM) is the improved *o2* germplasm that has superior protein quality to the normal endosperm maize but with desirable kernel characteristics and agronomic performance similar to normal endosperm maize.

Maize in Africa is grown by small scale farmers under extremely low-input systems where average maize yields are 1.3 t ha^{-1} (DeVries and Toenniessen, 2001; Banziger and Diallo, 2004). Among many production constraints, drought and low soil fertility, mainly N deficiency, are the main factors that most frequently limit maize production (Banziger and Lafitte, 1997; Banziger and Cooper, 2001). A considerable proportion of maize in the tropics is still grown under low N conditions (Banziger and Lafitte, 1997). Nitrogen deficiency is common where N is applied at below-optimal levels because of high cost relative to economic returns, or where there are significant risks of drought and frost or of excessive leaching of nitrate (Lafitte and Edmeades, 1994a). Nitrogen is an essential component of all enzymes and therefore necessary for plant growth and development. Thus, efficient N uptake and use by maize plants is of fundamental importance to maize production systems (Muza et al., 2004).

Low N increases the anthesis-silking interval, enhances kernel abortion, reduces final grain number and then grain yield (Banziger and Lafitte, 1997; Monneveux et al., 2005). Reduction of grain weight under low N conditions is more attributable to reduction in grain filling period than in growth rate (Monneveux et al., 2005). Improved maize varieties that tolerate low soil fertility will help maize farmers in stress-prone areas to obtain better harvests under the same stress conditions (Zaidi et al., 2003; CIMMYT, 2007). Selection for improved performance under low N stress based on grain yield alone has often been

considered inefficient, but the use of secondary traits such as anthesis-silking interval, leaf senescence, ears per plant, kernels per plant and kernel weight whose variance increases under stress and whose heritability remains high, are used to improve selection efficiency under low N stress (Banziger and Lafitte, 1997; Manda and Mwambula, 1999; Edmeades et al., 2006).

The use of cultivars that utilize nitrogen more efficiently could greatly improve maize productivity in maize-based cropping systems. The International Maize and Wheat Improvement Centre (CIMMYT) has made significant progress in developing maize germplasm tolerant to low N (Beck et al., 1996; Banziger and Lafitte, 1997; Banziger et al., 1997; Banziger and Diallo, 2004; Banziger et al., 2006). This germplasm includes normal maize inbred lines and populations developed through different breeding programs within CIMMYT. However, information on yield and agronomic performance of QPM germplasm under low N stress is scarce. Moreover, low N tolerant QPM populations, inbred lines or hybrids have not been released so far for commercial use.

Previous studies on heterosis and combining ability of QPM germplasm were conducted under non-stressed conditions. Vasal et al. (1993a;b) studied heterosis and combining ability of CIMMYT's tropical and subtropical QPM germplasm and reported maximum high-parent heterosis of 16% and the greater importance of GCA relative to SCA. Combining ability studies of QPM inbred lines identified the greater importance of GCA or additive gene action for grain yield and agronomic traits (Pixley and Bjarnason, 1993; Cordova et al., 2003; Fan et al., 2004; Hadji, 2004; Bhatnagar et al., 2004; Xingming et al., 2004). Environment can differentially affect the performance of hybrids and combining ability of inbred lines. Information on hybrid performance and combining ability of QPM inbreds for grain yield and agronomic traits under low N stress is required for breeders to utilize this germplasm for the development of stress tolerant, nutritionally enhanced maize cultivars. Thus, the objectives of this study were to estimate heterosis and combining ability of QPM inbred lines for yield and agronomic traits under low N stress and non-stress conditions.

4.3 Materials and methods

Environments and stress management

The study was conducted at CIMMYT-Harare Research Station, Zimbabwe during the 2006/07 cropping season and at Bako Agricultural Research Centre, Ethiopia during the 2007 cropping season under low N stress and optimum N conditions. The detailed descriptions of the environments were given in materials and methods of Chapter 3. Low N stress conditions were achieved by continuously cropping maize for a minimum of five years without applying N fertilizer. Optimum N conditions were maintained by applying the recommended N rate for the respective locations, managed by crop rotation and residue incorporation. No chemical N fertilizer was applied to the low N experiments. In the optimum N experiments, 28 kg ha^{-1} N was incorporated prior to sowing, and 69 kg ha^{-1} N was side-dressed each at 28 and 56 days after emergence at Harare and 100 kg ha^{-1} N was applied in two splits, half at planting and the rest at 37 days after emergence, at Bako. Other standard cultural and agronomic practices were followed in trial management as detailed in Chapter 3. Analytical results of soil samples taken at two depths prior to fertilizer application and sowing for each site are presented in Tables 4.1 and 4.2.

Germplasm

Fifteen inbred lines (Table 4.3) were selected based on diverse pedigree backgrounds from the 32 QPM inbred lines characterized in Chapter 3. These lines show better combining ability in top-cross evaluations and *per se* performance across a range of tropical and subtropical environments. Most of the lines are resistant/tolerant to major foliar diseases of the tropics (CIMMYT, 2004c). Diallel crosses were made among the 15 inbred lines in the winter of 2006 at Muzarabani, Zimbabwe. Seeds from reciprocal crosses were bulked to form a set of 105 F_1 hybrids. The F_1 hybrids were evaluated along with two QPM (SC527Q and CML144/CML159//CML176) and one normal maize (SC633) hybrid check at Harare, and two normal maize (BH540 and BH541) and one QPM (BHQP542) hybrid checks at Bako.

Table 4.1 Soil properties at two depths of the experimental fields at Harare, Zimbabwe

N site	Depth (cm)	Texture	pH ($CaCl_2$)	Mineral N (ppm)	Available P_2O_5 (ppm)	K (meq/100g)	Ca (meq/100g)	Mg (meq/100g)	Total exchangeable cations (meq/100g)
Optimum N	0-30	Sandy clay	5.2	43	66	0.49	7.82	2.78	11.1
	30-60	Sandy clay	5.4	22	16	0.13	7.50	2.84	10.5
Low N	0-30	Sandy clay	5.8	24	187	0.36	8.51	2.84	11.7
	30-60	Sandy clay	5.5	18	20	0.13	7.27	2.49	9.9

Analyzed by the Department of Agricultural Research and Extension Services (AREX), Harare, Zimbabwe

Table 4.2 Soil properties at two depths of the experimental fields at Bako, Ethiopia

N site	Depth (cm)	Texture	pH (H_2O)	Total N (%)	Available P (ppm)	Organic Matter (%)	K (meq/100g)	Ca (meq/100g)	Mg (meq/100g)	Total exchangeable cations (meq/100g)
Optimum N	0-30	Clay	5.95	0.19	35.69	6.33	0.73	7.09	2.25	10.07
	30-60	Clay	5.87	0.10	0.56	3.87	0.27	5.40	1.61	7.28
Low N	0-30	Clay	5.64	0.12	2.40	2.69	0.16	5.33	1.19	6.68
	30-60	Clay	6.65	0.08	0.92	1.61	0.18	4.53	1.63	6.34

Analyzed by the International Livestock Research Institute (IRLI), Addis Ababa, Ethiopia

Table 4.3 List of fixed QPM inbred lines used in the diallel study evaluated under optimum and low N stress conditions at Harare, Zimbabwe and Bako, Ethiopia, their pedigrees, and adaptation

No.	Name	Pedigree	Adaptation	Stress tolerance/ resistance
1	VL052	[CML141/[CML141/CML395]F2-1sx]-4-2-1-B*4-1-B	Tropical/Subtropical	HM, MSV, PP
2	VL05200	[CML144/[CML144/CML395]F2-8sx]-1-2-3-2-B*4-1-B	Tropical/Subtropical	HM, MSV, PP
3	VL05468	[CML144/SNSYNF2[N3/TUX-A-90]-102-1-2-2-BSR-B*4]-B-4-3-B*4-1-B	Tropical	HM, PP
4	VL054178	[CML159/[CML159/[MSRXPOOL9]C1F2-205-1(OSU23i)-5-3-X-X-1-BB]F2-3sx]-8-1-1-B-B-B-4-B	Tropical	HM, MSV, PP
5	VL052887	[CML181/[CML181/[MSRXPOOL9]C1F2-174-1(OSU31ss)-1-7(I)-X-X-1-B]F2-2sx]-1-3-3-1-B-B	Subtropical	MSV
6	VL05482	[CML182/TZMI703]-B-9-1-BB-#-B-2-B	Subtropical	
7	VL0523	[CML202/CML144]F2-1-1-3-B-1-B*5-2-B	Tropical/Subtropical	HM,PP, MSV, ET, PS
8	VL0524	[CML205/CML176]-B-2-1-1-2-B*4-1-B	Tropical/Subtropical	MSV, ET, PS
9	VL05561	[GQL5/[GQL5/[MSRXPOOL9]C1F2-205-1(OSU23i)-5-3-X-X-1-BB]F2-4sx]-11-3-1-1-B*4-1-B	Tropical	MSV
10	VL05483	[TZMI703/CML176]-B-3-2-B*4-1-B	Subtropical	
11	CML511	[CML389/CML176]-B-29-2-2-B*5	Subtropical	MSV
12	CML144	Pob62c5HC182-2-1-2-B-B-3-1-#-#	Tropical	HM, PP
13	CML159	Pob63c2HC5-1-3-1-B-2-1-1-B-#-#	Tropical	HM, PP
14	CML491	(6207QB/6207QA)-1-4-#-2-2-B-B	Tropical	PP
15	VL06375	(CLQRCWQ50/CML312SR)-2-2-1-B-1-B	Subtropical	MSV

ET= *Turcicum* leaf blight caused by *Exserohilum turcicum*; HM= leaf blight caused by *Helminthosporium maydis*; MSV= maize streak virus, PP= leaf rust caused by *Puccinia polysora*; PS= leaf rust caused by *Puccinia sorghi*

Experimental design and field measurements

The 108 hybrids (105 F_1s and three checks) were planted in an alpha-lattice design (Patterson and Williams, 1976) with two replicates and two row plots at each environment. The hybrids were tested under low and optimum N levels in adjacent blocks at both locations. The plots were over sown with two seeds per hill every 25 cm at Harare and every 30 cm at Bako in two rows of 4.0 m (Harare) and 4.8 m (Bako) in length spaced 75 cm apart. The plots were later thinned to the desired plant densities of 53 333 and 44 444 plants ha^{-1} at Harare and Bako, respectively.

Measurements were recorded on well-bordered plants by excluding the plant nearest to the alley of each row. Days to anthesis and silking were calculated as the number of days from planting to 50% pollen shed and silk emergence. Anthesis silking interval was calculated as the difference between days to silking and anthesis (ASI = DS – DA).Two weeks after pollen shed, plant height and ear height were measured as the distance from ground level to the first tassel branch or to the node bearing the main ear. Leaf senescence was scored for the low N experiments on a scale from 0 to 10 by dividing the percentage of estimated total leaf area that is dead by 10. A score of 1 = 10%; 2 = 20%; 3 = 30%, 4 = 40%; 5 = 50%; 6 = 60%; 7 = 70%; 8 = 80%; 9 = 90%, and 10 = 100% dead leaf area (Banziger et al., 2000). It was scored at 28 and 35 days after anthesis at Harare and Bako, respectively, when obvious genotypic differences for leaf senescence became apparent. Number of ears per plant was obtained by dividing the number of ears by number of plants harvested. An ear was counted if it had at least one fully developed grain. Five random ears were selected from all harvested ears of each plot to measure ear diameter and length, number of rows per ear and kernels per row. Ear diameter was measured at the mid way along the ear length as average of the five randomly selected ears. Ear length was measured as length of the ear from the base to tip, like ear diameter. An average of five ears was used. Ear diameter and ear length were recorded only at Bako. Number of kernels per plant was determined from number of rows per ear and number of kernels per row. Grain weight from all the ears of each experimental unit was measured and used to calculate grain yield (expressed in ton ha^{-1} and adjusted to 12.5% moisture content). For thousand kernel weight, random kernels from the bulk of each

experimental unit after shelling was counted using a photoelectric seed counter and weighed in grams after the moisture was adjusted to 12.5%.

Statistical analysis

Before data analysis, anthesis-silking interval (ASI) was normalized using $\ln\sqrt{(ASI+10)}$ as suggested by Bolaños and Edmeades (1996). Analysis of variance per environment was conducted with the PROC MIXED procedure in SAS (2003) considering genotypes as fixed effects and replications and blocks within replications as random. Relative reductions in grain yield and agronomic traits under low N was calculated as (1 - $MV_{low\ N}/MV_{optimum\ N}$), where $MV_{low\ N}$ and $MV_{optimum\ N}$ are mean traits values obtained in paired experiments under low and optimum N (Banziger et al., 1997). Entry means adjusted for block effects generated from individual location analyses according to the lattice design (Cochran and Cox, 1960) were used to perform across environments combined analyses using PROC GLM in SAS (SAS, 2003) and combining ability analysis using a modification of the DIALLEL-SAS program (Zhang and Kang, 1997). GCA effects of the parents and SCA effects of the crosses were estimated following Griffing's Method IV (crosses only) and Model I (fixed) of diallel analysis (Griffing, 1956). Combined analyses of variance were conducted for each trait that showed significant entry mean squares in individual environment analysis. Data were combined over optimum N, low N and across all environments. Combining ability was analyzed, and GCA and SCA effects were estimated accordingly. The mean squares for hybrids and environments were tested against the mean squares for hybrid x environment (E) as error term while hybrid x E interactions mean squares were tested against pooled error. The pooled error mean squares were obtained by dividing the sum of error sum of squares from all locations with the corresponding sum of the error degrees of freedom. The significance of GCA and SCA sources of variation was determined using the corresponding interactions with the environment as error terms. Because the combining ability mean squares were calculated based on entry means, error mean squares used to test the significance of GCA and SCA interactions with environment was obtained by dividing the pooled error mean squares from the ANOVA by the number of replications (Griffing, 1956; Singh, 1973; Dabholkar, 1992). Significance of GCA and SCA effects were determined by

the t-test, using standard errors of GCA and SCA effects, respectively (Griffing, 1956; Singh and Chaudhary, 1985).

Heterosis was estimated only for the optimum N experiments as the inbred lines were not evaluated under low N conditions. Mid-parent heterosis was calculated as: MPH=$\frac{(F_1 - MPV)}{MPV} \times 100$, where *F1* is the mean performance of the cross and *MPV* is mean of the two inbred parents. High parent heterosis was calculated as: $HPH = \frac{(F_1 - HPV)}{HPV} \times 100$, where *HPV* is the mean value of the highest performing parent. Pearson's phenotypic correlation coefficients were calculated between grain yield and agronomic traits to determine the relationships between grain yield and agronomic traits under optimum and low N conditions. Spearman's rank correlation coefficients were calculated between grain yield under low N stress and optimum N environments using the Statistical Package for the Social Sciences (SPSS, 2002) software.

4.4 Results

Hybrids exhibited significant differences in all traits under low and optimum N conditions at Harare except anthesis-silking interval under both conditions and ear height under low N (Table 4.4). At Bako, highly significant differences were observed among hybrids for all traits in both environmenrs except for anthesis-silking interval under low N conditions (Table 4.5). About 30% of the 105 F_1s had higher grain yield than the high yielding normal hybrid check at Bako (optimum N), but very few or none of the F_1s yielded higher than the highest yielding normal check at the other environments (data not presented). Low N stress reduced yield and field performance of the hybrids (Figure 4.1). Relative grain yield reduction was 88.5% and 48.8% at Harare and Bako, respectively. However, Spearman's rank correlation analysis showed that the correlations between hybrid means under optimum and low N environments were positive and highly significant at Harare (r = 0.40**) and at Bako (r= 0.51**). Days to anthesis and silking increased under low N while other agronomic traits decreased (Tables 4.4 and 4.5).

Table 4.4 Means, *F*-test and coefficient of variation (CV) for grain yield and agronomic traits of maize hybrids evaluated at Harare under optimum and low nitrogen stress conditions, 2006/07

Environment		GY	DA	DS	ASI	PH	EH	SEN	EPP	RPE	KPR	KPE	TKW
Optimum N	Grand mean	7.7	71.4	70.1	-1.4	256.1	136.3		1.12	14.3	37.4	536.5	295.0
	Minimum	3.1	65.9	63.9	-4.0	209.4	115.3		0.86	12.4	29.1	394.4	208.9
	Maximum	12.9	76.9	75.2	0.5	292.2	164.8		1.77	17.2	45.4	693.0	435.2
	Mean for QPM F_1s	7.7	71.5	70.1	-1.4	256.1	136.4		1.13	14.3	37.4	535.2	292.6
	Mean for QPM checks	8.1	71.2	69.8	-1.5	250.5	127.8		1.00	15.3	38.8	596.1	352.0
	Mean for normal check	11.6	66.0	65.7	-0.5	268.7	138.4		1.01	13.8	39.5	548.6	435.2
	F test	**	**	**	ns	**	**		**	**	**	**	**
	SE(m)	0.8	1.1	1.3	1.0	7.5	7.1		0.08	0.4	1.9	33.3	16.1
	CV(%)	13.7	2.2	2.6	7.7	4.1	7.4		10.18	4.2	7.0	8.8	7.7
Low N	Grand mean	0.9	76.0	80.3	4.5	172.6	78.2	4.8	0.64	13.2	18.7	252.0	182.9
	Minimum	0.1	69.0	72.6	0.6	132.8	52.8	3.0	0.20	8.2	7.9	80.9	122.3
	Maximum	1.9	84.5	90.8	11.0	195.4	94.9	6.5	0.92	16.8	28.4	432.1	260.1
	Mean for QPM F_1s	0.9	76.1	80.4	4.5	172.3	78.0	4.8	0.64	13.2	18.6	250.0	181.8
	Mean for QPM checks	1.0	71.3	75.5	4.5	185.5	82.1	5.8	0.65	14.3	23.8	341.2	197.9
	Mean for normal check	1.7	72.5	78.0	5.7	185.4	87.3	6.5	0.79	12.0	23.5	284.5	260.1
	F test	**	**	**	ns	**	ns	*	**	**	**	**	**
	SE (m)	0.2	0.9	1.9	1.9	8.1	7.1	0.6	0.09	1.0	3.1	49.9	17.0
	CV(%)	39.0	1.8	3.3	6.2	6.6	12.8	16.3	18.9	10.5	23.2	28.0	13.2
	Relative reduction[†]	88.5	-6.4	-14.6	431.1	32.6	42.6	-	42.9	8.0	50.0	53.0	38.0

[†] Percent relative reduction due to low N stress (1 - $MV_{low\ N}/MV_{optimum\ N}$); * $P \leq 0.05$; ** $P \leq 0.01$; ASI= anthesis-silking interval (d); DA= days to anthesis; DS= days to silking; EH= ear height (cm); EPP= ears per plant; GY= grain yield (t ha^{-1}); KPR= number of kernels per row; KPE= number of kernels per ear; ns= non-significant; PH= plant height (cm); RPE= number of rows per ear; SE(m)=standard error of the mean; SEN= leaf senescence (%); TKW= thousand kernel weight (g)

Table 4.5 Means, *F*-test and coefficient of variation (CV) for grain yield and agronomic traits of maize hybrids evaluated at Bako under optimum and low nitrogen stress conditions, 2007

Environment		GY	AD	SD	ASI	PH	EH	SEN	EPP	ED	EL	RPE	KPR	KPE	TKW
Optimum N	Grand mean	6.5	80.3	81.9	1.6	240.8	121.6		1.41	4.6	16.2	14.4	38.4	553.8	288.3
	Minimum	1.4	70.4	72.2	-2.0	178.8	90.0		0.81	3.8	10.7	11.8	22.2	261.5	176.8
	Maximum	9.7	93.6	97.1	5.5	293.5	155.0		2.02	5.0	20.3	17.2	45.0	685.2	417.2
	Mean for QPM F_1s	6.5	80.4	81.9	1.5	240.5	121.4		1.41	4.6	16.2	14.4	38.4	553.0	286.3
	Mean for QPM check	6.4	75.2	77.8	2.0	244.9	117.0		1.26	4.8	16.9	15.4	42.4	651.7	300.3
	Mean for normal checks	6.6	78.0	81.9	3.8	255.2	132.3		1.48	4.8	17.4	14.4	38.0	546.9	389.5
	F test	**	**	**	**	**	**		**	**	**	**	**	**	**
	SE(m)	0.4	1.0	1.4	0.7	7.1	7.4		0.10	0.1	0.6	0.4	1.7	31.2	11.9
	CV(%)	8.5	1.8	2.3	3.4	4.1	8.6		9.78	2.9	5.5	4.0	6.3	8.0	5.9
Low N	Grand Mean	3.3	87.2	87.9	0.7	161.1	66.5	3.4	1.07	4.1	12.2	13.7	30.9	424.3	240.4
	Minimum	0.4	76.0	76.5	-1.0	111.7	36.3	1.0	0.63	3.4	5.8	11.3	13.0	147.0	164.9
	Maximum	6.4	100.7	101.5	3.3	219.2	103.7	7.5	1.72	4.7	17.4	16.0	40.8	564.8	399.4
	Mean for QPM F_1s	3.3	87.2	88.0	0.7	160.1	65.8	3.4	1.06	4.1	12.1	13.7	30.9	423.0	238.4
	Mean for QPM check	2.9	83.7	84.7	0.7	166.1	60.8	4.2	1.11	4.4	12.2	14.4	33.6	487.4	192.2
	Mean for normal checks	5.8	84.7	85.5	0.8	212.9	102.2	1.5	1.19	4.7	16.4	13.6	33.8	461.9	369.3
	F test	**	**	**	ns	**	**	**	**	**	**	**	**	**	**
	SE(m)	0.7	1.9	2.0	0.6	9.8	7.5	0.6	0.15	0.1	0.9	0.5	2.2	37.4	16.5
	CV(%)	28.6	3.1	3.2	3.0	8.6	16.0	26.0	19.57	4.2	10.5	5.1	10.2	12.5	9.7
	Relative reduction[†]	48.8	-8.5	-7.4	53.2	33.1	45.3	-	24.11	9.9	24.7	4.8	19.5	23.4	16.6

[†] Percent relative reduction due to low N stress (1 - $MV_{low\ N}/MV_{optimum\ N}$); * $P \leq 0.05$; ** $P \leq 0.01$; ASI= anthesis-silking interval (d); DA= days to anthesis; DS= days to silking; ED= ear diameter (cm); EH= ear height (cm); EL= ear length (cm); EPP= ears per plant; GY= grain yield (t ha^{-1}); KPR= number of kernels per row; KPE= number of kernels per ear; ns= non-significant; PH= plant height (cm); RPE= number of rows per ear; SE(m)=standard error of the mean; SEN= leaf senescence (%); TKW= thousand kernel weight (g)

Figure 4.1 Performance of QPM hybrids under optimal and low N stress conditions

Highly significant GCA mean squares were observed for all traits at Harare under optimum N (Table 4.6). SCA mean squares were significant for all traits except for days to anthesis and silking. Under low N at Harare, GCA mean squares were significant for all traits and SCA mean squares were not significant for grain yield and leaf senescence. Similarly, GCA mean squares were significant for all traits at Bako under optimum and low N conditions (Table 4.6). SCA mean squares were significant for all traits except ear height and anthesis-silking interval under optimum N, and number of rows per ear under low N conditions.

Combined analysis of variance across optimum N environments revealed that environment effects were significant for all traits except number of rows per ear (Table 4.7). All traits exhibited highly significant differences among the hybrids. Grain yield ranged from 2.2 to 10.9 t ha^{-1} with a mean of 7.1 t ha^{-1}. The highest yielding hybrid was VL05483 x CML491 (10.9 t ha^{-1}) followed by VL05483 x CML511 (10.0 t ha^{-1}). Mean days to anthesis was 75.94 with a range of 68.5 – 84.3 days. Days to silking ranged from 68.4 to 84.7 with a mean of

76.0. Mean plant and ear height were 248.3 and 128.9 cm with ranges of 194.1 – 281.2 and 104.9 – 151.5 cm, respectively. Ears per plant ranged from 0.9 to 1.8 with a mean of 1.3. Mean number of rows per ear and kernels per row were 14.4 and 37.9 with ranges of 12.3 – 16.4 and 26.7 – 45.2, respectively. Number of kernels per ear ranged from 328.0 – 689.0 with a mean of 544.1. Mean thousand kernel weight was 289.5 g with a range of 192.8 – 355.5 g. Combining ability analysis revealed significant GCA mean squares for all traits. SCA mean squares were significant for grain yield, plant height, number of kernels per row and kernels per ear, and thousand kernel weight.

Hybrid x E interactions were also significant for all traits (Table 4.7). GCA x E mean squares were significant for all traits but the magnitudes were consistently smaller than the respective GCA mean squares. SCA x E effects were significant for all traits except ear height. Similarly, the magnitudes of SCA x E mean squares were smaller than that of SCA for most traits. Across low N environments, highly significant differences were observed between the environments for all traits (Table 4.8). The differences among hybrids were highly significant for grain yield, days to anthesis and silking, plant height, number of rows per ear and thousand kernel weight. Grain yield ranged from 0.4 to 3.4 t ha^{-1} with a mean of 2.1 t ha^{-1}. The highest yielding hybrid was VL05200 x VL06375 (3.7 t ha^{-1}) followed by CML491 x VL06375 (3.4 t ha^{-1}). Mean days to anthesis was 81.7 with a range of 73.6 – 91.4. Days to silking ranged from 75.9 to 93.7 with a mean of 84.2. Plant height ranged from 130.6 to 191.5 cm with a mean of 166.2 cm. Number of rows per ear ranged from 10.3 to 15.6 with a mean of 13.4. Mean thousand kernel weight was 210.1 g with a range of 146.7 – 290.5 g. Mean relative grain yield loss under low N was 70.6%. Spearman's rank correlation between hybrid means across optimum and low N environments were positive and highly significant (r = 0.61**). Days to anthesis and silking increased by 7.6 and 10.8%, respectively. Plant height, ears per plant, number of rows per ear, number of kernels per row, kernels per ear and thousand kernel weight decreased by 33.1, 32.8, 6.4, 34.8, 38.2 and 27.4%, respectively.

Combining ability analysis under low N conditions revealed significant GCA mean squares for grain yield, days to anthesis and silking, plant height, number of rows per ear and thousand kernel weight. SCA mean squares were significant for plant height and thousand

kernel weight. Hybrid x E, GCA x E and SCA x E interaction mean squares were significant for all traits (Table 4.8).

The effects of environments and hybrids were significant for all traits evaluated across all environments (Table 4.9). Mean grain yield was 4.6 t ha^{-1} with a range of 1.3 - 6.9 t ha^{-1}. The highest yielding hybrid across environments was VL05483 x CML491 (6.7 t ha^{-1}) followed by CML491 x VL06375 (6.4 t ha^{-1}). The former hybrid also showed the highest grain yield across optimum N while the latter showed higher grain yield across low N conditions. Mean days to anthesis was 78.8 (range 71.0 to 87.0) while mean days to silking was 80.1 (range 72.2 to 88.3). The range for plant height was from 162.5 to 229.5 cm with a mean of 207.2 cm while ear height ranged from 82.0 to 127.9 cm with a mean of 107.9 cm. Ears per plant ranged from 0.75 to 1.35 with a mean of 1.06. Mean ear diameter was 4.3 cm with a range of 3.6 to 4.8 cm. Ear length ranged from 8.2 to 17.3 cm with a mean of 14.1 cm. Mean number of rows per ear and kernels per row were 13.9 and 31.3 with ranges of 11.8 to 15.8 and 21.6 to 37.0, respectively. Number of kernels per ear ranged from 263.9 to 541.6 with a mean of 440.3. Mean thousand kernel weight was 449.8 g (range 171.8 to 313.0 g).

Table 4.6 Mean squares due to hybrids, general (GCA) and specific (SCA) combining ability for grain yield and agronomic traits evaluated under optimum and low N stress conditions at Harare and Bako, 2006 and 2007

Trait†	Harare optimum N			Harare low N			Bako optimum N			Bako low N		
	Hybrid Df=104	GCA df=14	SCA df=90	Hybrid Df=104	GCA df=14	SCA df=90	Hybrid Df=104	GCA df=14	SCA df=90	Hybrid Df=104	GCA df=14	SCA df=90
GY	2.3**	6.6**	1.7**	0.2**	0.7**	0.1	2.5**	8.3**	1.6**	1.4**	3.5**	1.0**
DA	6.6**	39.7**	1.5	10.2**	60.3**	2.5**	25.6**	161.9**	4.4**	25.9**	147.6**	7.0**
DS	7.5**	42.4**	2.1	16.6**	89.6**	5.3*	25.5**	157.8**	4.9**	26.6**	148.9**	7.5**
ASI	2.0	-	-	10.0	-	-	1.3**	5.2**	0.7	0.9	-	-
PH	212.7**	885.5**	108.1**	175.9**	642.4**	103.3*	294.7**	850.5**	208.2**	260.6**	590.6**	209.3**
EH	139.6**	537.9**	77.6*	129.3	-	-	140.4**	627.9**	64.6**	94.1**	111.3**	91.5*
SEN	-	-	-	0.4*	0.8**	0.3	-	-	-	-	1.6**	0.8**
EPP	0.02**	0.04**	0.02**	0.03**	0.12**	0.02**	0.07**	0.30**	0.03**	0.04**	0.04**	0.04**
ED	-	-	-	-	-	-	0.07**	0.26**	0.04**	0.06**	0.20**	0.04**
EL	-	-	-	-	-	-	3.2**	15.3**	1.3**	3.5**	12.6**	2.1**
RPE	0.9**	4.2**	0.3**	2.3**	6.3**	1.6**	0.8**	4.1**	0.3**	0.8**	3.8**	0.3
KPR	11.5**	41.6**	6.8**	18.6**	51.7**	13.5*	12.4**	37.6**	8.5**	19.6**	60.2**	13.3**
KPE	3842.2**	16062.5**	1941.3**	4931.6**	13046.2**	3669.3*	4346.9**	16332.3**	2482.5**	4066.8**	9823.9**	3171.2**
TKW	854.3**	3961.1**	371.0*	694.0**	2102.8**	474.9*	1691.0**	8893.0**	570.7**	1215.8**	4148.2**	759.7**

† GCA and SCA effects were not analyzed for traits with non significant mean squares in the ANOVA; * * $P \leq 0.05$; ** $P \leq 0.01$; ASI= anthesis-silking interval (d); DA= days to anthesis; DS= days to silking; ED= ear diameter (cm); EH= ear height (cm); EL= ear length (cm); EPP= ears per plant; GY= grain yield (t ha^{-1}); KPR= number of kernels per row; KPE= number of kernels per ear; ns= non-significant; PH= plant height (cm); RPE= number of rows per ear; SEN= leaf senescence (%); TKW= thousand kernel weight (g)

Table 4.7 Combined analysis of variance and means for grain yield and agronomic traits of hybrids evaluated across optimum nitrogen environments at Harare and Bako, 2006 -2007

Source of variation	df	GY	DA	DS	PH	EH	EPP	RPE	KPR	KPE	TKW
Environment (E)	1	70.8**	4204.9**	7326.6**	12701.6**	11811.0**	4.12**	0.2	57.4**	16598.5**	2091.9*
Hybrids	104	3.8**	26.3**	26.5**	401.6**	206.2**	0.05**	1.3**	19.1*	6458.4**	2138.4**
GCA	14	12.4**	173.8**	174.1**	1628.7**	1000.4**	0.25*	7.9**	71.5**	28616.1**	11743.0**
SCA	90	2.5**	3.3	3.6	211.0**	82.7	0.02	0.3	10.9**	3011.4**	644.5**
Hybrids x E	104	1.0**	5.9**	6.5**	105.8**	73.8*	0.03**	0.4**	4.8**	1730.7**	406.9**
GCA x E	14	2.5*	27.9**	26.1**	107.3*	165.4**	0.09**	0.5**	7.6**	3778.7**	1111.1**
SCA x E	90	0.7**	2.5**	3.4**	105.3**	59.5	0.02**	0.3**	4.4*	1412.4*	297.3*
Error	164	0.4	1.1	1.7	52.9	53.1	0.01	0.2	3.2	1038.5	201.0
Mean		7.1	75.9	76.0	248.3	128.9	1.27	14.4	37.9	544.1	289.5
Min		2.2	68.5	68.4	194.1	104.7	0.88	12.3	26.7	328.0	192.8
Max		10.9	84.3	84.7	281.2	151.5	1.75	16.4	45.2	689.0	355.5
SE(m)		0.6	1.1	1.3	7.3	7.3	0.09	0.4	1.8	32.2	14.2
CV(%)		11.9	2.0	2.5	4.1	8.00	10.0	4.1	6.7	8.4	6.9

* * $P \leq 0.05$; ** $P \leq 0.01$; CV(%)= coefficient of variation; DA= days to anthesis; DS= days to silking; EH= ear height (cm); EPP= ears per plant; GY= grain yield (t ha^{-1}); KPR= number of kernels per row; KPE= number of kernels per ear; PH= plant height (cm); RPE= number of rows per ear; SE(m)=standard error of the mean; TKW= thousand kernel weight (g)

Table 4.8 Combined analysis of variance and means for grain yield and agronomic traits of maize hybrids evaluated across low nitrogen stress environments at Harare and Bako, 2006 -2007

Source of variation	df	GY	DA	DS	PH	SEN	EPP	RPE	KPR	KPE	TKW
Environment (E)	1	307.0**	6458.5**	3068.2**	7816.5**	100.5**	9.30**	14.7**	7963.7**	1571774.2**	168096.4**
Hybrids	104	0.9*	29.5**	35.8**	306.7**	0.6	0.04	1.8*	21.6	4894.4	1414.7**
GCA	14	3.0*	185.9**	217.7**	1055.3**	1.1	0.10	7.9**	78.7	14867.6	5150.0**
SCA	90	0.6	5.2	7.4	190.2*	0.5	0.03	0.9*	12.7	3343.3	833.8**
Hybrids x E	104	0.6**	6.6**	7.4**	129.8**	0.8**	0.03*	1.2**	16.6**	4104.0**	495.1**
GCA x E	14	1.2**	22.1**	20.7**	177.8**	1.3**	0.06**	2.2**	33.2**	8002.5**	1101.0**
SCA x E	90	0.5**	4.2**	5.4*	122.4**	0.7**	0.03**	1.1**	14.0**	3497.2**	400.7*
Error	164	0.3	2.3	3.8	80.6	0.4	0.02	0.6	7.2	1942.2	281.4
Mean		2.1	81.7	84.2	166.2	4.1	0.85	13.4	24.8	336.5	210.1
SE(m)		0.5	1.5	1.9	9.0	0.6	0.12	0.8	2.7	44.1	16.8
Min		0.4	73.6	75.9	130.6	3.2	0.49	10.3	16.5	199.8	146.7
Max		3.7	91.4	93.7	191.4	5.8	1.30	15.6	31.6	448.7	290.5
CV(%)		33.6	2.6	3.3	7.6	20.5	19.9	8.2	15.3	18.4	11.2
Relative Reduction†		70.6	-7.6	-10.8	33.1	-53.8	32.8	6.4	34.8	38.2	27.4

† Percent relative reduction due to low N stress (1 - $MV_{low\ N}/MV_{optimum\ N}$); * $P \leq 0.05$; ** $P \leq 0.01$; CV(%)= coefficient of variation; DA= days to anthesis; DS= days to silking; EPP= ears per plant; GY= grain yield (t ha^{-1}); KPR= number of kernels per row; KPE= number of kernels per ear; PH= plant height (cm); RPE= number of rows per ear; SE(m)=standard error of the mean; TKW= thousand kernel weight (g)

GCA mean squares combined across environments were highly significant for all traits (Table 4.9). SCA mean squares were highly significant for most traits except ears per plant and number of rows per ear. SCA sums of squares were larger than GCA sums of squares for grain yield (55%) and ear diameter (51%) whereas GCA sums of squares were larger for the other measured traits. Hybrid x E interaction was significant for all traits except for ear height and ear diameter. There was highly significant GCA x E interaction for all traits except ear diameter. SCA x E interaction was significant for all traits except ear height, ear diameter and ear length.

Phenotypic correlation coefficients between grain yield and agronomic traits at each and across environments are presented in Table 4.10. Grain yield had highly significant and negative correlation with days to anthesis and silking under all conditions. Phenotypic correlation between grain yield and anthesis-silking interval was highly significant and negative under optimum N at Bako. Grain yield showed positive and significant correlations with plant and ear heights, ears per plant, ear diameter and length, number of rows per ear, kernels per row and kernels per ear, and thousand kernel weight at each and across environments. Leaf senescence had highly significant negative correlation with grain yield under low N at Bako but the correlation was weak at Harare.

The estimates of GCA effects of 15 QPM inbred lines evaluated in a diallel cross for grain yield and agronomic traits under optimum N at Harare are presented in Table 4.11. The inbred lines varied significantly in GCA for all traits. GCA for grain yield varied from – 0.96 to 1.21 t ha^{-1}. Inbred lines VL054178, VL05561, VL05483, CML511, CML491 and VL06375 showed highly significant positive GCA effects for grain yield. In contrast, VL052, VL05200, VL052887, VL05482, CML144 and CML159 had significant negative GCA effects for grain yield. GCA effects for days to anthesis and silking were lower for VL054178, VL05482, VL05561, VL05483 and VL06375, and higher for VL05200, VL05468, VL052887, VL0523, VL0524, CML491 and CML144. Inbred lines VL052, VL05200, VL05482 and CML144 showed highly significant negative GCA effects for ear and plant height while VL052887 and VL0524 had significant positive GCA effects for both traits. VL05482, VL05561 and VL05483 had significantly high positive GCA effects for ears

per plant while VL05468 showed significantly high negative GCA effect. Inbred lines VL05468, VL05561 and CML491 showed positive GCA effects for number of rows per ear, kernels per row and kernels per ear while VL052 and VL0524 had negative GCA effects for these traits. For thousand kernel weight, highly significant positive GCA effects were observed for VL05200, VL054178, CML159 and VL06375 while highly significant negative GCA effects were observed for VL05468, VL052887, VL05482 and CML144.

The estimates of GCA effects of the inbred lines for various traits under low N conditions at Harare are presented in Table 4.12. Inbreds VL054178, VL05483, CML511 and VL06375 had highly significant positive GCA effects for grain yield while VL052 and VL05468 had highly significant negative GCA effects. VL054178, VL05482, VL05483 and VL06375 had highly significant negative GCA effects for days to anthesis and silking while many inbred lines showed highly significant positive GCA effects for these traits. Highly significant negative GCA effects for plant height were observed for VL05200 and VL05482 while highly significant positive GCA effects were observed for VL054178, VL05483, CML159 and VL06375. Inbred lines VL052887 and CML144 showed significant negative GCA effects for leaf senescence while VL052, VL054178, CML511 and VL06375 had significant positive GCA effects for this trait. GCA effects for ears per plant were positive and highly significant for VL05482, VL05483, CML491 and VL06375 but negative and highly significant for VL05468, VL052887, VL0523 and VL05561. Inbred lines VL05483, CML511 and VL0675 had positive significant GCA effects at least for two traits among number of rows per ear, kernels per row and kernels per ear. For thousand kernel weight, VL05200, VL054178, CML159 and VL06375 showed significant positive GCA effects.

Table 4.9 Combined analysis of variance and means for grain yield and agronomic traits of maize hybrids evaluated across optimal and low N stress environments at Harare and Bako, 2006 – 2007

Source of variation	df	GY	AD	SD	PH	EPP	RPE	KPR	KPE	TKW	df	EH	df	ED	EL
Environment (E)	3	1007.6**	4710.5**	5807.2**	242846.8**	10.4**	34.1**	8747.5**	2038052.2**	276937.6**	2	120093.6**	1	10.79**	860.52**
Hybrids	104	3.6**	53.9**	58.9**	580.9**	0.06**	2.5**	31.5**	8719.6**	3134.3**	104	241.2**	104	0.12**	5.80**
GCA	14	12.1**	356.1**	386.3**	2322.5**	0.25**	14.4**	120.3**	34046.7**	15498.1**	14	931.0**	14	0.44**	25.21**
SCA	90	2.3**	6.7**	8.1**	310.4**	0.03	0.7	17.7**	4780.1**	1210.4**	90	115.7**	90	0.07**	2.71**
Hybrids x E	312	0.9**	4.8**	5.8**	121.0**	0.03**	0.7**	10.2**	2822.6**	440.3**	208	70.2	104	0.01	0.90*
GCA x E	42	2.3**	17.8**	17.5**	215.5**	0.09**	1.3**	23.6**	7072.7**	1202.3**	28	173.0**	14	0.02	2.66**
SCA x E	270	0.7**	2.9**	3.9**	106.2**	0.02**	0.6**	8.1**	2161.4**	322.0**	180	59.0	90	0.01	0.69
Error	328	0.3	1.7	2.8	66.8	0.01	0.4	5.2	1490.4	241.2	246	54.3	164	0.01	0.61
Mean		4.6	78.8	80.1	207.2	1.06	13.9	31.3	440.3	249.8		107.9		4.3	14.1
Min		1.3	71.0	72.2	162.5	0.75	11.8	21.6	263.9	171.8		82.0		3.6	8.2
Max		6.7	87.0	88.3	229.6	1.35	15.8	37.0	541.6	313.0		127.9		4.8	17.3
SE(m)		0.4	0.9	1.2	5.8	0.08	0.4	1.6	27.3	11.0		6.0		0.1	0.8
CV(%)		17.1	2.3	2.9	5.6	14.17	6.3	10.3	12.4	8.8		9.7		3.6	7.8

* $P \leq 0.05$; ** $P \leq 0.01$; CV(%)= coefficient of variation; DA= days to anthesis; DS= days to silking; ED= ear diameter (cm); EH= ear height (cm); EL= ear length (cm); EPP= ears per plant; GY= grain yield (t ha^{-1}); KPR= number of kernels per row; KPE= number of kernels per ear; PH= plant height (cm); RPE= number of rows per ear; SE(m)= standard error of the mean; SEN= leaf senescence (1-5); TKW= thousand kernel weight (g)

Table 4.10 Phenotypic correlation coefficients between grain yield and agronomic traits at each environment and across environments

Trait[†]	Harare		Bako		Across		
	Optimum N	Low N	Optimum N	Low N	Optimum N	Low N	All
DA	-0.38**	-0.60**	-0.40**	-0.53**	-0.43**	-0.59**	-0.53**
DS	-0.31**	-0.70**	-0.47**	-0.55**	-0.44**	-0.63**	-0.54**
ASI	-	-	-0.26**	-	-	-	-
PH	0.46**	0.43**	0.60**	0.60**	0.65**	0.63**	0.72**
EH	0.22*	-	0.37**	0.42**	0.38**	-	0.43**
SEN	-	0.15	-	-0.34**	-	-	-
EPP	0.54**	0.67**	0.41**	0.22*	0.43**	-	0.38**
ED	-	-	0.63**	0.67**	-	-	0.64**
EL	-	-	0.61**	0.80**	-	-	0.70**
RPE	0.12	0.52**	0.22*	0.14	0.21*	0.13	0.23*
KPR	0.33**	0.59**	0.63**	0.67**	0.58**	-	0.67**
KPE	0.32**	0.64**	0.58**	0.67**	0.55**	-	0.65**
TKW	0.47**	0.04	0.54**	0.76**	0.52**	0.68**	0.61**

[†] Correlation coefficients were not calculated for traits with non significant mean squares in the ANOVA; * $P \leq$ 0.05; ** $P \leq$ 0.01; DA= days to anthesis; DS= days to silking; ED= ear diameter (cm); EH= ear height (cm); EL= ear length (cm); EPP= ears per plant; GY= grain yield (t ha^{-1}); KPR= number of kernels per row; KPE= number of kernels per ear; PH= plant height (cm); RPE= number of rows per ear; SEN= leaf senescence (1-5); TKW= thousand kernel weight (g)

Under optimum N conditions at Bako, significant positive GCA effects were exhibited by VL052887, VL05561, VL05483, CML511, CML159, CML491 and VL06375 while all the other inbred lines showed significant negative GCA effects for grain yield (Table 4.13). VL054178, VL05482, VL05561, VL05483, CML511, CML159 and VL06375 showed highly significant negative GCA effects for days to anthesis and silking. Inbred lines VL05200, VL052887, VL05561 and CML144 had significant negative GCA effects for anthesis-silking interval. GCA effects for ear and plant heights were highly significant and negative for VL05200, VL054178 and VL05482. Inbred lines VL052887, VL05482, VL05483, CML511, CML144 and CML491 had significant positive GCA effects for ears per

plant. GCA effects for ear diameter and length were highly significant and positive for VL05561, CML159 and VL06375. Inbred lines VL05468, VL05483, CML511and CML159 had positive GCA effects for number of rows per ear, kernels per row and kernels per ear. VL05200, VL054178, VL05561, CML159 and VL06375 showed highly significant GCA effects for thousand kernel weight.

The estimates of GCA effects of the inbred lines for various traits under low N conditions at Bako are presented in Table 4.14. Inbreds VL054178, VL05561, CML159 and VL06375 had highly significant positive GCA effects for grain yield while VL052, VL52887 and CML144 showed highly significant negative GCA effects. VL054178, VL05482, VL05561, VL05483, CML159 and VL06375 showed highly significant negative GCA effects for days to anthesis and silking. GCA effects for plant height were negative and significant for VL05200, VL0523 and CML144. None of the inbred lines had significant negative GCA effects for ear height; however, VL0524 showed the highest positive GCA effect which is highly significant. VL0523, CML511 and CML491 showed significant negative GCA effects for leaf senescence. GCA effects for ears per plant were positive and significant for VL054178, VL0524 and CML491. VL05468, VL05561, CML159 and VL06375 exhibited positive GCA effects for ear length and diameter. Inbred lines VL05468, VL05561, CML511, CML491 and VL06375 showed significant positive GCA effects at least for two of the traits among number of rows per ear, kernels per row and kernels per ear. For thousand kernel weight, VL054178, CML159 and VL06375 showed highly significant positive GCA effects while VL052887 and CML144 had highly significant negative GCA effects.

Table 4.11 General combining ability effects (GCA) of 15 QPM inbred lines for grain yield and agronomic traits under optimum nitrogen condition at Harare, 2006/07

Line	GY	DA	DS	PH	EH	EPP	RPE	KPR	KPE	TKW
VL052	-0.78**	0.42	0.57	-6.25**	-5.51**	-0.04*	-0.35**	-2.17**	-43.55**	-0.24
VL05200	-0.85**	1.48*	0.52	-16.06**	-6.18**	-0.06*	0.38**	-3.36**	-35.59**	12.65**
VL05468	-0.22	1.63**	1.93**	0.03	1.40	-0.07**	1.12**	2.44**	78.25**	-22.12**
VL054178	0.87**	-2.75**	-3.03**	-3.29	-6.45**	-0.05*	-0.99**	1.34**	-19.93*	36.28**
VL052887	-0.42*	1.89**	1.59**	7.26**	6.34**	0.01	0.01	-0.70	-8.92	-25.62**
VL05482	-0.43*	-3.84**	-3.84**	-13.04**	-12.83**	0.07**	-0.53**	0.41	-13.85	-9.58**
VL0523	-0.29	1.39**	1.57**	3.44	6.95**	-0.02	-0.73**	1.17**	-11.99	-5.05
VL0524	-0.34	1.05**	1.81**	5.13*	9.42**	0.00	-0.78**	-0.73	-39.52**	-11.39*
VL05561	0.84**	-0.84**	-0.73	1.98	4.53*	0.04*	0.27*	3.52**	60.46**	5.91
VL05483	1.21**	-1.19**	-1.36**	12.57**	2.34	0.13**	0.41**	-1.53**	-7.34	-1.96
CML511	0.55**	0.26	0.64	9.99**	2.25	0.03	0.49**	1.11*	36.01**	-1.32
CML144	-0.96**	1.41**	1.08**	-9.01**	-5.95**	0.00	0.22*	-0.96	-5.72	-17.59**
CML159	-0.46*	0.19	0.35	1.75	-4.51*	-0.06*	0.09	-0.55	-3.70	11.79**
CML491	0.57**	0.88**	0.93**	-0.72	5.62**	0.02	0.29**	0.82	22.97*	-1.84
VL06375	0.71**	-1.97**	-2.05**	6.21**	2.58	0.00	0.11	-0.80	-7.59	30.08**
SE(g_i)	0.20	0.29	0.34	2.01	1.91	0.02	0.11	0.50	8.91	4.32

* $P \leq 0.05$; ** $P \leq 0.01$; DA= days to anthesis; DS= days to silking; EH= ear height (cm); EPP= ears per plant; GY= grain yield (t ha^{-1}); KPR= number of kernels per row; KPE= number of kernels per ear; PH= plant height (cm); RPE= number of rows per ear; SE(g_i)= standard error of GCA; TKW= thousand kernel weight (g)

Table 4.12 General combining ability effects (GCA) of 15 QPM inbred lines for grain yield and agronomic traits under low nitrogen stress at Harare, 2006/07

Line	GY	AD	SD	PH	SEN	EPP	RPE	KPR	KPE	TKW
VL052	-0.28**	1.27**	1.99**	-0.78	0.30*	-0.05*	-0.58*	-3.28**	-49.62**	-6.76
VL05200	-0.08	2.31**	2.10**	-17.82**	-0.16	-0.09*	-0.35	-2.28**	-37.57**	23.89**
VL05468	-0.32**	2.47**	3.37**	-2.11	0.18	-0.07**	-0.58*	-3.37**	-44.68**	3.34
VL054178	0.13*	-3.65**	-3.91**	5.96**	0.30*	-0.01	-0.80**	2.19**	12.59	18.22**
VL052887	-0.17*	1.93**	1.76**	-2.27	-0.39**	-0.06**	0.01	0.28	-0.58	-15.10**
VL05482	0.06	-3.65**	-3.67**	-6.08**	-0.13	0.09**	-0.25	1.99*	17.98	-14.11**
VL0523	-0.17*	1.66**	1.70**	1.59	0.03	-0.10**	-0.32	-0.82	-17.47	7.59
VL0524	-0.12	1.47**	2.27**	-2.11	-0.09	-0.09*	-0.98**	-1.19	-29.51*	6.13
VL05561	-0.12	-0.30	-1.06*	-0.01	-0.24	-0.11**	-0.24	1.55	17.31	1.22
VL05483	0.39**	-2.49**	-4.23**	12.46**	-0.01	0.18**	1.70**	2.18**	58.69**	-13.70**
CML511	0.17*	-1.46**	-0.50	1.22	0.33*	0.06*	0.67*	2.03*	38.38**	-7.27
CML144	-0.13*	1.70**	2.03**	-2.01	-0.33*	0.00	0.24	-1.11	-11.64	-12.42**
CML159	0.11	0.04	-0.11	7.22**	-0.13	-0.01	0.61*	0.39	15.81	10.50*
CML491	0.06	0.85**	1.58**	-3.14	-0.08	0.15**	0.52*	-0.64	0.00	-12.49**
VL06375	0.47**	-2.15**	-3.30**	7.87**	0.41**	0.12**	0.36	2.09*	30.31*	10.97**
SE(g_i)	0.07	0.25	0.50	2.17	0.15	0.02	0.26	0.82	13.36	4.57

* $P \leq 0.05$; ** $P \leq 0.01$; DA= days to anthesis; DS= days to silking; EPP= ears per plant; GY= grain yield (t ha^{-1}); KPR= number of kernels per row; KPE= number of kernels per ear; PH= plant height (cm); RPE= number of rows per ear; SE(g_i)= standard error of GCA; SEN= leaf senescence (1-5); TKW= thousand kernel weight (g)

Table 4.13 General combining ability effects (GCA) of 15 QPM inbred lines for grain yield and agronomic traits under optimum N conditions at Bako, 2007

Line	GY	DA	DS	ASI	PH	EH	EPP	ED	EL	RPE	KPR	KPE	TKW
VL052	-0.66**	0.90**	1.27**	0.34	-3.37	0.11	-0.01	0.03	-0.63**	-0.01	-1.78**	-26.43**	-8.69**
VL05200	-1.17**	0.91**	0.52	-0.47*	-18.01**	-9.96**	-0.19**	0.03	-0.90**	0.37**	-2.57**	-22.90**	6.66*
VL05468	-0.92**	2.66**	3.35**	0.76**	-2.22	0.88	-0.11**	-0.02	0.41*	0.92**	1.54**	58.45**	-22.38**
VL054178	-0.22*	-5.11**	-4.69**	0.41*	-8.64**	-6.39**	-0.27**	-0.02	1.57**	-0.85**	0.75	-24.82**	48.64**
VL052887	0.39**	4.87**	3.50**	-1.28**	3.58	4.60*	0.34**	-0.21**	-1.07**	-0.42**	-1.30**	-34.94**	-31.76**
VL05482	-0.38**	-6.15**	-5.58**	0.64**	-5.62**	-5.46**	0.12**	-0.18**	-0.20	-0.69**	-1.74**	-51.76**	-4.53
VL0523	-0.49**	3.07**	3.31**	0.14	5.34**	6.11**	-0.03	-0.13**	-0.16	-0.62**	0.30	-17.80*	-11.47**
VL0524	-0.32**	3.34**	3.98**	0.57**	7.35**	9.01**	-0.01	-0.16**	-0.36*	-0.62**	0.05	-20.28*	-6.70*
VL05561	1.58**	-0.26**	-1.59**	-1.24**	6.78**	14.76**	-0.03	0.13**	2.15**	-0.05	4.26**	58.51**	21.84**
VL05483	0.73**	-3.71**	-4.04**	-0.24	6.98**	-3.31	0.12**	0.14**	-0.82**	0.95**	0.47	43.55**	-10.13**
CML511	0.47**	-1.44**	-1.41**	-0.01	5.16**	0.31	0.06*	0.10**	-0.63**	0.33**	0.78	24.20**	1.94
CML144	-0.94**	3.36**	3.11**	-0.39*	-10.82**	-3.85	0.07**	-0.09**	-1.58**	-0.17	-1.48**	-28.16**	-40.39**
CML159	0.94**	-2.77**	-2.52**	0.22	1.66	-9.00**	-0.16**	0.21**	1.25**	0.35**	1.13*	30.41**	41.51**
CML491	0.26*	3.51**	4.11**	0.61**	0.29	-3.31	0.15**	-0.06*	-0.25	0.14	0.23	8.17	-18.03**
VL06375	0.72**	-3.19**	-3.31**	-0.05	11.52**	5.49**	-0.04	0.23**	1.21**	0.38**	-0.65	3.80	33.50**
$SE(g_i)$	0.11	0.27	0.36	0.18	1.89	1.99	0.03	0.03	0.17	0.11	0.46	8.35	3.20

* $P \leq 0.05$; ** $P \leq 0.01$; ASI= anthesis-silking interval (d); DA= days to anthesis; DS= days to silking; ED= ear diameter; EH= ear height (cm); EL= ear length (cm); EPP= ears per plant; GY= grain yield (t ha^{-1}); KPR= number of kernels per row; KPE= number of kernels per ear; PH= plant height (cm); RPE= number of rows per ear; $SE(g_i)$= standard error of GCA; TKW= thousand kernel weight (g)

Table 4.14 General combining ability effects (GCA) of 15 QPM inbred lines for grain yield and agronomic traits under low nitrogen stress at Bako, 2007

Inbred line	GY	DA	DS	PH	EH	SEN	EPP	ED	EL	RPE	KPR	KPE	TKW
VL052	-0.56**	0.86	1.06*	-1.63	-2.45	0.19	0.01	-0.01	-0.75**	-0.09	-1.82**	-28.22**	-1.69
VL05200	-0.32	1.33*	1.03	-10.29**	-3.68	0.00	-0.08*	0.05	-0.70**	0.60**	-3.27**	-27.14**	8.71
VL05468	-0.10	2.78**	3.06**	-5.11	-1.69	0.13	-0.08*	0.08*	0.17	0.72**	0.61	31.12**	-8.63
VL054178	0.62**	-5.10**	-5.21**	-2.71	-2.06	0.55**	0.08*	-0.07*	1.29**	-0.95**	1.08	-14.78	26.30**
VL052887	-0.56**	5.46**	5.79**	-0.30	0.71	0.18	0.01	-0.17**	-1.33**	-0.03	-2.80**	-39.65**	-21.61**
VL05482	0.10	-5.12**	-4.94**	-0.93	-1.32	0.53**	0.04	-0.20**	0.84**	-0.75**	2.91**	13.22	-8.37
VL0523	-0.42*	2.75**	2.75**	-7.66**	-1.80	-0.65**	-0.02	-0.10**	-0.39	-0.52**	-0.22	-14.48	-11.42*
VL0524	-0.32	1.75**	1.60**	1.29	6.57**	0.08	0.09*	-0.07*	-0.02	-0.72**	0.55	-14.02	-7.99
VL05561	0.72**	-2.55**	-2.81**	0.79	2.71	-0.04	-0.02	0.04	1.53**	-0.15	3.88**	48.80**	5.37
VL05483	-0.21	-2.59**	-2.84**	7.16**	2.75	0.23	0.01	0.05	-1.53**	0.58**	-2.59**	-18.73	-5.49
CML511	-0.19	-0.33	-0.27	5.27*	1.20	-0.37*	-0.06	0.07*	-0.31	0.42**	1.45*	32.69**	-9.33*
CML144	-0.59**	3.27**	3.06**	-6.77*	-2.94	-0.02	-0.03	-0.10**	-0.79**	-0.04	-1.42**	-20.15*	-26.46**
CML159	0.60**	-3.32**	-3.30**	10.10**	-2.78	0.10	-0.01	0.23**	0.03	0.48**	-1.42*	-2.96	31.57**
CML491	0.26	3.62**	3.40**	-3.16	2.79	-0.60**	0.09*	0.00	0.31	0.34*	1.56*	29.97**	-3.17
VL06375	0.98**	-2.79**	-2.40**	13.97**	1.99	-0.30	-0.02	0.20**	1.64**	0.12	1.49*	24.33*	32.23**
SE(g_i)	0.18	0.51	0.53	2.62	2.02	0.17	0.04	0.03	0.24	0.13	0.60	10.02	4.42

* $P \leq 0.05$; ** $P \leq 0.01$; DA= days to anthesis; DS= days to silking; ED= ear diameter (cm); EH= ear height (cm); EL= ear length (cm); EPP= ears per plant; GY= grain yield (t ha^{-1}); KPE= number of kernels per ear; KPR= number of kernels per row; PH= plant height (cm); RPE= number of rows per ear; SE(g_i)= standard error of GCA; SEN= leaf senescence (1-5); TKW= thousand kernel weight (g)

Across optimum N environments, VL054178, VL05561, VL05483, CML511, CML491 and VL06375 showed highly significant GCA effects for grain yield while VL052, VL05200 and CML144 showed significantly lower GCA effects (Table 4.15). Inbred lines VL054178, VL05482, VL05561, VL05483, CML159 and VL06375 had highly significant negative GCA effects for days to anthesis and silking. Inbred lines VL05200, VL054178, VL05482 and CML144 showed significantly negative GCA effects for plant and ear heights. Inbred lines with highly significant GCA effects for ears per plant were VL052887, VL05482, VL05483, CML511 and CML491. Inbred lines VL05468, VL05561, CML511, CML159 and CML491 had positive GCA effects for number of rows per ear, kernels per row and kernels per ear. For thousand kernel weight, VL05200, VL054178, VL05561, CML159 and VL06375 had highly significant positive GCA effects.

Table 4.16 shows the estimates of GCA effects for grain yield and agronomic traits of the inbred lines combined across low N stress environments. VL054178, VL5561, CML159 and VL06375 showed highly significant positive GCA effects for grain yield while VL052, VL052887, VL0523 and CML144 showed highly significant positive GCA effects. Inbred lines with highly significant negative GCA effects for days to anthesis and silking were VL054178, VL05482, VL05561, VL05483, CML159 and VL06375. GCA effects for plant height were significant and negative for VL05200, VL05468, VL05482 and CML144. For number of rows per ear VL05483, CML511, CML159 and CML491 showed highly significant positive GCA effects. VL05200, VL054178, CML159 and VL06375 showed highly significant positive GCA effects for thousand kernel weight.

Across all environments, highly significant positive GCA effects for grain yield were observed for VL054178, VL05561, VL05483, CML511, CML159, CML491 and VL06375 while the other inbred lines showed negative GCA effects for the same trait (Table 4.17). Highly significant negative GCA effects for days to anthesis and silking were observed for VL054178, VL05482, VL05561, VL05483, CML159 and VL06375. Inbred lines VL05200, VL05482 and CML144 showed highly significant GCA effects for plant and ear height. For ears per plant, VL052887, VL05482, VL05483 and CML491 exhibited highly significant positive GCA effects. GCA effects for ear diameter and length were positive and highly

Table 4.15 General combining ability effects (GCA) of 15 QPM inbred lines for grain yield and agronomic traits evaluated across optimum nitrogen environments at Harare and Bako, 2006 and 2007

Inbred line	GY	DA	DS	PH	EH	EPP	RPE	KPR	KPE	TKW
VL052	-0.72**	0.66**	0.91**	-4.81**	-2.70	-0.03*	-0.18*	-1.98**	-35.00**	-4.47
VL05200	-1.01**	1.19**	0.52*	-17.03**	-8.08**	-0.12**	0.38**	-2.96**	-29.24**	9.65**
VL05468	-0.57**	2.14**	2.64**	-1.10	1.14	-0.09**	1.02**	1.99**	68.36**	-22.25**
VL054178	0.32**	-3.93**	-3.85**	-5.96**	-6.42**	-0.16**	-0.93**	1.05**	-22.37**	42.45**
VL052887	-0.01	3.38**	2.55**	5.41**	5.47**	0.18**	-0.21**	-0.99**	-21.93**	-28.69**
VL05482	-0.40**	-5.00**	-4.71**	-9.33**	-9.14**	0.09**	-0.61**	-0.68*	-32.80**	-7.05**
VL0523	-0.39**	2.23**	2.43**	4.40**	6.53**	-0.03*	-0.68**	0.73**	-14.89*	-8.26**
VL0524	-0.33**	2.20**	2.90**	6.24**	9.22**	0.00	-0.70**	-0.34	-29.90**	-9.05**
VL05561	1.21**	-0.54**	-1.16**	4.38**	9.65**	0.00	0.11	3.88**	59.48**	13.87**
VL05483	0.97**	-2.46**	-2.70**	9.78**	-0.49	0.13**	0.67**	-0.53	18.11**	-6.05*
CML511	0.51**	-0.60**	-0.38	7.59**	1.28	0.05**	0.41**	0.94**	30.10**	0.31
CML144	-0.95**	2.39**	2.09**	-9.91**	-4.90**	0.04*	0.03	-1.22**	-16.95**	-29.00**
CML159	0.24*	-1.28**	-1.08**	1.70	-6.76**	-0.12**	0.22**	0.29	13.36*	26.65**
CML491	0.42**	2.19**	2.52**	-0.22	1.16	0.09**	0.28**	0.53	15.57*	-9.92**
VL06375	0.72**	-2.58**	-2.68**	8.87**	4.04**	-0.03*	0.25**	-0.73**	-1.90	31.80**
$SE(g_i)$	0.11	0.20	0.25	1.38	1.38	0.02	0.08	0.34	6.11	2.69

* $P \leq 0.05$; ** $P \leq 0.01$; DA= days to anthesis; DS= days to silking; EH= ear height (cm); EPP= ears per plant; GY= grain yield (t ha^{-1}); KPE= number of kernels per ear; KPR= number of kernels per row; PH= plant height (cm); RPE= number of rows per ear; $SE(g_i)$= standard error of GCA; TKW= thousand kernel weight (g)

Table 4.16 General combining ability effects (GCA) of 15 QPM inbred lines for grain yield and agronomic traits evaluated across low nitrogen environments at Harare and Bako, 2006 and 2007

Inbred lines	GY	DA	DS	PH	RPE	TKW
VL052	-0.42**	1.07**	1.52**	-1.21	-0.33*	-4.23
VL05200	-0.20*	1.82**	1.56**	-14.06**	0.12	16.29**
VL05468	-0.21*	2.62**	3.21**	-3.61*	0.06	-2.64
VL054178	0.38**	-4.38**	-4.54**	1.62	-0.88**	22.26**
VL052887	-0.37**	3.69**	3.77**	-1.28	-0.01	-18.36**
VL05482	0.08	-4.38**	-4.31**	-3.51*	-0.49**	-11.24**
VL0523	-0.29**	2.20**	2.23**	-3.03	-0.43**	-1.91
VL0524	-0.22*	1.61**	1.94**	-0.42	-0.85*	-0.94
VL05561	0.30**	-1.43**	-1.93**	0.40	-0.19	3.30
VL05483	0.09	-2.55**	-3.53**	9.81**	1.15**	-9.60**
CML511	-0.01	-0.89**	-0.39	3.25	0.54**	-8.29**
CML144	-0.36**	2.49**	2.54**	-4.39**	0.10	-19.43**
CML159	0.35**	-1.64**	-1.71**	8.65**	0.54**	21.03**
CML491	0.16	2.23**	2.49**	-3.15	0.42**	-7.83**
VL06375	0.73**	-2.48**	-2.85**	10.92**	0.25	21.59**
$SE(g_i)$	0.10	0.28	0.37	1.70	0.15	3.18

* $P \leq 0.05$; ** $P \leq 0.01$; DA= days to anthesis; DS= days to silking; GY= grain yield (t ha^{-1}); PH= plant height (cm); RPE= number of rows per ear; $SE(g_i)$= standard error of GCA; TKW= thousand kernel weight (g)

significant for VL05561, CML159 and VL06375. For number of rows per ear, kernels per row and kernels per ear, VL05468, VL05561, CML511and CML491 showed positive GCA effects. Inbred lines VL05200, VL054178, VL05561, CML159 and VL06375 showed highly significant positive GCA effects for thousand kernel weight.

Minimum and maximum values of the SCA effects for grain yield and agronomic traits along with standard errors of SCA effects are presented in Table 4.18. A wide range of SCA values (from high negative to high positive) were observed for all traits. The SCA effects for grain

yield were high for the crosses VL054178 x CML144, VL05483 x CML144, VL05483 x CML491 and CML511 x CML491 across optimum N and across all environments (Table 4.19).

The mean performance of the 15 QPM parental inbred lines for grain yield and agronomic traits across optimum N conditions are given in Table 4.20. VL052887, VL05561, VL05483, CML144 and VL06375 showed higher grain yield. Inbred lines VL054178 and VL05482 took smaller number of days to anthesis and silking, hence, earlier in maturity. VL05200, VL05482 and VL05561 had shorter ear and plant heights. VL05482, VL05483, CML144 and VL06375 were prolific inbreds as they showed higher number of ears per plant. VL052, VL05468, VL05561, VL05483 and VL06375 had bigger ears as shown by high values of ear diameter and length, number of rows per ear, kernels per row and kernels per ear. VL052, VL05200 and VL06375 had larger kernels as evident from the high values of thousand kernel weight.

Mid-parent (MPH) and high parent (HPH) heterosis of the crosses among 15 QPM inbred lines are summarized in Table 4.21. The mean percentage MPH ranged from -9.1% for days to silking to 112.7% for grain yield. Mean percentage HPH ranged from -12.0% for days to silking to 89.8% for grain yield. All the crosses showed negative MPH and HPH for days to anthesis and silking. On the other hand, all the crosses showed positive MPH for plant and ear heights, number of kernels per row and kernels per ear. The percentage MPH for grain yield ranged from -20.7 to 229.2% with a mean of 112.8% while the HPH ranged from -30.4 to 221.4% with a mean of 89.8% (Table 4.22). Crosses VL052 x VL054178, VL05468 x VL054178 and CML511x CML491 showed higher MPH and HPH (above 200%) for grain yield. Generally, about 65% and 38% of the crosses showed above 100% MPH and HPH values for grain yield, respectively.

Table 4.17 General combining ability effects (GCA) of 15 QPM inbred lines for grain yield (t ha^{-1}) and agronomic traits across low N stress and optimal environments at Harare and Bako, 2006 and 2007

Inbred Lines	GY	DA	DS	PH	EH	EPP	ED	EL	RPE	KPR	KPE	TKW
VL052	-0.57**	0.85**	1.22**	-3.03	-2.60	-0.02	0.00	-0.70**	-0.25*	-2.26**	-36.97**	-4.34
VL05200	-0.60**	1.49**	1.06**	-15.53**	-6.60**	-0.11**	0.04*	-0.81**	0.25*	-2.87**	-30.80**	12.97**
VL05468	-0.39**	2.36**	2.92**	-2.35	0.19	-0.08**	0.03	0.29*	0.55**	0.30	30.78**	-12.44**
VL054178	0.35**	-4.15**	-4.21**	-2.17	-4.96**	-0.06**	-0.04*	1.41**	-0.90**	1.34**	-11.73	32.35**
VL052887	-0.19	3.54**	3.16**	2.06	3.89**	0.08**	-0.21**	-1.19**	-0.12	-1.13**	-21.03**	-23.52**
VL05482	-0.16	-4.69**	-4.51**	-6.43**	-6.54**	0.08**	-0.18**	0.32**	-0.55**	0.89*	-8.60	-9.14**
VL0523	-0.34**	2.22**	2.33**	0.68	3.75**	-0.04*	-0.11**	-0.27	-0.55**	0.13	-15.43*	-5.09
VL0524	-0.28**	1.91**	2.41**	2.91	8.34**	0.00	-0.13**	-0.20	-0.79**	-0.34	-25.83**	-5.00
VL05561	0.76**	-0.99**	-1.54**	2.40	7.32**	-0.04*	0.08**	1.83**	-0.04	3.30**	46.27**	8.59**
VL05483	0.53**	-2.48**	-3.12**	9.80**	0.60	0.11**	0.10**	-1.17**	0.92**	-0.38	19.06**	-7.82**
CML511	0.25*	-0.74**	-0.38	5.42**	1.26	0.03	0.09**	-0.46**	0.49**	1.34**	32.83**	-4.00
CML144	-0.66**	2.44**	2.32**	-7.15**	-4.26**	0.01	-0.08**	-1.17**	0.07	-1.24**	-16.43*	-24.21**
CML159	0.30**	-1.45**	-1.40**	5.17**	-5.45**	-0.06**	0.23**	0.64**	0.39**	-0.11	9.90	23.84**
CML491	0.29**	2.22**	2.50**	-1.68	1.70	0.11**	-0.02	0.04	0.32**	0.50	15.28*	-8.87**
VL06375	0.72**	-2.52**	-2.78**	9.91**	3.37*	0.01	0.21**	1.42**	0.24*	0.53	12.70	26.69**
SE(g_i)	0.11	0.25	0.31	1.55	1.40	0.02	0.02	0.15	0.10	0.40	7.31	2.94

* $P \leq 0.05$; ** $P \leq 0.01$; DA= days to anthesis; DS= days to silking; ED= ear diameter (cm); EH= ear height (cm); EL= ear length (cm); EPP= ears per plant; GY= grain yield (t ha^{-1}); KPE= number of kernels per ear; KPR= number of kernels per row; PH= plant height (cm); RPE= number of rows per ear; SE(g_i)= standard error of GCA; TKW= thousand kernel weight (g)

Table 4.18 Minimum, maximum and standard error (SE) for estimates of specific combining ability (SCA) for grain yield and agronomic traits of crosses among 15 QPM inbred lines across optimum nitrogen, low nitrogen stress and across all environments

Environment	Trait	Minimum	Maximum	$SE(s_{ij})$
Optimum N	Grain yield (t ha^{-1})	-4.14	2.41	0.39
	Plant height (cm)	-31.78	31.60	4.76
	Kernel per row	-11.57	4.30	1.17
	Kernels per ear	-171.59	76.75	21.10
	Thousand kernel weight (g)	-68.82	42.93	9.28
Low N	Plant height (cm)	-24.14	16.97	5.88
	Thousand kernel weight (g)	-77.78	55.52	10.98
Across	Grain yield (t ha^{-1})	-2.64	2.41	0.37
	Days to anthesis	-2.87	3.37	0.85
	Plant height (cm)	-26.38	12.06	5.35
	Ear height (cm)	-15.44	11.12	4.82
	Days to silking	-2.60	4.20	1.08
	Ear diameter (cm)	-0.81	0.39	0.07
	Ear length (cm)	-5.45	2.15	0.51
	Thousand kernel weight (g)	-73.26	40.50	10.17
	Kernels per row	-9.50	4.98	1.49
	Kernels per ear	-135.51	77.40	25.27

$SE(s_{ij})$= standard error of SCA

Table 4.19 Estimates of specific combining ability (SCA) effects for grain yield (t ha^{-1}) of crosses among 15 QPM inbred lines evaluated across optimum nitrogen conditions (above diagonal, SE(s_{ij})= 0.39) and across environments (below diagonal, SE(s_{ij})= 0.36)

Cross	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10	P11	P12	P13	P14	P15
P1		-0.11	-0.14	1.29**	-1.31**	0.88*	-0.15	0.35	0.80*	0.46	0.76	-1.67**	0.52	-1.87**	0.37
P2	-0.26		-0.15	0.43	-0.23	0.49	0.12	0.65	0.43	-0.51	0.57	-1.27**	-0.01	-1.19**	0.96*
P3	-0.12	-0.31		1.01*	-0.56	0.16	0.18	-0.77*	0.14	0.38	0.21	-0.44	0.94*	-0.81*	0.04
P4	0.77*	0.75*	0.81*		0.42	-0.95*	1.09**	0.72	-1.29**	-0.86*	-0.60	1.40**	-2.78**	0.39	-0.08
P5	-0.92*	-0.44	-0.23	0.53		0.44	-0.11	-0.24	1.39**	0.85*	0.22	-2.04**	1.05**	-0.26	0.57
P6	0.72	0.32	0.00	-0.56	0.67		1.17**	0.42	-0.59	-1.10**	-0.13	0.92*	-0.33	0.03	-1.23**
P7	-0.13	-0.01	0.18	0.82*	-0.16	0.7		-4.14**	-0.37	0.61	0.16	0.24	0.66	-0.37	1.09**
P8	0.30	0.15	-0.36	0.32	-0.11	0.22	0.51		-0.13	0.64	0.54	0.26	0.64	0.58	0.66
P9	0.54	0.22	0.33	-0.89*	0.67	-0.18	-2.64**	-0.36		-0.56	0.17	1.40**	-0.46	0.12	-0.88*
P10	0.43	-0.21	-0.01	-0.93*	0.53	-0.73*	-0.14	0.47	-0.31		-2.03**	2.41**	-0.99*	2.39**	-1.51**
P11	0.31	0.44	0.05	-0.21	0.16	0.04	0.40	0.22	-0.21	-1.00**		0.13	0.20	2.02**	-2.04**
P12	-0.98**	-1.09**	-0.49	1.20**	-1.28**	0.60	0.12	0.17	1.14**	1.68**	0.25		0.19	-2.53**	-0.21
P13	0.43	0.33	0.78*	-2.33**	0.43	-0.33	0.02	0.66	-0.18	-0.56	0.25	0.07		0.58	-0.04
P14	-1.07**	-0.78*	-0.54	0.23	-0.30	-0.38	0.11	0.49	0.30	1.28**	0.85*	-1.54**	0.45		1.10**
P15	0.14	1.04**	0.06	-0.35	0.60	-0.94**	0.39	0.62	-0.78*	-0.87*	-1.10**	-0.73*	0.04	0.79*	

* $P \leq 0.05$; ** $P \leq 0.01$; P1= VL052; P2= VL05200; P3= VL05468; P4= VL054178; P5= VL052887; P6= VL05482; P7= VL0523; P8= VL0524; P9= VL05561; P10= VL05483; P11= CML511; P12= CML144; P13= CML159; P14= CML491; P15= VL06375; SE(sij)= standard error of SCA

Table 4.20 Mean performance of 15 QPM parental inbred lines for grain yield and agronomic traits evaluated under optimum nitrogen conditions at Harare and Bako, 2006 and 2007

Line	GY	DA	SD	PH	EH	EPP	ED	EL	RPE	KPR	KPE	TKW
VL052	2.5	88.5	89.8	183.8	86.3	0.9	4.1	12.8	13.6	25.3	343.8	249.4
VL05200	3.7	84.0	84.5	133.8	68.8	1.0	4.2	11.0	14.6	22.9	334.4	277.5
VL05468	2.7	86.8	88.8	172.5	85.0	1.0	4.0	12.0	16.2	28.7	465.3	153.6
VL054178	2.3	76.0	77.8	146.3	67.5	1.1	3.2	12.4	11.2	22.2	250.5	231.6
VL052887	4.1	84.9	84.5	178.6	90.8	1.3	3.8	11.6	12.6	19.9	255.6	217.9
VL05482	2.8	76.5	77.5	131.3	56.3	1.3	3.6	12.4	11.1	27.7	308.1	188.1
VL0523	3.2	86.8	87.3	173.8	91.3	1.3	3.6	11.8	11.9	27.8	329.8	211.7
VL0524	2.4	87.5	89.3	175.0	97.5	0.9	3.7	11.7	11.5	24.9	284.2	232.9
VL05561	4.1	82.5	81.8	140.0	73.8	1.3	3.7	13.6	13.6	28.4	386.0	215.5
VL05483	4.3	77.0	77.8	185.0	86.3	1.4	4.2	11.3	15.3	27.0	412.3	204.8
CML511	3.3	78.3	78.3	186.3	85.0	1.1	4.1	10.5	13.9	26.3	363.5	207.8
CML144	4.0	85.5	84.3	152.5	72.5	1.4	4.0	11.9	14.6	27.1	392.9	174.9
CML159	3.3	80.3	81.5	155.0	66.3	0.9	4.0	13.8	13.9	24.1	333.0	241.5
CML491	3.3	89.3	91.3	179.3	77.5	1.3	3.8	13.2	13.9	28.1	390.8	242.3
VL06375	4.6	79.8	81.0	198.8	90.0	1.3	3.5	13.5	12.9	26.5	350.8	252.5
Mean	3.4	82.9	83.7	166.1	79.6	1.2	3.8	12.2	13.4	25.8	346.7	220.1
Minimum	2.3	76.0	77.5	131.3	56.3	0.9	3.2	10.5	11.1	19.9	250.5	153.6
Maximum	4.6	89.3	91.3	198.8	97.5	1.4	4.2	13.8	16.2	28.7	465.3	277.5
$LSD_{0.05}$	1.2	4.1	4.1	24.0	17.9	0.3	0.2	1.3	1.0	2.5	38.1	23.0
CV%	24.8	3.4	3.4	10.0	15.5	19.9	4.3	7.1	4.9	6.8	7.6	7.2

CV(%)= coefficient of variation; DA= days to anthesis; DS= days to silking; ED= ear diameter (cm); EH= ear height (cm); EL= ear length (cm); EPP= ears per plant; GY= grain yield (t ha^{-1}); KPE= number of kernels per ear; KPR= number of kernels per row; LSD= least significant difference; PH= plant height (cm); RPE= number of rows per ear; TKW= thousand kernel weight (g)

Table 4.21 Minimum, maximum and mean of mid- parent heterosis and high-parent heterosis for grain yield and agronomic traits of crosses among 15 QPM inbred lines evaluated at Harare and Bako, 2006 and 2007

Trait	Mid-parent heterosis (%)			High-parent heterosis (%)		
	Minimum	Maximum	Mean	Minimum	Maximum	Mean
Grain yield (t ha^{-1})	-20.7	229.2	112.8	-30.4	221.4	89.8
Days to anthesis	-14.3	-2.3	-8.4	-20.1	-2.6	-11.3
Days to silking	-15.0	-2.3	-9.2	-20.8	-2.5	-12.0
Plant height (cm)	26.1	77.1	50.2	18.6	71.6	39.8
Ear height (cm)	39.9	91.9	62.6	27.3	86.7	49.8
Ears per plant	-20.6	50.0	9.1	-33.0	43.7	0.4
Ear diameter (cm)	-1.1	44.2	19.1	-2.5	39.7	14.1
Ear length (cm)	-8.9	56.6	32.0	-9.2	52.2	26.1
Thousand kernel weight (g)	-3.6	70.1	32.0	-11.5	50.3	21.9
Number of rows per ear	-2.2	19.8	7.5	-11.7	18.0	1.0
Number of kernels per row	1.7	87.0	47.4	-3.7	77.4	39.3
Number of kernels per ear	6.8	109.8	57.9	-0.6	105.2	44.1

Table 4.22 Percent mid-parent heterosis (below diagonal) and high parent heterosis (above diagonal) for grain yield (t ha^{-1}) of crosses among 15 QPM inbred lines evaluated at Harare and Bako, 2006 and 2007

Inbred line	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10	P11	P12	P13	P14	P15
P1		43.4	109.4	213.8	23.0	141.8	81.8	151.5	106.3	80.6	129.8	-6.5	114.2	47.2	63.2
P2	69.4		46.3	86.6	42.3	68.2	58.8	74.5	89.9	51.8	95.6	-3.8	71.9	44.8	69.7
P3	115.8	68.5		190.7	45.0	121.6	96.8	100.7	93.6	82.3	117.8	27.7	131.1	83.3	59.3
P4	228.7	128.9	213.3		90.5	114.1	152.8	221.4	80.5	74.2	120.0	95.8	46.2	145.9	76.1
P5	52.0	50.3	74.9	143.7		73.3	60.4	58.3	135.7	106.1	90.2	-0.5	103.7	76.1	83.0
P6	154.9	89.8	126.9	135.7	105.1		132.7	139.4	79.9	51.8	112.2	66.0	98.1	113.4	35.0
P7	102.8	69.4	113.6	193.8	80.1	147.2		-30.4	85.7	91.7	121.4	49.1	128.4	101.9	86.2
P8	157.3	110.0	111.5	229.2	99.0	157.8	-20.7		93.0	93.8	134.4	51.2	129.3	131.9	77.9
P9	153.8	99.6	132.5	130.1	136.9	112.0	107.5	141.6		101.7	121.1	115.5	98.9	117.7	78.1
P10	127.3	64.2	124.2	126.9	111.3	83.4	120.0	148.1	107.8		51.7	120.6	69.4	151.7	59.0
P11	160.7	105.0	140.5	159.6	110.1	129.3	125.6	171.2	143.1	71.3		68.8	141.4	200.5	37.3
P12	14.5	0.5	52.7	148.5	0.6	94.7	65.8	88.5	116.7	128.6	84.6		63.7	0.4	75.7
P13	143.0	80.2	155.2	72.6	125.0	114.1	132.7	165.3	118.7	91.3	141.4	79.0		149.2	75.3
P14	67.2	51.5	102.8	190.7	94.1	131.0	106.1	168.7	138.9	183.7	201.1	9.5	149.7		104.0
P15	109.7	88.3	100.2	133.8	92.8	66.7	118.9	132.3	88.6	63.5	58.9	87.1	102.8	135.7	

P1= VL052; P2= VL05200; P3= VL05468; P4= VL054178; P5= VL052887; P6= VL05482; P7= VL0523; P8= VL0524; P9= VL05561; P10= VL05483; P11= CML511; P12= CML144; P13= CML159; P14= CML491; P15= VL06375

4.5 Discussion

Significant differences observed among hybrids for individual and across environments indicate the existence of a high level of variation for various characteristics which makes selection possible for improved grain yield and agronomic traits under N stress and non-stress conditions. Similar results were reported for QPM diallel entries evaluated under non-stressed conditions (Pixley and Bjarnason, 1993; Vasal et al., 1993a; b; Bhatnagar et al., 2004; Xingming et al., 2004; Hadji, 2004). Variability in the performance of normal maize hybrids under low N conditions were reported by several investigators (Banziger and Lafitte, 1997; Betran et al., 2003e; Diallo et al., 2004; Banziger and Diallo, 2004; Mosisa et al.,

2007). Lower yield observed in QPM hybrids compared to the normal maize hybrid checks at most of the environments suggests the need for more breeding effort for the development of competent QPM germplasm. Special effort should be devoted to the development of low N stress tolerant QPM genotypes. Bhatnagar et al. (2004) also reported that QPM hybrids yield less than the commercial non-QPM hybrid checks.

The grain yield under low N stress at Harare was lower (Table 4.4) and at Bako was higher (Table 4.5) than the stipulated limit recommended by Banziger et al. (1997) who determined that average grain yield under low N stress has to be between 25% and 35% of what the average yield would have been in the same location under optimum N to be able to select varieties that perform reasonably well both under optimum and low N stress conditions. The results of this study indicated that the stress level at Harare low N is more severe than that of Bako which is less severe than the level recommended to identify low N tolerant germplasm. The grain yield loss due to low N was high at both locations (88.5% at Harare and 48.8% at Bako). However, positive and highly significant rank correlation between grain yields under stress and optimal conditions indicates that the hybrids had consistent performance under contrasting N conditions. Hence, simultaneous improvement for a wide range of N stress levels should be possible. This has been confirmed by other trials conducted under low and optimum N conditions (Lafitte and Edmeades, 1994a; Banziger et al., 1997; Presterl et al., 2003).

Hybrid x E interactions were significant for most traits across optimum N (Table 4.7), low N stress (Table 4.8) and all (Table 4.9) environments, suggesting that the hybrids did not perform consistently across locations. The mean grain yield across low N was 29.4% of the optimum N (Table 4.8), which is within the recommended range (Banziger and Lafitte, 1997). Nevertheless, different magnitudes of grain yield loss can be expected under low N conditions depending on the stress level of the environment (Banziger et al., 1997; Banziger and Lafitte, 1997; Banziger et al., 1999a; Betran et al., 2003e; Smalberger and Toit, 2004; Monneveux et al., 2005). The level of reduction in plant height, number of kernels per ear and thousand kernel weight observed across low N in these experiments were close to the amounts reported by Banziger and Laffite (1997), but the reduction observed for ears per

plant was high for this study (Table 4.8). Banziger and Lafitte (1997) observed a significant reduction in plant height (27.1%), ears per plant (11.2%), grains per ear (47.8%) and grain weight (30.7%) under low N.

The phenotypic correlations between grain yield and other agronomic traits (Table 4.10) indicated that early anthesis and silking, longer anthesis-silking interval and higher proportion of leaf senescence resulted in a decrease in grain yield under low and optimum N. An earlier maturing variety, owing to its shorter life cycle, is predisposed to lower yields than a later maturing variety which has the opportunity to draw on nutrients and photosynthesize over a longer period (Pswarayi and Vivek, 2008). Nitrogen stress delays silking of maize and thereby widens ASI (Jacobs and Pearson, 1991). Delayed leaf senescence indicates the ability of the plant or genotype to intercept light for a longer time (Wolfe et al., 1988; Banziger and Lafitte, 1997). The positive correlations of plant and ear height, ear diameter and length, number of rows per ear, kernels per row and kernels per ear, and thousand kernel weight with grain yield indicate that increases in these traits result in increased grain yield, thereby indicating the possibility of simultaneous improvement of these traits and grain yield. This finding is consistent with other reports (Banziger et al., 1997; Betran et al., 2003e; Monneveux et al., 2005; Pswarayi and Vivek, 2008). However, genotypes with taller plant and ear height are not desirable due to lodging susceptibility. Therefore while selecting for a high yielding genotype maintaining a balance between higher yield and shorter stature is critical.

GCA is associated with additive genetic effects while SCA is associated with non-additive genetic effects (Baker, 1978; Falconer and Mackay, 1996). Significance of GCA and SCA mean squares for most traits at each and across environments indicates the importance of both additive and non-additive genetic effects in the inheritance of these traits. This finding is in agreement with previous diallel studies on QPM inbred lines (Pixley and Bjarnason, 1993; Bhatnagar et al., 2004; Hadji, 2004; Fan et al., 2004). However, in combined analysis across low N (Table 4.8), SCA mean squares were not significant for most traits, including grain yield, indicating that non-additive genetic effects are less important under low N stress. This finding is not consistent with previous reports (Diallo et al., 2003; Betran et al., 2003e;

Makumbi et al., 2004). However, consistent with the current study, in QPM inbred lines Xingming et al. (2004) and in QPM pools and populations Vasal et al. (1993a; b) reported lack of non-additive gene action for grain yield and other agronomic traits. Beker (1978) indicated that when SCA mean squares are not significant, the performance of a single-cross progeny can be adequately predicted on the basis of GCA effects. If, on the other hand, the SCA mean square is significant the relative importance of GCA and SCA should be assessed.

The predominance of GCA sums of squares to SCA sums of squares indicates the relative importance of additive gene action to non-additive gene action while the predominance of SCA sums of squares implies the relative importance of non-additive gene action. Most of the inbred lines used in the current study were developed at CIMMYT-Zimbabwe by evaluation of top-cross performance and selection for better GCA across a range of environments in sub-Saharan Afirica. GCA was predominant for parents that have been developed through selection for GCA and for parents that have not been separated into heterotically complementary groups during their development (Pixley and Bjarnason, 1993). The absence of significant SCA effect for most of the traits under low N stress is undesirable because heterosis can not be expected to directly contribute gains for these traits. The expression of heterosis in the low N experiment is lower compared to the optimum N one, due to poor hybrid performance (Betran et al., 2003d).

Partitioning of hybrid x E interactions into GCA x E and SCA x E components showed that GCA x E and SCA x E interactions were significant for most traits across optimum N, low N and all environments. This indicates that GCA effects associated with parents and SCA effects associated with crosses were not consistent over environments. Similar findings were reported by others (Betran et al., 2003e; Gissa et al., 2007; Pswarayi and Vivek, 2008). Single crosses are more sensitive to environments than three-way or double crosses (Hallauer and Miranda, 1988). In addition, stress environments produce high genotype by environment interactions (Banziger et al., 2000). In most cases, the magnitudes of GCA x E and SCA x E mean squares were smaller than the respective GCA and SCA mean squares, suggesting the interaction effects may be of minor importance as compared to the main effects.

The estimate of GCA effects of a parent in the diallel is an important indicator of its potential for generating superior breeding genotypes. High positive GCA and SCA effects are desirable for grain yield, ears per plant, thousand kernel weight, number of rows per ear, kernels per row and kernels per ear, and thousand kernel weight while high negative effects are desirable for the other traits. Low absolute values of GCA effects indicate that the mean of a parent in crossing with the others does not differ greatly from the grand mean of the crosses. On the other hand, high absolute values of GCA estimate indicate that the parental mean is superior or inferior to the grand mean. SCA effect estimates the deviation of individual crosses from the average performance of the parents involved (Hallauer and Miranda, 1988).

Most parents in this study, showed significant GCA effects with different magnitudes and directions. This suggested the presence of adequate diversity in the genetic constitution of parents for most of the measured traits. Even though crossover interactions were observed for GCA effects of the inbred lines, there were some inbred lines with consistent GCA effects across the N conditions. Inbred lines VL054178, VL05561, VL05483, CML159, CML491 and VL06375 were the best general combiners for grain yield at each and across environments, indicating that these lines contributed to increased grain yield in their cross under optimum and low N stress conditions. VL054178, VL05482, VL05561, VL05483, CML159 and VL06375 were the best general combiners for early anthesis and silking, and hence, contributed significantly to earliness in their crosses as they showed significantly fewer mean number of days from planting to anthesis and silking. Early maturing maize genotypes are important as they escape terminal drought in areas with short rainy seasons. Inbreds VL05483 and VL06375 could reduce anthesis-silking interval. Inbred lines VL05200, VL05482 and CML144 significantly contributed to reduced plant stature.

Significant crossover interactions were observed for GCA effects of inbred lines for leaf senescence. Lines that contributed to delayed senescence in their crosses were VL052887 and CML144 at Harare and VL0523, CML511 and CML491 at Bako under low N conditions. VL05482, VL05483 and CML491 were good general combiners for ears per plant. Ears per plant is an important agronomic trait linked to low N stress tolerance in maize,

as it reflects bareness or prolificacy of a genotype under stress (Banziger et al., 1997; Pswarayi and Vivek, 2008). VL05561, VL05483, CML511, CML159 and VL06375 were good general combiners for ear diameter while VL054178, VL05482, VL05561 and VL06375 combined well for ear length. Good general combining inbred lines for kernel traits were VL05483, CML511 and CML159 for number of rows per ear, VL05561 and CML511 for number of kernels per row, VL05483 and CML511 for number of kernels per ear, and VL05200, VL054178, CML159 and VL06375 for thousand kernel weight.

Statistically significant positive or negative SCA effects for grain yield and agronomic traits shows that the crosses performed better or poorer than what would be expected from the GCA effects of their respective parents (Tables 4.18 and 4.19). VL054178 x CML144, VL05483 x CML144, VL05483 x CML491 and CML511 x CML491 were best combinations with favourable SCA estimates for grain yield (Table 4.19). These crosses contain parents with high GCA effects for grain yield, indicating the increased concentration of favourable alleles. Vasal et al. (1992c) argued that positive SCA effects indicate that lines are in opposite heterotic groups while negative SCA effects indicate that lines are in the same heterotic group.

A large number of hybrids showed superiority over their parents for various traits indicating the existence of substantial heterosis in the hybrids (Tables 4.21 and 4.22) and the potential of these inbred lines for hybrid development. The lower heterosis observed for days to anthesis and silking is desirable as it indicates the earlier flowering of hybrids compared to the parental inbred lines. The ranges of heterotic responses observed in this study were on average higher than that reported by Gissa et al. (2007) for normal maize inbred lines. However, Tollenaar et al. (2004) observed higher mean grain yield MPH of 167% and Betran et al. (2003e) reported MPH and HPH of 157 and 126%, respectively, compared to 112.8% and 89.8%, observed in this study. The extent of heterotic response of the F_1 hybrids largely depends on the breeding value and genetic diversity of the parents included in crosses, and on the environmental conditions under which hybrids are grown (Hallauer and Miranda, 1988; Young and Virmani, 1990; Glover et al., 2005). As expected, the levels of heterosis observed in this study were high, since the parents used are fixed inbred lines.

4.6 Conclusions

Nitrogen deficiency is among the major factors limiting maize production in Africa. The use of maize cultivars that perform well under limited nitrogen availability could greatly improve maize productivity in maize-based cropping systems of the continent. The results of this experiment indicated the existence of a high level of variability and the possibility of selection among the hybrids for grain yield and agronomic traits under low N stress. As it can be concluded from the positive and highly significant rank correlations between hybrid grain yields under low N and optimum N, some hybrids performed better under both conditions. Most QPM hybrids performed lower than the normal commercial checks, indicating the need for more effort to develop efficient QPM germplasm.

Combining ability analysis is important in identifying the best parents or parental combinations for a hybridization program. GCA and SCA mean squares where significant for most traits at each and across environments except SCA across low N stress environments which showed significant mean squares only for plant height and thousand kernel weight. It is concluded that non additive gene effects are less important for the inheritance of characters under low N stress condition. Estimates of GCA effects of the parents showed that individually parents contributed to specific traits. However, parents such as VL054178, VL05561, VL05483, CML511, CML144, CML159, CML491 and VL06375 showed desirable GCA effects for most traits and could be used in the breeding program for the development of low N stress tolerant hybrids. Moreover, cross combinations with good SCA effects (VL054178 x CML144, VL05483 x CML144, VL05483 x CML491 and CML511 x CML491), high MPH and HPH (VL052 x VL054178, VL05468 x VL054178 and CML511x CML491) for grain yield contain at least one of these inbred lines as their parents. This study identified good combining QPM inbred lines and good performing QPM hybrid combinations under both optimum and low N stress environments. Multilocation evaluation under low N and optimal conditions is required to confirm the findings of this study.

Chapter 5

Genetic analysis of quality protein maize inbred lines under abiotic stress and optimal conditions

5.1 Abstract

Growing maize hybrids tolerant to drought and low N stress would significantly reduce yield losses occurring in Africa. This study estimated the combining ability and the genetic control and modes of gene action for grain yield and related traits in quality protein maize (QPM) inbred lines. Fifteen QPM inbred lines were used in a diallel study. The diallel crosses were evaluated separately in trials under drought stress, low nitrogen (N) stress and optimal conditions in a total of 13 environments in eastern and southern African regions. The mean squares for general (GCA) and specific (SCA) combining ability were significant for most measured traits in each environment. GCA effects were significant while SCA effects were not significant for most traits across sites with drought and low N stress. Across optimal environments, both GCA and SCA effects were significant for all traits. Combined across all environments, both GCA and SCA effects were significant for most traits. Additive genetic effects were important under stress, and both additive and non-additive genetic effects were important under optimal conditions. This study identified QPM inbred lines with good GCA effects across stress and optimal conditions, indicating that the genetic systems controlling a given trait under different conditions are at least partially similar. The estimate of predictability ratio for grain yield was close to unity for stress environments, indicating the possibility of predicting progeny performance based on parental GCA alone. Thus, QPM grain yield under stress can be improved using recurrent selection methods, which exploit additive genetic effects. Plant and ear height showed high predictability ratios in each environment and across environments. These traits also showed high broad and narrow sense heritability, indicating that environment had a small effect on the inheritance of these traits. In general, this study provided evidence that good performance can be achieved under stress and non-stress conditions in QPM germplasm.

5.2 Introduction

Drought and low N stress are factors most frequently limiting maize production, food security, and economic growth in sub-Saharan Africa. The unprecedented combination of climatic risk, declining soil fertility, the need to expand food production into more marginal areas as population pressure increases, high input costs, extreme poverty, and unavailability of credit systems, have resulted in small holder farmers in southern and eastern Africa producing maize in extremely low-input/low risk systems (Banziger and Diallo, 2004). As a consequence, crop yields are falling to very low levels and food insecurity is widespread amongst agricultural communities (Kamara et al., 2004). The development of maize germplasm able to tolerate drought and low N stress is crucial if the productivity of maize based farming systems is to be sustained or increased (Betran et al., 2003e).

Maize genotypes perform differently under drought and low N conditions due to the existence of genetic variability for tolerance to these stresses (Bolaños and Edmeades, 1993b; Lafitte and Edmeades, 1994c; Vasal et al., 1997b; Banziger et al., 2000; Diallo et al., 2004). Betran et al. (2003e) observed hybrids performing well under stress and suggested the possibility of combining stress tolerance and yield potential in tropical maize hybrids. Tolerance of maize to stress from low N and drought is partly related to the development of the root system, which in turn influences water and nutrient uptake by crop plants (Moll et al., 1982; Kamara et al., 2004). In general, however, the amount of grain yields recorded from maize genotypes fall with the severity of low N and drought stress (Betran et al., 2003e). Breeding strategies to develop stress tolerant maize inbred lines include screening and selection of inbreds under managed stress conditions, multi-location testing of progeny in a representative sample of the target environments, and selection under high plant populations (Beck et al., 1997). Additional information from adaptive secondary traits (ears per plant, anthesis-silking interval and leaf senescence) that show differential expression between optimal and stress conditions is genetically variable and is correlated with grain yield and is commonly used to increase selection efficiency (Bolaños et al., 1993; Bolaños and Edmeades, 1996; Banziger and Lafitte, 1997). When genetic variance and heritability for grain yield declines under drought stress (Blum, 1988; Bolaños and Edmeades, 1996),

variances and heritability of anthesis-silking interval and ears per plant remain stable across drought stress levels or may even increase (Bolaños and Edmeades, 1996). Anthesis-silking interval and ears per plant have, therefore, been used in selection indices to increase selection efficiency for drought tolerance (Bolaños et al., 1993; Bolaños and Edmeades, 1996). Similarly, Banziger and Lafitte (1997) showed that ears per plant, leaf senescence, and anthesis-silking interval can increase the efficiency of selection for grain yield in low N environments.

The choice of the most effective breeding scheme and the rate of the genetic improvement are dependent upon the relative magnitude of various gene effects (Dhillon and Pollmer, 1978). The expression and genetic variation of grain yield and secondary traits in maize vary with stress level. Additive genetic effects are more important for grain yield under drought and well-watered conditions and non-additive genetic effects are found to be more important under low N stress conditions (Betran et al., 2003e; Makumbi et al., 2004). Betran et al. (1999) reported that as drought stress increases so does the importance of GCA and additive genetic effects. For ears per plant, Makumbi et al. (2004) reported the importance of non-additive genetic effects under low N stress conditions. Derera et al. (2008) reported the preponderance of additive effects for grain yield and ears per plant under drought and the importance of both additive and non-additive effects in controlling grain yield under well-watered conditions. Both additive and non-additive gene effects are important for days to anthesis, silking and anthesis-silking interval under both drought and non-drought environments (Derera et al., 2008).

A few studies conducted on genetic analysis of stress tolerance in maize have focused on the normal maize germplasm. The impact of drought and low N stress on the mode of gene action controlling grain yield and related traits of QPM germplasm has not been studied. Quantitative analysis of the mode of gene action controlling yield and secondary traits in QPM germplasm under drought, low N and optimal conditions would help in devising a viable conventional breeding strategy to develop nutritionally enhanced cultivars adapted to stress and optimal environments. Since QPM germplasm contains increased lysine and tryptophan concentrations and higher biological value, increasing its production among the

low input farming community can help alleviate food insecurity and malnutrition. The present study evaluated (i) the combining ability and (ii) modes of gene action for grain yield and related traits in QPM inbred lines under drought and low N stress, and optimal (well-watered and well-fertilized) conditions.

5.3 Materials and methods

Environments and stress management

The study was conducted at 13 locations in four countries of eastern and southern Africa, viz. Ethiopia, Kenya, Zambia and Zimbabwe from 2006 to 2008 (Figure 5.1 and Table 5.1). Nine environments at Harare (HAOM), Rattray Arnorld (RAOM), Mpongwe (MPOM), Bako (BKOM), Melkassa (MLOM), Pawe (PWOM), Awassa (AWOM), Jimma (JMOM) and Kiboko (KBOM) research stations comprised optimum management (optimal fertilization and supplemental irrigation as needed to avoid drought stress). Fertilizer rates at each location were adjusted to reflect the agronomic recommendations for each location. The trials were conducted during the summer (main cropping) seasons of the respective countries. Two experiments (HALN and BKLN) were conducted under low N stress at Harare, Zimbabwe and Bako, Ethiopia, research stations respectively, during the summer seasons. The low N stress management for these environments is described in the materials and methods of Chapter 4. Two experiments were grown under drought stress during the winter (dry) seasons at Chiredzi, Zimbabwe(CHDS) and Kiboko, Kenya (KBDS) research stations.

Both Chiredzi and Kiboko are largely rain free during the winter season, allowing the control of drought stress intensity by withdrawing or delaying irrigation for varying lengths of time during flowering and grain filling stages (Edmeades et al., 1999). At Chiredzi, drought stress was achieved by applying a total of 220 mm irrigation water in the first 50 days from planting. This regime caused severe drought stress at flowering and grain filling time. The trials at Kiboko were irrigated from planting until 15 days before male flowering after which watering was withheld until 15 days after male flowering when additional irrigation was applied to prevent zero-yield (Banziger et al., 2000). Care was taken so that irrigation, and hence stress, was as uniform as possible and the drought blocks were not contaminated with

irrigation water from neighbouring blocks or leaking pipes and wind drift. Sufficient fertilization and crop management practices were applied, except irrigation management to avoid confined effects from other factors. Apart from targeted stress, management of experiments at the same locations was the same across irrigation and N levels.

Germplasm

All the details are given in the materials and methods section of Chapter 4. The F_1 hybrids were evaluated along with two QPM (SC527Q and CML144/CML159//CML176) and one normal maize (SC633) hybrid checks in all experiments conducted in Kenya, Zambia and Zimbabwe, and two normal maize (BH540 and BH541) and one QPM (BHQP542) hybrid checks in all experiments conducted in Ethiopia.

Experimental design and field measurements

All experiments were laid out as 9 x 12 alpha-lattice designs (Patterson and Williams, 1976) with two replications. Plant densities and spacing for each location are given in Table 5.1. Measurements were recorded on grain yield (GY), days to anthesis (DA), days to silking (DS), anthesis-silking interval (ASI), plant height (PH), ear height (EH), leaf senescence (SEN) and ears per plant (EPP) on well bordered plants by excluding plants next to the allay. The detail descriptions of the traits recorded are given in the materials and methods section of Chapter 4.

Statistical analysis

Before data analysis, anthesis-silking interval (ASI) was normalized using $\ln\sqrt{(ASI+10)}$ as suggested by Bolaños and Edmeades (1996). Analysis of variance per environment was conducted with the PROC MIXED procedure in SAS (SAS, 2003) considering genotypes as fixed effects and replications and blocks within replications as random. Entry means adjusted for block effects generated from individual location analyses according to a lattice design (Cochran and Cox, 1960) were used to perform across environments combined analyses using PROC GLM in SAS (SAS, 2003) and combining ability analysis using a modification of the DIALLEL-SAS program (Zhang and Kang, 1997).

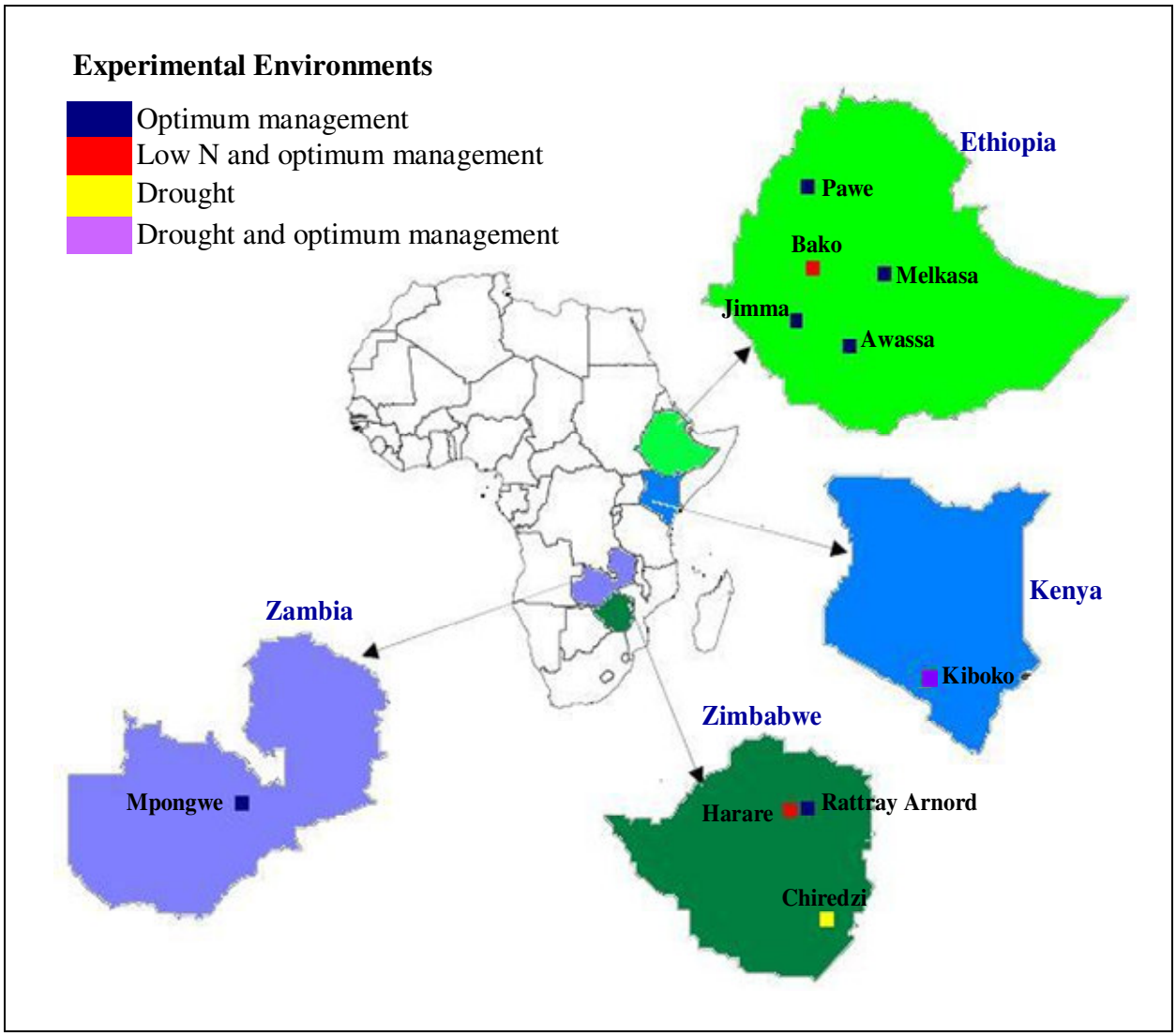

Figure 5.1 Experimental environments used to evaluate quality protein maize F1 hybrids

GCA effects of the parents and SCA effects of the crosses were estimated following Griffing's Method IV (crosses only) and Model I (fixed) of diallel analysis (Griffing, 1956). Combined analyses of variance were conducted for each trait that showed significant entry mean squares in individual environment analysis. Data were combined across drought, low N, optimal and all environments. Combining ability was analyzed, and GCA and SCA effects were estimated accordingly. The mean squares for hybrids and environments were tested against the mean squares for hybrid x environment (E) as error term while hybrid x E interactions mean squares were tested against pooled error.

Table 5.1 Locations and environments used to evaluate F_1 hybrids, with their characteristics and codes

Location	Country	Year	Latitude	Longitude	Altitude	Rainfall Mm	Temperature °C		Type of environment	Code	Fertilization kg ha^{-1}			Plot size (m x m)	Density plants ha^{-1}
							Min	Max			N	P_2O_5	K‡		
Harare	Zimbabwe	2006/7	17°49'S	31°1'E	1489	890	14.2	26.8	Optimum	HAOM	166	56	24	4.0 x 1.50	53,333
Harare	Zimbabwe	2006/7	17°49'S	31°1'E	1489	890	14.2	26.8	Low N stress	HALN	0	56	24	4.0 x 1.50	53,333
RARS	Zimbabwe	2006/7	17°16'S	31°03'E	1341	865	14.2	27.0	Optimum	RAOM	208	35	21	4.0 x 0.75	53,333
Mpongwe	Zambia	2006/7	13°32'S	28°03'E	1300	1500	n/a†	n/a	Optimum	MPOM	208	35	21	4.0 x 0.75	53,333
Bako	Ethiopia	2007	9°06'N	37°09'E	1650	1245	14.0	28.1	Optimum	BKOM	100	100	-	4.8 x 1.50	44,444
Bako	Ethiopia	2007	9°06'N	37°09'E	1650	1245	14.0	28.1	Low N stress	BKLN	0	100	-	4.8 x 1.50	44,444
Melkasa	Ethiopia	2007	8°24'N	39°21'E	1550	680	14.6	28.6	Optimum	MLOM	50	25	-	4.8 x 1.50	44,444
Pawe	Ethiopia	2007	11°09'N	36°03'E	1100	1577	16.6	33.4	Optimum	PWOM	64	46	-	4.8 x 1.50	44,444
Awassa	Ethiopia	2007	7°08'N	38°48'E	1700	1100	12.6	26.8	Optimum	AWOM	110	46	-	4.8 x 1.50	44,444
Jimma	Ethiopia	2007	7° 46' N	36°00'E	1753	1530	12.0	26.2	Optimum	JMOM	75	70	-	4.8 x 1.50	44,444
Chiredzi	Zimbabwe	2007	21°02' S	31°58' E	433	300	14.0	34.2	Drought stress	CHDS	148	56	24	4.0 x 1.50	53,333
Kiboko	Kenya	2007	2°10'S	37°40'E	975	561	14.0	33.0	Drought stress	KBDS	156	92	-	4.0 x 1.50	53,333
Kiboko	Kenya	2008	2°10'S	37°40'E	975	561	14.0	33.0	Optimum	KBOM	156	92	-	4.0 x 1.50	53,333

† n/a= not available; ‡K= potassium fertilizer was not used in Ethiopia and Kenya; RARS= Rattray Arnold Research Station

Since means (over replication) of each of the genotypes were used for combined analysis of variance, estimate of pooled error mean squares were calculated following the procedure of Dabholkar (1999) as: $\sum_{i=1}^{n} K_i S_i^2 \Big/ \sum_{i=1}^{n} K_i r$, where K_i and S_i^2 are error degrees of freedom and error mean square at i^{th} environment, respectively, n is the number of environments and r is the number of replications in each environment. The significance of GCA and SCA sources of variation was determined using the corresponding interactions with the environment as error terms. Error mean squares calculated above were used to test the significance of GCA and SCA interactions with environment; because the combining ability mean squares were calculated based on entry means of each genotype from each environment (Griffing, 1956; Singh, 1973; Dabholkar, 1992). For GCA effects of the inbred lines, the restriction $\sum gi = 0$ was imposed. Significance of GCA effects was determined by the t-test, using standard errors of GCA effects (Griffing, 1956; Singh and Chaudhary, 1985).

GCA and SCA equivalent variance components of mean squares were estimated by a fixed model for the diallel design (Griffing, 1956; Singh, 1973; Baker, 1978). In the case where parents are completely inbred, Griffing (1956) has shown that the total genetic variance among single cross progeny is equal to twice the general combining ability component of variance ($2\sigma_{gca}^2$) plus the specific combining ability component of variance (σ_{sca}^2). Based on this relationship, additive (σ_A^2) and dominance (σ_D^2) variances were estimated as $\sigma_A^2 = 2\sigma_{gca}^2$ and $\sigma_D^2 = \sigma_{sca}^2$. Genotypic ($\sigma_g^2$) and phenotypic ($\sigma_p^2$) variances were also calculated as $\sigma_g^2 = \sigma_A^2 + \sigma_D^2$, and $\sigma_p^2 = \sigma_g^2 + \sigma_e^2$. Broad ($H^2$) and narrow ($h^2$) sense heritability was calculated from the estimated components of variances as: $H^2 = \sigma_g^2 / \sigma_p^2$ and $h^2 = \sigma_A^2 / \sigma_p^2$. The relative importance of GCA and SCA variances in determining progeny performance was estimated based on Baker's predictability ratio (PR) (Baker, 1978) as:

$$PR = 2\sigma_{gca}^2 / (2\sigma_{gca}^2 + \sigma_{sca}^2),$$

where, σ_{gca}^2 and σ_{sca}^2 are variance components for GCA and SCA, respectively. Standard errors associated with σ_{gca}^2 and σ_{sca}^2 were calculated following the procedure described by

Dabholkar (1999). Then, significance of variance components was determined by the t-test using the standard errors.

5.4 Results

Analysis of variance for each environment revealed the existence of significant differences among hybrids for most traits except anthesis-silking interval at HAOM, HALN, MPOM, BKLN and PWOM, and ear height at HALN (Table 5.2). Mean squares due to GCA were highly significant for all traits studied at all environments. SCA effects were also significant for most traits. Mean grain yields for the QPM hybrids (excluding the checks) ranged from 0.6 t ha^{-1} under severe drought at CHDS to 8.4 t ha^{-1} under optimum management at MPOM (Table 5.3). The percentage of QPM hybrids with higher grain yield than the best check ranged from zero (no QPM hybrids yielded higher than the best check) under low N stress at BKLN to 73.3% under optimum management at KBOM. At Kiboko, average grain yield of the hybrids tested under drought stress (KBDS) was 35.7% of grain yield under optimal conditions (KBOM). Average grain yields tested under low N stress at HALN and BKLN were 11.5 and 51.2% of grain yields under optimal conditions at the same locations, HAOM and BKOM, respectively.

Combined analysis of variance across drought stress environments revealed highly significant mean squares due to environments and hybrids for all traits analyzed (Table 5.4). Mean grain yield across drought stress environments ranged from 0.3 to 3.7 t ha^{-1} with a mean of 1.8 t ha^{-1}. Higher grain yields were recorded for VL052 x VL05561 (3.7 t ha^{-1}), VL05561 x CML159 (3.5 t ha^{-1}), VL054178 x VL06375 (3.4 t ha^{-1}), VL05482 x VL05561 (3.3 t ha^{-1}) and VL054178 x VL05561 (3.0 t ha^{-1}), in order listed. Mean grain yield across drought stress environments (Table 5.4) was 27.4% of the mean grain yield across optimal environments (Table 5.6). Mean days to anthesis was 92.3 with a range of 82.8 – 103.5. Days to silking ranged from 83.7 to 120.0 with a mean of 102.0. Anthesis-silking interval ranged from 0.4 to 21.4 days with a mean of 9.7. Ears per plant ranged from 0.10 to 0.88 with a mean 0.50. Combining ability analysis revealed non-significant GCA mean square for grain yield but significant GCA mean squares for days to anthesis and silking, anthesis-silking

interval and ears per plant. SCA mean squares, however, were not significant for all traits. Hybrid x E, GCA x E and SCA x E interaction mean squares were significant for all traits tested.

Combined analysis of variance across low N stress environments revealed that environment effects were significant for all traits (Table 5.5). All traits exhibited highly significant differences among the hybrids except leaf senescence and ears per plant. Grain yield ranged from 0.4 to 3.7 t ha^{-1} with a mean of 2.1 t ha^{-1}. The highest yielding hybrids were VL05200 x VL06375 (3.7 t ha^{-1}), CML491 x VL06375 (3.4 t ha^{-1}), VL05200 x VL054178 (3.3 t ha^{-1}), CML159 x VL06375 (3.3 t ha^{-1}) and VL0524 x VL06375 (3.2 t ha^{-1}). Mean grain yield across low N stress environments (Table 5.5) was 32.5% of the mean yield across optimal environments (Table 5.6). Mean days to anthesis was 81.7 with a range of 73.6 – 91.4. Days to silking ranged from 75.9 to 93.7 with a mean of 84.2. Mean plant height was 166.2 cm with ranges of 130.6 – 191.4 cm. Leaf senescence ranged from 31.6 to 57.5% with a mean of 41.0%. Ears per plant ranged from 0.59 to 1.30 with a mean 0.85. Mean squares due to GCA were significant for grain yield, days to anthesis and silking, and plant height but not significant for leaf senescence and ears per plant. SCA mean squares were significant only for plant height. The interaction of drought stress environments with hybrids, GCA and SCA were significant for all traits.

Table 5.2 Mean squares for hybrids, general (GCA) and specific (SCA) combining ability for grain yield and agronomic traits at 13 stressed and optimal environments, 2006 – 2008

Environment†	Source of variation	DF	GY	DA	DS	ASI	PH	EH	EPP	SEN
HAOM	Hybrids	104	4.6**	13.3**	15. 0**	2.0	425.4**	279.1**	0.04**	-
	GCA	14	6.6**	39.7**	42.4**	-	885.5**	537.9**	0.04**	-
	SCA	90	1.7**	1.5	2.1	-	108.1**	77.6*	0.02**	-
HALN	Hybrids	104	0.3**	20.5**	33.3**	10.0	351.8**	129.3	0.06**	0.8*
	GCA	14	0.7**	60.3**	89.6**	-	642.4**	-	0.12**	0.8**
	SCA	90	0.1	2.5**	5.3*	-	103.3*	-	0.02**	0.3
RAOM	Hybrids	104	5.5**	12.7**	15.9**	2.1**	341.5**	298.1**	0.05**	-
	GCA	14	6.9**	35.9**	42.6**	3.2**	467.5**	364.5**	0.07**	-
	SCA	90	2.1**	1.7**	2.6**	0.7	124.6**	115.5**	0.02**	-
MPOM	Hybrids	104	10.1**	3.6**	3.3**	0.8	986.7**	459.0**	0.03*	-
	GCA	14	15.8**	6.4**	5.1**	-	1278.1**	703.1**	0.02**	-
	SCA	90	3.4**	1.1	1.1	-	371.3**	155.8**	0.01	-
BKOM	Hybrids	104	5.0**	51.2**	51.0**	2.5**	589.4**	280.9**	0.13**	-
	GCA	14	8.3**	161.9**	157.8**	5.2**	850.5**	627.9**	0.30**	-
	SCA	90	1.6**	4.4**	4.9**	0.7	208.2**	64.6	0.03**	-
BKLN	Hybrids	104	2.7**	51.8**	53.1**	0.9	521.2**	188.2**	0.08**	1.9**
	GCA	14	3.5**	147.6**	148.9**	-	590.6**	111.3*	0.04*	1.6**
	SCA	90	1.0**	7.00**	7.5**	-	209.3**	91.5*	0.04**	0.8**
MLOM	Hybrids	104	3.9**	22.2**	22.2**	1.5**	570.6**	357.9**	0.11**	-
	GCA	14	6.2**	66.3**	62.5**	2.5**	633.0**	420.7**	0.26**	-
	SCA	90	1.3**	2.5*	3.1*	0.5*	231.2**	141.4*	0.02**	-
PWOM	Hybrids	104	3.6**	35.3**	36.6**	1.8	367.7**	212.8**	0.04**	-
	GCA	14	4.4**	77.5**	85.9**	-	335.9*	150.5**	0.03**	-
	SCA	90	1.4	8.4**	7.8**	-	160.2**	99.5**	0.02**	-
AWOM	Hybrids	104	2.6**	20.0**	18.3**	4.4**	571.9**	278.4**	0.12**	-
	GCA	14	2.9**	63.1**	55.7**	5.4**	757.9**	381.2**	0.16**	-
	SCA	90	1.0**	1.8**	1.9*	1.7*	212.5**	101.5**	0.04*	-
JMOM	Hybrids	104	3.2**	39.9**	35.4**	1.7**	598.3**	308.6**	0.07**	-
	GCA	14	4.8**	124.9**	110.2**	1.1**	924.7**	409.7**	0.13**	-
	SCA	90	1.1**	3.6**	3.3**	0.8**	201.9**	114.6	0.02**	-
CHDS	Hybrids	104	0.3**	71.2**	309.2**	108.4**	762.6**	293.3**	0.08**	0.8**
	GCA	14	0.5**	207.6**	900.5**	271.4**	1598.7**	314.3**	0.19**	1.2**
	SCA	90	0.1*	8.9**	38.6**	20.4*	191.9**	120.6**	0.02**	0.3
KBDS	Hybrids	104	3.8**	34.5**	90.9**	20.6**	-	-	0.09**	-
	GCA	14	10.2**	115.0**	254.7**	33.1**	-	-	0.22**	-
	SCA	90	0.6**	2.0**	12.9**	6.8**	-	-	0.02*	-
KBOM	Hybrids	104	9.4**	17.4**	18.4**	2.2**	427.0**	204.5**	0.03**	-
	GCA	14	14.7**	56.2**	56.7**	5.5**	807.6**	492.3**	0.05**	-
	SCA	90	3.2**	1.3**	1.8**	0.4	121.1**	41.5*	0.01**	-

† Environment codes as explained in Table 5.1; * $P \leq 0.05$; ** $P \leq 0.01$; DF= degrees of freedom; GY= grain yield; AD= days to anthesis; DS= days to silking; ASI= anthesis-silking interval; PH= plant height; EH= ear height; EPP= ears per plant; SEN= leaf senescence

Table 5.3 Means of QPM hybrids, and best normal and QPM checks for grain yield (t ha^{-1}) in 13 stress and optimal environments, 2006 -2008

Means	Optimal									Low N stress		Drought stress	
	HAOM	RAOM	MPOM	BKOM	MLOM	PWOM	AWOM	JMOM	KBOM	HALN	BKLN	CHDS	KBDS
Grand mean	7.7	6.5	8.4	6.5	6.7	4.9	4.7	4.6	8.1	0.9	3.3	0.6	2.9
Hybrid mean	7.7	6.4	8.4	6.5	6.7	4.9	4.7	4.6	8.2	0.9	3.3	0.6	2.9
Best hybrid	12.9	10.6	13.8	9.7	10.6	8.8	7.2	7.9	12.1	1.9	6.4	2.1	5.7
Best QPM check	9.1	7.8	9.2	6.4	5.9	3.8	4.7	4.9	7.5	1.0	2.9	1.0	2.4
Best normal check	11.6	10.0	8.6	7.4	6.5	6.1	6.0	2.5	5.5	1.7	6.4	0.3	3.2
SE (m)	0.6	0.9	0.7	0.3	0.5	0.8	0.5	0.4	0.5	0.2	0.6	0.2	0.5
% high yielding hybs[‡]	1.0	1.0	41.9	31.4	61.0	14.3	10.5	41.0	73.3	2.9	0.0	13.3	45.7

[†] Environment codes are as explained in Table 5.1; [‡] proportion of QPM hybrid with higher grain yield than the best check (normal maize or QPM); SE(M)= standard error of the mean

Table 5.4 Combined analysis of variance and means for grain yield and agronomic traits of QPM hybrids across drought stress environments at Chiredzi and Kiboko, 2007

Source of variation	df	Mean squares				
		GY	DA	DS	ASI	EPP
Environment (E)	1	275.0**	65614.0**	116716.3**	7339.6**	14.24**
Hybrid	104	1.3**	46.7**	159.8**	42.4**	0.07**
GCA	14	7.3	308.8**	1030.3**	233.0**	0.39**
SCA	90	0.4	5.9	24.3	12.7	0.02
Hybrid x E	104	0.7**	6.1**	40.3**	22.1**	0.02**
GCA x E	14	3.3**	13.8**	124.9**	71.5**	0.02**
SCA x E	90	0.3**	5.0**	27.1**	14.4*	0.02**
Error	164	0.2	2.5	11.8	8.8	0.01
Mean		1.8	92.3	102.0	9.7	0.50
Minimum		0.3	82.8	83.7	0.4	0.10
Maximum		3.7	103.5	120.0	21.4	0.88
SE (m)		0.3	1.1	2.4	2.1	0.07
CV (%)		24.1	1.7	3.4	30.7	20.0

* $P \leq 0.05$; ** $P \leq 0.01$; ASI= Anthesis silking interval (d); CV= coefficient of variation (%); DA= days to anthesis; DF= degrees of freedom; DS= days to silking; EPP= ears per plant; GCA= general combining ability; GY= grain yield (t ha^{-1}); SCA= specific combining ability; SE (m)= standard error of the mean

Across optimal environments, the effects of environments, hybrids, GCA and SCA were highly significant for all the traits evaluated (Table 5.6). Grain yields ranged from 1.8 to 9.4 t ha^{-1} with a mean of 6.5 t ha^{-1}. The highest yielding hybrids were VL05483 x CML491 (9.4 t ha^{-1}), CML511 x CML491 (8.8 t ha^{-1}), VL05561 x CML491 (8.7 t ha^{-1}), CML159 x CML491 (8.5 t ha^{-1}) and VL054178 x CML491 (8.1 t ha^{-1}). Mean days to anthesis was 73.8 with a range of 66.9 – 80.4. Days to silking ranged from 68.9 to 82.8 with a mean of 75.1. Mean plant and ear height was 225.5 and 110.9 cm with ranges of 189.0 – 248.4 cm and 89.9 – 131.7 cm. Mean ears per plant was 1.14 with ranges of 0.79 – 1.48. Anthesis-silking interval ranged from -0.2 to 3.3 d with a mean of 1.6 d. Hybrid x E, GCA x E and SCA x E interactions were highly significant for all traits except SCA x E for ear height and anthesis-silking interval.

Table 5.5 Combined analysis of variance and means for grain yield and agronomic traits of QPM hybrids across low nitrogen stress environments at Harare and Bako, 2006 - 2007

Source of variation	df	Mean squares					
		GY	DA	DS	PH	SEN	EPP
Environment (E)	1	307.0**	6458.5**	3068.2**	7816.5**	100.5**	9.30**
Hybrids	104	0.9*	29.5**	35.8**	306.7**	0.6	0.04
GCA	14	3.0*	185.9**	217.7**	1055.3**	1.1	0.10
SCA	90	0.6	5.2	7.4	190.2*	0.5	0.03
Hybrids x E	104	0.6**	6.6**	7.4**	129.8**	0.8**	0.03*
GCA x E†	14	1.2**	22.1**	20.7**	177.8**	1.3**	0.06**
SCA x E†	90	0.5**	4.2**	5.4*	122.4**	0.7**	0.03**
Error	164	0.3	2.3	3.8	80.6	0.4	0.02
Mean		2.1	81.7	84.2	166.2	4.1	0.85
Minimum		0.4	73.6	75.9	130.6	3.2	0.49
Maximum		3.7	91.4	93.7	191.4	5.8	1.30
SE (m)		0.5	1.5	1.9	9.0	0.6	0.12
CV (%)		24.4	1.8	2.3	5.4	14.4	16.6

* $P \leq 0.05$; ** $P \leq 0.01$; CV= coefficient of variation (%); DA= days to anthesis; DF= degrees of freedom; DS= days to silking; EPP= ears per plant; GCA= general combining ability; GY= grain yield (t ha^{-1}); PH= plant height (cm); SCA= specific combining ability; SE (m)= standard error of the mean; SEN= leaf senescence (1-5)

Combined analysis of variance across all environments showed that environment and hybrid effects were highly significant for all traits except hybrid effects for leaf senescence. Mean grain yield was 5.1 t ha^{-1} and ranged from 1.4 to 7.2 t ha^{-1}. Hybrids VL05482 x VL05561 (5.7 t ha^{-1}), VL05561 x CML159 (5.4 t ha^{-1}), VL052 x VL05561 (5.3 t ha^{-1}), VL05200 x VL05561 (5.3 t ha^{-1}) and VL054178 x CML511 (5.3 t ha^{-1}) showed higher grain yields. Days to anthesis ranged from 70.4 to 84.3 with a mean of 77.9. Mean days to silking was 80.7 with a range of 72.3 – 89.4. Ears per plant ranged from 0.66 to 1.25 with a mean of 1.00. Mean anthesis silking interval was 3.6 d with a range of 0.7 – 7.5 d. Mean plant and ear height was 211.3 cm and 106.4 cm with ranges of 175.9 – 232.0 cm and 87.1 – 127.9 cm, respectively. Leaf senescence ranged from 38.3 to 61.9% with a mean of 46.4%. GCA and SCA mean

squares were significant for all traits except both GCA and SCA for leaf senescence and SCA for anthesis-silking interval. Hybrid x E, GCA x E and SCA x E were significant for all traits evaluated.

Estimates of GCA effects for grain yield showed that inbred lines VL05561, VL05483, CML511, CML159 and VL06375 combined well in most of the environments (Table 5.8). These inbred lines showed positive and highly significant GCA effects in seven or more out of 13 environments. On the other hand, VL052, VL052887, VL0523 and CML144 showed negative and highly significant GCA effects in most of the environments. VL054178, VL05561, CML159 and VL06375 showed positive and highly significant GCA effects across low N environments. Inbred lines VL05561, VL05483 and CML511 showed high positive GCA effects across optimum and combined environments. VL054178, VL05561, CML159 and VL06375 had positive and highly significant GCA effects across low N, optimal and combined environments.

For days to anthesis, VL054178, VL05482, VL05561, VL05483, CML511 and VL06375 had negative and highly significant GCA effects in most environments (Table 5.9). On the other hand, inbred lines VL05200, VL054178, VL052887, VL0523, VL05561 and CML144 showed positive and highly significant GCA effects in most environments. VL054178, VL05482, VL05561, VL05483, CML511, CML159 and VL06375 had highly significant negative GCA effects for days to silking across drought stress, low N stress, optimal and combined environments.

Inbred lines VL054178, VL05482, VL05561, VL05483 and VL06375 had negative and highly significant GCA effects for days to silking (Table 5.10). On the other hand, VL05468, VL052887, VL0523, VL0524, CML144 and CML491 showed positive and highly significant GCA effects. VL054178, VL05482, VL05561, VL05483, CML159 and VL06375 had highly significant negative GCA effects for days to anthesis across drought stress, low N stress, optimal and combined environments.

Table 5.6 Combined analysis of variance and means for grain yield and agronomic traits of QPM hybrids across nine optimal environments, 2006 - 2008

Sources of variation	df	Mean squares						df	Mean squares
		GY	DA	DS	PH	EH	EPP		ASI
Environment (E)	8	231.4**	5263.9**	7362.0**	61527.2**	46311.2**	3.09**	5	509.0**
Hybrids	104	14.4**	69.8**	71.1**	1356.2**	643.5**	0.11**	104	2.8**
GCA	14	46.8**	477.1**	472.7**	5289.2**	2925.7**	0.58**	14	13.2**
SCA	90	9.4**	6.5**	8.6**	744.4**	288.5**	0.04**	90	1.2**
Hybrids x E	832	1.2**	4.7**	4.6**	135.4**	87.0**	0.02**	520	0.9**
GCA x E	112	2.6**	17.2**	16.2**	183.5**	129.1**	0.05**	70	1.6**
SCA x E	720	0.8**	2.2**	2.2**	110.5**	69.3	0.02**	450	0.6
Error	738	0.6	1.5	1.8	73.1	61.7	0.01	492	0.6
Mean		6.5	73.8	75.1	225.5	110.9	1.14		1.6
Minimum		1.8	66.9	68.9	189.0	89.9	0.79		-0.2
Maximum		9.4	80.4	82.8	248.4	131.7	1.48		3.3
SE (m)		0.3	0.4	0.5	2.9	2.6	0.03		0.3
CV(%)		11.6	1.7	1.8	3.8	7.1	8.8		47.8

* $P \leq 0.05$; ** $P \leq 0.01$; ASI= anthesis-silking interval (d); CV= coefficient of variation (%); DA= days to anthesis; DF= degrees of freedom; DS= days to silking; EH= ear height (cm); EPP= ears per plant; GCA= general combining ability; GY= grain yield (t ha^{-1}); PH= plant height (cm); SCA= specific combining ability; SE (m)= standard error of the mean

Table 5.7 Combined analysis of variance and means for grain yield and agronomic traits of QPM hybrids across 13 stress and optimal environments, 2006 - 2008

Trait	df	Mean squares				df	Mean squares	df	Mean square	df	Mean squares	df	Mean squares
		GY	DA	DS	EPP		ASI		PH		EH		SEN
Environment (E)	12	700.9**	14771.6**	25562.4**	10.36**	7	2892.0**	11	115037.7**	10	56210.9**	2	142.7**
Hybrids	104	14.0**	130.8**	191.5**	0.119**	104	13.2**	104	1664.1**	104	708.1**	104	0.6
GCA	14	50.7**	906.4**	1307.7**	0.60**	14	70.9*	14	6397.4**	14	3010.9**	14	1.8
SCA	90	8.3**	10.1**	17.9**	0.04**	90	4.2	90	927.8**	90	349.9**	90	0.4
Hybrids x E	1248	1.1**	5.5**	13.3**	0.028**	728	8.4**	1144	144.8**	1040	87.2**	208	0.6**
GCA x E	168	2.9**	21.3**	58.7**	0.09**	98	36.6**	154	306.8**	140	150.2**	28	0.9**
SCA x E	1080	0.9**	3.0**	6.3**	0.02**	630	4.0**	990	119.6**	900	77.4**	180	0.5**
Pooled error	1066	0.5	1.8	3.6	0.01	656	2.6	984	77.1	902	62.0	246	0.3
Mean		5.1	77.9	80.7	1.00		3.6		211.3		106.4		4.6
Minimum		1.4	70.4	72.3	0.66		0.7		175.9		87.1		3.8
Maximum		7.2	84.3	89.4	1.25		7.5		232.0		127.9		6.2
SE (m)		0.2	0.4	0.5	0.03		0.6		2.5		2.4		0.3
CV (%)		13.4	1.7	2.4	10.0		44.9		4.2		7.4		12.0

** $P \leq 0.01$; ASI= anthesis-silking interval (d); CV= coefficient of variation (%); DA= days to anthesis; DF= degrees of freedom; DS= days to silking; EH= ear height (%); EPP= ears per plant; GCA= general combining ability; GY= grain yield (t ha^{-1}); PH= plant height (cm); SCA= specific combining ability; SE(m)= standard error of the mean; SEN= leaf senescence (1-5)

Table 5.8 Estimates of general combining ability (GCA) effects of 15 QPM inbred lines for grain yield (t ha^{-1}) per environment and across environments, 2006 -2008

Environment[†]	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10	P11	P12	P13	P14	P15	SE(gi)
HAOM	-0.78**	-0.85**	-0.22	0.87**	-0.42*	-0.43*	-0.29	-0.34	0.84**	1.21**	0.55**	-0.96**	-0.46*	0.57**	0.71**	0.20
HALN	-0.28**	-0.08	-0.32**	0.13*	-0.17*	0.06	-0.17*	-0.12	-0.12	0.39**	0.17*	-0.13*	0.11	0.06	0.47**	0.07
RAOM	-0.97**	-0.89**	-0.08	0.30	-0.57*	-0.22	-0.41	-0.27	1.17**	0.89**	1.28**	-0.88**	-0.19	0.50	0.34	0.28
MPOM	-0.73**	-0.75**	-0.58*	0.51*	-0.40	-0.27	-0.92**	-1.23**	1.73**	1.46**	1.85**	-1.50**	-0.76**	0.58*	1.00**	0.23
BKOM	-0.66**	-1.17**	-0.92**	-0.22*	0.39**	-0.38**	-0.49**	-0.32**	1.58**	0.73**	0.47**	-0.94**	0.94**	0.26*	0.72**	0.11
BKLN	-0.56**	-0.32	-0.10	0.62**	-0.56**	0.10	-0.42*	-0.32	0.72**	-0.21	-0.19	-0.59**	0.60**	0.26	0.98**	0.18
MLOM	-0.34*	-0.36*	-0.79**	0.12	-0.24	1.20**	-1.09**	-0.87**	0.84**	0.78**	0.30*	-0.66**	0.57**	0.32*	0.22	0.14
PWOM	-0.76**	-0.10	-0.08	0.03	-0.71*	0.59*	-0.43	0.19	0.85**	-0.41	0.26	-0.89**	0.99**	0.56*	-0.08	0.27
AWOM	-0.49**	0.11	-0.50**	-0.02	-0.18	0.23	-0.56**	-0.38*	0.88**	0.29	0.61**	-0.54**	0.35	0.56**	-0.35	0.18
JMOM	-0.30*	-0.01	0.33*	-0.89**	1.31**	0.43**	0.04	0.25	-0.97**	0.51**	0.12	0.43**	-0.74**	-0.57**	0.07	0.14
CHDS	-0.04	-0.04	-0.20**	0.30**	-0.18**	0.21**	-0.26**	-0.20**	0.19**	0.06	0.03	-0.19**	0.22**	-0.11	0.22**	0.06
KBDS	-0.57**	-0.49**	-0.84**	1.11**	-0.97**	1.00**	-0.72**	-0.68**	1.63**	0.44**	0.39*	-1.19**	0.55**	-0.43**	0.78**	0.16
KBOM	-1.08**	-1.19**	-0.59**	0.20	-0.52**	-0.32	-0.82**	-0.66**	2.26**	1.19**	1.24**	-1.42**	0.86**	0.16	0.69**	0.18
ACLN[§]	-0.42**	-0.20*	-0.21*	0.38**	-0.37**	0.08	-0.29**	-0.22*	0.30**	0.09	-0.01	-0.36**	0.35**	0.16	0.73**	0.10
ACOPT[#]	-0.68**	-0.55**	-0.52**	0.25**	-0.28**	0.09	-0.64**	-0.50**	1.14**	0.68**	0.76**	-0.97**	0.40**	0.44**	0.37**	0.07
ACALL[$]	-0.58**	-0.45**	-0.48**	0.34**	-0.34**	0.17**	-0.56**	-0.45**	0.97**	0.52**	0.56**	-0.83**	0.39**	0.29**	0.44**	0.05

[†] Environment codes are as explained in Table 5.1; * $P \leq 0.05$; ** $P \leq 0.01$; [$] ACALL= across all environments; [§] ACLN= across low N stress environments; [#] ACOPT= across optimum N environments; P1= VL052; P2= VL05200; P3= VL05468; P4= VL054178; P5= VL052887; P6= VL05482; P7= VL0523; P8= VL0524; P9= VL05561; P10= VL05483; P11= CML511; P12= CML144; P13= CML159; P14= CML491; P15= VL06375; SE(gi)= standard error of GCA effects

Table 5.9 Estimates of general combining ability (GCA) effects of 15 QPM inbred lines for days to anthesis per environment and across environments, 2006 - 2008

Environment[†]	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10	P11	P12	P13	P14	P15	SE(gi)
HAOM	0.42	1.48*	1.63**	-2.75**	1.89**	-3.84**	1.39**	1.05**	-0.84**	-1.19**	0.26	1.41**	0.19	0.88**	-1.97**	0.29
HALN	1.27**	2.31**	2.47**	-3.65**	1.93**	-3.65**	1.66**	1.47**	-0.30	-2.49**	-1.46**	1.70**	0.04	0.85**	-2.15**	0.25
RAOM	0.46*	0.69**	1.87**	-2.32**	1.81**	-2.80**	2.19**	1.52**	-1.03**	-1.56**	-0.61*	1.62**	-0.22	0.39	-2.03**	0.20
MPOM	-0.68**	-0.29	0.12	0.12	-0.46	0.68**	0.17	-0.36	0.14	0.14	1.74**	-1.50**	-0.25	0.16	0.28	0.25
BKOM	0.90**	0.91**	2.66**	-5.11**	4.87**	-6.15**	3.07**	3.34**	-0.26**	-3.71**	-1.44**	3.36**	-2.77**	3.51**	-3.19**	0.27
BKLN	0.86	1.33*	2.78**	-5.10**	5.46**	-5.12**	2.75**	1.75**	-2.55**	-2.59**	-0.33	3.27**	-3.32**	3.62**	-2.79**	0.51
MLOM	0.58	0.78*	1.81**	-2.83**	3.11**	-5.02**	2.28**	2.04**	-0.63	-2.22**	-0.73*	1.58**	0.02	1.38**	-2.15**	0.35
PWOM	1.37*	1.42*	1.79**	-3.48**	3.98**	-4.36**	1.33*	2.16**	-2.89**	-1.39*	1.05	1.87**	-1.97**	0.92	-1.81**	0.58
AWOM	1.00**	1.51**	1.55**	-2.88**	3.00**	-4.22**	1.51**	1.39**	-0.76**	-2.30**	-0.99**	2.16**	-1.07**	2.32**	-2.22**	0.25
JMOM	1.01**	-2.74**	-2.05**	1.99**	-1.65**	2.72**	-2.74**	-0.16	2.66**	-4.26**	4.21**	-6.00**	3.26**	3.20**	0.55	0.36
CHDS	2.36**	1.72**	1.35*	-5.31**	3.50**	-5.78**	4.88**	2.79**	-0.81	-3.25**	-3.89**	5.17**	-3.51**	4.98**	-4.20**	0.54
KBDS	1.88**	1.21**	1.83**	-4.03**	4.46**	-5.00**	2.05**	2.06**	-1.23**	-3.25**	-2.37**	3.66**	-1.77**	2.66**	-2.17**	0.26
KBOM	1.01**	0.58**	1.51**	-2.81**	2.66**	-4.16**	2.14**	1.61**	-1.17**	-1.86**	-1.09**	2.57**	-0.89**	1.38**	-1.46**	0.20
ACDRT[‡]	2.12**	1.46**	1.59**	-4.67**	3.98**	-5.39**	3.46**	2.42**	-1.02**	-3.25**	-3.13**	4.41**	-2.64**	3.82**	-3.19**	0.30
ACLN[§]	1.07**	1.82**	2.62**	-4.38**	3.69**	-4.38**	2.20**	1.61**	-1.43**	-2.55**	-0.89**	2.49**	-1.64**	2.23**	-2.48**	0.28
ACOPT[#]	0.67**	0.77**	1.73**	-2.92**	2.79**	-3.99**	1.93**	1.77**	-0.77**	-1.87**	-0.43**	1.67**	-0.96**	1.52**	-1.92**	0.11
ACALL[ŝ]	0.96**	1.04**	1.85**	-3.42**	3.11**	-4.26**	2.21**	1.85**	-0.91**	-2.19**	-0.92**	2.22**	-1.32**	1.98**	-2.20**	0.10

[†] Environment codes are as explained in Table 5.1; * $P \leq 0.05$; ** $P \leq 0.01$; [ŝ] ACALL= across all environments; [‡] ACDRT= across drought stress environments; [§] ACLN= across low N stress environments; [#] ACOPT= across optimum N environments; P1= VL052; P2= VL05200; P3= VL05468; P4= VL054178; P5= VL052887; P6= VL05482; P7= VL0523; P8= VL0524; P9= VL05561; P10= VL05483; P11= CML511; P12= CML144; P13= CML159; P14= CML491; P15= VL06375; SE(gi)= standard error of GCA effects

Table 5.10 Estimates of general combining ability (GCA) effects of 15 QPM inbred lines for days to silking per environment and across environments, 2006 - 2008

Environment[†]	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10	P11	P12	P13	P14	P15	SE(gi)
HAOM	0.57	0.52	1.93**	-3.03**	1.59**	-3.84**	1.57**	1.81**	-0.73	-1.36**	0.64	1.08**	0.35	0.93**	-2.05**	0.34
HALN	1.99**	2.10**	3.37**	-3.91**	1.76**	-3.67**	1.70**	2.27**	-1.06*	-4.23**	-0.50	2.03**	-0.11	1.58**	-3.30**	0.50
RAOM	0.51	0.75*	3.36**	-2.48**	1.55**	-2.36**	1.89**	1.28**	-1.78**	-1.68**	-0.55	1.44**	-0.16	0.61*	-2.36**	0.29
MPOM	-0.53*	-0.33	0.13	0.04	-0.52*	0.45	0.27	-0.04	0.05	0.22	1.56**	-1.35**	-0.35	0.21	0.19	0.24
BKOM	1.27**	0.52	3.35**	-4.69**	3.50**	-5.58**	3.31**	3.98**	-1.59**	-4.04**	-1.41**	3.11**	-2.52**	4.11**	-3.31**	0.36
BKLN	1.06*	1.03	3.06**	-5.21**	5.79**	-4.94**	2.75**	1.60**	-2.81**	-2.84**	-0.27	3.06**	-3.30**	3.40**	-2.40**	0.53
MLOM	0.83*	0.97*	2.55**	-2.40**	2.62**	-4.75**	2.09**	1.87**	-1.57**	-2.22**	-0.56	0.99*	0.20	1.60**	-2.20**	0.39
PWOM	1.49*	1.47*	1.88**	-3.66**	4.16**	-4.59**	1.50*	2.14**	-3.17**	-1.68**	0.14	1.91**	-1.84**	1.87**	-1.60**	0.57
AWOM	0.61*	0.75*	2.53**	-2.25**	2.56**	-3.40**	2.25**	1.86**	-1.59**	-2.78**	-1.22**	1.24**	-0.83**	2.00**	-1.72**	0.30
JMOM	0.71	-2.73**	-2.16**	1.99**	-1.49**	2.53**	-2.28**	0.26	2.44**	-4.16**	3.71**	-5.51**	3.20**	3.27**	0.23	0.37
CHDS	4.28**	2.92*	7.35**	-13.41**	6.00**	-11.57**	11.49**	8.14**	-4.04**	-8.23**	-6.18**	9.08**	-5.59**	7.12**	-7.37**	1.14
KBDS	3.18**	1.43*	4.33**	-5.32**	6.65**	-6.50**	3.28**	3.24**	-4.01**	-4.48**	-3.72**	5.16**	-2.54**	3.11**	-3.82**	0.62
KBOM	0.93**	1.20**	2.56**	-2.78**	2.11**	-3.28**	1.66**	1.52**	-2.51**	-1.35**	-0.71**	2.45**	-1.35**	1.73**	-2.18**	0.23
ACDRT[‡]	3.73**	2.18**	5.84**	-9.36**	6.32**	-9.04**	7.39**	5.69**	-4.02**	-6.35**	-4.95**	7.12**	-4.06**	5.12**	-5.60**	0.65
ACLN[§]	1.52**	1.56**	3.21**	-4.54**	3.77**	-4.31**	2.23**	1.94**	-1.93**	-3.53**	-0.39	2.54**	-1.71**	2.49**	-2.85**	0.37
ACOPT[#]	0.71**	0.68**	2.30**	-2.82**	2.36**	-3.65**	1.97**	1.97**	-1.41**	-1.96**	-0.47**	1.43**	-0.89**	1.73**	-1.95**	0.12
ACALL[ŝ]	1.30**	1.05**	2.99**	-4.10**	3.19**	-4.58**	2.84**	2.53**	-1.89**	-2.88**	-1.15**	2.47**	-1.50**	2.37**	-2.65**	0.14

[†] Environment codes are as explained in Table 5.1; * $P \leq 0.05$; ** $P \leq 0.01$; [ŝ] ACALL= across all environments; [‡] ACDRT= across drought stress environments; [§] ACLN= across low N stress environments; [#] ACOPT= across optimum N environments; P1= VL052; P2= VL05200; P3= VL05468; P4= VL054178; P5= VL052887; P6= VL05482; P7= VL0523; P8= VL0524; P9= VL05561; P10= VL05483; P11= CML511; P12= CML144; P13= CML159; P14= CML491; P15= VL06375; SE(gi)= standard error of GCA effects

The GCA effects for anthesis-silking interval were negative and highly significant for VL05561 but positive and highly significant for VL054178 in almost all environments (Table 5.11). Across drought stress environments, inbred lines VL054178 and VL05482 showed lower GCA effects. VL052887, VL05561 and CML144 had negative and highly significant GCA effects across optimal environments. Across all environments, VL054178, VL05561, VL05483 and VL06375 showed lower GCA effects for anthesis-silking interval.

Inbred lines VL05200, VL054178, VL05482, CML144 and CML159 showed negative and significant GCA effects for plant and ear height in most environments (Tables 5.12 and 6.13). However, VL05483 and VL06375 had positive and significant GCA effects for plant height while VL053, VL0524 and VL5561 had positive and significant GCA effects for ear height in most environments. For plant height, inbred lines VL05200, VL05468, VL05482 and CML144 showed negative and highly significant GCA effects across low N stress, optimal and combined environments. For ear height, VL05200, VL054178, VL05482, CML144 and CML159 had negative and significant GCA effects across optimal and combined environments.

For ears per plant, inbred lines VL05482, VL05483 and CML511 showed positive and significant whereas VL05200, VL05468, VL0523, VL0524 and CML159 showed negative and highly significant GCA effects in most environments and in drought, optimal and combined environments (Table 5.14). GCA effects of the lines were not consistent for leaf senescence across the two low N stress environments. GCA effects were negative and significant for VL052887 and CML144 under low N stress at Harare while VL0523, CML511 and CML491 had negative and significant GCA effects under low N stress condition at Bako (Table 5.15). Positive and highly significant GCA effects were observed for VL06375 at Harare and for VL054178 and VL05482 at Bako low N stress. At Chirezi under drought stress, VL05482, CML511 and CML491 showed negative and significant GCA effects while VL054178 and CML159 showed positive and highly significant GCA effects for leaf senescence.

Table 5.11 Estimates of general combining ability (GCA) effects of 15 QPM inbred lines for anthesis-silking interval per environment and across environments, 2006 - 2008

Environment[†]	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10	P11	P12	P13	P14	P15	SE(gi)
RAOM	0.05	0.09	1.47**	-0.14	-0.22	0.47**	-0.30	-0.22	-0.80**	-0.14	0.01	-0.18	0.05	0.20	-0.34	0.23
BAOM	0.34	-0.47*	0.76**	0.41*	-1.28**	0.64**	0.10	0.57**	-1.24**	-0.24	-0.01	-0.39*	0.22	0.61**	-0.05	0.18
MLOM	0.24	0.16	0.74**	0.39*	-0.45**	0.28	-0.30	-0.18	-1.03**	0.01	0.16	-0.53**	0.16	0.32*	-0.03	0.15
AWOM	-0.35	-0.78**	0.92**	0.57*	-0.51	0.84**	0.68*	0.61*	-0.78**	-0.39	-0.32	-0.93**	0.34	-0.35	0.45	0.28
JMOM	-0.31	0.02	-0.03	-0.05	0.06	-0.19	0.52**	0.37*	-0.27	0.12	-0.46*	0.45*	-0.01	0.10	-0.31	0.18
CHDS	1.85	1.18	6.01**	-8.08**	2.45*	-5.71**	6.62**	5.39**	-3.24**	-5.00**	-2.27*	3.89**	-2.12*	2.16*	-3.11**	1.01
KBDS	1.24*	0.23	2.47**	-1.23*	2.23**	-1.53**	1.17*	1.16*	-2.73**	-1.19*	-1.30**	1.47**	-0.84	0.50	-1.65**	0.49
KBOM	-0.10	0.69**	1.07**	-0.02	-0.55**	0.88**	-0.55**	-0.02	-1.29**	0.46**	0.35*	-0.14	-0.46**	0.39*	-0.69**	0.16
ACDRT[‡]	1.55**	0.71	4.24**	-4.65**	2.34**	-3.62**	3.89**	3.27**	-2.99**	-3.09**	-1.79**	2.68**	-1.48**	1.33*	-2.38**	0.56
ACOPT[#]	-0.02	0.01	0.78**	0.22**	-0.58**	0.59**	-0.10	0.14	-0.91**	-0.05	0.03	-0.37**	0.06	0.16*	-0.02	0.08
ACALL[ŝ]	0.37*	0.18	1.65**	-1.00**	0.15	-0.46**	0.94**	0.92**	-1.43**	-0.81**	-0.43**	0.39*	-0.32*	0.45**	-0.61**	0.15

[†] Environment codes are as explained in Table 5.1; * $P \leq 0.05$; ** $P \leq 0.01$; [ŝ] ACALL= across all environments; [‡] ACDRT= across drought stress environments; [#] ACOPT= across optimum N environments; [ŝ] P1= VL052; P2= VL05200; P3= VL05468; P4= VL054178; P5= VL052887; P6= VL05482; P7= VL0523; P8= VL0524; P9= VL05561; P10= VL05483; P11= CML511; P12= CML144; P13= CML159; P14= CML491; P15= VL06375; SE(gi)= standard error of GCA effects

Table 5.12 Estimates of general combining ability (GCA) effects of 15 QPM inbred lines for plant height (cm) per environment and across environments, 2006 - 2008

Environment[†]	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10	P11	P12	P13	P14	P15	SE(gi)
HAOM	-6.25**	-16.06**	0.03	-3.29	7.26**	-13.04**	3.44	5.13*	1.98	12.57**	9.99**	-9.01**	1.75	-0.72	6.21**	2.01
HALN	-0.78	-17.82**	-2.11	5.96**	-2.27	-6.08**	1.59	-2.11	-0.01	12.46**	1.22	-2.01	7.22**	-3.14	7.87**	2.17
RAOM	-1.55	-12.35**	2.35	-0.05	4.05*	-10.13**	0.91	4.76*	-2.21	5.98**	9.25*	-6.85**	4.38*	-1.1	2.56	2.01
MPOM	-3.02	-15.17**	-12.29**	-0.36	8.10*	-4.4	8.10*	5.21	9.25**	7.17*	15.41**	-19.21**	-3.25	-2.48	6.94*	3.21
BKOM	-3.37	-18.01**	-2.22	-8.64**	3.58	-5.62**	5.34**	7.35**	6.78**	6.98**	5.16**	-10.82**	1.66	0.29	11.52**	1.89
BKLN	-1.63	-10.29**	-5.11	-2.71	-0.30	-0.93	-7.66**	1.29	0.79	7.16**	5.27*	-6.77*	10.10**	-3.16	13.97**	2.62
MLOM	2.43	-12.27**	-1.40	-3.68	3.26	-10.33**	-0.60	-1.53	4.41	12.82**	11.71**	-3.66	0.04	-5.83*	4.63*	2.31
PWOM	-0.98	-7.42**	-0.23	-6.34*	-0.18	-3.61	5.24*	5.36*	-3.79	7.33**	-1.28	-7.63**	3.79	3.05	6.68*	2.60
AWOM	-2.37	-17.74**	-8.71**	-10.92**	7.69**	1.69	3.13	6.67**	-0.85	8.85**	9.82**	-1.18	1.26	0.17	2.47	2.26
JMOM	-0.40	6.40**	4.96*	-6.58**	6.03*	0.88	4.72*	-22.85**	-8.58**	-5.79*	10.04**	0.52	9.74**	1.41	-0.48	2.31
CHDS	-4.07	-13.24**	-5.92*	9.93**	-11.98**	15.15**	-3.53	-1.70	2.23	9.56**	9.05**	-17.05**	9.13**	-13.83**	16.25**	2.76
KBOM	-6.88**	-11.76**	-6.03**	-7.09**	1.95	-5.18**	2.21	3.08	6.29**	10.22**	13.77**	-11.29**	4.32*	-1.91	8.31**	1.66
ACLN[§]	-1.21	-14.06**	-3.61*	1.62	-1.28	-3.51*	-3.03	-0.42	0.40	9.81**	3.25	-4.39**	8.65**	-3.15	10.92**	1.70
ACOPT[#]	-2.49**	-14.85**	-4.12**	-5.13**	5.08**	-5.56**	4.17**	4.16**	2.38**	8.70**	8.75**	-8.47**	2.22**	-0.85	6.01**	0.76
ACALL[§]	-2.41**	-14.58**	-4.18**	-2.75**	2.60**	-3.50**	2.33**	2.91**	2.03**	8.96**	7.86**	-8.51**	3.87**	-2.31**	7.68**	0.68

[†] Environment codes are as explained in Table 5.1; [§] ACALL= across all environments; * $P \leq 0.05$; ** $P \leq 0.01$; [§] ACLN= across low N stress environments; [#] ACOPT= across optimum N environments; P1= VL052; P2= VL05200; P3= VL05468; P4= VL054178; P5= VL052887; P6= VL05482; P7= VL0523; P8= VL0524; P9= VL05561; P10= VL05483; P11= CML511; P12= CML144; P13= CML159; P14= CML491; P15= VL06375; SE(gi)= standard error of GCA effects

Table 5.13 Estimates of general combining ability (GCA) effects of 15 QPM inbred lines for ear height (cm) per environment and across environments, 2006 – 2008

Environment[†]	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10	P11	P12	P13	P14	P15	SE(gi)
HAOM	-5.51**	-6.18**	1.40	-6.45**	6.34**	-12.83**	6.95**	9.42**	4.53*	2.34	2.25	-5.95**	-4.51*	5.62**	2.58	1.91
RAOM	-0.38	-8.54**	5.81**	-1.72	2.83	-8.24**	4.39*	6.25**	6.01**	-1.07	5.78**	-7.69**	-2.62	1.98	-2.79	2.13
MPOM	2.16	-8.57**	-6.48**	-13.21**	4.66	-6.88**	3.68	6.21*	12.01**	6.96**	7.58**	-8.82**	-2.28	2.93	0.04	2.38
BKOM	0.11	-9.96**	0.88	-6.39**	4.60*	-5.46**	6.11**	9.01**	14.76**	-3.31	0.31	-3.85	-9.00**	-3.31	5.49**	1.99
BKLN	-2.45	-3.68	-1.69	-2.06	0.71	-1.32	-1.80	6.57**	2.71	2.75	1.20	-2.94	-2.78	2.79	1.99	2.02
MLOM	-0.2	-12.66**	0.34	1.80	1.57	-3.3	5.07*	5.17*	11.35**	3.30	1.57	-7.27**	-5.17*	-0.30	-1.28	2.5
PWOM	-0.77	-4.67*	-0.82	-1.56	-0.64	-1.46	6.28**	6.68**	-0.70	1.18	-3.87	-4.14*	-0.35	3.87	0.97	1.98
AWOM	-0.72	-10.80**	-4.93*	-7.43**	5.07*	-0.29	4.08*	8.02**	2.36	5.20*	5.77**	0.63	-6.38**	-0.21	-0.36	1.99
JMOM	-0.3	-0.43	0.32	-1.51	-4.02	0.54	-1.50	-10.83**	-6.90**	-2.95	8.32**	-2.11	10.35**	7.03**	4.00	2.44
CHDS	0.83	-6.67**	-4.77*	3.86	-5.04*	1.33	5.64*	5.95**	9.31**	0.9	-0.21	-6.35**	-4.39	-2.84	2.46	2.24
KBOM	-1.92	-10.05**	-0.87	-3.90**	1.82	-8.61**	8.35**	9.46**	10.55**	-0.45	1.48	-3.61*	-6.18**	1.64	2.30	1.40
ACOPT[#]	-0.84	-9.14**	-1.29	-4.64**	3.84**	-5.46**	6.14**	7.47**	7.21**	1.53*	2.35**	-4.69**	-4.50**	1.42*	0.60	0.70
ACALL[§]	-0.83	-8.42**	-1.64*	-3.64**	2.75**	-4.47**	5.37**	7.25**	6.99**	1.58*	2.02**	-4.68**	-4.34**	1.16	0.90	0.64

[†] Environment codes are as explained in Table 5.1; * $P \leq 0.05$; ** $P \leq 0.01$; [§] ACALL= across all environments; [#] ACOPT= across optimum N environments; P1= VL052; P2= VL05200; P3= VL05468; P4= VL054178; P5= VL052887; P6= VL05482; P7= VL0523; P8= VL0524; P9= VL05561; P10= VL05483; P11= CML511; P12= CML144; P13= CML159; P14= CML491; P15= VL06375; SE(gi)= standard error of GCA effects

Table 5.14 Estimates of general combining ability (GCA) effects of 15 QPM inbred lines for number of ears per plant per environment and across environments, 2006 - 2008

Environment[†]	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10	P11	P12	P13	P14	P15	SE(gi)
HAOM	-0.04*	-0.06*	-0.07**	-0.05*	0.01	0.07**	-0.02	0.00	0.04*	0.13**	0.03	0.00	-0.06*	0.02	0.00	0.02
HALN	-0.05*	-0.09*	-0.07**	-0.01	-0.06**	0.09**	-0.10**	-0.09*	-0.11**	0.18**	0.06*	0.00	-0.01	0.15**	0.12**	0.02
RAOM	-0.08**	-0.08**	-0.01	-0.03	0.07**	-0.01	-0.05*	0.03	0.02	0.07*	0.19**	-0.09**	-0.07**	0.05*	0.00	0.02
MPOM	-0.01	0.00	-0.07**	-0.01	0.01	0.03	0.00	-0.07**	0.03	0.08**	0.05	0.02	-0.07*	0.00	0.00	0.03
BKOM	-0.01	-0.19**	-0.11**	-0.27**	0.34**	0.12**	-0.03	-0.01	-0.03	0.12**	0.06*	0.07**	-0.16**	0.15**	-0.04	0.03
BKLN	0.01	-0.08*	-0.08*	0.08*	0.01	0.04	-0.02	0.09*	-0.02	0.01	-0.06	-0.03	-0.01	0.09*	-0.02	0.04
MLOM	0.01	-0.04*	-0.05*	-0.18**	0.24**	0.20**	-0.18**	-0.09**	-0.09**	0.14**	0.10**	0.09**	-0.21**	0.12**	-0.07**	0.02
PWOM	-0.01	-0.03	-0.05*	-0.02	-0.05	0.07*	0.00	-0.06*	0.07**	-0.01	0.03	-0.02	0.01	0.09**	-0.01	0.03
AWOM	-0.01	-0.04	-0.08	-0.09*	0.17**	0.21**	-0.06	0.09	-0.05	0.05	0.00	0.03	-0.21**	0.09	-0.10*	0.05
JMOM	-0.06*	0.00	0.12**	-0.01	-0.04	0.09**	-0.07**	0.00	-0.18**	0.02	0.23**	0.10**	-0.07*	-0.06*	-0.07**	0.03
CHDS	-0.03	-0.03	-0.13**	0.19**	-0.11**	0.16**	-0.18**	-0.16**	0.05	0.06*	0.08**	-0.09**	0.15**	-0.04	0.10**	0.03
KBDS	-0.10**	-0.06*	-0.12**	0.13**	-0.14**	0.15**	-0.18**	-0.15**	0.19**	0.13**	0.07**	-0.14**	0.09**	0.02	0.12**	0.03
KBOM	-0.06**	-0.05**	-0.01	-0.07**	0.13**	0.04*	-0.08**	-0.05**	0.02	0.11**	0.05**	-0.03	-0.04*	0.02	0.03	0.02
ACDRT[‡]	-0.07**	-0.04*	-0.13**	0.16**	-0.13**	0.15**	-0.18**	-0.16**	0.12**	0.10**	0.07**	-0.12**	0.12**	-0.01	0.11**	0.02
ACOPT[#]	-0.03**	-0.06**	-0.07**	-0.08**	0.13**	0.09**	-0.05**	-0.02*	-0.01	0.08**	0.07**	0.01	-0.10**	0.07**	-0.03*	0.01
ACALL[§]	-0.03**	-0.06**	-0.08**	-0.02**	0.07**	0.10**	-0.07**	-0.04**	0.00	0.08**	0.06**	-0.01	-0.05**	0.07**	0.00	0.01

[†] Environment codes are as explained in Table 5.1; * $P \leq 0.05$; ** $P \leq 0.01$; [§] ACALL= across all environments; [‡] ACDRT= across drought stress environments; [#] ACOPT= across optimum N environments; P1= VL052; P2= VL05200; P3= VL05468; P4= VL054178; P5= VL052887; P6= VL05482; P7= VL0523; P8= VL0524; P9= VL05561; P10= VL05483; P11= CML511; P12= CML144; P13= CML159; P14= CML491; P15= VL06375; SE(gi)= standard error of GCA effects

Table 5.15 Estimates of general combining ability (GCA) effects of 15 QPM inbred lines for leaf senescence (1-5 score) under low N and drought stress environments, 2006 - 2007

Inbred line	Harare low N	Bako low N	Chiredzi drought
VL052	0.30*	0.19	0.21
VL05200	-0.16	0.00	-0.08
VL05468	0.18	0.13	0.24
VL054178	0.30*	0.55**	0.70**
VL052887	-0.39**	0.18	-0.05
VL05482	-0.13	0.53**	-0.34**
VL0523	0.03	-0.65**	-0.28*
VL0524	-0.09	0.08	-0.11
VL05561	-0.24	-0.04	-0.09
VL05483	-0.01	0.23	0.15
CML511	0.33*	-0.37*	-0.38**
CML144	-0.33*	-0.02	0.19
CML159	-0.13	0.10	0.39**
CML491	-0.08	-0.60**	-0.35**
VL06375	0.41**	-0.30	-0.20
SE(gi)	0.15	0.17	0.13

* $P \leq 0.05$; ** $P \leq 0.01$; SE(gi)= standard errors of GCA effects

SCA variances (σ^2_{sca}) were higher than GCA effects (σ^2_{gca}) for grain yield under optimal environments except at JMOM (Table 5.16 and Figure 5.2). Under low N stress, GCA variance was much higher than SCA variance at HALN while SCA variance was higher at BKLN. Under drought stress, GCA variance was higher than SCA variance at KBDS while the two variance components were equal at CHDS. SCA variances were higher than GCA variances across low N stress, optimal and combined environments. High broad sense heritability was observed for grain yield under all environments except at PWOM. Narrow sense heritability was higher at HALN under low N and at KBDS under drought stress environments. The relative contribution of additive genetic variance estimated as predictability ratio (PR) indicated that additive genetic variance accounted for 90% of the

total genetic variation at HALN under low N stress (Fig. 5.2). Under drought stress at CHDS and KBDS additive genetic variance accounted for 71 and 83% of the genetic variation, respectively. Across environments, additive genetic variance accounted for 56, 45 and 50% of the total genetic variation across low N stress, optimal and combined environments, respectively.

Variances due to GCA were consistently higher than that of SCA in all cases for days to anthesis (Table 5.17) and silking (Table 5.18). Broad and narrow sense heritability was high in each and across environments except at MPOM. For both traits, additive genetic variances accounted for more than 75% of the total genetic variance in all environments except for days to silking at MPOM under optimal management. Across environments, additive genetic variance accounted for more than 90% of the genetic variation for days to anthesis and silking. For anthesis-silking interval, GCA variances were higher than SCA variances at BKOM, RAOM, CHDS and KBOM whereas SCA variances were higher than GCA variances at MLOM, AWOM, JMOM and KBDS (Table 5.19). However, GCA variances were consistently higher than that of SCA across drought stress, optimal and combined environments. Heritability was relatively higher at BKOM and KBOM under optimal conditions, at CHDS and KBDS under drought stress conditions, and across drought stress environments. The contribution of additive genetic variance to the total genetic variance for anthesis-silking interval was higher in most environments and across environments.

GCA variances for plant height were higher than SCA variances at HAOM (optimal condition), HALN (low N stress condition) and CHDS (drought stress condition) whereas SCA variances were higher than that of GCA for other environments and across low N stress, optimal and combined environments (Table 5.20). Broad sense heritability was higher for most environments while narrow sense heritability was higher only for HAOM and CHDS. Predictability ratios were higher for plant height at HAOM (71%), HALN (70%) and CHDS (73%). Similarly, SCA variances were higher than GCA variances for ear height in most environments and across optimal and combined environments (Table 5.21). Broad sense heritability was higher at HAOM, MPOM and KBOM while high narrow sense heritability

was observed at BKOM and KBOM. Additive genetic variances accounted for 90, 83 and 74% of the total genetic variance at BKOM, KBOM and HAOM, respectively.

For ears per plant, SCA components of variances were higher than that of GCA under low N stress and most optimal conditions while GCA components of variances were higher than that of SCA under drought stress conditions at CHDS and KBDS (Table 5.22). Across drought stress, optimal and combined environments, GCA variances were higher than SCA variances. Broad and narrow sense heritability, and predictability ratios were higher under optimal (BKOM and MLOM), drought stress (CHDS and KBDS) and across drought stress conditions. A higher predictability ratio was observed under drought stress environments. Variance components due to SCA were higher than that of GCA for leaf senescence under low N stress at HALN and BKLN while GCA variance was higher than SCA variance under drought stress at CHDS (Table 5.23). Broad sense heritability was high for BKLN and predictability ratio was high (81%) at CHDS while narrow sense heritability was low under all conditions for leaf senescence.

Table 5.16 Estimates of genetic parameters for grain yield (t ha^{-1}) in a diallel cross among 15 QPM inbred lines per environment and across environments, 2006 – 2008

Environment[†]	σ^2_{gca} ±SE	σ^2_{sca} ±SE	σ^2_A	σ^2_D	σ^2_e	H^2(%)	h^2(%)	PR
HAOM	0.46 ± 0.18	1.09 ± 0.26	0.93	1.09	0.56	78.1	36.0	0.46
HALN	0.05 ± 0.02	0.01 ± 0.01	0.09	0.01	0.06	63.8	57.5	0.90
RAOM	0.45 ± 0.19	1.02 ± 0.36	0.89	1.02	1.10	63.4	29.6	0.47
MPOM	1.16 ± 0.43	2.61 ± 0.51	2.31	2.61	0.77	86.5	40.7	0.47
BKOM	0.63 ± 0.23	1.45 ± 0.24	1.25	1.45	0.15	94.6	43.9	0.46
BKLN	0.23 ± 0.09	0.57 ± 0.17	0.47	0.57	0.46	69.4	31.3	0.45
MLOM	0.45 ± 0.17	1.01 ± 0.20	0.90	1.01	0.29	86.8	41.0	0.47
PWOM	0.26 ± 0.12	0.38 ± 0.26	0.52	0.38	1.02	46.6	27.0	0.58
AWOM	0.19 ± 0.08	0.59 ± 0.17	0.38	0.59	0.45	68.4	26.6	0.39
JMOM	0.35 ± 0.13	0.82 ± 0.16	0.71	0.82	0.26	85.7	39.6	0.46
CHDS	0.03 ± 0.01	0.03 ± 0.01	0.06	0.03	0.05	62.7	44.5	0.71
KBDS	0.76 ± 0.28	0.31 ± 0.10	1.52	0.31	0.30	85.9	71.2	0.83
KBOM	1.09 ± 0.40	2.70 ± 0.47	2.18	2.70	0.46	91.5	40.9	0.45
ACLN[§]	0.10 ± 0.04	0.16 ± 0.05	0.21	0.16	0.26	58.5	33.0	0.56
ACOPT[#]	0.40 ± 0.14	0.98 ± 0.15	0.79	0.98	0.56	75.9	33.9	0.45
ACALL[$]	0.30 ± 0.11	0.60 ± 0.09	0.59	0.60	0.46	72.4	35.9	0.50

[†] Environment codes are as explained in Table 5.1; [$] ACALL= across all environments; [§] ACLN= across low N stress environments; [#] ACOPT= across optimum N environments; H^2= broad sense heritability; h^2= narrow sense heritability; PR= predictability ratio; SE= standard error

Table 5.17 Estimates of genetic parameters for days to anthesis in a diallel cross among 15 QPM inbred lines per environment and across environments, 2006 – 2008

Environment[†]	σ^2_{gca} ± SE	σ^2_{sca} ± SE	σ^2_A	σ^2_D	σ^2_e	H^2(%)	h^2(%)	PR
HAOM	2.97 ± 1.08	0.31 ± 0.28	5.93	0.31	1.18	84.1	80.0	0.95
HALN	4.57 ± 1.64	1.56 ± 0.39	9.14	1.56	0.89	92.3	78.9	0.85
RAOM	2.72 ± 0.98	1.18 ± 0.27	5.43	1.18	0.56	92.2	75.8	0.82
MPOM	0.43 ± 0.17	0.24 ± 0.21	0.85	0.24	0.84	56.4	44.1	0.78
BKOM	12.38 ± 4.40	3.32 ± 0.66	24.75	3.32	1.05	96.4	85.0	0.88
BKLN	11.08 ± 4.01	3.37 ± 1.17	22.15	3.37	3.62	87.6	76.0	0.87
MLOM	4.97 ± 1.80	0.84 ± 0.45	9.94	0.84	1.69	86.5	79.7	0.92
PWOM	5.59 ± 2.11	3.59 ± 1.43	11.18	3.59	4.76	75.6	57.2	0.76
AWOM	4.79 ± 1.72	0.89 ± 0.29	9.57	0.89	0.87	92.3	84.5	0.92
JMOM	9.47 ± 3.40	1.84 ± 0.60	18.94	1.84	1.78	92.1	83.9	0.91
CHDS	15.66 ± 5.65	4.78 ± 1.45	31.31	4.78	4.07	89.9	78.0	0.87
KBDS	8.78 ± 3.13	1.09 ± 0.33	17.55	1.09	0.93	95.3	89.7	0.94
KBOM	4.28 ± 1.53	0.75 ± 0.21	8.56	0.75	0.55	94.5	86.8	0.92
ACDRT[‡]	11.78 ± 4.20	1.71 ± 0.46	23.56	1.71	2.50	91.0	84.8	0.93
ACLN[§]	7.06 ± 2.53	1.48 ± 0.40	14.13	1.48	2.26	87.4	79.1	0.91
ACOPT[#]	4.07 ± 1.44	0.56 ± 0.11	8.13	0.56	1.48	85.5	80.0	0.94
ACALL[§]	5.35 ± 1.90	0.64 ± 0.11	10.71	0.64	1.75	86.6	81.7	0.94

[†] Environment codes are as explained in Table 5.1; [§] ACALL= across all environments; [‡] ACDRT= across drought stress environments; [§] ACLN= across low N stress environments; [#] ACOPT= across optimum N environments; H^2= broad sense heritability; h^2= narrow sense heritability; PR= predictability ratio; SE= standard error

Table 5.18 Estimates of genetic parameters for days to silking in a diallel cross among 15 QPM inbred lines per environment and across environments, 2006 – 2008

Environment[†]	σ^2_{gca} ± SE	σ^2_{sca} ± SE	σ^2_A	σ^2_D	σ^2_e	H^2(%)	h^2(%)	PR
HAOM	3.14 ± 1.15	0.42 ± 0.40	6.27	0.42	1.65	80.3	75.2	0.94
HALN	6.62 ± 2.44	1.75 ± 0.95	13.23	1.75	3.54	80.9	71.5	0.88
RAOM	3.18 ± 1.16	1.40 ± 0.42	6.37	1.40	1.17	86.9	71.3	0.82
MPOM	0.33 ± 0.14	0.31 ± 0.21	0.65	0.31	0.83	53.6	36.3	0.68
BKOM	12.00 ± 4.29	3.08 ± 0.78	23.99	3.08	1.83	93.7	83.0	0.89
BKLN	11.15 ± 4.05	3.56 ± 1.27	22.30	3.56	3.96	86.7	74.8	0.86
MLOM	4.64 ± 1.70	0.95 ± 0.56	9.28	0.95	2.15	82.7	75.0	0.91
PWOM	6.25 ± 2.34	3.21 ± 1.35	12.51	3.21	4.56	77.5	61.7	0.80
AWOM	4.18 ± 1.51	0.64 ± 0.34	8.37	0.64	1.26	87.7	81.5	0.93
JMOM	8.33 ± 3.00	1.38 ± 0.57	16.67	1.38	1.91	90.5	83.5	0.92
CHDS	67.87 ± 24.49	20.32 ± 6.34	135.73	20.32	18.24	89.5	77.9	0.87
KBDS	19.18 ± 6.93	7.62 ± 2.07	38.37	7.62	5.30	89.7	74.8	0.83
KBOM	4.31 ± 1.54	1.12 ± 0.29	8.62	1.12	0.71	93.2	82.5	0.89
ACDRT[‡]	39.17 ± 14.01	6.28 ± 1.91	78.35	6.28	11.78	87.8	81.3	0.93
ACLN[§]	8.23 ± 2.96	1.83 ± 0.58	16.46	1.83	3.75	83.0	74.7	0.90
ACOPT[#]	4.03 ± 1.43	0.75 ± 0.14	8.05	0.75	1.79	83.1	76.0	0.91
ACALL[§]	7.72 ± 2.74	1.10 ± 0.20	15.43	1.10	3.62	82.0	76.6	0.93

[†] Environment codes are as explained in Table 5.1; [§] ACALL= across all environments; [‡] ACDRT= across drought stress environments; [§] ACLN= across low N stress environments; [#] ACOPT= across optimum N environments; H^2= broad sense heritability; h^2= narrow sense heritability; PR= predictability ratio; SE= standard error

Table 5.19 Estimates of genetic parameters for anthesis-silking interval in a diallel cross among 15 QPM inbred lines per environment and across environments, 2006 – 2008

Environment[†]	σ^2_{gca} ± SE	σ^2_{sca} ± SE	σ^2_A	σ^2_D	σ^2_e	H^2(%)	h^2(%)	PR
RAOM	0.19 ± 0.09	-0.01 ± 0.16	0.38	-0.00	0.73	34.0	34.5	1.00
BKOM	0.37 ± 0.14	0.19 ± 0.12	0.74	0.19	0.45	67.2	53.3	0.79
MLOM	0.17 ± 0.07	0.18 ± 0.09	0.33	0.18	0.32	61.8	40.2	0.65
AWOM	0.33 ± 0.15	0.60 ± 0.30	0.67	0.60	1.11	53.2	28.1	0.53
JMOM	0.05 ± 0.03	0.35 ± 0.14	0.09	0.35	0.46	49.5	10.4	0.21
CHDS	19.78 ± 7.38	6.23 ± 3.72	39.57	6.23	14.18	76.4	66.0	0.86
KBDS	2.28 ± 0.90	3.36 ± 1.13	4.56	3.36	3.40	69.9	40.3	0.58
KBOM	0.39 ± 0.15	0.03 ± 0.08	0.78	0.03	0.37	68.8	66.6	0.97
ACDRT[‡]	8.62 ± 3.17	1.97 ± 1.06	17.24	1.97	8.80	68.6	61.6	0.90
ACOPT[#]	0.16 ± 0.04	0.11 ± 0.02	0.32	0.11	0.57	43.1	32.1	0.74
ACALL[§]	0.66 ± 0.24	0.20 ± 0.08	1.31	0.20	2.63	36.5	31.7	0.87

[†] Environment codes are as explained in Table 5.1; [§] ACALL= across all environments; [‡] ACDRT= across drought stress environments; [#] ACOPT= across optimum N environments; H^2= broad sense heritability; h^2= narrow sense heritability; PR= predictability ratio; SE= standard error

Table 5.20 Estimates of genetic parameters for plant height in a diallel cross among 15 QPM inbred lines per environment and across environments, 2006 – 2008

Environment[†]	σ^2_{gca} ± SE	σ^2_{sca} ± SE	σ^2_A	σ^2_D	σ^2_e	H^2(%)	h^2(%)	PR
HAOM	63.81 ± 24.09	52.05 ± 18.13	127.62	52.05	56.01	76.2	54.2	0.71
HALN	44.38 ± 17.49	37.86 ± 18.28	88.76	37.86	65.47	65.9	46.2	0.70
RAOM	31.64 ± 12.73	68.45 ± 20.30	63.29	68.45	56.12	70.1	33.7	0.48
MPOM	87.29 ± 34.80	227.91 ± 59.04	174.57	227.91	143.37	73.7	32.0	0.43
BKOM	61.60 ± 23.14	158.47 ± 31.64	123.19	158.47	49.74	85.0	37.2	0.44
BKLN	38.06 ± 16.10	113.48 ± 34.21	76.13	113.48	95.79	66.4	26.7	0.40
MLOM	42.99 ± 17.24	157.15 ± 35.96	85.99	157.15	74.07	76.7	27.1	0.35
PWOM	18.61 ± 9.20	66.27 ± 27.71	37.22	66.27	93.94	52.4	18.9	0.36
AWOM	52.80 ± 20.63	141.10 ± 33.22	105.60	141.10	71.43	77.6	33.2	0.43
JMOM	65.40 ± 25.16	127.37 ± 31.90	130.80	127.37	74.48	77.6	39.3	0.51
CHDS	114.83 ± 43.50	85.99 ± 32.68	229.66	85.99	105.92	74.9	54.5	0.73
KBOM	59.17 ± 21.97	82.68 ± 18.81	118.33	82.68	38.41	84.0	49.4	0.59
ACLN[§]	37.49 ± 14.35	54.81 ± 14.71	74.97	54.81	80.63	61.7	35.6	0.58
ACOPT[#]	44.58 ± 15.98	74.60 ± 12.22	89.16	74.60	73.06	69.2	37.7	0.54
ACALL[š]	40.52 ± 14.50	70.90 ± 11.40	81.03	70.90	77.06	66.4	35.4	0.53

[†] Environment codes are as explained in Table 5.1; [š] ACALL= across all environments; [§] ACLN= across low N stress environments; [#] ACOPT= across optimum N environments; H^2= broad sense heritability; h^2= narrow sense heritability; PR= predictability ratio; SE= standard error

Table 5.21 Estimates of genetic parameters for ear height in a diallel cross among 15 QPM inbred lines per environment and across environments, 2006 - 2008

Environment	σ^2_{gca} ± SE	σ^2_{sca} ± SE	σ^2_A	σ^2_D	σ^2_e	H^2(%)	h^2(%)	PR
HAOM	37.46 ± 14.64	26.61 ± 13.88	74.92	26.61	50.97	66.6	49.1	0.74
RAOM	23.18 ± 9.94	52.39 ± 19.62	46.36	52.39	63.14	61.0	28.6	0.47
MPOM	48.00 ± 19.15	76.76 ± 26.02	96.01	76.76	79.08	68.6	38.1	0.56
BKOM	44.06 ± 17.09	9.44 ± 12.78	88.11	9.44	55.17	63.9	57.7	0.90
BKLN	4.20 ± 3.10	34.79 ± 16.07	8.40	34.79	56.66	43.3	8.4	0.19
MLOM	25.68 ± 11.49	54.47 ± 24.78	51.36	54.47	86.89	54.9	26.7	0.49
PWOM	7.36 ± 4.14	44.71 ± 16.94	14.72	44.71	54.82	52.0	12.9	0.25
AWOM	25.09 ± 10.39	46.45 ± 17.21	50.17	46.45	55.08	63.7	33.1	0.52
JMOM	25.12 ± 11.18	31.51 ± 21.21	50.24	31.51	83.09	49.6	30.5	0.61
CHDS	18.81 ± 8.59	50.90 ± 20.78	37.63	50.90	69.69	56.0	23.8	0.43
KBOM	35.78 ± 13.39	14.43 ± 7.42	71.57	14.43	27.11	76.0	63.3	0.83
ACOPT[#]	24.48 ± 8.84	25.20 ± 4.75	48.96	25.20	61.71	54.6	36.0	0.66
ACALL[§]	20.62 ± 7.44	26.17 ± 4.70	41.24	26.17	61.97	52.1	31.9	0.61

[†] Environment codes are as explained in Table 5.1; [§] ACALL= across all environments; [#] ACOPT= across optimum N environments; H^2= broad sense heritability; h^2= narrow sense heritability; PR= predictability ratio; SE= standard error

Table 5.22 Estimates of genetic parameters for number of ears per plant in a diallel cross among 15 QPM inbred lines per environment and across environments, 2006 - 2008

Environment[†]	σ^2_{gca} ±SE	σ^2_{sca} ±SE	σ^2_A	σ^2_D	σ^2_e	H^2(%)	h^2(%)	PR
HAOM	0.003 ± 0.001	0.009 ± 0.002	0.005	0.009	0.007	68.1	25.5	0.37
HALN	0.009 ± 0.003	0.010 ± 0.003	0.018	0.010	0.007	79.0	51.2	0.65
RAOM	0.005 ± 0.002	0.007 ± 0.003	0.010	0.007	0.009	65.9	39.8	0.60
MPOM	0.001 ± 0.001	0.003 ± 0.002	0.002	0.003	0.009	36.6	16.6	0.45
BKOM	0.022 ± 0.008	0.019 ± 0.004	0.045	0.019	0.009	86.9	61.5	0.71
BKLN	0.001 ± 0.001	0.019 ± 0.007	0.003	0.019	0.022	50.2	6.3	0.13
MLOM	0.020 ± 0.007	0.014 ± 0.004	0.039	0.014	0.008	86.9	63.6	0.73
PWOM	0.001 ± 0.001	0.008 ± 0.003	0.003	0.008	0.010	51.4	13.3	0.26
AWOM	0.010 ± 0.004	0.014 ± 0.008	0.020	0.014	0.031	51.9	30.5	0.59
JMOM	0.009 ± 0.004	0.009 ± 0.003	0.019	0.009	0.009	74.8	49.8	0.67
CHDS	0.014 ± 0.005	0.007 ± 0.003	0.028	0.007	0.009	79.5	63.4	0.80
KBDS	0.016 ± 0.006	0.007 ± 0.003	0.033	0.007	0.011	79.0	65.4	0.83
KBOM	0.004 ± 0.001	0.006 ± 0.002	0.008	0.006	0.004	75.7	42.6	0.56
ACDRT[‡]	0.015 ± 0.005	0.005 ± 0.002	0.029	0.005	0.010	77.4	66.1	0.85
ACOPT[#]	0.005 ± 0.002	0.003 ± 0.001	0.010	0.003	0.011	55.1	41.1	0.75
ACALL[š]	0.004 ± 0.001	0.002 ± 0.000	0.007	0.002	0.011	46.0	33.9	0.74

[†] Environment codes are as explained in Table 5.1; [š] ACALL= across all environments; [‡] ACDRT= across drought stress environments; [#] ACOPT= across optimum N environments; H^2= broad sense heritability; h^2= narrow sense heritability; PR= predictability ratio; SE= standard error

Table 5.23 Estimates of genetic parameters for leaf senescence (1-5) in a diallel cross among 15 QPM inbred lines per environment and across environments, 2006 - 2008

Environment	σ^2_{gca} ± SE	σ^2_{sca} ± SE	σ^2_A	σ^2_D	σ^2_e	H^2(%)	h^2(%)	PR
HALN	0.04 ± 0.02	0.09 ± 0.06	0.09	0.09	0.25	41.5	20.2	0.49
BKLN	0.10 ± 0.04	0.43 ± 0.13	0.19	0.43	0.39	61.4	18.9	0.31
CHDS	0.08 ± 0.03	0.04 ± 0.05	0.16	0.04	0.23	45.8	37.2	0.81

† Environment codes are as explained in Table 5.1; H^2= broad sense heritability; h^2= narrow sense heritability; PR= predictability ratio; SE= standard error

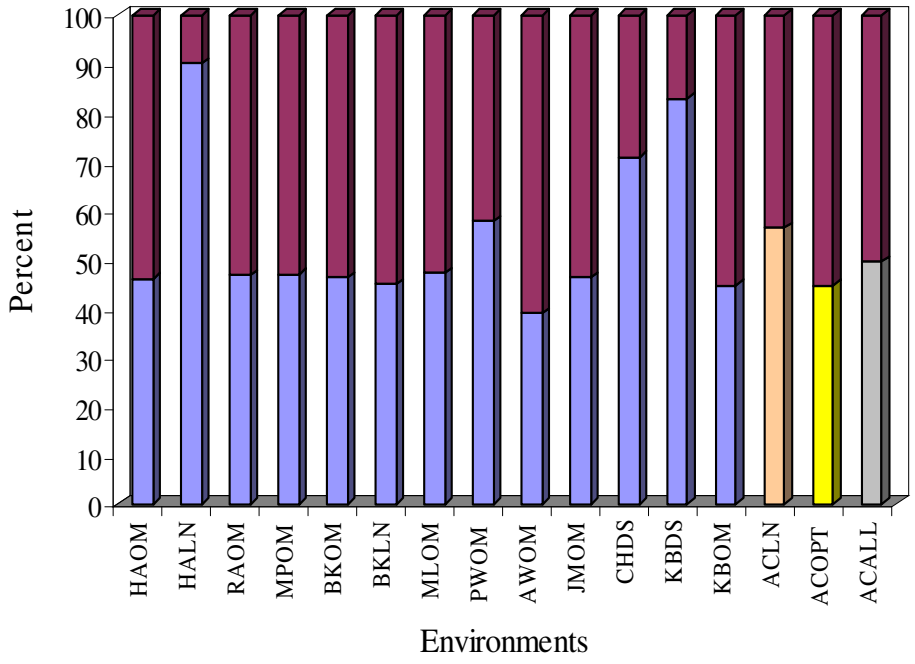

Figure 5.2 Proportion of additive (lower bar) and non-additive (upper bar) genetic variance for grain yield (t ha^{-1}) per environment and across environments in a diallel cross among 15 QPM inbred lines evaluated at 13 locations from 2006 to 2008**.** Environment codes are as explained in Table 5.1.

5.5 Discussion

The results observed in various environments (Table 5.2) showed that drought and low N stress significantly affected grain yield, as previously reported (Bolaños and Edmeades, 1993b, 1996; Banziger et al., 1997; Banziger and Lafitte, 1997; Banziger et al., 1999c; Derera et al., 2008). High levels of variation observed among hybrids under drought stress, low N stress and optimal environments indicate the possibility of selecting for improved grain yield and agronomic traits under stress and non-stress conditions. The existence of genetic variability in maize evaluated under stress conditions has been reported by several investigators (Bolaños et al., 1993; Bolaños and Edmeades, 1996; Banziger and Lafitte, 1997; Beck et al., 1997; Banziger et al., 1997; 1999b; Betran et al., 2003e; Derera et al., 2008). In some environments (HAOM, HALN, ROM and BKLN), only a few or no QPM hybrids yielded higher than the best standard check (Table 5.3) indicating the inferior yielding ability of the QPM hybrids. This indicates that more research efforts are needed for the development of high yielding QPM genotypes, especially for low N stress environments. Significant GCA and SCA mean squares for most traits in each environment indicate the importance of both additive and non-additive effects for the traits studied. This suggests that effective selection or systematic hybridization could be employed in improving these traits.

Combined analysis of variance across drought stress (Table 5.4), low N stress (Table 5.5), optimal (Table 5.6) and combined (Table 5.7) environments indicated the existence of significant variation among hybrids and environments for all traits except for leaf senescence and ears per plant across low N stress. Both additive and non-additive genetic effects were not important for grain yield across drought stress environments while only additive effect was important for days to anthesis and silking, anthesis-silking interval and ears per plant. This finding is contrary to the reports of other researchers (Betran et al., 1999; 2003e; Makumbi et al., 2004; Derera et al., 2008), who reported the importance of additive effects for grain yield of normal maize under drought stress. When genetic variance for grain yield is not apparent, secondary traits of adaptive value whose genetic variability increases and whose heritability remains high under drought can increase selection efficiency (Bolaños and Edmeades, 1996; Edmeades et al., 1997; Banziger and Lafitte, 1997; Banziger et al., 1999a).

Under low N stress, additive effects were important for all traits except leaf senescence and ears per plant while SCA was important only for plant height. Highly significant GCA and SCA mean squares for all traits under optimal environments indicate the importance of both additive and non-additive gene effects for the inheritance of these traits. Similar results have been reported in diallel studies of QPM inbred lines under optimal environments (Pixley and Bjarnason, 1993; Bhatnagar et al., 2004; Hadji, 2004; Fan et al., 2004). Derera et al. (2008) reported the importance of both additive and non-additive effects in conditioning grain yield, days to anthesis and silking, and anthesis-silking interval in Design-II crosses of normal maize inbred lines. Similarly, additive and non-additive effects were important for all traits evaluated across environments except leaf senescence which had non-significant GCA and SCA effects and anthesis silking interval which had non significant SCA effects. Significant mean squares of Hybrid x E, GCA x E and SCA x E interactions for most traits across environments indicate that these effects were not consistent over environments. This implies that different genes are involved in controlling these traits under low-N stress, drought stress and optimal conditions. Cooper and Byth (1996) explained that the larger the degree of genotype-by-environment interaction, the more dissimilar the genetic systems controlling the physiological processes conferring adaptation to different environments.

Even though significant cross-over interactions were observed for GCA effects of the inbred lines, some inbred lines were identified with consistent GCA effects across environments. This implies that the genetic systems controlling a given trait under different stress and non-stress conditions are at least partially similar. Hence, it is possible to identify QPM hybrids that perform well across stress levels in Africa. Similar conclusions have been drawn by Betran et al. (2003e) who evaluated tropical normal maize inbred lines and their hybrids for grain yield under optimal, drought and low N stress conditions.

Inbred lines VL054178, VL05561, VL05483, CML511, CML159 and VL06375 were good general combiners for grain yield in most environments and across drought, low N, optimal and combined environments indicating that these inbred lines contributed to increased grain yield in their crosses under all environmental conditions. Inbred lines VL054178, VL05482, VL05561, VL05483, CML159 and VL06375 contributed to earliness under most

environments as inferred from the negative and highly significant GCA effects of days to anthesis and silking. VL05561 was the best general combiner for anthesis-silking interval. Inbred lines VL05200, VL054178, VL05482, CML144 and CML159 were good combiners for plant stature as they contributed to reduced plant and ear height in the crosses. VL05482, VL05483 and CML511 contributed to increased ears per plant in the crosses. Significant cross-over interactions were observed for GCA effects of the inbred lines for leaf senescence under drought and low N stress (Table 5.15). At Harare low N, VL052887 and CML144, at Bako Low N, VL0523 and at Chiredzi drought stress, VL0582, CML511 and CML491 were the best general combiners for leaf senescence. Anthesis-silking interval, ears per plant and leaf senescence are important secondary traits to be considered in increasing the efficiency of selection for grain yield under stresses. The highest grain yielding genotypes under low N and drought tended to show lower anthesis-silking interval, delayed senescence, and a higher number of ears per plant (Bolaños and Edmeades, 1993b; Banziger and Lafitte, 1997; Banziger et al., 1999b; Diallo et al., 2004).

Higher SCA variances than GCA variances for grain yield in most optimal environments indicate that non-additive variability was of greater importance in the inheritance of grain yield under optimal conditions. Under low N and drought stress conditions, however, additive variability was more important than non-additive variability except for BKLN (low N stress). This might be due to the reason that the stress level at BKLN is not that severe as it can be understood from the lower level of grain yield loss (48.8%) as compared to the grain yield under optimal conditions (BKOM) at the same location and during the same season. Additive effects were more important across drought (85%) and low N (56%) stress conditions while both additive and non-additive effects expressed as predictability ratio were equally important for grain yield across all environments (50% each) (Table 5.16). The predominance of additive effects under drought condition has been reported by several researchers (Betran et al., 2003e; Diallo et al., 2003; Makumbi et al., 2004; Derera et al., 2008). Contrary to findings in the current study Betran et al. (2003e) reported the greater importance of non-additive genetic effects for grain yield under low N stress. The discrepancy might be caused due to the fact that most of the lines used for their study have already been improved for drought tolerance. The higher estimates of broad sense heritability

observed for grain yield in most environments was mainly due to the non-additive genetic effects which can be exploited through employing systematic hybridization. Lower estimates of narrow sense heritability in most environments and across environments further indicate the lower proportion of additive effects in the total variance of grain yield.

Additive effects were more important that non-additive effects in the inheritance of days to anthesis and silking in all cases. Similarly, additive effects were more important for anthesis-silking interval, plant and ear height, and ears per plant in most cases. In general, high estimates of broad and narrow sense heritability were recorded in most of these traits, which indicates the greater importance of additive effects in their inheritance. The low heritability observed in some traits indicates that environmental effects had more pronounced effects relative to the genetic effects.

According to Baker (1978), when SCA mean squares are not significant, the hypothesis that the performance of a single-cross progeny can be adequately predicted on the basis of GCA would be accepted. On the other hand, if the SCA mean squares are significant, the relative importance of GCA and SCA should be assessed by estimating components of variance in determining progeny performance. The closer the predictability ratio to unity, the greater the predictability based on GCA alone. The results of this study revealed that the predictability ratios (PR) for grain yield, plant and ear height, and leaf senescence were low and that of days to anthesis and silking, and anthesis-silking interval were high in most cases. Therefore, the possibility of determining progeny performance for days to anthesis and silking, and anthesis-silking interval from parent GCA alone is high under most of the environmental conditions used for the current study.

5.6 Conclusions

A large proportion of the maize crop in Africa is grown by small scale farmers under low input systems, without adequate fertilization and irrigation. Significant yield losses due to drought and low N stress were realized in this study. The results indicated the availability of considerable variation among QPM hybrids and the possibility of making selections for grain yield and agronomic traits under stress and non-stress conditions. Significant GCA and SCA mean squares, and hence the importance of both additive and non-additive effects was observed for most traits in most environments. Both additive and non-additive genetic effects were not important for grain yield across drought environments. In this case, secondary traits such as anthesis-silking interval and ears per plant with high genetic variability and heritability can be used to increase selection efficiency. Additive effects were important under low N stress while both additive and non-additive effects were important under optimal conditions for most traits.

Estimates of GCA effects showed that inbred lines VL054178, VL05482, VL05561, VL05483, CML511, CML159, CML491 and VL06375 had good GCA effects for most traits under stress and non-stress conditions. These inbred lines can be used for the development of QPM hybrids and synthetics that perform well across stress and non-stress environments. Estimates of GCA and SCA variance components revealed that non-additive genetic effects were more important than additive genetic effects for grain yield under most optimal environments. However, under stress conditions such as HALN, CHDS and KBDS, additive effects were more important than non-additive effects for grain yield. Plant height and ear height showed high broad and narrow sense heritability under all conditions, indicating that environment had a relatively small influence on their expression. The high predictability ratios observed for some traits showed that the prediction of progeny performance only from the GCA effects of inbred lines could be possible. In general, the inbred lines used in this study were found to be useful sources for genetic variability for the development of new genotypes for stress tolerance and the study confirmed the possibility of achieving good performances across stress and non-stress conditions in QPM germplasm.

Chapter 6

Association of parental genetic distance with hybrid performance, heterosis and specific combining ability in quality protein maize under stress and optimal environments

6.1 Abstract

Analysis of genetic distance among quality protein maize (QPM) inbred lines and the correlation of genetic distance with hybrid performance, heterosis and specific combining ability (SCA) would help to design breeding strategy and predict hybrid performance. The present study was carried out to determine the amount of genetic diversity among QPM inbred lines using SSR markers and morphological distances; to classify the inbred lines according to their relationship; and to estimate the correlations of SSR markers and morphological distances with hybrid performance, heterosis and SCA under stress and optimal environments. One-hundred and five hybrids generated by diallel crossing of 15 QPM inbred lines were evaluated across 13 low N and drought stress, and optimal conditions. The 15 parents were evaluated for 17 morphological traits at Harare and Bako and for DNA polymorphism using 40 SSR markers. Low N and drought stress significantly decreased grain yield, plant and ear height, and number of ears per plant; and increased days to anthesis and silking. Grain yield had the highest heterosis, indicating the potential of the inbred lines for hybrid development. Days to anthesis and silking expressed negative heterosis indicating earlier anthesis and silking of hybrids than their parental inbred lines. SSR markers and morphological methods of genetic distance estimates showed moderately high genetic distance among the inbred lines studied. Cluster analysis based on the two distance measures grouped the 15 parental lines differently. SSR markers grouped the inbred lines more reliably and efficiently according to pedigree relationship. The SSR marker-based genetic distance was positively and highly significantly correlated with grain yield; and negatively and highly significantly with days to anthesis and silking. These relationships suggest that high grain yield and earliness of QPM hybrids can be predicted from SSR marker determined distances of the parents. The correlations of SSR marker distance with heterosis and SCA were too low to be of predictive value. Morphological distances were of

low importance in predicting performance, heterosis and SCA effects of hybrids. Environment affected the correlations of genetic distance with hybrid performance, heterosis and SCA, with lower values revealed under stress conditions.

6.2 Introduction

In maize, hybrid breeding remains the method of choice for attaining maximum genetic gain from the effects of heterosis. Nevertheless, identification of lines with superior cross performance is the most costly and time consuming phase in hybrid development programs (Melchinger et al., 1990a). This is because it is necessary to cross the available inbred lines and evaluate the hybrids in extensive yield trails. If inbred lines themselves could be screened, and superior crosses predicted before field evaluation, this would greatly enhance the efficiency of hybrid breeding programs. However, *per se* performance of maize inbred lines does not predict the performance of maize hybrids for grain yield and agronomic traits (Hallauer and Miranda, 1988). In addition, trait expression is often significantly influenced by environmental factors. The efficiency of hybrid breeding programs could be increased if the inbred lines could be screened for genetic diversity using molecular markers and superior crosses accurately predicted prior to field evaluation (Melchinger et al., 1991).

Genetic diversity in relation to hybrid performance and heterosis has been studied extensively in maize. Moll et al. (1965) reported positive correlations between morphological markers based genetic diversity of the parents with heterosis in maize hybrids. The amount of heterosis measured between crosses of maize populations and races from different geographical regions increased as the genetic distance between populations increased (Paternaini and Lonnquist, 1963; Moll et al., 1965). Studies with isozymes demonstrated that genetic distance estimates were in most cases positively associated with F_1 performance for grain yield (Stuber, 1994a). Several studies have attempted to use isozyme variation to measure genetic diversity among inbred lines and to examine the relationship between genetic diversity and grain yield (Frei et al., 1986; Price et al., 1986; Lamkey et al., 1987; Smith and Smith, 1989b). In general, diversity or genetic distance, as measured by isozyme

differences, has not been a good predictor of grain yield or grain yield heterosis. Isozyme diversity, as measured by isozyme loci, may not contribute to heterosis or may not be linked to loci that contribute to heterosis (Hadjinov et al., 1980; Lamkey et al., 1987).

DNA markers have been used to analyze the genetic relationships among maize inbred lines and to examine the relationship between DNA marker-based genetic distance and single-cross grain yields and heterosis in maize. Several reports have demonstrated the high correlation between RFLP distance and hybrid performance in maize (Lee et al., 1989; Smith et al., 1990; Ajmone-Marsan et al., 1998; Betran et al., 2003d; Makumbi, 2005). Melchinger et al. (1990a) and Makumbi (2005), however, reported that RFLP-based genetic distance measures are of limited use in predicting heterotic performance of single crosses between unrelated lines. Lanza et al. (1997) observed positive correlations between RAPD-based genetic distances and maize single-cross hybrid grain yield whereas Parentoni et al. (2001) reported that correlation between RAPD markers estimated genetic distance and SCA for yield was too low to be of predictive value. Ajmone-Marsan et al. (1998) and Kiula et al. (2007) reported that the correlation between AFLP markers, hybrid performance and SCA estimates may have a practical utility in predicting hybrid performance. Legesse et al. (2008) reported low correlation of AFLP measured genetic distance with hybrid performance and heterosis. SSR markers offer advantages in reliability, reproducibility, discrimination, standardization, and cost effectiveness over other marker types (Smith et al., 1997; Melchinger, 1999). SSR markers provide an effective method for predicting hybrid performance and heterosis (Drinic et al., 2002). Genetic distance based on SSR markers was found to be significantly correlated with hybrid yield in maize (Xu et al., 2004).

The degree of heterosis depends on the relative performance of inbred parents and the corresponding hybrids. Environment can have different effects on the performance of hybrids, altering the relationship between genetic distance and heterosis. Betran et al. (2003d) estimated correlation of genetic diversity with hybrid performance, heterosis and specific combining ability of normal maize inbred lines under stress and non-stress environments, and observed lower correlation values under more stressed conditions. In Africa, limited and erratic supply of water and nutrients create contrasting environments.

Information on the influence of low N and drought stress on the use of genetic distance as a predictor of hybrid performance in QPM germplasm is not available. Therefore the objectives of this study were (i) to determine SSR marker and morphological traits based genetic distances among QPM inbred lines; (ii) to classify the inbred lines according to their relationship based on these markers (iii) to estimate the correlations of SSR markers and morphological distances with hybrid performance, heterosis and specific combining ability in quality protein maize under stress and optimal environments

6.3 Materials and methods

Environments and stress management

The inbred lines were evaluated under optimal management conditions at Harare, Zimbabwe and Bako, Ethiopia. The detail descriptions of environmental conditions of the two locations are given in Chapter 3. Similarly, detail descriptions of the 13 environments and stress management practices used for the evaluation the F_1 hybrids are given in materials and methods of Chapters 4 and 5.

Germplasm and field measurements

Fifteen QPM inbred lines used in the diversity study and diallel cross are described in the materials and methods section of Chapter 4. Grain yield, days to anthesis, anthesis-silking interval, plant height, ear height, plant aspect (rating of overall phenotypic appearance of plants), ear diameter, ear length, thousand kernel weight, number of rows per ear, number of kernels per row, leaf length, leaf width, leaf area, tassel size, leaf orientation and foliage rating were used for morphological characterization of the 15 parental inbred lines. One-hundred and five F_1 hybrids resulted from a diallel cross of the inbred lines were evaluated across two low N stress, two drought stress and eight optimum management conditions in Ethiopia, Kenya, Zambia and Zimbabwe. For this study, measurements were taken on grain yield, days to anthesis, days to silking, plant height, ear height and ears per plant of the hybrids.

SSR analysis

Details of SSR analysis used are given in the materials and methods section of Chapter 3. Briefly, 40 selected SSR markers were used in this study. Fluorescently labelled SSR primers were multiplexed in polymerase chain reactions (PCRs) for maximum efficiency. PCR products were subsequently fractionated on an ABI 3130xl Genetic Analyser (PE Applied Biosystems, Foster City, Calif.). The electropherograms were analysed with Genemapper 4.0 software (PE Applied Biosystems, Foster City, Calif.). Bands were coded as present (1) or absent (0) for all the genotypes. A matrix of binary data was constructed with rows equal to number of inbred lines, columns equal to SSR markers alleles and the body of the matrix was filled in with zeros and ones.

Statistical analysis

Analyses of variance for grain yeld and agronomic traits were conducted following the procedures described in materials and methods of Chapters 4 and 5. The formula for estimating mid parent heterosis (MPH) and high parent heterosis (HPH) are presented in the materials and methods part of Chapter 4. The parental lines were evaluated only at two locations (Harare and Bako); therefore, the heterosis was estimated for these two locations only. SCA effects were analyzed as described in the materials and methods part of Chapter 4.

As indicated in materials and methods of Chapter 3, Euclidean distance was computed from 17 morphological traits after the mean observation for each line was standardized (subtracting from each observation the mean value of the trait and dividing by its respective standard deviation). Band profiles generated by SSR markers as 1 or 0 for presence or absence of a specific band, respectively, were used to estimate the Euclidian distances among all possible pairs of the 15 inbred lines. The distances were computed using the Number Cruncher Statistical System, NCSS 2000 (Hintze, 1998). A dendrogram was constructed from the distance matrix using the unweighted pair group method with the arithmetic averages (UPGMA) method of cluster analysis. Pearson correlation coefficient was

computed to estimate the association of SSR marker- and morphological distances with F_1 hybrid performance, MPH, HPH and SCA.

6.4 Results

Analysis of variance for individual environment and across environments showed significant differences among inbred lines and hybrids for all the traits evaluated, except ear height for hybrids at Harare low N (HALN). The inbred lines showed higher yield and earlier maturity at Harare than at Bako (Table 6.1). Hybrid grain yield averaged 5.1 t ha^{-1} across all environments and ranged from 0.6 t ha^{-1} at Chiredzi drought stress (CHDS) to 8.4 t ha^{-1} at Mpongwe optimum management (MPOM) (Table 6.2). Average days to anthesis were 77.9 days with a range of 67.7 days at MPOM to 110.0 days at CHDS. Days to silking ranged from 68.3 days at MPOM to 125.5 days at CHDS with overall average of 80.7 days. Plant height averaged 211.3 cm and ranged from 161.1 cm at Bako low N (BKLN) to 256.1 at HAOM. Ear height ranged from 66.5 cm at BKLN to 136.3 cm at Harare optimum management (HAOM) with an average of 105.4. Average number of ears per plant was 1.00 with a range of 0.24 at Chiredzi drought stress (CHDS) to 1.41 at Bako optimum management (BKOM).

Drought and low N stress decreased grain yield, plant and ear height and number of ears per plant and increased days to anthesis and silking. At Harare, grain yield for hybrids grown under low N (HALN) was 11.5% of grain yield under optimum management (HAOM) during the same season. Grain yield under low N at Bako (BKLN) was 51.2% of grain yield under optimum management (BKOM) at the same location during the same season. At Kiboko, grain yield under controlled drought (KBDS) during the dry season was 35.7% of grain yield under the well-watered regime (KBOM). Grain yield of the hybrids decreased relatively more under drought stress when compared to low N stress environments. However, at Kiboko, drought and well-watered trials were plant in different season.

Table 6.1 Mean, minimum and maximum performance of QPM inbred lines for grain yield and agronomic traits at Harare, Bako and across both locations

Environment		GY	DA	DS	PH	EH	EPP
Harare	Mean	4.0	77.7	77.4	178.2	86.5	1.07
	Min	2.6	69.4	69.2	137.5	57.5	0.62
	Max	7.0	83.6	83.1	242.5	105.0	1.42
	$LSD_{0.05}$	2.4	3.3	4.4	46.0	31.0	0.56
Bako	Mean	2.8	88.1	90.0	154.0	72.8	1.26
	Min	1.8	80.5	81.5	127.2	54.0	0.84
	Max	4.2	98.5	101.0	190.0	101.2	1.68
	$LSD_{0.05}$	1.2	7.7	7.3	18.5	18.8	0.45
Across	Mean	3.4	82.9	83.7	166.1	79.6	1.17
	Min	2.3	76.0	77.5	131.3	56.3	0.91
	Max	4.6	89.3	91.3	198.8	97.5	1.40
	$LSD_{0.05}$	1.2	4.1	4.1	24.0	17.9	0.34

DA= days to anthesis; DS= days to silking; EH= ear height (cm); EPP= number of ears per plant; GY= grain yield (t ha^{-1}); PH= plant height (cm)

Table 6.2 Mean, minimum and maximum values of QPM hybrids for grain yield and agronomic traits in 13 stress and optimal environments; and across environments

Environment†		GY	DA	DS	PH	EH	EPP
HAOM	Mean	7.7	71.4	70.1	256.1	136.3	1.12
	Minimum	3.1	65.9	63.9	209.4	115.3	0.86
	Maximum	12.9	76.9	75.2	292.2	164.8	1.77
	$LSD_{0.05}$	2.1	3.1	3.6	21.0	20.1	0.23
HALN	Mean	0.9	76.0	80.3	172.6	78.2	0.64
	Minimum	0.1	69.0	72.6	132.8	52.8	0.20
	Maximum	1.9	84.5	90.8	195.4	94.8	0.92
	$LSD_{0.05}$	0.7	2.7	5.3	22.8	19.8	0.24
MPOM	Mean	8.4	67.7	68.3	231.0	115.5	1.04
	Minimum	2.4	64.0	64.9	165.0	79.9	0.78
	Maximum	13.8	71.4	72.8	275.0	155.0	1.39
	$LSD_{0.05}$	2.5	2.6	2.6	33.7	25.0	0.27
RAOM	Mean	6.5	70.2	69.7	240.9	132.4	0.95
	Minimum	1.8	65.6	64.6	201.2	104.7	0.44
	Maximum	10.6	75.3	75.6	269.4	157.4	1.50
	$LSD_{0.05}$	3.0	2.1	3.0	21.1	22.3	0.26
BKOM	Mean	6.5	80.3	81.9	240.8	121.6	1.41
	Minimum	1.4	70.4	72.2	178.8	90.0	0.81
	Maximum	9.7	93.6	97.1	293.5	155.0	2.02
	$LSD_{0.05}$	1.1	2.9	3.8	19.8	20.9	0.27
BKLN	Mean	3.3	87.2	87.9	161.1	66.5	1.07
	Minimum	0.4	76.0	76.5	111.7	36.3	0.63
	Maximum	6.4	100.7	101.5	219.2	103.7	1.72
	$LSD_{0.05}$	1.9	5.4	5.6	27.5	21.2	0.41
MLOM	Mean	6.7	77.3	76.9	248.7	126.5	1.28
	Minimum	1.6	67.9	68.4	185.2	92.1	0.65
	Maximum	10.6	85.8	86.9	283.3	155.2	2.02
	$LSD_{0.05}$	1.5	3.7	4.1	24.2	26.2	0.25
PWOM	Mean	4.9	71.2	74.4	185.8	74.7	0.98
	Minimum	1.9	62.0	64.5	147.6	52.2	0.32
	Maximum	8.8	81.2	84.9	217.2	97.6	1.51
	$LSD_{0.05}$	2.6	6.1	6.0	27.3	20.8	0.28
AWOM	Mean	4.7	79.3	81.7	194.6	92.2	1.38
	Minimum	1.7	71.0	74.8	136.8	63.5	0.84
	Maximum	7.2	84.5	89.5	229.1	126.5	2.13
	$LSD_{0.05}$	1.8	2.6	3.2	23.8	20.9	0.50

Table 6.2 Continued

Environment†		GY	DA	DS	PH	EH	EPP
CHDS	Mean	0.6	110.0	125.5	174.1	107.2	0.24
	Minimum	0.2	99.1	100.2	117.2	79.8	0.01
	Maximum	2.1	124.6	148.5	205.1	139.3	0.76
	$LSD_{0.05}$	0.7	5.7	12.1	28.9	23.5	0.27
KBDS	Mean	2.9	74.7	78.5	-	-	0.76
	Minimum	0.2	65.3	67.0	-	-	0.17
	Maximum	5.7	86.2	104.5	-	-	1.02
	$LSD_{0.05}$	1.5	2.7	6.5	-	-	0.29
JMOM	Mean	4.6	84.5	89.9	218.3	106.4	1.05
	Minimum	0.5	73.1	80.5	160.9	75.3	0.37
	Maximum	7.9	94.5	101.7	256.4	128.6	1.74
	$LSD_{0.05}$	1.4	3.8	3.9	24.3	25.6	0.27
KBOM	Mean	8.1	62.0	63.0	214.5	92.2	1.05
	Minimum	1.5	55.2	56.8	176.2	70.6	0.76
	Maximum	12.1	69.8	71.4	243.6	113.9	1.65
	$LSD_{0.05}$	1.8	2.1	2.4	17.4	14.6	0.18
Across drought	Mean	1.8	92.33	101.97	-	-	0.5
	Minimum	0.3	82.76	83.68	-	-	0.1
	Maximum	3.7	103.5	120.02	-	-	0.88
	$LSD_{0.05}$	0.8	3.13	6.79	-	-	0.20
Across low N	Mean	2.1	81.69	84.2	166.17	-	0.85
	Minimum	0.4	73.6	75.87	130.55	-	0.49
	Maximum	3.7	91.35	93.7	191.41	-	1.3
	$LSD_{0.05}$	1.4	4.19	5.42	25.08	-	0.34
Across optimal	Mean	6.5	73.81	75.14	225.48	110.86	1.14
	Minimum	1.8	66.9	68.91	188.97	89.88	0.79
	Maximum	9.4	80.36	82.79	248.39	131.74	1.48
	$LSD_{0.05}$	0.7	1.12	1.26	7.96	7.32	0.08
Across all environments	Mean	5.1	77.88	80.68	211.29	106.44	1.00
	Minimum	1.4	70.37	72.25	175.87	87.09	0.66
	Maximum	7.2	84.28	89.36	231.99	127.9	1.25
	$LSD_{0.05}$	0.5	1.03	1.48	7.06	6.62	0.08

† HAOM= Harare optimum management; HALN= Harare low nitrogen; RAOM= Rattrey-Arnorld optimum management; MPOM= Mpongwe optimum management; BKOM= Bako optimum management; BKLN= Bako low nitrogen; MLOM= Melkassa optimum management; PWOM= Pawe optimum management; AWOM= Awassa optimum management; JMOM= Jimma optimum management; CHDS= Chiredzi drought stress; KBDS= Kiboko drought stress; KBOM= Kiboko optimum management. DA= days to anthesis; DS= days to silking; EH= ear height (cm); EPP= number of ears per plant; GY= grain yield (t ha^{-1}); PH= plant height (cm)

Heterosis was estimated both as MPH and HPH in two non-stress (Harare and Bako) environments where the hybrids and inbred lines were evaluated in adjacent experiments. Average MPH determined for grain yield across all F_1 hybrids was 98.4% at Harare with a range of -9.4 to 235.5% (Table 6.3). At Bako, MPH for grain yield ranged from -45.4 to 304.2% with a mean of 139.1%. Across the two locations MPH averaged 112.8% with a range of -20.7 to 229.2%. All the hybrids showed negative MPH for days to anthesis and silking across locations. MPH for plant height ranged from 26.1 to 77.1% with an average of 50.2% while MPH for ear height ranged from 39.9 to 91.9% with an average of 62.6%. For ears per plant, it averaged 9.1% and ranged from -20.6 to 50.0%. HPH for gain yield averaged 74.1% and ranged from -15.3 to 225.0% at Harare and averaged 111.7% and ranged from -50.6 to 275.3% at Bako. Across both locations, grain yield HPH ranged from -30.4 to 221.4 and averaged 89.8%. Days to anthesis showed an average HPH of -11.3% and range of -20.1 to -2.61% while days to silking showed an average HPH of -12.0% and range of -20.8 to -2.5%. Average HPH for plant height was 39.8% with a range of 18.6 to 71.6% while that of ear height averaged 49.8% and ranged 27.3 to 86.7%. HPH for number of ears per plant averaged 0.4% and ranged from -33.0 to 43.7%.

Most traits studied showed highly significant SCA mean squares in individual environments. SCA mean squares were also significant for all traits for optimal management and across all environments; but were not significant for most traits in low N and drought stress conditions. SCA effects were not computed for the environments that showed non-significant SCA mean squares. SCA effects for grain yield were relatively lower under stress than optimal conditions. A higher maximum SCA effect (5.67 t ha^{-1}) for grain yield was observed at MPOM while a lower value (1.36 t ha^{-1}) was recorded at CHDS (Table 6.4). No clear trends were observed on the effect of drought and low N stress on the magnitude of SCA effects for the other agronomic traits.

Table 6.3 Mean, minimum and maximum mid- parent heterosis and high-parent heterosis for grain yield and agronomic traits of crosses among 15 QPM inbred lines evaluated at Harare, Bako, and across both locations

Environment		Mid-parent heterosis						High-parent heterosis					
		GY	DA	DS	PH	EH	EPP	GY	DA	DS	PH	EH	EPP
Harare	Mean	98.4	-8.0	-9.4	44.8	58.7	6.5	74.1	-11.0	-12.3	33.2	45.4	-3.7
	Minimum	-9.4	-15.1	-16.8	15.6	27.3	-30.2	-15.3	-20.1	-22.0	-1.5	12.5	-39.6
	Maximum	235.5	-1.9	-2.1	71.9	101.7	64.0	225.0	-3.9	-3.3	70.5	94.9	33.4
Bako	Mean	139.1	-8.7	-8.9	57.1	68.3	12.3	111.7	-12.0	-12.3	46.8	52.7	1.6
	Minimum	-45.4	-17.4	-18.3	23.3	32.5	-36.9	-50.6	-21.7	-21.8	11.1	11.8	-41.2
	Maximum	304.2	3.7	2.6	100.3	121.4	61.3	275.3	1.3	1.1	92.2	113.8	54.0
Across	Mean	112.8	-8.4	-9.2	50.2	62.6	9.1	89.8	-11.3	-12.0	39.8	49.8	0.4
	Minimum	-20.7	-14.3	-15.0	26.1	39.9	-20.6	-30.4	-20.1	-20.8	18.6	27.3	-33.0
	Maximum	229.2	-2.3	-2.3	77.1	91.9	50.0	221.4	-2.6	-2.5	71.6	86.7	43.7

DA= days to anthesis; DS= days to silking; EH= ear height; EPP= number of ears per plant; GY= grain yield; PH= plant height

Table 6.4 Minimum, maximum and standard error (SE) for estimates of specific combining ability (SCA) for grain yield and agronomic traits of crosses among 15 QPM inbred lines evaluated in 13 stress and optimal environments; across environments

Environment†		GY	DA	DS	PH	EH	EPP
HAOM	Maximum	3.58	2.65	3.31	18.49	21.01	0.54
	Minimum	-3.93	-4.73	-4.73	-25.58	-18.01	-0.23
	$SE(s_{ij})$	0.70	1.01	1.19	6.93	6.61	0.07
HALN	Maximum	0.61	4.74	6.29	21.33	17.20	0.27
	Minimum	-0.59	-4.92	-5.31	-28.99	-20.05	-0.31
	$SE(s_{ij})$	0.23	0.87	1.74	7.49	6.53	0.08
MPOM	Maximum	5.67	2.82	2.75	40.38	31.17	0.28
	Minimum	-3.81	-3.04	-2.06	-69.04	-45.25	-0.25
	$SE(s_{ij})$	0.81	0.85	0.84	11.09	8.23	0.09
RAOM	Maximum	3.59	2.80	4.04	19.10	19.56	0.29
	Minimum	-3.94	-5.02	-5.47	-36.67	-30.83	-0.40
	$SE(s_{ij})$	0.97	0.69	1.00	6.94	7.36	0.09
BKOM	Maximum	2.42	6.73	7.92	70.76	18.12	0.39
	Minimum	-4.45	-3.85	-4.27	-38.04	-22.01	-0.57
	$SE(s_{ij})$	0.36	0.95	1.25	6.53	6.88	0.09
BKLN	Maximum	2.17	6.67	6.77	30.77	19.28	0.67
	Minimum	-3.65	-13.43	-13.63	-43.45	-24.68	-0.70
	$SE(s_{ij})$	0.63	1.76	1.84	9.06	6.97	0.14
MLOM	Maximum	2.35	4.25	6.06	40.65	28.84	0.36
	Minimum	-3.63	-2.93	-3.27	-60.94	-31.60	-0.39
	$SE(s_{ij})$	0.50	1.20	1.36	7.97	8.63	0.08
PWOM	Maximum	2.85	8.80	9.17	24.55	19.84	0.37
	Minimum	-2.87	-7.95	-7.67	-48.55	-33.23	-0.61
	$SE(s_{ij})$	0.94	1.98	2.02	8.97	6.85	0.09
AWOM	Maximum	1.88	3.59	3.54	22.39	21.22	0.51
	Minimum	-2.64	-3.10	-4.03	-53.90	-26.67	-0.42
	$SE(s_{ij})$	0.62	1.04	0.86	7.82	6.87	0.16
CHDS	Maximum	1.36	13.18	7.59	25.38	27.07	0.40
	Minimum	-0.69	-13.06	-8.41	-41.96	-36.23	-0.38
	$SE(s_{ij})$	0.21	3.95	1.87	9.53	7.73	0.09

Table 6.4 Continued

Environment†		GY	DS	DA	PH	EH	EPP
KBLN	Maximum	1.74	16.83	4.51	-	-	0.25
	Minimum	-2.54	-5.07	-2.58	-	-	-0.38
	$SE(s_{ij})$	0.51	2.13	0.89	-	-	0.09
JMOM	Maximum	1.77	5.47	4.93	23.36	22.24	0.35
	Minimum	-3.49	-3.07	-8.48	-43.18	-23.77	-0.56
	$SE(s_{ij})$	0.47	1.28	1.24	7.99	8.44	0.09
KBOM	Maximum	3.44	5.24	4.07	27.38	13.95	0.42
	Minimum	-5.21	-2.33	-2.18	-26.85	-18.32	-0.21
	$SE(s_{ij})$	0.63	0.78	0.68	5.74	4.82	0.06
Across optimal environments	Maximum	1.82	3.70	2.88	11.49	11.96	0.14
	Minimum	-3.48	-1.47	-1.53	-44.76	-23.41	-0.27
	$SE(s_{ij})$	0.23	0.41	0.37	2.64	2.42	0.03
Across all environments	Maximum	1.32	4.14	3.05	10.76	12.71	0.11
	Minimum	-2.67	-2.21	-1.73	-40.56	-24.03	-0.22
	$SE(s_{ij})$	0.17	0.49	0.34	2.35	2.20	0.03

† HAOM= Harare optimum management; HALN= Harare low nitrogen; RAOM= Rattrey-Arnorld optimum management; MPOM= Mpongwe optimum management; BKOM= Bako optimum management; BKLN= Bako low nitrogen; MLOM= Melkassa optimum management; PWOM= Pawe optimum management; AWOM= Awassa optimum management; JMOM= Jimma optimum management; CHDS= Chiredzi drought stress; KBDS= Kiboko drought stress; KBOM= Kiboko optimum management. DA= days to anthesis; DS= days to silking; EH= ear height; EPP= number of ears per plant; GY= grain yield; PH= plant height

Analysis of 40 SSR markers yielded a total of 169 alleles among the 15 QPM inbred lines. The number of amplified alleles per locus varied from two to seven with a mean value of 4.2. Primers with a low number of alleles (two per primer) were *phi006*, *phi029*, *phi032*, *phi050*, *phi089* and *umc1993* whereas primers *phi041*, *phi053*, *phi96100* and *umc1757* showed a higher number of alleles (seven alleles per primer). A total of 37 unique alleles were detected among the 15 inbred lines. Parental inbred lines VL05482, VL05561, CML144 and VL05200 contained a high number of unique alleles of seven, six, five and four, respectively.

SSR genetic marker and morphological distances calculated for all 105 possible combinations of the 15 parents are presented in Table 6.5. The pairwise genetic dissimilarity values determined using Euclidean distance based on SSR markers ranged from 0.25 (between VL0523 and VL0524) to 0.67 (between VL05200 and VL05561) with a mean of

0.57. Euclidean distance based on morphological evaluation ranged from 0.73 (between VL052 and VL0524) to 2.17 (between VL052887 and VL05482) with a mean of 1.39. Higher genetic distances for SSR markers were observed between VL05200 and VL05561 (0.67), VL05482 and CML144 (0.66), VL05561 and CML159 (0.66), VL05483 and CML144 (0.66), and CML511 and CML159 (0.66). Higher morphological distance was observed between VL054178 and VL052887 (2.06), VL054178 and CML144 (2.04), and VL052887 and VL05482 (2.17). Parental inbred lines VL05561 and CML144 showed the highest mean SSR measured genetic distance (0.62) while VL052 had the lowest (0.51). On the other hand, mean morphological distance was higher for VL054178 (1.75), VL052887 (1.62) and VL05482 (1.58). The correlation coefficient between the two distance measures was non-significant (r= 0.14).

Table 6.5 Estimates of genetic distance based on morphological (above diagonal) and SSR marker (below diagonal) data for all pair-wise combinations of fifteen QPM parental inbred lines

Inbred lines[†]	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10	P11	P12	P13	P14	P15	Mean MD[‡]
P1		1.15	1.11	1.81	1.62	1.63	1.15	0.73	1.34	1.38	1.11	1.27	1.12	1.09	1.35	1.28
P2	0.45		1.51	1.99	1.42	1.88	1.40	1.26	1.30	1.64	1.36	1.03	1.23	1.35	1.51	1.43
P3	0.43	0.58		1.89	1.83	1.71	1.02	1.09	1.37	1.34	1.15	1.31	1.45	1.50	1.65	1.42
P4	0.59	0.59	0.57		2.06	1.24	1.74	1.43	1.64	1.88	1.41	2.17	1.44	1.93	1.85	1.75
P5	0.38	0.52	0.44	0.54		2.04	1.47	1.45	1.58	1.76	1.43	1.31	1.64	1.57	1.55	1.62
P6	0.60	0.65	0.6	0.57	0.57		1.72	1.42	1.35	1.54	1.32	1.69	1.20	1.72	1.70	1.58
P7	0.41	0.55	0.47	0.59	0.47	0.63		0.77	1.08	1.41	1.17	1.24	1.37	1.38	1.37	1.31
P8	0.45	0.54	0.50	0.59	0.51	0.64	0.25		1.25	1.38	1.08	1.39	1.10	1.15	1.34	1.20
P9	0.61	0.67	0.60	0.62	0.61	0.61	0.61	0.60		1.19	1.15	0.95	0.90	1.20	1.06	1.24
P10	0.61	0.62	0.61	0.63	0.61	0.61	0.56	0.59	0.66		1.01	1.43	1.06	1.44	1.27	1.41
P11	0.56	0.65	0.61	0.65	0.61	0.58	0.56	0.56	0.62	0.51		1.23	1.10	1.41	1.32	1.23
P12	0.57	0.57	0.59	0.65	0.60	0.66	0.64	0.61	0.63	0.66	0.63		1.27	1.31	1.38	1.35
P13	0.63	0.60	0.60	0.41	0.59	0.55	0.64	0.63	0.66	0.65	0.66	0.65		0.96	1.05	1.21
P14	0.39	0.52	0.44	0.59	0.39	0.55	0.48	0.51	0.60	0.60	0.56	0.58	0.63		1.06	1.36
P15	0.45	0.58	0.48	0.54	0.48	0.61	0.47	0.53	0.61	0.65	0.59	0.63	0.60	0.44		1.39
Mean SSR[ζ]	0.51	0.58	0.54	0.58	0.52	0.60	0.52	0.54	0.62	0.61	0.60	0.62	0.61	0.52	0.55	

[†] P1= VL052; P2= VL05200; P3= VL05468; P4= VL054178; P5= VL052887; P6= VL05482; P7= VL0523; P8= VL0524; P9= VL05561; P10= VL05483; P11= CML511; P12= CML144; P13= CML159; P14= CML491; P15= VL06375. [‡] MD= morphological data. [ζ] SSR= simple sequence repeat

Cluster analyses based on SSR marker and morphological distances classified the parental inbred lines into different groups (Figures 6.1 and 6.2). However, the two distance measures grouped the 15 inbred lines quite differently. Cluster analyses based on SSR marker grouped the inbred lines into three clusters and two outliers while morphological distances grouped the inbred lines into four clusters and one outlier. Cluster I of the SSR marker distance contained eight of the 15 inbred lines (Figure 6.1). In this cluster the most closely related inbred lines were VL052, VL052887 and CML491, and VL0523 and VL0524. The inbred lines were not related by pedigree. However, the former group shared some common phenotypic characteristics such as late anthesis and silking, taller plant and ear heights, high amount of foliage and small tassel size. The latter group had similar performance in almost all morphological traits. The two inbred lines in cluster II have close pedigree relationship; both of them are the recycled versions of CML176. Cluster III contains three inbred lines among which CML159 and VL054178 have a very close pedigree relationship. Inbred lines VL05561 and CML144 were clustered distantly from the other inbred lines. In a few cases, morphological distance based clustering of the inbred lines followed the pedigree relationship among the materials (Figure 6.2). On the basis of this distance measure, inbred lines with closely related pedigrees such as CML144 and VL05200 (cluster III), and CML511 and VL05483 (cluster II) were tightly clustered. An inbred lines VL052887 was clustered separately from the others.

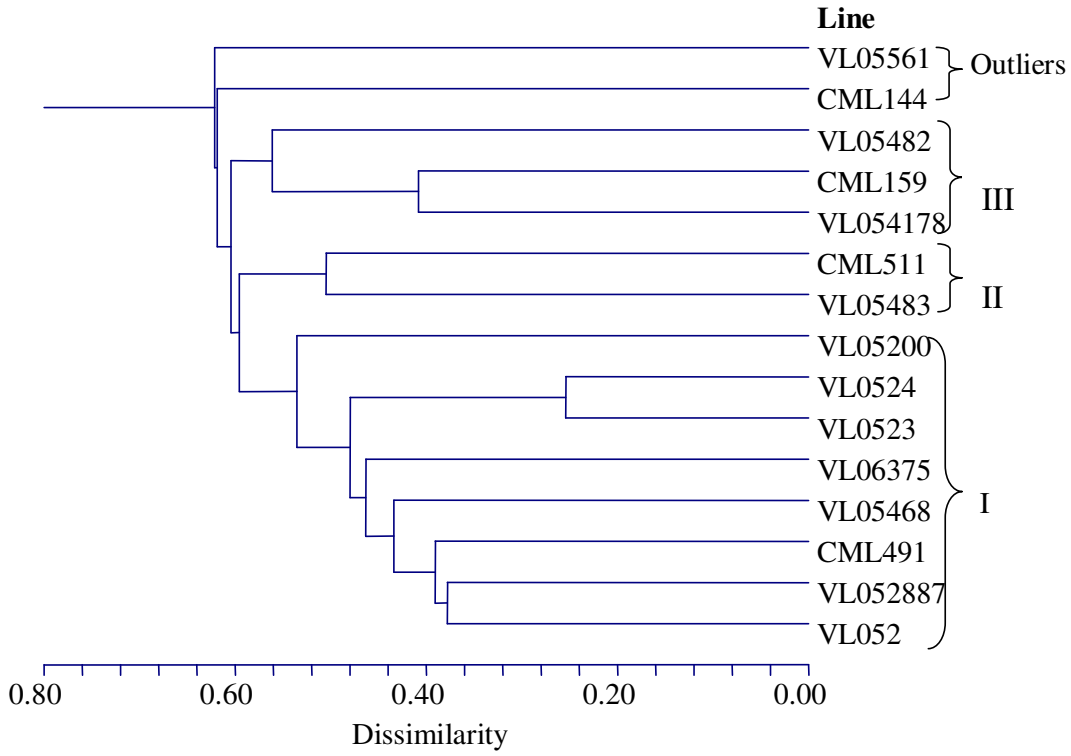

Figure 6.1 Dendrogram depicting genetic relationships among 15 QPM inbred lines revealed by UPGMA cluster analysis based on SSR markers

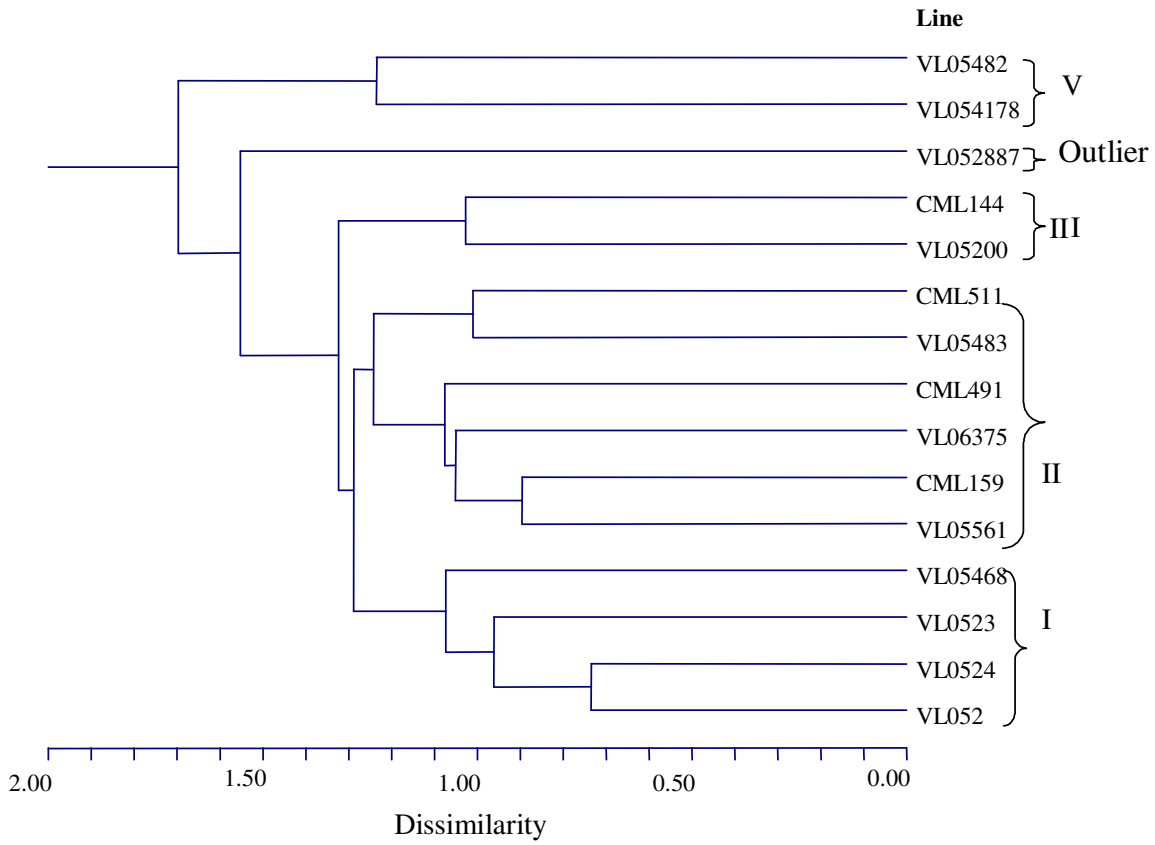

Figure 6.2 Dendrogram depicting genetic relationships among 15 QPM inbred lines revealed by UPGMA cluster analysis based on 17 morphological traits

Table 6.6 illustrates the correlation coefficients of SSR markers and morphological distances with F_1 hybrid performance under different environments. SSR marker distance had a strong correlation with hybrid grain yield under all stress and optimal environments. SSR distance was inversely correlated with days to anthesis and silking in all environments, except MPOM. The correlation values of genetic distance measured by SSR markers with plant height was highly significant under low N stress (BKLN), drought stress (CHDS), across low N environments (ACLN), across drought environments (ACDRT) and across all environments (ACALL). However, ear height showed a non-significant correlation coefficient with SSR distance under all conditions. Higher correlation values between SSR distance and number of ears per plant was observed under drought stress conditions. In most cases, morphological distance showed non-significant correlation with hybrid performance for grain yield and agronomic traits, except with days to anthesis and silking. Highly

significant correlation with grain yield was observed only at MLOM and JMOM; and with number of ears per plant at JMOM and across all environments. An inverse correlation was observed between morphological distances, and days to anthesis and silking under most environments.

Table 6.6 Pearson correlation coefficients of SSR marker and morphological distances with F1 performance for grain yield and agronomic traits in a diallel cross among 15 QPM inbred lines per environment and across environments

Environment†	Genetic distance						Morphological distance					
	GY	DA	DS	PH	EH	EPP	GY	DA	DS	PH	EH	EPP
HAOM	0.32**	-0.32**	-0.31**	0.06	-0.18	0.19	0.23*	-0.32**	-0.39**	-0.05	-0.19*	0.06
HALN	0.21*	-0.35**	-0.35**	0.10	-	0.10	0.09	-0.32**	-0.30**	-0.01	-	0.15
MPOM	0.35**	0.18	0.09	0.11	0.01	0.25**	0.15	0.13	0.07	0.01	-0.26**	0.22*
RAOM	0.36**	-0.35**	-0.39**	0.14	-0.00	0.11	0.03	-0.28**	-0.24*	0.02	-0.08	-0.03
BKOM	0.42**	-0.48**	-0.53**	0.11	-0.04	-0.03	0.05	-0.29**	-0.30**	-0.05	-0.15	0.11
BKLN	0.35**	-0.42**	-0.44**	0.34**	0.16	-0.05	0.16	-0.14	-0.14	0.10	0.03	0.14
MLOM	0.55**	-0.44**	-0.49**	0.17	0.05	0.03	0.28**	-0.30**	-0.27**	-0.10	-0.00	0.25*
PWOM	0.38**	-0.38**	-0.44**	0.12	-0.11	0.32**	0.06	-0.14	-0.13	0.06	0.04	0.10
AWOM	0.47**	-0.40**	-0.56**	0.22*	0.09	-0.09	0.13	-0.19	-0.22*	0.06	-0.01	0.12
CHDS	0.32**	-0.38**	-0.39**	0.39**	0.16	0.38**	0.10	-0.17	-0.17	0.13	-0.03	0.13
KBLN	0.50**	-0.51**	-0.58**	-	-	0.53**	0.17	-0.22*	-0.17	-	-	0.19
JMOM	0.46**	-0.48**	-0.50**	0.22*	0.11	0.20*	0.27**	-0.28**	-0.31**	0.10	0.02	0.36**
KBOM	0.52**	-0.51**	-0.53**	0.24*	-0.07	0.20*	0.12	-0.32**	-0.24*	-0.09	-0.20*	0.19
ACLN	0.36**	-0.42**	-0.44**	0.27**	0.16	0.03	0.17	-0.23*	-0.28*	0.06	0.03	0.19
ACDRT	0.49**	-0.45**	-0.49**	0.39**	0.16	0.51**	0.17	-0.20*	-0.18	0.13	-0.03	0.18
ACOPT	0.53**	-0.47**	-0.53**	0.21*	-0.02	0.15	0.18	-0.29**	-0.29**	-0.00	-0.14	0.25*
ACALL	0.54**	-0.47**	-0.52**	0.26**	0.03	0.28**	0.19	-0.26**	-0.25*	0.03	-0.12	0.30**

* $P \leq 0.05$; ** $P \leq 0.01$; † HAOM= Harare optimum management; HALN= Harare low nitrogen; RAOM= Rattray-Arnold optimum management; MPOM= Mpongwe optimum management; BKOM= Bako optimum management; BKLN= Bako low nitrogen; MLOM= Melkassa optimum management; PWOM= Pawe optimum management; AWOM= Awassa optimum management; JMOM= Jimma optimum management; CHDS= Chiredzi drought stress; KBDS= Kiboko drought stress; KBOM= Kiboko optimum management; ACLN= Across low N environments; ACDRT= Across drought environments; ACOPT= Across optimum environments; ACALL= Across all environments. DA= days to anthesis; DS= days to silking; EH= ear height; EPP= number of ears per plant; GY= grain yield; PH= plant height

The relationship between SSR and morphological distances with MPH and HPH of grain yield and agronomic traits are presented in Table 6.7. The MPH for grain yield showed positive association with morphological distance at Harare and with SSR distance at Bako. Across environments, the two distance measures showed positive and significant correlation with MPH. HPH for grain yield had positive and significant correlation with SSR marker distance at Harare and across the two locations; but no strong association was observed between morphological distance and HPH. The two distance measures had negative correlations with MPH and HPH of days to anthesis and silking. In some cases, the distance measures had positive and significant correlations with plant and ear height. The correlation of SSR marker and morphological distances with MPH and HPH of number of ears per plant was non-significant for the two locations and across locations.

Table 6.7 Pearson correlation coefficients of SSR marker and morphological distances with mid-parent (MP) and high-parent (HP) heterosis for grain yield and agronomic traits in a diallel cross among 15 QPM inbred lines per environment and across environments

Trait	Heterosis	Harare		Bako		Combined	
		SSRD	MD	SSRD	MD	SSRD	MD
Grain Yield	MP	0.18	0.28*	0.24*	0.09	0.26**	0.21*
	HP	0.22*	0.13	0.18	0.02	0.28**	0.09
Days to anthesis	MP	0.14	-0.14	-0.20*	-0.09	-0.12	-0.15
	HP	-0.01	-0.40**	-0.25**	-0.20*	-0.22*	-0.32**
Plant height	MP	0.48**	0.07	0.35**	0.20*	0.54**	0.21*
	HP	0.32**	0.01	0.21*	0.12	0.30**	0.08
Ear height	MP	0.32**	-0.06	0.29**	0.13	0.42**	0.12
	HP	0.12	-0.18	0.19*	0.06	0.19	-0.06
Days to silking	MP	0.17	-0.29**	-0.18	-0.11	-0.08	-0.23*
	HP	0.07	-0.39**	-0.24*	-0.20*	-0.15	-0.33**
Ears per plant	MP	-0.01	-0.12	-0.09	-0.08	-0.08	-0.13
	HP	0.07	-0.07	-0.08	-0.06	-0.03	-0.09

* $P \leq 0.05$; ** $P \leq 0.01$; SSRD= SSR marker-based genetic distance; MD= morphological distance

The correlation of SSR marker-based genetic distance with grain yield SCA was positive and significant in most environments, except at HALN and CHDS (Table 6.8). SCA effects for days to anthesis and silking were negatively correlated with SSR marker distance; but not significant in most cases. Plant and ear height, and number of ears per plant had positive and significant correlation coefficients with SSR distance measures in some environments. Only a few traits showed strong association with morphological distances (Table 6.8). Positive and highly significant correlation coefficients of morphological distance with grain yield and plant height were revealed under optimum management conditions.

6.5 Discussion

Highly significant differences observed among the hybrids and inbred lines for various traits indicated the existence of considerable variation among these sets of genotypes. This indicates good probability for the improvement of QPM germplasm under stress and optimal conditions and also across a range of environmental variables. The ability of the hybrids to perform well under different environmental conditions indicated the adaptation of the hybrids to the locations of evaluation. Variations in response of maize hybrids to environmental stress were previously reported by several researchers (Betran et al., 2003d; e; Mosisa et al., 2007; Derera et al., 2008). As revealed by significant environmental effects, results of the current study generally showed that low N and drought stress decreased grain yield, plant height, ear height and number of ears per plant; and increased days to anthesis and silking, which is consistent with the findings of other researchers (Bolaños and Edmeades, 1996; Banziger and Lafitte, 1997; Betran et al., 2003e; Derera et al., 2008; Pswarayi and Vivek, 2008).

Table 6.8 Pearson correlation coefficients of SSR marker and morphological distances with specific combining ability (SCA) of grain yield and agronomic traits in a diallel cross among 15 QPM inbred lines per environment and across environments

Environment	Genetic distance						Morphological distance					
	GY	AD	SD	PH	EH	EPP	GY	AD	SD	PH	EH	EPP
HAOM	0.27**	-0.08	-0.04	0.18	0.07	0.01	0.23*	-0.08	-0.08	0.16	0.03	0.05
HALN	-0.01	-0.08	-0.05	0.02	-0.03	0.04	0.04	-0.13	-0.08	0.05	-0.01	0.03
MPOM	0.24*	0.17	0.08	0.18	0.08	0.11	0.19	0.18	0.15	0.12	0.04	0.17
RAOM	0.23*	-0.05	-0.12	0.27**	0.20*	0.1	0.11	-0.12	-0.13	0.20*	0.11	0.01
BKOM	0.35**	-0.26**	-0.26**	0.24*	0.17	0.15	0.23*	-0.20*	-0.20*	0.19	0.1	0.13
BKLN	0.25**	-0.07	-0.09	0.30**	0.21*	0.00	0.16	-0.05	-0.06	0.24*	0.13	0.07
MLOM	0.34**	-0.19	-0.18	0.15	0.11	0.04	0.27**	-0.11	-0.11	0.05	0.09	0.11
PWOM	0.28**	-0.06	-0.1	0.28**	0.06	0.25*	0.21*	0.00	0.01	0.24*	0.14	0.18
AWOM	0.30**	-0.06	-0.24*	0.28**	0.16	-0.03	0.22*	-0.01	-0.17	0.27**	0.18	-0.02
CHDS	0.06	-0.05	-0.02	0.26**	0.18	0.04	-0.05	0.02	0.14	0.13	0.05	-0.07
KBLN	0.27**	-0.31**	-0.36**	-0.33**	-0.32**	0.28**	0.18	-0.20*	-0.15	-0.1	-0.1	0.17
JMOM	0.40**	-0.22*	-0.25**	0.39**	0.32**	0.28**	0.27**	-0.11	-0.17	0.26**	0.13	0.16
KBOM	0.37**	-0.33**	-0.36**	0.24*	0.19	0.17	0.29**	-0.27**	-0.23*	0.19	0.13	0.09
ACLN	0.40**	-0.24*	-0.29**	0.37**	0.26**	0.24*	0.29**	-0.16	-0.19	0.27**	0.18	0.19
ACDRT	0.26**	-0.18	-0.20*	-	-	0.22*	0.14	-0.06	0.05	-	-	0.07
ACOPT	0.40**	-0.24*	-0.29**	0.36**	0.28**	0.25*	0.28**	-0.15	-0.11	0.27**	0.18	0.20*
ACALL	0.24*	-0.1	-0.09	0.23*	0.21*	0.02	0.16	-0.1	-0.09	0.20*	0.13	0.09

* $P \leq 0.05$; ** $P \leq 0.01$; † HAOM= Harare optimum management; HALN= Harare low nitrogen; RAOM= Rattray-Arnorld optimum management; MPOM= Mpongwe optimum management; BKOM= Bako optimum management; BKLN= Bako low nitrogen; MLOM= Melkassa optimum management; PWOM= Pawe optimum management; AWOM= Awassa optimum management; JMOM= Jimma optimum management; CHDS= Chiredzi drought stress; KBDS= Kiboko drought stress; KBOM= Kiboko optimum management; ACLN= Across low N environments; ACDRT= Across drought environments; ACOPT= Across optimum environments; ACALL= Across all environments. DA= days to anthesis; DS= days to silking; EH= ear height; EPP= number of ears per plant; GY= grain yield; PH= plant height

Most parents showed positive heterosis for grain yield in both locations and across locations, indicating the existence of substantial heterosis in the hybrids. Among all the traits studied, both MPH and HPH were the highest for grain yield, which is consistent with other reports in maize (Saleh et al., 2002; Legesse et al., 2008). The level of mean MPH (112.8%) and HPH (89.8%) for grain yield observed in the current study is higher than that reported by Xu et al. (2004), Gissa et al. (2007) and Legesse et al. (2008), but lower than that reported by Saleh et

al. (2002), Betran et al. (2003d), Tollenaar et al. (2004) and Makumbi (2005). All hybrids showed desirable negative MPH and HPH for days to anthesis and silking, showing that the hybrids were earlier in anthesis and silking than their parental inbred lines. Moderately high positive MPH and HPH for plant and ear height indicates the preponderance of dominance effects among the parental inbred lines for taller plant stature. Similar results were reported previously (Saleh et al., 2002; Legesse et al., 2008). Significant SCA effect indicates the deviation of specific crosses from the average performance of the parents involved (Hallauer and Miranda, 1988).

The mean (4.2) and range (2 – 7) of alleles amplified per primer in the current study were close to results of previous studies using SSRs in maize inbred lines (Xu et al., 2004; Legesse et al., 2007). Xu et al. (2004) reported a mean of 4.4 and a range of 2 – 9 alleles per locus for 43 SSR primers in 15 key inbred lines of Chinese maize. Legesse et al. (2007) genotyped 56 highland and mid-altitude maize inbred lines from CIMMYT programs in Ethiopia and Zimbabwe using 27 SSR loci and reported a mean of 3.85 and range of 2 – 7 alleles per SSR locus. Parental inbred lines VL05482, VL05561, CML144 and VL05200 with abundant unique alleles could easily be differentiated from the other inbred lines. Similar findings were reported previously (Bantte and Prasanna, 2003; Choukan et al., 2006).

The ability to provide distance measures between the inbred lines that reflect pedigree relationship ensures a more stringent evaluation of the adequacy of a marker profile data. The fact that maximum distance revealed by both SSR markers and morphological distance between inbred lines with unrelated pedigree is a good indication conferring the ability of the two distance measures to distinguish between maize inbred lines. The efficiency of SSR markers in genetic diversity analysis of maize inbred lines has been proven valuable (Smith et al., 1997; Pejic et al., 1998; Warburton et al., 2002; Pinto et al., 2003; Bantte and Prasanna, 2003; Legesse et al., 2007). Morphological traits are also useful for preliminary evaluation because it is fast, simple, and can be used as a general approach for assessing genetic diversity among morphologically distinguishable accessions (Yoseph et al., 2005). However, compared with morphological traits, SSR markers were more reliable and efficient in grouping the inbred lines according to their pedigree relationships. Morphological markers

have shortcomings to detect differences among closely related genotypes and are influenced by prevailing environmental conditions (Smith and Smith, 1992).

In maize, breeding for hybrid varieties is a well recognized approach for yield increment through the exploitation of heterosis. The role of genetically divergent germplasm is of primary importance for the phenomenon of heterosis to occur. Such phenomenon has been reported repeatedly in maize where genetically unrelated parents will have better cross performance (Hallauer and Miranda, 1988; Saleh et al., 2002). In the current study, highly significant positive correlations manifested between SSR marker-based genetic distance and hybrid performance for grain yield, indicating the effectiveness of molecular markers for prediction of hybrid performance. Such significant correlations between genetic distance and grain yield, and suitability of molecular distance for predicting the maize single cross performance were reported by several investigators (Betran et al., 2003d; Barbosa et al., 2003; Xu et al., 2004; Legesse et al., 2008; Kiula et al., 2008). Highly significant negative correlation of SSR marker distance with days to anthesis and silking indicated the dominance for earliness. Bernardo (1992) indicated that molecular genetic distance can only account for variation in performance due to the dominance effects. Consistent with the current study, Legesse et al. (2008) reported positive and significant correlation between plant height and molecular genetic distance. The correlation coefficients of morphological distance with grain yield and agronomic traits were mostly non-significant; except with days to anthesis and silking. Where the correlation coefficients were significant, the magnitudes were low suggesting that morphological distance in this set of maize inbred lines is of limited value in predicting F_1 hybrid grain yield and agronomic traits.

The magnitude of correlation coefficients of SSR marker and morphological distances with MPH, HPH and SCA of grain yield and agronomic traits were mostly low. This indicates that the two distance measures may not be suitable predictors of heterosis and SCA effects in the set of materials studied. Similar results were previously reported (Melchinger et al., 1990b; Ajmone-Marsan et al., 1998; Parentoni et al., 2001; Makumbi, 2005; Legesse et al., 2008). Contrary to the current finding, Betran et al. (2003d) reported a highly significant correlation (r = 0.80) between genetic distance and SCA effects in tropical maize inbreds grown under

stress and non-stress environments. Melchinger (1999) and Betran et al. (2003d) suggested that hybrid performance and heterosis can better be predicted when genetic distance is smaller than a certain threshold, depending on the germplasm under consideration. In this study, the range of genetic distance estimates of the inbred lines were as high as the genetic distances among unrelated inbred lines in which the correlation between marker-estimated genetic distance and MPH is expected to be weak (Melchinger, 1999). Melchinger et al. (1990a) and Saghai-Maroof et al. (1997) noted that the level of correlations between genetic distance, and hybrid performance and heterosis depend on the germplasm used.

Several suggestions have been given concerning the low correlation of genetic distance with hybrid performance, heterosis and SCA. These include lack of linkage between genes controlling the traits measured, unequal genome coverage, random marker distribution and diversified effect of dominance (Melchinger et al., 1990b; Charcosset et al., 1991; Bernardo, 1992; Kwon et al., 2002). Effective prediction of hybrid performance and heterosis using molecular marker would be feasible when a significant proportion (50%) of the selected markers used in the calculation of genetic distance are linked with quantitative trait loci (QTL) affecting performance and heterosis of the target trait in the germplasm under study (Melchinger et al., 1990b; Charcosset et al., 1991; Bernardo, 1992).

The comparison of correlation coefficients for those experiments in the same environment with different stress levels indicated that the magnitude of correlation coefficients of SSR and morphological distances with hybrid performance and SCA decreased under stress conditions. The different environments mostly changed the degree of correlations, but not the signs. Similarly, Betran et al. (2003d) observed that the correlations of genetic distance with F_1 hybrids, SCA, MPH and HPH increased when the drought stress levels decreased. They, however, observed similar magnitudes of correlations within different levels of N stress.

6.6 Conclusions

Drought and low N stress decreased grain yield, plant and ear heights and number of ears per plant and increased days to anthesis and silking. Grain yield showed the highest MPH and HPH among all the traits studied. Negative MPH and HPH for days to anthesis and silking showed that the hybrids were earlier in anthesis and silking than their parental inbred lines. The desirable heterosis observed in this study for grain yield and earliness indicates the potential of the inbred lines for hybrid development. SCA effects for grain yield were lower under stressed than optimal conditions; hence, heterosis can not be expected to directly contribute to gains for grain yield under stress. SSR markers and morphological distances estimated between all possible pair-wise comparisons indicated the presence of considerable variations among the inbred lines studied, which can systematically be exploited in the breeding program. Between the two distance measures, however, SSR markers more reliably and efficiently grouped the inbred lines in accordance with pedigree relationship. SSR marker-based genetic distances showed higher correlation values with grain yield and some agronomic traits than morphological distances, indicating the efficiency of SSR markers in predicting hybrid performance. Even though the correlations of SSR marker and morphological distances with heterosis and SCA effects were significant in some cases, the magnitudes were very low to be of predictive value. Low N and drought stress decreases the magnitude of correlations of genetic distance with hybrid performance, heterosis and SCA. In general, the two distance measures can be useful for the identification of genetically similar/different genotypes; but of limited importance for predicting heterosis and SCA, especially when stress environments are targeted.

Chapter 7

Genotype-environment interaction and stability analysis for grain yield in quality protein maize single-cross hybrids

7.1 Abstract

Genotype-environment (G x E) interaction indicates differential reaction of genotypes to changes in environmental conditions; it becomes more important as the differences in stress intensity among the environments increase. This study was conducted to analyze genotype x environment interaction and grain yield stability of QPM single-cross hybrids for grain yield across stress and optimal environments; and observe the pattern of grouping of the environments based on grain yield responses of the hybrids. One-hundred and five QPM F_1 hybrids resulting from diallel crosses among 15 inbred lines were evaluated under two drought stress, two low N stress and eight optimal environments in eastern and southern African regions. G x E interaction and yield stability were assessed using additive main effects and multiplicative interaction (AMMI), and joint linear regression models. Combined analysis of variance showed significant environment, genotype and G x E effects. The largest proportion of the total variation was explained by environmental effects as a result of inclusion of environments with varying stress conditions. Spearman's rank correlation showed that both AMMI stability value (ASV) and linear regression were positively correlated in ranking the stability of hybrids. The positive rank correlation between the two stability statistics indicated the importance of the models in determining the relative stability of genotypes. AMMI analysis based on inbred line means and selected hybrids clearly discriminated the genotypes on the bases of adaptation patterns. Hierarchical clustering using Ward's minimum variance based on hybrid grain yield and inbred line means grouped the 13 environments mainly according to geographical locations and prevailing growing conditions at different environments.

7.2 Introduction

Maize in Africa is grown in many variable environments by smallholder farmers. Drought and low N stress are the most important environmental variables frequently limiting maize production in Africa (Diallo et al., 2004; Banziger and Diallo, 2004; Setimela et al., 2007). These variable environments affect or influence the ranking of genotypes for grain yield performance across environments and growing seasons. G x E interaction, which is the differential response of cultivars to environmental changes, is an important factor determining the performance of cultivars (Hallauer et al., 1988; Crossa et al., 1990; Vargas et al., 1999). G x E interaction is reflected in various responses of genotypes to environmental conditions. Some genotypes are characterized by stable phenotypic performance in a wide range of environments, while others display considerable variation over environments. Most interesting from the point of view of both breeding and cultivation are those genotypes which have stable or only slightly influenced agronomic traits in a wide range of environments (Ceccarelli, 1989; Gauch and Zobel, 1997; Kang, 1998; Kaczmarek et al., 1999). Multi-environment trials are systematic approaches exploited to increase yield stability of crop varieties in stress prone environments (Shakhatreh et al., 2001).

Determination of the mode of response of genotypes to environmental conditions, particularly identification of stable genotypes, has been of interest to researchers for many years. There is an extensive set of methods for analysis of multi environment trials attempting to interpret omnipresent genotype by environment interactions. The G x E interaction expressed as the linear regression coefficient of the genotype on the site mean was first proposed by Yates and Cochran (1938). This was later used by Finlay and Wilkinson (1963) and modified by Eberhart and Russell (1966), who incorporated the deviation from regression as stability parameter. According to the joint regression model, a stable variety is one with a high mean yield, regression coefficient equals to one (b_i= 1) and deviation from regression equals to zero (s^2d_i= 0) (Eberhart and Russell, 1966). In most cases, s^2d_i is considered as stability parameter rather than b_i (Eberhart and Russell, 1966; Becker and Leon, 1988). According to Zobel et al. (1988), however, linear regression accounts for only a small portion of the interaction sum of squares.

The AMMI model offers a more appropriate first statistical model of choice when main effects and interaction are both important (Zobel et al., 1988; Crossa et al., 1990; Gauch and Zobel, 1997). AMMI model combines analysis of variance for the genotype and environment main effects with principal components analysis of the G x E interactions (Gauch and Zobel, 1996). It is gaining popularity and is currently the main alternative multivariate approach to the joint regression analyses in many breeding programs (Annicchiarico, 1997). The AMMI model is considered appropriate to optimize growers' yields, despite G x E interactions that cause no one genotype to be superior everywhere and always. It is used to subdivide the growing regions to relatively homogeneous mega-environments and target appropriate genotypes for specific mega-environment (Gauch and Zobel, 1997; Annicchiarico, 1997). The results can be graphed in a very informative biplot that shows both main and interaction effects for both genotypes and environments (Gauch and Zobel, 1996). AMMI increases the precision of yield estimation and selection of higher yielding genotypes than treatment means (Crossa et al., 1990). AMMI has no specific experimental design requirements, except for a two-way data structure (Zobel et al., 1988).

The existence of G x E interaction in QPM hybrids was reported by several researchers (Vasal et al., 1993a; b; Pixley and Bjarnason, 1993; 2002; Glover et al., 2005). Pixley and Bjarnason (2002) evaluated G x E interaction and stability of different types of QPM hybrids and open pollinated cultivars grown at 13 tropical locations on four continents and reported high grain yield stability of open pollinated cultivars followed by double crosses, three-way cross and single cross, successively. Recent QPM research activities conducted in Africa by CIMMYT and National Agricultural Research Systems (NARS) partners has resulted in the development of well adapted QPM inbred lines. However, no information is available on the stability in grain yield performance for the hybrids from these inbred lines across the target environments. The objectives of this study were, therefore, to analyze G x E interaction and stability of QPM single-cross hybrids for grain yield across stress and optimal environments; and observe the pattern of grouping of the environments based on grain yield responses of the hybrids.

7.3 Materials and Methods

Environments and stress management

The details of environments and stress management used for this study are given in materials and methods section of Chapters 4 and 5.

Germplasm

One-hundred and five QPM F_1 hybrids resulting from diallel crosses among 15 inbred lines were used for the study. Standard checks were not included as different checks were used at different locations. Further details of the genotypes are given in the materials and methods section of Chapter 4.

Experimental design and field measurements

These are also presented in the materials and methods sections of Chapters 4 and 5.

Statistical analysis

Analysis of variance for grain yield for each environment was conducted with the PROC MIXED procedure in SAS (2003) considering genotypes as fixed effects and replications and blocks within replications as random. This analysis adjusted the mean grain yield and resulted in the greatest efficiency for each site. Entry means adjusted for block effects generated from individual location analyses according to the lattice design (Cochran and Cox, 1960) were used to perform across environments combined analyses as well as stability analysis.

Joint linear regression of the mean of the genotype on the environmental mean as an independent variable was performed using IRRISTAT (IRRI, 2003) according to the procedure proposed by Eberhart and Russell (1966). According to these authors, regression coefficient (b_i), deviation from regression for each genotype (s^2d_i) and mean grain yield (t ha^{-1}) of the genotype over all environments are important factors.

The linear model proposed by Eberhart and Russell (1966) is:

$$Y_{ij} = \mu_i + \beta_i I_j + \delta_{ij}$$

where Y_{ij} is the mean performance of i^{th} hybrid in j^{th} environment; μ_i is the mean of i^{th} hybrid over all environments; β_i is the regression coefficient which measures the response of i^{th} hybrid to varying environments; δ_{ij} is the deviation from regression of i^{th} hybrid in the j^{th} environment, and I_j is the environmental index of j^{th} environment.

The AMMI model, which combines the standard analysis of variance with principal component analysis (Zobel et al., 1988), was used to investigate the agronomic nature of G x E interaction. The AMMI model first fits additive effects for the main effects of genotypes and environments, using the additive usual transpose analysis of variance procedure. Subsequently the program fits multiplicative effects for G x E by principal component analysis (Zobel et al., 1988; Gauch and Zobel, 1996; Gauch and Zobel, 1997). The AMMI model as proposed by Zobel et al. (1998) is:

$$Y_{ge} = \mu + \alpha_g + \beta_e + \sum_{n=1}^{N} \lambda_n \gamma_{gn} \eta_{en} + \theta_{ge},$$

where Y_{ge} is the yield of genotype, g, in environment, e; μ is the grand mean; α_g is the genotype mean deviation; β_e is the environment mean deviation; λ_n is the eigenvalue of the principal component (PCA) axis, *n*; γ_{gn} and η_{en} are the genotype and environment PCA scores for the PCA axis, *n*; N is the number of PCA axis retained in the model; and θ_{ge} is the residual.

The AMMI analyses were computed using adjusted means from 13 locations for the 105 hybrids using a SAS program from the CIMMYT (Burgueño et al., 2001). AMMI biplots were constructed using Biplot v1.1 (http://www.stat.vt.edu/facstaff/epsmith.html) for the 15 inbred lines, averaging the grain yield values in hybrids and for the top 20% of the hybrids (21 hybrids) as it is difficult to accommodate all 105 hybrids in the AMMI biplot graph. Biplots of the first two principal components were used to illustrate the relationships among genotypes, environments, and between genotypes and environments. Environments are represented as vectors and genotypes are represented as points. Genotypes and environments that are close together tend to be similar. The angle between two environment vectors

indicates the degree of association or correlation. Small angles indicate similarity, 90^o angles indicate orthogonality and no association, and angles $>90^o$ indicate a negative correlation of genotype performance between these environments. The orthogonal projections of genotypes on environment vectors indicate the relative performance of genotypes in a given environment; that is the greater the projection of the genotype in the positive direction, the better the performance of that genotype in that environment.

In order to rank the hybrids used in the current study in terms of stability, AMMI stability value (ASV) was calculated for each hybrid following the procedure proposed by Purchase (1997) as follows:

$$\text{ASV}= \sqrt{\left[\frac{IPCA1SS}{IPCA2SS}(IPCA1score)\right]^2 + [IPCA2score]^2}$$

where, ASV= AMMI stability value; SS= sum of squares; IPCA1 and IPCA2= the first and the second interaction principal component axes, respectively.

Hybrids with lower ASV values were considered more stable than hybrids with higher ASV values. Spearman's rank correlation coefficients were calculated between the two stability statistics using Statistical Package for the Social Sciences (SPSS, 2002) software.

The environments were grouped by a hierarchical agglomerative clustering with Ward's minimum variance as a method of fusion. The groupings were made based on adjusted mean grain yield of the hybrids and mean grain yield of the inbred lines in hybrids using IRRISTAT (IRRI, 2003) software.

7.4 Results

Combined analysis of variance showed that environments, hybrids or genotypes, and G x E interaction were highly significant (Table 7.1). Sum of squares of environments, hybrids and G x E accounted for 74.6, 12.9 and 12.4% of the treatment combination (environments, hybrids and G x E) sum of squares, respectively. G x E interaction effects were further

partitioned into interaction principal component axes (IPCA) using the AMMI model. The first four IPCA axes explained 67.7% of the G x E interactions and all were highly significant. The first, second, third and fourth IPCA explained 32.0, 18.7, 8.9 and 8.1% of the G x E interaction, respectively (Table 7.1).

Table 7.1 Analysis of variance for additive main effect and multiplicative interaction (AMMI) model for grain yield (t ha^{-1}) of QPM single-cross hybrids evaluated across 13 stress and optimal environments

Source of variation	Degrees of freedom	Sum of squares	Mean Squares	Total variation explained (%)	G x E explained (%)	G x E cumulative (%)
Environments (E)	12	8411.1	700.9**	74.6	-	-
Hybrids	104	1457.3	14.0**	12.9	-	-
Hybrids x E	1248	1402.1	1.1**	12.4	-	-
IPCA1	115	448.8	3.9**	-	32.0	32.0
IPCA2	113	262.2	2.3**	-	18.7	50.7
IPCA3	111	124.2	1.1**	-	8.9	59.6
IPCA4	109	113.6	1.0**	-	8.1	67.7
G x E residual	800	453.2	0.6	-	-	-
Pooled error	1066	490.4	0.5	-	-	-

** $P \leq 0.01$; IPCA= interaction principal component axis

Stability analysis conducted to assess the grain yield performance of hybrids across stress and optimal environments showed a significant variation in stability of hybrids as measured by mean grain yield, slope of linear regression (b), and deviation from regression (s^2d) (Table 7.2). Similarly, AMMI stability value (ASV) of each genotype revealed variation among hybrids in yield stability. Mean grain yield ranged from 1.4 – 7.2 t ha^{-1}, b ranged from 0.28 – 1.63, absolute values of s^2d ranged from 0.01 to 4.93 and ASV ranged from 0.04 to 2.30. A stable variety is defined as one with high mean grain yield, b= 1.0 and s^2d =0 (Eberhart and Russel, 1966) and ASV=0 (Purchase, 1997). Hybrids with higher grain yield generally had b>1 and s^2d significantly different from zero while hybrids with lower grain yield had b<1 and s^2d not significantly different from zero.

Highest yielding hybrids were VL05483 x CML491 (mean= 7.2 t ha^{-1}, b= 1.63, s^2d= 0.64), VL05561 x CML491 (mean= 6.9 t ha^{-1}, b= 1.26, s^2d = 0.94) and CML159 x CML491 (mean= 6.6 t ha^{-1}, b= 1.20, s^2d= 0.62). All these hybrids showed higher values of b and s^2d. Relatively better stability was shown by VL054178 x CML491 (mean= 6.39, b= 1.12, s^2d= 0.01), VL052 x VL05561 (mean= 6.2 t ha^{-1}, b= 1.15, s^2d= 0.20), and CML511 x CML159 (mean= 5.9 t ha^{-1}, b= 1.08, s^2d= -0.15), which had higher grain yield, b close to unity and s^2d not significantly different from zero. ASV also identified stable hybrids as indicated in the rank order given in Table 7.2. However, discrepancies were observed between the two models in ranking the hybrids. The hybrid identified as stable by both analysis methods was VL054178 x CML491 (mean= 6.4, b= 1.12, s^2d= 0.01, ASV= 0.28). Most interestingly, significant Spearman's coefficient of rank correlation (r= 0.247, P≤0.05) was observed between the deviation from regression (s^2d) and ASV.

Mean grain yield for the inbred lines ranged from 4.3 t ha^{-1} for CML144 to 6.0 t ha^{-1} for VL05561 (Table 7.3). The highest yielding inbred lines were VL05561 (6.0 t ha^{-1}), CML511 (5.6 t ha^{-1}), VL05483 (5.6 t ha^{-1}) and VL06375 (5.5 t ha^{-1}). Mean grain yield for hybrids ranged from 0.6 t ha^{-1} for Chiredzi under drought stress to 8.4 t ha^{-1} for Mpongwe under optimal management. As expected, drought and low N stress environments gave significantly lower yields than optimal management environments at the same location and season. High yielding environments were Mpongwe (8.4 t ha^{-1}), Kiboko (8.2 t ha^{-1}) and Harare (7.7 t ha^{-1}) optimum management while Chiredzi drought stress (0.6 t ha^{-1}), Harare low nitrogen stress (0.9 t ha^{-1}) and Kiboko drought stress (2.9 t ha^{-1}) were low yielding environemtns in order listed. Between the two stresses (drought and low N) drought stress caused more yield reduction than low N stress (Table 7.4).

Table 7.2 Mean grain yield (t ha^{-1}), linear regression coefficient (b), deviation from regression (s^2d), and AMMI stability value (ASV) for grain yield of QPM single crosses evaluated across 13 stress and optimal environments

No.	Hybrid	Mean	Rank	b	S^2_d	Rank	ASV	Rank	No.	Hybrid	Mean	Rank	b	S^2_d	Rank	ASV	Rank
1	P1xP2	3.1	100	0.64*	0.03	7	1.27	93	54	P5xP9	6.08	11	1.34*	0.73**	83	1.02	82
2	P1xP3	3.9	90	0.84	0.35	55	0.61	49	55	P5xP10	5.79	21	1.31*	0.87**	90	0.98	80
3	P1xP4	5.5	37	1.10	-0.07	20	0.34	22	56	P5xP11	5.95	13	1.35*	0.59*	73	1.42	96
4	P1xP5	3.1	99	0.72*	0.06	14	1.00	81	57	P5xP12	2.74	102	0.61*	-0.03	10	1.23	91
5	P1xP6	5.3	59	1.03	0.53*	66	0.56	42	58	P5xP13	5.52	40	1.09	1.10**	98	0.57	44
6	P1xP7	4.0	87	0.82	0.09	25	0.54	39	59	P5xP14	4.68	79	1.07	0.87**	89	0.82	68
7	P1xP8	4.0	88	0.79*	0.01	2	0.86	74	60	P5xP15	5.84	17	1.17	0.79**	84	0.86	72
8	P1xP9	6.2	9	1.15	0.20	39	0.72	57	61	P6xP7	5.47	44	1.17	2.37**	104	1.51	100
9	P1xP10	5.5	38	1.22*	-0.06	18	0.80	66	62	P6xP8	4.85	75	0.86	0.21	42	0.55	41
10	P1xP11	5.7	25	1.30	1.11**	99	1.44	98	63	P6xP9	5.89	15	1.01	0.62**	75	0.22	8
11	P1xP12	2.3	104	0.53*	0.04	13	1.53	101	64	P6xP10	4.81	76	0.84	0.80**	85	0.74	61
12	P1xP13	5.4	47	0.97	0.56*	69	0.71	55	65	P6xP11	5.39	50	0.94	0.34	54	0.17	6
13	P1xP14	3.6	94	0.72*	-0.27	48	1.03	83	66	P6xP12	5.02	67	0.94	0.24	45	0.57	45
14	P1xP15	5.5	43	1.08	-0.20	41	0.43	26	67	P6xP13	4.99	70	0.84*	-0.34	53	0.55	40
15	P2xP3	3.5	96	0.80*	0.04	11	0.82	69	68	P6xP14	5.84	18	1.10	1.47**	103	0.51	36
16	P2xP4	5.7	26	0.85	0.40*	58	0.51	35	69	P6xP15	5.02	68	0.83*	0.01	3	0.53	38
17	P2xP5	3.6	95	0.69*	0.98**	94	1.34	95	70	P7xP8	1.37	105	0.28*	-0.06	15	2.30	105
18	P2xP6	5.5	41	0.98	0.91**	92	0.47	30	71	P7xP9	4.91	73	1.06	0.69**	82	0.56	43
19	P2xP7	4.2	83	0.85*	-0.17	37	0.63	51	72	P7xP10	5.38	52	1.16	0.32	51	0.74	60
20	P2xP8	4.3	81	0.91	-0.17	38	0.51	34	73	P7xP11	4.95	72	0.99	0.80**	86	0.41	24
21	P2xP9	6.3	7	1.24*	0.31	49	0.96	78	74	P7xP12	3.80	91	0.86	0.02	5	0.65	52
22	P2xP10	5.1	63	0.97	-0.13	29	0.30	17	75	P7xP13	5.47	45	1.04	1.15**	101	0.90	75
23	P2xP11	5.9	16	1.26*	0.41*	59	0.98	79	76	P7xP14	4.99	71	0.95	0.14	34	0.31	18
24	P2xP12	2.7	103	0.64*	0.06	17	1.11	88	77	P7xP15	5.30	58	1.17	0.63**	76	0.95	77
25	P2xP13	5.7	27	0.82	1.13**	100	1.10	87	78	P8xP9	5.24	61	1.10	0.12	28	0.50	32
26	P2xP14	3.8	92	0.72*	0.02	6	1.08	85	79	P8xP10	5.81	20	1.29*	0.07	19	1.20	90
27	P2xP15	5.7	29	1.01	0.13	32	0.23	10	80	P8xP11	5.25	60	1.13	-0.04	12	0.44	27
28	P3xP4	5.6	33	1.07	0.31	50	0.39	23	81	P8xP12	3.70	93	0.79*	0.06	16	0.83	71
29	P3xP5	3.9	89	0.88	-0.03	9	0.47	29	82	P8xP13	5.67	31	0.92	1.04**	95	0.90	76
30	P3xP6	5.0	69	0.86	0.43*	60	0.81	67	83	P8xP14	5.06	66	1.09	0.22	43	0.31	19
31	P3xP7	4.0	86	0.93	1.05**	96	0.74	62	84	P8xP15	5.75	23	1.03	-0.08	22	0.04	1
32	P3xP8	4.1	85	0.96	-0.03	8	0.07	3	85	P9xP10	6.12	10	1.26	1.10**	97	1.43	97
33	P3xP9	5.8	22	1.22	0.52*	65	0.71	54	86	P9xP11	5.99	12	1.22	0.63**	77	0.86	73
34	P3xP10	5.3	55	1.15*	-0.26	47	0.59	46	87	P9xP12	6.32	8	1.33*	0.14	33	1.23	92
35	P3xP11	5.4	53	1.23	0.88**	91	1.32	94	88	P9xP13	6.40	5	1.07	0.34	52	0.59	47
36	P3xP12	3.3	97	0.72*	0.68**	81	1.14	89	89	P9xP14	6.88	2	1.26	0.94**	93	0.82	70
37	P3xP13	5.2	62	0.97	0.63**	78	0.72	58	90	P9xP15	5.60	34	1.08	0.57**	71	0.61	50
38	P3xP14	4.3	82	0.91	-0.23	44	0.32	20	91	P10xP11	4.90	74	1.01	-0.09	23	0.28	15
39	P3xP15	5.3	56	1.09	0.08	21	0.28	14	92	P10xP12	5.84	19	1.18	0.54*	67	0.52	37
40	P4xP5	5.5	46	1.04	0.36	56	0.46	28	93	P10xP13	5.36	54	0.98	-0.13	30	0.06	2
41	P4xP6	4.7	78	0.71*	0.11	27	1.09	86	94	P10xP14	7.19	1	1.63*	0.64**	79	2.27	104
42	P4xP7	5.5	42	1.04	0.10	26	0.22	7	95	P10xP15	5.39	51	1.11	0.82**	87	0.79	64
43	P4xP8	5.7	30	1.06	0.55*	68	0.16	5	96	P11xP12	5.57	35	1.16	0.58*	72	0.79	65
44	P4xP9	5.7	28	1.04	-0.09	24	0.34	21	97	P11xP13	5.90	14	1.08	-0.15	35	0.43	25
45	P4xP10	5.1	65	0.99	0.43*	61	0.12	4	98	P11xP14	6.61	4	1.49*	-0.02	4	1.45	99
46	P4xP11	5.6	36	0.99	0.20	40	0.23	11	99	P11xP15	5.08	64	0.92	-0.13	31	0.22	9
47	P4xP12	5.7	32	1.21	0.51*	63	0.77	63	100	P12xP13	4.78	77	0.83	4.93**	105	2.00	103
48	P4xP13	3.3	98	0.72*	0.65**	80	1.04	84	101	P12xP14	2.92	101	0.54*	0.36	57	1.64	102
49	P4xP14	6.4	6	1.12	0.01	1	0.28	13	102	P12xP15	5.41	48	1.05	-0.25	46	0.27	12
50	P4xP15	5.4	49	0.93	0.52*	64	0.49	31	103	P13xP14	6.62	3	1.20	0.62**	74	0.51	33
51	P5XP6	5.3	57	0.95	0.57*	70	0.60	48	104	P13xP15	5.54	39	0.89	0.48*	62	0.73	59
52	P5xP7	4.2	84	0.91	0.16	36	0.30	16	105	P14xP15	5.75	24	1.13	1.39**	102	0.72	56
53	P5xP8	4.3	80	0.89	0.84**	88	0.65	53									

* $P \leq 0.05$; ** $P \leq 0.01$; P1= VL052; P2= VL05200; P3= VL05468; P4= VL054178; P5= VL052887; P6= VL05482; P7= VL0523; P8= VL0524; P9= VL05561; P10= VL05483; P11= CML511; P12= CML144; P13= CML159; P14= CML491; P15= VL06375

Table 7.3 Mean grain yield (t ha^{-1}) of 15 QPM inbred lines in hybrids across 13 stress and optimal environments

No.	Inbred line	Grain yield (t ha^{-1})	Rank
1	VL052	4.5	14
2	VL05200	4.6	11
3	VL05468	4.6	12
4	VL054178	5.4	6
5	VL052887	4.8	9
6	VL05482	5.2	8
7	VL0523	4.5	13
8	VL0524	4.7	10
9	VL05561	6.0	1
10	VL05483	5.6	3
11	CML511	5.6	2
12	CML144	4.3	15
13	CML159	5.4	5
14	CML491	5.3	7
15	VL06375	5.5	4

Table 7.4 Mean grain yield (t ha^{-1}) of the 13 stress and optimal experimental environments for 105 QPM hybrids

Environment	Code	Grain yield	Rank
Harare optimum management	HAOM	7.7	3
Harare low nitrogen stress	HALN	0.9	12
Rattray-Arnold optimum management	RAOM	6.4	6
Mpongwe optimum management	MPOM	8.4	1
Bako optimum management	BKOM	6.5	5
Bako low nitrogen stress	BKLN	3.3	10
Melkasa optimum management	MLOM	6.7	4
Pawe optimum management	PWOM	4.9	7
Awassa optimum management	AWOM	4.7	8
Jimma optimum management	JMOM	4.6	9
Chiredzi drought stress	CHDS	0.6	13
Kiboko drought stress	KBDS	2.9	11
Kiboko optimum management	KBOM	8.2	2

Mean performance of the 15 inbred lines in hybrids and top yielding 21 hybrids (Table 7.2) were used to graph the AMMI biplot. The AMMI biplot generated using the first two principal component scores showed a clear association between genotypes and environments (Figures 7.1 and 7.2). The first principal components explained 47.5% (PCA1) and 16.9% (PCA2) of the G x E interaction for the inbred line (Figure 7.1). The biplot showed that optimum management environments, KBOM and MPOM, were the most discriminating environments for the genotypes. Moreover, the angle between the vectors for these two environments was small. Vectors of stress environments, HALN, BKLN and CHDS, except KBDS projected in the opposite direction to KBOM and MPOM. For the environments, closer relationships were observed between PWOM and JMOM (Ethiopian optimum management environments), BKLN and AWOM (both in Ethiopia but low N and optimum management), HALN and CHDS (low N and drought stress Zimbabwean environments), HAOM and RAOM (optimum management Zimbabwean environments), and BKOM and KBOM (optimum management Ethiopian and Kenyan environments).

The AMMI biplot also clearly indicated the relationship among the inbred lines. P9 was different from the other inbred lines in its hybrid performance as it is located far apart from the other inbred lines in the biplot. P10 and P11, P6 and P13, P2 and P12, P4 and P14 were quite similar in their hybrid performances for grain yield. Projection of inbred lines points to environmental vectors indicated specific interactions between an inbred line and an environment. P4, P5 and P15 were the inbred lines with stable performance across environments, as the points for these inbred lines were close to the origin of the biplot. On the other hand, inbred lines P13, P9, P10, P11, P12 and P2 had unstable performance. P9 had smaller projection on the vector for environment KBOM. Inbred lines P10 and P11 showed smaller projection on the vector of MPOM. P12 performed well at stress environments of CHDS and HALN, and P6 performed well at JMOM.

AMMI analysis of the top yielding 20% hybrids revealed that the first two principal components accounted for 45.8% of the total variation in G x E sums of squares (Figure 7.2). Environments RAOM and HAOM were the most discriminating among these groups of hybrids and the angle between the vectors of these environments was large. Environments

BKOM and HALN had shorter vectors. Strong associations were observed among the three stress environments (KBDS, BKLN and CHDS). Environments JMOM and AWOM were highly correlated. HALN was strongly associated with HAOM, rather than other stress environments. Hybrids C2, C3, C5, C7, C9, C14 and C15 projected positively on the vectors of three of the four stress environments. Hybrids C8, C12, C20, C18 and C10 showed greater affinity for RAOM and MPOM. C1 had relatively smaller projection on the vector of MPOM and HAOM. Hybrid C19 had smaller projection on the vector of KBOM. C11 and C21 projected positively on the vector of MLOM, and C17 showed smaller projection on the vectors of JMOM, AWOM and MLOM. C16 was positioned closest to the origin of the biplot.

Pattern analysis was used to further investigate the relationships among the environments used for this study. Cluster analysis conducted using lattice adjusted mean grain yields of the hybrids revealed three groups of environments (Figure 7.3). The first group contained optimally managed environments except BKLN, which is a low N stress environment. All the environments are located in Ethiopia and Kenya (eastern African region). The second group contained environments which received optimum crop management and all are located in southern African region (Zimbabwe and Zambia). The third group consisted of two drought stress (CHDS and KBDS) and one low N stress (HALN) environments. Clustering the environments based on grain yields of the inbred lines in hybrids showed clear grouping based on the prevalent growing conditions (Figure 7.4). The first group consisted of all stress environments; within this group, the two drought stress environments (CHDS and KBDS) were more closely associated. The second group contained optimally managed Ethiopian environments. Most of the environments (PWOM, JMOM and AWOM) had similar mean grain yield levels (Table 7.1). The third group contained high yielding environments located in four different countries; Ethiopia (BKOM), Kenya (KBOM), Zimbabwe (HAOM and RAOM), and Zambia (MPOM).

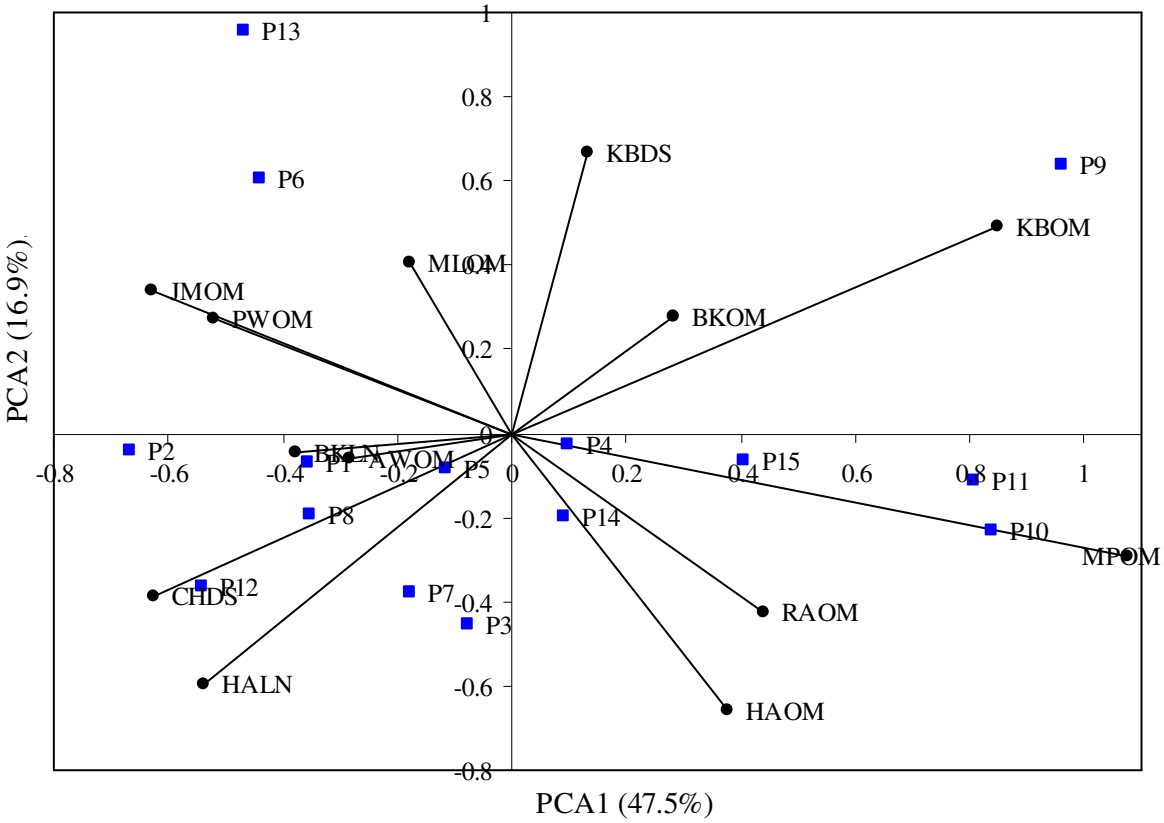

Figure 7.1 Additive main effect and multiplicative interaction (AMMI) biplots for grain yield of inbred lines in hybrids in a diallel cross among 15 QPM inbred lines evaluated across 13 stress and optimal environments. P1= VL052; P2= VL05200; P3= VL05468; P4= VL054178; P5= VL052887; P6= VL05482; P7= VL0523; P8= VL0524; P9= VL05561; P10= VL05483; P11= CML511; P12= CML144; P13= CML159; P14= CML491; P15= VL06375

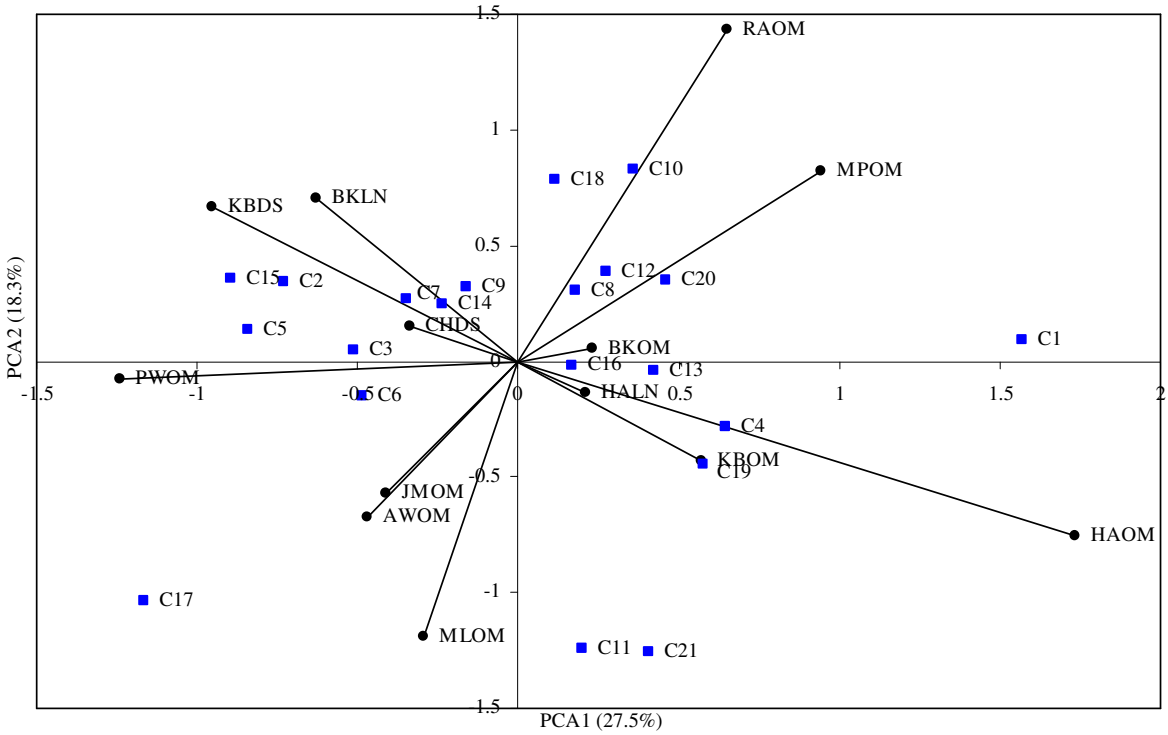

Figure 7.2 Additive main effect and multiplicative interaction (AMMI) biplots for grain yield (t ha^{-1}) for 21 top yielding single-crosses across 13 stress and optimal environments.

C1= VL05483 x CML491; C2= VL05561 x CML491; C3= CML159 x CML491; C4= CML511 x CML491; C5= VL05561x CML159; C6= VL054178 x CML491; C7= VL05200 x VL05561; C8= VL05561 x CML144; C9= VL052 x VL05561; C10= VL05561 x VL05483; C11= VL052887 x VL05561; C12= VL05561 x CML511; C13= VL052887 x CML511; C14= CML511 x CML159; C15= VL05482 x VL05561; C16= VL05200 x CML511; C17= VL05482 x CML491; C18= VL052887 x VL06375; C19= VL05483 x CML144; C20= VL0524 x VL05483; C21= VL052887 x VL05483

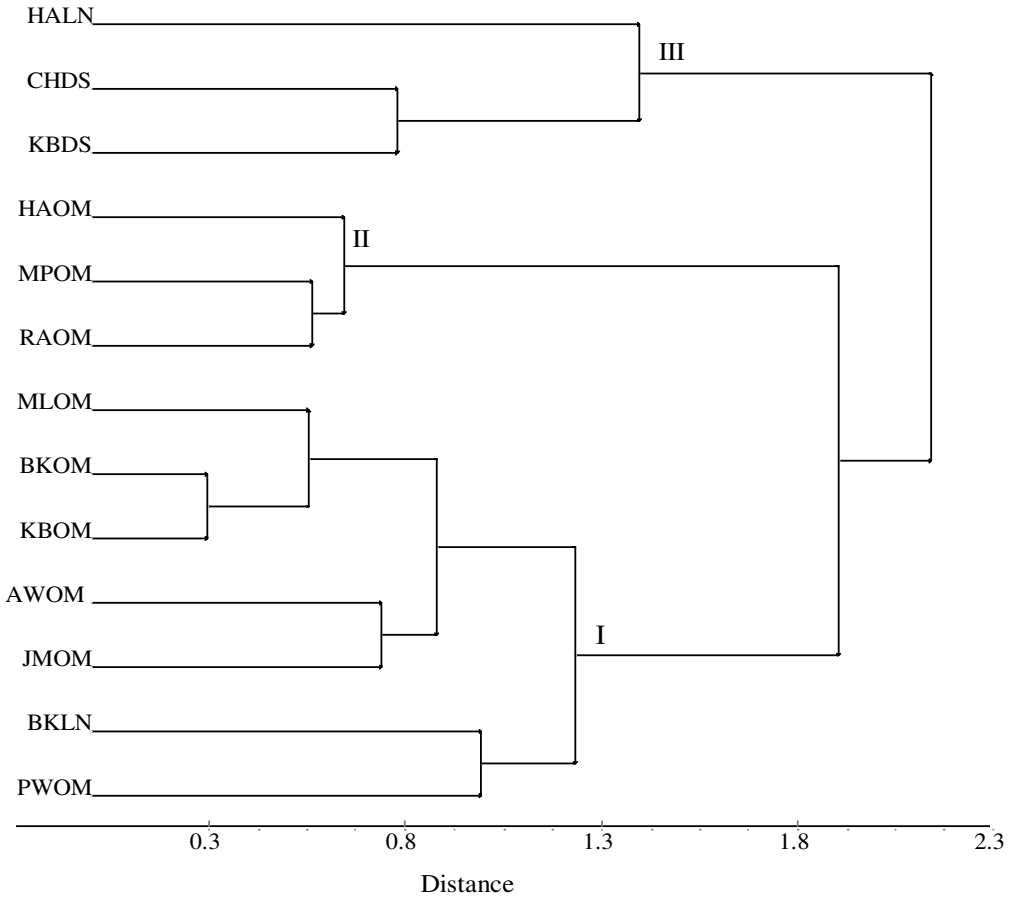

Figure 7.3 Cluster analysis (Ward's minimum variance) of 13 stress and optimal environments base on grain of hybrids in diallel crosses among 15 QPM inbred lines. Environment codes are as explained in Table 7.3

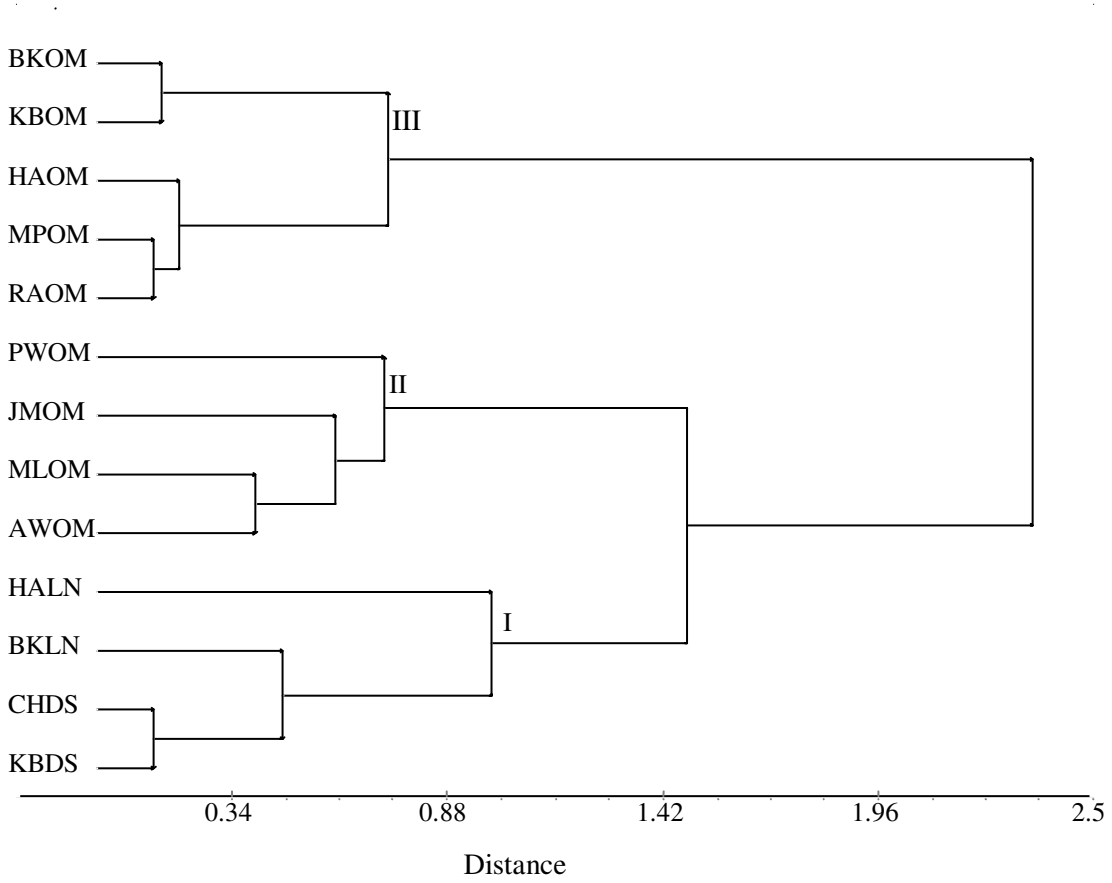

Figure 7.4 Cluster analysis (Ward's minimum variance) of 13 stress and optimal environments based on grain yield of inbred lines in hybrids in diallel crosses among 15 QPM inbred lines. Environment codes are as explained in Table 7.3

7.5 Discussion

The highly significant differences observed among hybrids across environments indicated the existence of variation for grain yield among the single crosses. Significant variation among the environments indicated that each of the targeted environments were unique as desired. Differences in maize grain yield among stress and optimal environments were reported by several researchers (Betran et al., 2003e; Presterl et al., 2003; Mosisa et al., 2007; Derera et al., 2008; Pswarayi and Vivek, 2008). Highly significant G x E interaction effects indicated fluctuating responses of maize hybrids to different environmental stresses. Single crosses are more sensitive to environments than other types of crosses and open pollinated cultivars

(Hallauer and Miranda, 1988; Pixley and Bjarnason, 2002). Moreover, stress environments produce high genotype by environment interactions (Banziger et al., 2000; Banziger and Diallo, 2004). The largest proportion of total sum of square was accounted for by environment effects while genotypic and G x E interaction effects were almost equally important. This is mainly due to the variation in levels and types of stress among the environments. The dominance of environment effects in combined analysis of grain yield across stress and non-stress environments was reported by other researchers (Makumbi, 2005; Gezahegn et al., 2008). The first two IPCAs accounted for more than 50% of the G x E interaction and therefore AMMI2 was identified as the best-fit model to elucidate interpretable patterns of the interactions.

According to linear regression stability model of Eberhart and Russell (1966), stable varieties are those with high grain yield, b= 1.0 and s^2d= 0. Among the joint regression stability measures, s^2d was largely used to rank the relative stability of cultivars (Becker and Leon, 1988). The indication was that b could be used to describe the general response to the goodness of environmental conditions, whereas s^2d actually measures the yield stability. Consistent to the current study, association of high mean yield and regression coefficients were reported by Betran et al. (2003e) for tropical maize single-crosses evaluated under stress and non-stress environments. In this study, the linear regression stability model (Eberhart and Russel, 1966) identified VL054178 x CML491, VL052 x VL05561 and CML511 x CML159 as relatively stable hybrids. The PCA scores of a genotype in the AMMI analysis indicate the stability of a genotype across environments (Zobel et al., 1988; Gauch and Zobel, 1996). The closer the IPCA scores are to zero, the more stable the genotypes are across their testing environments (Purchase, 1997; Adugna and Labuschagne, 2002). ASV calculated based on the PCA1 and PCA2 identified hybrids VL0524 x VL06375, VL05483 x CML159, VL05468 x VL0524 as the most stable ones, with lower ASV values. Even though there is difference between the two stability statistics in ranking the genotype, Spearman's rank correlation between these models is significant. This indicated that both stability measures are important in determining the comparative stability of the hybrids evaluated in the current experiments. Similar results were reported by Adugna and

Labuschagne (2002), who analyzed the genotype-environment interactions and phenotypic stability of linseed in Ethiopia.

Mean grain yield of the inbred lines in hybrids indicates the potential contribution of the parents to progeny performance. Accordingly, VL05561, CML511, VL05483 and VL06375 significantly contributed to increased grain yield in their crosses. The lower mean grain yield under stress than optimal environments, even when the hybrids were planted at the same location and season, showed that drought and low N stresses strongly affected grain yield. Similar results were reported by other authors (Betran et al., 2003e; Makumbi, 2005; Mosisa et al., 2007; Derera et al., 2008).

AMMI2 analysis positioned the inbred lines in different locations, indicating the adaptation pattern of the inbred lines. KBOM and MPOM had longer vectors from the origin; and hence, these locations had high discrimination power and gave good information on the performance of the hybrids. The two environments were similar in genotype discrimination; and different from stress environments, HALN, CHDS, and BKLN. In general, high yielding environments, BKOM, KBOM, MPOM, RAOM, and HAOM except MLOM discriminate the inbred lines similarly. Environments with medium grain yield, JMOM, PWOM and AWOM were closely associated, suggesting that the same information about the inbred lines can be obtained from these environments. The low N stress severity at BKLN was relatively less than HALN; hence, BKLN was more closely associated with AWOM (optimal environment) than with HALN. These results are in line with the findings of Mosisa et al. (2007) who reported greater dissimilarity between high N and severe stress low N environments than between either high N and medium N or medium N and low N environments. G x E interaction increases as the difference in stress intensity between two environments increased (Banziger et al., 1997; Mosisa et al., 2007; Derera et al., 2008). However, HAOM and HALN, KBOM and KBLN were closely related in inbred line discrimination, indicating that environments with different stress levels but sharing the same location ranked the inbred lines similarly. The exception was BKOM and BKLN that were very dissimilar in discriminating the inbred lines (Figure 7.1). Similar results were reported by Betran et al. (2003e). In this study, inbred lines P1, P2, P7, P8 and P12 showed good

performance in hybrids under stress environments whereas, P9, P10 and P11 had high grain yield under high yielding environments. P6 and P13 performed better under medium yielding environments (JMOM and PWOM) while P4, P5 and P15 had relatively a stable performance in hybrids across environments.

RAOM and HAOM had high discrimination power among the selected hybrids (Figure 7.2); however, there was no relationship between the two environments, indicating the difference between these environments in discrimination of selected hybrids. BKOM and HALN were less discriminating; such environments provide little information on the genotypes (Yan and Tinker, 2006). The close association between HALN and HAOM indicated similar response of the hybrids to low N stress and optimum N environments. This further indicated a strong genetic correlation between low N and optimum N environments as previously reported (Banziger et al., 1997; Presterl et al., 2003). The identification of hybrids with superior performance in both stress and optimal environments would enhance maize production in Africa. The stress environments, KBDS, BKLN and CHDS, were positively correlated; and hence ranked the hybrids similarly. Hybrids with superior performance under both drought and low N stress environments are highly desirable for African farmers who produce maize under these conditions. Cultivars well adapted to both stress conditions can significantly contribute to enhanced maize production in Africa. Similar to this, Banziger et al. (1999b) reported that selection for drought stress increases maize grain yield under low N stress. HAOM had strong negative correlation with stress environments (KBDS, BKLN and CHDS), indicating strong cross over G x E interaction. Hybrids C2, C3, C5, C7, C9, C14 and C15 showed better performance under drought and low N stress environments, KBDS, BKLN and CHDS. C10, C1, C19, C11 and C21 were well adapted to high yielding environments such as RAOM, MPOM, HAOM, KBOM and MLOM while C16 was the most stable hybrid.

Pattern analysis based on hybrid grain yield clustered the 13 environments mainly based on geographical location and stress conditions. The results indicated marked differences between eastern African (cluster I) and southern African (cluster II) optimally managed environments. Most of the environments used for this study belong to dry and sub-humid

mid-altitude maize growing mega-environments (Hartkamp et al., 2000); however, the clustering patterns did not follow the known mega-environment groups. Alagarswamy and Chandra (1998) also reported clustering of environments that was largely geographical for sorghum grain yield across countries in Africa, Asia and Central America. Cluster analysis based on inbred line means grouped the environments mainly based on the prevailing growing conditions at different environments. For example, drought stress environments (CHDS and KBDS), which are distant geographical locations, were grouped together. Results of the current study were similar to that of Chapman et al. (1997) and Makumbi (2005), who reported that high yielding environments cluster differently from stress environments for tropical maize populations and hybrids, respectively.

7.6 Conclusions

In combined analysis of variance across stress and optimal environments, the highest proportion of variation was explained by environments; mainly due to the inclusion of environments with varying stress conditions. Highly significant G x E indicated the sensitivity of single-cross hybrids to environmental changes. Joint regression and ASV models were used to analyze the stability of the hybrids. Even though the two models ranked the hybrids differently, Spearman's rank correlation showed significant association between these models, indicating the importance of the models in determining the relative stability of the hybrids. AMMI analysis unambiguously positioned the inbred lines and selected hybrids in different locations based on the adaptation pattern of the genotypes. Environments with vectors projecting in the same direction were positively correlated and discriminated the genotypes in the same manner. Projection of environmental vectors in opposite direction indicated dissimilarity between the environments in genotype discrimination. The high yielding environments discriminated the genotypes differently from the stress environments. In some cases, environments with different stress levels but sharing the same location discriminated the genotypes similarly, which indicated the possibility of developing better performing genotypes under stress and optimal conditions. The smaller the projection of genotype point onto the environment vector, the better the performance of that genotype in

that environment. Genotypes positioned closer to each other in the biplots tended to have a similar pattern of response to a given environment. In this study, AMMI analysis identified inbred lines and hybrids well adapted to stress and optimal environments as well as relatively stable genotypes. Cluster analysis using Ward's minimum variance based on hybrid grain yield and inbred line means grouped the 13 environments mainly according to geographical locations and prevailing growing conditions at different environments.

Chapter 8

Combining ability of quality protein maize inbred lines for endosperm modification and protein quality under low nitrogen stress and optimal conditions

8.1 Abstract

Quality protein maize (QPM) breeding involves the combined use of the *opaque-2* (*o2*) gene and the genetic modifiers of the *o2* locus to develop cultivars with modified kernel endosperm, and increased concentrations of lysine and tryptophan. This study was designed to assess general (GCA) and specific (SCA) combining ability effects for endosperm modification, tryptophan and protein concentration in grain, and protein quality index, identify QPM donor parents, and measure the relationship among these traits under low N stress and optimal conditions. A 15-parent diallel cross was evaluated under two low N stress and two optimal environments at Harare and Bako. Most QPM hybrids showed higher protein quality trait values than the best normal check under both conditions. Low N stress relatively increased the frequency of soft or poorly modified grains as compared to the optimum N conditions. Low N stress decreased tryptophan and protein concentrations in grain and increased protein quality index. However, the levels of endosperm modification, tryptophan and protein concentration observed under low N condition were within acceptable range. Tryptophan concentration was more stable than protein concentration across N levels. Endosperm modification had an undesirable relationship with tryptophan concentration and protein quality index, suggesting that selection for endosperm modification should be accompanied by selection for protein quality. GCA mean squares were highly significant for most traits for each environment and across environments whereas SCA mean squares were not significant in most cases. This indicates that additive gene effects were primarily responsible for variation of most traits evaluated and hence progeny performance can adequately be predicted on the basis of GCA effects of the parents. Furthermore, higher correlation and regression coefficients observed between sum of GCA effects of the two parents and hybrid values for all traits across low N stress and optimal environments. Inbred lines VL05200, VL05468, VL054178 and CML144 were identified as good donor parents in QPM breeding. Results of the current study suggest that hybrids with the highest values of protein quality traits under low N stress and optimal conditions will be crosses between lines with the highest GCA values for these traits.

8.2 Introduction

Maize is the dominant staple crop grown by the vast majority of rural households in Africa. Nutritionally, however, the protein of maize is deficient in two essential amino acids, lysine and tryptophan (Bhatia and Rabson, 1987). Maize endosperm protein is comprised of different fractions; namely, albumins, globulins, zeins or prolamines and glutelins. In normal maize, the endosperm contains a high proportion of zein fraction (especially α-zein) which is completely devoid of lysine and tryptophan. The high proportion of this particular fraction is the primary cause of poor protein quality in maize. A reduction in the zein fraction thus results in a proportional elevation of other fractions rich in lysine and an elevation of these two amino acids in protein (Vasal, 2000). The discovery of the biochemical effects of mutant allele *o2* (Mertz et al., 1964) opened an exciting opportunity for improving the quality of maize endosperm protein. This mutant alters amino acid profile and composition of maize endosperm protein and results in twofold increase in the levels of lysine and tryptophan compared to what is encountered in normal maize genotypes (Vasal et al., 1984b; Mertz, 1992; Villegas et al., 1992). High quality protein mutants increase the levels of lysine and tryptophan by suppressing synthesis of the lysine-deficient zein fraction (Vasal, 2001).

However, some undesirable effects of the *o2* mutation such as low grain yield and many other undesirable kernel characteristics jeopardized its commercial exploitation (Wessel-Beaver and Lambert, 1982; Vasal et al., 1984a; Villegas et al., 1992; Lin et al., 1997; Vasal, 2001; Prasanna et al., 2001). Breeders have achieved some inspiring success in the development of hard endosperm *o2* maize through the use of endosperm modifiers. Endosperm hardness modifier genes convert the soft/opaque mutant endosperm to a hard/vitreous endosperm with little loss of protein quality (Hohls et al., 1996; Vasal, 2002). The inheritance of *o2* modifier genes for endosperm texture is complex (Vasal et al., 1980; Wessel-Beaver and Lambert, 1982). Several researchers reported that additive genetic effects are more important than non-additive effects for endosperm hardness in the *o2* background of QPM (Sriwatanapongse et al., 1974; Vasal et al., 1980; Wessel-Beaver and Lambert, 1982; Ortega and Bates, 1983; Wessel-Beaver et al., 1985; Pixley and Bjarnason, 1993; Vasal et al., 1993a; Vasal et al., 1993b; De-quan and Shi-Huang, 1995). Non-additive genetic

components also contribute to the expression of kernel vitreousness (Sriwatanapongse et al., 1974; Wessel-Beaver and Lambert, 1982).

Published data describing the types of gene action regulating expression of protein quality traits indicated the greater importance of additive genetic variance relative to dominance genetic variance for percentage protein in grain and percentage tryptophan in grain for different *o2* germplasm (Sreeramulu and Baumann, 1970; Bjarnason et al., 1977; Motto et al., 1978; Wessel-Beaver et al., 1985; Pixley and Bjarnason, 1993; De-quan and Shi-Huang, 1995). This indicates that effective selection can increase the frequency of favourable alleles for endosperm modification. However, Ngaboyisonga et al. (2008) reported the significance of both additive and non-additive gene action in conferring protein and tryptophan concentrations in QPM kernels. Environmental conditions such as soil nitrogen level and irrigation affect the gene action governing protein and tryptophan concentration (Kniep and Mason, 1991; Ngaboyisonga et al., 2008).

In Africa, maize is frequently produced under environmental stress from low soil N. The impacts of low N stress on grain yield and related traits of maize have been extensively studied (Banziger and Cooper, 2001; Banziger and Diallo, 2004; Diallo et al., 2004; Mosisa et al., 2004; Banziger et al., 2006). However, very little data has been published indicating the impact of this stress on endosperm modification, protein quality and quantity of QPM. CIMMYT (2003b) reported the negative effects of low N stress on endosperm modification of QPM germplasm. Percent protein and tryptophan in grain are lower under low N compared to optimum N (CIMMYT, 2003b). However, the tryptophan level of QPM under both low nitrogen and optimum conditions is higher than the tryptophan level of normal maize under optimum conditions (CIMMYT, 2003b; Mosisa, 2005). Similary, Pixley and Bjarnason (2002) reported that protein quality is very stable, whereas protein content and endosperm modification of QPM varieties are less stable across environments.

This study was conducted (i) to assess GCA and SCA effects for endosperm modification and protein quality traits for QPM inbred lines under optimum N and low N stress conditions; and (ii) to identify good QPM donor parents (iii) to measure the phenotypic

correlation coefficients between endosperm modification, protein quality and quantity of QPM hybrids under low N stress and non-stress conditions.

8.3 Materials and methods

The details of environments, stress management procedures and experimental designs used are given in the materials and methods section of Chapter 4.

Germplasm

One-hundred and five hybrids generated by a diallel cross of 15 QPM inbred lines and three checks were evaluated in the field as described in Chapter 4. Endosperm modification and protein quality of the inbred lines are given Table 8.1. In each experimental unit, five plants were full sib-mated plant-to-plant to avoid cross pollination between QPM and normal maize varieties in the field. At harvest, the sib-mated plants in each plot were harvested separately for laboratory analysis while the rest of the plants in the plot were used for estimation of grain yield per hectare by adjusting to the corresponding plot area. The F_2 grains were shelled from the middle of five ears for all self-pollinated plots. Then 20 seeds of uniform size from the middle of the cob were taken from the bulk grains of each plot for laboratory analysis.

Laboratory methods

Protein content and quality were determined at the CIMMYT Cereal Quality Laboratory following procedures described by Villegas (1975) and Villegas et al. (1984). Briefly, whole-grain samples were finely ground using 0.5 mm setting of a cyclone mill, the resulting flour was defatted with hexane, and concentrations of nitrogen and tryptophan were colorimetrically determined for duplicate samples. With a view that nitrogen from cereal samples is mainly derived from protein; and the amino acid composition of endosperm protein is constant enough to have a relatively fixed nitrogen to protein ratio within a give cereal (Nkonge and Balance, 1982), protein concentration was estimated from the nitrogen value as: %protein= %nitrogen x 6.25 (conversion factor for maize). Tryptophan and protein concentrations in grain were expressed as g kg^{-1} for statistical analysis. Lysine concentration

was not measured because the procedure is more costly and lengthy than tryptophan analysis, and because lysine and tryptophan concentrations in the protein of *o2* endosperm are highly correlated (r= 0.85**) (Hernandez and Bates, 1969). The use of whole grain for colorimetric determination of protein quantity and quality has been used effectively to improve QPM germplasm at CIMMYT and seems justifiable in light of the considerable cost savings realized (Pixley and Bjarnason, 1993).

Endosperm modification score was assessed at the CIMMYT laboratory in Harare, Zimbabwe and Bako National Maize Research laboratory in Ethiopia. A random 100-kernel sample was taken from five self pollinated ears from each plot. Only full-size kernels, taken from the centre of well-filled ears were used. The kernels were sorted on a back-lit (candling) table and sorted from 1 to 5, where 1= completely modified (that is translucent normal phenotype); 2= 75% modified; 3= 50% modified; 4= 25% modified; and 5= completely opaque. The endosperm modification score for a plot was the mean score for the 100-kernel sample. Protein quality index (QI) was calculated as the ratio of tryptophan concentration to protein concentration in the grain, expressed as a percentage and indicates the percent of tryptophan in grain.

Statistical analysis

Variances, GCA and SCA effects were analyzed and tested for significance as described in the materials and methods of Chapter 4. Pearson phenotypic correlation coefficients were calculated between endosperm modification and protein quality traits using Statistical Package for Social Sciences (SPSS, 2002). Similarly, correlation coefficients were calculated and pair-wise t-tests were done to compare optimum and low N stress conditions for each trait. Predicted values of hybrids were calculated as the sum of GCA effects of the two parents across low N and optimum N separately. The mean values of each trait across low N and optimum N environments were correlated with and regressed on the predicted values of the traits for the respective environmental condition to determine the relationship between GCA effects of the parental lines and performance of the hybrid progeny.

Table 8.1 Endosperm modification (1-5), tryptophan and protein concentration in grain (g kg^{-1}) and protein quality index (%) for QPM inbred lines used in the diallel study

No.	Name	Modification (1 – 5)[†]	Tryptophan (g kg^{-1})[‡]	Protein (g kg^{-1})[‡]	Quality Index (%)[§]
1	VL052	2.3	1.02	104.4	0.97
2	VL05200	1.7	0.85	108.7	0.78
3	VL05468	1.9	1.10	116.4	0.95
4	VL054178	1.0	0.46	105.6	0.44
5	VL052887	2.0	0.91	112.1	0.81
6	VL05482	2.5	0.77	106.9	0.72
7	VL0523	2.5	1.02	102.2	1.00
8	VL0524	2.9	0.95	110.1	0.86
9	VL05561	1.3	0.71	114.2	0.62
10	VL05483	3.0	0.80	109.2	0.73
11	CML511	2.0	0.94	112.9	0.83
12	CML144	2.0	0.71	104.2	0.68
13	CML159	1.8	0.82	104.6	0.79
14	CML491	2.1	0.92	106.9	0.86
15	VL06375	2.0	0.85	113.3	0.75

[†] Endosperm modification scores taken as the mean scores from two locations, Harare and Bako;

[‡] Tryptophan and protein concentrations in grain were analyzed at CIMMYT Cereal Quality Laboratory, Mexico;

[§] Protein quality index, calculated as the ratio of tryptophan to protein concentration in grain

8.4 Results

Significant differences were observed among the hybrids for endosperm modification, tryptophan and protein concentration in the grain, and protein quality index under both optimum N and low N stress conditions at Harare and Bako (Tables 8.2 and 8.3). Figure 8.1 illustrates segregation of QPM cobs for endosperm modification. At Harare, where only one normal check hybrid was used, the proportion of QPM hybrids with higher values than the normal check were 86.7% for tryptophan concentration in grain, 17.1% for protein concentrations in grain, and 93.3% for quality index under optimum N conditions (Table 8.1). Under low N stress, 93.3% of the QPM hybrids for tryptophan, 70.5% for and protein, and 90.5% for quality index, showed higher values than the normal check hybrid. At Bako, where two normal maize hybrid checks were used, 85.7 and 93.3% of the QPM hybrids showed higher values of tryptophan concentration in grain and protein quality index, respectively, than the best normal check under optimum N conditions. Nevertheless, no QPM hybrid had higher protein concentrations in grain than the best normal check under optimum N conditions. Under low N stress, 97.1, 33.3, 33.3 and 97.1% of the QPM hybrids showed higher values of tryptophan and protein concentration in the grain and protein quality index, respectively than the best normal hybrid check (Table 8.2). At Harare, mean tryptophan concentration (0.68 g kg^{-1}) in grain for the QPM hybrids under low N stress was higher than the tryptophan concentration (0.65 g kg^{-1}) of the best normal check under optimum N, while similar concentrations were observed at Bako. On the mean bases, higher values of endosperm modification and quality index, and lower values of tryptophan and protein concentrations in grain were observed under low N stress than under optimum N conditions at both locations. Under low N stress, endosperm modification score increased by 40.2% at Harare and by 5.5% at Bako while protein quality index increased by 13.4% at Harare and by 5.1% at Bako (Table 8.2). On the other hand, tryptophan and protein concentrations in grain decreased by 15.0 and 25.2%, respectively, at Harare low N stress while the decrease was 11.8 and 15.7% for tryptophan and protein concentrations in grain, respectively, at Bako under low N stress.

Table 8.2 Means, standard error of the mean, *F*-test and coefficient of variation for endosperm modification (MOD, 1-5), tryptophan concentration in grain (TRP, g kg^{-1}), protein concentration in grain (g kg^{-1}) and protein quality index (QI, %) of maize hybrids evaluated under optimum and low N stress conditions at Bako and Harare, 2006 – 2007

Trait	Harare optimum N				Harare low N				Bako optimum N				Bako low N			
	MOD[†]	TRP	Protein	QI	MOD	TRP	Protein	QI	MOD	TRP	Protein	QI	MOD	TRP	Protein	QI
Mean	2.28	0.80	98.2	0.81	3.21	0.67	73.2	0.92	2.53	0.85	108.9	0.78	2.68	0.75	91.8	0.82
Minimum	1.41	0.53	81.8	0.52	2.23	0.41	55.4	0.68	1.50	0.50	91.6	0.50	1.45	0.48	75.7	0.44
Maximum	3.10	1.06	115.6	1.01	4.91	0.93	102.7	1.30	3.53	1.07	128.1	1.01	3.60	1.07	127.2	1.06
Best QPM hybrid	1.41	1.06	115.6	1.01	2.23	0.93	102.7	1.30	1.50	1.07	125.4	1.01	1.45	1.07	127.2	1.06
Mean for QPM hybrids	2.29	0.80	98.2	0.82	3.21	0.68	73.5	0.93	2.55	0.85	108.8	0.79	2.69	0.75	91.7	0.83
Best QPM Check	1.88	0.73	98.9	0.80	3.23	0.58	70.2	0.89	2.81	0.84	106.2	0.79	2.80	0.65	110.2	0.80
Best normal Check	-	0.65	105.2	0.62	-	0.53	66.4	0.77	-	0.75	128.1	0.58	-	0.55	94.3	0.59
F test	**	**	**	**	**	**	**	**	**	**	**	**	**	**	*	**
SE(M)	0.18	0.06	4.72	0.05	0.32	0.06	7.72	0.06	0.19	0.04	3.23	0.04	0.28	0.05	6.86	0.06
CV (%)	11.1	9.9	6.8	9.3	14.1	13.5	14.9	9.8	10.4	6.8	4.2	6.6	14.6	8.8	10.6	10.1
Relative reduction[‡]	-	-	-	-	-40.2	15.0	25.2	-13.4	-	-	-	-	-5.5	11.8	15.7	-5.1
QPM hybrids better than normal check (%)	-	86.7	17.1	93.3	-	93.3	70.5	90.5	-	85.7	0.0	93.3	-	97.1	33.3	97.1

[†] best hybrid for endosperm modification is the one with lowest score; [‡] percent relative reduction due to low N stress (1 - $MV_{low\ N}/MV_{optimum\ N}$), negative values indicate an increase under low N stress in that particular trait; CV= coefficient of variation; SE(m)= standard error of the mean

Figure 8.1 Segregation of QPM F_2 cobs for endosperm modification (bleached white kernels are completely opaque)

The mean performance of inbred lines in hybrids showed that endosperm modification score was consistently higher under low N stress at Harare followed by low N stress at Bako (Figure 8.2a). Minimum scores were realized under optimum N at Harare for all inbred lines as compared to other environments. Tryptophan concentration in grain was higher under optimum N and lower under low N stress at both locations (Figure 8.2b). Protein concentration was higher under optimum conditions but very low under low N stress at Harare where the stress was very severe (Figure 8.2c). On the other hand, protein quality index was higher under low N stress especially at Harare (Figure 8.2d).

Endosperm modification showed highly significant GCA and SCA mean squares under both optimum and low N conditions at both locations (Table 8.3). GCA mean squares for tryptophan concentration in grain were significant under all conditions while SCA mean

squares were highly significant only at Bako under both low N stress and optimal conditions. For tryptophan and protein concentrations, GCA mean squares were significant at all environments and SCA mean squares were significant under optimal conditions at both locations. Quality index had highly significant GCA mean squares under all conditions while SCA mean squares for the trait were significant at Harare low N and Bako optimum N.

Highly significant environment (E) and hybrid effects were observed for all traits evaluated across optimum N conditions (Table 8.4). GCA mean squares were also highly significant for all traits while SCA effects were significant for endosperm modification and protein concentration in grain. Endosperm modification score ranged from 1.56 to 3.17 with a mean of 2.41. Mean tryptophan in grain was 0.83 g kg^{-1} with a range of 0.50 – 1.03 g kg^{-1}. Protein in grain ranged from 87.96 to 119.81 g kg^{-1} with a mean of 103.49 g kg^{-1}. Mean protein quality index was 0.80% with a range of 0.50 – 1.00%. Hybrid x E, GCA x E and SCA x E mean squares were significant for all traits.

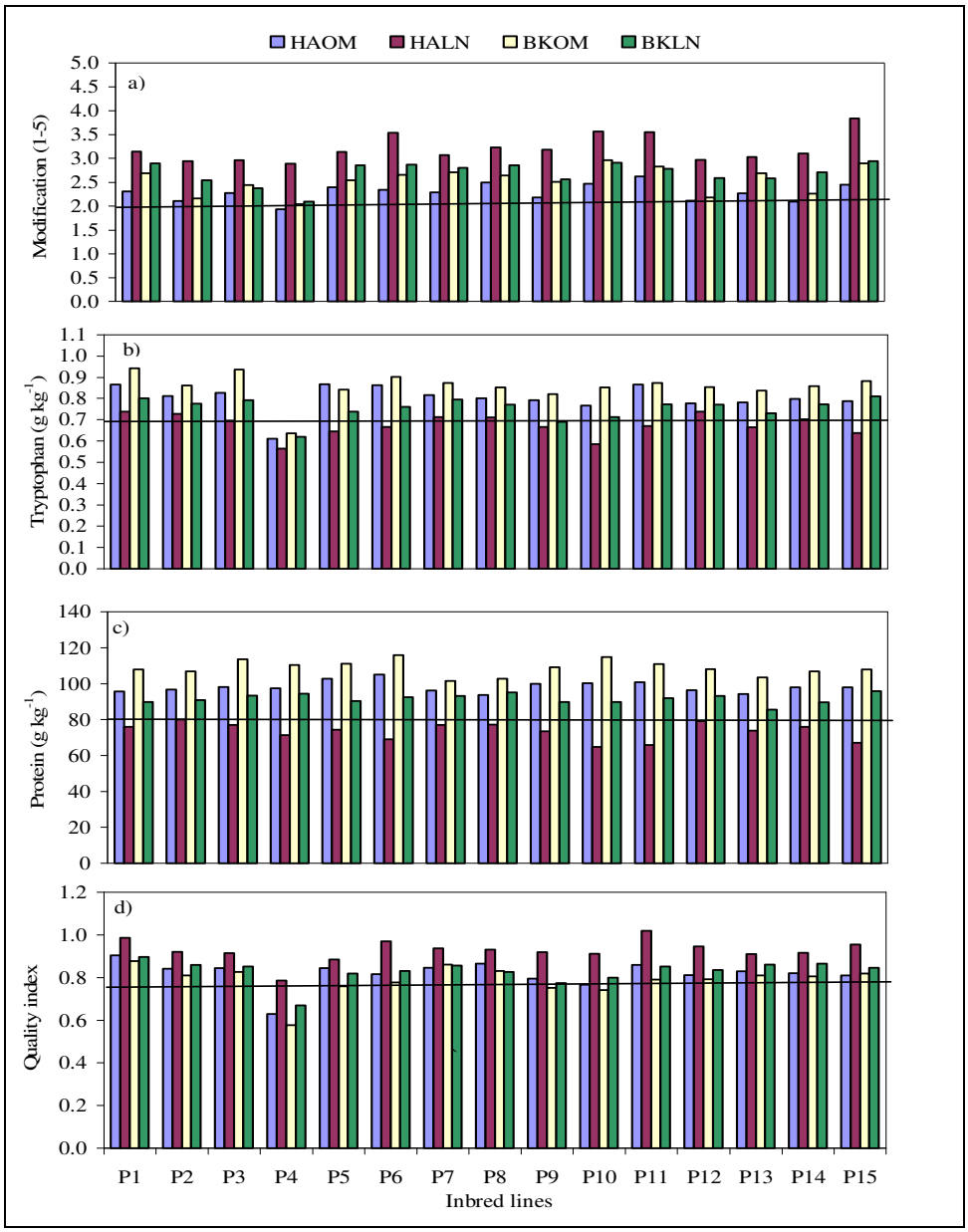

Figure 8.2 Performance of 15 QPM inbred lines in hybrids in each environment for a) endosperm modification (1-5), b) tryptophan concentration in grain (g kg^{-1}), c) protein concentration in grain (g kg^{-1}) and d) protein quality index (%) under optimum and low nitrogen stress conditions at Bako and Harare. Horizontal lines indicate minimum acceptable values. Environments are: HAOM and HALN= Harare optimal management and low N stress, and BKOM and BKLN= Bako optimal management and low N stress. Parental inbred lines are: P1= VL052; P2= VL05200; P3= VL05468; P4= VL054178; P5= VL052887; P6= VL05482; P7= VL0523; P8= VL0524; P9= VL05561; P10= VL05483; P11= CML511; P12= CML144; P13= CML159; P14= CML491; P15= VL06375

Table 8.3 Mean squares for hybrids, general (GCA) and specific (SCA) combining ability for endosperm modification (1-5), tryptophan concentration in grain (g kg^{-1}), protein concentration in grain (g kg^{-1}) and protein quality index (%) for QPM hybrid evaluated under optimum and low N stress conditions at Harare and Bako, 2006 – 2007

Traits	Source	Harare optimal	Harare low N	Bako optimal	Bako low N
Modification	Hybrids	0.11**	0.29**	0.25**	0.21**
	GCA	0.49**	1.19**	1.17**	0.85**
	SCA	0.05**	0.15*	0.11**	0.11*
Tryptophan	Hybrids	0.012**	0.010**	0.012**	0.009**
	GCA	0.060**	0.041**	0.072**	0.037**
	SCA	0.004	0.005	0.003**	0.004**
Protein	Hybrids	55.0**	110.2**	52.8**	66.6*
	GCA	146.2**	349.3**	267.8**	106.7**
	SCA	40.8**	73.0	19.4**	60.3
Quality	Hybrids	0.011**	0.011**	0.011**	0.009**
index	GCA	0.057**	0.041**	0.071**	0.043**
	SCA	0.004	0.007**	0.002*	0.004

* $P \leq 0.05$; ** $P \leq 0.01$

Across low N stress environments, environment and hybrid effects were highly significant for all traits, except for protein concentration in grain (Table 8.5). GCA mean squares were significant for endosperm modification, tryptophan and quality index whereas SCA was not significant for all traits. Mean endosperm modification score (1 – 5 scale) was 2.93 with a range of 1.89 – 4.18. Tryptophan in grain ranged from 0.48 to 0.97 g kg^{-1} with a mean of 0.71 g kg^{-1}. Quality index ranged from 0.44 to 1.14% with a mean of 0.88%. Mean endosperm modification score across optimum N was 82.3% of the score across low N. Tryptophan concentration in grain across low N stress was 85.5% of the concentration across optimum N. Protein concentrations across low N stress were 79.8% of the concentration across optimum N. On the other hand, protein quality index across optimum N was 90.9% of the index across low N stress condition. In general, across location data revealed that, endosperm modification score and quality index of hybrids increased, and tryptophan and

protein concentrations in grain decreased under low N stress (Table 8.6). The same trend was observed for inbred lines in hybrids (Figure 8.3). Significant hybrids x E, GCA x E and SCA x E effects were observed for all traits except SCA x E for protein concentrations in grain, and quality index (Table 8.5).

Table 8.4 Combined analysis of variance and means for endosperm modification (1-5), tryptophan concentration in grain (g kg^{-1}), protein concentration in grain (g kg^{-1}) and protein quality index (%) of QPM hybrids across optimum N environments at Harare and Bako, 2006 – 2007

Sources of variation	DF	Modification	Tryptophan	Protein	Quality index
Environment (E)	1	3.42**	0.144**	5838.9**	0.046**
Hybrids	104	0.28**	0.020**	80.4**	0.019**
GCA	14	1.51**	0.123**	364.4**	0.123**
SCA	90	0.10*	0.004	36.2*	0.003
Hybrids x E	104	0.08**	0.004**	27.4**	0.003*
GCA x E	14	0.15**	0.009	49.6	0.005
SCA x E	90	0.07**	0.003	24.0	0.003
Error	164	0.03	0.002	15.7	0.002
Mean		2.41	0.83	103.5	0.80
Minimum		1.56	0.50	88.0	0.50
Maximum		3.17	1.03	119.8	1.00
SE(M)		0.13	0.03	2.81	0.03
CV%		7.6	5.8	3.8	5.7

* $P \leq$ 0.05; ** $P \leq$ 0.01; CV= coefficient of variation; GCA= general combining ability; SCA= specific combining ability; SE(m)= standard error of the mean

Table 8.5 Combined analysis of variance and means for endosperm modification (1-5), tryptophan concentration in grain (g kg^{-1}), protein concentration in grain (g kg^{-1}) and protein quality index (%) of QPM hybrids across low N stress environments at Harare and Bako, 2006 – 2007

Sources of Variation	df	Modification	Tryptophan	Protein	Quality index (%)
Environment (E)	1	13.99**	0.323**	17440.4**	0.493**
Hybrids	104	0.35**	0.013**	86.5	0.015**
GCA	14	1.70**	0.068**	-	0.074**
SCA	90	0.13	0.005	-	0.006
Hybrids x E	104	0.15**	0.005**	90.3**	0.006*
GCA x E	14	0.34**	0.011**	238.2**	0.009**
SCA x E	90	0.13*	0.004*	67.3	0.005
Error	164	0.09	0.003	53.7	0.004
Mean		2.93	0.71	82.6	0.88
Minimum		1.89	0.48	67.4	0.44
Maximum		4.18	0.97	110.2	1.14
SE(M)		0.21	0.04	5.18	0.04
CV%		10.2	7.8	8.9	7.0

* $P \leq$ 0.05; ** $P \leq$ 0.01; CV= coefficient of variation; GCA= general combining ability; SCA= specific combining ability; SE(m)= standard error of the mean

Across all environments, highly significant environment mean squares were observed for all traits (Table 8.7). Mean squares for hybrids were significant for endosperm modification, tryptophan concentration in grain and protein quality index. GCA and SCA mean squares were significant for endosperm modification and protein quality index. Endosperm modification score ranged from 1.72 to 3.63 with a mean of 2.67. Mean tryptophan concentration in grain was 0.77 g kg^{-1} with a range of 0.49 – 0.95 g kg^{-1}. Quality index ranged from 0.47 to 1.01% with a mean of 0.84%. Hybrid x E, GCA x E and SCA x E effects were significant for all traits.

Table 8.6 Mean of endosperm modification (MOD, 1-5), tryptophan concentration in grain (TRP, g kg^{-1}), protein concentration in grain and protein quality index (QI, %) of selected 20 of the 105 QPM hybrids across environments at Harare and Bako, 2006 – 2007

Cross†	Across optimum N				Across low N				Across all			
	MOD	TRP	Protein	QI	MOD	TRP	Protein	QI	MOD	TRP	Protein	QI
Top 10												
P1xP2	2.00	0.93	105.6	0.88	2.68	0.85	88.9	0.98	2.34	0.89	97.3	0.93
P1xP6	2.48	0.98	111.5	0.88	3.13	0.79	79.4	1.01	2.81	0.88	95.5	0.94
P1xP13	2.54	0.96	96.9	1.00	3.11	0.81	82.9	0.99	2.82	0.89	89.9	0.99
P1xP14	2.15	0.96	97.5	0.98	3.05	0.9	87.7	1.01	2.6	0.93	92.6	1.00
P1xP15	3.07	0.97	102.0	0.94	3.78	0.81	75.5	1.08	3.43	0.89	88.7	1.01
P2xP6	2.02	0.91	111.3	0.81	3.03	0.81	90.9	0.93	2.53	0.86	101.1	0.87
P3xP6	2.52	1.03	119.8	0.86	2.73	0.71	80.3	0.93	2.63	0.87	100.1	0.89
P3xP7	2.69	0.93	100.2	0.93	2.93	0.8	94.9	0.86	2.81	0.87	97.6	0.89
P3xP8	2.46	0.93	104.3	0.89	2.33	0.86	97.4	0.91	2.39	0.89	100.8	0.90
P7xP8	2.56	0.93	105.6	0.87	3.01	0.97	100.5	0.96	2.79	0.95	103.1	0.92
Lowest 10												
P2xP4	1.74	0.59	97.3	0.61	2.21	0.56	80.3	0.69	1.98	0.57	88.8	0.65
P3xP4	1.74	0.67	110.6	0.6	2.26	0.59	88.3	0.68	2.00	0.63	99.5	0.64
P4xP5	2.52	0.62	107.9	0.57	2.81	0.55	77.9	0.70	2.67	0.58	92.9	0.64
P4xP6	1.76	0.62	114.2	0.55	2.58	0.58	85.9	0.70	2.17	0.60	100.0	0.62
P4xP7	1.90	0.64	96.9	0.67	2.54	0.57	77.7	0.76	2.22	0.60	87.3	0.72
P4xP9	2.18	0.61	109.4	0.55	2.33	0.58	83.2	0.74	2.25	0.59	96.3	0.65
P4xP10	2.49	0.59	105.8	0.57	3.30	0.52	77.3	0.70	2.90	0.56	91.5	0.64
P4xP12	1.77	0.56	101.0	0.56	2.16	0.68	89.6	0.78	1.97	0.62	95.3	0.67
P4xP13	1.56	0.58	98.9	0.59	1.89	0.54	85.2	0.64	1.72	0.56	92.1	0.61
P4xP15	1.82	0.62	104.6	0.60	2.82	0.55	73.0	0.75	2.32	0.59	88.8	0.67

† Crosses were selected based on tryptophan concentration; P1= VL052; P2= VL05200; P3= VL05468; P4= VL054178; P5= VL052887; P6= VL05482; P7= VL0523; P8= VL0524; P9= VL05561; P10= VL05483; P12= CML144; P13= CML159; P14= CML491; P15= VL06375

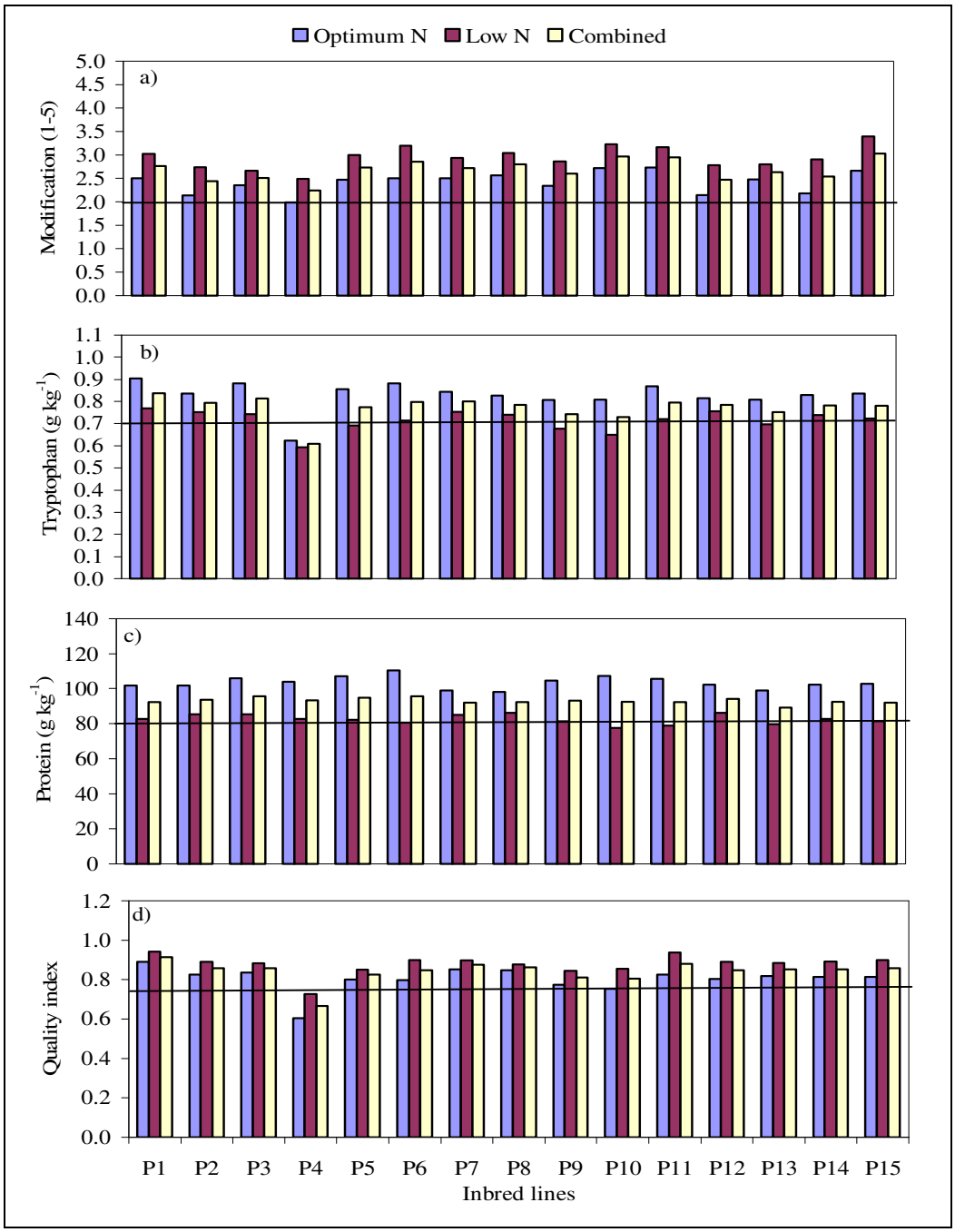

Figure 8.3 Performance of 15 QPM inbred lines in hybrids for a) endosperm modification, b) tryptophan concentration in grain, c) protein concentration in grain and d) protein quality index across environments. Horizontal lines indicate minimum acceptable values. Parental inbred lines are: P1= VL052; P2= VL05200; P3= VL05468; P4= VL054178; P5= VL052887; P6= VL05482; P7= VL0523; P8= VL0524; P9= VL05561; P10= VL05483; P11= CML511; P12= CML144; P13= CML159; P14= CML491; P15= VL06375

Table 8.7 Combined analysis of variance and means for endosperm modification (1-5), tryptophan concentration in grain (g kg^{-1}), protein concentration in grain (g kg^{-1}) and protein quality index (%) of QPM hybrids across all environments at Bako and Harare, 2006 – 2007

Sources of variation	df	Modification (1-5)	Tryptophan (g kg^{-1})	Protein (g kg^{-1})	Quality index (%)
Environment (E)	3	15.69**	0.605**	23053.1**	0.375**
Hybrids	104	0.52**	0.027**	81.8	0.030**
GCA	14	2.99**	0.068	-	0.074**
SCA	90	0.14**	0.005	-	0.006**
Hybrids x E	312	0.12**	0.005**	67.6**	0.004**
GCA x E	42	0.24**	0.048**	217.4**	0.046**
SCA x E	270	0.09**	0.004**	42.5	0.004
Error	328	0.06	0.003	34.7	0.003
Mean		2.67	0.77	93.0	0.84
Minimum		1.72	0.49	79.5	0.47
Maximum		3.63	0.95	106.5	1.01
SE(M)		0.12	0.03	2.95	0.03
CV%		9.3	6.8	6.3	6.5

* $P< 0.05$; ** $P< 0.01$; CV= coefficient of variation; GCA= general combining ability; SCA= specific combining ability; SE(m)= standard error of the mean

Spearman's rank correlation analysis among the traits showed endosperm modification had positive and highly significant correlation coefficients with tryptophan concentration and protein quality index across optimum N and across all environments (Table 8.8). Across low stress environments, endosperm modification showed positive and highly significant correlation coefficients with protein quality index. The correlations between endosperm modification and protein concentration in grain were negative and highly significant across optimum N but non-significant across low N stress and across all environments. Tryptophan had positive and significant correlation coefficients with protein concentration and protein quality index across optimum N, low N and all environments. The correlations between protein concentration and protein quality index were negative and significant in all conditions. The correlation between low N stress and optimum N environments was positive

and highly significant for all traits except protein concentration in grain (Table 8.8). Pair-wise t-tests between low N and optimum N environments were highly significant (P< 0.01) for all traits.

Table 8.8 Pearson phenotypic correlation coefficients among endosperm modification (MOD, 1-5), tryptophan concentration in grain (TRP, g kg^{-1}), protein concentration in grain (g kg^{-1}) and protein quality index (QI, %) of QPM hybrids across environments, and between optimum N and low N stress conditions for these traits at Harare and Bako, 2006 – 2007

Trait	Across optimum N			Across low N			Across all			*r* between
	TRP	Protein	QI	TRP	Protein	QI	TRP	Protein	QI	ON and LN
MOD	0.48**	0.11	0.41**	0.08	-0.42**	0.45**	0.34**	-0.18	0.45**	0.65**
TRP		0.21*	0.86**		0.50**	0.71**		0.25*	0.88**	0.64**
Protein			-0.31**			-0.22*			-0.22*	-0.02
QI										0.73**

* $P \leq 0.05$; ** $P \leq 0.01$; *r*= correlation coefficient; LN= low nitrogen stress condition; ON= optimum nitrogen condition

Considerable variation was observed among the 15 QPM inbred lines evaluated for GCA effects for all traits under all environmental conditions. For endosperm modification, inbred lines VL05200, VL05468, VL054178 and CML144 exhibited highly significant negative GCA effects under all environmental conditions (Table 8.9). CML491 showed significantly low GCA effects under optimum N conditions at both locations. In most environments, VL05482, VL0524, VL05483, CML511 and VL06375 had positive and significant GCA effects.

Inbred lines VL052 and VL05468 had positive and highly significant GCA effects for tryptophan concentration in grain under most conditions (Table 8.10). These inbred lines showed consistently higher tryptophan content across different N conditions. VL05482 showed positive and highly significant GCA effects under optimum N conditions at each and across environments. Inbred line VL06375 showed positive and highly significant GCA effects under both conditions at Bako, but not elsewhere. Inbred lines VL054178, VL05561

and VL05483 showed poor GCA effects for the same trait under most conditions. For protein concentrations in grain, inbred lines VL052887, VL05482 and CML511 showed positive and significant GCA effects under optimum N conditions (Table 8.11). Negative and significant GCA effects were observed for VL0524 under optimum N and for CML159 under most conditions. Cross-over interactions were observed for GCA effects of lines for protein concentrations in grain under low N stress conditions. At Harare low N, VL05200 and CML144 had positive and highly significant GCA effects while VL05483, CML511 and VL06375 showed highly significant negative GCA effects. At Bako low N, VL0524 and VL06375 showed positive and significant GCA effects while CML159 had negative and highly significant GCA effects.

Table 8.9 General combining ability effects (GCA) of 15 QPM inbred lines for endosperm modification (1-5) at Harare and Bako, 2006 - 2007

Inbred Lines	Harare optimal	Harare low N	Bako optimal	Bako low N	Across locations		
					Optimal	Low N	All
VL052	0.00	-0.06	0.15**	0.22**	0.08*	0.08	0.08*
VL05200	-0.19**	-0.29**	-0.40**	-0.17*	-0.30**	-0.22**	-0.27**
VL05468	-0.01	-0.27**	-0.13**	-0.35**	-0.06	-0.31**	-0.20**
VL054178	-0.40**	-0.35**	-0.55**	-0.65**	-0.47**	-0.49**	-0.48**
VL052887	0.12*	-0.08	0.01	0.19*	0.05	0.05	0.07*
VL05482	0.06	0.35**	0.14**	0.18*	0.09**	0.27**	0.18**
VL0523	0.01	-0.15	0.19**	0.10	0.09**	-0.02	0.04
VL0524	0.22**	0.02	0.09	0.18*	0.16**	0.10	0.13**
VL05561	-0.10*	-0.04	-0.05	-0.13	-0.08*	-0.09	-0.07*
VL05483	0.18**	0.37**	0.44**	0.24**	0.32**	0.30**	0.32**
CML511	0.36**	0.37**	0.31**	0.11	0.33**	0.23**	0.29**
CML144	-0.19**	-0.24**	-0.39**	-0.10	-0.29**	-0.18**	-0.23**
CML159	-0.03	-0.20*	0.15**	-0.12	0.06	-0.15**	-0.04
CML491	-0.20**	-0.11	-0.31**	0.03	-0.26**	-0.05	-0.16**
VL06375	0.16**	0.68**	0.36**	0.27**	0.27**	0.48**	0.36**
SE(gi)	0.05	0.09	0.05	0.07	0.04	0.06	0.03

* $P \leq 0.05$; ** $P \leq 0.01$; SE(gi)= standard error of GCA

Table 8.10 General combining ability effects (GCA) of 15 QPM inbred lines for grain trypthophan concentration (g kg^{-1}) at Harare and Bako, 2006 – 2007

Inbred lines	Harare optimal	Harare low N	Bako optimal	Bako low N	Across	
					Optimal	Low N
VL052	0.068**	0.069**	0.094**	0.051**	0.081**	0.060**
VL05200	0.010	0.057**	0.005	0.023	0.008	0.040**
VL05468	0.026	0.022	0.089**	0.041**	0.058**	0.032**
VL054178	-0.205**	-0.121*	-0.234**	-0.145**	-0.219**	-0.133**
VL052887	0.071**	-0.033	-0.013	-0.018	0.029**	-0.026*
VL05482	0.067**	-0.009	0.050**	0.008	0.059**	-0.001
VL0523	0.014	0.041*	0.020	0.042**	0.017	0.042**
VL0524	-0.002	0.039*	-0.003	0.019	-0.002	0.029**
VL05561	-0.011	-0.009	-0.039**	-0.070**	-0.025**	-0.039**
VL05483	-0.039*	-0.096*	-0.001	-0.041**	-0.020*	-0.069**
CML511	0.068**	-0.005	0.020	0.019	0.044**	0.007
CML144	-0.027	0.069**	0.000	0.019	-0.013	0.044**
CML159	-0.020	-0.014	-0.020	-0.027*	-0.020*	-0.020
CML491	-0.004	0.028	0.004	0.019	0.000	0.024*
VL06375	-0.015	-0.039*	0.028**	0.059**	0.006	0.010
SE(gi)	0.015	0.017	0.011	0.012	0.009	0.011

$P \leq 0.05$; ** $P \leq 0.01$; SE(gi)= standard error of GCA

GCA effects of VL052 were positive and highly significant for protein quality index under all conditions (Table 8.12). Inbred lines VL0523 and VL0524 showed positive and highly significant GCA effects under optimal environments and across all environments. CML511 had significantly positive GCA effects at Harare under both stress and non-stress conditions and across environments. On the other hand, inbred lines VL054178, VL052887, VL05561 and VL05483 showed negative and significant GCA effects for protein quality index in most environments.

Highly significant and positive correlation coefficients were observed between sum of GCA effects of the two parents and hybrid values for all traits across low N stress and across optimal environments (Figures 8.4 and 8.5). The correlations ranged from 0.74 for protein quality index to 0.91 for tryptophan concentration in grain, both across optimum N environments. The regression of hybrid performance on parental inbred line GCA effects resulted in positive and highly significant regression coefficients of 1.00 for all traits with R^2 values ranging from 54% for protein quality index (Figure 8.5a) to 83% for tryptophan concentration in grain (Figure 8.4c) across optimum N environments.

Table 8.11 General combining ability effects (GCA) of 15 QPM inbred lines for grain protein concentration (g kg^{-1}) at Harare and Bako, 2006 - 2007

Inbred lines	Harare optimal	Harare low N	Bako optimal	Bako low N	Across optimal
VL052	-2.70*	2.68	-0.92	-1.96	-1.81*
VL05200	-1.64	7.09**	-2.00*	-0.96	-1.82*
VL05468	-0.07	3.77	5.28**	1.98	2.61**
VL054178	-0.77	-2.31	1.76*	2.83	0.49
VL052887	5.01**	0.92	2.50**	-1.31	3.76**
VL05482	7.41**	-4.82*	7.82**	0.82	7.62**
VL0523	-2.20	3.70	-7.67**	1.63	-4.94**
VL0524	-4.85**	4.05	-6.46**	3.63*	-5.66**
VL05561	1.93	-0.16	0.28	-2.06	1.11
VL05483	2.09	-9.22**	6.57**	-1.88	4.33**
CML511	2.72*	-8.12**	2.21*	0.14	2.46**
CML144	-1.86	6.16**	-0.69	1.50	-1.27
CML159	-4.39**	0.54	-5.51**	-6.66**	-4.95**
CML491	-0.32	2.67	-2.10*	-2.23	-1.21
VL06375	-0.35	-6.97**	-1.07	4.54*	-0.71
SE(gi)	1.24	2.10	0.85	1.82	0.75

$P \leq 0.05$; ** $P \leq 0.01$; SE(gi)= standard error of GCA

Table 8.12 General combining ability effects (GCA) of 15 QPM inbred lines for protein quality index (%) per at Harare and Bako, 2006 - 2007

Inbred lines	Harare optimal	Harare low N	Bako optimal	Bako low N	Across		
					Optimal	Low N	All
VL052	0.091**	0.066**	0.095**	0.072**	0.093**	0.069**	0.081**
VL05200	0.024	-0.006	0.022*	0.031	0.023*	0.012	0.018*
VL05468	0.027	-0.013	0.041**	0.025	0.034**	0.006	0.020**
VL054178	-0.203**	-0.151**	-0.224**	-0.174**	-0.214**	-0.162**	-0.188**
VL052887	0.027	-0.047**	-0.031**	-0.012	-0.002	-0.030*	-0.016*
VL05482	-0.001	0.044*	-0.012	0.002	-0.007	0.023*	0.008
VL0523	0.032*	0.011	0.079**	0.029	0.055**	0.020	0.038**
VL0524	0.049**	0.004	0.045**	-0.003	0.047**	0.000	0.024**
VL05561	-0.026	-0.012	-0.039**	-0.059**	-0.032**	-0.036**	-0.034**
VL05483	-0.056**	-0.017	-0.051**	-0.033*	-0.053**	-0.025*	-0.039**
CML511	0.043**	0.100**	0.002	0.025	0.022*	0.063**	0.043**
CML144	-0.007	0.019	0.003	0.007	-0.002	0.013	0.006
CML159	0.011	-0.020	0.023*	0.032*	0.017	0.006	0.011
CML491	0.000	-0.009	0.016	0.039*	0.008	0.015	0.012
VL06375	-0.011	0.029	0.033**	0.018	0.011	0.024*	0.017*
SE(gi)	0.014	0.017	0.010	0.016	0.009	0.012	0.007

$P \leq 0.05$; ** $P \leq 0.01$; SE(gi)= standard error of GCA

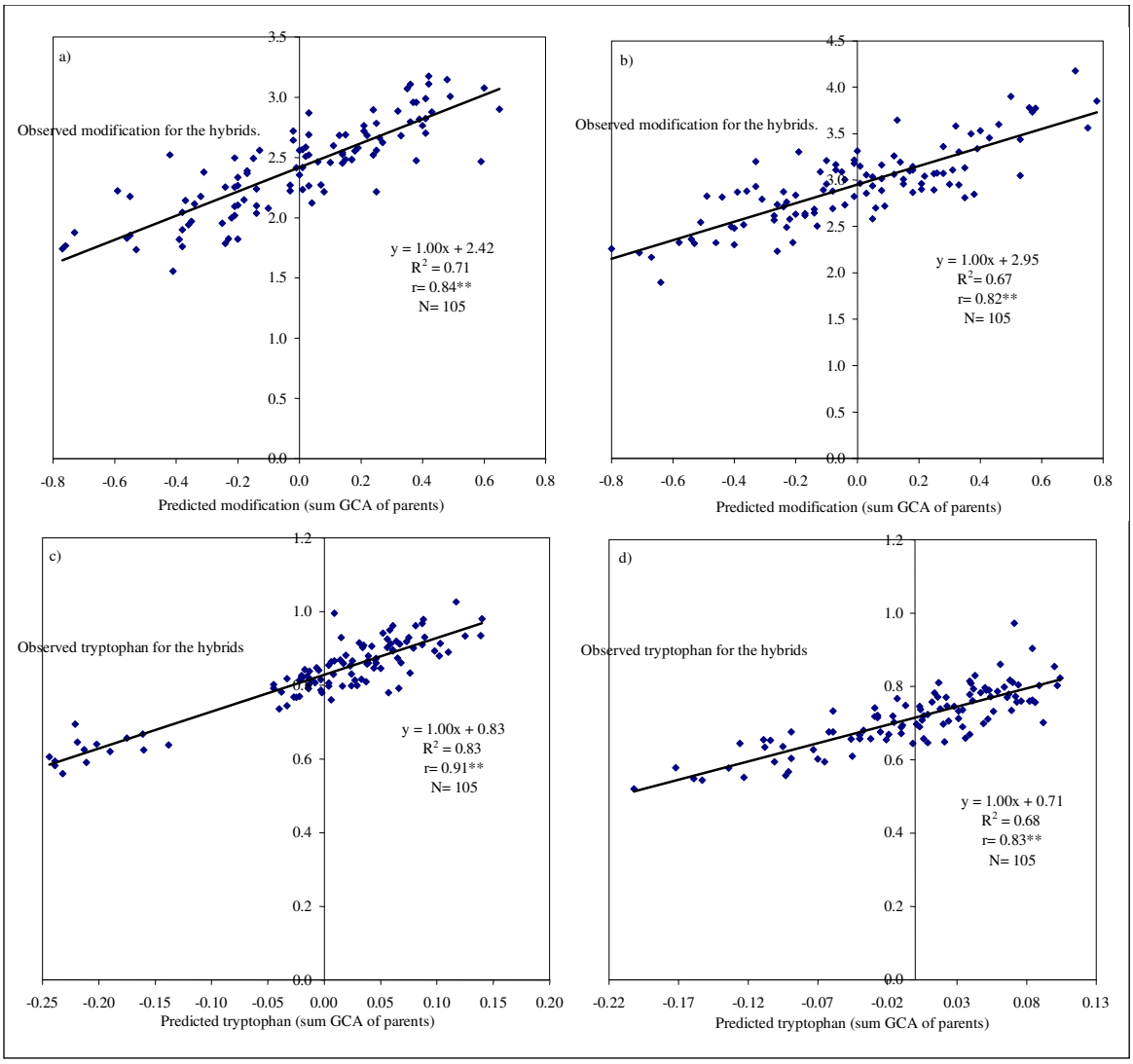

Figure 8.4 Regression of observed cross performances on GCA effects (sum of the two parents) for: a) endosperm modification score (1 - 5) across optimum N; b) endosperm modification score (1 - 5) across low N stress; c) tryptophan concentration in grain (g kg-1) across optimum N; d) tryptophan concentration in grain (g kg-1) across low N stress environments. ** $P < 0.01$; r= correlation coefficient; R2= coefficient of determination

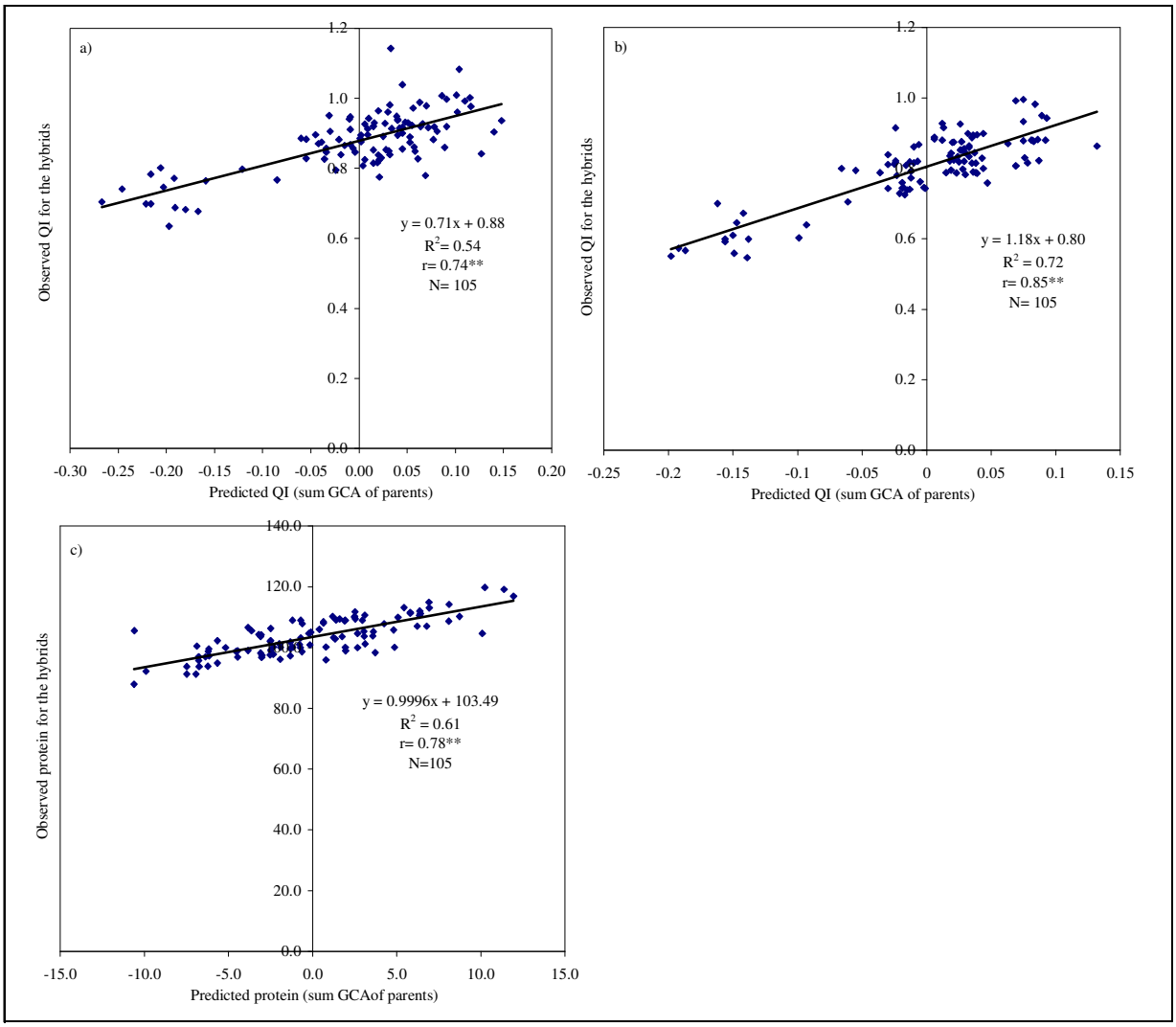

Figure 8.5 Regression of observed cross performances on GCA effects (sum of the two parents) for: a) protein quality index (QI) across optimum N; b) protein quality index (QI) across low N stress; c) protein concentration in grain (g kg-1) across optimum N environments. ** $P \leq 0.01$; r= correlation coefficient; R^2= coefficient of determination

8.5 Discussion

The results indicated the existence of a high level of variation among the hybrids for endosperm modification and most protein quality traits under stressed and optimal conditions, indicating the possibility of selection for modified endosperm phenotype and improved protein quality under both conditions. Significant variations were also observed

among the environments. The performances of the hybrids were not consistent across environments as observed from the significant interactions between environment and hybrids across low N stress, optimum N and all environments. Previously, several researchers reported similar results for endosperm modification (Wessel-Beaver and Lambert, 1982; Wessel-Beaver et al., 1985; Vasal et al., 1993a; b; Hohls et al., 1996; Pixley and Bjarnason, 2002), protein and tryptophan concentration in grain (Pixley and Bjarnason, 1993; Moro et al., 1995; Pixley and Bjarnason, 2002; Ngaboyisonga et al., 2008). Under both low N stress and optimal conditions, the protein quality traits (tryptophan concentration in grain and protein quality index) of most QPM hybrids were higher than the best normal check, indicating the relative stability of protein quality across soil N levels. However, protein concentrations in grain were higher only for few QPM hybrids as compared to the concentrations for the best normal maize check hybrid. Similarly, Pixley and Bjarnason (2002) reported that tryptophan concentration in protein is more stable than protein concentration in grain across environments. CIMMYT (2003b) reported that tryptophan level of QPM under both low nitrogen and optimum conditions is higher than the tryptophan level of normal maize under optimum conditions, which is consistent with observations in the current study.

Endosperm modification scores increased under low N stress conditions. Since the lower score indicates the better modification, this finding indicates that low N stress increased the frequency of soft or poorly modified grains relative to the same hybrids under optimal growing conditions. However, the level of endosperm modification under low N condition was within acceptable range. Ngaboyisonga et al. (2006) observed a similar trend under drought and low N stress conditions. Endosperm modification of QPM varieties is less stable across environments (Pixley and Bjarnason, 2002). Although QPM cultivars were superior to non-QPM cultivars in protein quality in all environments, tryptophan and protein concentrations in grain were affected by N conditions. As expected, higher concentrations of tryptophan and protein in grain were observed under optimum N than under low N stress because N is an important component of amino acids and proteins. Similar results were previously reported by others (Kniep and Mason, 1991; CIMMYT, 2003b; Mosisa, 2005). Higher protein quality index value was observed under low N stress than optimum N mainly due to a sharp decrease

in protein concentration under the same conditions. An increase in total protein in the maize kernel results in an increase in the zein fraction in endosperm proteins (Frey et al., 1949; Glover, 1992). Given that the zein fraction has poor nutritional quality due to its lack of tryptophan and lysine, it seems likely that higher protein content will result in lower protein quality (Glover, 1992; Darrigues et al., 2006). This can further be confirmed by the negative relationship between protein concentration and protein quality index. In general, the reductions due to low N in endosperm modification, protein quality and quantity were higher at Harare than at Bako, as the stress level at Harare was more severe than the stress level at Bako, as was observed for grain yield and agronomic traits (Chapter 4). The data for this experiment were obtained from only two low N stress and two optimal conditions. Moreover, among the two low N stress environments, the stress level at Bako was not as severe as the level required for germplasm screening. So, further investigations with increased number of locations are required to come up with conclusive results.

Positive phenotypic correlations observed between endosperm modification and tryptophan concentration in grain, and between endosperm modification and protein quality index indicates the low protein quality of genotypes with well modified endosperm texture. However, the correlation values were very low and may not complicate simultaneous improvement of these traits. It is because of this that QPM development has been successful. Nevertheless, if selection for endosperm modification is accompanied by selection for protein quality, desired levels of quality would be ensured. The negative or absence of relationship between endosperm modification and protein concentration in grain is desirable as both traits can be improved simultaneously. Similarly, tryptophan concentration in grain had a desirable relationship with protein concentration and protein quality index. Similar results were reported for *o2* and QPM germplasm (Wessel-Beaver et al., 1985; Kniep and Mason, 1991; Pixley and Bjarnason, 1993; 2002). The positive and highly significant correlations between low N stress and optimum N for most traits indicate that the hybrids had consistent performance under both conditions, and hence improvement for these traits under optimal conditions can simultaneously improve the performance under low N stress.

Significant variation observed among the hybrids for most traits was mainly due to GCA components of variation, indicating the importance of additive genetic effects in the inheritance of these traits under most environmental conditions. Non-additive effects were not important in most cases. Several researchers reported that additive genetic effects are more important than non-additive effects for endosperm hardness in the *o2* background of QPM (Ortega and Bates, 1983; Pixley and Bjarnason, 1993; Vasal et al., 1993a; b; De-quan and Shi-Huang, 1995; Hohls et al., 1996). In line with the current study, Pixley and Bjarnason (1993) reported the greater importance of additive gene action for protein concentration in grain and tryptophan concentration in grain.

Significant GCA x E and SCA x E interactions observed for most traits across low N stress, optimum N and all environments indicate that GCA effects of the inbred lines and SCA effects of the crosses were not consistent for these traits. This finding agrees with other reports (Pixley and Bjarnason, 1993; Vasal et al., 1993a; b; Hohls et al., 1996). However, comparison of GCA effects of lines for individual environments and across environments suggests that significant GCA x E interaction reflects small changes in rank for GCA effects that would not preclude identification of the best and worst lines for GCA effects for some traits. Accordingly, inbred lines VL05200, VL05468, VL054178 and CML144 were identified as the best general combiners for endosperm modification in most individual environments and across environments. These inbred lines can be used as the donor parents for the conversion of normal maize germplasm to QPM counterparts. Inbred lines VL052 and VL05468 were the best general combiners for tryptophan concentration in grain. Inbred lines VL052887, VL05482 and CML511 were best general combiners under optimal conditions for protein concentrations in grain. For protein quality index, VL052 and CML511 were the best general combiners under most environments while VL0523 and VL0524 were best only under optimal conditions.

If the SCA mean squares are not significant, as is the case for most traits in the current study, Baker (1978) argued that the performance of a single cross progeny can be adequately predicted on the basis of GCA. Hence, the higher correlation and regression coefficients observed between sum of GCA effects of the two parents and hybrid values for all traits

across low N stress and optimal conditions agrees with the hypothesis of Baker (1978). The absence of SCA effects for protein quality traits is regrettable because heterosis cannot be exploited to directly contribute gains for these traits (Pixley and Bjarnason, 1993).

8.6 Conclusions

Significant variation exists in QPM germplasm for endosperm modification, protein quality and quantity under low N stress and non-stress conditions. This indicates the possibility of improving QPM germplasm for these traits under different N levels. Tryptophan concentration of most QPM hybrids under both low N and optimal conditions was higher than the tryptophan concentration of normal maize under optimal conditions. Low N stress increased the frequency of soft or poorly modified grains as compared to the optimum N condition. Protein concentration in grain was more sensitive to low N stress than tryptophan concentration in grain. Undesirable associations were observed between endosperm modification and protein quality, and between protein concentration and protein quality index. However, the values are very low to be of detrimental effect for simultaneous improvement of these traits. It is recommended that selection for endosperm modification needs to be accompanied by monitoring protein quality to ensure desired quality level. Tryptophan and protein concentrations in grain can be simultaneously improved. Lack of undesirable relationships between hybrids under low N stress and optimum N for all traits should facilitate QPM cultivar development adapted to both environmental conditions. GCA effects and hence additive gene effects were primarily responsible for variation of most traits evaluated, under both low N stress and optimal conditions. Interaction of environment with GCA effects were significant for all traits across environments but consistently best general combining parents were identified, especially for endosperm modification, tryptophan concentration in grain and protein quality index. Lack of significant SCA effects for most traits indicates that progeny performance of the inbred lines can be adequately predicted on the basis of GCA effects of the parents. Therefore selection of parents for the formation of QPM hybrids, synthetics or open pollinated cultivars can be based on evaluation of GCA effects for the traits of interest among agronomically acceptable lines. The absence of significant SCA effects for most traits was undesirable, as heterosis cannot be exploited for these traits. Inbred lines VL05200, VL05468, VL054178 and CML144 were identified as good donor parents for the conversion normal maize genotypes to QPM.

Chapter 9

Summary/Opsomming

9.1 Summary

Maize is the dominant staple crop in most regions of Africa. The nutritional value of maize protein, however, is deficient in the essential amino acids such as lysine and tryptophan. This study was conducted to (1) investigate the level of variability among elite QPM inbred lines, (2) analyze combining ability of the inbred lines and G x E interaction of the resulting hybrids under stress and optimal conditions, (3) study the associations of parental genetic distances with F_1 performance, heterosis and SCA of the hybrids under stress and optimal environments, and (4) investigate the effects of low N stress on endosperm modification, protein quantity and quality of QPM and identify best donor parents.

The genetic variability of 35 maize inbred lines (32 QPM and three normal maize line checks) was studied using morpho-agronomic traits and SSR markers. Both methods indicated genetic variability among the lines. UPGMA cluster analysis based on morpho-agronomic data grouped the inbred lines into four clusters and two outliers mainly based on grain yield, days to anthesis, plant height and leaf area. SSR markers grouped the inbred lines into six clusters which were different from the morpho-agronomic clustering. SSR markers grouped the inbred lines more efficiently in accordance with pedigree relationships. A diallel analysis of 15 QPM inbred lines showed significant GCA and SCA mean squares for most traits under optimal environments. GCA effects were significant while SCA effects were not significant for most traits across sites with drought and low N stress. Additive genetic effects were important under stress, and both additive and non-additive genetic effects were important under optimal conditions. Inbred lines VL054178, VL05482, VL05561, VL05483, CML511, CML159, CML491 and VL06375, which had good GCA effects for most traits under stress and non-stress conditions can potentially be used in QPM breeding programs in Africa and similar environments worldwide. Mean MPH ranged from -9.1% for days to silking to 112.7% for grain yield and HPH ranged from -12.0% for days to silking to 89.8%

for grain yield. All the crosses showed negative MPH and HPH for days to anthesis and silking, and positive MPH for plant and ear height, number of kernels per row and kernels per ear.

SSR marker-based genetic distance was positively and highly significantly correlated with grain yield; and negatively and highly significantly correlated with days to anthesis and silking. The correlations of SSR marker distance with heterosis and SCA were low to be of predictive value. Morphological distances were not useful in predicting heterosis and SCA effects of hybrids. Environment affected the correlations of genetic distance with hybrid performance, heterosis and SCA, with lower values under stress conditions. AMMI stability value and linear regression models were positively correlated in ranking the stability of QPM hybrids. AMMI analysis based on inbred line means and selected hybrids clearly discriminated the genotypes on the base of adaptation patterns. Hierarchical clustering based on hybrid grain yield and inbred line means grouped the 13 environments mainly according to geographical location and prevailing growing conditions.

QPM hybrids showed higher levels of tryptophan content and protein quality index than the normal maize hybrids under both low N stress and optimal conditions. Low N stress increased the frequency of soft or poorly modified grains and decreased tryptophan and protein concentration in grain and increased protein quality index. Tryptophan concentration was more stable than protein concentration across low N stress and optimal conditions. Additive gene effects were primarily responsible for variation in endosperm modification and protein quality in the QPM inbred lines. Inbred lines VL05200, VL05468, VL054178 and CML144 were the best general combiners for endosperm modification; hence can be used as *o2* donor parents.

Information from the genetic diversity analyses of the inbred lines can be used for effective utilization of the inbred lines in the breeding programs for the formation of heterotic populations and development of desirable varieties. The inbred lines used in this study, in general, were found to be useful sources for genetic variability for the development of new genotypes for stress tolerance and the study confirmed the possibility of achieving good

performances across stress and non-stress conditions in QPM germplasm. However, more breeding efforts should be devoted to the development of QPM inbred lines with better field performance and acceptable levels of protein quality and quantity under both stress and optimal conditions. Inbred lines identified as good *o2* donors can be used for the conversion of well adapted normal maize genotypes into QPM counterparts.

9.2 Opsomming

Mielies is die dominante stapelvoedsel in die grootste deel van Afrika. Die voedingswaarde van mielieproteïene skiet egter tekort aan essensiële aminosure soos lisien en triptofaan. Hierdie studie is gedoen om te bepaal (1) die vlak van variasie in elite ingeteelde QPM lyne, (2) die kombineervermoë van ingeteelde lyne en G x E interaksie van die basters onder stremmings en optimale toestande, (3) die assosiasies van ouer genetiese afstande met F_1 prestasie, heterose en SCA van die basters onder stremmings en optimale toestande, en (4) die effek van lae N stremming op QPM endosperm modifikasie, proteïen hoeveelheid en kwaliteit en om die beste donor ouers te bepaal.

Die genetiese variasie van 39 mielie ingeteelde lyne (32 QPM en drie normale mielielyn standaarde) is geëvalueer met gebruik van morfo-agronomiese eienskappe en SSR merkers. Beide metodes het genetiese variasie in die ingeteelde lyne aangetoon. UPGMA trosanalise gebaseer op morfo-agronomiese data het die lyne in ses groepe verdeel gebaseer op graan opbrengs, dae tot blom, plant hoogte en blaar area. SSR merkers het ook die ingeteelde lyne in ses groepe verdeel, maar verskillend van die SSR merker groepe. SSR merkers het die lyne meer effektief gegroepeer volgens stambome. ‘n Dialleel analise van 15 QPM ingeteelde lyne het betekenisvolle GCA en SCA gemiddelde kwadrate vir meeste eienskappe in optimale omgewings getoon. GCA effekte was betekenisvol terwyl SCA effekte nie betekenisvol was vir meeste eienskappe oor droogte en lae N stremmings toestande. Additiewe geeneffekte was belangrik onder stremming, en beide additiewe en nie-additiewe genetiese effekte was belangrik in optimale toestande. Ingeteelde lyne VL054178, VL05482, VL05561, VL05483, CML511, CML159, CML491 en VL06375, wat goeie GCA effekte vir meeste eienskappe onder beide stremmings en optimal toestande gehad het kan potensieël vir QPM teelprogramme in Afrika en soortgelyme omgewings wêreldwyd gebruik word. Gemiddelde MPH het gewissel van -9.1% vir dae tot baardvorming tot 112.7% vir graanopbrengs, en HPH het gewissel van -12.0% vir dae tot baardvorming tot 89.8% vir graanopbrengs. Alle kruisings het negatiewe MPH en HPH vir dae tot blom en baardvorming getoon, en positiewe MPH vir plant en kophoogte, aantal pitte per ry en pitte per kop.

Die SSR merker-gebaseerde genetiese afstande was positief en hoogs betekenisvol gekorreleer met graanopbrengs; en negatief en hoogs betekenisvol met dae tot blom en baardvorming. Die korrelasies van SSR merker afstande met heterose en SCA was te laag om vir voorspelling te gebruik. Morfologiese afstande was onbruikbaar vir voorspelling van heterose en SCA in basters. Omgewing het die korrelasie van genetiese afstand met baster prestasie, heterose en SCA beïnvloed, met laer waardes onder stremmings toestande. AMMI stabiliteitswaarde en liniêre regressie modelle was positief gekorreleer in die rangordebepaling van stabiliteit van QPM basters. AMMI analise gebaseer op ingeteelde lyn gemiddeldes en geselekteerde basters het die genotipes duidelik onderskei op grond van aanpassingspatrone. Hierargale groepering op grond van baster graanopbrengs het die 13 omgewings hoofsaaklik volgens geografiese ligging en produksietoestande gegroepeer.

QPM basters het hoër vlakke van triptofaan en proteïenkwaliteitsindeks getoon as normale mielie basters onder beide lae en optimale N toestande. Lae N stremming het die frekwensie van sagte of swak gemodifiseerde pitte verhoog en het triptofaan en proteïeninhoud verlaag, maar het proteïenkwaliteitsindeks verhoog. Triptofaan konsentrasie was meer stabiel as proteïen konsentrasie oor lae N en optimale toestande. Additiewe geeneffekte was hoofsaaklik verantwoordelik vir variasie in endosperm modifikasie en proteïenkwaliteit in die QPM ingeteelde lyne. Lyne VL05200, VL05468, VL054178 en CML144 is geïdentifiseer as die beste algemene kombineerders vir endosperm modifikasie; en kan dus gebruik word as *o2* donors.

Inligting van die genetiese diversiteits analises van die ingeteelde lyne kan gebruik word in teelprogramme vir die vorming van heterotiese populasies. Die ingeteelde lyne wat in hierdie studie gebruik is, is oor die algemeen bruikbaar as bron van geneties variasie vir die ontwikkeling van nuwe genotipes met stremmings toleransie, en die studie het die moontlikheid bevestig om goeie opbrengste in QPM te kry onder beide stremmings en optimale toestande. Meer klem moet geplaas word op die ontwikkeling van QPM ingeteelde lyne met beter opbrengste en aanvaarbare vlakke van proteïen kwaliteit en kwantiteit onder beide stremmings en optimal toestande. Ingteelde lyne wat as goeie *o2* donors geïdentifiseer

is kan gebruik word vir die omskakeling van goed aangepaste gewone mielie genotipes na QPM.

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APPENDICES

Appendix 1 Mean performances for grain yield and agronomic traits in a diallel crosses among fifteen QPM inbred lines evaluated under drought stress conditions at Chirezi and Kiboko

Cross	GY	DA	DS	ASI	PH	EH	EPP	Cross	GY	DA	DS	ASI	PH	EH	EPP
P1 x P2	0.9	97.9	112.1	14.1	132.9	93.9	0.3	P5 x P9	1.8	96.2	107.3	11.3	165.3	121.1	0.5
P1 x P3	1.2	96.9	112.6	15.7	179.4	115.1	0.3	P5 x P10	1.7	94.2	106.3	12.2	180.7	105.9	0.5
P1 x P4	2.0	88.5	89.9	1.4	187.1	109.4	0.7	P5 x P11	1.9	93.4	101.8	8.2	183.1	112.4	0.6
P1 x P5	0.3	98.5	120.0	21.4	133.9	86.4	0.1	P5 x P12	0.4	99.3	113.5	14.1	117.2	87.2	0.1
P1 x P6	1.9	87.5	93.7	6.1	205.1	119.2	0.7	P5 x P1\3	1.4	93.4	105.9	12.6	180.2	112.8	0.5
P1 x P7	1.8	97.5	111.1	13.3	168.9	119.9	0.2	P5 x P14	0.8	101.6	115.4	13.9	145.0	101.2	0.3
P1 x P8	0.8	97.1	111.6	14.3	181.1	127.3	0.3	P5 x P15	2.2	94.2	100.2	6.2	184.7	110.5	0.6
P1 x P9	3.7	92.1	93.7	1.6	176.2	112.2	0.8	P6 x P7	1.8	90.6	104.4	13.5	189.5	128.4	0.4
P1 x P10	1.3	89.5	93.8	4.3	193.6	124.3	0.5	P6 x P8	2.3	90.0	97.6	7.6	183.4	130.6	0.6
P1 x P11	1.6	91.8	103.6	11.9	184.3	100.7	0.5	P6 x P9	3.3	86.1	86.6	0.4	193.6	112.4	0.7
P1 x P12	0.5	102.0	119.6	17.7	135.3	93.2	0.2	P6 x P10	2.6	84.4	85.6	1.4	179.6	94.1	0.8
P1 x P13	1.7	90.7	100.4	9.5	175.8	96.9	0.5	P6 x P11	2.8	83.5	85.2	1.7	184.0	99.5	0.7
P1 x P14	0.9	102.0	116.8	14.7	137.7	103.0	0.4	P6 x P12	1.9	93.1	103.9	11.0	184.7	104.8	0.7
P1 x P15	2.1	89.3	99.3	9.7	188.8	111.0	0.6	P6 x P13	2.4	85.4	88.8	3.4	193.7	108.5	0.7
P2 x P3	0.5	94.4	109.6	15.3	161.3	94.2	0.2	P6 x P14	2.3	89.1	95.9	6.8	175.3	101.0	0.7
P2 x P4	3.0	87.3	92.1	5.0	177.5	103.4	0.7	P6 x P15	2.8	84.3	87.1	2.9	198.7	102.3	0.7
P2 x P5	0.9	96.8	107.6	10.8	155.7	97.6	0.2	P7 x P8	0.3	98.9	118.9	20.1	126.4	82.5	0.1
P2 x P6	2.0	87.2	96.0	8.8	177.7	97.1	0.6	P7 x P9	1.2	98.7	109.9	11.4	157.5	112.0	0.4
P2 x P7	1.0	97.3	111.2	13.7	147.2	92.2	0.3	P7 x P10	1.6	93.0	104.8	11.9	205.0	128.1	0.4
P2 x P8	0.9	100.4	115.5	15.4	149.0	100.9	0.3	P7 x P11	1.5	92.5	104.7	12.4	186.2	120.3	0.4
P2 x P9	2.9	92.2	103.3	11.2	166.3	99.5	0.6	P7 x P12	0.4	101.9	115.9	14.0	148.0	99.1	0.2
P2 x P10	1.9	92.0	99.7	7.6	177.0	107.2	0.7	P7 x P13	2.3	91.9	104.9	12.9	185.1	107.6	0.4
P2 x P11	1.4	91.8	95.3	3.5	187.4	108.3	0.5	P7 x P14	1.2	97.1	108.8	11.7	168.8	121.1	0.5
P2 x P12	0.5	99.3	110.7	11.3	131.7	93.7	0.2	P7 x P15	1.7	93.1	106.0	12.8	194.0	112.4	0.4
P2 x P13	2.7	86.1	93.3	7.1	177.9	106.3	0.9	P8 x P9	1.9	95.0	106.5	11.6	174.3	124.3	0.5
P2 x P14	0.7	100.5	113.3	12.7	124.0	90.7	0.3	P8 x P10	1.6	91.2	100.2	8.9	193.4	139.3	0.4
P2 x P15	2.1	89.7	98.2	8.4	195.2	130.0	0.6	P8 x P11	1.4	90.4	103.4	12.8	198.4	125.3	0.4
P3 x P4	2.1	89.9	99.4	9.6	171.9	104.2	0.6	P8 x P12	0.5	98.6	114.0	15.4	160.6	94.7	0.2
P3 x P5	0.6	101.6	116.9	15.4	137.2	79.8	0.2	P8 x P13	2.2	91.2	104.0	12.8	192.7	106.5	0.4
P3 x P6	2.6	88.7	102.2	13.4	175.8	96.4	0.6	P8 x P14	0.9	96.5	109.2	12.8	166.9	110.8	0.3
P3 x P7	0.4	96.6	113.9	17.2	150.2	106.8	0.2	P8 x P15	2.2	92.1	104.4	12.2	181.1	109.6	0.4
P3 x P8	0.8	97.9	113.9	15.9	168.1	109.5	0.3	P9 x P10	2.9	88.2	91.9	3.6	162.9	101.1	0.6
P3 x P9	1.9	92.4	104.4	12.0	168.0	112.8	0.4	P9 x P11	2.9	88.0	95.6	7.6	171.5	103.7	0.7
P3 x P10	1.8	90.2	103.0	12.8	186.8	107.4	0.5	P9 x P12	2.0	94.8	103.0	8.1	179.0	122.8	0.6
P3 x P11	1.6	88.8	97.0	8.3	189.4	106.9	0.5	P9 x P13	3.5	89.0	90.7	1.8	193.9	120.6	0.9
P3 x P12	0.5	96.2	109.3	13.1	154.3	102.1	0.2	P9 x P14	2.4	93.2	102.4	9.1	177.1	129.0	0.6
P3 x P13	1.5	91.6	105.4	13.7	175.8	97.7	0.5	P9 x P15	3.0	88.6	94.6	6.1	190.8	123.4	0.7
P3 x P14	1.1	98.7	114.8	15.9	150.9	105.6	0.3	P10 x P11	1.3	86.3	93.0	6.8	177.6	103.6	0.5
P3 x P15	1.3	90.7	103.0	12.4	186.9	101.1	0.4	P10 x P12	1.8	92.0	100.2	8.3	170.3	112.0	0.6
P4 x P5	2.3	89.3	94.1	4.6	193.9	105.3	0.7	P10 x P13	2.2	86.7	91.2	4.3	183.6	87.9	0.7
P4 x P6	2.5	82.8	83.7	1.2	199.1	114.9	0.8	P10 x P14	2.0	93.4	100.5	7.4	170.2	86.3	0.6
P4 x P7	2.3	89.7	97.1	7.3	195.8	133.9	0.5	P10 x P15	2.2	85.5	88.2	2.6	190.9	103.6	0.7
P4 x P8	2.2	90.0	97.3	7.5	189.3	122.2	0.5	P11 x P12	1.6	91.7	101.6	9.9	186.9	113.6	0.6
P4 x P9	3.0	86.1	87.4	1.0	185.6	127.8	0.7	P11 x P13	2.9	87.8	93.2	5.3	172.9	90.8	0.7
P4 x P10	2.8	84.8	88.6	3.6	185.6	112.6	0.7	P11 x P14	1.4	93.2	105.6	12.5	172.9	111.8	0.5
P4 x P11	3.0	86.5	90.2	3.8	180.3	102.9	0.7	P11 x P15	2.0	87.6	95.2	7.8	175.7	99.1	0.6
P4 x P12	1.4	91.4	101.9	10.4	163.8	106.9	0.5	P12 x P13	1.4	96.3	108.4	11.9	172.3	98.4	0.5
P4 x P13	1.2	89.0	98.4	9.5	169.4	98.1	0.5	P12 x P14	0.7	103.5	117.3	13.8	125.4	79.9	0.4
P4 x P14	2.5	91.3	98.3	7.1	166.0	104.8	0.7	P12 x P15	2.0	91.2	102.8	11.5	181.8	110.7	0.5
P4 x P15	3.3	86.5	89.7	3.3	196.8	105.4	0.9	P13 x P14	2.1	92.1	101.0	8.7	186.3	108.8	0.7
P5 x P6	1.4	91.0	101.4	10.5	189.7	109.7	0.5	P13 x P15	2.0	88.2	91.2	2.9	192.1	103.7	0.7
P5 x P7	0.9	100.2	114.2	13.9	164.5	110.7	0.3	P14 x P15	2.1	91.2	96.8	5.7	186.7	110.8	0.7
P5 x P8	0.8	95.9	107.0	10.9	146.1	95.5	0.2								
Mean									1.8	92.3	102.0	9.6	174.1	107.2	0.5
F-test									**	**	**	**	**	**	**
$LSD_{0.05}$									0.8	3.1	6.7	5.9	28.9	23.5	0.2
CV%									24.1	1.7	3.4	30.4	8.4	11.0	20.0
No. of sites									2	2	2	2	1	1	2

* $P \leq 0.05$; ** $P \leq 0.01$; CV= coefficient of variation; DA= days to anthesis; DS= days to silking; ED= ear diameter; EL= ear length; GY= grain yield; KPR= number of kernels per row; KPE= number of kernels per ear; P1= VL052; P2= VL05200; P3= VL05468; P4= VL054178; P5= VL052887; P6= VL05482; P7= VL0523; P8= VL0524; P9= VL05561; P10= VL05483; P11= CML511; P12= CML144; P13= CML159; P14= CML491; P15= VL06375; PH= plant height; TKW= thousand kernel weight

Appendix 2 Mean performances for grain yield and agronomic traits in a diallel crosses among fifteen QPM inbred lines evaluated under low nitrogen conditions at Harare and Bako

Cross	GY	DA	DS	PH	ED	EL	RPE	TKW	Cross	GY	DA	DS	PH	ED	EL	RPE	TKW
P1 x P2	1.0	78.5	81.0	143.7	3.9	10.1	12.3	185.9	P5 x P9	2.0	84.7	85.7	170.2	3.9	12.2	13.2	195.4
P1 x P3	1.4	87.9	90.2	163.7	4.3	10.7	11.5	218.3	P5 x P10	2.0	82.5	84.5	173.2	4.1	9.8	13.6	190.0
P1 x P4	2.3	77.9	80.7	159.2	4.1	12.4	12.6	277.7	P5 x P11	1.8	85.6	86.6	171.8	4.1	11.0	14.0	190.2
P1 x P5	0.8	86.8	90.6	161.5	3.8	9.5	13.8	167.6	P5 x P12	0.8	90.8	93.3	146.7	3.7	8.7	13.7	150.7
P1 x P6	2.3	78.5	82.7	164.4	4.1	13.0	13.5	197.6	P5 x P13	1.9	83.8	87.9	182.1	4.4	10.5	14.1	225.1
P1 x P7	1.3	85.8	88.6	156.1	3.9	9.9	12.8	205.7	P5 x P14	1.5	85.0	87.6	159.3	3.7	10.0	14.5	179.1
P1 x P8	1.7	84.4	88.1	168.7	4.0	12.0	12.3	199.1	P5 x P15	3.1	81.2	84.7	180.8	4.2	15.0	12.9	224.7
P1 x P9	2.2	81.8	84.9	167.2	4.4	13.5	12.8	215.5	P6 x P7	2.1	79.6	81.5	155.2	3.6	12.2	14.3	178.1
P1 x P10	2.1	81.0	81.3	185.1	4.2	10.0	14.7	222.9	P6 x P8	1.9	78.8	80.9	164.6	4.0	14.3	12.0	192.2
P1 x P11	1.5	83.2	86.0	178.2	4.3	11.3	13.2	186.3	P6 x P9	2.7	75.7	78.0	163.8	4.1	15.7	12.6	206.9
P1 x P12	1.0	85.9	89.2	165.4	3.6	9.3	13.0	146.7	P6 x P10	1.9	74.9	77.3	158.8	3.9	10.2	13.5	193.0
P1 x P13	2.3	80.4	83.8	180.6	4.6	12.9	14.7	241.2	P6 x P11	2.4	76.0	77.4	165.2	4.0	12.4	13.9	182.2
P1 x P14	1.5	84.9	87.5	146.4	3.8	11.0	13.4	184.6	P6 x P12	2.1	80.3	82.9	161.2	3.9	12.7	13.0	179.4
P1 x P15	2.3	80.6	84.0	170.7	4.3	14.0	13.4	237.9	P6 x P13	2.2	76.8	79.3	167.8	3.9	11.2	13.0	221.8
P2 x P3	1.2	87.1	89.7	134.2	4.4	11.5	13.3	220.9	P6 x P14	1.5	78.4	83.2	164.8	3.9	13.1	13.1	206.7
P2 x P4	3.3	76.9	77.4	161.0	4.2	14.1	13.1	267.2	P6 x P15	2.2	76.7	79.7	159.6	4.0	12.9	12.4	216.7
P2 x P5	0.9	91.4	93.6	130.6	3.8	9.6	13.3	183.4	P7 x P8	0.4	87.3	89.4	141.7	3.4	5.8	12.0	190.6
P2 x P6	2.1	78.8	80.3	165.5	4.0	12.2	12.9	231.2	P7 x P9	2.2	83.2	86.1	155.6	4.0	14.7	12.3	212.2
P2 x P7	1.4	87.7	91.3	149.1	3.9	9.5	12.7	224.6	P7 x P10	2.1	82.5	84.1	178.7	4.1	11.4	14.9	196.9
P2 x P8	1.3	85.9	89.8	156.8	4.0	10.3	13.0	222.3	P7 x P11	1.9	81.4	85.2	177.1	4.2	11.4	13.3	216.5
P2 x P9	2.2	79.9	81.6	156.4	4.4	13.5	14.2	251.6	P7 x P12	1.2	83.5	86.3	159.4	4.0	11.0	13.3	182.8
P2 x P10	2.0	82.1	83.9	173.5	4.1	10.6	15.0	215.4	P7 x P13	1.7	84.5	86.9	170.0	4.4	13.4	13.2	235.8
P2 x P11	2.2	83.7	84.8	160.9	4.5	12.6	14.5	230.6	P7 x P14	3.1	83.9	85.4	170.5	4.2	13.2	13.1	224.5
P2 x P12	0.6	88.1	93.7	130.8	3.8	8.3	13.4	173.8	P7 x P15	2.4	81.8	85.0	184.5	4.4	14.4	12.9	229.9
P2 x P13	2.9	80.1	81.8	170.5	4.4	12.3	14.2	267.9	P8 x P9	1.6	81.8	83.1	163.0	3.7	12.3	12.8	192.8
P2 x P14	1.7	88.7	90.7	137.9	4.2	11.6	13.9	188.8	P8 x P10	2.2	79.6	80.6	177.9	4.1	12.2	14.5	198.0
P2 x P15	3.7	78.3	79.4	172.7	4.5	14.1	14.0	290.5	P8 x P11	1.8	83.5	88.8	173.6	4.1	12.1	11.7	210.4
P3 x P4	2.9	78.3	82.4	173.1	4.1	15.2	13.2	247.8	P8 x P12	1.6	84.2	86.3	166.1	4.0	12.6	13.6	182.9
P3 x P5	1.6	88.9	91.9	168.9	3.9	11.1	12.4	182.1	P8 x P13	2.9	81.7	83.6	174.4	4.5	14.8	13.4	242.1
P3 x P6	1.8	78.9	81.8	157.9	3.9	12.6	12.9	196.9	P8 x P14	2.4	85.2	88.5	153.5	4.1	12.5	13.1	188.3
P3 x P7	1.7	86.7	88.9	155.8	4.2	13.0	12.4	207.6	P8 x P15	3.2	82.5	84.3	183.4	4.4	14.0	13.1	246.3
P3 x P8	1.7	85.8	90.5	164.7	4.3	11.6	11.8	199.7	P9 x P10	2.4	77.7	78.6	177.6	4.4	11.4	15.2	199.5
P3 x P9	2.7	83.7	85.0	168.4	4.3	14.7	12.8	195.7	P9 x P11	1.8	78.5	82.0	155.1	4.0	11.3	13.3	177.2
P3 x P10	1.6	80.9	83.9	168.9	4.2	10.2	15.2	190.1	P9 x P12	2.9	82.0	83.0	167.9	4.2	14.3	12.2	249.0
P3 x P11	1.7	81.7	86.8	164.0	4.0	11.6	15.3	190.9	P9 x P13	2.8	78.8	80.8	166.8	4.3	12.1	13.2	231.2
P3 x P12	1.0	87.7	90.8	149.4	3.9	9.1	14.0	205.6	P9 x P14	3.0	82.4	85.2	175.8	4.2	16.1	14.4	211.5
P3 x P13	2.8	80.7	83.6	184.1	4.6	13.7	15.4	241.4	P9 x P15	2.4	77.7	79.5	189.5	4.1	13.3	14.2	222.3
P3 x P14	1.8	86.7	90.5	163.8	4.0	12.4	14.4	180.9	P10 x P11	2.2	78.4	80.0	169.0	4.0	9.7	14.7	192.1
P3 x P15	2.7	82.7	84.6	162.7	4.4	14.2	14.5	230.0	P10 x P12	2.8	80.1	81.6	181.2	4.3	11.1	13.5	202.3
P4 x P5	2.7	80.5	83.4	178.2	4.1	12.2	13.0	222.8	P10 x P13	2.4	76.9	79.3	183.8	4.5	11.1	14.9	220.2
P4 x P6	2.3	73.6	75.9	158.3	3.7	15.1	11.7	196.5	P10 x P14	2.5	80.6	82.2	184.8	4.2	10.7	14.8	204.7
P4 x P7	2.7	78.3	81.0	177.3	4.0	14.6	12.3	229.2	P10 x P15	2.7	76.5	78.2	173.2	4.3	12.4	15.6	196.0
P4 x P8	2.2	78.6	82.2	175.7	4.1	14.6	10.3	252.6	P11 x P12	2.1	82.3	85.7	176.8	4.2	11.7	14.5	199.1
P4 x P9	2.3	77.2	80.1	154.4	4.0	14.2	12.2	224.1	P11 x P13	2.7	78.1	82.4	167.2	4.3	11.5	14.4	222.8
P4 x P10	1.5	76.9	77.6	168.2	3.7	8.7	13.0	196.1	P11 x P14	1.9	84.8	89.2	165.9	4.1	11.4	14.4	207.3
P4 x P11	2.6	77.3	78.7	178.0	4.1	13.2	13.4	220.6	P11 x P15	2.6	77.6	80.2	165.9	4.4	14.1	14.5	208.1
P4 x P12	3.1	77.1	78.8	171.0	4.5	14.5	12.6	250.4	P12 x P13	2.0	83.0	84.8	176.2	4.2	12.0	15.0	207.1
P4 x P13	0.9	78.7	81.4	152.3	3.4	9.3	13.0	175.1	P12 x P14	1.3	89.0	91.9	142.5	3.8	11.0	14.0	157.5
P4 x P14	2.7	80.1	82.8	165.0	4.2	15.0	13.3	246.2	P12 x P15	2.0	82.0	83.3	174.9	4.1	12.8	13.9	202.2
P4 x P15	2.6	75.3	77.4	175.8	4.3	13.0	12.9	225.3	P13 x P14	2.9	81.5	82.9	171.9	4.6	11.9	13.4	225.5
P5 x P6	2.7	79.5	81.9	173.6	3.8	12.7	13.0	196.8	P13 x P15	3.3	77.1	78.1	191.4	4.3	13.0	13.2	258.3
P5 x P7	1.2	85.9	88.1	156.1	3.9	9.8	13.0	182.9	P14 x P15	3.4	81.4	83.5	183.3	4.4	13.5	13.8	234.6
P5 x P8	1.5	85.2	88.0	156.9	3.8	10.0	13.5	212.6									
Mean										2.1	81.7	84.2	167.0	4.1	12.2	13.4	212.3
F test										*	**	**	**	**	**	*	**
$LSD_{0.05}$										1.0	3.0	3.8	17.9	0.3	2.5	1.5	33.4
CV%										33.6	2.6	3.3	7.6	4.2	10.5	8.2	11.2
No. of location										2	2	2	2	1	1	2	2

* $P \leq 0.05$; ** $P \leq 0.01$; CV= coefficient of variation; DA= days to anthesis; DS= days to silking; ED= ear diameter; EL= ear length; GY= grain yield; P1= VL052; P2= VL05200; P3= VL05468; P4= VL054178; P5= VL052887; P6= VL05482; P7= VL0523; P8= VL0524; P9= VL05561; P10= VL05483; P11= CML511; P12= CML144; P13= CML159; P14= CML491; P15= VL06375; PH= plant height; RPE= number of rows per ear; TKW= thousand kernel weight

Appendix 3 Mean performance for grain yield and agronomic traits in a diallel crosses among fifteen QPM inbred lines evaluated under optimal conditions

Cross	GY	DA	DS	ASI	PH	EH	EPP	ED	EL	RPE	KPR	KPE	TKW
P1 x P2	4.02	76.7	78.4	1.9	204.6	101.6	1.07	4.5	13.3	14.1	30.2	425.8	280.3
P1 x P3	5.11	76.5	78.3	2.2	212.3	102.8	1.05	4.8	16.2	15.5	38.0	590.0	255.1
P1 x P4	7.04	70.6	71.6	1.8	220.1	103.9	1.03	4.8	17.1	13.3	38.0	503.8	346.1
P1 x P5	4.26	77.3	77.8	0.6	220.1	112.0	1.16	4.2	14.0	13.9	32.7	452.8	237.4
P1 x P6	6.67	70.3	71.8	1.7	225.9	106.6	1.22	4.6	15.5	13.6	36.2	492.0	298.9
P1 x P7	5.11	75.8	77.4	1.7	225.7	118.0	1.13	4.5	15.5	13.2	38.8	511.0	268.1
P1 x P8	5.23	75.5	77.0	1.5	222.1	115.0	1.10	4.3	15.3	13.5	35.9	489.0	277.3
P1 x P9	7.67	73.2	74.3	1.0	230.7	121.7	1.06	4.9	18.6	14.7	40.9	600.5	322.8
P1 x P10	7.23	72.4	73.1	1.1	239.9	115.3	1.22	4.7	14.7	14.1	34.6	489.1	297.5
P1 x P11	7.58	74.2	75.9	2.2	243.1	116.9	1.28	4.8	16.3	15.0	39.2	590.5	293.5
P1 x P12	3.03	77.3	78.7	1.5	200.7	98.7	0.97	4.0	12.1	14.1	32.1	449.4	230.0
P1 x P13	6.94	73.6	75.1	1.5	224.1	104.3	1.06	4.7	17.9	14.8	37.3	553.1	328.9
P1 x P14	4.69	76.6	78.1	1.7	218.8	107.7	1.12	4.4	14.1	14.1	35.3	497.9	237.0
P1 x P15	6.95	72.0	73.6	1.5	236.2	116.6	1.13	5.0	17.3	14.6	35.4	517.8	321.7
P2 x P3	4.63	76.6	78.6	2.9	199.8	99.4	0.97	4.6	15.4	15.9	34.4	547.8	266.8
P2 x P4	6.88	70.5	72.0	2.1	206.3	99.7	1.07	4.7	17.4	14.4	34.4	492.7	336.3
P2 x P5	4.76	78.3	79.1	1.1	205.7	102.4	1.20	4.3	13.0	14.3	33.1	472.6	255.7
P2 x P6	7.04	69.7	71.3	2.2	205.5	99.1	1.14	4.5	16.3	14.1	37.4	525.8	282.6
P2 x P7	5.50	76.2	77.0	0.6	216.6	111.6	1.04	4.5	14.5	14.1	34.3	482.8	314.9
P2 x P8	5.68	76.0	77.1	1.4	218.5	111.2	1.12	4.5	14.4	13.6	34.2	466.8	303.1
P2 x P9	8.02	73.4	73.9	0.4	214.3	107.5	1.14	5.0	18.9	14.6	42.1	614.9	341.3
P2 x P10	6.55	72.6	73.9	1.5	227.8	101.8	1.14	4.8	15.6	15.2	38.7	589.4	297.6
P2 x P11	7.70	74.1	75.3	1.4	224.3	105.9	1.16	4.7	16.3	14.9	36.2	540.5	314.2
P2 x P12	3.58	78.5	79.9	1.6	192.6	89.9	1.05	4.2	12.8	14.4	32.8	472.5	251.7
P2 x P13	7.01	72.7	73.9	1.6	220.1	102.5	1.00	4.8	16.7	16.2	37.1	605.2	319.9
P2 x P14	4.89	76.8	77.6	1.4	206.8	96.1	1.10	4.4	14.4	14.8	33.5	493.6	278.2
P2 x P15	6.94	71.1	72.7	2.1	220.7	104.5	1.05	4.7	15.3	15.2	33.3	507.1	335.5
P3 x P4	7.01	72.3	74.1	2.3	224.2	106.7	1.05	4.6	18.8	14.3	41.6	593.4	320.9
P3 x P5	5.20	78.5	79.9	1.5	223.6	113.6	1.21	4.1	15.7	15.1	38.5	580.9	227.7
P3 x P6	6.26	71.7	73.3	1.7	216.1	104.2	1.14	4.4	16.7	14.3	36.9	528.5	275.3
P3 x P7	5.37	77.2	79.6	3.0	225.8	119.0	1.00	4.5	16.5	14.4	41.3	596.2	258.5
P3 x P8	5.36	78.2	80.5	3.2	230.6	122.4	1.05	4.4	16.7	14.7	40.1	593.2	260.7
P3 x P9	7.33	75.3	76.5	1.1	230.6	123.4	1.06	4.8	19.7	15.2	45.2	689.0	286.9
P3 x P10	6.92	72.8	74.6	2.2	234.4	115.9	1.15	4.7	15.4	16.3	41.0	670.0	269.1
P3 x P11	7.00	74.1	76.0	2.4	232.6	110.6	1.10	4.6	15.2	16.2	40.2	654.9	267.3
P3 x P12	4.45	77.7	79.2	2.0	200.8	94.7	1.07	4.4	15.0	15.4	40.7	624.8	216.8
P3 x P13	6.56	75.0	76.9	2.6	224.7	102.7	1.01	4.8	16.9	15.8	40.0	628.3	310.8
P3 x P14	5.53	76.9	79.5	3.1	217.7	105.2	1.16	4.2	15.6	15.1	39.6	597.4	237.3
P3 x P15	6.80	73.0	75.0	2.2	230.0	114.8	1.06	4.6	17.6	15.8	38.7	611.8	310.4
P4 x P5	6.77	73.5	74.5	1.2	222.2	107.1	1.14	4.3	17.3	13.3	39.4	524.4	306.5
P4 x P6	5.68	66.9	68.9	2.7	211.7	100.0	1.15	4.1	16.0	13.0	36.0	467.8	286.7
P4 x P7	6.82	72.5	73.5	1.4	231.4	115.9	1.08	4.5	18.8	12.7	42.3	536.4	348.1
P4 x P8	7.25	71.9	73.7	2.0	228.4	116.6	1.04	4.6	18.6	13.3	42.2	560.7	338.9
P4 x P9	7.06	70.8	71.5	0.6	214.3	109.5	1.02	4.5	20.3	13.5	42.3	574.8	331.9
P4 x P10	6.33	68.8	70.7	2.5	221.9	103.8	1.06	4.7	16.1	13.6	36.9	501.4	313.3
P4 x P11	6.78	71.0	72.7	2.0	233.5	113.4	1.12	4.6	16.7	13.1	40.6	533.6	336.3
P4 x P12	7.15	71.2	72.3	1.3	219.7	102.9	1.08	4.8	17.4	13.8	38.4	528.3	345.7
P4 x P13	4.30	72.8	74.5	1.8	206.4	95.4	0.93	3.9	14.4	13.2	33.7	444.3	289.6
P4 x P14	8.08	72.7	74.3	1.8	222.5	108.6	1.15	4.6	18.8	13.6	42.4	576.8	348.7
P4 x P15	6.49	69.8	70.9	1.6	227.5	108.2	1.04	4.8	18.7	13.6	35.9	488.5	355.5
P5 x P6	6.75	72.9	74.2	1.7	231.9	109.6	1.48	4	14.9	13.2	35.0	463.3	264.8
P5 x P7	5.55	77.8	78.6	1.1	231.5	117.2	1.24	4.3	14.4	13.5	36.7	495.1	248.7
P5 x P8	5.70	77.8	78.9	1.4	235.2	118.0	1.24	4.2	14.5	13.6	37.8	514.4	246.6
P5 x P9	7.95	76.4	76.4	-0.2	239.7	126.7	1.34	4.5	16.5	14.0	41.1	573.8	292.9
P5 x P10	7.53	74.9	76.3	1.5	248.4	123.3	1.43	4.4	15.4	14.5	35.7	514.5	272.6
P5 x P11	7.77	76.6	77.2	0.6	245.3	123.7	1.42	4.5	15.1	14.5	38.0	550.8	279.1
P5 x P12	3.69	78.3	79.1	1.0	207.8	104.2	1.14	4.3	11.5	14.3	32.5	466.6	192.8
P5 x P13	7.26	75.8	77.0	1.0	242.5	108.5	1.18	4.8	17.6	14.8	38.3	565.2	305.9
P5 x P14	6.25	76.9	78.3	1.2	231.2	119.8	1.28	4.3	14.7	14.9	38.6	576.9	250.3
P5 x P15	7.26	74.5	75.5	0.9	237.7	115.7	1.20	4.8	17.5	14.5	40.0	581.3	298.5

Appendix 3 Continued

Cross	GY	DA	DS	ASI	PH	EH	EPP	ED	EL	RPE	KPR	KPE	TKW
P6 x P7	7.03	72.9	74.1	1.7	231.6	118.1	1.13	4.3	16.2	13.7	40.7	560.3	277.1
P6 x P8	6.07	72.8	74.4	2.0	225.6	111.3	1.23	4.3	15.6	13.5	40.5	546.5	271.1
P6 x P9	7.18	68.5	70.0	1.9	223.7	112.4	1.20	4.6	17.0	14.2	41.1	582.1	293.8
P6 x P10	5.96	67.4	69.1	2.6	214.6	97.0	1.23	4.4	14.8	13.6	37.6	511.1	265.5
P6 x P11	6.63	68.9	70.7	2.3	218.1	104.4	1.23	4.4	14.7	13.9	38.1	531.3	269.9
P6 x P12	6.36	70.8	72.1	1.7	221.1	105.5	1.36	4.3	15.0	14.1	37.3	526.5	261.1
P6 x P13	6.18	69.5	72.0	3.2	215.0	95.9	1.10	4.5	17.6	13.5	36.1	487.6	316.8
P6 x P14	7.59	71.2	72.9	2.3	226.6	112.8	1.39	4.4	15.7	14.1	34.1	483.4	289.5
P6 x P15	6.15	68.0	69.6	2.1	217.1	104.0	1.17	4.7	17.5	14.0	34.5	484.8	308.0
P7 x P8	1.82	80.4	82.8	3.3	189.0	101.0	0.79	3.8	10.7	12.3	26.7	328.0	259.5
P7 x P9	6.34	75.3	76.0	0.4	229.6	120.8	1.07	4.3	17.6	13.8	43.0	591.1	278.5
P7 x P10	6.97	74.0	75.2	1.3	244.0	120.3	1.20	4.6	16.1	15.1	40.9	620.2	278.1
P7 x P11	6.41	74.8	75.8	1.3	247.0	119.6	1.13	4.7	16.0	14.2	39.2	559.5	274.2
P7 x P12	5.13	76.6	77.6	0.8	229.0	116.2	1.14	4.3	14.7	13.8	38.9	537.0	248.8
P7 x P13	7.02	74.3	75.8	1.9	239.4	118.0	1.04	4.7	17.8	13.4	38.4	515.8	307.5
P7 x P14	6.26	76.1	77.7	1.5	229.0	119.3	1.23	4.4	17.0	13.9	40.3	557.4	274.0
P7 x P15	6.73	74.6	76.3	1.7	241.4	117.1	1.04	4.7	18.1	14.0	38.2	533.5	309.2
P8 x P9	6.78	74.2	75.2	0.9	231.6	119.8	1.10	4.3	18.3	13.3	42.2	559.3	282.6
P8 x P10	7.53	74.0	75.3	1.1	248.3	131.7	1.26	4.5	15.2	14.4	34.4	501.7	264.1
P8 x P11	6.87	75.2	76.8	1.7	246.6	123.6	1.24	4.6	15.5	14.0	37.3	523.9	293.5
P8 x P12	4.89	76.5	77.2	0.3	227.5	114.5	1.14	4.2	14.8	13.2	38.6	508.8	235.3
P8 x P13	7.05	74.2	75.5	1.2	238.9	118.6	1.08	4.9	18.7	14.1	40.7	571.7	323.8
P8 x P14	6.58	75.9	77.7	2.0	227.9	122.6	1.14	4.4	16.6	14.2	38.3	544.3	267.4
P8 x P15	7.09	73.7	75.3	1.8	240.5	122.7	1.17	4.7	16.5	14.2	36.9	520.6	311.1
P9 x P10	7.66	71.5	71.8	0.7	227.0	114.8	1.08	5.0	17.0	16.4	38.7	634.6	291.3
P9 x P11	7.62	72.6	73.0	0.8	229.6	118.0	1.20	4.7	17.0	15.0	40.3	609.2	292.4
P9 x P12	8.04	73.7	74.0	-0.2	228.2	121.0	1.19	4.8	17.1	14.8	37.8	560.6	291.6
P9 x P13	7.84	72.1	72.6	0.8	231.4	118.4	1.07	4.8	19.8	14.1	41.6	588.7	320.6
P9 x P14	8.72	74.3	75.6	1.2	226.8	119.2	1.21	4.6	17.7	14.4	42.7	618.0	295.0
P9 x P15	6.89	72.1	72.7	0.8	230.2	112.6	1.12	4.7	18.5	14.3	41.7	594.2	311.4
P10 x P11	6.30	72.1	73.7	1.8	223.0	106.8	1.24	4.7	13.0	15.1	36.5	549.0	253.7
P10 x P12	7.42	73.2	73.8	0.8	236.9	117.7	1.37	4.7	14.7	15.0	36.1	540.6	260.5
P10 x P13	6.72	70.6	72.1	2.0	230.8	100.1	1.05	4.9	15.9	15.2	36.2	553.2	312.4
P10 x P14	9.38	74.1	75.1	1.1	242.9	118.0	1.41	4.7	16.3	15.3	40.5	618.7	282.5
P10 x P15	6.70	70.5	71.6	1.3	230.0	105.2	1.15	4.8	15.2	15.7	35.7	559.8	315.9
P11 x P12	7.23	75.0	75.9	1.1	229.9	114.5	1.26	4.7	14.0	14.9	40.9	608.7	283.4
P11 x P13	7.28	72.2	73.4	1.6	232.0	109.3	1.08	4.8	16.5	15.1	39.5	600.3	310.4
P11 x P14	8.80	75.6	77.2	1.6	234.8	114.2	1.36	4.6	15.2	15.5	40.1	620.5	288.3
P11 x P15	6.32	71.2	72.2	1.7	230.7	101.8	1.06	4.7	16.4	14.7	36.4	536.2	300.3
P12 x P13	6.13	73.7	75.0	1.4	225.2	102.9	1.02	5	16.8	14.4	37.4	538.0	290.1
P12 x P14	3.77	78.8	80.9	2.7	196.1	97.0	1.13	4.1	12.5	14.3	34.4	491.7	246.5
P12 x P15	6.91	73.7	74.7	1.4	230.8	111.3	1.17	4.8	17.1	14.7	36.7	543.8	321.4
P13 x P14	8.45	73.6	74.8	1.1	228.7	110.7	1.08	5	16.9	14.9	38.9	584.9	312.1
P13 x P15	6.82	70.8	71.7	1.2	226.2	106.1	1.03	4.9	18.8	14.3	38.9	555.0	350.1
P14 x P15	7.08	73.3	74.7	1.5	235.7	119.3	1.18	4.9	17.3	14.5	38.5	558.6	316.7
mean	6.45	73.8	75.1	1.6	225.6	110.8	1.14	4.6	16.2	14.4	37.9	545.1	291.7
F test	**	**	**	**	**	**	**	**	**	**	**	**	**
LSD	0.70	1.1	1.3	0.9	8.0	7.4	0.10	0.3	1.8	0.8	3.6	64.1	28.2
CV%	16.4	2.3	2.5	66.8	5.4	10.0	12.8	2.9	5.5	4.1	6.7	8.4	6.9
No. of sites	8	9	9	6	9	9	9	1	1	2	2	2	2

** $P \leq 0.05$; CV= coefficient of variation; ASI= anthesis-silking interval; DA= days to anthesis; DS= days to silking; EH= ear height; EPP= ears per plant; ED= ear diameter; EL= ear length; GY= grain yield; KPR= number of kernels per row; KPE= number of kernels per ear; P1= VL052; P2= VL05200; P3= VL05468; P4= VL054178; P5= VL052887; P6= VL05482; P7= VL0523; P8= VL0524; P9= VL05561; P10= VL05483; P11= CML511; P12= CML144; P13= CML159; P14= CML491; P15= VL06375; PH= plant height; RPE= number of rows per ear; TKW= thousand kernel weight

Appendix 4 Mean performance for grain yield and agronomic traits in a diallel crosses among fifteen QPM inbred lines evaluated under stress and optimal conditions

Cross	GY	DA	DS	ASI	PH	EH	SEN	EPP	ED	EL	RPE	KPR	KPE	TKW
P1 x P2	3.1	80.2	84.0	4.9	188.5	96.9	4.5	0.9	4.2	11.7	13.2	25.2	341.3	233.1
P1 x P3	3.9	81.4	85.4	5.5	201.5	101.0	5.5	0.9	4.5	13.4	13.5	28.4	417.7	236.7
P1 x P4	5.5	74.5	75.8	1.7	207.2	99.5	5.2	1.0	4.5	14.7	13.0	31.4	408.4	311.9
P1 x P5	3.1	82.0	86.3	5.8	203.1	105.5	5.2	0.9	4.0	11.8	13.8	25.4	350.4	202.5
P1 x P6	5.3	74.2	76.9	2.8	213.9	103.7	4.9	1.1	4.4	14.2	13.6	31.4	426.7	248.3
P1 x P7	4.0	80.7	84.3	4.6	209.4	111.8	4.3	0.9	4.2	12.7	13.0	29.4	385.9	236.9
P1 x P8	4.0	80.2	84.0	4.7	209.8	112.4	4.8	1.0	4.1	13.7	12.9	28.8	381.1	238.2
P1 x P9	6.2	77.4	78.9	1.1	215.6	116.9	4.2	1.0	4.6	16.0	13.8	33.5	473.9	269.2
P1 x P10	5.5	76.4	77.5	1.9	226.9	112.0	4.6	1.1	4.5	12.3	14.4	28.7	409.2	260.2
P1 x P11	5.7	78.3	81.7	4.6	227.4	111.2	4.7	1.1	4.5	13.8	14.1	31.7	461.1	239.9
P1 x P12	2.3	82.4	86.6	5.6	189.4	94.4	5.2	0.9	3.8	10.7	13.5	24.9	343.2	188.3
P1 x P13	5.4	77.3	80.4	3.5	212.9	100.0	5.5	0.9	4.7	15.4	14.7	31.4	462.5	285.1
P1 x P14	3.6	81.8	85.5	4.9	200.0	103.7	4.5	1.0	4.1	12.6	13.7	28.0	392.0	210.8
P1 x P15	5.5	76.0	79.2	3.5	221.3	110.5	4.9	1.0	4.6	15.6	14.0	30.5	430.2	279.8
P2 x P3	3.5	81.0	85.1	6.0	185.7	94.5	5.2	0.8	4.5	13.4	14.6	27.0	419.4	243.8
P2 x P4	5.7	74.0	76.0	2.8	196.3	97.0	5.3	1.0	4.5	15.7	13.7	30.7	423.4	301.7
P2 x P5	3.6	83.2	85.7	3.5	189.0	96.7	4.4	1.0	4.0	11.3	13.8	25.6	358.8	219.5
P2 x P6	5.5	73.8	76.5	3.8	196.5	97.2	4.4	1.0	4.3	14.3	13.5	30.5	417.1	256.9
P2 x P7	4.2	81.2	84.5	3.9	199.5	105.1	4.0	0.9	4.2	12.0	13.4	27.3	372.8	269.8
P2 x P8	4.3	81.3	85.0	4.9	202.4	106.9	5.0	0.9	4.2	12.3	13.3	27.2	368.0	262.7
P2 x P9	6.3	77.3	79.6	3.1	200.7	102.3	5.1	1.0	4.7	16.2	14.4	34.4	498.0	296.4
P2 x P10	5.1	77.1	79.4	3.0	214.5	98.8	4.6	1.0	4.5	13.1	15.1	30.6	463.1	256.5
P2 x P11	5.9	78.3	79.8	1.9	210.7	102.9	4.0	1.0	4.6	14.4	14.7	30.0	444.0	272.4
P2 x P12	2.6	83.2	86.7	4.0	177.2	87.1	4.4	0.9	4.0	10.6	13.9	25.9	363.2	212.7
P2 x P13	5.7	75.9	78.1	3.0	208.4	98.9	4.4	0.9	4.6	14.5	15.2	29.5	460.1	293.9
P2 x P14	3.8	82.3	85.1	4.2	188.4	91.8	4.0	1.0	4.3	13.0	14.3	27.7	405.5	233.5
P2 x P15	5.7	75.1	77.7	3.7	210.6	104.7	4.5	1.0	4.6	14.7	14.6	29.1	429.2	313.0
P3 x P4	5.6	75.9	79.3	4.1	211.3	103.1	4.7	1.0	4.3	17.0	13.8	34.5	483.5	284.3
P3 x P5	3.9	83.7	87.4	5.0	207.3	107.1	4.8	1.0	4.0	13.4	13.7	29.1	419.5	204.9
P3 x P6	5.0	75.4	79.1	4.7	203.0	99.5	4.9	1.0	4.1	14.7	13.6	30.5	419.0	236.1
P3 x P7	4.0	81.7	86.3	6.6	207.8	112.0	4.3	0.8	4.4	14.8	13.4	31.0	442.0	233.0
P3 x P8	4.1	82.4	87.2	6.4	214.4	117.3	4.9	0.9	4.4	14.1	13.3	30.2	431.8	230.2
P3 x P9	5.8	79.2	82.1	3.8	215.0	117.6	4.2	0.9	4.5	17.2	14.0	35.7	520.8	241.3
P3 x P10	5.3	76.7	80.4	4.8	219.5	111.0	5.2	1.0	4.5	12.8	15.8	31.5	502.9	229.6
P3 x P11	5.4	77.5	80.9	3.8	217.6	105.6	5.0	1.0	4.3	13.4	15.8	33.8	536.0	229.1
P3 x P12	3.3	82.1	85.6	4.8	188.4	91.9	4.7	0.9	4.2	12.1	14.7	31.4	466.4	211.2
P3 x P13	5.2	78.4	82.3	5.4	213.9	98.9	4.7	0.9	4.7	15.3	15.6	32.6	513.1	276.1
P3 x P14	4.3	81.8	86.6	6.3	203.2	101.3	5.0	1.0	4.1	14.0	14.8	34.3	505.0	209.1
P3 x P15	5.3	77.2	80.8	4.8	215.1	108.1	4.3	0.9	4.5	15.9	15.1	32.0	487.3	270.2
P4 x P5	5.5	77.0	78.9	2.0	212.5	104.1	5.0	1.0	4.2	14.7	13.1	32.4	427.4	264.6
P4 x P6	4.7	70.4	72.3	2.3	201.7	97.5	5.6	1.1	3.9	15.5	12.4	32.8	403.1	241.6
P4 x P7	5.5	76.0	78.3	2.9	219.4	113.2	4.8	0.9	4.3	16.7	12.5	37.0	465.1	288.6
P4 x P8	5.7	75.7	78.6	3.4	216.4	114.2	4.6	0.9	4.4	16.6	11.8	33.4	426.5	295.7
P4 x P9	5.7	74.1	75.3	0.7	201.9	106.4	4.5	0.9	4.2	17.3	12.9	34.4	450.3	278.0
P4 x P10	5.1	72.5	74.5	2.8	209.9	100.5	5.4	1.0	4.2	12.4	13.3	28.8	385.9	254.7
P4 x P11	5.6	74.4	76.3	2.5	219.8	108.3	5.4	1.0	4.4	14.9	13.2	35.6	471.5	278.4
P4 x P12	5.7	75.2	77.8	3.5	207.0	99.4	5.0	0.9	4.6	15.9	13.2	31.8	429.1	298.1
P4 x P13	3.3	76.2	79.2	3.7	194.3	90.3	6.2	0.9	3.7	11.9	13.1	27.5	360.4	232.4
P4 x P14	6.4	76.7	79.3	3.1	208.2	104.9	4.4	1.0	4.4	16.9	13.5	35.0	472.1	297.5
P4 x P15	5.4	73.2	74.8	2.0	216.3	104.5	5.5	1.0	4.5	15.8	13.3	30.2	405.0	290.4
P5 x P6	5.3	76.7	79.6	3.9	218.6	106.7	5.0	1.2	3.9	13.8	13.1	31.3	409.1	230.8
P5 x P7	4.2	82.5	85.5	4.3	213.3	111.6	4.3	1.0	4.1	12.1	13.3	29.3	386.9	215.8
P5 x P8	4.3	81.7	84.6	3.8	214.7	111.1	4.4	1.1	4.0	12.3	13.5	29.5	400.3	229.6
P5 x P9	6.1	80.7	82.6	2.7	221.9	120.4	4.6	1.1	4.2	14.3	13.6	33.8	461.9	244.2
P5 x P10	5.8	79.1	82.1	4.2	230.2	116.3	4.7	1.2	4.2	12.6	14.0	28.9	408.4	231.3
P5 x P11	5.9	80.5	82.5	2.5	227.9	118.4	4.0	1.2	4.3	13.1	14.2	32.2	459.9	234.7
P5 x P12	2.7	83.4	86.6	4.3	190.1	98.7	4.3	0.9	4.0	10.1	14.0	27.1	382.1	171.8
P5 x P13	5.5	79.8	83.1	3.9	227.3	103.6	4.7	1.0	4.6	14.1	14.4	30.5	445.8	265.5
P5 x P14	4.7	81.9	85.4	4.4	212.0	113.9	4.4	1.1	4.0	12.4	14.7	32.6	481.3	214.7

Appendix 4 Continued

Cross	GY	DA	DS	ASI	PH	EH	SEN	EPP	ED	EL	RPE	KPR	KPE	TKW
P5 x P15	5.8	78.5	80.7	2.2	223.8	111.7	4.3	1.1	4.5	16.2	13.7	35.7	499.1	261.6
P6 x P7	5.5	76.7	79.9	4.7	215.4	114.5	4.5	1.0	3.9	14.2	14.0	35.0	487.8	227.6
P6 x P8	4.9	76.3	79.0	3.4	212.0	109.7	4.5	1.1	4.2	15.0	12.7	34.8	447.0	231.7
P6 x P9	5.9	72.4	73.8	1.5	211.2	109.7	4.9	1.1	4.4	16.3	13.4	34.8	479.5	250.3
P6 x P10	4.8	71.1	72.9	2.3	202.4	93.1	4.1	1.1	4.1	12.5	13.5	31.9	433.5	229.2
P6 x P11	5.4	72.3	73.9	2.2	206.4	99.5	5.2	1.1	4.2	13.5	13.9	34.4	479.4	226.1
P6 x P12	5.0	75.7	78.7	4.0	208.1	101.0	4.1	1.2	4.1	13.8	13.5	31.9	434.7	220.2
P6 x P13	5.0	73.1	75.7	3.2	205.3	93.2	4.2	1.0	4.2	14.4	13.3	31.2	415.5	269.3
P6 x P14	5.8	75.1	78.0	3.4	212.1	107.9	4.5	1.2	4.2	14.4	13.6	29.7	407.3	248.1
P6 x P15	5.0	71.8	73.8	2.3	206.0	98.9	4.6	1.1	4.4	15.2	13.2	29.4	392.8	262.3
P7 x P8	1.4	84.3	89.4	7.5	175.9	95.0	4.7	0.7	3.6	8.2	12.1	21.6	263.9	225.0
P7 x P9	4.9	80.1	82.8	3.2	211.2	114.4	3.8	0.9	4.2	16.1	13.0	35.6	470.1	245.4
P7 x P10	5.4	78.2	81.1	3.9	229.8	116.7	4.3	1.0	4.4	13.8	15.0	34.8	521.7	237.5
P7 x P11	4.9	78.6	81.7	4.1	230.3	115.3	4.2	1.0	4.4	13.7	13.8	31.7	445.5	245.3
P7 x P12	3.8	81.5	84.9	4.1	210.7	109.7	4.2	0.9	4.2	12.9	13.6	30.4	414.2	215.8
P7 x P13	5.5	78.6	82.0	4.6	223.3	112.9	4.4	1.0	4.5	15.6	13.3	30.7	409.8	271.6
P7 x P14	5.0	80.6	83.7	4.0	214.2	115.1	4.1	1.1	4.3	15.1	13.5	32.5	440.9	249.3
P7 x P15	5.3	78.6	82.2	4.5	227.9	112.7	5.2	0.9	4.5	16.3	13.4	33.4	457.1	269.5
P8 x P9	5.2	78.6	81.2	3.6	215.4	115.4	4.5	0.9	4.0	15.3	13.0	36.3	474.0	237.7
P8 x P10	5.8	77.5	80.0	3.0	232.0	127.9	4.6	1.1	4.3	13.7	14.4	30.8	446.4	231.0
P8 x P11	5.2	78.8	82.8	4.5	230.4	117.6	4.2	1.0	4.3	13.8	12.9	31.3	416.9	251.9
P8 x P12	3.7	81.1	84.3	4.1	211.7	109.2	5.1	0.9	4.1	13.7	13.4	31.5	419.3	209.1
P8 x P13	5.7	78.0	81.1	4.1	224.3	113.6	4.4	0.9	4.7	16.7	13.7	34.0	470.0	282.9
P8 x P14	5.1	80.5	84.2	4.7	210.5	116.4	4.3	1.0	4.2	14.5	13.6	32.1	445.0	227.9
P8 x P15	5.7	77.9	81.2	4.4	226.0	117.6	4.5	1.0	4.5	15.2	13.6	32.1	438.2	278.7
P9 x P10	6.1	75.0	75.9	1.5	213.4	109.7	5.1	1.0	4.7	14.2	15.8	34.1	541.6	245.4
P9 x P11	6.0	75.9	77.8	2.5	212.3	111.4	4.9	1.1	4.3	14.2	14.2	33.3	479.4	234.8
P9 x P12	6.3	78.2	79.9	1.9	214.1	116.2	4.0	1.0	4.5	15.7	13.5	30.6	431.8	270.3
P9 x P13	6.4	75.7	76.7	1.1	217.5	113.8	4.4	1.0	4.6	15.9	13.7	33.4	466.5	275.9
P9 x P14	6.9	78.5	81.2	3.2	214.1	116.0	4.6	1.1	4.4	16.9	14.4	35.3	509.0	253.2
P9 x P15	5.6	75.5	77.1	2.2	220.1	110.8	4.6	1.0	4.4	15.9	14.3	35.8	508.9	266.8
P10 x P11	4.9	75.3	77.7	3.1	210.2	102.4	4.1	1.1	4.4	11.4	14.9	30.5	455.2	222.9
P10 x P12	5.8	77.1	79.1	2.7	222.1	113.8	5.0	1.2	4.5	12.9	14.3	30.1	433.2	231.4
P10 x P13	5.4	74.0	76.2	2.6	219.0	96.2	5.4	1.0	4.7	13.5	15.1	29.8	451.7	266.3
P10 x P14	7.2	78.1	80.1	2.7	227.1	111.2	4.3	1.2	4.5	13.5	15.1	32.3	488.3	243.6
P10 x P15	5.4	73.8	75.2	1.6	217.3	101.0	5.1	1.1	4.5	13.8	15.7	30.3	470.9	256.0
P11 x P12	5.6	78.7	81.4	3.3	217.5	110.8	4.5	1.1	4.5	12.9	14.7	34.3	504.9	241.2
P11 x P13	5.9	75.5	77.8	2.5	216.3	104.5	4.8	1.0	4.6	14.0	14.8	31.3	468.4	266.6
P11 x P14	6.6	79.7	83.4	4.3	218.2	110.8	4.0	1.2	4.4	13.3	15.0	32.8	491.7	247.8
P11 x P15	5.1	74.7	77.0	3.2	215.3	97.6	4.2	1.0	4.6	15.3	14.6	32.6	477.2	254.2
P12 x P13	4.8	78.6	81.7	4.0	212.7	98.7	4.7	0.9	4.6	14.4	14.7	31.8	465.2	248.6
P12 x P14	2.9	84.2	88.2	5.5	181.3	90.9	4.4	1.0	4.0	11.8	14.1	28.7	406.7	202.0
P12 x P15	5.4	77.7	80.4	3.9	217.4	107.4	4.6	1.0	4.5	15.0	14.3	31.6	456.7	261.8
P13 x P14	6.6	77.7	80.1	3.0	215.7	107.0	4.2	1.0	4.8	14.4	14.2	32.1	472.7	268.8
P13 x P15	5.5	74.5	75.7	1.6	217.6	102.2	4.5	1.0	4.6	15.9	13.7	30.8	431.3	304.2
P14 x P15	5.8	77.3	79.4	2.5	222.9	114.1	4.0	1.1	4.7	15.4	14.1	31.5	445.4	275.7
mean	5.1	77.8	80.6	3.6	211.6	106.5	4.6	1.0	4.3	14.2	13.9	31.4	442.0	252.0
F test	**	**	**	**	**	**	ns	**	**	**	**	**	**	**
LSD	0.5	1.0	1.5	1.6	7.1	6.7	-	0.1	0.2	1.6	0.9	3.2	54.3	21.8
CV%	13.4	1.7	2.4	44.9	4.2	7.4	12.0	10.0	3.5	7.8	6.3	10.3	12.4	8.7
No. of location	13	13	13	8	12	11	3	13	2	2	4	4	4	4

** $P \leq 0.05$; ASI= anthesis-silking interval; CV= coefficient of variation; DA= days to anthesis; DS= days to silking; ED= ear diameter; EH= ear height; EL= ear length; EPP= ears per plant; GY= grain yield; KPE= kernels per ear; KPR= kernels per row; ns= non-significant; P1= VL052; P2= VL05200; P3= VL05468; P4= VL054178; P5= VL052887; P6= VL05482; P7= VL0523; P8= VL0524; P9= VL05561; P10= VL05483; P11= CML511; P12= CML144; P13= CML159; P14= CML491; P15= VL06375; PH= plant height; RPE= rows per ear; SEN= leaf senescence; TKW= thousand kernel weight

Appendix 5 Estimates of specific combining ability (SCA) effects for various agronomic traits of diallel crosses among fifteen QPM inbred lines evaluated across stress and optimal environments

Cross	GY	DA	DS	PH	EH	EPP	ED	EL	KPR	KPE	TKW
P1 x P2	-0.94**	0.34	0.98*	-5.73*	-0.19	-0.01	-0.18*	-0.91	-0.98	-31.6	-24.99*
P1 x P3	-0.06	0.72*	0.41	-3.13	-2.94	0.00	0.14*	-0.31	-0.96	-16.78	4.01
P1 x P4	0.73**	-0.96**	-2.08**	1.17	-2.39	0.02	0.21**	-0.12	1.00	16.44	34.42**
P1 x P5	-1.02**	0.08	1.07*	-8.28**	-2.76	-0.11**	-0.13	-0.42	-2.53	-32.27	-19.1
P1 x P6	0.62**	-0.36	-0.57	8.60**	2.58	0.03	0.25**	0.47	1.46	31.6	12.31
P1 x P7	0.11	-0.39	-0.53	-1.73	0.87	0.04	-0.02	-0.45	0.22	-2.37	-3.13
P1 x P8	-0.02	-0.52	-0.52	-1.93	-0.37	0.04	-0.11	0.49	0.09	3.24	-1.93
P1 x P9	0.79**	-0.53	-1.19*	4.72*	4.34*	-0.01	0.19*	0.75	1.14	23.94	15.49
P1 x P10	0.54**	-0.28	-1.58**	9.13**	4.85*	0.03	0.06	0.05	0.02	-13.55	22.90*
P1 x P11	0.70**	0.36	0.89	10.76**	3.61	0.07*	0.08	0.85	1.30	24.57	-1.23
P1 x P12	-1.31**	1.35**	2.13**	-10.92**	-6.46**	-0.08**	-0.45**	-1.55**	-2.92	-44.07	-32.61**
P1 x P13	0.57**	-0.25	-0.12	0.18	-1.23	0.01	0.14*	1.35**	2.46	48.9	16.14
P1 x P14	-1.13**	0.95**	1.12*	-6.45**	-2.99	-0.06*	-0.21**	-0.85	-1.56	-26.98	-25.46*
P1 x P15	0.57**	-0.66	-0.20	4.84*	4.08	0.05	0.06	0.76	0.91	13.81	7.99
P2 x P3	-0.66**	0.18	0.36	-6.77**	-1.84	-0.08**	0.10	-0.2	-1.74	-21.25	-6.19
P2 x P4	0.79**	-1.46**	-1.71**	2.47	2.66	0.10**	0.17*	0.99	0.92	25.26	6.91
P2 x P5	-0.69**	1.13**	0.79	-10.19**	-3.97	-0.03	-0.17*	-0.81	-1.71	-30.05	-19.41
P2 x P6	0.74**	-0.85*	-0.69	3.39	3.74	-0.01	0.11	0.68	1.17	15.82	3.61
P2 x P7	0.15	0.04	-0.14	0.58	1.75	-0.01	-0.06	-1.04*	-1.27	-21.65	12.46
P2 x P8	0.12	0.54	0.69	2.92	1.74	0.02	-0.04	-0.81	-0.9	-16.04	5.27
P2 x P9	0.77**	-0.72*	-0.23	2.01	-2.65	0.04	0.25**	1.06*	2.66	41.86	25.38*
P2 x P10	0.02	0.33	0.58	8.93**	-0.75	0.00	0.02	0.96	2.54	34.17	1.89
P2 x P11	0.72**	0.32	-0.78	6.19**	2.94	0.01	0.14*	1.55**	0.22	1.29	13.97
P2 x P12	-1.12**	2.03**	2.52**	-10.91**	-6.17**	-0.07**	-0.29**	-1.54**	-1.31	-30.25	-25.52*
P2 x P13	0.73**	-1.73**	-2.15**	7.88**	5.23*	0.06*	0.00	0.55	1.17	40.32	7.63
P2 x P14	-1.13**	1.36**	1.00*	-5.85*	-7.29**	-0.04	-0.05	-0.35	-1.24	-19.65	-20.06*
P2 x P15	0.66**	-1.64**	-1.42**	6.32**	5.81**	0.03	0.02	-0.03	0.12	6.63	23.88*
P3 x P4	0.70**	-0.41	-0.33	7.02**	2.02	0.07**	-0.01	1.19*	1.54	23.79	14.92
P3 x P5	-0.30	0.81*	0.53	-2.33	-0.41	0.03	-0.15*	0.19	-1.39	-30.92	-8.6
P3 x P6	0.26	-0.08	-0.05	-0.48	-0.77	-0.01	-0.08	-0.02	-2.01	-43.85	8.21
P3 x P7	0.03	-0.28	-0.18	-1.50	1.89	0.00	0.16*	0.66	-0.74	-14.02	1.07
P3 x P8	-0.04	0.81*	0.97*	4.49	5.31*	0.00	0.17*	-0.11	-1.08	-13.81	-1.83
P3 x P9	0.24	0.37	0.32	5.93*	5.88**	0.02	0.06	0.96	0.78	3.09	-4.31
P3 x P10	0.22	-0.83*	-0.39	3.55	4.73*	-0.01	0.04	-0.44	0.26	12.39	0.40
P3 x P11	0.23	-1.28**	-1.67**	2.72	-1.15	-0.02	-0.14*	-0.55	0.84	31.72	-3.93
P3 x P12	-0.43*	0.12	-0.58	-10.15**	-8.11**	-0.01	-0.08	-1.14*	1.02	11.38	-1.61
P3 x P13	0.25	-0.01	0.12	2.97	-1.51	0.01	0.12	0.25	1.09	31.75	15.24
P3 x P14	-0.59**	0.05	0.57	-1.54	-4.56*	0.00	-0.24**	-0.45	2.18	18.27	-19.06
P3 x P15	0.31	-0.30	-0.25	0.46	2.45	0.00	-0.07	0.07	-0.15	3.15	6.49
P4 x P5	0.41*	-0.56	-0.92	1.44	-1.37	-0.02	0.12	0.37	0.87	19.49	6.31
P4 x P6	-0.88**	0.15	0.24	-3.22	-0.80	-0.01	-0.21**	-0.34	-0.74	-17.24	-31.08**
P4 x P7	0.67**	-0.65	-1.17*	8.62**	5.05*	0.05	0.12	1.45**	4.22**	51.59**	11.87
P4 x P8	0.75**	-0.59	-0.50	5.02*	4.23	-0.04	0.24**	1.28*	1.09	23.4	18.88
P4 x P9	-0.66**	0.57	0.58	-8.55**	-3.27	-0.05	-0.17*	-0.05	-1.56	-24.9	-12.4
P4 x P10	-0.86**	0.24	0.79	-7.51**	-3.85	-0.04	-0.19**	-1.95**	-3.48*	-62.09**	-19.29
P4 x P11	-0.39*	0.80*	0.83	3.50	3.57	-0.02	0.02	-0.16	1.60	9.73	0.58
P4 x P12	1.09**	-1.47**	-1.23*	7.01**	1.37	-0.01	0.39**	1.55**	0.38	16.59	40.50**
P4 x P13	-2.47**	3.05**	4.14**	-18.00**	-8.14**	-0.06*	-0.81**	-4.26**	-5.04**	-78.44**	-73.26**
P4 x P14	0.71**	0.23	0.35	2.10	1.05	0.01	0.13	1.34**	1.84	27.89	24.55*
P4 x P15	-0.43*	0.93**	0.83	0.17	0.86	0.02	0.00	-1.15*	-2.99*	-36.63	-18.10
P5 x P6	0.42*	-0.04	0.28	8.33**	2.05	0.09**	-0.04	0.56	0.22	-1.95	14.00
P5 x P7	0.01	-0.76*	-1.22*	-2.78	-2.86	0.05	0.09	-0.55	-1.01	-17.31	-5.05
P5 x P8	0.04	-1.11**	-1.79**	-2.03	-5.32*	0.04	0.00	-0.42	-0.34	6.49	8.66
P5 x P9	0.40*	0.61	0.62	6.09**	4.27	0.06*	-0.01	-0.45	0.31	-4.01	9.67
P5 x P10	0.55**	0.24	1.13*	7.46**	5.64*	0.06*	-0.03	0.85	-0.91	-30.30	13.18
P5 x P11	0.68**	0.45	-0.27	6.22**	7.31**	0.07**	0.09	0.64	0.67	7.42	12.76
P5 x P12	-1.14**	0.22	0.20	-15.19**	-5.69**	-0.12**	-0.04	-1.65**	-1.85	-21.11	-29.93**
P5 x P13	0.42*	0.07	0.73	9.61**	-1.22	-0.02	0.25**	0.54	0.42	16.25	15.72
P5 x P14	-0.32	-1.02**	-0.82	0.52	3.59	-0.07**	-0.11	-0.56	1.91	46.38	-2.37
P5 x P15	0.69**	-0.25	-0.52	2.36	1.74	0.00	0.16*	1.85**	4.98**	66.76**	8.97
P6 x P7	0.81**	0.82*	0.95	5.36*	7.23**	-0.04	-0.14	0.04	2.67	71.15**	-7.63
P6 x P8	0.08	0.87*	0.35	1.35	0.52	0.02	0.18*	0.77	2.94	40.76	-3.63
P6 x P9	-0.30	-0.36	-0.42	1.46	0.77	-0.02	0.17*	0.04	-0.71	1.16	1.39

Appendix 5 Continued

Cross	GY	DA	DS	PH	EH	EPP	ED	EL	KPR	KPE	TKW
P6 x P10	-0.93**	-0.29	-0.34	-14.28**	-10.38**	-0.06*	-0.15*	-0.76	0.08	-17.63	-3.3
P6 x P11	-0.39*	-0.45	-1.03*	-9.16**	-4.37*	-0.04	-0.04	-0.47	0.86	14.49	-10.23
P6 x P12	0.64**	-0.16	0.08	8.88**	3.79	0.11**	0.03	0.54	0.93	19.05	4.09
P6 x P13	-0.62**	0.77*	1.10*	-6.26**	-4.36*	-0.00	-0.18*	-0.67	-0.89	-26.48	5.14
P6 x P14	0.34*	-0.54	-0.44	6.67**	4.88*	0.05	0.07	-0.07	-3.01*	-40.05	16.64
P6 x P15	-0.64**	0.40	0.37	-9.43**	-3.88	-0.04	0.04	-0.65	-3.34*	-51.97**	-4.71
P7 x P8	-2.67**	2.33**	3.28**	-40.56**	-24.03**	-0.22**	0.07	1.03*	-9.50**	19.16	-1.56
P7 x P9	-0.55**	0.89**	1.12*	-4.33	-4.35*	-0.02	-0.49**	-5.45**	0.86	-135.51**	-14.37
P7 x P10	0.38*	0.34	0.46	7.37**	3.41	0.01	-0.10	0.42	3.74*	-1.41	-7.56
P7 x P11	-0.10	-0.62	-0.68	8.88**	1.53	-0.02	0.08	1.12*	-1.08	77.40**	0.95
P7 x P12	0.14	-0.80*	-1.13*	5.63*	2.63	0.02	0.09	0.32	0.19	-12.58	4.93
P7 x P13	0.59**	-0.21	-0.05	5.92*	5.51*	0.08**	0.06	0.22	-0.63	5.39	-4.36
P7 x P14	0.22	-1.52**	-2.21**	3.01	2.26	0.10**	0.06	1.12*	0.56	-25.35	3.39
P7 x P15	0.37*	0.68*	1.31**	6.75**	0.10	-0.03	0.10	1.22*	1.42	0.38	13.8
P8 x P9	-0.34	-0.26	-0.13	-0.72	-5.21*	-0.03	-0.28**	-0.45	2.02	12.9	-15.35
P8 x P10	0.68**	-0.04	-0.40	8.92**	12.71**	0.08**	-0.01	0.95	0.21	12.51	-5.64
P8 x P11	0.09	0.02	0.67	8.42**	1.99	0.02	0.01	0.35	-1.01	-30.77	11.44
P8 x P12	-0.07	-0.86*	-1.41**	6.13**	0.27	0.01	-0.02	0.95	1.76	20.89	-11.15
P8 x P13	0.67**	-0.44	-0.60	6.29**	4.37*	0.02	0.27**	2.15**	3.14*	45.26	0.00
P8 x P14	0.17	-1.22**	-1.38**	-1.34	1.63	0.01	0.02	0.55	0.62	14.89	-7.69
P8 x P15	0.70**	0.35	0.59	4.26	3.14	0.06*	0.09	-0.14	0.59	10.67	7.55
P9 x P10	-0.42*	0.25	0.00	-8.76**	-5.23*	-0.11**	0.19*	-0.58	-0.14	35.61	-4.83
P9 x P11	-0.59**	-0.19	0.17	-8.76**	-3.98	0.00	-0.20**	-1.28*	-2.66	-40.37	-19.25
P9 x P12	1.13**	-0.99**	-1.42**	9.35**	7.52**	0.06*	0.17*	0.92	-2.78	-38.71	36.47**
P9 x P13	-0.02	0.05	-0.60	0.41	4.81*	0.04	-0.04	-0.68	-1.11	-30.34	-5.99
P9 x P14	0.57**	-0.50	0.05	3.18	1.51	0.00	0.01	0.92	0.18	6.79	4.02
P9 x P15	-0.86**	0.69*	0.96	-0.81	-3.41	0.01	-0.22**	-1.47**	0.65	9.27	-17.93
P10 x P11	-1.23**	0.46	0.98*	-17.78**	-7.52**	-0.05	-0.12	-1.08*	-1.78	-37.36	-14.74
P10 x P12	1.10**	-0.81*	-1.22*	10.44**	10.50**	0.11**	0.15*	1.12*	0.4	-10.1	13.97
P10 x P13	-0.60**	-0.36	-0.14	-5.01*	-7.38**	-0.06*	0.04	-0.08	-1.02	-17.93	0.82
P10 x P14	1.32**	0.38	-0.09	9.28**	2.14	0.07**	0.09	0.52	0.86	13.29	10.83
P10 x P15	-0.63**	0.25	0.03	-10.52**	-7.87**	-0.02	-0.14*	-0.57	-1.17	-1.52	-12.33
P11 x P12	0.79**	-0.51	-0.65	6.92**	7.10**	0.05*	0.16*	0.42	2.88	47.82	19.95
P11 x P13	-0.10	-0.14	-0.24	-6.68**	0.45	-0.02	-0.04	-0.29	-1.24	-15.01	-2.70
P11 x P14	0.71**	0.77*	1.48**	1.41	1.22	0.06*	0.00	-0.39	-0.36	2.92	11.21
P11 x P15	-0.97**	-0.11	0.11	-11.40**	-11.71**	-0.11**	-0.03	0.22	-0.59	-9.00	-17.95
P12 x P13	0.17	-0.16	0.02	6.08**	1.36	-0.01	0.12	0.82	1.83	31.05	-0.49
P12 x P14	-1.59**	2.13**	2.65**	-19.07**	-11.90**	-0.06*	-0.23**	-1.18*	-1.88	-32.82	-14.38
P12 x P15	-0.37*	0.76*	1.27**	-2.21	-2.66	-0.03	-0.13	-0.28	3.74*	58.10**	-26.26*
P13 x P14	0.89**	-0.86*	-1.51**	2.99	3.83	-0.04	0.26**	-0.39	0.39	6.85	4.37
P13 x P15	-0.34	0.10	-0.88	-5.15*	-0.73	0.02	-0.17*	-0.28	-0.94	-31.97	4.21
P14 x P15	-0.03	-0.34	-0.96*	6.34**	5.63*	0.00	0.18*	-0.18	-0.85	-23.25	8.42
$SE(S_{ij})$	0.17	0.34	0.49	2.35	2.20	0.03	0.07	0.51	1.45	25.27	10.17

** $P \leq 0.05$; * $P \leq 0.01$; DA= days to anthesis; DS= days to silking; ED= ear diameter; EH= ear height; EL= ear length; EPP= ears per plant; GY= grain yield; KPE= kernels per ear; KPR= kernels per row; P1= VL052; P2= VL05200; P3= VL05468; P4= VL054178; P5= VL052887; P6= VL05482; P7= VL0523; P8= VL0524; P9= VL05561; P10= VL05483; P11= CML511; P12= CML144; P13= CML159; P14= CML491; P15= VL06375; PH= plant height; $SE(S_{ij})$= standard error of SCA; TKW= thousand kernel weight

Appendix 6 Percentage mid-parent heterosis of diallel crosses among fifteen QPM inbred lines evaluated at Harare and Bako under optimum N conditions

Cross	DA	DS	PH	EH	EPP	ED	EL	RPE	KPR	KPE	TKW
P1 x P2	-9.4	-9.8	44.9	71.6	14.6	9.0	12.0	-0.1	25.3	25.6	6.4
P1 x P3	-9.6	-10.1	30.8	42.9	24.5	17.8	31.0	4.2	40.9	45.8	26.6
P1 x P4	-12.9	-15.0	43.8	54.2	14.3	31.3	36.2	7.4	59.8	69.5	43.9
P1 x P5	-6.5	-9.0	35.2	48.9	12.0	6.7	15.1	6.5	44.6	51.1	1.6
P1 x P6	-14.3	-15.0	53.2	64.3	15.8	18.6	23.3	10.0	36.6	51.0	36.7
P1 x P7	-10.2	-9.9	34.9	50.4	14.1	15.7	26.3	3.7	46.3	51.7	16.3
P1 x P8	-10.6	-10.8	37.6	42.4	39.8	10.4	25.1	7.8	43.3	55.7	15.0
P1 x P9	-12.1	-11.9	58.4	75.1	9.1	26.4	41.2	7.8	52.4	64.5	38.9
P1 x P10	-12.2	-13.1	44.8	39.9	20.2	14.7	22.0	-2.2	32.4	29.4	31.0
P1 x P11	-8.1	-7.9	40.5	54.5	33.8	17.0	40.2	9.0	52.1	67.0	28.4
P1 x P12	-6.9	-7.0	29.6	48.2	-0.4	-1.1	-1.9	-0.2	22.6	22.0	8.4
P1 x P13	-10.4	-10.9	47.0	57.9	27.7	16.7	34.8	7.9	51.1	63.4	34.0
P1 x P14	-10.7	-11.6	26.1	43.6	10.0	10.2	8.8	2.6	32.1	35.6	-3.6
P1 x P15	-13.1	-14.1	36.1	51.7	11.3	31.5	31.6	10.4	36.6	49.1	28.2
P2 x P3	-7.2	-8.7	43.7	59.9	2.4	12.0	34.1	3.3	33.4	37.0	23.8
P2 x P4	-10.2	-11.5	61.5	65.7	-7.0	26.7	49.1	11.5	52.4	68.5	32.1
P2 x P5	-3.6	-5.4	47.0	51.8	5.1	6.4	15.2	5.2	54.7	60.2	3.2
P2 x P6	-11.0	-12.0	68.7	87.3	-4.2	15.4	39.4	9.7	47.8	63.7	21.4
P2 x P7	-8.0	-9.3	53.1	66.4	-3.0	14.0	27.3	6.4	35.5	45.4	28.8
P2 x P8	-6.7	-8.6	54.1	52.5	50.0	13.1	26.8	4.3	43.3	50.9	18.8
P2 x P9	-9.0	-11.1	68.0	73.3	-0.2	27.8	53.8	3.7	64.3	70.7	38.5
P2 x P10	-6.8	-8.0	55.9	59.6	5.2	15.5	39.7	1.8	55.2	57.9	23.4
P2 x P11	-5.9	-6.2	51.2	67.0	22.2	14.4	51.7	4.7	47.3	54.9	29.5
P2 x P12	-3.1	-3.2	35.6	49.3	-3.0	2.1	11.8	-1.2	31.4	29.9	11.3
P2 x P13	-9.0	-9.8	62.4	68.5	5.4	17.0	34.7	13.9	58.2	81.4	23.3
P2 x P14	-6.1	-9.7	67.8	54.2	8.0	10.9	19.2	3.6	31.2	36.1	7.0
P2 x P15	-11.1	-12.6	44.7	57.7	2.0	21.9	24.8	10.5	34.8	48.0	26.6
P3 x P4	-9.7	-11.9	57.4	66.4	2.8	25.7	54.5	4.4	63.4	65.8	66.6
P3 x P5	-2.9	-4.7	42.1	50.7	32.8	5.2	33.3	4.8	58.4	61.2	22.6
P3 x P6	-11.3	-11.7	55.8	66.1	7.7	15.8	37.1	5.0	31.0	36.7	61.1
P3 x P7	-7.6	-7.3	50.1	63.7	5.3	16.9	38.9	2.5	46.5	50.0	41.5
P3 x P8	-6.9	-7.8	52.0	66.0	22.7	15.1	41.0	6.6	49.6	58.3	34.9
P3 x P9	-7.4	-7.8	62.5	88.8	5.1	26.1	54.1	2.0	58.4	61.9	55.5
P3 x P10	-8.9	-9.0	40.4	43.8	12.1	15.6	32.1	3.7	47.3	52.7	50.2
P3 x P11	-7.7	-7.5	38.8	46.1	13.7	14.2	35.2	8.1	46.2	58.0	47.9
P3 x P12	-4.4	-5.8	45.7	57.1	-4.6	10.6	25.6	0.1	45.9	45.6	32.0
P3 x P13	-9.2	-10.6	56.3	61.4	24.0	18.8	31.1	4.9	51.7	57.4	57.3
P3 x P14	-8.6	-9.2	36.7	53.5	8.3	6.2	24.1	0.3	39.3	39.6	19.9
P3 x P15	-10.8	-11.2	40.5	53.2	-4.3	23.1	38.0	8.6	40.2	49.9	52.9
P4 x P5	-8.3	-9.0	49.9	60.5	9.1	22.6	44.6	11.9	87.0	107.2	36.4
P4 x P6	-10.2	-11.7	64.6	83.7	-0.7	19.5	29.3	16.6	44.3	67.5	36.6
P4 x P7	-10.6	-11.3	61.1	67.2	-9.7	31.0	55.8	10.4	69.4	84.9	57.0
P4 x P8	-10.8	-11.5	54.9	66.1	1.1	33.8	54.6	17.7	79.3	109.7	45.9
P4 x P9	-8.1	-10.2	71.3	91.0	-16.8	29.9	56.5	9.0	67.4	80.6	48.5
P4 x P10	-8.7	-9.6	57.9	75.1	-0.1	25.7	36.0	2.7	49.9	51.3	43.6
P4 x P11	-5.8	-6.0	53.3	61.7	6.8	26.1	46.2	4.4	67.5	73.8	53.1
P4 x P12	-9.8	-10.3	60.8	65.9	-11.2	31.6	43.5	6.9	55.8	64.2	70.1
P4 x P13	-4.6	-6.3	47.4	56.8	3.1	7.9	10.1	5.2	45.5	52.3	22.4
P4 x P14	-10.1	-11.1	45.3	64.2	2.2	29.5	47.4	8.5	68.6	79.9	47.2
P4 x P15	-9.9	-11.0	42.6	51.9	-10.9	44.2	44.5	13.2	47.6	62.5	46.9
P5 x P6	-8.8	-9.2	61.9	63.9	20.0	7.2	24.3	11.6	46.8	64.4	30.4
P5 x P7	-6.2	-7.5	45.0	49.9	15.5	15.1	23.3	10.5	54.0	69.2	15.8
P5 x P8	-5.9	-7.1	49.3	54.1	33.0	10.6	24.5	13.2	69.0	90.6	9.4
P5 x P9	-5.2	-6.0	59.5	83.2	11.1	20.6	31.2	7.0	70.1	78.9	35.2
P5 x P10	-6.0	-6.8	48.2	58.6	19.5	10.6	34.4	3.9	52.0	54.1	29.0
P5 x P11	-2.5	-3.0	46.2	62.3	24.3	15.2	36.8	9.5	64.7	77.9	31.1
P5 x P12	-2.3	-2.3	42.0	56.1	-2.0	10.3	-2.0	5.2	38.2	43.9	-1.8
P5 x P13	-6.2	-7.0	57.6	49.7	23.2	24.0	38.7	11.9	74.0	92.1	33.2
P5 x P14	-7.8	-9.6	43.2	71.3	9.6	14.0	18.9	12.6	61.0	78.5	8.8
P5 x P15	-7.1	-7.8	40.0	53.6	10.7	31.3	39.4	13.8	72.3	91.7	26.9
P6 x P7	-9.0	-9.8	65.3	79.5	-1.4	17.6	34.1	19.3	46.9	75.7	38.6
P6 x P8	-9.3	-8.9	60.2	61.5	27.3	17.9	29.5	19.8	54.2	84.6	28.8
P6 x P9	-11.6	-11.7	77.1	90.1	5.2	27.0	30.9	15.0	46.4	67.7	45.6

Appendix 6 Continued…

Cross	DA	DS	PH	EH	EPP	ED	EL	RPE	KPR	KPE	TKW
P6 x P10	-10.3	-11.9	47.0	54.4	7.3	12.9	24.8	3.3	37.5	41.9	35.2
P6 x P11	-10.0	-10.0	49.6	68.9	15.6	13.8	28.4	11.7	41.4	58.2	36.3
P6 x P12	-10.3	-9.5	71.7	91.9	9.2	13.3	23.5	9.9	36.4	50.2	43.8
P6 x P13	-10.9	-11.0	67.8	85.5	0.1	17.9	34.4	8.4	39.4	52.1	47.5
P6 x P14	-12.0	-13.0	57.5	86.8	21.6	19.7	22.9	12.5	22.3	38.3	34.5
P6 x P15	-11.9	-13.2	44.6	75.9	-3.6	33.3	35.0	16.7	27.3	47.2	39.8
P7 x P8	-4.6	-5.1	30.2	40.8	-20.6	2.3	-8.9	5.0	1.6	6.8	16.7
P7 x P9	-7.0	-6.7	64.6	67.4	3.6	18.4	38.8	7.9	53.3	65.1	30.4
P7 x P10	-7.7	-8.7	46.8	53.0	12.7	17.6	39.3	10.8	49.3	67.1	33.6
P7 x P11	-7.9	-7.9	48.2	48.9	1.1	22.1	43.6	10.6	45.3	61.4	30.7
P7 x P12	-8.0	-7.0	48.7	57.4	-5.2	11.8	24.1	4.2	41.9	48.6	28.7
P7 x P13	-6.4	-7.2	56.0	66.8	-3.8	22.2	39.2	4.4	48.3	55.6	35.7
P7 x P14	-9.3	-10.5	39.7	67.6	-4.0	17.5	36.3	7.6	44.4	54.7	20.7
P7 x P15	-7.8	-7.6	45.5	51.8	-0.3	34.0	43.0	12.5	40.7	56.8	33.2
P8 x P9	-10.5	-10.0	66.2	63.8	20.6	17.7	44.7	5.9	58.6	66.9	26.1
P8 x P10	-7.9	-9.1	56.2	64.1	28.9	14.9	31.9	7.4	32.8	44.1	20.7
P8 x P11	-6.1	-6.3	51.8	52.3	32.2	18.4	39.6	10.7	46.0	61.8	33.2
P8 x P12	-8.7	-8.0	53.7	66.7	13.3	9.2	25.3	1.3	48.7	50.3	15.4
P8 x P13	-9.1	-9.8	52.6	61.0	29.5	26.7	46.6	11.2	66.5	85.3	36.5
P8 x P14	-10.2	-9.7	39.0	54.8	13.1	17.4	33.5	12.2	44.6	61.3	12.6
P8 x P15	-9.2	-9.8	37.3	46.4	17.5	30.4	30.7	16.3	43.5	64.0	28.2
P9 x P10	-7.5	-10.4	58.5	66.8	-7.3	26.8	36.4	13.5	39.6	59.0	38.6
P9 x P11	-7.1	-8.0	51.5	67.5	19.5	23.0	41.2	9.5	47.6	62.5	38.1
P9 x P12	-9.3	-9.7	70.4	88.3	6.7	23.4	34.2	5.0	36.4	43.9	49.4
P9 x P13	-8.6	-9.0	74.2	87.5	10.0	25.4	44.6	2.9	58.5	63.7	40.3
P9 x P14	-11.0	-10.4	60.1	89.4	3.3	22.7	32.4	5.1	51.1	59.1	28.9
P9 x P15	-8.6	-9.8	57.8	83.6	-3.3	31.1	36.5	8.0	51.9	61.3	33.1
P10 x P11	-3.1	-2.3	33.2	44.0	4.5	14.2	19.1	3.6	36.9	41.5	23.0
P10 x P12	-8.4	-9.4	50.7	55.6	27.4	13.2	26.5	0.6	33.4	34.3	37.2
P10 x P13	-8.4	-9.3	51.6	60.4	0.0	20.6	26.5	4.6	41.9	48.4	40.0
P10 x P14	-9.1	-10.9	42.1	62.1	31.1	17.4	33.1	5.0	47.1	54.1	26.4
P10 x P15	-8.2	-9.5	31.9	40.6	-13.2	24.7	22.3	11.4	33.6	46.7	38.2
P11 x P12	-7.5	-6.1	52.2	68.3	4.4	16.2	25.0	4.8	53.6	61.0	48.1
P11 x P13	-6.5	-6.3	48.4	72.3	21.3	20.2	35.8	9.0	57.2	72.4	38.1
P11 x P14	-7.4	-8.9	45.1	65.7	36.2	17.1	28.5	11.8	47.5	64.5	28.1
P11 x P15	-7.0	-8.0	31.6	45.4	-7.2	26.2	36.5	10.1	38.1	50.1	30.5
P12 x P13	-7.6	-6.7	64.3	69.4	-3.5	24.2	30.7	0.9	46.3	48.2	39.3
P12 x P14	-3.5	-3.5	29.1	52.0	-4.8	4.1	-0.3	0.5	24.8	25.5	18.2
P12 x P15	-9.9	-11.7	46.4	61.4	1.5	29.1	34.5	7.0	37.2	46.2	50.4
P13 x P14	-11.5	-12.3	49.8	84.5	11.8	26.5	25.4	7.5	49.3	61.6	29.0
P13 x P15	-9.7	-13.2	44.2	62.9	-6.7	30.3	37.6	6.7	53.9	62.3	41.8
P14 x P15	-11.1	-11.6	41.5	70.1	11.0	34.0	29.6	8.4	41.1	50.6	28.0

DA= days to anthesis; DS= days to silking; ED= ear diameter; EH= ear height; EL= ear length; EPP= ears per plant; KPR= number of kernels per row; KPE= number of kernels per ear; P1= VL052; P2= VL05200; P3= VL05468; P4= VL054178; P5= VL052887; P6= VL05482; P7= VL0523; P8= VL0524; P9= VL05561; P10= VL05483; P11= CML511; P12= CML144; P13= CML159; P14= CML491; P15= VL06375; PH= plant height; RPE= number of rows per ear; TKW= thousand kernel weight

Appendix 7 Percentage high-parent heterosis of diallel crosses among fifteen QPM inbred lines evaluated at Harare and Bako under optimum N conditions

Cross	AD	SD	PH	EH	EPP	ED	EL	RPE	KPR	KPE	TKW
P1 x P2	-11.7	-12.5	25.2	54.2	11.2	7.6	4.2	-3.5	19.4	23.8	1.0
P1 x P3	-10.5	-10.6	26.8	41.9	22.4	16.6	27.0	-4.2	32.6	26.8	2.3
P1 x P4	-19.0	-20.7	29.1	37.4	5.8	17.6	34.0	-2.1	50.0	46.5	38.8
P1 x P5	-8.5	-11.7	33.3	45.2	-4.6	2.9	9.7	2.4	29.3	31.7	-4.8
P1 x P6	-20.1	-20.8	31.3	35.7	-1.7	11.6	21.5	-0.1	30.7	43.1	19.9
P1 x P7	-11.1	-11.2	31.2	46.3	-2.6	9.1	21.5	-2.7	39.8	48.6	7.5
P1 x P8	-11.1	-11.0	34.3	34.2	38.0	5.2	19.9	-0.7	42.0	42.2	11.2
P1 x P9	-15.1	-15.9	39.6	62.4	-5.3	19.7	36.9	7.8	44.1	55.6	29.4
P1 x P10	-17.9	-18.9	44.3	39.9	1.6	13.4	15.2	-7.7	28.2	18.6	19.3
P1 x P11	-13.4	-13.8	39.6	53.4	24.0	16.4	27.7	8.0	49.4	62.5	17.7
P1 x P12	-8.5	-9.8	18.5	36.4	-17.0	-1.8	-5.2	-3.6	18.6	14.4	-7.8
P1 x P13	-14.6	-15.0	35.5	39.6	27.5	15.6	29.7	6.9	47.4	60.9	31.9
P1 x P14	-11.1	-12.3	24.6	36.3	-4.8	6.5	7.1	1.5	25.5	27.4	-5.0
P1 x P15	-17.4	-18.3	30.9	48.6	-5.3	21.2	27.9	7.5	33.6	47.6	27.4
P2 x P3	-8.7	-10.9	27.5	44.6	1.1	9.4	28.5	-1.8	19.9	17.7	-3.9
P2 x P4	-14.5	-15.1	54.6	64.2	-11.5	12.2	40.9	-1.5	50.1	47.3	21.2
P2 x P5	-4.1	-5.4	28.6	33.4	-8.2	1.3	12.3	-2.2	44.6	41.3	-7.8
P2 x P6	-15.0	-15.7	67.2	70.2	-16.6	7.2	31.6	-3.4	35.0	57.2	1.8
P2 x P7	-9.5	-10.7	35.5	45.9	-15.1	6.2	23.1	-3.5	23.7	44.4	13.5
P2 x P8	-8.5	-11.0	35.9	30.0	43.7	6.5	23.0	-6.9	37.7	39.6	9.2
P2 x P9	-9.8	-12.6	64.2	67.5	-11.1	19.6	39.1	0.1	48.4	59.3	23.0
P2 x P10	-10.7	-11.7	34.3	43.4	-8.8	15.2	37.6	-0.5	43.4	43.0	7.3
P2 x P11	-9.1	-9.7	29.9	51.0	16.5	12.3	48.2	2.0	37.9	48.7	13.2
P2 x P12	-3.9	-3.4	27.3	45.4	-17.1	0.1	7.5	-1.2	21.3	20.3	-9.3
P2 x P13	-11.0	-11.4	51.2	65.4	2.5	14.4	21.0	11.0	54.5	81.0	15.3
P2 x P14	-8.9	-13.1	46.5	45.5	-4.2	5.9	9.4	1.2	19.1	26.3	0.3
P2 x P15	-13.3	-14.4	21.1	39.1	-11.0	11.1	13.1	4.1	25.7	44.6	20.9
P3 x P4	-15.3	-17.4	45.4	49.2	-3.3	13.6	52.2	-11.7	44.9	27.5	38.5
P3 x P5	-3.9	-7.0	39.7	45.9	14.7	2.4	31.1	-7.0	34.2	24.8	4.5
P3 x P6	-16.5	-17.3	37.2	38.0	-7.2	10.0	34.8	-11.6	28.7	13.6	46.3
P3 x P7	-7.6	-8.1	49.6	58.1	-8.8	11.3	37.7	-11.1	44.1	28.1	22.1
P3 x P8	-7.3	-8.1	50.9	55.4	19.0	10.9	39.4	-9.0	39.6	27.5	11.9
P3 x P9	-9.7	-11.4	47.2	76.3	-7.4	20.7	45.0	-6.2	57.6	48.1	33.1
P3 x P10	-14.0	-14.6	35.7	42.7	-3.9	13.1	28.5	0.8	43.0	44.0	31.4
P3 x P11	-12.3	-13.0	33.7	46.1	7.1	13.6	26.9	0.3	40.0	40.7	28.6
P3 x P12	-5.1	-8.2	37.3	45.6	-19.3	10.1	25.2	-4.8	41.7	34.3	23.9
P3 x P13	-12.6	-14.3	48.3	43.6	22.1	18.7	22.5	-2.7	39.4	35.0	28.7
P3 x P14	-9.9	-10.5	34.1	46.7	-4.9	3.8	18.5	-6.8	37.8	28.4	-2.1
P3 x P15	-14.4	-15.0	31.3	48.9	-17.4	14.6	30.1	-2.5	34.8	31.5	23.0
P4 x P5	-13.1	-12.6	36.3	40.0	-0.4	13.6	40.1	5.9	77.4	105.2	32.3
P4 x P6	-10.5	-11.8	56.1	68.4	-9.6	13.5	29.1	16.1	30.0	51.8	23.8
P4 x P7	-16.2	-16.1	48.3	45.4	-17.4	24.1	52.2	7.1	52.4	62.6	50.3
P4 x P8	-16.6	-17.2	42.2	40.5	-7.6	25.2	50.6	16.4	69.7	97.3	45.5
P4 x P9	-11.7	-12.4	67.6	82.9	-22.4	22.5	49.4	-0.6	49.1	48.9	43.3
P4 x P10	-9.3	-9.6	41.4	56.1	-9.5	11.5	30.4	-11.1	36.5	21.6	35.3
P4 x P11	-7.2	-6.3	36.8	45.1	6.6	13.5	35.2	-5.6	54.6	46.8	45.2
P4 x P12	-14.8	-13.8	57.5	60.2	-20.8	18.6	40.9	-5.6	41.8	34.4	49.3
P4 x P13	-7.2	-8.4	43.2	55.3	-4.4	-2.5	4.3	-4.8	39.9	33.4	19.9
P4 x P14	-16.7	-17.7	31.9	53.6	-5.1	19.6	42.9	-2.0	50.9	47.6	43.9
P4 x P15	-12.0	-12.8	23.8	32.9	-18.8	39.7	38.2	5.7	35.6	39.3	40.8
P5 x P6	-13.3	-13.0	40.4	32.8	19.5	4.4	20.3	5.2	26.2	50.4	21.5
P5 x P7	-7.3	-8.9	43.0	49.5	15.3	12.4	22.2	7.6	32.3	50.1	14.1
P5 x P8	-7.3	-9.6	47.7	48.8	12.1	9.4	23.8	8.2	52.3	81.0	5.9
P5 x P9	-6.5	-7.5	42.2	66.1	8.7	18.5	21.5	2.9	44.7	48.6	34.4
P5 x P10	-10.4	-10.5	45.7	54.7	18.4	5.5	33.0	-5.5	32.1	24.8	25.1
P5 x P11	-6.3	-6.6	43.2	57.2	13.4	11.7	30.5	4.3	44.9	51.5	28.1
P5 x P12	-2.6	-2.5	31.7	40.4	-4.6	7.0	-3.4	-2.2	20.0	18.8	-11.5
P5 x P13	-8.8	-8.6	47.2	29.5	5.1	20.6	27.5	6.7	59.1	69.7	26.7
P5 x P14	-10.0	-12.9	43.0	58.8	7.6	13.6	11.7	7.1	37.5	47.6	3.3
P5 x P15	-9.9	-9.7	32.9	53.0	10.5	25.3	29.3	12.3	50.9	65.7	18.3
P6 x P7	-14.3	-14.9	45.1	45.0	-2.0	17.3	30.8	15.3	46.8	69.9	30.9
P6 x P8	-15.0	-14.9	40.1	27.3	6.9	16.2	25.9	18.0	46.2	77.4	16.4
P6 x P9	-14.8	-14.0	71.6	67.6	2.5	26.0	25.1	4.4	44.6	50.8	36.3

Appendix 7 Continued…

Cross	AD	SD	PH	EH	EPP	ED	EL	RPE	KPR	KPE	TKW
P6 x P10	-10.6	-12.0	25.6	27.5	6.7	5.0	19.5	-10.9	35.7	24.0	29.7
P6 x P11	-11.0	-10.4	27.5	40.4	5.1	7.6	18.6	0.6	37.7	46.2	29.8
P6 x P12	-15.0	-13.1	59.7	70.4	6.8	7.2	21.1	-3.3	34.8	34.0	38.8
P6 x P13	-13.0	-13.2	54.9	71.5	-14.9	11.8	27.5	-2.3	30.3	46.4	31.1
P6 x P14	-18.3	-19.6	36.4	61.2	19.0	16.3	19.3	1.2	21.5	23.7	19.5
P6 x P15	-13.7	-15.0	20.0	42.9	-3.8	30.6	29.3	8.6	24.6	38.2	22.0
P7 x P8	-5.0	-6.1	29.8	36.3	-33.0	1.1	-9.2	3.0	-3.7	-0.6	11.4
P7 x P9	-9.3	-9.6	48.6	51.3	1.6	17.8	29.6	1.2	51.6	53.1	29.2
P7 x P10	-12.9	-13.7	42.3	48.8	11.5	9.7	36.7	-1.5	47.3	50.4	31.4
P7 x P11	-12.4	-12.7	43.2	43.8	-7.6	15.8	35.8	2.8	41.3	53.9	29.5
P7 x P12	-8.7	-8.6	39.6	41.2	-7.8	6.0	23.5	-5.5	40.1	36.7	17.5
P7 x P13	-9.9	-10.3	47.5	43.9	-17.9	16.3	29.0	-2.9	38.4	54.9	27.3
P7 x P14	-10.6	-12.5	37.5	54.9	-5.6	14.5	29.2	-0.1	43.5	42.6	13.1
P7 x P15	-11.5	-11.0	36.4	50.7	-0.7	30.8	33.8	8.2	37.5	52.1	22.5
P8 x P9	-13.0	-13.8	49.6	43.9	3.5	16.9	34.7	-2.5	48.7	44.9	21.4
P8 x P10	-13.4	-14.9	52.0	54.6	7.8	8.4	29.8	-6.1	27.5	21.7	13.4
P8 x P11	-11.0	-12.1	47.2	42.5	21.0	13.5	32.4	1.1	42.1	44.1	26.0
P8 x P12	-9.8	-10.6	43.8	45.3	-6.6	4.7	24.3	-9.7	42.7	29.5	1.0
P8 x P13	-12.9	-13.7	43.9	35.2	27.6	21.9	35.5	1.5	63.8	71.7	34.0
P8 x P14	-11.0	-10.7	37.3	38.9	-3.3	15.7	26.1	2.3	36.3	39.3	10.4
P8 x P15	-13.2	-14.0	29.1	40.8	-1.2	25.9	22.0	9.7	39.1	48.4	23.2
P9 x P10	-10.6	-12.6	39.2	54.7	-10.1	18.9	25.1	7.2	36.2	53.9	35.2
P9 x P11	-9.5	-10.0	32.6	56.4	11.3	17.2	25.1	8.6	42.0	57.8	35.7
P9 x P12	-10.9	-11.0	63.4	86.7	1.8	17.6	25.9	1.4	33.1	42.7	35.3
P9 x P13	-9.9	-9.1	65.7	78.0	-4.4	19.9	43.5	2.0	46.4	52.5	32.7
P9 x P14	-14.4	-15.0	42.5	84.8	2.9	20.1	30.3	3.9	50.3	58.1	21.7
P9 x P15	-10.1	-10.2	34.5	67.1	-5.6	27.4	36.2	5.2	46.8	53.9	23.4
P10 x P11	-3.9	-2.6	32.8	43.0	-5.5	12.3	14.7	-1.3	35.0	33.2	22.0
P10 x P12	-12.9	-12.9	37.5	43.2	25.2	11.2	23.5	-1.7	33.3	31.1	27.2
P10 x P13	-10.3	-11.4	39.3	41.8	-15.4	18.2	15.2	-0.4	34.2	34.2	29.3
P10 x P14	-15.4	-17.5	39.9	53.8	27.6	12.3	23.9	0.2	44.2	50.1	16.6
P10 x P15	-9.8	-11.3	27.4	37.7	-13.9	13.8	12.3	2.7	32.4	35.8	25.1
P11 x P12	-11.4	-9.5	38.5	55.9	-7.0	16.1	17.6	2.2	51.3	54.9	36.4
P11 x P13	-7.7	-8.2	36.0	53.3	12.6	19.7	19.6	9.0	50.7	65.2	28.5
P11 x P14	-13.1	-15.4	42.4	58.4	26.4	13.8	15.5	11.6	42.7	58.8	19.0
P11 x P15	-7.9	-9.6	27.5	41.3	-15.5	17.0	21.2	6.3	37.5	47.5	18.9
P12 x P13	-10.4	-8.2	63.0	62.1	-19.5	23.8	21.7	-1.7	38.2	36.9	20.1
P12 x P14	-5.5	-7.2	19.5	47.1	-8.9	1.3	-5.0	-1.9	22.5	25.1	1.7
P12 x P15	-13.0	-13.4	29.4	45.7	-1.0	19.7	26.4	0.8	35.8	38.4	27.3
P13 x P14	-16.0	-17.0	39.6	71.1	-3.2	23.5	22.5	7.3	38.5	49.7	28.8
P13 x P15	-10.0	-13.4	28.3	41.4	-20.5	21.2	36.2	3.0	46.8	58.2	38.7
P14 x P15	-15.8	-16.5	34.5	58.3	8.8	27.6	27.9	4.5	37.1	42.9	25.5

DA= days to anthesis; DS= days to silking; ED= ear diameter; EH= ear height; EL= ear length; EPP= ears per plant; KPR= number of kernels per row; KPE= number of kernels per ear; P1= VL052; P2= VL05200; P3= VL05468; P4= VL054178; P5= VL052887; P6= VL05482; P7= VL0523; P8= VL0524; P9= VL05561; P10= VL05483; P11= CML511; P12= CML144; P13= CML159; P14= CML491; P15= VL06375; PH= plant height; RPE= number of rows per ear; TKW= thousand kernel weight

Appendix 8 Means for endosperm modification, tryptophan concentration in grain, protein concentration in grain and protein quality index of QPM hybrids evaluated at Harare and Bako

Cross	Low N				Optimum N				Across			
	MOD	TRP	Protein	QI	MOD	TRP	Protein	QI	MOD	TRP	Protein	QI
P1 x P2	2.7	0.85	88.9	1.0	2.0	0.93	105.6	0.9	2.3	0.89	97.3	0.9
P1 x P3	2.5	0.70	83.4	0.8	2.5	0.93	100.2	0.9	2.5	0.82	91.8	0.9
P1 x P4	2.5	0.63	82.5	0.8	1.8	0.64	99.6	0.6	2.2	0.63	91.1	0.7
P1 x P5	3.6	0.74	77.0	1.0	2.7	0.89	100.0	0.9	3.2	0.81	88.5	0.9
P1 x P6	3.1	0.79	79.4	1.0	2.5	0.98	111.5	0.9	2.8	0.88	95.5	0.9
P1 x P7	2.7	0.80	87.8	0.9	2.5	0.89	93.7	0.9	2.6	0.85	90.7	0.9
P1 x P8	2.9	0.80	86.6	0.9	2.9	0.90	91.2	1.0	2.9	0.85	88.9	0.9
P1 x P9	3.2	0.65	79.2	0.8	2.4	0.90	108.9	0.8	2.8	0.78	94.1	0.8
P1 x P10	2.8	0.69	82.3	0.9	2.8	0.89	111.8	0.8	2.8	0.79	97.0	0.8
P1 x P11	3.1	0.78	79.6	1.0	2.7	0.93	108.1	0.9	2.9	0.86	93.8	0.9
P1 x P12	3.2	0.82	88.3	0.9	2.5	0.86	98.2	0.9	2.9	0.84	93.3	0.9
P1 x P13	3.1	0.81	82.9	1.0	2.5	0.96	96.9	1.0	2.8	0.89	89.9	1.0
P1 x P14	3.1	0.90	87.7	1.0	2.1	0.96	97.5	1.0	2.6	0.93	92.6	1.0
P1 x P15	3.8	0.81	75.5	1.1	3.1	0.97	102.0	0.9	3.4	0.89	88.7	1.0
P2 x P3	2.3	0.77	86.8	0.9	1.9	0.79	95.9	0.8	2.1	0.78	91.3	0.8
P2 x P4	2.2	0.56	80.3	0.7	1.7	0.59	97.3	0.6	2.0	0.57	88.8	0.6
P2 x P5	2.6	0.78	99.3	0.8	2.0	0.81	108.9	0.7	2.3	0.80	104.1	0.8
P2 x P6	3.0	0.81	90.9	0.9	2.0	0.91	111.3	0.8	2.5	0.86	101.1	0.9
P2 x P7	2.7	0.76	82.9	0.9	2.1	0.87	95.8	0.9	2.4	0.81	89.3	0.9
P2 x P8	3.1	0.73	75.6	1.0	2.1	0.86	93.7	0.9	2.6	0.80	84.7	1.0
P2 x P9	2.8	0.70	82.9	0.9	2.0	0.84	103.1	0.8	2.4	0.77	93.0	0.8
P2 x P10	3.2	0.72	79.8	0.9	2.6	0.81	110.2	0.7	2.9	0.77	95.0	0.8
P2 x P11	3.1	0.78	78.0	1.0	2.9	0.94	108.4	0.9	3.0	0.86	93.2	1.0
P2 x P12	2.5	0.76	93.9	0.8	2.2	0.84	103.6	0.8	2.4	0.80	98.8	0.8
P2 x P13	2.5	0.70	75.5	0.9	2.3	0.81	97.0	0.8	2.4	0.75	86.3	0.9
P2 x P14	2.6	0.80	93.3	0.8	1.8	0.83	96.8	0.9	2.2	0.81	95.0	0.9
P2 x P15	3.1	0.80	87.8	0.9	2.2	0.87	97.6	0.9	2.6	0.83	92.7	0.9
P3 x P4	2.3	0.59	88.3	0.7	1.7	0.67	110.6	0.6	2.0	0.63	99.5	0.6
P3 x P5	2.7	0.72	89.1	0.8	2.4	0.91	112.0	0.8	2.6	0.82	100.5	0.8
P3 x P6	2.7	0.71	80.3	0.9	2.5	1.03	119.8	0.9	2.6	0.87	100.1	0.9
P3 x P7	2.9	0.80	94.9	0.9	2.7	0.93	100.2	0.9	2.8	0.87	97.6	0.9
P3 x P8	2.3	0.86	97.3	0.9	2.5	0.93	104.3	0.9	2.4	0.89	100.8	0.9
P3 x P9	2.3	0.75	84.0	0.9	2.0	0.82	98.3	0.8	2.2	0.78	91.2	0.9
P3 x P10	3.2	0.68	81.4	0.8	2.7	0.86	113.0	0.8	2.9	0.77	97.2	0.8
P3 x P11	2.9	0.78	80.1	1.0	2.6	0.88	109.9	0.8	2.8	0.83	95.0	0.9
P3 x P12	2.8	0.76	79.1	1.0	2.0	0.87	102.9	0.8	2.4	0.81	91.0	0.9
P3 x P13	2.3	0.76	82.5	0.9	2.6	0.86	97.8	0.9	2.4	0.81	90.1	0.9
P3 x P14	2.9	0.73	80.1	0.9	2.2	0.95	109.1	0.9	2.5	0.84	94.6	0.9
P3 x P15	3.1	0.79	86.2	0.9	2.7	0.92	108.8	0.8	2.9	0.86	97.5	0.9
P4 x P5	2.8	0.55	77.9	0.7	2.5	0.62	107.9	0.6	2.7	0.58	92.9	0.6
P4 x P6	2.6	0.58	85.9	0.7	1.8	0.62	114.2	0.5	2.2	0.60	100.0	0.6
P4 x P7	2.5	0.57	77.7	0.8	1.9	0.64	96.9	0.7	2.2	0.60	87.3	0.7
P4 x P8	2.9	0.65	92.7	0.7	2.4	0.69	99.9	0.7	2.6	0.67	96.3	0.7
P4 x P9	2.3	0.58	83.2	0.7	2.2	0.61	109.4	0.6	2.3	0.59	96.3	0.6
P4 x P10	3.3	0.52	77.3	0.7	2.5	0.59	105.8	0.6	2.9	0.56	91.5	0.6
P4 x P11	2.2	0.64	84.1	0.8	2.2	0.66	109.0	0.6	2.2	0.65	96.6	0.7
P4 x P12	2.2	0.68	89.6	0.8	1.8	0.56	101.0	0.6	2.0	0.62	95.3	0.7
P4 x P13	1.9	0.54	85.2	0.6	1.6	0.58	98.9	0.6	1.7	0.56	92.1	0.6
P4 x P14	2.4	0.65	82.0	0.8	1.9	0.65	100.0	0.6	2.1	0.65	91.0	0.7
P4 x P15	2.8	0.55	73.0	0.7	1.8	0.62	104.6	0.6	2.3	0.59	88.8	0.7
P5 x P6	3.6	0.72	80.0	0.9	2.5	0.98	119.2	0.8	3.1	0.85	99.6	0.9
P5 x P7	2.9	0.77	88.4	0.9	2.5	0.86	100.1	0.9	2.7	0.82	94.2	0.9
P5 x P8	3.0	0.75	83.7	0.9	2.8	0.81	100.1	0.8	2.9	0.78	91.9	0.9
P5 x P9	3.0	0.59	71.3	0.8	2.3	0.80	100.1	0.8	2.6	0.70	85.7	0.8
P5 x P10	2.8	0.64	78.0	0.8	3.0	0.87	108.7	0.8	2.9	0.75	93.4	0.8
P5 x P11	3.1	0.67	80.9	0.8	2.5	0.92	107.0	0.9	2.8	0.79	94.0	0.8
P5 x P12	2.5	0.74	89.6	0.8	1.8	0.80	110.0	0.7	2.1	0.77	99.8	0.8
P5 x P13	3.0	0.66	80.4	0.8	2.6	0.99	109.0	0.9	2.8	0.83	94.7	0.9
P5 x P14	3.3	0.64	77.7	0.8	2.3	0.80	109.4	0.7	2.8	0.72	93.5	0.8
P5 x P15	3.0	0.72	80.2	0.9	2.9	0.91	105.4	0.9	3.0	0.81	92.8	0.9
P6 x P7	3.1	0.76	82.8	0.9	2.6	0.83	99.9	0.8	2.8	0.80	91.4	0.9
P6 x P8	3.5	0.75	80.1	0.9	2.2	0.78	98.9	0.8	2.9	0.76	89.5	0.9
P6 x P9	3.1	0.67	77.6	0.9	2.6	0.90	110.3	0.8	2.9	0.78	93.9	0.8

Appendix 8 Continued

Cross	Low N				Optimum N				Across			
	MOD	TRP	Protein	QI	MOD	TRP	Protein	QI	MOD	TRP	Protein	QI
P6 x P10	3.7	0.60	67.4	0.9	3.0	0.88	116.9	0.7	3.4	0.74	92.2	0.8
P6 x P11	3.9	0.66	70.3	0.9	3.1	0.91	104.6	0.9	3.5	0.79	87.5	0.9
P6 x P12	2.7	0.83	88.5	0.9	2.1	0.87	110.5	0.8	2.4	0.85	99.5	0.9
P6 x P13	3.1	0.65	70.9	0.9	2.7	0.86	104.7	0.8	2.9	0.76	87.8	0.9
P6 x P14	3.0	0.75	86.1	0.9	2.4	0.91	111.1	0.8	2.7	0.83	98.6	0.9
P6 x P15	3.6	0.72	89.8	0.8	3.1	0.87	114.9	0.8	3.3	0.80	102.4	0.8
P7 x P8	3.0	0.97	100.5	1.0	2.6	0.93	105.6	0.9	2.8	0.95	103.1	0.9
P7 x P9	2.9	0.69	81.9	0.8	2.2	0.81	99.1	0.8	2.6	0.75	90.5	0.8
P7 x P10	3.4	0.72	83.3	0.9	2.8	0.82	107.9	0.8	3.1	0.77	95.6	0.8
P7 x P11	3.0	0.70	80.7	0.9	3.2	0.90	102.2	0.9	3.1	0.80	91.5	0.9
P7 x P12	2.6	0.76	86.8	0.9	2.3	0.85	98.8	0.9	2.5	0.81	92.8	0.9
P7 x P13	2.6	0.77	86.7	0.9	2.5	0.79	92.2	0.9	2.6	0.78	89.5	0.9
P7 x P14	3.2	0.77	79.0	1.0	2.4	0.86	97.3	0.9	2.8	0.81	88.2	0.9
P7 x P15	3.6	0.71	77.5	0.9	2.8	0.85	94.9	0.9	3.2	0.78	86.2	0.9
P8 x P9	3.0	0.69	82.4	0.9	2.2	0.77	98.7	0.8	2.6	0.73	90.5	0.8
P8 x P10	3.5	0.66	78.0	0.9	3.1	0.81	101.9	0.8	3.3	0.74	89.9	0.8
P8 x P11	3.3	0.66	94.7	0.8	3.0	0.91	104.3	0.9	3.2	0.78	99.5	0.8
P8 x P12	2.7	0.76	96.8	0.9	2.6	0.82	91.2	0.9	2.6	0.79	94.0	0.9
P8 x P13	3.1	0.65	71.0	0.9	2.7	0.77	88.0	0.9	2.9	0.71	79.5	0.9
P8 x P14	2.6	0.79	85.7	0.9	2.1	0.78	100.5	0.8	2.3	0.78	93.1	0.9
P8 x P15	3.8	0.67	80.9	0.8	2.9	0.81	97.0	0.8	3.3	0.74	89.0	0.8
P9 x P10	2.9	0.63	83.5	0.8	2.5	0.79	113.1	0.7	2.7	0.71	98.3	0.7
P9 x P11	3.2	0.66	71.6	0.9	2.8	0.88	103.8	0.9	3.0	0.77	87.7	0.9
P9 x P12	2.6	0.71	83.9	0.9	2.1	0.78	100.9	0.8	2.4	0.75	92.4	0.8
P9 x P13	2.9	0.73	87.0	0.9	2.7	0.80	106.6	0.7	2.8	0.77	96.8	0.8
P9 x P14	2.6	0.70	88.1	0.8	2.1	0.77	105.0	0.7	2.4	0.73	96.6	0.8
P9 x P15	3.3	0.74	85.2	0.9	2.6	0.82	105.9	0.8	3.0	0.78	95.6	0.8
P10 x P11	3.4	0.68	72.5	1.0	2.9	0.83	107.0	0.8	3.2	0.75	89.8	0.9
P10 x P12	3.3	0.68	78.0	0.9	2.3	0.82	103.7	0.8	2.8	0.75	90.9	0.8
P10 x P13	3.0	0.60	75.0	0.8	3.0	0.74	98.6	0.7	3.0	0.67	86.8	0.8
P10 x P14	2.9	0.61	68.3	0.9	2.5	0.83	101.2	0.8	2.7	0.72	84.8	0.9
P10 x P15	3.9	0.68	79.1	0.9	2.5	0.79	105.3	0.7	3.2	0.73	92.2	0.8
P11 x P12	2.9	0.79	81.5	1.0	2.1	0.92	110.3	0.8	2.5	0.85	95.9	0.9
P11 x P13	2.9	0.77	80.8	0.9	2.8	0.80	99.2	0.8	2.9	0.78	90.0	0.9
P11 x P14	3.1	0.73	75.4	1.0	2.3	0.85	103.3	0.8	2.7	0.79	89.4	0.9
P11 x P15	4.2	0.81	74.0	1.1	3.1	0.85	103.6	0.8	3.6	0.83	88.8	1.0
P12 x P13	3.2	0.71	76.3	0.9	1.8	0.74	93.8	0.8	2.5	0.73	85.0	0.9
P12 x P14	2.8	0.82	86.7	0.9	1.9	0.84	106.3	0.8	2.3	0.83	96.5	0.9
P12 x P15	3.0	0.77	87.0	0.9	2.6	0.85	101.2	0.8	2.8	0.81	94.1	0.9
P13 x P14	2.8	0.74	83.4	0.9	2.3	0.82	99.6	0.8	2.6	0.78	91.5	0.9
P13 x P15	2.9	0.67	78.8	0.9	2.7	0.80	102.3	0.8	2.8	0.74	90.5	0.8
P14 x P15	3.5	0.69	85.5	0.8	2.4	0.76	96.1	0.8	2.9	0.72	90.8	0.8
Mean	2.9	0.71	82.6	0.9	2.4	0.83	103.5	0.8	2.7	0.77	93.0	8.4
F test	**	**	ns	**	**	**	**	**	**	**	ns	**
$LSD_{0.05}$	0.59	0.11	14.46	0.11	0.36	0.08	7.85	0.08	0.34	0.08	8.24	0.08
CV%	10.2	7.8	8.9	7.0	7.6	5.8	3.8	5.7	9.3	6.8	6.3	6.5

** $P \leq 0.01$; CV= coefficient of variation; LSD= least significance difference; MOD= endosperm modification; ns= non-significant; P1= VL052; P2= VL05200; P3= VL05468; P4= VL054178; P5= VL052887; P6= VL05482; P7= VL0523; P8= VL0524; P9= VL05561; P10= VL05483; P11= CML511; P12= CML144; P13= CML159; P14= CML491; P15= VL06375; QI= quality index; TRP= tryptophan