

**Recurrent Selection for Drought Tolerance in Maize (*Zea mays*
L.) and a Study of Heterotic Patterns of Maize Populations from
Eastern Kenya**

Philip Kipkoech Leley

BSc Hons Egerton University, Kenya; MPhil Moi University, Kenya

Supervisors

Principal supervisor: Prof Pangirayi Tongoona

Co-supervisor: Dr John Derera

In-country supervisor: Dr Jane Ininda

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Thesis Abstract

There are few maize varieties that are drought tolerant in semi-arid eastern Kenya and farmer perceptions of drought tolerant maize cultivars have not been studied in this region. Farmers in this region use maize landraces that have not been studied for their potential future hybridization. The main objectives of this study were therefore to: (i) study farmer perceptions of drought and preference for maize varieties, (ii) improve drought tolerance in maize populations in the semi-arid eastern Kenya using S_1 family recurrent selection, and (iii) classify maize landraces according to their heterotic patterns.

A participatory rural appraisal (PRA) was conducted in Machakos and Makueni districts in semi-arid eastern Kenya. A total of 175 farmers were involved in focus group discussions. An open ended questionnaire and a checklist were used to guide the farmers during the discussion sessions. Scoring and ranking techniques were used to assess farmers' preferences of maize varieties and constraints to maize production. The farmers grew maize as their major crop followed by beans. Nearly 60% of the farmers grew local maize landraces, whose seed they recycled from season to season; 40% grew improved varieties, but mainly composites rather than hybrids. The key farmers' criteria for choosing a maize variety in order of importance were drought tolerance, early maturity, high yield, and disease resistance. The major constraints to maize production were drought, lack of technical know-how, pests, poor soils, and inadequate seed supply. Maize traits preferred by farmers in a drought tolerant variety included high yield, recovery after a dry spell and the stay green characteristic.

Two maize landrace populations MKS and KTU from semi-arid eastern Kenya and three CIMMYT populations V032, ZM423, and ZM523 were subjected to two cycles of S_1 progeny recurrent selection for drought tolerance in yield and traits indicative of drought tolerance were measured during flowering and grain filling from February 2005 to September 2007. Evaluation to determine selection gains was done in one trial replicated five times. It was laid out as a 4x4 lattice design and drought was imposed at reproductive stage by withholding irrigation one week before flowering and resumed during grain filling. The trial was repeated under well-watered conditions which served as a control experiment. After two cycles of selection under drought stress conditions, KTU population had a realized gain in yield of 0.2 t ha^{-1} , MKS population 1.2 t ha^{-1} and ZM423 0.4 t ha^{-1} , whereas in V032 and ZM523, grain yield reduced by 1.1 t ha^{-1} and 0.6 t ha^{-1} , respectively. Under well watered conditions, the realized gains in grain yield were positive in all the populations except V032, where there was a reduction of 0.1 t ha^{-1} . Selection increased the genetic variability and heritability estimates for yield in S_1 lines of MKS and ZM423 populations, but decreased in KTU, V032 and ZM523 populations.

The research to identify heterotic patterns was undertaken using ten maize landraces from the semi-arid eastern Kenya, six maize landraces from coastal Kenya, and three maize populations from CIMMYT. These populations were planted at Kiboko Research Farm during the short rains of October-December 2005 and crossed to two population testers, Embu 11 and Embu 12. The evaluation of the test crosses was done during the long rains of March-June 2006. Percentage heterosis for yield ranged from -17.7% to 397.4%, -79.4 to 22.2% for anthesis-silking interval, -23.9% to 29.2% for ear height, -0.1 to 1.1 for ear diameter, -7.1 to 21.2% for ear length and -5.9% to 30.3% for plant height.

General combining ability (GCA) effects were significant ($p=0.05$) for all the traits, while specific combining ability (SCA) effects were not significant ($p>0.05$), implying that variation among these crosses was mainly due to additive rather than nonadditive gene effects. Since SCA was not significant ($p>0.05$) for yield, maize populations were classified based on percentage heterosis for yield alone. The maize populations therefore, were grouped into three different heterotic groups P, Q and R. Twelve landrace populations and two CIMMYT populations showed heterosis with Embu 11 and no heterosis with Embu 12 were put in one group P. Two landrace populations that showed no heterosis with either tester were put in group Q. Two landrace populations and one CIMMYT population showed heterosis with both testers were put in group R. None of the populations showed heterosis only with Embu 12 and no heterosis with Embu 11.

The main constraint to maize production was drought and the farmers preferred their landraces whose seed they recycled season to season. After two cycles of recurrent selection, the landrace populations showed improved progress in yield. Thus, further selection will be beneficial in the populations where genetic variability increased. Therefore, these populations can further be improved *per se* and released as varieties and/or incorporated into the existing maize germplasm to broaden their genetic base, given that their heterotic patterns have been identified. Considering that farmers recycle seed, breeding should be towards the development of open-pollinated varieties which are drought tolerant.

Declaration

The experimental work in this thesis was carried out in the School of Biochemistry, Genetics, Plant Microbiology, and Pathology, University of Kwa Zulu Natal, Pietermaritzburg, from January 2003 to December 2007, under the supervision of Professor Pangirayi Tongoona and Doctor John Derera

This thesis study represents my original work and ideas. It has not otherwise been submitted in any form for degree to any University. Where use has been made of the work of others, it has been duly acknowledged in the text.

Signed:.....Date

Philip Kipkoech Leley (Candidate)

Signed:.....Date.....

Prof Pangirayi Tongoona (Principal supervisor)

Signed:.....Date.....

Dr John Derera (Co-supervisor)

Dedication

This work is dedicated to my wife JEPCHIRCHIR TARUS, my children ABEL KIGEN, LINUS KIPTOO and JEAN JEPTEPKENY, and my late mother JANE JEPTEPKENY

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Abbreviations

ASI – Anthesis-silking interval

CGIAR – Consultative Group on International Agricultural Research

CIMMYT – International Maize and Wheat Improvement Centre

DNA – Deoxyribonucleic acid

FAO – Food and Agriculture Organization

GCA – General combining ability

IITA – International Institute of Tropical Agriculture

KARI – Kenya Agricultural Research Institute

PRA – Participatory rural appraisal

RAPD – Randomly amplified polymorphic DNA

RLFP – Restriction fragment length polymorphism

SCA – Specific combining ability

SSRs – Single sequence repeats

S1 – Inbred line which has been selfed once

S2 – Inbred line which has been selfed in two successive generations

δ^2 – Variance

C₀ – Cycle zero (Original population)

C₁ – Cycle one

C₂ – Cycle two

Introduction to Thesis

Importance of Maize

Maize was introduced into the Kenyan coast in the sixteenth century, by 1903, it covered an estimated 20% of Kenya's crop area and by 1960, this area had risen to 44% (De Groot et al., 2002). Its annual production in Kenya stands at 2.3 million tons produced on 1.5 million ha at an average grain yield of 1.5 t ha⁻¹ (Pingali and Pandey, 2001). The national food security in Kenya is often pegged to the availability of adequate supplies of maize to meet domestic demands. Maize is grown in almost all agro-ecological zones, including marginal areas on both large and small scale farms (Odendo et al., 2002). It accounts for more than 20% of all agricultural production, and 25% of agricultural employment (Ouma et al., 2002). It is a major source of income for the majority of the rural population and it accounts for over 80 % of the total cereals consumed.

Maize is high yielding, easy to process, readily digested and costs less to buy than other cereals. It has three possible uses: as human food, livestock feed and as raw material for industry (FAO, 1992). Where it is grown for human food, maize is an important source of calories for the poor. Subsistence farmers grow the crop widely in mixed cropping systems. Average annual per capita human consumption of maize is 20 kg in developing countries, but it approaches 80 kg in Latin America and the Caribbean, and, in Sub-Saharan Africa, 60 kg (CGIAR, 2002)

Constraints to Maize Production

The major constraints to maize production include both biotic and abiotic factors. The main biotic factors are pests and diseases. The most common abiotic factors are drought, extreme temperatures, low soil fertility (especially low nitrogen), high soil aluminium (soil acidity), flooding and salinity (Tuberosa et al., 2005). Drought is a common phenomenon in tropical environments, and it is one of the major factors contributing to yield losses in maize production. It is thought to cause average annual yield losses of about 17% in the tropics (Edmeades et al., 1999), and upto 60% in

severe drought conditions (Zaidi et al., 2004). Even though agriculture is the mainstay of Kenya's economy, with over 90% of the population relying on agriculture for their livelihood, only about 30% of Kenya's total land area is arable, and half of this is semi-arid (Njoroge and Ngure, 1986).

Maize Breeding in Eastern Kenya

Maize breeding work for the semi-arid areas in Kenya started in 1956 at Katumani Research Centre with the objective of developing improved early-maturing maize varieties. The early breeding policy at Katumani was to develop synthetic and composite varieties. The varieties developed initially included eight synthetic varieties and three composites (KARI, 2000). Of these varieties, Katumani composite B is the most widely grown in the semi-arid areas. However, this variety did not meet the preferences of farmers, especially in the drier areas of eastern Kenya (Njoroge and Ngure, 1986). Hence, there is still a strong need to develop drought tolerant varieties that will meet the farmers' preferences and are suitable for these drier areas.

Problem Statement and Justification

Maize in Kenya is produced in a wide range of agro-ecological zones, ranging from the wet highlands to the dry lowlands. The yields are unpredictable because of variability in weather patterns. The bulk of the maize comes from the wet highland areas however, with an increasing population, the area under maize is steadily declining in these high potential areas. Hence, expanding maize production to the dry regions is necessary to provide for the shortfall. In these areas however, the major constraint is drought caused by irregular rainfall distribution and this is accentuated by the low water holding capacity of the soils. At the same time, maize is grown without irrigation due to the high cost of installation of irrigation facilities, which of the resource-poor smallholder farmers cannot afford.

Drought affects maize grain yield by suppressing plant growth and development at all stages of the growth cycle, but the maize crop is most sensitive during the flowering

period (Bänziger et al., 2000). Complete barrenness can occur if maize plants are stressed in the interval from just before tassel emergence to the beginning of grain filling (Grant et al., 1989). Escaping drought by manipulating the planting date and using early maturing varieties is an effective strategy for the early and later parts of the growing cycle. However, this does not address the problem of drought occurring in the middle of the main growing season, when maize is at the flowering stage. Selection and breeding for drought tolerance is one way of reducing the impact of water deficit on crop yield. Edmeades et al. (1999) demonstrated that drought tolerance can be obtained in lowland tropical maize populations by either recurrent selection to increase the frequency of drought-adaptive alleles, or by assembling populations from sources in which these types of alleles are already present at a relatively high frequency.

Farmers in the semi-arid areas in Kenya use mainly unimproved maize landraces, where most of the maize is planted using farm-saved grain as seed. Thus, the improvement of maize landrace populations from these dryland areas, which can be used to develop open-pollinated varieties (OPVs), becomes an option. Improved OPVs are yielding than landraces, with less risk than hybrids regarding availability and the cost of the hybrid seed is prohibitive to the resource-poor farmers. Currently, public institutions such as CIMMYT and IITA are investing considerable resources developing and promoting OPVs for the marginal areas in their maize breeding programmes as an alternative to the landraces and hybrid varieties (Pixley and Bänziger, 2004; Pixley, 2006). The purpose of this research, therefore, was to assess the progress of selection for drought tolerance in dryland maize populations while maintaining high yields and genetic variability.

Information about heterotic patterns is essential in a maize breeding programme in order to maximize the use of genetic resources. However, information on possible heterotic groups and patterns of the maize landrace populations grown by farmers in the semi-arid eastern Kenya is lacking. Knowledge of the heterotic groups and heterotic patterns of these populations is useful in that they can be improved *per se* and used to broaden as well as diversify the genetic base of the existing maize breeding populations in Kenya.

Farmer preferences for drought tolerant varieties have not been well documented, hence, this information is lacking. At the same time, there is low adoption of improved varieties in the semi-arid eastern Kenya. Njoroge and Ngure (1986) reported that about

70% of the farmers in this region did not grow the recommended and available commercial maize varieties. Farmers' perceptions of drought and drought tolerant varieties have to be captured and included in varietal development. In addition to drought tolerance, farmers sometimes have certain preferences which breeders might be unaware. This, therefore, makes a participatory breeding approach a way integrating farmers' experiences in the breeding objectives. In order to capture the farmer preferences and incorporate their views into the maize breeding, therefore, it is necessary to conduct a participatory rural appraisal. This is expected to increase the adoption of the developed maize varieties.

General Objectives

The main objectives of the study were to improve drought tolerance in maize populations in semi-arid eastern Kenya, using S_1 family recurrent selection, and to classify collected landraces according to their heterotic patterns.

Specific Objectives

The objectives of the study were to:

1. assess farmers' perception of, and preference for, drought tolerant traits in maize varieties grown in semi-arid eastern Kenya;
2. determine the changes in genetic variability in five maize populations after two cycles of recurrent selection;
3. determine the genetic gain in drought tolerance and other agronomic traits of maize populations in semi-arid eastern Kenya after two cycles of recurrent selection and
4. determine the heterotic patterns and combining ability of the landraces in semi-arid eastern and coastal Kenya.

Hypotheses

The following hypotheses were tested:

1. The farmers in south eastern Kenya have knowledge of which traits contribute to drought tolerance in a maize variety;
2. Sufficient genetic variability is maintained in five maize populations after two cycles of recurrent selection;
3. Recurrent selection improves drought tolerance and other agronomic traits of maize populations in the semi-arid eastern Kenya after two cycles of recurrent selection;
4. The landraces from the semi-arid eastern and coastal Kenya belong to the same heterotic group.

Structure of the Thesis

The thesis is presented in the following order:

1. General introduction
2. Chapter one: Literature review
3. Chapter two: Farmers' perception on drought and preferences for drought tolerant traits in maize varieties in south eastern Kenya
4. Chapter three: Response to two cycles of S_1 progeny recurrent selection for drought tolerance and effect of selection on genetic variability in maize populations in semi-arid eastern Kenya
5. Chapter four: Heterotic patterns and combining ability of some maize landraces from south eastern and coastal Kenya
6. Chapter five: Overview of the thesis and way forward

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Chapter 1: Literature Review

1.1 Drought and its Effects in Maize

Drought is the main abiotic factor most responsible for limiting maize production and productivity in the developing world (Edmeades et al., 1992). May and Milthorpe (1962) defined drought as a meteorological and environmental event which is caused by the absence of rainfall for a period of time long enough to cause depletion of soil moisture and damage to plants. Agricultural drought is said to exist when the level and distribution of precipitation is sufficiently low to cause serious shortfalls in crop yields (Hulse, 1989). A plant experiences drought when the demand from the above ground parts for water exceeds the supply from the roots. Water uptake by a plant is based on the phenomenon of soil-plant-atmosphere continuum (SPAC), which is dependent on available gradient of potential among these three components (Zaidi, 2002).

Drought stresses affect both physiological and biochemical processes that in turn affect photochemical and photosynthetic activities of the plant, thereby affecting agronomic traits (Ronno, 1999). Plant damage is therefore a consequence of a disturbance of these processes. Hugh and Richard (2003) attributed the yield reduction in maize, due to drought stress, to three main mechanisms: (i) reduced canopy absorption of incident photosynthetically active radiation (PAR), (ii) reduced radiation use efficiency (RUE), and (iii) reduced harvest index (HI). The effect of water stress therefore depends on the growth stage at which it occurs. In general, water stress, except at the most critical time, will have less effect on the yield of grain than on the plant's total growth (Arnon, 1982). Maize is considered more susceptible than most other cereals to drought stresses at flowering, when yield losses can be severe through barrenness, due to complete pollination failure, or reduction in kernels per ear (Campos et al., 2006). Thus evaluating maize that is moisture stressed during flowering makes it possible to identify maize genotypes capable of maintaining a shorter anthesis-silking interval and achieving high grain yields (Magorokosho et al., 2003).

1.1.1 Flowering, Pollination and Grain Filling

There is abundant evidence showing that in cereal grain crop's life cycle, the most sensitive period to drought, is the stage of floral development and flowering. Desiccation at this time frequently causes a reduction in the number of seeds set by the plant and even if a subsequent improvement in water availability occurs, yield remains depressed (Salter and Goode, 1967). Maize being a cross-pollinated crop is more sensitive than other cereals to water deficits and high temperature at flowering, because anthers are separated in space by about 1cm on the plant and pollen and stigma are fully exposed to the environment (Bolaños and Edmeades, 1993b).

In maize, water deficits can disrupt reproductive development and induce large yield reductions. Water deficit at flowering will impair the development of flower primordia, while anthesis and fertilization will not be fully effective. Moisture regime during this phase largely determines the number of fruits which will be produced (Grant et al., 1989). The effects are largest around anthesis and pollination, when grain number can be decreased (Zinselmeier et al., 1995) and this has been attributed to abnormal embryo-sac development (Moss and Downey, 1971) or decreased silk receptivity (Bassetti and Westgate, 1993b), depending on when water deficits occur. Nesmith and Ritchie (1992) recorded a yield reduction as high as 90% and an incidence of barrenness reaching 77%, when plants were stressed in the interval from just prior to tassel emergence to the beginning of grain filling. Studies on the timing of drought stress have indicated that flowering is the most sensitive stage for yield determination in maize and losses in grain yield and kernels per plant can exceed 50% when drought coincides with this period (Bolaños and Edmeades, 1993b). All these can be attributed to the fact that maize being outcrossing, pollen must be transferred from the anthers at the top of the plant to the exposed silks of the same plant and the surrounding ones. Thus, in a dry environment both the female and the male flowers are subject to desiccation before pollination.

Drought also increases the anthesis-silking interval (ASI) (DuPlessis and Dijkhuis, 1967; Edmeades et al., 2000). Hence, pollen can reach the silks after it has desiccated, or when silks have withered or senesced (Bassetti and Westgate, 1993a, b) or after ovaries have exhausted their starch reserves (Zinselmeier et al., 2000; Bruce et al., 2002). This leads to a decrease in the grain number formed in the maize ear. Delayed silk

emergence may be due to a reduced rate of silk elongation, a process which is strongly affected by plant water status. It has also been associated with reduced photo-assimilation per plant caused by high plant density (Bolaños and Edmeades, 1993b). In this context, ASI is considered more valuable as a diagnostic trait of cultivar performance than silking date per se, since ASI is largely independent of maturity among cultivars. The ASI has been one component of selection index used to identify superior genotypes for recombination during recurrent selection programmes in CIMMYT, for improved performance of maize under drought (Bänziger et al., 2004).

During grain filling, the supply of assimilates determines the extent to which ears, kernels and endosperm cells established during flowering are filled. Thus, if the crop is exposed to drought at this critical stage, grain filling is adversely affected, resulting in small or shrivelled grains (Zaidi, 2002). However, the effects of stress during grain maturation are far less marked than during flowering. Wardlaw (1967) found in wheat (*Triticum aestivum*), that the development of the grain, which constituted the main “sink” for the flag leaf assimilates, was initially unaffected by a water deficit that caused wilting of the leaves and reduced photosynthetic rates. The reduced photosynthetic activity of the leaves and ear were compensated by an increased translocation of assimilates to the grain from the lower parts of the plant (Arnon, 1982).

The efficiency of selection for drought tolerance depends, in part, upon an understanding of drought-sensitive periods in the crop’s phenology so that tolerance is not confounded with drought escape. Where drought stress is induced by withdrawal of irrigation, or by the onset of a dry season, moisture stress increases with time. In these circumstances, early maturing cultivars may be identified incorrectly as drought tolerant because they complete stress-sensitive processes, such as flowering or grain filling, at lower stress levels than their late maturing counterparts (Bolaños and Edmeades, 1993b).

1.1.2 Grain Yield

Soil and plant water deficits limit the yield of many crops and it has been reported in a large body of literature that water deficits limit yield and/or that irrigation increases yield (Turner, 1979). Grain yield is the product of many growth processes occurring throughout the development of the plant. In *Gramineae*, these include the number and growth rates of inflorescences and the number and growth rates of the seeds set. These processes are in turn integrated with leaf growth and senescence to form a balanced system of sources and sinks for assimilates and nutrients. All these processes are affected by water stress which results in yield reduction (Morgan, 1984). Yield can be analyzed in terms of three components: (i) the number of ears ha^{-1} , (ii) the number of grains ear^{-1} , and (iii) the mean weight grain $^{-1}$. These components are determined at different stages of growth and so are affected in different ways by drought (Austin, 1989).

The effect of water stress on yield will depend largely on what proportion of the total dry matter produced is considered as useful material (Fisher and Hagan, 1965). For grain crops, where the dry matter is stored in the seeds or grain, photosynthesis that occurs after flowering is the limiting factor (Throne, 1966). The effect of water stress will, therefore, depend on the stage of growth at which it occurs.

Grain yields in maize have been reported to be sensitive to moisture stress especially during the period beginning approximately at silking and continuing through grain filling (Grant et al., 1989). The critical development period of determining grain yield in maize, centres on flowering and early grain filling (Boyer and Westgate, 2004). This is due to water-stress inhibiting the flow of photosynthates during both ovule/pollen and seed development (Moreno et al., 2005).

This information on the critical stage, in the growth stage of maize, to drought stress is useful in the improvement of drought tolerance in maize, as regards to when to apply moisture stress. In the current study, moisture stress was induced at flowering, which is the critical stage, with the objective to select germplasm that tolerates water stress and still give high yields.

1.2 Mechanism of Adaptation to Drought Stress in Maize

The ability of a crop species or variety to grow and yield satisfactorily in areas subjected to periodic water deficits has been termed as drought resistance (Ashley, 1993). No distinction is usually made between drought resistance and tolerance as the two terms are used interchangeably. Several morphological, anatomical, physiological and biochemical attributes of a plant confer drought resistance. These attributes, which confer drought resistance, can occur singly or together in any plant. These adaptations can be heritable or non-heritable, constitutive or facultative (Turner, 1986a). Turner (1979) suggested that the mechanisms of adaptation to water deficits can be divided into three categories:

1. Drought escape: The ability of a plant to complete its life cycle before serious soil and plant water deficits develop;
2. Drought tolerance with low plant water potential: the ability of a plant to endure periods without significant rainfall and endure low tissue water status i.e., dehydration tolerance;
3. Drought tolerance with high plant water potential: the ability of the plant to endure periods without significant rainfall whilst maintaining a high plant water status i.e., dehydration postponement.

Drought escape is the ability of a plant to complete its life cycle before the onset of severe soil water deficits. In nature, drought escapers are characterized by rapid phenological development after the incidence of rain and extension of the reproductive phase of development while good soil moisture conditions prevail (Turner, 1986b). Earliness, however, reduces the potential yield of the crop by reducing the dry matter at anthesis and the sites for post-anthesis grain filling (Turner, 1986a), resulting in lower yields in years of adequate water supply (Magorokosho et al., 2003). A mild water deficit between floral initiation and anthesis has been shown to hasten anthesis and maturity in wheat (Turner, 1979).

Drought tolerance with low plant water potential, allows the plants to sustain osmotic stress through the re-establishment of cellular homeostasis, the structural and functional protection of proteins and membranes (Moreno et al., 2005). The major mechanism of turgor maintenance is osmotic adjustment through the accumulation of solutes under

conditions of water deficit thereby decreasing the osmotic potential and increasing turgor pressure of the cells (Turner, 1986b). Osmotic adjustment is considered to influence a range of physiological processes. It maintains stomatal opening and photosynthesis to lower leaf water potentials (Turner, 1986a). Tolerance to dehydration is considered to arise at the molecular level and depends on membrane structure and enzyme activity. It depends on the ability of the cells to withstand mechanical injury, the ability of the membranes to withstand degradation and the ability of the membrane and cytoplasm to withstand denaturing of proteins (Gaff, 1980).

Drought tolerance with high plant water potential permits the plants to reduce water loss from leaves by regulating stomatal function, or to increase water absorption by adapting root architecture (Moreno et al., 2005). Maintenance of water uptake requires the development of roots into water-containing soil and their continued extraction of water in the absence of rain. The growth of roots into deeper soil layers is a function of both genotype and environment (Turner, 1986a). Mechanisms for reducing water loss include decreased stomatal conductance, leaf rolling and a decrease in leaf area. However, all these processes decrease productivity (Turner, 1979). They increase water use efficiency by reducing water loss at critical times of the day when water vapour pressure deficits are large, but allow photosynthesis to continue in the early morning or late afternoon when vapour pressure deficits are less severe. Midday stomatal closure and leaf wilting or leaf rolling allow this. Likewise, a reduction in photosynthesis and water use early in the life of the plant may enable a greater grain yield to be achieved by conserving water for the period after anthesis (Passioura, 1977).

1.3 Genes Controlling Drought Tolerance in Maize

Water-deficit stress leads to a series of physiological and molecular responses that will enable plants to overcome this unfavourable situation. These responses are controlled by several hundreds of genes conferring drought tolerance to crops. These genes have already been identified and characterized (Coraggio and Tuberosa, 2004). The products of these genes are thought to function directly or indirectly in protecting cells from dehydration (Ingram and Bartels, 1996), and can be classified into two groups: functional proteins and regulatory proteins (Moreno et al., 2005). The functional proteins include

proteins that participate in stress tolerance. These proteins include (i) aquaporins and ion channels, (ii) enzymes required for the biosynthesis of various compatible solutes, (iii) osmoprotectants such as late embryogenesis abundant (Lea) proteins and chaperones, and (iv) detoxification enzymes. The regulatory proteins consist of proteins that are involved in dehydration/abscisic acid (ABA) signal transduction cascades and gene expression regulators. These include (i) metabolic enzymes, (i) protein kinases and phosphatases, and (i) transcription factors (Shinozaki and Yamaguchi-Shinozaki, 1997). Recently, genetic screening has allowed the identification of a set of genes induced in maize seedlings during water-deficit stress which include enzymes of amino acid and carbohydrate metabolism, kinases and transcription factors that are thought to be involved in drought signalling pathway (Zheng et al., 2004). In the current study, drought was imposed during the reproductive stage and as such, genes that are expressed during this time of the crops' growing stage were selected for.

1.4 Breeding for Drought Tolerance in Maize

With most maize in the developing world being grown under rain-fed conditions and the proportion of maize grown in marginal areas increasing, breeding for maize cultivars with high and stable grain yields under drought is an important priority. Moreover, the use of drought tolerant cultivars may be the only affordable option for many small-scale farmers (Bolaños and Edmeades, 1993a).

There has been considerable effort devoted to breeding for improved drought resistance in cultivars of major crops, although there has been little progress. There are many reasons for this. The most obvious is that selecting for drought resistance is difficult, as the response is complex and it interacts with other factors such as high temperature and nutrient uptake. Moreover, further problems exist in obtaining a consistent response following the exposure of large plant populations to conditions which simulate realistic drought conditions in the field (McWilliam, 1989). In breeding for drought tolerance, one needs to identify the type of drought that the crop is likely to encounter. Using cluster analysis, five types of drought crops encounter have been identified as: early drought; mid-season drought; late-season drought; drought with relief near harvest; progressive moderate drought and progressive severe drought (Turner, 1986b).

Due to the low heritability of yield under drought, secondary traits (in contrast to the primary trait i.e., yield) whose genetic variances increase under stress or are reduced less than that of yield, can increase selection efficiency provided they have a clear adaptive value under stress, relatively high heritability and are easy to measure (Bolaños et al., 1993; Bolaños and Edmeades, 1996). This means that the alternative physiological characters associated with drought resistance must be employed to augment selection for yield (Fischer et al., 1989).

According to Edmeades et al. (1998), secondary traits have maximum utility in selection when they are: (i) genetically associated in a desired direction with grain yield under stress; (ii) highly heritable; (iii) cheap, fast to measure and non-destructive; (iv) stable over the measurement period; (v) observed at or before flowering, so that undesirable parents are not crossed; (vi) an estimator of yield potential before final harvest; (vii) not associated with yield loss under non-stressed conditions; and (viii) an actual measurement rather than a subjective score, when being used for QTL analysis. The following secondary traits according to Bänziger et al. (2000) are normally used in selecting for drought tolerance: ears per plant, anthesis-silking interval (ASI), leaf senescence, tassel size and leaf rolling. Bolaños and Edmeades (1993b) using secondary traits in selecting for improved drought tolerance in Tuxpeño Sesquía maize population for six cycles of recurrent selection, reported a 14% increase cycle⁻¹ in ear mass and a reduction of 1.7% cycle⁻¹ in tassel size under drought.

Edmeades et al. (1999) have demonstrated that drought tolerance can be obtained in lowland tropical maize populations either by recurrent selection to increase frequency of drought-adaptive alleles or by assembling populations from sources in which these types of alleles are already present at a relatively high frequency. Breeding maize for drought prone environments has two major goals, to develop cultivars that can escape drought or those that are drought tolerant (Bänziger et al., 2000). Cultivars that escape drought mature early enough so as to complete their life cycle within a given season length. Drought tolerant cultivars, on the other hand, are characterized by increased production under drought (Bänziger et al., 2000). Numerous QTL studies examining drought tolerance and related traits in maize, rice (*Oryza sativa*), barley (*Hordium vulgare*) and wheat have demonstrated that drought tolerance is affected by several loci, each of which have relatively small effects (McCouch and Deorge, 1995; Quarrie, 1996). This

makes the use of recurrent selection methods appropriate in improving maize for drought tolerance.

1.4.1 Selection Strategy for Drought Tolerance in Maize

The major objective of any breeding programme is to improve yield potential. Thus, the choice of a selection strategy is critical to breeding for stress tolerance. Byrne et al. (1995) summarized three selection strategies that breeders use in selecting maize for drought tolerance: selecting only under well-watered conditions, selecting only under stress conditions, and selecting in a combination of stressed and unstressed environments.

Selection for high yields under optimal conditions is to breed for yield potential and then to assume that this will provide a yield advantage under suboptimal conditions. A review of breeding progress pointed out that selection for high yield in stress-free conditions has to some extent, indirectly improved yield in drought-prone environments (Cattivelli et al., 2008). Johnson and Gealdelmann (1989) found that gains from selection under well-watered conditions were equal to those from selection under drought stress when evaluated in stress conditions and that such gains were superior when evaluated in favourable conditions. However, Martinez-Barajas et al. (1992) found that progress from selection for high yield under well-watered conditions was greatly reduced under crop water deficits. This method, therefore, may not be effective in breeding for drought tolerance.

Selection only under stress conditions requires the identification of the characters in each generation. However, selection under drought compared with selection under non-stressed conditions has often been considered less efficient, because of a decline in heritability for grain yield under stress (Bolaños and Edmeades, 1996), as environmental variance rises and observed genetic variance falls (Johnson and Gealdelmann, 1989). This decline in heritability for grain yield is attributed to the fact that genetic variances for yield decrease more rapidly than the environmental variances among plots with increasing stress (Bolaños et al., 1993). Another drawback to this approach is that some traits that contribute to survival under drought may lower productivity under favourable

conditions (Ludlow and Muchow, 1990). However, this strategy was employed with reasonable success by Arboleda-Rivera and Compton (1974) who realized an increased yield in both stressed and unstressed environments. Using this strategy also, Zaidi et al. (2004) reported improved mid-season drought tolerance in tropical maize without significant yield penalties under optimal input conditions. Venuprasad et al. (2007) reported greater responses in rice from direct selection under stress than indirect selection under non-stress conditions.

Selection can also be undertaken using a combination of stressed and unstressed environments. This is the intrinsic goal of multilocational testing schemes although, in the presence of a large genotype x stress-level interaction, progress from selection based on combined data may be limited (Byrne et al., 1995). Using this strategy, Chapman and Edmeades (1999) reported increased grain yield under drought at flowering by 30 to 50% in three lowland tropical maize populations.

The choice of the best selection strategy to use for best results remains unresolved. This difficulty in choosing appropriate selection environments has restricted breeding progress for drought tolerance in highly-variable target environments (Bänziger et al., 2004). This has resulted in breeders using a combination of two or more methods in selecting maize for drought tolerance. In CIMMYT, for example breeders use three carefully managed water supply levels: (i) flowering drought stress, (ii) grain filling drought stress, and (iii) well-watered conditions. This screening approach has been reported to have wider merit (Bänziger and Meyer, 2002). Therefore, the decision on which selection method to use remains the prerogative of the breeder. In the current study, selection was done using the combination of both flowering and grain filling drought stresses.

1.5 Recurrent Selection

Recurrent selection has been practised ever since crop breeding became a profession, but the term “recurrent selection” was first coined by Hull (1945). It is a population improvement method, which involves cyclic selection in a breeding population to increase the frequency of favourable alleles and thus increasing the mean performance

(Doerksen et al., 2003). Except for mass selection, all recurrent selection methods include three distinct, but equally important phases: (i) sampling of individuals from target population and development of progenies, (ii) evaluation, and (iii) selection of progenies, and recombination of selected progenies. Each of these is very important and can dramatically influence progress towards goals of the recurrent selection programme (Weyhrich et al., 1998a).

Recurrent selection is commonly used for the improvement of quantitatively inherited traits by which the frequencies of favourable genes are increased whilst maintaining the genetic variability in populations of plants for future cycles of selection (Hallauer, 1992). The mean of the trait under selection will improve gradually and the shift will continue as long as genetic variability exists in the population. The recurrent selection programme should, therefore, maintain genetic variability within the population in order to facilitate improvement in future cycles of selection and its success is determined by evaluating improvement in the mean of the target population, as well as the best individuals (Schnicker and Lamkey, 1993). However, with selection, genetic variability in a population decreases until the selected alleles become fixed. Alleles are fixed rapidly and deleterious homozygous alleles are eliminated early in selection (Weyhrich et al., 1998a). This problem of reduction in genetic variability with selection is overcome by recombining an appropriate number of plants. The balance would be to recombine few individuals that a reasonable response could be expected in the short term, but not too few that a sharp decrease in genetic variance would compromise long term genetic progress (Weyhrich et al., 1998b). Hallauer (1992), after reviewing literature on effective population sizes, suggested that approximately 25-35 progenies should be intermated.

The populations considered in recurrent selection may include open-pollinated cultivars developed by intermating germplasm that possess specific traits, F_2 populations formed by intermating crosses of inbred lines, and populations that include exotic germplasm. Recurrent selection methods emphasize continued improvement of the same population, which may be either closed (no germplasm introduced) or open (germplasm introduced on either a regular or irregular basis). Recurrent selection programmes are usually planned on a long term basis. The number of individuals recombined in the recurrent selection programme, along with the breeding structure of the population, directly impacts the effective population size. The number also affects the genetic variation

remaining after selection, as well as the selection intensity. Both these variables are important in establishing and maintaining a desirable rate of progress from recurrent selection. Traditionally, maize breeders have recombined between 10 and 25 individuals in recurrent selection programmes (Weyhrich et al., 1998b). In the current study, 20 individual plants were recombined in each of the populations in the recurrent selection programme.

The improvement of maize populations through recurrent selection has been effective for increasing frequency of favourable alleles of economic value. These improved populations have been commercially used as open-pollinated varieties and in intervarietal hybrids, as well as sources of inbred lines (Ramírez-Díaz et al., 2000)). The rates of gain may not always be evident from cycle to cycle and, in some cases, erratic response can occur. However, a gradual improvement is realized (Hallauer, 1992). Doerksen et al. (2003) reported a genetic improvement in their maize population breeding programme. Previous estimates for grain yield improvement indicate that for different methods of selection in different populations, for the same method in different populations, and for different methods in the same populations, a 2 to 7% increase per cycle in grain yield can be expected, depending on the germplasm and selection method (Weyrich et al., 1998a). Similarly, Vales et al. (2001) reported a linear increase in grain yield in interpopulation crosses and in two Spanish synthetic populations with recurrent selection procedures.

1.5.1 Methods of Recurrent Selection

Various methods of recurrent selection and their application have been discussed by Hallauer and Miranda (1988). The improvement of maize through recurrent selection can be done either through intrapopulation selection or interpopulation selection methods, the former being more frequently used than the latter method in maize improvement because it is not as complex, flexible, and more amenable to use for most plant, ear and kernel traits (Hallauer, 1992).

1.5.1.1 Intrapopulation Recurrent Selection

Intrapopulation selection involves the improvement of one population. The most common methods are mass selection and family selection with all its variants: paternal or maternal half-sib families, full-sib families, or inbred lines S_1 and S_2 (Ramírez-Díaz et al., 2000). Mass selection involves the selection of plants from a population on the basis of their phenotype, bulk sowing of their seeds and growing of the next generation in order to obtain new cultivars or to maintain the varietal purity of existing cultivars. It can be applied to both self-pollinated and cross-pollinated crop species and its success depends to a large extent on the heritability of the desired traits (Borojević, 1990). Selection for traits with low heritability is relatively ineffective, because plants superior due to genotype may not be distinguished from plants superior due to environmental effects. Since selection is based on the maternal parent only, and there is no control over pollination, this amounts to a form of random mating with selection (Hallauer and Miranda, 1988). Mass selection has been used to improve grain yield, to change ear length, kernel size, maturity and to increase the number of ears in maize (Hallauer, 1992)

Half-sib family selection procedure is based on a progeny test and the new population is constituted by compositing half-sib lines selected from progeny performance rather than from phenotypic appearance, as is the case with mass selection. Half-sib in this case refers to plants with a common parent or pollen source (Hallauer, 1992). Half-sib family selection method has been used to improve grain yield in maize (Hallauer, 1992) and Feng et al. (2004) reported an increase of soybean (*Glycine max*) oil content at a rate of $1.1 \pm 0.2\text{g kg}^{-1}\text{cycle}^{-1}$.

With full-sib family selection, crosses are made between selected pairs of plants in the source population with the crossed seed used for progeny tests in a replicated trial and the remnant full-sib seed used to recombine the best families. Each cycle requires two seasons and new full-sib families are obtained from the recombination block (Hallauer and Miranda, 1988). Theoretically, the full-sib method is more efficient than mass or half-sib methods, since it allows parental control and, therefore, the selection response is of greater magnitude, but its disadvantage is that it is more expensive than the others due to the creation of families using manual pollination (Ramírez-Díaz et al., 2000). Moll (1991) reported a 2.4% gain cycle⁻¹ in maize grain yield after 16 cycles of full-sib family

selection. It has been used to reduce plant height and to increase resistance to root lodging (Ramírez-Díaz et al., 2000). Recurrent selection for performance under drought practised among 250 full-sib progeny in Tuxpeño maize population for eight cycles increased grain yields by 9.5% per cycle (Edmeades et al., 1986). Bruce et al. (2002) reported improved performance of 126 kg ha⁻¹ cycle⁻¹ in elite lowland tropical white dent and Tuxpeño Sesquía maize populations after 28 cycles of recurrent selection among full-sib and/or S₁ families. Omuigui et al. (2006) reported an increase in genetic gains in tropical maize populations of 2.3% after three cycles of full-sib recurrent selection for low nitrogen tolerance. Pixley et al. (2006) demonstrated increased resistance to maize streak virus and other traits in maize by selection using full-sib families.

In selfed progeny selection schemes, the selection units are either S₁ or S₂ family means compared with the grand mean of all the S₁ or the S₂ families, respectively. Remnant seeds from the selfed ears are used for recombination (Hallauer and Miranda, 1988). Selfed progeny selection is considered to be superior to other methods of recurrent selection for the improvement of the population *per se*, since alleles are fixed rapidly and deleterious homozygous alleles are exposed and eliminated early in selection (Doerksen et al., 2003). The additive genetic variance available for selection among selfed families (S₁ and S₂) is greater than that among half-sib and full-sib families. Selection among S₁ or S₂ families is useful for characters having low heritability, because a larger portion of additive genetic variance contributes to genetic advance than with full-sib or half-sib selection. S₁ recurrent selection has been used in the improvement of performance in various crops. Using S₁ family selection, Ramírez-Díaz et al. (2000) managed to effectively modify ear and plant heights as well as reduce ear rot and root lodging rates in maize. Zaidi et al. (2004), using S₁ families to improve maize populations for drought tolerance, found decreased ear abortion and increased assimilate supply during grain filling. Chapman and Edmeades (1999) reported that under drought, 12.6% gain per cycle was achieved using S₁ recurrent selection in tropical maize populations. After three cycles of recurrent S₁ selection in La Posta Sesquía and pool 26 Sesquía there was a 38% increase in grain yield in water stressed environments (Edmeades et al., 1999). In the current study, the S₁ recurrent selection method was used to improve drought tolerance in maize populations in semi-arid eastern Kenya.

1.5.1.2 Interpopulation Recurrent Selection

Interpopulation recurrent selection (reciprocal recurrent selection) is a cyclical breeding procedure in which progressively improved populations of two germplasm pools are used reciprocally as testers and direct effects of selection are estimated in the population cross (Doerksen et al, 2003). Interpopulation recurrent procedures are appropriate only when heterosis is important in cultivar crosses and exploits all types of gene action responsible for heterosis. Its important feature is that selection is toward the improvement of populations themselves as well as the increase of heterosis in the crossed population. In all instances, crossed families are evaluated in replicated trials (Hallauer, 1992). Interpopulation half-sib or full-sib progenies are used as evaluation units and interpopulation S_1 progenies as recombination units (Santos et al., 2005).

Reciprocal recurrent selection has been effective for improving grain yield *per se* of maize populations, especially their crosses (Moreno-Pérez et al., 2004), root lodging and stalk lodging, with small or desirable changes in other agronomic traits (Schnicker and Lamkey, 1993.). It was highly effective in improving grain yield and prolificacy in IG-1 and IG-2 maize populations and directly related to the improvement of hybrids from inbred lines (Santos et al., 2005). Betrán and Hallauer (1996), using this procedure, have shown that single-crosses developed from advanced cycles of selection showed higher yields and lower lodging than those from original non-improved populations.

1.6 Heterosis and Heterotic Patterns

The term heterosis, coined by Shull, was first proposed in 1914 and is described in terms of superiority of F_1 hybrid performance over some measure of the performance of the parents (Stuber, 1994). Although many hypotheses have been suggested to explain heterosis, its genetical, physiological and biochemical bases still remain largely unexplained (Reif et al., 2005). The manifestation of heterosis usually depends on genetic divergence of the parental varieties. Genetic divergence of the two parental varieties is inferred from the heterotic patterns manifested in the series of variety crosses (Hallauer and Miranda, 1988). If heterosis between the two parental varieties is large, then it shows that the two parents are genetically diverse. To fully exploit heterosis in

hybrid breeding, the concept of heterotic groups and patterns was suggested and knowledge of heterotic patterns can contribute to broadening of the maize breeding germplasm base (Mungoma and Pollak, 1988).

A heterotic group as defined by Melchinger and Gumber (1998), “is a group of related or unrelated genotypes from the same or different populations which show similar combining ability or heterotic response when crossed with genotypes from other genetically distinct germplasm groups and by comparison heterotic pattern refers to a specific pair of two heterotic groups which express high heterosis and consequently high hybrid performance in their cross”. The establishment of heterotic patterns among varieties is important in selecting inbred lines as parental seed stocks in hybrid production. Examples for determining heterotic patterns of varieties and diversity in the manifestation of heterosis were reported by Moll et al. (1965).

1.6.1. Methods of Studying Heterotic Patterns

There are various ways which can be used to group different maize populations into different heterotic patterns. Heterotic patterns can be analyzed either by crossing the germplasm in question with common testers which are known to be of different heterotic patterns, using molecular markers or by crossing the germplasm in a diallel mating system. To assign germplasm into different heterotic patterns, Reif et al. (2005) suggested two strategies to be used: (i) a higher mean heterosis and hybrid performance and (ii) a reduced specific combining ability variance and a lower ratio of specific combining ability to general combining ability variance ($\delta^2_{SCA}:\delta^2_{GCA}$).

The testers are usually broad based (open-pollinated varieties) and can be two or more. The lines are crossed to these testers and the crosses evaluated in a replicated trial in order to determine the performance of these crosses in relation to the parents and the testers. Heterosis can either be determined by using the average performance of the two parents (mid-parent heterosis) or the high parent heterosis (Hallauer and Miranda, 1988). Based on the evaluation of the test crosses, the varieties can then be assigned to various gene pools, depending on their heterotic patterns. Examples of determining

heterotic patterns of maize varieties or populations using testers have been reported by Santos et al. (2001) and Mosisa et al. (1996).

The diallel mating design has been largely utilized to identify heterotic patterns and it involves the crossing of a number of parents in all possible combinations (Melani and Carena, 2005). The parents used in the diallel mating system can either be a set of inbred lines or individuals from a heterogeneous random mating population, such as an open-pollinated variety. The diallel design has been the most widely used for estimation of variances in crop plants (Christie and Shattuck, 1992). The data from the evaluation of crosses is used to estimate variances due to general and specific combining abilities. A reduced specific combining ability variance and a lower ratio of specific combining ability to general combining ability ($\delta^2_{SCA}:\delta^2_{GCA}$) implies that the two parents that formed the cross are not genetically divergent and could belong to the same heterotic group (Reif et al., 2005). Mungoma and Pollark (1988) also used the diallel mating system to study the heterotic patterns of yellow and white-endosperm American and South African maize populations. Similarly, Viana and Matta (2003) used diallel analysis to group popcorn maize populations into inter- and intra-population breeding programmes. Like the diallel mating design, any other mating design that produces hybrids for evaluation can be utilized to identify heterotic patterns among population crosses.

Genetic diversity can also be studied using molecular or DNA markers, which reveal sites of variation. These markers arise from different classes of DNA mutations such as substitutions (point mutations), rearrangements (insertions or deletions) or errors in replication of tandemly repeated DNA. They are selectively neutral because they are usually located in non-coding regions of DNA (Collard et al., 2005). The most common molecular markers that have been used to estimate genetic diversity include restriction fragment length polymorphism (RFLP), random amplified polymorphic DNA (RAPD), single sequence repeats (SSRs) or microsatellites and amplified fragment length polymorphism (AFLP). Farooq and Azam (2002) have reported that RFLP markers are the most reliable, as exemplified in wheat, sugar cane (*Saccharum* spp), alfalfa (*Medicago sativa*), rice, and several other crop species. These markers are also robust and transferable across populations. However, RFLP markers are time consuming, laborious and expensive (Beckmann and Soller, 1986). Thus, this limits their application. Random amplified polymorphic DNA markers are quick and simple to obtain, enabling

genetic diversity analyses in several types of plant materials, such as natural populations, populations in breeding programmes and germplasm collections. However, they have problems with reproductivity and are not transferable (Collard et al., 2005). Warburton et al. (2005) characterized 218 elite CIMMYT maize inbred lines using 32 RFLP markers and defined their heterotic groups. Betrán et al. (2003) also used RFLP markers to determine the genetic diversity within a set of tropical maize lines and classified them according to their genetic distances.

Single sequence repeats (SSRs) are technically simple, robust, reliable and transferable between populations and are commonly. Their only limitation is that they are time consuming during their development and require labour for the production of primers (Collard et al., 2005). Xia et al. (2004) investigated genetic diversity with SSRs among CIMMYT lowland tropical maize inbred lines and grouped them into two heterotic patterns. Barata and Carena (2006) also used SSRs to classify elite North Dakota maize inbred lines into heterotic groups. Teng and Li (2004) also used these markers to classify maize populations in China into different heterotic groups and patterns.

Amplified fragment length polymorphisms (AFLPs) are multi-loci and high levels of polymorphism are generated. The limitation to their application is that large amounts of DNA are required and it is a complicated method (Collard et al., 2005). This method has been utilized to identify heterotic patterns in maize populations.

The weakness of molecular markers is that the genetic distance identified does not necessarily translate into heterosis. In a study of ten maize varieties, Prasad and Singh (1986) reported that heterosis was not linearly related to genetic divergence since most of the diverse parental varieties did not necessarily show the greatest heterotic response. Thus, the results of molecular markers should be verified by evaluation of the crosses in replicated field trials.

1.6.2. Status of Heterotic Patterns in Different Regions

There are roughly 250 races of maize in the world and they are either temperate or tropical. Temperate maize populations are grouped into two main heterotic groups, the flints and the dents, which have evolved separately over the last 2500 years (Troyer,

1999). Tropical maize, however, has a broad genetic base and shows greater genetic diversity than temperate maize. The tropical germplasm, however, cannot be classified as easily as temperate germplasm, due to different breeding practices and objectives, including a strong effort towards open-pollinated variety (OPV) development (Warburton et al., 2005). The following paragraphs present the maize heterotic patterns in various regions of the world.

In America, particularly in the US, the main group is the dent type. Within this group there are numerous populations that are generally referred to as the old open-pollinated (OP) populations e.g. Leaming, Krug, Lancaster, Ohio Queen (Warburton et al., 2005; Lee, 2007). The main heterotic groups as listed by Reif et al. (2005) are Reid yellow dent (Wf9, LH80 types), germplasm comprising of Iodent Reid (LH82 and MBS402), Troyer dent, Osterland dent, Stiff stalk synthetic (B14, B37, B73 types), Reid *per se* and Funk Reid, Minnesota, Lancaster (C103, Oh43 types), Sure Crop, North Western dent and Leaming corn.

In Europe, the flint and dent are the major groups in the north, and Lancaster and long stiff stalk predominate in the southern parts (Warburton et al., 2005). Rebourg et al. (2001) studied 130 European traditional maize populations using RFLP analysis and grouped them into six major groups, namely: German flint, North-Eastern European Flint, Southern European Flint, Italian Orange Flint, Pyrenees-Galicia Flint and the Czechoslovakian type.

The maize heterotic groups being utilized in China are both native and introductions from America. The native group consists of Tangsipingtou and Ludahonggu while the exotic consist of Reid Yellow Dent, Lancaster Sure Crop and germplasm derived from the Pioneer hybrids (Teng and Li, 2004; Reif et al., 2005).

Maize germplasm accessions in Kenya were acquired through both local collections and exotic introductions. These have been characterized into different heterotic groups according to the different maize agro-ecological zones in Kenya (KARI, 1992). The national maize improvement programme is divided into five broad mega-environments, each of which encompasses a number of agro-ecological zones. These are: Coast (0-1000 m), mid-altitude moisture stressed (1000-1600 m), mid-altitude non-moisture

stressed (1600-1700 m), high altitude (1700-2300 m) and very high altitude (over 2300 m) (KARI, 1992). Generally, there are eleven major maize heterotic groups in Kenya. The high altitude programme has three heterotic groups; Kitale Synthetic I and II, and Ecuador 573. The mid-altitude programme has six heterotic groups; Embu 11, Embu 12, Muguga A, Muguga B, Kakamega pool A and Kakamega pool B (KARI, 1992; KARI, 2000). The eastern and coastal regions have no known existing heterotic patterns in their maize breeding programme. This is largely because the main objective of maize breeding in these regions has been to produce mainly open-pollinated varieties rather than hybrids. The eastern and coastal regions fall under different agro-ecological zones and they are geographically separated far apart. Farmers in these two regions grow different types of maize landraces which they have been passing on from generation to generation. Thus, there could be some variability in these landrace populations. In view of this, an attempt was made in the current research to identify heterotic groups in these regions using the maize landraces collected from the framers.

1.7 Participatory Rural Appraisal

Participatory rural appraisal (PRA) tools are usually applied to capture farmers' perceptions and preferences (Odendo et al., 2002). Formal plant breeding approaches have been less effective in doing so, as is evident in both the slow adoption of improved varieties by farmers, and the lack of breeding progress in the performance of adopted varieties under low input conditions (Bänziger and Cooper, 2001). Farmers have an extensive knowledge of their environments, crops and cropping patterns, built up over many seasons and generations (Bänziger et al., 2000). Therefore, an assessment of attributes of maize varieties preferred by farmers, and the socio-economic environment under which the farmers operate, is an important starting point. The acceptability of new varieties and production packages by farmers depends on how well researchers have identified farmers' objectives and constraints (Upton, 1987).

Farmer evaluations help scientists to design, test and recommend innovations. In this context, farmer participation is crucial as it allows for the incorporation of farmers' indigenous technical knowledge, identification of farmers' criteria and priorities, and appropriate definition of the research agenda. Participatory rural appraisal is designed to

better incorporate perspectives of the end users rather than formal plant breeding, reach resource-poor farmers, breed for high-stress and diverse conditions, and incorporate wide variation in traits for specific client preferences (Dorward et al., 2007). Therefore, by integrating farmers' concerns and conditions into agricultural research, it is hoped that research will develop drought tolerant maize varieties that will be widely adopted, resulting in more productive, stable, equitable and sustainable agricultural systems. Thus, in the current study, a PRA was carried out to assess the farmers' perceptions of, and preferences for, drought tolerant traits in maize varieties in semi-arid eastern Kenya. Their views were thereafter considered during selection for the improvement of maize populations for drought tolerance.

Since the introduction of PRA into Kenya in the mid-1980's (Lelo et al., 1995), several PRA studies have been conducted in the country. Bett et al., 2000: Ouma et al., 2002 conducted PRA studies in eastern Kenya and reported that maize is the most important crop grown in the region, and constraints to its production were mainly drought and soil fertility. However, none of the PRA studies done in eastern Kenya has specifically addressed the farmers' perception of drought tolerance and preferences for drought tolerant traits in maize varieties. It was for this reason that, in the current study, a PRA was carried out to address these issues.

1.8 Summary

Literature review established that:

Drought is the main abiotic factor responsible for significant yield losses in maize production in semi-arid areas. Maize is most sensitive to drought during the reproductive stage, i.e. flowering to grain filling stages. Drought occurring during this period causes a delay in silking resulting in an increase in anthesis-silking period resulting in lack of synchronization between silking and anthesis. Therefore, an understanding of the drought-sensitive period in the maize plant's growth cycle will improve the efficiency for selection for drought tolerance.

Crops have evolved various mechanisms to cope with water-deficit periods. These are: drought escape, drought tolerance with low water potential and drought tolerance with high water potential. These drought tolerance mechanisms are controlled by several genes that have already been identified and characterized. The products of these genes are thought to function directly or indirectly in protecting cells from dehydration and can be classified into two groups: functional proteins and regulatory proteins.

Owing to the complexity of drought tolerance, direct selection for drought tolerance using yield alone is not efficient. Thus, this necessitates the use of indirect selection using secondary traits such as number of ears per plant, anthesis-silking interval, leaf senescence, tassel size and leaf rolling. Selection for drought tolerance can either be done under optimal conditions, under drought conditions or a combination of both strategies. The most common practice is to use a combination of both strategies and carryout multilocational testing.

The improvement of maize for drought tolerance can be undertaken using recurrent selection procedures, through either intrapopulation or interpopulation selection. Intrapopulation selection methods are mass selection and family selection with all its variants: paternal or maternal half-sib families, full-sib families, or inbred lines S_1 and S_2 .

Knowledge of heterosis and heterotic patterns is important in breeding maize hybrids. Methods of identifying heterotic patterns are: crossing the germplasm with testers, using molecular markers or crossing the germplasm in a diallel mating system. To assign the germplasm into different heterotic patterns two strategies can be used:(i) a higher mean heterosis and hybrid performance and (ii) a reduced specific combining ability variance and a lower ratio of specific combining ability to general combining ability variance ($\bar{\sigma}_{SCA}^2 : \bar{\sigma}_{GCA}^2$). Maize heterotic patterns have been established in the western Kenya but have not been established in the eastern and coastal regions. This study therefore, investigated the heterotic patterns and groups of maize landraces from eastern Kenya using two testers.

Participatory rural appraisal is carried out to assess farmers' preferences and perceptions. The PRA is crucial as it allows for the incorporation of farmers' indigenous technical expertise, criteria and priorities into the research objectives. Formal plant breeding approaches have been less effective in doing so, as is evident in both the slow

adoption of improved varieties by farmers, and the lack of breeding progress in the performance of adopted varieties under low input conditions. Therefore, an assessment of attributes of maize varieties preferred by farmers, and the socio-economic environment under which the farmers operate, becomes important.

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Chapter 2: Farmers' Perceptions of Drought and Preferences for Drought Tolerant Traits in Maize Varieties in Semi-Arid South Eastern Kenya

Abstract

Farmer participation in agricultural research is increasingly seen as a powerful methodology to increase the probability of adoption of new crop varieties. A participatory rural appraisal was therefore undertaken in the semi-arid region of south eastern Kenya to determine the maize varieties farmers grow and to assess farmers' perceptions of drought and preference for drought tolerant traits in maize varieties. The study was conducted in 2005 in four villages sampled from two districts, Makueni and Machakos representing dry transitional and dry mid-altitude maize zones, respectively, in south eastern Kenya. The study included literature reviews, interviews with key informants and group discussions with farmers from representative villages. There were eight focus group discussions involving of 92 male and 83 female farmers utilizing an open ended questionnaire and a check list. Scoring and ranking techniques were used to assess farmers' preferences and constraints. Secondary data was also collected and analyzed. The farmers in both districts grew maize as their major crop followed by beans (*Phaseolus vulgaris*). A total of 60% of the farmers grew local maize landraces, whose seed they recycled from season to season, whereas 40% grew improved varieties which were mainly composites rather than hybrids. The key farmers' criteria for choosing a maize variety in order of importance were drought tolerance, early maturity, high yield and disease resistance. The major constraints to maize production were drought, lack of technical know-how, pests, poor soils and lack of sufficient seed. Maize traits preferred by farmers in a drought tolerant variety included high yield, recovery after a dry spell and stay green. The study established that maize was the main crop grown, landraces were preferred most by the farmers to the improved varieties, and drought was the most important criteria considered in choosing a maize variety the farmers grew in each season. Therefore, these farmers' preferences and circumstances should be taken into consideration in developing new maize varieties for this region. This will increase the chances of adoption of the developed varieties, leading to increased maize production.

2.1 Introduction

The arid and semi-arid regions of Kenya make up 85% of the total land area. They are characterized by low and unreliable rainfall, with mean annual precipitation falling within 200 – 1000mm range. These regions are inhabited by about 20% of Kenya's population (Republic of Kenya, 1993). Farmers' perceptions about drought and drought tolerant varieties have to be established and included in varietal development. In addition to drought tolerance, farmers sometimes have certain preferences which breeders may be unaware of. This, therefore, makes a participatory approach more effective in knowing these farmers' experiences so as to include them in the breeding objectives.

In recent years, there has been an increasing consensus that the farmers' participation in technology development increases the likelihood of technology adoption (Ashby and Lilja, 2004). Participatory plant breeding may have many motivations, among them increased and more stable productivity, better understanding of farmers' varietal selection criteria and adoption of varieties. Formal plant breeding approaches have been ineffective as is evident in both non-adoption of improved varieties by farmers and lack of breeding progress as reflected by poor performance of adopted varieties under low input conditions (Bänziger and Cooper, 2001). Farmers have an extensive and well-adapted knowledge base of their environments, crops and cropping patterns built up over many seasons and generations (Bänziger et al., 2000). Participatory crop improvement involves farmers directly in the process of variety improvement and testing at an earlier stage than in a conventional breeding process. It is designed to incorporate perspectives of end users better than is formal plant breeding, reach resource-poor farmers, breed for high-stress and diverse conditions and incorporate wide variation in traits for specific client preferences (Dorward et al., 2007). There has been success and impact of conventional and centralized plant breeding programmes in high input areas but relatively low impact in marginal and small-scale farming sector. Thus, for such marginal regions a participatory breeding approach may be effective (Morris and Bellon, 2004). A participatory breeding approach has been used and reported to be quite effective in several cases such as in barley (*Hordeum vulgare*) in the dry Mediterranean regions (Ceccarelli et al., 2001), and maize in Mexico and Honduras (Smith et al., 2001), and India (Witcombe et al., 2003).

In order to estimate potential adoption of new varieties and facilitate overall evaluation of potential benefits of developing varieties, an assessment of attributes of maize varieties preferred by farmers and the socio-economic environment under which the farmers operate is an important starting point. Acceptability of agricultural technologies by farmers depends on how well researchers have identified farmers' objectives and constraints (Upton, 1987). As breeders involve farmers as participants, they will be able to learn more about the most important criteria of male and female farmers for preferred cultivars. This encourages the use of locally adapted cultivars (Danial et al., 2007). Farmer evaluations help scientists to design, test and recommend new technologies in light of information about farmers' opinions on usefulness of the innovation. In this context, participation is crucial. Participatory research allows incorporation of farmers' indigenous technical knowledge, identification of farmers' criteria and priorities, and definition of research agenda (Chambers, 1994). Participatory rural appraisal (PRA) tools are usually applied to determine farmers' perceptions and preferences (Odendo et al, 2002). De Groote and Bellon (2000) emphasized that PRA, which involves local people in gathering and analyzing information, allows establishing the actual local conditions, and fosters dialogue between scientists and farmers. By integrating farmers' concerns and conditions into agricultural research, it is hoped that research will develop technologies that become widely adopted, resulting in more productive, stable, equitable and sustainable agricultural systems.

Participatory rural appraisal was first conducted in Kenya in 1986 (Lelo et al., 1995) and has gained popularity since its inception. Since then, several PRA's have been conducted in the semi-arid areas of eastern Kenya. Sillah (1998) conducted a PRA in Embu district and identified constraints limiting agricultural production as mainly low income, lack of market, drought, poor infrastructure, pests and diseases. Ouma et al. (2002) reported that farmers in the moist transitional zone in eastern Kenya were interested in early maturing maize varieties. Bett et al. (2000) conducted a PRA in Kitui, Machakos, and Makueni districts, and found that drought and soil fertility were the major constraints limiting maize production in these districts. Songa and Overholt (2001) reported that farmers in eastern Kenya planted mainly local landraces and Katumani composite. Other PRA studies by Ikombo et al. (1996) and Gachimbi (2002) in Kasikeu, Makueni district, revealed that poor soils is one of the main constraints limiting crop production in the area. A PRA study done in the low and mid-altitude zones of western

Kenya revealed that maize was the most important crop. However, yields were low due to mainly two factors: low soil fertility and use of unimproved maize varieties (Achieng et al., 2001).

The objectives of this PRA study were to determine the maize varieties farmers grow and assess farmers' perceptions of drought and preference for drought tolerant traits in maize varieties grown in the semi-arid areas of Kenya. The hypothesis of the PRA study was that farmers in the semi-arid areas have preferences and knowledge of which traits contribute to drought tolerance in a maize variety.

2.2 Materials and Methods

2.2.1 The study Area

The PRA was carried out in the two districts, Machakos and Makueni, of the eastern province of Kenya. The dry mid-altitude (DM) maize zone covers most of Machakos, Makueni, Kitui and Mwingi districts. The dry transitional (DT) maize zone covers some parts of Machakos and a substantial part of Makueni district. This study covered two maize zones, the dry mid-altitude and the dry transitional zones. The PRA study was conducted in two sub-locations of the dry mid-altitude maize zone in Machakos district, Katanga and Kyangala. Similarly, the PRA exercise covered two sub-locations of the dry transitional maize zones of Makueni district, Uvaleni and Muani (Table 2.1).

Table 2.1 Sites and dates of the PRA study conducted in Machakos and Makueni districts in 2005

Agro-ecozone	District	Division	Sub-location	Village	No of farmers attending	GPS	Dates of the PRA
DM	Machakos	Kalama	Katanga	Katitu	44	37°20'E,1°38'S	06.04.2005
DM	Machakos	Kalama	Kyangala	Kyuluni	34	37°22'E,1°41'S	07.04.2005
DT	Makueni	Kasikeu	Uvaleni	Mbiini	71	37°21'E,1°54'S	11.04.2005
DT	Makueni	Kasikeu	Muani	Muani	26	37°23'E,1°58'S	12.04.2005
TOTAL					175		

DM – Dry mid-altitude zone, DT – Dry transitional zone.

2.2.1.1 Machakos District

Machakos district is one of the 13 districts in the eastern province of Kenya and it borders Makueni district to the south, Kajiado and Nairobi to the west, Embu, and Murang'a to the North and Kitui to the east. It covers an area of about 6,281.4 km² with 1,982.5 km² of arable land and 4298.9 km² of rangelands. The district has a potential irrigable land area of 10,027 ha but currently only 2,960 ha are under irrigation (Anon 1, 2004).

The district has an altitude that ranges from 700 m – 1700 m above sea level. It is generally hot and dry with two main rain seasons, i.e., the long rains of March to May and short rains of October to December with an average rainfall of 500 – 1300 mm per annum with 60% rainfall reliability occurring during the growing period of the first rains being 50 – 45 mm and the second rains being 60 – 530 mm. The temperatures in the district range from 18°C to 25°C, with June to July being the coldest months and October to February the hottest months (Jaetzold and Schmidt, 1983).

The district has a population of 906,644 persons as per the 1999 population census, with a growth rate of 3.09% and a density of 152 persons per km² (Anon 1, 2004). The breakdown of the population, per division, is shown in Table 2.2. Land use patterns in the district are mainly based on the agro-ecological zones and influenced by soil type.

The district can be divided into 5 major agro-ecological zones according to Jaetzold and Schmidt (1983). Land use details are summarized in Table 2.3. The PRA exercise was conducted in Kalama division, which falls in the agro-ecological zones UM3 and UM4 (Table 2.3).

Table 2.2 Population per division in Machakos district

Division	Population
Kalama	41,000
Kangundo	91,238
Kathiani	95,096
Machakos central	143,374
Masinga	74,478
Matungulu	99 731
Mavoko	48,938
Mwala	82,211
Ndithini	32,358
Yathui	65,567
Yatta	125,755

Source: Anon 1 (2004)

Table 2.3 Major agro-ecological zones in Machakos district

Agro-Ecological Zone	Altitude (m above sea level)	Mean annual rainfall (mm)	Annual mean temp (°C)	Description
LH2 – Lower Highland	1830 – 2130	1000 – 1300	16.0 – 17.9	Maize/Wheat-Pyrethrum zone.
UM3 – Upper Midland	1400 – 1770	900 – 1050	17.9 – 20.5	Marginal Coffee zone
UM4 – Upper Midland	1340 – 1830	700 – 950	17.9 – 20.9	Sunflower/Maize zone
UM5 – Upper Midland	1460 – 1710	550 – 750	18.6 – 20.2	Livestock/Sunflower zone
UM6 – Upper Midland				Ranching zone

Source: Jaetzold and Schmidt (1983)

2.2.1.2 Makueni District

Makueni district is also one of the 13 districts in the eastern province and is situated at the extreme southern part of the province. It borders Machakos to the north, Taita Taveta district to the south, Kajiado to the west and Kitui to the east. It covers an area of about 7965.8km² with 6245.2km² arable land and 1720.6km² of rangelands (Anon 2, 2004).

The district has an altitude that ranges from 600 m – 1900 m above sea level. It is characterized by a generally hot and dry climate, with two main rainy seasons, i.e. long rains, which occur from March to May and short rains from October to December, with an average rainfall of 664 mm per annum. The short rains are usually more reliable than the long rains. The temperatures in the district range from 17°C to 24°C with July to August being the coldest months and December to February the hottest months (Jaetzold and Schmidt, 1983).

The district has a population of 739,906 people, as per the 1999 population census giving, a population density of 93 persons per km² (Anon 2, 2004). The breakdown of population per division is shown in Table 2.4. Land use patterns in the district are mainly based on the agro-ecological zones and influenced by soil type. This makes the district's agricultural potential varied, with the high potential zones in the highlands being suitable for rain-fed crop and livestock production, whereas the lower potential zones are suitable for the production of small livestock, zebu cattle and drought tolerant crops. Maize is the main food crop grown in the area just as is the case in Machakos district.

The district is divided into eight major agro-ecological zones according to Jaetzold and Schmidt (1983). Land use details are summarized in Table 2.5. Kasikeu division, where the PRA was carried out, falls within the agro-ecological zones UM3, UM4, LM3 and LM4 (Table 2.5).

Table 2.4 Population per division in Makueni district

Division	Population
Kaiti	46,107
Kalama	14,039
Kasikeu	35,719
Kathonzweni	65,738
Kibwezi	80,236
Kilome	46,204
Kilungu	67,741
Kisau	50,510
Makindu	50,299
Matiliku	38,868
Mbitini	48,729
Mbooni	55,984
Mtito-Andei	66,663
Tilimani	32,717
Wote	40,353

Table 2.5 Major agro-ecological zones in Makueni district

Agro-ecological zone	Altitude (m above sea level)	Mean annual rainfall (mm)	Annual mean temp (°C)	Description
LH2 – Lower Highland	1830 – 2130	1000 – 1300	16.0 – 17.9	Wheat/Maize/Pyrethrum /Dairy zone
UM3 – Upper Midland	1400 – 1770	900 – 1050	17.9 – 20.5	Marginal Coffee zone
UM4 – Upper Midland	1340 – 1830	700 – 850	17.9 – 20.9	Sunflower/Maize zone
LM3 – Lower Midland	1160 – 1350	700 – 850	20.9 – 22.0	Cotton zone
LM4 – Lower Midland	1160 – 1280	700 - 850	21.3 – 23.3	Marginal Cotton zone
LM5 – Lower Midland	790 – 1220	600 – 750	21.6 – 24.0	Livestock/Millet zone
LM6 – Lower Midland				Ranching zone
L6 – Lowland				Lowland Ranching zone

Source: Jaetzold and Schmidt (1983)

2.2.2 Data Sources

Primary and secondary data sources were utilized. Primary data were generated through focused group discussions composed of 92 male and 83 female farmers, as well as key informants using, PRA approaches. The research team comprised of a socio-economist, maize breeder and a technical assistant who was conversant with the local language. The key informants were experienced farmers (those who have been farming for many years) in the villages, local administrative leaders and agricultural extension officers. Secondary data were obtained from Kenya government establishments, some relevant public and private institutions.

Secondary data were collected for both Machakos and Makueni districts from the Ministry of Agriculture annual reports on maize production, areas under maize production and mean annual rainfall.

2.2.3 Sampling Procedure

A multi-stage sampling procedure was used to select the sites that represented diverse ecological and socio-economic environments in the dry-mid altitude and dry transitional maize agro-ecological zones. The criteria for stratification were the relative importance of maize, severity of drought and agro-ecological zone. Two districts were chosen from the four districts in the two agro-ecological zones using a stratified random sampling procedure. Machakos district was chosen to represent the dry mid-altitude zone, whereas Makueni district was chosen to represent the dry transitional zone. In each of the districts selected, one division was randomly selected. A list of all locations in each of the selected divisions was obtained from respective divisional agricultural and administrative staff and one location was randomly selected from these. Then a list of all sub-locations was obtained from which one was randomly selected. Finally, One village was randomly selected using the list of villages as the sampling frames.

2.2.4 Data Collection and Analyses

Farmers' meetings were organized in each of the selected villages with assistance from the extension staff and the provincial administration, in particular the area assistant chiefs. Four villages were covered and, in each case, focused group discussions/interviews were conducted separately for male and female farmers using the same open-ended questionnaire and check lists. In total, 175 farmers were involved in the exercise from the four villages chosen (Table 2.1). The meetings were held either in a church or at a school. Introductions preceded all the meetings during which the purpose of the exercise was explained to the farmers. The farmers were encouraged to use the language they were most familiar with. One member of the research team who was conversant with the local dialect facilitated the group discussions while one recorded the responses on the flip charts.

The farmers were first asked to record the past major important events they could remember. They then listed the major crops in order of their importance. Next, the farmers were asked to record the maize varieties they grew and the criteria they used to select these varieties. They then scored the varieties for each of the criteria on a scale of 1 (very bad) to 5 (very good). Then the farmers recorded the timing of activities in maize production. The farmers were then asked to rank the constraints they faced in maize production in order of importance.

The farmers also recorded the occurrence of drought over the last five years (ten seasons) and also estimated the crop loss under different levels of drought severity. They then ranked the maize characteristics they considered important in a drought tolerant maize variety. Thereafter they rated the performance of each of the maize varieties they had listed earlier with respect to each of these traits using a scale of 1 (very bad) to 5 (Very good). After the group discussions, there was an open discussion with both men and women together to enable them to raise any questions.

After the PRA exercise, the farmers' responses from all the study sites were compiled and summarized in tables. The different criteria used by farmers to select their maize varieties are presented in order of importance. The different criteria and rankings were combined from different groups and villages into a derived score, devised to represent the number of times a criterion ranks highly. For each group, the criterion received a

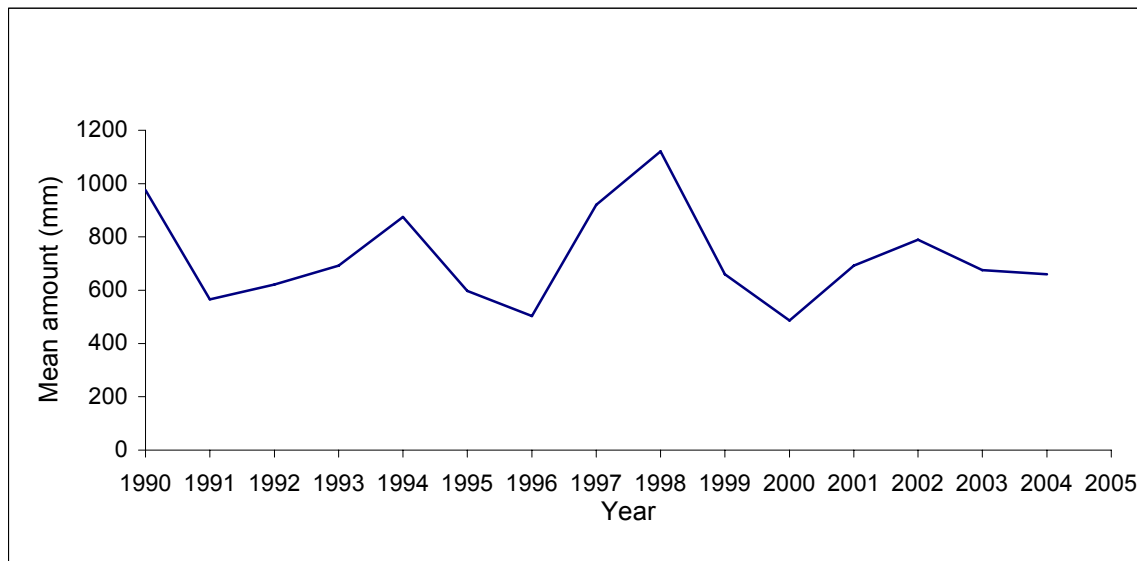
value inversely related to its rank, i.e., when a criterion is ranked first it receives a derived score of 5, second scores 4, third scores 3, fourth scores 2 and other rankings score 1. The mean derived score (mds) indicates the overall importance of the derived scores and ranges from 0 (criterion was not ranked) to 5 (criterion ranked first by all groups). This method of analysis was adopted from De Groote et al. (2002).

2.3 Results

2.3.1 Secondary Data

2.3.1.1 Machakos District

The average annual rainfall trend during 1990 – 2004 for Machakos district (Fig. 2.1). showed that, the district tends to receive less rainfall after every 3 to 4 years, which often translates into drought.

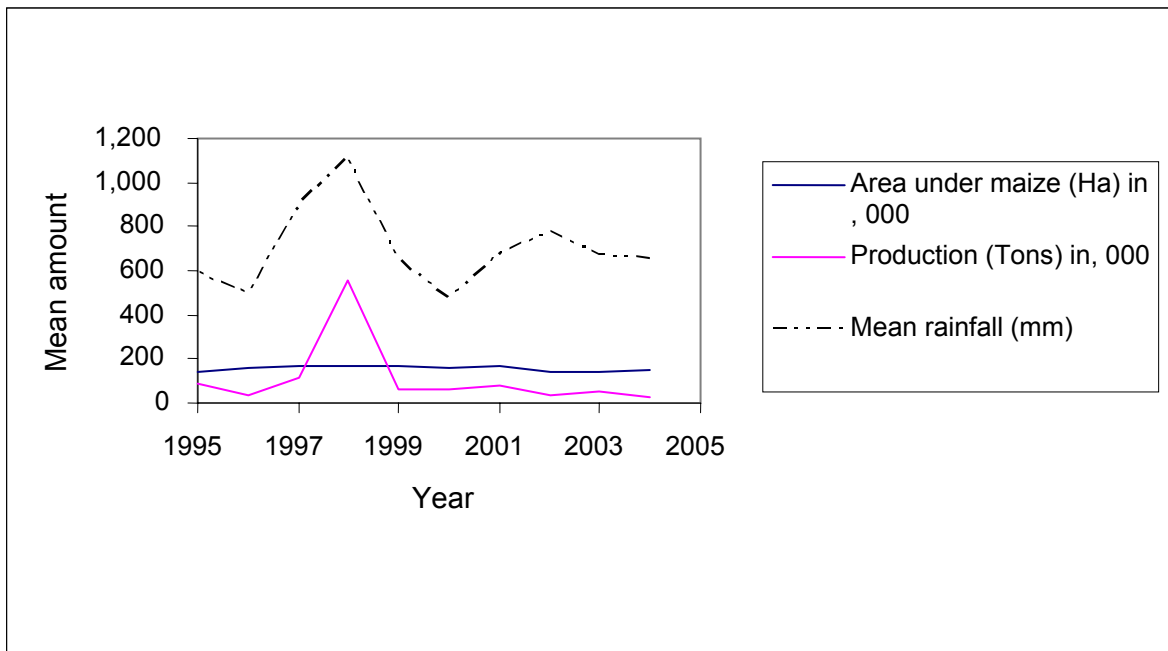


Source: Ministry of Agriculture (1990 – 2004)

Figure 2.1 Rainfall trends during 1990 – 2004 years in Machakos district

Crop production in the district is diversified ranging from intensive farming on smallholdings to large company farms with varieties of food, high value crops, and livestock. Farming methods range from use of traditional cultivation tools with little or no manure and fertilizer use (low management level) to mechanized and the use of

appropriate husbandry practices and improved crop seeds (Anon 1, 2004). Maize production trend in the district during 1995 – 2005 is shown in Fig. 2.2. The maize production went up in the district during the 1997 and 1998 cropping seasons (Fig. 2.2). Other crops of importance grown in the district include beans, cowpea (*Vigna unguiculata*), green grams (*Vigna aureus*), cassava (*Manihot* spp), pigeon pea (*Cajanus cajan*), and sweet potatoes (*Ipomea babatus*). Livestock production also forms an important economic activity in the district. Mainly large-scale farmers in the agro-ecological zone UM6 practice ranching (Table 2.3). The rest of the farmers in the remaining zones practice small-scale dairy and beef production. Goat and sheep production were also practiced alongside cattle keeping.

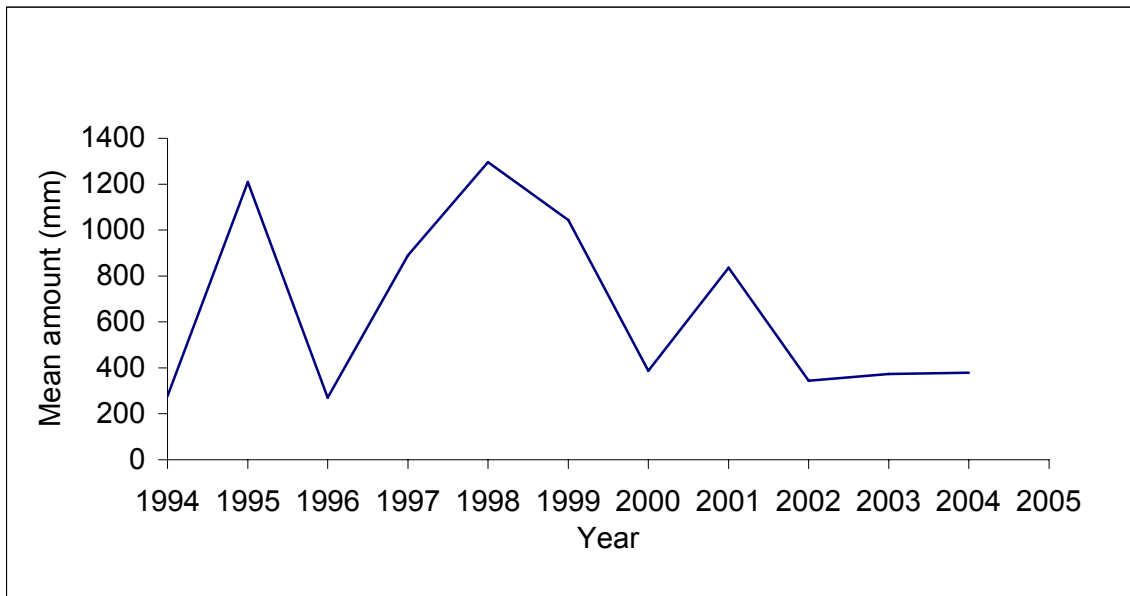


Source of data: Ministry of Agriculture annual reports (1995 – 2004)

Figure 2.2 Maize production during 1995 – 2005 in Machakos district

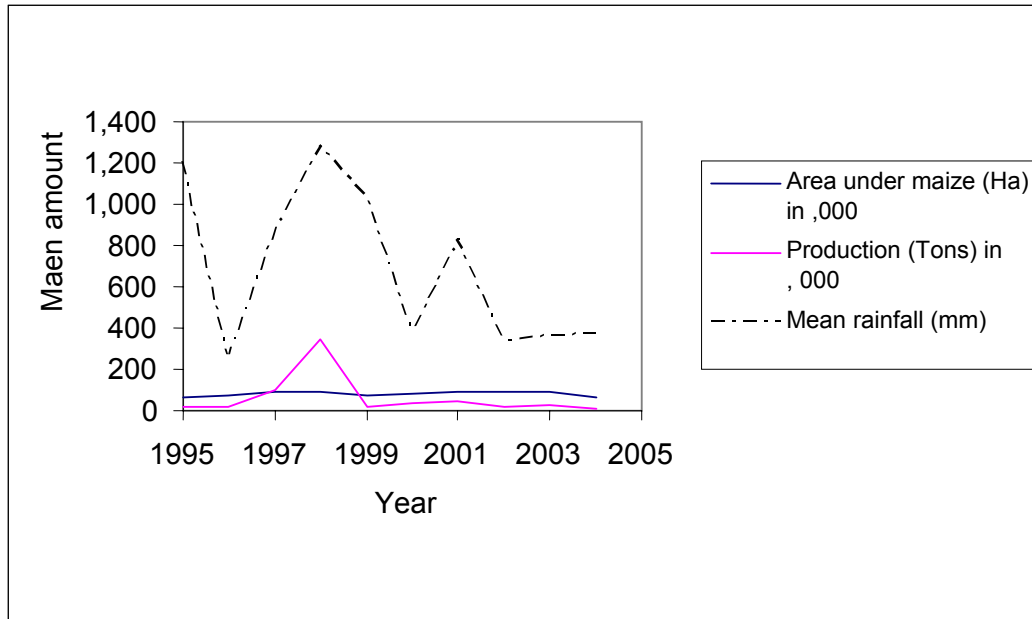
2.3.1.2. Makueni District

The average rainfall trend in the district during 1994 – 2005 is shown in Fig. 2.3. Maize production trends and the area under maize year⁻¹ for the same period are shown in Figure 2.4. Maize production was highest during the 1997/1998 cropping. Generally, during periods of low rainfall, the district also experiences also low maize yields. Beans, millet (*Eleusine coracana*), sorghum (*Sorghum vulgare*), and pigeon pea are the other food crops produced in the district.



Source: Ministry of Agriculture annual reports (1994 – 2004)

Figure 2.3 Rainfall trend during 1994 – 2005 in Makueni district



Source: Ministry of Agriculture annual reports (1995 – 2004)

Figure 2.4 Maize production trends during 1994 – 2004 in Makueni district

2.3.2 Primary Data

2.3.2.1 Major Crops Grown

Table 2.6 shows the various types of crops, in order of importance, grown in Machakos and Makueni districts as ranked by both males and females. At all the study sites in the two districts, maize was the main crop grown, followed by beans. The males generally ranked the crops differently than the ranking the females in both divisions. However, both the females and males mentioned maize as a major crop, followed by beans. Other crops of importance included pigeon peas, cowpea, cassava, sweet potatoes, sorghum, finger millet, pumpkin (*Cucurbita* spp) , and green grams though their rankings were not consistent in both districts (Table 2.6).

Table 2.6 Major crops grown listed in order of importance by both male and female farmers

District	Machakos		Makueni	
Division	Kalama		Kasikeu	
Rank	Male	Female	Male	Female
1	Maize	Maize	Maize	Maize
2	Beans	Beans	Beans	Beans
3	Pigeon pea	Cowpea	Pigeon pea	Cowpea
4	Cassava	Pigeon pea	Cowpea	Pigeon pea
5	Cowpea	Cassava	Sorghum	Sorghum
6	Sweet potato	Sweet potatoe	Finger millet	Finger millet
7	Pumpkin	Pearl millet	Pumpkin	Green grams
8	Sorghum/Millet	Finger millet	Cassava	Cassava
9		Sorghum	Sweet potato	Sweet potato
10			Green grams	

2.3.2.2. Maize Varieties Grown

Farmers grew a wide range of varieties (Table 2.7), from the local landraces and improved open-pollinated varieties (OPVs) to old hybrids from Kenya Seed Company (KSC) and newly introduced hybrid varieties from Pioneer, Pannar, Seed Co. and Cargill (now Monsanto/Dekalb). The farmers could not, however, say which type of Pioneer nor Pannar hybrid varieties they grew. The local landrace *Kinyanya* was the most popular maize variety grown. Across all the study sites, 60% of the respondents preferred the local maize landrace, *Kinyanya*. Katumani composite (KCB) was ranked second, with 16% of the respondents growing it and Pioneer came third with 10.5% of the respondents growing this variety. Other maize varieties grown by the respondents, to a lesser extent included Pannar, SC Duma, CG4141, H511, and Dryland composite/Makueni (DLC) (Table 2.7). The varieties KCB, DLC and H511 are produced locally by KARI and KSC, whereas Pioneer, Pannar, SC Duma, and CG4141 hybrid varieties are imported.

Table 2.7 Percentage of farmers growing different maize varieties in Kalama and Kasikeu divisions

Variety	Type	Kalama Division	Kasikeu Division	Overall %
Kinyanya	Landrace	58	62	60.0
KCB	Composite	19	13	16.0
Pioneer hybrids	Hybrid	7	14	10.5
Pannar hybrids	Hybrid	7	3	5.0
SC Duma hybrids	Hybrid	3	3	3.0
H511	Hybrid	2	4	3.0
CG4141 hybrids	Hybrid	4	0	2.0
DLC	Composite	0	1	0.5

2.3.2.3 Farmers' Criteria for Maize Variety Selection

The most important criteria across the sites based on mean derived scores (mds) in ranked order, were drought tolerance, early maturity, disease resistance, yield and pest resistance, ear placement and grain size (Table 2.8). Other criteria considered by farmers in choosing the maize varieties they grew, though less important, included seed availability, ear size, taste and management. Criteria such as taste and management were not mentioned by all the groups at all the sites though they were also considered in choosing a variety.

The male and female farmers at all the study sites ranked the criteria for choosing the maize varieties differently. In some instances, both ranked a criterion equally. In Muani, for example, the male and female respondents ranked drought second, whereas the male and female respondents in Kalama division, Machakos district ranked drought first and second, respectively (Table 2.8). The farmers also indicated that they have changed variety use in the last ten years due to the introduction of new varieties into the country, such as Pioneer, SC Duma and Pannar, by foreign seed companies. The farmers could not remember these maize hybrids by their brand names, but could only identify them by their company names.

Table 2.8 Rankings and mean derived scores of criteria for maize variety selection

District	Machakos				Makueni				Mean derived score*
Division	Katanga		Kyangala		Uvaleni		Muani		
Criteria	Men	Women	Men	Women	Men	Women	Men	Women	
Drought tolerance	1	-	1	2	1	2	2	2	4.4
Early maturity	-	1	2	3	1	1	3	1	4.3
Disease resistance	2	-	-	2	3	-	4	-	3.3
Yield	3	2	3	-	4	4	1	3	3.1
Pest resistance	7	-	-	2	3	-	4	-	2.5
Ear placement	-	3	-	4	-	7	-	4	2.0
Grain size	-	5	4	8	-	5	-	1	2.0
No. rows per ear	-	-	-	5	-	3	-	-	2.0
Seed availability	4	-	-	-	6	-	6	-	1.3
Ear size		5	5	7		6	-	-	1.0
Taste	9	-	-	-	5	-	-	-	1.0
Management	5	-	-	-	7	-	-	-	1.0

- Not mentioned

*Every time a criterion is ranked first, it receives a score of 5, second scores 4, third scores 3, fourth scores 2 and other rankings score 1.

2.3.2.4 Time Lines

The time lines for important past events were gathered from discussions with men and women from the four villages in Kalama and Kasikeu divisions. The farmers in Kalama division were able to recall a total of 21 important past events (Table 2.9), whereas those from Kasikeu division could recall a total of 23 (Table 2.10). In both divisions, most of these events were related to drought and famine indicating that shortage of food and lack of water are the main problems. The farmers in both districts could recall that severe drought had occurred nine times and during these times of drought, there was no food and thus they resorted to eating hides and skins in some cases. However, there were also some years when rainfall was sufficient and this resulted in bumper harvests.

For example, in 1997, they experienced *El Nino* rain and had good harvests, but their livestock died due to diseases. They reported also two occasions in which pests such as armyworms (*Spodoptera exempta*), locusts (*Oxya yezoensis*) and chaffer grubs (*Schizonycha* spp) invaded their crops and this resulted in poor or no harvests (Tables 2.9 and 2.10).

Table 2.9 Time lines for Kalama division – Machakos district during 1928 to 2002

Year	Major event	Comments
1928	Drought	Ate hides & skins
1936	Locust invasion	
1941	Drought/Serena sorghum introduced	Famine
1944	Invasion of Locusts, army worms & scabies	
1946	Heavy rains/Measles outbreak	
1947	Bumper harvest	Good rains
1950	Drought	Famine
1951	Heavy rains	
1960	Drought/Maasai cattle raids	Famine
1961	Drought followed by floods	Famine
1964	Drought	Famine
1975	Drought	Famine, cattle died
1980-1981	Drought	Famine
1982	Bumper harvest	Good rains
1984	Army worm invasion & drought	Livestock deaths
1985	Bumper harvest	Good rains
1991	Bumper harvest	Good rains
1993	Bumper harvest	Good rains
1997	<i>El Nino</i> rains/livestock deaths-diseases	Good harvest
2000	Drought	Famine
2002	Chaffer grub infestation	Poor yields

Table 2.10 Time lines for Kasikeu division – Makueni district during 1910 to 2002

Year	Major event	Comments
1910-1920	First settlement in Kasikeu	
1927	Locust invasion	Crops destroyed
1928-1929	Drought	Famine
1930-1931	Locust invasion	Crops destroyed
1932-1934	Drought	Famine- (<i>yua ya ukuku</i>)-grass harvested from forest and eaten
1933	Kasikeu primary & dispensary built	
1939	Kasikeu market started	
1942	Drought	Famine
1943	Drought	Famine
1943-1945	Drought	Famine
1945-1946	Land registration for sale	
1949-1951	Building of dams	White man collected cattle
1961-1962	Floods	Famine/relief food dropped by planes
1961	Bumper harvest	Good rains
1965-66	Famine- <i>Atta</i>	There was no maize harvest
1972-1973	Drought	Caused movement of cattle
1980-1981	Drought -Famine- <i>Nikw'a ngwete</i>	People had money but no food to buy
1984	Drought	Famine – yellow maize, food for work programme initiated
1985	Army worm invasion	Poor yields
1988	Bumper harvest	Good rains
1997	<i>El Nino</i> rains	Good harvest
2000	Drought	Famine
2002	Chaffer grub infestation	Poor yields

2.3.2.5 Constraints to Maize Production

The farmers in the study areas encountered several constraints in maize farming and are presented in a ranked order in Table 2.11. The male and female farmers from all the study sites ranked the constraints differently although some constraints were ranked the same. For example, drought was ranked the most important constraint by all the sexes in all the study sites, whereas pest problems were ranked differently by different sexes in all the study sites (Table 2.11). The two major pests given by the farmers in all study sites, which hampered their maize production, were chaffer grubs and stem borers (*Busseola fusca*). Lack of technical agricultural knowledge of crop management and poor soils were ranked second and third, respectively. Lack of sufficient seeds at

planting time and high prices of inputs, were ranked fourth and fifth, respectively. Other constraints though considered less important, included pests, low market prices and disease problems.

Table 2.11 Rankings and mean derived scores of maize production constraints at each division

Division	Rank								Mean derived score*
	Katanga		Kyangala		Uvaleni		Muani		
	Men	Women	Men	Women	Men	Women	Men	Women	
Drought	1	1	1	-	1	-	1	-	5.0
Lack of technical know-how	3	-	-	2	4	2	2	4	3.2
Poor soils	4	-	2	-	3	-	3	6	2.6
Inadequate seeds	6	3	-	-	5	3	-	2	2.4
High prices of inputs	-	2	-	3	-	6	6	-	2.3
Pests	5	4	3	4	7	4	3	5	1.9
Low market prices	7	-	-	-	-	-	7	3	1.7
Diseases	-	5	4	5	8	5	4	-	1.3

- Not mentioned

*Every time a constraint is ranked first, it receives a score of 5, second scores 4, third scores 3, fourth scores 2 and other rankings score 1.

2.3.2.6 Maize Traits Preferred in a Drought Tolerant Variety

For the maize traits preferred in a drought tolerant variety, the farmers identified 7 and 6 preferred traits in Kalama and Kasikeu divisions, respectively, although the ranking of these traits differed slightly (Table 2.12). The farmers in both the divisions considered yield as the most important trait. Farmers in Kalama division ranked stay green and plant recovery from stress after a dry spell, second and third, respectively. Farmers in Kasikeu division ranked plant recovery from stress after a dry spell and leaf rolling second and third, respectively. The number of ears per plant and short stem were considered as the least important traits by the farmers in both divisions.

Table 2.12 Rankings of traits preferred by farmers in a drought tolerant maize variety

Division	Kalama	Kasikeu
Trait	Rank	Rank
Yield	1	1
Stay green	2	4
Recovery after a dry spell	3	2
Rooting pattern	4	-
Leaf rolling	5	3
Leaf senescence	6	5
Ears per plant	7	-
Short stem	-	6

- Not mentioned

Farmers also ranked the performance of the varieties they grew with respect to the traits listed above. The rankings differed between sites and between groups. Male farmers from Kalama division ranked *Kinyanya* (maize local landrace) as the best performing variety in all the traits listed followed by Katumani composite (KCB). Pioneer hybrids were ranked as the worst performing (Table 2.13). Female farmers from the same division ranked SC Duma as the best performing variety, while Pannar and Pioneer hybrids were ranked second and third, respectively (Table 2.14). *Kinyanya* and KCB were ranked the worst performing varieties which was opposite of male farmer rankings.

Table 2.13 Male farmer rankings of varieties for drought tolerance traits in Kalama division, Machakos district.

Variety	Trait							Overall rank
	Yield	Stay green	Recovery after dry spell	Root structure	Leaf rolling	Leaf senescence	Ears per plant	
<i>Kinyanya</i>	1	2	1	1	1	1	1	1
KCB	2	1	2	1	1	2	2	2
Pioneer	3	1	3	2	2	3	3	3

Table 2.14 Female farmer rankings of varieties for drought tolerance traits in Kalama division, Machakos district

Variety	Rank					Overall rank
	Yield	Stay green	Recovery after dry spell	Root structure	Leaf senescence	
SC Duma	1	1	1	1	1	1
Pannar	2	1	2	2	2	2
Pionner	3	2	2	3	3	3
<i>Kinyanya</i>	2	3	3	4	2	4
KCB	1	3	3	4	3	4

Male farmers from Kasikeu division ranked Katumani composite (KCB) as the best performing variety and *Kinyanya* second (Table 2.15). They ranked SC Duma third. Pioneer and Pannar hybrid varieties were ranked fourth and fifth, respectively. Female farmers from Kasikeu division ranked DLC as the best performing variety, while both KCB and SC Duma were ranked second. They ranked *Kinyanya* third and both Pioneer and Pannar hybrids fourth (Table 2.16).

Table 2.15 Male farmer rankings of varieties for drought tolerance traits in Kasikeu division, Makueni district

Variety	Trait				Overall rank
	Yield	Stay green	Recovery after dry spell	Root structure	
KCB	1	1	2	2	1
<i>Kinyanya</i>	2	2	2	1	2
SC Duma	2	2	2	3	3
Pioneer	4	3	1	5	4
Pannar	3	4	3	4	5

Table 2.16 Female farmer rankings of varieties for drought tolerance traits in Kasikeu division, Makueni district

Variety	Trait				Overall rank
	Yield	Stay green	Recovery after dry spell	Root structure	
DLC	2	1	1	1	1
KCB	3	2	1	1	2
SC Duma	2	1	2	2	2
<i>Kinyanya</i>	2	1	3	3	3
Pannar	1	1	4	4	4
Pioneer	1	1	4	4	4

2.2.7 Drought Occurrence and Crop Losses Attributed to Drought

Drought severities were given scores ranging from 0 (no drought) to 3 (severe drought). From the farmers' responses, it became evident that, during the past five years (ten seasons), drought incidences were experienced more frequently in Kasikeu division in the Makueni district than in the Kalama division in Machakos district (Table 2.17). The short rains, which are normally experienced from November to January, were more reliable than the long rains, which are experienced from March to June, and more so for Kalama division. In Kalama division, there was no drought during the short rains of 2000, 2002 and 2003 (Table 2.17).

Table 2.17 Drought occurrences during the last 5 years (10 seasons) for Kalama division (Machakos district) and Kasikeu division (Makueni district)

Division	Year	2000		2001		2002		2003		2004	
		lr	sr	lr	sr	lr	sr	lr	sr	lr	sr
Kalama	Season										
	Drought severity*	2	0	2	2	3	0	3	0	2	2
Kasikeu	Season										
	Drought severity*	2	2	2	2	1	1	2	2	3	3

* 0= None (800 – 1000 mm), 1= Mild (600 – 700 mm), 2 = Moderate (400 – 500 mm), 3 = Severe (0 – 100 mm).

lr = Long rains, sr = Short rains.

The farmers estimated maize yields by stating the number of 90 kg bags acre⁻¹ they would get under different drought severities. These were converted into t ha⁻¹. The responses differed substantially between sites and between groups. Female farmers gave higher yields than male farmers in both two divisions (Table 2.18). Female farmers in Kalama division gave a harvest estimate of 2.3 – 3.7 t ha⁻¹ in good rainfall seasons, whereas the male farmers gave an estimate of 0.7 – 1.1 t ha⁻¹. Female farmers in Kasikeu division indicated that in good rainfall seasons, they harvest an about 2.3 – 2.4 t ha⁻¹, while the male farmers gave an estimate of 0.9 – 1.8 t ha⁻¹. Generally both female and male respondents in all the areas indicated that during severe drought there is usually a total crop failure (Table 2.18).

Table 2.18 Estimated maize yield (t ha⁻¹) under different drought severities

Gender drought severity*	Machakos district		Makueni district	
	Kalama		Kasikeu	
	Male Yield (t ha ⁻¹)	Female Yield (t ha ⁻¹)	Male Yield (t ha ⁻¹)	Female Yield (t ha ⁻¹)
None	0.7 – 1.1	2.3 – 2.7	0.9 – 1.8	2.3 – 3.4
Mild	0.5 – 0.7	0.9 – 1.6	0.5 – 0.9	1.1 – 1.4
Moderate	0.2 – 0.5	0.5 – 0.7	0.3	0.5 – 0.7
Severe	0.0	0.0	0.0	0.0

* 0= None (800 – 1000 mm), 1= Mild (600 – 700 mm), 2 = Moderate (400 – 500 mm), 3 = Severe (0 – 100 mm)

Farmers in both Kalama and Kasikeu divisions indicated that they were interested in growing a variety that is tolerant to drought. However, the female farmers indicated that they would only adopt it if the cost of production does not exceed 25% above the usual production cost. The male farmers said they would adopt it if the additional cost was between 25 to 50% above the usual production cost.

2.4 Discussion

The farmers could recall time lines, dating back to 1910, and this was supported by the secondary data collected from the Ministry of Agriculture records. The two districts have experienced frequent droughts and isolated cases of locust and army worm infestations. These two districts have been associated with great famine as drought leads to total crop failure, while pest attacks lead to crop destruction. Makueni district appears to experience drought more frequently than Machakos district. However, there have been years with sufficient and even more than usual rainfall amounts. For example, in 1961 there were floods in both districts and, in 1997 there were *El Nino* rains. During these periods of sufficient rainfall, the farmers got bumper harvests. They keep the surplus in store for use during dry periods and also sell their surplus.

The results of the PRA study showed that farmers grew a wide range of maize varieties but they preferred their local varieties to the improved varieties such as Katumani composite, Pioneer, SC Duma and Pannar hybrids, which are available in the market. A total of 76% of the respondents grew local landraces and Katumani composite, whilst only 24% grow hybrid varieties. A similar case was observed in PRA studies done in the same region by Songa and Overholt (2001). The farmers preferred their local landraces to the improved varieties, because it matures early, has large grains, is higher yielding than the improved varieties and has a good taste. They indicated that Pannar and Pioneer hybrids were prone to leaf blight infection during wet seasons and their grains are not large as compared to the local landraces. The farmers also indicated that they recycled the seed from the previous season's harvest more so for their local varieties and Katumani composite as opposed to the hybrids. The reason given by the farmers was that their local maize variety and the Katumani composite do not decline in yield like the hybrids, which declined in yields when their seeds recycle.

Another reason why the farmers preferred their local maize cultivars rather than the improved hybrids is the cost and the availability of seed at planting time. Their local maize cultivars are less costly as they recycle the seed from the previous season and the seed is readily available at planting time as opposed to hybrid seed which has to be purchased every planting season. This is because the local maize is usually an open-pollinated variety and its seed can be recycled without the risk of yield reduction like the hybrids. This recycling of seed has also been reported, in several previous PRA studies,

as a common practice by farmers throughout the country (Odendo et al., 2002; Ouma et al., 2002; Mose et al., 2002). Although the farmers preferred to grow their local varieties, they were willing to test new drought tolerant varieties. However, the farmers indicated that the new variety should not cost more than 25 – 50% above their normal production costs. This is largely due to heavy crop losses they incur in the event of a severe drought. Therefore, this greatly supports the need to improve their local maize populations *per se* for drought tolerance or the development of open-pollinated varieties (OPVs), as they will recycle the seed, thus reducing production costs.

Farmers use a combination of criteria in selecting the maize varieties they grow. Among the main criteria are drought tolerance, early maturity, yield and disease resistance. Mose et al. (2002) found the same criteria used by farmers in moist transitional and high tropical zones. Drought is the major criterion because droughts are frequent in the study areas. Early maturity is desirable as it allows the crop to escape drought. Early maturity also allows farmers to prepare land in order to plant two crops per year to fit the bimodal rainfall pattern. They also want a variety which is high yielding so that, in the event of optimum rainfall, they will obtain high yields and have surplus harvests for storage to use in future or sell for income.

Drought is a major constraint to maize production in this region. The area experiences frequent droughts as the farmers indicated during discussion groups. This was also evident in the time lines given by the farmers. A study done by Bett et al. (2000) in Kitui, Machakos and Makueni in eastern Kenya, also revealed drought as being the major constraint to maize production in the region. Other PRA studies by Ouma et al. (2002) revealed similar problems particularly low or erratic rainfall, low soil fertility and pests. The region receives two main rain seasons in a year, the long rains and the short rains. Usually the short rains are more reliable than the long rains. Drought in the region usually leads to a reduction in maize yields and in severe drought, there is a complete crop loss. This, therefore, necessitates a need to develop maize varieties that are drought tolerant for this region.

During the discussions, the farmers indicated that early maturity, yield and disease resistance were the most important traits to consider in a drought tolerant variety. Other traits they considered important included: stay green, recovery after a dry spell and leaf

rolling. Njoroge and Ngure (1986) reported that the varieties in the semi-arid regions still fall short of the farmers' requirements. It is, therefore, important that during the development of drought tolerant maize varieties these farmers' perceptions of a drought tolerant variety must be taken into account. This will increase the chances of them accepting and growing the developed variety. Crucially the new variety should actually perform better than their local varieties. This is because they ranked their local landrace *Kinyanya* the best in performance with regards to the traits they preferred in a maize variety. *Kinyanya* landrace, as the farmers pointed out, has larger grains, and can withstand pounding and this could explain why the farmers prefer it to the improved maize varieties in the market. The farmers have been growing this landrace since maize was introduced into the country and they are familiar to it.

During the discussion sessions, the male and female farmers held separate discussion groups. This was done in order to create more freedom so that the farmers, especially the female farmers could, be free to air their views. There was gender parity in the views as regards to the aspects that were undertaken in the study. In some cases, they concurred. However, this did not affect the overall perspective of the farmers. The case could have been different if the farmers were put in one group discussion as the female farmers are sometimes dominated by the male farmers. So it was advantageous to have them separate and later compare their views.

2.5 Conclusions

The study revealed that maize production is the main activity in the region, thus, the development of improved maize varieties should be a major priority. The region receives little and unreliable rainfall thus the maize varieties developed should be drought tolerant and/or early maturing. Farmers' selection criteria were identified. Considering also that the farmers prefer recycling seed as a strategy for coping with cash flow constraints, an effort should be made to develop open-pollinated varieties (OPVs), such as composites. To achieve this, local landraces should be improved and incorporated in the maize breeding programme in the drylands. Likewise, farmers' views and preferences should be taken into account when developing the new varieties for this region. This will enhance faster adoption of these varieties and thus lead to increased food security in the region.

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Chapter 3: Response to Two Cycles of S₁ Progeny Recurrent Selection on Drought Tolerance and Effect of Selection on Genetic Diversity in Maize populations in Semi-Arid Eastern Kenya

Abstract

Drought is the main cause of yield losses in semi-arid areas in tropical environments. The objectives of this study were (i) to improve drought tolerance in maize populations in semi-arid areas of Kenya through S₁ progeny recurrent selection, and (ii) to determine the genetic variability in these maize populations after two cycles of selection. Two maize landrace populations from semi-arid eastern Kenya and three CIMMYT populations V032, ZM423 and ZM523 were subjected to two cycles of S₁ progeny recurrent selection for yield and traits indicative of drought tolerance during flowering and grain filling from February 2005 to September 2007. Selection gains were determined in one trial laid out as a 4x4 balanced lattice design. Drought stress was imposed at reproductive stage by withholding irrigation one week before flowering and was not resumed until grain filling. The trial was repeated under well-watered conditions which served as a control experiment. The experiment to determine genetic variability was conducted under stress conditions and was laid out as a randomized complete block design with two replications. Under drought stress conditions, KTU population had a realized gain in yield of 0.2 t ha⁻¹, MKS population 1.2 t ha⁻¹ and ZM423 0.4 t ha⁻¹, whereas in V032 and ZM523, grain yield was reduced by 1.1 t ha⁻¹ and 0.6 t ha⁻¹, respectively. Under well watered conditions, the realized gains in grain yield were positive in all the populations except V032, where there was a reduction of 0.1t ha⁻¹. The genetic variability and heritability estimates for yield increased in S₁ lines of MKS and ZM423 populations, but decreased in KTU, V032 and ZM523 populations. The genetic variability of the secondary traits were reduced in some of the populations and increased in some populations. Grain yield was negatively correlated with anthesis-silking interval, leaf rolling and leaf senescence whereas it was positively correlated with ears per plant under drought conditions. This confirms the value of using anthesis-silking interval as a secondary trait when selecting for drought tolerance in maize. After two cycles of recurrent selection, grain yield improved in KTU, MKS, and ZM423 maize populations, whereas it reduced in V032 and ZM523 maize populations.

3.1 Introduction

Drought is the major abiotic factor responsible for limiting maize production and productivity in the developing world (Edmeades et al., 1992). Throughout the humid tropics, unpredictable periods of drought are responsible for significant yield reduction in maize. Thus, drought is a major source of food insecurity for many households as it has been estimated to cause annual maize yield loss of 24 million tons in the developing world (Magorokosho et al., 2003). Hugh and Richard (2003) attributed this reduction in yield of maize due to drought stress to three main mechanisms: (i) reduced canopy absorption of incident photosynthetically active radiation (PAR), (ii) reduced radiation use efficiency (RUE), and (iii) reduced harvest index (HI). In Kenya only about 30% of the total land area can be considered to be arable. Half of this arable area is semi-arid, hence agricultural production is hampered by low, unreliable and poorly distributed rainfall (Kiarie and Ngure, 1986).

Drought affects maize yields by restricting season length and through unpredictable stress that can occur at any time during the cropping cycle (Edmeades et al., 1994). The critical development period in maize for determining grain yield centres on flowering and early grain filling (Boyer and Westgate, 2004). The importance of a steady photoassimilate flow during both ovule /pollen and seed development has been shown. Moisture stress inhibits photosynthesis by inducing stomatal closure and limiting carbon dioxide availability. Dehydration also negatively affects the activity of carbon metabolic enzymes such as acid invertase, which play a central role in providing the necessary sugars for the growth of the developing ear (Moreno et al., 2005). Hence, genetic improvement of maize for increased drought stress tolerance is desirable.

Breeding for drought tolerance in maize is a complex task mainly due to the complexity of drought tolerance mechanisms and this has slowed down breeding progress (Moreno et al., 2005; Cattivelli et al., 2008). There has been considerable effort devoted to breeding for improved drought tolerance in cultivars of major crops, although with little progress being achieved. There are many reasons for this. The most obvious is that selecting for drought tolerance is difficult, as the response is complex and it interacts with other factors such as high temperature and nutrient uptake. Moreover, further problems exist in obtaining a consistent response following the exposure of large plant populations to conditions which simulate realistic drought conditions in the field

(McWilliam, 1989). Turner (1986) suggested five types of drought crops encounter as early drought; mid-season drought; late-season drought; drought with relief near harvest; progressive moderate drought, and progressive severe drought. In breeding for drought tolerance, one needs to identify the type of drought that the crop is likely to encounter. In this study, mid-season drought was targeted as drought stress was imposed at the reproductive stage.

Direct selection for yield is difficult owing to its low heritability under drought conditions. Thus, the use of secondary traits (in contrast to the primary trait i.e., yield) whose genetic variances increase under stress or are reduced less than that of yield, can increase selection efficiency provided they have a clear adaptive value under stress, relatively high heritability and are easy to measure (Bolaños and Edmeades, 1996). The secondary traits that are normally used in selecting for drought tolerance include number of ears per plant, anthesis-silking interval (ASI), leaf senescence, tassel size and leaf rolling (Bänziger et al., 2000). Under drought stress maize shows a delayed silking, leading to incomplete or no fertilization and decreased or no kernel development. Evaluating maize under moisture stress conditions during flowering allows for the identification of genotypes with a short ASI and high yield (Magorokosho et al., 2003). However, there is no consensus on the most effective approach to screening maize for drought tolerance. Although direct selection for yield is difficult, recent studies of broad sense heritability of grain yield under reproductive-stage drought stress, have revealed that, grain yield estimated is comparable to that in non-stress conditions, indicating that direct selection for yield under drought is likely to be effective as well (Venuprasad et al., 2007).

Improvement of maize populations through recurrent selection has been effective for increasing the frequency of favourable alleles of economic value. The improvement of crops through recurrent selection can either be done through intrapopulation selection or interpopulation selection methods. Intrapopulation selection method is more frequently in maize improvement, because it is not as complex and is more amenable to use for most plant, ear and kernel traits (Hallauer, 1992). Intrapopulation selection involves improving of one population. The most common methods are mass selection and family selection with all its variants: parental or maternal half-sib families, full-sib families or inbred lines (S_1 or S_2) (Ramírez-Díaz et al., 2000). Selfed progeny selection is considered to be

superior to other methods of recurrent selection for the improvement of the population *per se* since alleles are fixed rapidly and deleterious, homozygous alleles are exposed and eliminated early in selection (Doerksen et al, 2003). In this study, S₁ family selection was used. Edmeades et al. (1999) have demonstrated that drought tolerance can be obtained in lowland tropical maize populations either by recurrent selection to increase frequency of drought-adaptive alleles or by assembling populations from sources in which these types of alleles are already present at a relatively high frequency. The effectiveness of selection depends on the heritability of the trait under selection, the level of genetic variation and the intensity of selection (Hill et al., 1998).

Progress from selection is dependent upon the presence of adequate genetic variability in the population and accurate evaluation of breeding values of parental plants (Menkir et al., 2007). The mean of the trait under selection will improve gradually and the shift will continue as long as genetic variability exists in the population. The recurrent selection programme should, therefore, maintain genetic variability within the population in order to facilitate improvement in future cycles of selection and its success is determined by evaluating improvement in the mean of the target population, as well as the best individuals (Schnicker and Lamkey, 1993). With selection, genetic variability in a population decreases until the selected alleles become fixed (Weyhrich et al., 1998). However, Hinze et al. (2005) indicated that direct response to selection for yield increased after 11 cycles while the genetic variance within populations showed an insignificant decrease.

Two major processes operate to change the mean over cycles of recurrent selection in a population of finite size: selection acting to increase the mean and inbreeding depression due to genetic drift acting to decrease the mean (Helms et al., 1989). Inbreeding depression, an observed outcome of directional dominance, has been measured extensively in maize. Hallauer and Miranda (1988) summarized 99 experiments in maize in which genetic dominance variance was measured, and found that dominance makes a substantial general contribution to genetic variance for grain yield in maize populations. Given the importance of dominance variance in maize, it is clear that additive genetic expectations will lead to incorrect assumptions concerning changes in genotypic covariance components in populations undergoing inbreeding or genetic drift. Where S₁ progenies are used as recombination units, a reduction in

population sizes will occur and, as a consequence, genetic drift is expected to take place in the selected population (Souza Jr. et al., 2000). Hence, because of the joint effects of selection and genetic drift, the genetic variability of the traits being selected could be reduced after some cycles of selection and, consequently, the selection response could also be reduced in the selected populations (Santos et al., 2005). Generally, genetic diversity is a requirement for genetic variance and response to selection.

The objectives of this study were to (i) improve mid-season drought tolerance in five maize populations through S_1 family recurrent selection, (ii) determine the genetic gain in drought tolerance, and (iii) determine the genetic variability in maize populations in semi-arid eastern Kenya after two cycles of recurrent selection.

The hypotheses tested were that after two cycles of recurrent selection, (i) there is improvement of mid-season drought tolerance, (ii) there is genetic gain in drought tolerance, and (iii) there is genetic variability in five maize populations in semi-arid eastern Kenya after two cycles of recurrent selection.

3.2 Materials and Methods

3.2.1 Germplasm

Two landrace populations sourced from the farmers in Machakos and Kitui districts of semi-arid eastern Kenya and three populations from CIMMYT-Zimbabwe (V032, ZM423 and ZM523) were used in the S_1 family recurrent selection procedure. The landrace populations have never been improved, whereas the CIMMYT populations are open-pollinated varieties which were developed at CIMMYT-Zimbabwe. The profiles of these populations are shown in Table 3.1.

Table 3.1 Profiles of the germplasm used in the recurrent selection process

Maize population	Origin	Province	District	Kernel colour	Variety type
MKS-CEN	Kenya	Eastern	Machakos	White	Landrace
KTU-CEN	Kenya	Eastern	Kitui	White	Landrace
V032	CIMMYT-Zimbabwe			White	Improved
ZM423	CIMMYT-Zimbabwe			White	Improved
ZM523	CIMMYT-Zimbabwe			White	Improved

3.2.2 Experimental Site and Cultural Practices

The experiment was done at KARI-Kiboko Research Sub-Station in Makueni district which has an elevation of 927 m above sea level and a GPS reading of 37° 43' E, 02° 13' S. Generally, the site is hot and dry and receives a bimodal type of rainfall, with long rains occurring from March – May and short rains from October – December with a mean annual rainfall of 538.8 mm. The short rains generally have more rainfall amount (season mean of 328 mm) and are more reliable than the long rains (season mean of 233 mm). The soils at Kiboko Research Farm are ferric fluvisol, which are mainly sandy-clay soil type with a top soil pH of 7.9 (Hornetz et al., 2000). The rainfall amounts during the entire period of the experiment are shown in Table 3.2. The spacing used during the entire selection procedure was 75 cm between the rows and 25 cm within the rows. The experiment used the recommended fertilization and cultural practices of conventional maize production. The rainfall was supplemented with irrigation during the entire period of the selection process. The irrigation was usually done at least twice a week for two hours. The irrigation water was applied with 3/4" dual nozzle sprinklers spaced at 6.7 m with risers 2.15m high at a rate of $9.6 \pm 0.58 \text{ mm hr}^{-1} \text{ ha}^{-1}$.

Table 3.2 Rainfall amounts during the entire selection period (2005 to 2007)

Month	Year		
	2005	2006	2007
	Rainfall (mm)	Rainfall (mm)	Rainfall (mm)
January	6.5	12.4	5.6
February	0.0	6.0	0.0
March	40.5	85.7	50.4
April	186.5	205.8	165.3
May	13.8	43.5	16.2
June	0.0	0.0	0.0
July	0.0	0.0	4.5
August	2.5	0.0	0.0
September	0.5	0.0	0.0
October	20.5	0.0	-
November	57.5	0.0	-
December	9.2	0.0	-
Total	337.5	353.4	242.0*

*This represents the rainfall amount during the experimental time only

3.2.3 Formation of S₁ Lines

The S₁ lines for cycle one (C₁) were formed from cycle zero (C₀) populations during the long rains of March – June 2005 and for cycle two (C₂) from cycle one (C₁) populations, during the later parts of long rains in March – June 2006. A total of 600 seeds from C₀ were planted for each of the populations for each cycle. At flowering, individual plants were self pollinated to obtain S₁ plants. In each of the populations, 300 to 400 selfed plants/ears were selected on the basis of the following criteria:

1. Earliness – early to medium maturing (90-110days);
2. Ear height – short (80cm – 100cm for CIMMYT materials and 60 cm – 80 cm for local landraces);
3. Disease resistance – visual observation on both the foliar and the ear;
4. Ear size – medium to large;
5. Kernel characteristics: (i) Kernel type – flint;
(ii) Kernel colour – white;

Out of the selected S₁ plants, 200 were selected again per population for screening/evaluation for drought tolerance. At harvest, rotten and small or partially filled

ears were discarded. The selected ears from the S₁ lines in each population were then bulked and the seeds used for evaluation. This procedure was then repeated in cycle two.

3.2.4 Evaluation and Random Mating of the S₁ Lines

The 200 S₁ lines selected from each of the five populations were evaluated for drought tolerance during the off seasons (dry period) of 2005 for cycle one and 2006 for cycle two. For both cycles, the S₁ lines were planted at the Kiboko Research Farm in two replicates. The S₁ lines were planted in sets of 25, i.e. 5 lines per population in a set/block, giving a total of 40 sets per replicate. In total, 200 S₁ lines were planted per population in each replicate. The evaluation was done under managed drought stress, with withdrawal of irrigation water one week before flowering and irrigation was not resumed until two weeks after flowering. Tensiometers and neutron probes were used to monitor the soil moisture levels during the water stress period. The readings were taken at a 2 – 4 day interval. The soil moisture level at the start of withdrawal of irrigation was at about pF value of 2, when soil water was easily available to the plant and by the time irrigation was resumed the soil moisture was at around pF values of 3.8, when soil water becomes difficult to absorb i.e. early wilting.

Data was collected on the agronomic traits based on the standard procedures used by CIMMYT (Bänziger et al., 2000). The traits used to select 20 S₁ lines in each population, which represent 10% selection intensity, are shown in Table 3.3.

Table 3.3 Selection criteria during the evaluation of the S₁ lines

Trait	Description
Days to anthesis (DA)	Days from planting to 50% pollen shed
Days to Silking (DS)	Days from planting to 50% silk emergence
Anthesis-silking interval (ASI)	Anthesis date minus silking date
Ears per plant (EPP)	Number of ears with at least one grain, divided by the total number of plants per plot
Leaf rolling (LR)	Visual score: 1 (Unrolled leaves) to 5 (rolled leaves). Measured 2 – 3 times at weekly interval from commencement of flowering
Leaf senescence (LS)	Visual score 0 (0% dead leaf area) to 10 (100% dead leaf area). Measured 2-3 times at weekly interval at commencement of flowering
Yield	Grain yield measured after harvesting

Ears harvested from each line in each of the populations were shelled, grains dried and weighed. In each population, 20 S₁ lines with good performance in the traits mentioned above were selected for random mating. The S₁ lines were planted for random mating during the short rains of January – April 2006 for cycle one and January – April 2007 for cycle two. These 20 S₁ selected families from each population were planted in 20 rows of 30 hills, giving a plant population of 600 plants. These S₁ lines were then randomly mated by bulking pollen from the S₁ plants and using it to make crosses by hand in all possible combinations. This procedure was done for each separate population. At harvest, ears were harvested, shelled, dried and bulked in each of the five different populations to form seed for the next cycle. This procedure was repeated for cycle two.

3.2.5 Evaluation of the Populations after Two Cycles of Recurrent Selection

Evaluation for genetic gain

The evaluation for genetic gain in the five populations after two cycles of recurrent selection was done in June – September 2007. This is the off season period when rainfall is not expected to occur. The experiment was laid out as a 4 x 4 balanced lattice design with 5 replications. There were 4 rows of 15 hills planted in each population,

giving a plant population of 60 plants per cycle (C_0 , C_1 , and C_2). Included in each replication was a commercial check, Katumani composite (KCB). The evaluation was conducted under both optimal conditions and controlled drought stressed conditions. Under optimal conditions, irrigation was applied throughout the entire crops' growth period, until the plants reached physiological maturity. Under the drought stressed conditions, irrigation was stopped one week before flowering and resumed during grain filling.

Data were collected on the traits shown in Table 3.3. Under optimal conditions, the traits leaf rolling and leaf senescence were not measured. Ears harvested from each of the populations were bulked, shelled, grain dried and weighed. Grain yield adjusted to 12.5% moisture content and converted to $t\ ha^{-1}$, was calculated using the following formula:

$$\text{Grain yield (t ha}^{-1}\text{)} = [\text{Grain weight (Kg plot}^{-1}\text{)} \times 10 \times (100-\text{mc}) / (100-12.5) / (\text{Plot area})], \text{ where mc} = \text{measured grain moisture content.}$$

Determination of genetic variability

The evaluation of S_1 progenies to determine the genetic variability in the five populations after two cycles of recurrent selection was done in June – September 2007. The experiment was laid out as a randomized complete block design with two replications. In each population, 30 S_1 families in each population per cycle were evaluated for genetic variability. There were 30 rows of 10 hills planted in each population, each row representing an S_1 family. The evaluation was done under controlled drought stressed conditions whereby irrigation was withdrawn one week prior to flowering and not resumed until grain filling. The data was collected on the traits shown in Table 3.3. Ears harvested from each of the S_1 lines in each population were bulked, shelled, grains dried, weighed. Grain yield was adjusted to 12.5% moisture content, using the same formula as described previously in section 3.2.5.1.

3.2.6 Data Analyses

Genetic gain

All the data collected from the evaluation for genetic gain, were subjected to analyses of variance (ANOVA) based on a row x column design (Cochran and Cox, 1992) using SAS v 9.1.3 (SAS Institute, 2004). The SAS procedure used for the ANOVA was GLM (General linear model) procedure as a fixed model for experimental populations. The linear model was as follows:

$$Y_{ijklm} = \mu + R_i (r_m) + C_j (r_m) + p_k + c_i + r_m + \varepsilon_{ijklm},$$

where,

Y_{ijklm} = the observation made in the m^{th} replication on the k^{th} population, in the i^{th} cycle in the j^{th} row and in the l^{th} column, μ = general mean, R_i = effect of the i^{th} row, C_j = effect of the j^{th} column, p_k = population effect, c_i = Effect of the i^{th} cycle of selection, $j = 1, 2$ and ε_{ijklm} = experimental error.

Selection gains were determined from C_0 to C_1 , C_1 to C_2 and C_0 to C_2 . Realized net gain to selection in each cycle was calculated as:

$$\mu c_{n+1} - \mu c_n,$$

where, μc_{n+1} and μc_n stand for the means of the traits evaluated at $n^{\text{th}} + 1$ cycle and cycle n^{th} , respectively.

Genetic variability

The data collected from the experiment to determine genetic variability, was subjected to analysis of variances (ANOVA) based on a randomized complete block design (RCBD) (Cochran and Cox, 1992) using GenStat release 9th edition statistical software (Payne et al., 2006). The analysis was based on the following linear model:

$$Y_{ijkl} = \mu + f_i + p_j + c_k + \beta_l + \epsilon_{ijkl},$$

where,

Y_{ijkl} = the observation made on the i^{th} S_1 family in the j^{th} population, in the k^{th} cycle, in the l^{th} block/replication, μ = general mean, f_i = effect of the S_1 family, p_j = population effect, c_k = effect of the k^{th} cycle of selection: $k = 1, 2$ and ϵ_{ijkl} = experimental error.

The genetic and phenotypic variance components were estimated using the restricted maximum likelihood (REML) random model in GenStat, the S_1 lines being considered random. These variance components were used to estimate the broad sense heritability of the traits using the formula: $H^2 = \delta_g^2 / \delta_{ph}^2$ (Hill et al., 1998). Where: H^2 = heritability broad sense, δ_g^2 = genetic variance and δ_{ph}^2 = phenotypic variance.

3.3 Results

3.3.1 Analysis of Variance

Evaluation for genetic gain

The analyses of variance (ANOVA), showing the mean squares of days to anthesis, days to silking, anthesis-silking interval, leaf rolling, leaf senescence, ears per plant, and yield for the stressed and well watered conditions are shown in Tables 3.4 and 3.5, respectively.

In the drought stressed conditions, the mean squares for the number of days to anthesis was highly significant at $p=0.01$ for cycle, populations effects and the cycle x population interaction effects. The number of days to silking was significant at $p=0.05$ for cycle effects whereas, it was highly significant at $p=0.01$ for population and cycle x population interaction effects. The anthesis-silking interval was significant at $p=0.05$ for population effects and not significant ($p>0.05$) for cycle and cycle x population interaction effects. Leaf rolling was significant at $p=0.05$ for cycle x population interaction effects, whereas it was not significant ($p>0.05$) for cycle and population effect. Ears per plant were not

significant ($p>0.05$) for all the effects. Yield was significant at $p=0.05$ for population effects only (Table 3.4).

Table 3.4 Mean squares for days to anthesis (DA), days to silking (DS), anthesis-silking interval (ASI), leaf rolling (LR) scores, leaf senescence (LS) scores, ears per plant (EPP), and yield under stressed conditions

Source	df	MEAN SQUARES						
		DA	DS	ASI	LR	LS	EPP	Yield
Replications	4	9.77*	19.75**	4.55**	2.74**	0.12*	0.01	5.77**
Col (Rep)	15	34.31**	38.50**	1.34*	0.29**	0.43*	0.05*	0.88
Row (Rep)	15	16.53**	17.77**	1.16	0.26*	0.01	0.037	1.53**
Cycle	2	16.84**	12.44*	0.75	0.12*	0.02	0.009	0.98
Population	4	150.20**	118.77**	4.35*	0.20*	0.72	0.067	1.78*
PopulationxCycle	8	10.75**	15.38**	1.52	0.17*	0.05*	0.026	0.85
Error	26	2.62	2.94	1.21	0.09	0.03	0.02	0.05
Overall mean		63.47	65.79	2.32	1.34	1.04	1.11	4.59
CV%		2.55	2.61	31.60	22.96	16.91	13.41	14.8
LSD _{0.05}		2.34	2.78	1.36	0.53	0.23	0.21	1.01

*, ** Significant at $p=0.05$ and $p=0.01$, respectively.

In the well watered conditions, the number of days to anthesis were significant ($p=0.05$) for cycle effects. Yield was highly significant ($p=0.01$) for cycle effects. The number of days to silking, anthesis-silking interval, and ears per plant were not significant ($p>0.05$) for cycle effects. The number of days to silking, number of days to anthesis, ears per plant and yield were highly significant at $p=0.01$, whereas anthesis-silking interval was significant at $p=0.05$. None of the traits were significant ($p>0.05$) for population x cycle interaction effects (Table 3.5).

Table 3.5 Mean squares for days to anthesis (DA), days to silking (DS), anthesis-silking interval (ASI), ears per plant (EPP), and yield under well watered conditions

Source	MEAN SQUARES					
	df	DA	DS	ASI	EPP	Yield
Replications	4	17.70**	9.41*	3.59*	0.06	6.28**
Col (Rep)	15	25.70**	25.46**	1.74	0.05	0.80
Row (Rep)	15	14.72**	13.47**	1.45	0.05	1.12
Cycle	2	1.58*	1.18	0.13	0.04	4.74**
Population	4	149.12**	116.18**	2.48*	0.29**	3.81**
PopulationxCycle	8	1.66	2.02	0.74	0.06	1.03
Error	26	2.12	3.19	0.88	0.04	0.77
Overall mean		64.00	66.12	2.11	1.19	4.68
CV%		2.27	2.70	44.54	17.27	18.71
LSD _{0.05}		2.54	2.94	1.36	0.25	1.12

*, ** Significant at $p=0.05$ and $p=0.01$, respectively.

Genetic variability

The analysis of variance showed significant differences among the means of the agronomic traits of the S₁ lines for the five populations (Table 3.6). Yields were significantly different ($p=0.05$) in MKS S₁ lines in C₁, but was not in C₂. In KTU and V032, yields were highly significant ($p=0.01$) in C₂, but was not ($p>0.05$) in C₁. In ZM423 yields were not significantly different ($p>0.05$) in C₁, but highly significantly different ($p=0.01$) in C₂. Yields were not significantly different ($p>0.05$) in both cycles in ZM523.

There were highly significant differences in the number of days to anthesis (DA) at $p=0.01$ in C₁ and C₂ for landrace population KTU, while there were highly significant differences ($p=0.01$) for MKS in C₁ and no significant differences ($p>0.05$) in C₂. In V032 S₁ lines, the number of days to anthesis were highly significantly different ($p=0.01$) in C₁ and not significant ($p>0.05$) in C₂. In ZM423, DA were not significantly different ($p>0.05$) in C₁, but were highly significantly different ($p=0.01$) in C₂. In ZM523, DA were significantly different at $p=0.05$ and $p=0.01$ in C₁ and C₂, respectively.

Days to silking (DS) were significantly different ($p=0.05$) in C₁ and not ($p>0.05$) in C₂ in MKS S₁ lines. In KTU, DS were highly significantly different ($p=0.01$) in both cycles. In V032, DS were significantly different ($p=0.01$) in C₁ and not significantly different ($p>0.05$) in C₂. There were significant differences ($p=0.05$) in C₁ of the ZM423 and

ZM523 S₁ lines. In the same populations there were highly significant differences ($p=0.01$) in C₂.

Leaf rolling (LR) was not significantly different ($p>0.05$) in both MKS and KTU S₁ lines in both cycles. It was significantly different ($p=0.01$) in V032 in both cycles. In ZM423, LR was not significantly different ($p>0.05$) in C₁, but significant ($p=0.01$) in C₂. In ZM523, it was only significantly different ($p=0.05$) in C₁.

The plant height (PH) was significantly different ($p=0.05$) in MKS and ZM423 S₁ lines in C₂, but was not ($p>0.05$) in C₁. Plant height was not significantly different ($p>0.05$) in KTU and ZM523 in both cycles. In V032, PH was highly significantly different ($p=0.01$) in C₁ and significant ($p=0.05$) in C₂.

Table 3.6 Mean squares, means, minimum and maximum values for yield ($t\ ha^{-1}$), days to 50% anthesis (DA), days to 50% silking (DS), leaf rolling (LR) scores and plant height (PH) of the S_1 lines in five populations

Traits		Populations									
		MKS		KTU		V032		ZM423		ZM523	
		Cycle 1	Cycle 2	Cycle 1	Cycle 2	Cycle 1	Cycle 2	Cycle 1	Cycle 2	Cycle 1	Cycle 2
Yield	Max	0.7	0.7	0.7	0.7	0.7	0.7	0.7	0.7	0.7	1.54
	Mean	2.4	3.5	2.8	2.7	3.9	4.3	5.1	4.7	3.8	4.0
	Min	5.6	8.75	8.4	7.0	9.8	9.8	10.5	10.5	10.5	10.5
	MS	1.9*	3.5	4.3**	1.9	6.9**	5.2	4.4	7.0**	4.9	2.9
	LSD	2.1	3.7	2.7	2.1	3.5	3.6	4.2	3.1	3.4	3.1
DA	Max	53.0	54.0	52.0	54.0	58.0	60.0	60.0	61.0	62.0	62.0
	Mean	58.6	60.6	57.9	60.3	64.4	65.7	65.1	65.1	69.1	68.3
	Min	66.0	69.0	65.0	69.0	72.0	75.0	74.0	71.0	77.0	77.0
	MS	15.7**	11.6	12.8**	20.3**	15.6**	15	8.0	8.6**	11.9*	14.0**
	LSD	4.9	5.5	3.9	4.4	4.4	6.2	4.7	3.1	5.1	3.1
DS	Min	54.0	58.0	53.0	57.0	60.0	61.0	62.0	63.0	65.0	65.0
	Mean	61.3	64.6	60.9	64.0	67.8	68.5	67.6	67.8	72.3	71.6
	MS	21.4*	19.7	22.5**	19.2**	29.4**	15.76	14.0*	15.2**	13.4*	20.3**
	Max	71.0	74.0	71.0	72.0	60.0	61.0	62.0	63.0	65.0	64.0
	LSD	6.4	7.4	5.1	2.4	4.7	7.4	5.1	4.1	5.0	4.3
LR	Min	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
	Mean	1.5	1.4	1.3	1.3	1.4	1.3	1.3	1.5	1.8	1.2
	Max	5.0	2.3	3.0	3.5	3.0	3.5	3.0	2.0	4.0	2.0
	MS	0.4	0.2	0.2	0.2	0.5**	0.4**	0.2	0.7**	0.7*	0.1
	LSD	1.4	0.8	0.9	0.9	0.8	0.7	0.9	1.1	1.2	0.6
PH	Min	85.0	101.0	75.0	93.0	75.0	55.0	90.0	100.0	78.0	105.0
	Mean	136.5	135.3	136.1	131.5	129.7	134.4	143.9	137.2	140.8	142.9
	Max	181.0	186.0	180.0	160.0	171.0	171.0	171.0	177.0	175.0	
	MS	509.9	397.2*	632.0	282.3	648.9**	697.3*	347.5	500.9*	407.1	245.2
	LSD	36.1	30.3	43.6	28.9	32.9	38.7	36.7	30.6	37.6	28.4

*, ** Significant at ($p=0.05$) and ($p=0.01$), respectively.

3.3.2 Realized Gains from Selection in five Maize Populations under Stress and Non-stress Environments

The realized gains from selection in the five maize populations from C_0 to C_1 , C_1 to C_2 and C_0 to C_2 for the agronomic traits under drought stress and well watered conditions are presented in Table 3.7. Selection generally increased the net gains in all the traits in the local landrace populations KTU and MKS, whereas, in the CIMMYT populations V032, ZM423 and ZM523, there were both decreases and increases in some of the traits under both environments. There was generally no gain in leaf rolling (LR) and leaf senescence (LS), whereas, number of ears per plant (EPP) were only increased by a small margin in all the populations.

There was generally a net improvement in all the traits after two cycles of selection in the landrace population KTU. Yield increased by 0.2 t ha^{-1} and 0.5 t ha^{-1} under drought and well watered conditions, respectively. The number of days to anthesis (DA) was increased by one day and by a 0.6 of day under drought and well watered conditions, respectively. The number of days to silking (DS) increased by 1.8 and 1.2 under drought and well watered conditions, respectively. Anthesis-silking interval (ASI) increased by 0.8 under both conditions.

There was also generally a net improvement in all the traits in the landrace population MKS. Selection increased the net gain in yield by 1.2 t ha^{-1} , which was the highest net gain under drought stress conditions compared to other populations. Under well watered conditions, yield increased by 0.8 t ha^{-1} . The number of days to anthesis increased by 1.2 and 3.2 under drought and well watered conditions respectively. Selection decreased ASI by one day and 0.2 of a day under drought stress and well watered conditions, respectively.

In V032 population, there was generally a net improvement in all traits except in yield where there was a net decrease of 1.1 t ha^{-1} under drought conditions, which was the largest decrease in the selection process. Under well watered condition, yield was decreased by 0.1 t ha^{-1} . The number of days to anthesis increased by 3.8 and 0.2 under drought and well watered conditions, respectively. The number of days to silking increased by 4.2 and 1.8 under drought and well watered conditions, respectively. The

highest net increase was realized in ASI where there was an increase of 1.6 days under well watered conditions. Under drought conditions ASI increased by 0.5 days.

In the ZM423 population, there was generally a decrease in net gain in all the traits except number of ears per plant and yield. Yield increased by 0.4 t ha⁻¹ and 2.5 t ha⁻¹ under drought and well watered conditions, respectively. The number of days to anthesis was decreased by 2.7 days under drought conditions, but was increased under well watered conditions by 1.5 days. The number of days to silking reduced by 4.2 days, and increased by 1.4 days under drought and well watered conditions, respectively. The anthesis-silking interval was decreased by 0.6 days and 0.4 days under drought and well watered conditions, respectively.

Generally, ZM523 population had increases in all the traits except in yield where there was a net decrease of 0.6 t ha⁻¹ under drought stress conditions. However, there was increased yield under well watered conditions of 0.8 t ha⁻¹. The number of days to anthesis increased by 2 and 0.4 under drought and well watered conditions, respectively. Days to silking increased by 4.2 and 0.6 under drought and well watered conditions, respectively. The anthesis-silking interval increased by 2.2 days and 0.2 0 of a day under drought and well watered conditions, respectively.

Table 3.7 Effect of selection on agronomic traits under drought stress (Drt) and non-stress environments (WW)

Trait Population	Days to anthesis		Days to silking		Anthesis-silking interval		Leaf rolling	Leaf senescence	Eears plant ⁻¹		Yield (t ha ⁻¹)	
	Drt	WW	Drt	WW	Drt	WW	Drt	Drt	Drt	WW	Drt	WW
KTU												
Gain C ₀ -C ₁	1.2	-0.4	2.2	0.0	1.0	0.4	0.2	0.0	0.0	0.0	0.0	-0.4
Gain C ₁ -C ₂	-0.2	1.0	0.4	1.2	-0.2	0.4	0.0	0.0	0.0	0.1	0.2	0.9
Net gain C₀-C₂	1.0	0.6	1.8	1.2	0.8	0.8	0.2	0.0	0.0	0.1	0.2	0.5
MKS												
Gain C ₀ -C ₁	0.8	3.4	0.4	3.6	-0.4	0.2	-0.2	0.0	0.0	0.0	0.6	-0.6
Gain C ₁ -C ₂	0.4	-0.2	-0.2	-0.6	-0.6	-0.4	0.2	0.0	0.0	0.1	0.6	1.4
Net gain C₀-C₂	1.2	3.2	0.2	3.00	-1.0	-0.2	0.0	0.0	0.0	0.1	1.2	0.8
V032												
Gain C ₀ -C ₁	1.5	0.6	1.7	1.8	0.2	1.2	0.2	0.2	0.2	-0.2	-0.2	-0.2
Gain C ₁ -C ₂	2.3	-0.4	2.5	0.0	0.3	0.4	0.0	0.1	0.0	0.1	-0.9	0.1
Net gain C₀-C₂	3.8	0.2	4.2	1.8	0.5	1.6	0.2	0.1	0.2	-0.1	-1.1	-0.1
ZM423												
Gain C ₀ -C ₁	-4.5	-0.5	-6.2	-0.4	-0.8	-0.2	-0.8	0.0	0.4	0.3	0.6	1.2
Gain C ₁ -C ₂	1.8	2.0	2.0	1.8	0.2	-0.2	0.3	0.0	-0.3	0.1	-0.2	1.3
Net gain C₀-C₂	-2.7	1.5	-4.2	1.40	-0.6	-0.4	-0.5	0.0	0.1	0.4	0.4	2.5
ZM523												
Gain C ₀ -C ₁	-2.2	-0.4	-1.6	-1.2	0.6	-0.8	-0.1	0.0	0.0	0.2	0.9	0.3
Gain C ₁ -C ₂	4.2	0.8	5.8	1.8	1.6	1.0	0.1	0.0	0.2	0.1	-1.5	0.5
Net gain C₀-C₂	2.0	0.4	4.20	0.6	2.2	0.2	0.0	0.0	0.2	0.3	-0.6	0.8

3.3.3 Genetic Variability and Heritability Estimates

The genetic variances (σ_g^2), phenotypic variances (σ_{ph}^2) and broad sense heritability (H^2) estimates for the agronomic traits of days to 50% anthesis, days to 50% silking, leaf rolling scores, plant height and grain yield of the S_1 progenies of five maize populations are presented in Table 3.8. The genetic variance for yield increased by a larger magnitude in the S_1 progenies of MKS and ZM423 populations while it decreased in KTU, V032 and ZM523 populations. Heritability estimates for yield decreased in four populations MKS, KTU, V032 and ZM523 but it increased in ZM423. The genetic variance was only significant in KTU at $p=0.05$ and $p=0.01$ in cycle one and cycle two, respectively.

There was a reduction of the genetic variances in S_1 progenies for days to anthesis by almost half in two populations, MKS and V032, whereas there was an increase in genetic variability for KTU and ZM423, but there was a reduction in ZM523. There was a decrease in heritability estimates of both the local landraces and V032, whereas there was an increase in heritability estimates in ZM423 and ZM523 for days to anthesis. The genetic variation for days to anthesis was significant ($p=0.05$) only in MKS, KTU V032 populations in cycle one, whereas it was not significant ($p>0.05$) in all the populations in cycle two. The genetic variance for days to silking in MKS and V032 decreased by a larger margin than in KTU. The trend was similar with the heritability estimates for days to silking in the same populations. There was no effect of selection on genetic variance for days to silking in both ZM423 and ZM523. The heritability of days to silking in ZM423 reduced, whereas it increased in ZM523 population. Genetic variation in days to silking was significant ($p=0.05$) in both cycles in KTU and in cycle two in ZM425. There was no significant variation ($p>0.05$) in MKS, V032 and ZM523 populations in both cycles.

The genetic variance for leaf rolling remained constant after selection in the S_1 s for KTU and V032 populations. However, genetic variance increased in ZM423 and MKS, whereas, it decreased in ZM523 S_1 s. Heritability estimates for KTU and V032 remained constant, but decreased in MKS and ZM523 while the value increased in ZM423 S_1 s. The genetic variation in leaf rolling was only significant ($p=0.05$) in V032 in both cycles, whereas it was not significant ($p>0.05$) in all the other populations in both cycles.

The genetic variance for plant height increased by a larger amount in the S₁ progenies of the three CIMMYT populations V032, ZM423, and ZM423, than in the local landrace population KTU. The genetic variance in the MKS population was decreased by almost half in cycle two. The heritability estimates for plant height increased after selection in the S₁ progenies of KTU, V032 and ZM423 populations, whereas, it decreased in MKS and ZM523 populations. The genetic variance was not significant ($p>0.05$) in all the populations in both cycles.

Table 3.8 Estimates of genetic variance and heritability for yield, days to 50% anthesis (DA), days to 50% silking (DS), leaf rolling (LR), and plant height (PH) in the S₁ progenies of five populations

Traits		Populations									
		MKS		KTU		V032		ZM423		ZM523	
		Cycle 1	Cycle 2	Cycle 1	Cycle 2	Cycle 1	Cycle 2	Cycle 1	Cycle 2	Cycle 1	Cycle 2
Yield	δ^2g	0.30	0.57	1.30*	0.30**	1.90	1.10	0.20	1.00	0.80	0.20
	δ^2ph	1.30	3.40	1.70	1.20	3.00	3.10	4.00	2.40	3.10	2.50
	H ²	0.23	0.17	0.76	0.25	0.63	0.35	0.05	0.42	0.26	0.08
	δ^2g SE	0.30	0.67	0.63	0.03	1.04	0.88	0.85	0.57	0.79	0.53
DA	δ^2g	4.70*	1.50	3.90*	4.60	4.80*	2.70	0.60	0.90	0.50	3.00
	δ^2ph	6.30	8.70	4.40	7.90	6.10	9.60	6.80	6.90	10.90	7.90
	H ²	0.75	0.17	0.89	0.58	0.79	0.28	0.09	0.13	0.05	0.38
	δ^2g SE	2.22	1.89	1.75	2.73	2.20	2.32	1.37	1.44	2.11	2.10
DS	δ^2g	5.70	2.60	6.10*	5.85*	6.80	1.10	3.50	3.40	0.70	6.70*
	δ^2ph	10.00	14.60	8.20	6.70	11.30	13.50	7.00	8.50	14.90	6.90
	H ²	0.57	0.18	0.74	0.87	0.60	0.08	0.50	0.40	0.05	0.97
	δ^2g SE	3.09	3.20	3.05	2.63	3.96	2.71	2.05	2.28	2.60	2.81
LR	δ^2g	0.10	0.01	0.01	0.01	0.14*	0.12*	0.02	0.12	0.17	0.02
	δ^2ph	0.70	0.20	0.20	0.20	0.17	0.14	0.18	0.47	1.09	0.15
	H ²	0.14	0.05	0.05	0.05	0.82	0.86	0.08	0.26	0.16	0.13
	δ^2g SE	0.10	0.04	0.04	0.04	0.07	0.05	0.06	0.11	0.17	0.02
PH	δ^2g	92.50	46.60	30.70	37.40	84.60	175.30	15.10	80.70	52.50	15.90
	δ^2ph	325.00	490.30	570.50	207.40	479.80	346.70	317.20	339.50	512.10	277.00
	H ²	0.28	0.10	0.05	0.18	0.18	0.51	0.05	0.24	0.10	0.06
	δ^2g SE	79.00	82.00	111.00	45.70	105.30	101.90	61.30	79.00	85.00	48.00

*, ** Significant at $p=0.05$ and $p=0.01$, respectively.

δ^2g – Genetic variance, δ^2ph – Genotypic variance, H² – Broad sense Heritability, and SE – Standard error.

3.3.4 Phenotypic Correlation between Agronomic Traits

Phenotypic correlation between traits under well watered and drought stressed conditions are shown in Table 3.9. Leaf rolling and senescence scores were not measured under well watered conditions. Under drought conditions, anthesis-silking interval (ASI) was positively correlated with leaf rolling and leaf senescence, although it was highly significant only with leaf rolling at $p=0.01$. It was positively correlated with leaf rolling but the correlation was not significant ($p>0.05$). It was negatively and highly significantly correlated with yield ($p=0.01$) and significant ($p=0.05$) with number of ears per plant under drought conditions. Under well watered conditions, it was positively correlated to yield whereas it was negatively correlated with ears per plant, though the correlation was not significant ($p>0.05$).

There was no significant correlation ($p>0.05$) between ears per plant and leaf rolling, leaf senescence and yield under drought conditions. However, the correlation between leaf rolling and leaf senescence was negative but positive with yield, although the correlation was not significant ($p>0.05$). Under well watered conditions it was positively correlated with yield but not significant ($p>0.05$). Under drought conditions, leaf rolling was positively correlated to leaf senescence but this was not significant ($p>0.05$). The correlation between leaf rolling and yield was highly significant ($p=0.01$) and negative. Leaf senescence was negatively correlated with yield and significant at $p=0.05$.

Table 4.9 Simple phenotypic correlation coefficients for 50% days to anthesis (DA), 50% days to silking (DS), leaf rolling (LR), leaf senescence (LS), ears per plant (EPP) and yield under both well watered (above diagonal) and drought stressed conditions (below diagonal)

	ASI	EPP	LR	LS	Yield
ASI		-0.212			0.082
EPP	-0.235*				0.143
LR	0.352**	-0.113			
LS	0.218	-0.052	0.177		
Yield	-0.659**	0.087	-0.432**	-0.231*	

*, ** significant at $p=0.05$ and $p=0.01$, respectively.

3.5 Discussion

Selection increased the number of days to anthesis and reduced the number of days to silking in MKS and ZM423, thereby reducing the anthesis-silking interval in these two populations. This implies that, in these two populations, drought tolerance was improved with selection, as a reduced anthesis-silking interval, is associated with drought tolerance. Drought stress at flowering usually does not greatly affect the number of days to anthesis, but usually affects silking by slowing the silk elongation thus increasing the anthesis-silking interval in drought susceptible genotypes (Magorokosho et al., 2003). Studies done by Omoigui et al. (2006) and Tuberosa et al. (2005) also found similar trends in regards to the silking in maize under stress environments.

Selection under drought stress increased yields for landraces, KTU and MKS, and the CIMMYT population, ZM423. Delayed silking is associated with yield losses due to a decrease in the number of grains formed in the maize ear (Zinselmeier et al., 2000; Bruce et al., 2002). But, in these three populations, there was a reduced anthesis silking-interval under drought stressed conditions, allowing pollination to take place effective. There was also an increase in genetic variability in MKS and ZM423 populations. This could explain the observed increase in yield with selection in these populations. However, the reduced genetic variability in KTU population had no penalty in yield responses. The CIMMYT populations, V032 and ZM523 had depressed yields after two cycles of selection under drought conditions. These two populations had increased anthesis-silking interval and this could possibly explain the reduction in their yields. The genetic variability in these populations was also reduced with selection, leading to the reduction in the yield in these two populations. The local landrace populations have never been improved, while the CIMMYT populations are improved. In the unimproved landrace populations, the variation is greater, while in the improved populations, the genetic base is probably narrow. This could explain why there was a higher net gain in yield in the landrace populations than in the CIMMYT populations.

There was also a general increase in yield from C_0 to C_2 , under well watered conditions in all populations except for V032 that showed a decline of $0.1t\ ha^{-1}$. This trend suggests that genetic gains can be achieved not only during normal growth conditions, but also during stress conditions. This would imply that these populations would do well under both optimal and water stressed conditions. Given that in the semi-arid regions, the

rainfall is unreliable and cannot be predicted. It can be low or sufficient, depending on the seasons. Therefore, these populations can do well under both these conditions. Ideally, a drought tolerant maize crop should have high grain yield and stability under both water-deficit and well-watered conditions (Bruce et al., 2002).

The genetic variability and heritability estimates for yield increased in S₁ lines of MKS and ZM423 populations, but decreased in KTU, V032 and ZM523 populations. KTU landrace population was most affected by selfing since its genetic variability in yield was decreased. Since selected progeny were only selfed once, it can be expected that there is still genetic variation as the S₁ progenies are still undergoing segregation and that with further selfing inbreeding depression will eventually be greater and variability will be reduced. Grain yield is greatly affected by the environment since it is a quantitatively inherited trait. Hence, the decrease in heritability could also be a result of environmental factors. Genetic variance and heritability for grain yield are generally lower under stress than optimal conditions (Campos et al., 2006). These results are in conformity with the studies done by Bänziger and Lafitte (1997) who found a greater reduction of genetic variance of grain yield under low yielding environments than under high yielding environments. Pinto et al. (2003) also reported a decrease in genetic variance for yield in BSSS and BSCB1 maize population after 12 cycles of recurrent selection. Despite this reduction in genetic variability, the yields of the S₁ lines in the current study only declined by a small margin.

The genetic variability for the number of days to anthesis was increased with selection while the genetic variability of the number of days to silking was generally reduced among the S₁ families, across the populations. This decrease in the genetic variability in the number of days to silking did not affect silking as the silking was generally delayed in the populations. This can be explained by the fact that under drought stress conditions, pollen shed is less likely to be affected but the silking is adversely affected (Magorokosho et al., 2003). The genetic variability and heritability estimates of leaf rolling were affected by selection. Where the genetic variability increased, the heritability of the trait increased. Leaf rolling is a trait, which is greatly affected by environment. In case of drought stress, the plants respond by rolling the leaves and in well watered conditions, the plants do not roll the leaves.

The genetic variability and heritability estimates of the S₁ progenies in all the populations showed a reduction in plant height, except in V032 and ZM423 populations, where there was an increase. This occurred because with selfing plant height is usually reduced because traits such as plant height show inbreeding depression. Given also that maize is an outcrossing crop, it shows high inbreeding depression when it is subjected to selfing as was the case in the current study. Several studies of inbreeding in maize on phenotypic and agronomic characters have reported significant inbreeding depression (Edwards and Lamkey, 2002). The S₁ lines of V032 and ZM423 populations had large variability in plant height after two selection cycles. This is against the expected effects of inbreed to plant height. Theoretically, it has been established that in the presence of directional dominance, inbreeding does not necessarily reduce genetic variance and may actually increase (Edwards and Lamkey, 2003). Thus, this could offer an explanation as to why there was an increase in genetic variances of these two populations. However, with further inbreeding there will be a reduction in genetic variability since these populations were only selfed once.

The correlation between yield with the secondary traits anthesis-silking interval, leaf rolling and leaf senescence was negative while it was positive with ears per plant. These results are agreement to those reported by Byrne et al. (1995). Chapman and Edmeades (1999) also reported a strong negative correlation of grain yield with anthesis-silking interval and positive correlation with ears per plant. This confirms the usefulness of these secondary traits as indirect selection traits for yield in breeding for drought tolerance in maize. The use of these secondary traits has been a strategy utilized by CIMMYT in its maize breeding programme (Bänziger et al., 2004).

The results of the present study confirm the effectiveness of S₁ family recurrent selection as a population improvement procedure capable of improving the performance of maize populations for drought tolerance. This method has been used elsewhere as reported by Edmeades et al (1999) and it resulted in annual gains of about 50% in grain yield in maize populations after selection. Using S₁ family selection, Ramírez-Díaz et al. (2000) also managed to effectively modify ear and plant heights as well as reduce ear rot and root lodging rates in maize. This is because S₁ progeny performance reflects mainly additive genetic effects (Goulas and Lonquist, 1976), which is useful in the population improvement through recurrent selection.

3.6 Conclusions

The two local landrace populations MKS and KTU, and one CIMMYT population ZM423 did improve in yield after two cycles of S_1 recurrent selection under drought conditions. This implies that selection improved drought tolerance in these populations. Also, the positive linear increase in grain yield in these three populations after two cycles of selection, suggests that with further selection there will be subsequent gains realized. It is envisaged that this rate of progress will be maintained in subsequent selection cycles provided that the same S_1 recurrent selection method is practiced using an effective population size in order to avoid genetic drift. With the two CIMMYT populations V032 and ZM523, any further selection may not lead to any increased performance.

The results of the present study have found that the genetic variability of yield and the secondary traits were reduced after two cycles of selection in some of populations and increased in some populations. Given that selection was only done for two cycles, these results may not be adequate to make any conclusive statements on the trends observed but they form a basis for further selection in these populations.

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Chapter 4: Heterotic Patterns and Combining Ability of Maize Landraces from South-Eastern and Coastal Kenya

Abstract

Maize breeding programmes are based on the identification and utilization of heterotic groups. Little emphasis has been placed on identifying new sources of maize germplasm that can be used in the maize breeding programme in Kenya. This research was undertaken to identify heterotic patterns of landraces from the semi-arid areas and determine their combining ability. Ten landrace maize populations from the semi-arid south eastern Kenya, six landraces from coastal Kenya and three populations from CIMMYT were planted at Kiboko Research Farm during the short rains of October – December 2005 and crossed to two population testers, Embu 11 and Embu 12. The evaluation of the test crosses was done during the long rains of March – June 2006. The trial was laid out as a randomized complete block design with three replications. Percentage heterosis for yield ranged from -17.7% to 397.4%, -79.4 to 22.2% for anthesis-silking interval, -23.9% to 29.2% for ear height, -0.1 to 1.1 for ear diameter, -7.1 to 21.2% for ear length and -5.9% to 30.3% for plant height. General combining ability (GCA) effects were significant ($p=0.05$) for all the traits, whereas specific combining ability (SCA) effects were only significant ($p=0.05$) for ear and plant heights. All the traits showed positive correlation with yield, with only anthesis-silking interval which was negatively correlated to yield. Since SCA was not significant ($p>0.05$) for yield, the maize populations were classified based on percentage heterosis for yield alone. The maize populations therefore, were grouped into three different heterotic groups P, Q and R. Twelve landrace populations and two CIMMYT populations showed heterosis with Embu 11 and no heterosis with Embu 12 were put in one group P. Two landrace populations showed no heterosis with either tester were put in group Q Two landrace populations and one CIMMYT population showed heterosis with both testers and were put in group R. None of the populations showed heterosis only with Embu 12 and no heterosis with Embu 11. The 19 maize populations were classified into three distinct heterotic groups and that the coastal landrace and CIMMYT maize populations showed a higher heterosis than landrace populations from eastern Kenya. Additive gene effects were significant whereas nonadditive gene effects were not significant implying that variation among these crosses was mainly due to additive rather than nonadditive gene effects.

4.1 Introduction

Heterosis is the superiority of F_1 performance over some measure of the performance of the parents, such as increase of size, yield and vigour (Stuber, 1994). Duvick (1999) defined heterosis as the increase in size or rate of growth of offspring over parents. Heterosis is a major yield factor in all breeding categories, except line breeding, and to exploit heterosis the concept of heterotic groups and patterns was suggested (Reif et al., 2005). The manifestation of heterosis usually depends on genetic divergence of the parents. Genetic divergence of the two parents is inferred from the heterotic patterns manifested in the series of variety crosses. If heterosis between the two parents is large, then it shows that the two parents are genetically diverse (Hallauer and Miranda, 1988).

A heterotic group is a population of genotypes that, when crossed with individuals from another heterotic group or population, consistently outperforms intra-population crosses (Hallauer and Miranda, 1988). Studies on maize heterotic groups and patterns are very helpful to increase breeding efficiency. Thus, establishment of heterotic patterns among varieties is important in selecting inbred lines as parental seed stocks in hybrid production (Santos et al., 2001). Examples for determining heterotic pattern of varieties and diversity in the manifestation of heterosis have been reported by Moll et al. (1962, 1965). Heterotic patterns can be analyzed either by crossing the germplasm in question to two or more common testers which are known to be of different heterotic patterns or by using molecular markers or by crossing the germplasm in a diallel mating design and using the combining ability variances generated through the experimental data (Hallauer and Miranda, 1988).

The concepts of general combining ability (GCA) and specific combining ability (SCA) have been used extensively in the breeding of several economic crop species. The GCA is associated with additive effects of the genes, while SCA is related to dominance and epistatic effects (non-additive effects) of the genes. The variance of SCA also contains deviations due to the interaction between different non-additive effects, in addition to those that are due to dominance and epistasis (Aguar et al., 2003). In cross-pollinating species, the GCA effect is an indicator of the relative value of the population in terms of frequency of favourable genes (Viana and Matta, 2003). Thus, the analysis of GCA effects enables the identification of superior parents.

The SCA effect of two populations expresses the differences of gene frequencies between them and measures their divergence. Therefore, GCA and SCA effects should be considered in the selection of populations for hybrid production and for reciprocal recurrent selection programmes (Viana and Matta, 2003). The specific combining ability variance estimated from experimental data is also used to classify germplasm into different heterotic groups. Lower variance for SCA and a lower ratio of SCA to GCA variance ($\delta^2_{SCA}:\delta^2_{GCA}$) would imply the two germplasm sources are not genetically divergent and could belong to the same heterotic group (Reif et al., 2005).

Genetic diversity in maize plays a key role for future breeding programmes, thus the choice of heterotic groups is fundamental in hybrid breeding of maize (Reif et al., 2003). The estimation of genetic distance among maize lines and the correlation between genetic distance (GD) and hybrid performance could determine breeding strategies, classify maize lines, define heterotic groups and predict hybrid performance (Betrán et al., 2003). The importance of genetic diversity has been emphasized since the shift from double-cross to single-cross hybrids. Thus, the identification of populations which can be used as sources of inbred lines is based on their agronomic performance and presence of useful genetic variance (Melani and Carena, 2005). There is currently an increased interest in commercializing outstanding populations. Thus, extensive testing of populations has the advantage of identifying new heterotic patterns and of assessing the commercial potential of improved populations (Carena, 2005).

Heterotic patterns in temperate maize were established more than 50 years ago (Reif et al., 2005). A clearly defined heterotic pattern does not exist in the tropical maize landraces grown in the semi-arid parts of eastern and coastal Kenya. If the heterotic patterns of these landrace populations are known, they can be used to broaden the genetic base of the existing breeding populations, and also lines can be extracted from these populations which can be utilized in the production of hybrids and/or open pollinated varieties for the semi-arid areas. The objective of this study therefore, was to determine the heterotic groups and patterns of landraces from the semi-arid eastern and coastal regions of Kenya and to estimate their general and specific combining abilities. The hypothesis tested was that the landraces from eastern and coastal semi-arid Kenya belong to the same heterotic group.

4.2 Materials and Methods

4.2.1 Genetic Materials

Ten landrace populations from the drier districts of eastern and six from coastal regions of Kenya were used in the study. These landraces were sourced from the farmers. Also included were three improved populations from CIMMYT-Zimbabwe (V032, ZM423 and ZM523). These three CIMMYT populations are open-pollinated varieties (OPVs) developed by crossing synthetics belonging to heterotic groups A and B with good performance and GCA. However, their heterotic patterns have not been studied. Embu 11 and Embu 12 were used as testers and were sourced from KARI-Embu Research Centre. These two populations form the main parental breeding populations of the Embu maize breeding programme for the medium potential mid-altitude regions in eastern Kenya. Embu 11 was developed in 1964 using the early OPVs from the parental maize breeding programme for the highland areas in western Kenya at Kitale Research Centre whereas Embu 12 was developed from the late parental breeding populations from Katumani maize breeding programmes (KARI, 1992). The profile of the maize populations used in the study of heterotic patterns is shown in Table 4.1.

Table 4.1 Profile of maize populations used in the study of heterotic patterns

Population	Province of origin	District	AEZ*
KTU-CEN-1	Eastern	Kitui	DM
KTU-CEN-2	Eastern	Kitui	DM
KTU-KBI	Eastern	Kitui	DT
MAK-KIS-1	Eastern	Makueni	DT
MAK-KIS-2	Eastern	Makueni	DT
MKS-CEN	Eastern	Machakos	DM
MKS-YTA	Eastern	Machakos	DM
MKS-YTU	Eastern	Machakos	DM
MWI-CEN	Eastern	Mwingi	DT
MWI-MMI	Eastern	Mwingi	DT
KLF-GAN	Coast	Kilifi	DT
KLF-VIT	Coast	Kilifi	DT
KWL-KIN-1	Coast	Kwale	DT

Population	Province of origin	District	AEZ*
KWL-KIN-2	Coast	Kwale	DT
TTA-TVT-1	Coast	Taita Taveta	DT
TTA-TVT-2	Coast	Taita Taveta	DT
V032			
ZM423			
ZM523			
EMBU11	Eastern	Embu	MM
EMBU12	Eastern	Embu	MM

* AEZ – Agro-ecological zone, DT – Dry transitional, DM – Dry mid-altitude and MM – Moist mid-altitude.

4.2.2 Experimental Site

The experiment was conducted at KARI – Kiboko Research Sub-station Farm in Makueni district, with an elevation of 927 m above sea level and a GPS reading of 37° 43' E, 02° 13' S. Generally, the site is hot and dry and receives a bimodal type of rainfall, with long rains occurring from March – May and short rains from October – December with a mean annual rainfall of 538.8 mm. The short rains generally have more rainfall amounts (season mean of 328mm) and are more reliable than the long rains (season mean of 233 mm). The soils at Kiboko Research Sub-station Farm are ferric fluvisol, which are mainly sandy-clayey soil type with a top soil pH of 7.9 (Hornetz et al., 2000). The rainfall amounts received during the entire period of the experiment are shown in Table 4.2.

Table 4.2 Rainfall amount received in 2005 and 2006 at KARI – Kiboko Research Sub-station Farm

Month	Rainfall amount (mm)	
	2005	2006
January	6.5	12.4
February	0.0	6.0
March	40.5	85.7
April	186.5	205.8
May	13.8	43.5
June	0.0	0.0
July	0.0	0.0
August	2.5	0.0
September	0.5	0.0
October	20.5	0.0
November	57.5	0.0
December	9.2	0.0
Total	337.5	353.4

4.2.3 Crossing Nursery

The crossing block was set out during the short rains of October – December 2005. In order to synchronize pollination between the testers and the accessions, planting was staggered over a three week interval. Two rows of 25 hills of each population were planted, one to be crossed with Embu 11(1st row) and the other with Embu 12 (2nd row). The spacing used was 75 cm between the rows and 25 cm within the rows. The recommended maize production practices were used. Irrigation was done at least twice a week for two hours. Irrigation water was applied with 3/4" dual nozzle sprinklers spaced at 6.7 m with risers 2.15 m high at a rate of $9.6 \pm 0.58 \text{ mm hr}^{-1} \text{ ha}^{-1}$. The landraces and the CIMMYT populations were used as females. Crossing the testers to the populations was done by hand, using standard maize pollination procedure, in January 2006. Each population had at least 25 crosses with each tester. At harvest, the empty

and rotten ears were discarded. The seed from each of the population cross with the respective testers were bulked and used for evaluation.

4.2.4 Evaluation of Test Crosses

The harvested seed from the 38 population crosses plus the two testers were planted during the long rains of March – May 2006. These were planted at Kiboko Research Farm, in three replicates and laid out as a randomized complete block design (RCBD). Two rows of 20 hills per entry were planted. The two testers Embu 11 and Embu 12 were used as checks in the experiment. The spacing used was 75 cm between the rows and 25 cm within the rows. The recommended cultural practices of conventional maize production were used. The rainfall was supplemented with irrigation during the entire period of the experiment. Irrigation was usually done at least twice a week for two hours.

Data were recorded on the following agronomic traits, while the crop was in the field: plant height (cm) measured from the base of the plant to the base of the tassel, anthesis date (50% pollen shed), silking date (50% silk emergence), ear height (cm) measured from the base of the plant to the node bearing the top ear, and ear number per plot. Harvesting was done in the last week of August 2006. At harvesting and thereafter, data were recorded for ear length, ear diameter and grain yield. The grain yield adjusted to 12.5% moisture content and converted to $t\ ha^{-1}$ was calculated using the following formula:

$$\text{Grain Yield (t ha}^{-1}\text{)} = \frac{[\text{Grain weight (kg plot}^{-1}\text{)} \times 10 \times (100 - \text{MC}) / (100 - 12.5)]}{\text{(Plot area)}}$$

where MC = measured grain moisture content.

4.2.5 Statistical Analyses

All the data collected were subjected to analyses of variances (ANOVA) based on a randomized complete block design model, using GenStat release 9.1 edition, statistical software (Payne et al., 2006). The estimates of GCA and SCA effects of landraces and CIMMYT populations were obtained using line x tester analysis according to Sigh and Chaudhary (1977). The maize populations in the study were regarded as lines. The linear model on which the analysis was based is:

$$Y_{ij} = \mu + g_i + g_j + s_{ij} + r + \varepsilon_{ijk},$$

where,

Y_{ij} is the mean for the cross of the i^{th} line with j^{th} tester, μ is the grand mean (trial mean), g_i is the line main effect (GCA for the lines), g_j is the main tester effects (GCA for testers), s_{ij} is the specific combining ability (SCA) that occurs when the i^{th} line is crossed with j^{th} tester, r is the replications and ε_{ijk} is the experimental error. The replications were treated as random effects. Sum of squares due to test crosses were divided into lines, testers and line x tester interaction effects. The three sources of variation were assumed to be fixed effects. The mean squares for line and testers correspond to GCA variation, whereas the mean squares of the line x tester interaction effects are related to the SCA variation. Simple correlation coefficients were calculated between the traits using Genstat Release 9th edition statistical software.

The GCA and SCA effects were determined according to Sigh and Chaudhary (1977).

GCA for lines was calculated using the formula:

$g_i = M_{ij} - OM$, where g_i is the GCA of i^{th} line, M_{ij} is the Mean of i^{th} line across j testers and OM is the Overall mean.

The GCA for testers was calculated using the formula:

$g_j = M_{ji} - OM$, where, g_j is the GCA of j^{th} tester, M_{ji} is the Mean of j^{th} tester across i lines and OM is the Overall mean.

The SCA was calculated using the following formula:

$s_{ij} = M_{ixj} - M_{ij} - M_{ji} + OM$, where, M_{ixj} is the mean of the cross between i^{th} line with j^{th} tester, M_{ij} is the Mean of i^{th} line across j testers, M_{ji} is the Mean of j^{th} tester across i lines and OM is the Overall mean.

The percentage heterosis was calculated using the formula:

$$\%H = [(F_1 - MT) / MT] \times 100,$$

Where, $\%H$ is the percentage heterosis, MT is the mean of the tester and F_1 is the mean of the test cross.

The percentage heterosis for yield was used to determine the heterotic groups of the populations. The means of the test crosses were tested whether they are significantly different from zero using the t-test formula (McCouway and et al., 1999). The t was calculated as:

$$t_c = (\%H - 0) / s.e,$$

where, t_c is the t calculated, $\%H$ is the percentage heterosis of the test cross and $s.e$ is the standard error. The calculated t was compared to the t from the statistical tables and if $t_c > t_{table}$ ($p=0.05$), then it is significant and thus heterotic to the tester.

4.3 Results

4.3.1 Heterosis for Grain Yield

Generally, all the crosses of coastal landrace and CIMMYT maize populations showed a higher percentage heterosis ($\%H$) with Embu 11 than the crosses of landraces from eastern Kenya (Table 4.3). Percentage heterosis for yield ranged from -17.7% to 397.4% with the cross MAK-KIS-2 x Embu 12 having the lowest $\%H$ heterosis and ZM523 x

Embu 11 cross having the highest %H heterosis. Generally, all crosses with Embu 11 showed highly significant positive ($p=0.01$) %H heterosis for yield with the exception of the crosses with MWI-CEN and MWI-MMI which were significant ($p=0.5$). Only two crosses, MKS-YTA X Embu11 and MAK-KIS-2, had their %H not significant ($p>0.05$). All the crosses with Embu 12 showed non-significant ($p>0.05$) %H heterosis with the exception of the crosses with KWL-KIN-2, TTA-TVT-1 and ZM523 which had significant ($p=0.05$) %H for yield (Table 4.3).

Generally, the SCA effects for yield were not significant ($p=0.05$) in all the crosses with both testers (Table 4.3). Since SCA effects, were not significant, heterosis for yield was used to group the maize populations into different heterotic groups.

Table 4.3 Percentage heterosis (%H) and specific combining ability (SCA) for yield for maize populations used in the study of heterotic patterns

Line	Origin	%H Yield		Yield SCA	
		Embu11	Embu12	Embu11	Embu12
MKS-YTA	Eastern	3.5	-15.5	-0.72	0.72
MKS-YTU	Eastern	277.8**	24.1	0.30	-0.30
MKS-CEN	Eastern	174.6**	34.0	-0.54	0.54
KTU-CEN-1	Eastern	218.1**	26.2	-0.11	0.11
KTU-CEN-2	Eastern	150.0**	13.9	-0.37	0.37
KTU-KBI	Eastern	237.4**	17.9	0.13	-0.13
MWI-CEN	Eastern	84.4*	4.4	-0.51	0.51
MWI-MMI	Eastern	106.9*	-4.2	-0.27	0.27
MAK-KIS-1	Eastern	131.7**	9.5	-1.04	1.04
MAK-KIS-2	Eastern	19.5	-17.7	0.04	-0.04
KLF-VIT	Coast	321.2**	66	-0.22	0.22
KLF-GAN	Coast	332.4**	35.4	0.41	-0.41
KWL-KIN-1	Coast	178.2**	14.2	-0.22	0.22
KWL-KIN-2	Coast	345.4**	83.5*	-0.19	0.19
TTA-TVT-1	Coast	393.9**	106.6*	-0.17	0.17
TTA-TVT-2	Coast	310.6**	50.4	0.13	-0.13
ZM423	CIMMYT	337.5**	53.4	0.18	-0.18
V032	CIMMYT	352.7**	64.6	0.21	-0.21
ZM523	CIMMYT	397.4**	93.1*	-0.02	0.02
SE		41.2	41.2	1.07	1.07

*, ** Significant at $p=0.05$ and $p=0.01$, respectively.

4.3.2 Performance of Test Crosses

There were highly significant ($p=0.01$) differences among test crosses for anthesis-silking interval (ASI), plant height (PH), ear height (EH) and ear diameter (ED) (Table 4.4). There were significant ($p=0.05$) differences among test crosses for yield (Y). There were no significant ($p>0.05$) differences among test crosses for ear length (EL) (Table 4.4).

Table 4.4 Mean squares for anthesis-silking interval (ASI), ear diameter (ED), ear height (EH), ear length (EL), plant height (PH) and yield

Source	MEAN SQUARES						
	d.f.	ASI	ED	EH	EL	PH	Yield
Replications	2	11.7	0.58	1631.9	2.588	5990	9.969
Testcrosses	39	4.6**	0.21**	359**	2.83	556**	5.62*
Error	78	2.25	0.068	76.32	1.99	92.13	3.24
CV%		44.4	5.4	6.6	8.5	3.9	44.0

*, ** Significant at $p=0.05$ and $p=0.01$ level respectively.

There was a large variability for anthesis-silking interval (ASI), ear height (EH), plant height (PH) and yield (Y) (Table 4.5). However, there was a small variability for ear diameter (ED), and ear length (EL). The plant height means ranged from 2133 cm to 261.7 cm. The mean plant height for the tester Embu 11 (check) was 201.7 cm which was the shortest height of the mean heights from all crosses. The shortest mean heights for plant height were observed generally from crosses with landraces from the eastern province, whereas the crosses from the coastal province landraces gave higher mean heights. TTA-TVT-2 x Embu 11 cross showed the greatest height which was 261.7cm. Anthesis-silking interval mean values ranged from 1.3 days to 7.7 days with most crosses of landraces from both the eastern and coastal areas, with Embu 11 exhibiting larger ASI. Crosses of ZM523 with both testers showed smaller ASI values while KWL-KIN-1 x Embu 11 cross had the largest ASI.

The mean ear heights ranged from 108 cm to 155 cm with crosses of landraces from the coastal region having the highest ear heights and those from the eastern region having lower ear heights. KWL-KIN-1 x Embu 12 showed the highest height while MKS-YTA x Embu 11 and MWI-CEN x Embu 12 showed the lowest height. The mean ear diameter ranged from 4.4 cm to 5.7 cm. Generally, the crosses of accessions from the coastal region had larger ear diameters than those from the eastern region. The mean ear length ranged from 14.5cm (KTU-CEN-1 x Embu 11 and MAK-KIS-1 x Embu 11) to 18.9cm (MKS-YTA x Embu 11). The mean yield ranged from 1.5 t ha⁻¹ to 6.2 t ha⁻¹ with crosses from the coastal region and the CIMMYT populations having the highest yields compared to the crosses with landraces from the eastern region. The crosses TVA-TVT-1 X Embu 11 and ZM523 X Embu 11 had the highest yields of 6.2 t ha⁻¹ and 6.1 t ha⁻¹, respectively, while MAK-YTA x Embu 11 had the lowest yield of 1.5 t ha⁻¹.

Table 4.5 Mean values of test crosses and testers for anthesis-silking interval (ASI), ear diameter (ED), ear height (EH), ear length (EL), plant height (PH), and yield

Test cross	ASI	ED	EH	EL	PH	Yield
MKS-YTAXE11	2.7	4.5	108.0	18.9	213.3	1.5
MKS-YTAXE12	3.0	4.5	122.0	17.8	233.3	2.5
MKS-YTUXE11	3.3	4.9	132.0	17.8	243.3	4.7
MKS-YTUXE12	3.3	4.6	130.0	17.4	231.7	3.6
MKS-CENXE11	4.7	5.0	123.0	15.7	233.3	3.3
MKS-CENXE12	3.3	4.8	132.0	17.0	258.3	3.9
KTU-CEN-1XE11	2.7	4.9	132.0	14.5	241.7	3.9
KTU-CEN-1XE12	3.0	5.0	137.0	15.2	250.0	3.7
KTU-CEN-2XE11	2.3	4.8	128.0	17.5	231.7	3.0
KTU-CEN-2XE12	2.7	4.6	145.0	15.9	255.0	3.3
KTU-KBIxE11	3.7	4.7	128.0	15.6	240.0	4.1
KTU-KBIxE12	4.7	4.5	132.0	15.9	251.7	3.4
MWI-CENXE11	4.3	4.8	125.0	15.8	225.0	2.4
MWI-CENXE12	2.3	4.7	108.0	15.5	248.3	3.0
MWI-MMIXE11	4.3	4.7	127.0	16.1	240.0	2.8
MWI-MMIXE12	3.0	4.4	135.0	16.6	251.7	2.9

Test cross	ASI	ED	EH	EL	PH	Yield
MAK-KIS-1xE11	4.3	4.9	130.0	14.5	228.3	1.6
MAK-KIS-1xE12	3.0	4.9	125.0	16.0	235.0	3.2
MAK-KIS-2xE11	2.0	4.7	118.0	16.9	238.3	3.0
MAK-KIS-1xE12	2.3	4.9	122.0	16.4	240.0	2.5
KLF-VITxE11	4.0	4.9	153.0	16.0	256.7	4.9
KLF-VITxE12	4.0	4.9	153.0	16.0	256.7	4.9
KLF-GANxE11	3.3	4.9	147.0	17.0	258.3	5.3
KLF-GANxE12	4.3	4.8	143.0	15.7	251.7	4.0
KWL-KIN-1xE11	7.7	5.0	140.0	16.8	250.0	3.4
KWL-KIN-1xE12	4.7	4.6	155.0	15.9	260.0	3.4
KWL-KIN-2xE11	3.7	4.9	148.0	17.6	261.7	5.4
KWL-KIN-2xE12	2.0	5.2	135.0	17.5	253.3	5.4
TTA-TVT-1xE11	3.0	5.7	138.0	17.4	245.0	6.2
TTA-TVT-1xE12	2.3	5.3	148.0	17.0	258.3	6.1
TTA-TVT-2xE11	2.7	5.2	138.0	16.4.0	261.7	5.2
TTA-TVT-2xE12	2.0	5.1	132.0	17.0	256.7	4.5
ZM423xE11	2.7	5.0	130.0	17.4	251.7	5.4
ZM423xE12	4.0	4.9	135.0	18.4	256.7	4.5
V032xE11	3.0	5.0	142.0	16.9	258.3	5.6
V032xE12	3.3	4.9	118.0	17.3	240.0	4.8
ZM523xE11	1.3	5.1	127.0	17.0	236.7	6.1
ZM523xE12	1.3	4.9	135.0	17.4	258.3	5.7
EMBU11 _a	6.3	4.6	118.0	15.6	201.7	1.3
EMBU12 _b	4.0	4.5	142.0	16.6	255.0	3.0
Mean	3.4	4.8	108.0	16.6	245.5	4.1
LSD	2.4	0.4	14.3.0	2.3	15.6	2.9

a, b, - checks.

4.3.3 Heterosis for Secondary Traits

Generally, most of the landrace crosses with Embu 11 showed a higher percentage heterosis (%H) for secondary traits, anthesis-silking interval (ASI), ear height (EH), ear diameter (ED), ear length (EL) and plant height (PH), than those with Embu 12 (Table 4.6). The heterosis for ASI ranged from -79.4% to 22.2%, with the cross ZM523 x Embu 11 showing the lowest heterosis and the cross KWL-KIN-1 x Embu 11 showing the highest heterosis. Heterosis for ear height ranged from -23.9% to 29.7%, with the cross MWI-CEN x Embu 12 having the lowest heterosis and KLF-VIT x Embu 11 with the highest heterosis. Heterosis for ear diameter ranged from -0.1% to 1.1%, with two crosses, MWI-MMI x Embu 12 and MKS-YTA x Embu 11 having the lowest heterosis, whereas TTA-TVT-1 x Embu 11 had the highest heterosis (Table 4.6). The heterosis for ear length ranged from -7.1% to 21.2%, with the two crosses KTU-CEN-1 x Embu 11 and MAK-KIS-1 x Embu 11 having the lowest heterosis, and the cross MKS-YTA x Embu 11 having the highest heterosis. The heterosis for plant height ranged from -5.9 to 30.2%, with V032 x Embu 12 cross having the lowest heterosis while the crosses TTA-TVT-2 x Embu 11 and KWL-KIN-2 x Embu 11 had the highest heterosis (Table 4.6).

Table 4.6 Estimates of percentage heterosis (%H) for the secondary traits anthesis-silking interval (ASI), ear diameter (ED), ear height (EH), ear length (EL) and plant height (PH)

Population/Line	Origin	Tester	%H ASI	%H ED	%H EH	%H EL	%H PH
MKS-YTA	Eastern	Embu 11	-57.1	-0.1	-8.5	21.2	6.1
MKS-YTA	Eastern	Embu 12	-25.0	0.0	-14.1	7.2	-8.5
MKS-YTU	Eastern	Embu 11	-47.6	0.3	11.9	14.1	21.0
MKS-YTU	Eastern	Embu 12	-17.5	0.1	-8.5	4.8	-9.1
MKS-CEN	Eastern	Embu 11	-25.4	0.4	4.2	0.6	16.1
MKS-CEN	Eastern	Embu 12	-17.5	0.3	-7.0	2.4	1.3
KTU-CEN-1	Eastern	Embu 11	-57.1	0.3	11.9	-7.1	20.2
KTU-CEN-1	Eastern	Embu 12	-25.0	0.5	-3.5	-8.4	-2.0
KTU-CEN-2	Eastern	Embu 11	-63.5	0.2	8.5	12.2	15.3
KTU-CEN-2	Eastern	Embu 12	-32.5	0.1	2.1	-4.2	0.0
KTU-KBI	Eastern	Embu 11	-41.3	0.1	8.5	0.0	19.4
KTU-KBI	Eastern	Embu 12	17.5	0.0	-7.0	-4.2	-1.3

Population/Line	Origin	Tester	%H ASI	%H ED	%H EH	%H EL	%H PH
MWI-CEN	Eastern	Embu 11	-31.7	0.2	5.9	1.3	11.9
MWI-CEN	Eastern	Embu 12	-42.5	0.2	-23.9	-6.6	-2.6
MWI-MMI	Eastern	Embu 11	-31.7	0.1	7.6	3.2	19.4
MWI-MMI	Eastern	Embu 12	-25.0	-0.1	-4.9	0.0	-1.3
MAK-KIS-1	Eastern	Embu 11	-31.7	0.3	10.2	-7.1	13.6
MAK-KIS-1	Eastern	Embu 12	-42.5	0.9	-12.0	-3.6	-7.8
MAK-KIS-2	Eastern	Embu 11	-68.3	0.1	-16.9	8.3	18.6
MAK-KIS-2	Eastern	Embu 12	-25.0	0.4	-14.1	-1.2	-5.9
KLF-VIT	Coast	Embu 11	-2.3	0.3	29.7	2.6	27.7
KLF-VIT	Coast	Embu 12	0.0	0.4	7.7	-3.6	0.7
KLF-GAN	Coast	Embu 11	-47.6	0.3	24.6	9.0	28.5
KLF-GAN	Coast	Embu 12	7.5	0.3	0.7	-5.4	-1.3
KWL-KIN-1	Coast	Embu 11	22.2	0.4	18.6	7.7	24.4
KWL-KIN-1	Coast	Embu 12	17.5	0.1	9.2	-4.2	2.0
KWL-KIN-2	Coast	Embu 11	-41.3	0.3	25.4	12.8	30.2
KWL-KIN-2	Coast	Embu 12	-50.0	0.7	-4.9	5.4	-0.7
TTA-TVT-1	Coast	Embu 11	-52.4	1.1	16.9	11.5	21.9
TTA-TVT-1	Coast	Embu 12	-42.5	0.8	4.2	2.4	1.3
TTA-TVT-2	Coast	Embu 11	-57.1	0.6	16.9	5.1	30.2
TTA-TVT-2	Coast	Embu 12	-50.0	0.6	-7.0	2.4	0.7
ZM423	CIMMYT	Embu 11	-57.1	0.4	10.2	11.5	25.2
ZM423	CIMMYT	Embu 12	0.0	0.4	-4.9	10.8	0.7
V032	CIMMYT	Embu 11	-52.4	0.4	20.3	8.3	28.5
V032	CIMMYT	Embu 12	-17.5	0.4	-16.9	4.2	-5.9
ZM523	CIMMYT	Embu 11	-79.4	0.5	7.6	9.0	17.8
ZM523	CIMMYT	Embu 12	-67.5	0.4	0.0	4.8	1.3

4.3.4 Combining Ability Analyses

The analysis of variance of test crosses between the populations and the two testers showed significant differences for all the traits except ear length (Table 4.4). The source of variation due to general combining ability (GCA) of maize populations was highly significant ($p=0.01$) for all the traits, whereas SCA of the testers was only significant ($p=0.05$) for ear diameter and highly significant ($p=0.01$) for plant height. The GCA estimates ranged from -1.95 to 2.89 for anthesis-silking interval, -0.42 to 0.67 for ear diameter, -17.76 to 14.74 for ear height, -1.79 to 1.23 for ear length, -23.03 to 11.14 for plant height and -1.46 to 1.96 for yield (Table 4.7). Generally, coastal landraces showed significant GCA effects for all traits, while all the CIMMYT populations showed significant ($p=0.05$) GCA effects for ear diameter (Table 4.8). The specific combining ability estimates (SCA) were highly significant ($p=0.01$) for only two traits, ear height and plant height (Table 4.7). The CIMMYT population V032 showed high positive significant ($p=0.05$) SCA for ear height and plant height with Embu 11 and negative with Embu 12 (Table 4.9).

Table 4.7 Mean squares of Line x Tester analysis for anthesis-silking interval (ASI), ear diameter (ED), ear height (EH), plant height (PH), ear length (EL), and yield

Source	Mean squares						
	d.f.	ASI	ED	EH	EL	PH	Yield
Rep	2	11.85	0.55	1438.82	3.461	5694.96	9.95
Line	18	6.19**	0.35**	538.91**	4.794*	540.84**	7.93**
Tester	1	4.25	0.32*	116.01	0.022	1368.64**	5.62
Line x Tester	18	1.97	0.07	183.6**	1.162	247.81**	2.39
Residual	74	2.22	0.07	78.46	1.883	83.92	3.41
Total	113						
LSD		1.71	0.03	10.19	1.58	10.54	2.12
CV%		45.40	5.40	6.70	8.20	14.90	44.10

*, ** Significant at $p=0.05$ and $p=0.01$ level, respectively.

Table 4.8 General combining ability (GCA) for maize populations/line and testers based on anthesis silking interval (ASI), ear diameter (ED), ear height (EH), plant height (PH), ear length (EL), and yield

Populations/Line	Traits					
	ASI	ED	EH	EL	PH	Yield
KLF-GAN	0.55	-0.03	12.24**	-0.32	8.64*	0.45
KLF-VIT	0.89	-0.08	14.74**	-0.39	10.31*	0.74
KTU-CEN1	-0.45	0.112	1.41	-1.79	-0.53	-0.38
KTU-CEN2	-0.78	-0.15	3.91	0.08	-3.03	-1.04
KTU-KBI	0.89	-0.22	-2.76	-0.88	-0.53	-0.41
KWL-KIN1	2.89**	-0.08	14.74**	-0.29	8.64*	-0.76
KWL-KIN2	-0.45	0.2**	8.91**	0.9	11.14*	1.21
MAK-KIS2	-1.11	-0.05	-12.76	0.01	-7.2	-1.46
MAK-KIS1	0.39	0.05**	-5.26	-1.36	-14.7	-1.78*
MKS-CEN	0.72	0.07**	-5.26	-0.26	-0.53	-0.58
MKS-YTA	-0.45	-0.32	-17.76	1.71**	-23.03	-2.19*
MKS-YTU	0.05	-0.10	-1.93	0.96	-8.86	-0.04
MWI-CEN	0.05	-0.22	-16.1	-0.98	-9.7	-1.46
MWI-MMI	0.39	-0.42	-1.93	-0.29	-0.53	-1.34
TTA-TVT1	-0.61	0.67**	10.57**	0.55	5.31	1.96*
TTA-TVT2	-0.95	0.28**	2.24	0.06	12.81**	0.63
V032	-0.11	0.1**	-2.76	0.49	2.81	1.04
ZM423	0.05	0.05**	-0.26	1.23**	7.81*	0.75
ZM523	-1.95	0.15**	-1.93	0.56	1.14	1.71*
SE populations/lines	0.61	0.01	3.60	0.56	3.74	0.75
Embu11	0.19	-0.05	-1.01	0.02	-3.41	0.22
Embu12	-0.19	0.05	1.01	-0.01	3.46	-0.22
SE Testers	0.21	0.04	1.23	0.19	1.27	0.26

*, ** Significant at $P=0.05$ and $P=0.01$ level, respectively.

Table 4.9 Specific combining ability (SCA) estimates for the maize populations/lines based on ear height (EH), and plant height (PH)

Population/Line	EH		PH	
	Testers			
	Embu11	Embu12	Embu11	Embu12
KLF-GAN	2.68	-2.68	6.80	-6.79
KLF-VIT	-4.82	4.82	3.47	-3.46
KTU-CEN4	-1.49	1.49	-0.70	0.70
KTU-CEN5	-7.33	7.32	-8.20	8.20
KTU-KBI	-0.66	0.66	-2.37	2.37
KWL-KIN13	-6.49	6.49	-1.54	1.54
KWL-KIN14	7.67	-7.68	7.64	-7.63
MAK-KIS10	-0.66	0.66	2.63	-2.63
MAK-KIS9	3.51	-3.51	0.13	-0.13
MKS-CEN3	-3.16	3.16	-9.04	9.04
MKS-YTA	-5.66	5.66	-6.54	6.54
MKS-YTU	1.84	-1.85	9.30	-9.29
MWI-CEN	9.34	-9.35	-8.20	8.20
MWI-MMI	-3.16	3.15	-2.37	2.37
TTA-TVT15	-3.99	3.99	-3.20	3.20
TTA-TVT16	4.34	-4.34	5.97	-5.96
V032	12.68*	-12.68*	12.63*	-12.63*
ZM423	-1.49	1.49	0.97	-0.96
ZM523	-3.16	3.15	-7.37	7.37
SE	5.1	5.1	5.0	5.0

* Significant at $p=0.05$.

4.3.5 Correlations between Agronomic Traits

The traits ear diameter (ED), ear height (EH), ear length (EL) and plant height (PH) were positively correlated to yield, except ASI which was negatively correlated (Table 4.10). Ear height was the only trait positively correlated to ASI, while the rest of the traits were

negatively correlated to ASI. Ear diameter was positively correlated to all the traits. Ear height was negatively correlated to EL, but positively correlated to PH and yield. Ear length was negatively correlated with PH.

Table 4.10 Phenotypic correlation coefficients of silking interval (ASI days), ear diameter (ED cm), ear height (EH cm), ear length (EL cm), plant height (PH cm), and yield

Trait	ASI	ED	EH	EL	PH
ASI					
ED	-0.099				
EH	0.056	0.2*			
EL	-0.178	0.212*	-0.089		
PH	-0.117	0.179	0.681**	-0.035	
Yield	-0.27**	0.519**	0.462**	0.229*	0.521**

*, ** Significant at $p=0.05$ and $p=0.01$ level, respectively.

4.6 Discussion

The general trend from the results shows that the accessions had a higher heterosis with Embu 11 than with Embu 12. This suggests that these landrace populations and the CIMMYT populations are more genetically diverse with Embu 11 than with Embu 12. This trend can be viewed from three perspectives. The two testers were developed in the middle 1960s by KARI maize breeding programmes. Embu 11 was developed in 1964 from the early open pollinated varieties from the Kitale maize breeding programme for the highland areas in western Kenya while Embu 12 was developed from late materials from the Katumani maize breeding programme for the semi-arid areas in eastern Kenya (KARI, 1992). This implies that Embu 11 is genetically diverse from the materials from the eastern and coastal areas whereas, Embu 12 having been developed from materials from Katumani (Eastern Kenya) was not genetically different from materials from the same region. Another explanation could be that the maize was introduced into Kenya by the Portuguese around the 16th century via the East African coast (Njoroge and Ngure, 1986). Then it later spread inland. The south eastern part of

Kenya borders the coastal area so there is a possibility that the farmers in these areas exchange maize seeds. Maize is an outcrossing crop, so there is cross pollination between the maize in the neighbouring farmers' fields in these two regions. The other explanation could be attributed to the fact that these two regions are drylands, the farmers have not adopted the growing of hybrid maize but instead grow unimproved landraces which they usually recycle from season to season. With these movements of maize between the two regions, there is gene flow between the maize populations in these two regions, making the maize populations in these areas less genetically divergent from Embu 12.

Despite the fact that most of these populations were heterotic to Embu 11, the coastal landrace and the CIMMYT maize populations showed higher heterosis than the maize landraces from eastern Kenya with Embu 11. The CIMMYT populations were developed by crossing synthetics belonging to heterotic groups A and B (heterotic grouping of CIMMYT) from the CIMMYT maize breeding programme in Zimbabwe. These two heterotic groups are different from Embu 11 and Embu 12, thus explaining the high heterosis. The two testers Embu 11 and Embu 12 have been used to develop maize hybrids for the moist mid-altitude maize zone which borders the region where the landrace materials from eastern Kenya were collected from, but geographically far apart from the coastal region. Thus, there is the possibility of maize from moist mid-altitude zone outcrossing with those from the areas where landraces were collected from eastern rather than with those from coastal region. The coastal region is not suitable for growing hybrids developed from Embu 11 and Embu 12 owing to its low altitude and high temperatures, hence, the farmers in this region do not grow these hybrids. This explains why the crosses of maize populations from coastal region showed a higher heterosis with Embu 11 rather than the materials from eastern Kenya. The fact that the landraces from the coastal region had a higher heterosis with Embu 11 than the landraces from eastern region, could suggest that these populations may be different from each other. Therefore, a further study of these populations may be necessary to ascertain this observed trend.

However, there were deviations from this general trend. Two populations from eastern Kenya, MKS-YTA, and MAK-KIS-2 showed low heterosis with both testers. This means that they are not genetically divergent from the two testers hence could belong to both of

the heterotic groups. These two populations were collected from dry mid-altitude maize zones which border the moist mid-altitude maize zone, where the farmers grow hybrids developed from inbred lines extracted from Embu 11 and Embu 12. Thus, there is a possibility of these hybrids outcrossing with the landraces in the region. Another deviation from the general trend is that three populations, KWL-KIN-2, TTA-TVT-1, both from coastal Kenya, and ZM523 population from CIMMYT, showed high heterosis with both testers which implies that these populations are genetically different from the testers and could not belong to either heterotic grouping of the testers. This implies that these three materials have a different origin from the two testers and that there has never been any outcrossing with the testers. It also suggests that the farmers from the region where the two coastal populations were collected might not be growing any improved cultivars developed from the two testers.

The expression of heterosis depends on the level of genetic divergence between parents and this depends on the differences in allele frequencies which are responsible for the expression of heterosis (Ricardo and Filho, 2003). Other studies using crosses with tropical maize populations have also shown high yield heterosis ranging from negative values to high positive values. Gama et al. (1982) found yield heterosis values ranging from 17% to 117%. In this study, there were only two exceptions, both from eastern region (MKS-YTA and MAK-KIS-2) that showed low heterosis with both testers. This can be explained by the fact that in some instances, crosses with broad based open-pollinated populations express low heterosis (Miranda, 1999). In the current study, all the accessions and the testers used were broad based populations, thus the low heterosis expressed by the MKS-YTA and MAK-KIS-2 crosses is not an exception. Studies by Beck et al. (1990), Crossa et al. (1990), Vasal et al. (1992), and Rezende and Souza Jnr. (2000) on crosses between broad based populations also reported low heterosis. Low levels of heterosis have been reported in extremely divergent crosses. In a study of ten maize varieties, Prasad and Singh (1986) reported that heterosis was not linearly related to genetic divergence since most of the diverse parental varieties did not necessarily show the greatest heterotic response.

The general combining ability (GCA) effects for populations were highly significant for all the traits, whereas the specific combining ability (SCA) effects were only significant for ear and plant height. Mungoma and Pollak (1998) reported a similar trend in Corn Belt

maize populations. The trend showed that the variation among these crosses was mainly due to additive rather than nonadditive effects. It also implies that additive gene effects were important in controlling anthesis-silking interval, ear diameter, ear length, and yield, while both additive and non-additive gene effects were important in controlling ear and plant heights. Soengas et al. (2006) found similar results in their combining ability and heterosis studies with flint maize populations. The implication of this trend is that selection would be effective in improving yield in these populations.

Given that SCA effects were not significant for yield, heterosis for yield was therefore used to group the populations into the different heterotic groups. Santos et al. (2001) also used the mean yield heterosis values to group maize accessions from Latin America into different heterotic groups. The non-significant SCA in yield cannot be explained in this case given that there was high heterosis observed in yield from the crosses. So, further study in these populations need to be done either using more than two testers or different methods to ascertain this observed trend with SCA.

The maize populations were categorized into three different heterotic groups, P, Q, and R (Table 4.11). Those that showed no heterosis with Embu 12 and significant heterosis with Embu 11 were put in group P. These populations in the P heterotic group were further subdivided into two subgroups based on their different levels of percentage heterosis to Embu11. The landraces from coastal region and two CIMMYT populations ZM423 and V032 were grouped in one subgroup due to their high heterosis with Embu11, whereas the landraces from eastern Kenya were grouped in another subgroup. The populations that were not heterotic with both Embu 11 and Embu 12 were put in group Q, and those heterotic with both Embu 11 and Embu 12 were put in group R. None of the populations showed heterosis only with Embu 12 and no heterosis with Embu 11. All the landraces from the eastern and coastal areas belong to the Embu 12 heterotic group (P heterotic group), except two populations from the coastal region KWL-KIN-2 and TTA-TVT-1 from Kwale and Taita Taveta districts, respectively, and one CIMMYT population ZM523. These populations showed heterosis with both testers and thus were grouped together into the second heterotic group R. Two populations from the eastern province MKS-YTA and MAK-KIS-2 from Machakos and Makueni districts, respectively, showed low heterosis with both testers and were thus grouped into the third heterotic group Q (Table 4.11).

Table 4.11 Heterotic grouping of the populations used in the study of heterotic patterns

Heterotic group			
P (Embu 12)		Q (Embu 11/Embu12)	R
Eastern sub-group	Coastal sub-group		
MKS-YTU	KLF-VIT	MKS-YTA	KWL-KIN-2
MKS-CEN	KLF-GAN	MAK-KIS-2	TTA-TVT-1
KTU-CEN-1	KWL-KIN-1		ZM523
KTUCEN-2	TTA-TVT-2		
KTU-KBI	ZM423		
MWI-MMI	V032		
MWI-CEN			
MAK-KIS-1			

There was a high positive correlation between yield and the agronomic traits ear diameter, ear height ear length and plant height. These traits contribute to yield, hence, this observation is the desired correlation. Plant height had the highest positive correlation with yield and this agrees with results reported by Hallauer and Miranda (1988). This means that selection for a larger ear diameter and longer ears will be also selecting for high yields. Yield was negatively correlated to anthesis-silking interval (ASI). Since ASI is inversely correlated with yield, selecting for smaller ASI implies selecting for high yields. This is due to the fact that a smaller ASI enables good synchronization of pollination leading to high chances of grain formation.

4.7 Conclusions and Recommendations

The 19 maize populations were classified into three distinct heterotic groups. The coastal landrace and CIMMYT maize populations showed higher heterosis than landrace populations from eastern Kenya with a few exceptions that showed low heterosis with both testers and high heterosis with both testers. This observation needs further study of the populations from coastal and eastern regions to ascertain whether there is any genetic diversity between these populations. This information on the heterotic patterns is

useful in the maize breeding programme, since these populations can be infused into the existing maize germplasm in the maize breeding programme to broaden its genetic base.

Additive gene effects were significant whereas nonadditive gene effects were not significant. Therefore, additive gene effects were responsible for the variation in the crosses. Given that, additive gene effects were more important than the non-additive gene effects, these populations can be improved through recurrent selection methods.

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Chapter 5: Overview and Way Forward

5.1 Introduction

This chapter summarizes all the research findings of this study. The main objectives of this study were to improve drought tolerance in five maize populations in the semi-arid eastern Kenya using S_1 family recurrent selection and to classify 19 maize populations (16 landraces and three CIMMYT populations) according to their heterotic patterns. The specific objectives of this study were to:

1. assess farmers' perception of and preference for drought tolerant traits in maize varieties grown in semi-arid areas of Kenya,
2. determine the changes in genetic variability in the S_1 families after two cycles of recurrent selection,
3. determine the genetic gain in drought tolerance and other agronomic traits of maize populations grown in semi-arid areas of Kenya after two cycles of recurrent selection and
4. determine the heterotic patterns and combining ability of maize landrace populations.

5.2 Summary of the Research Findings and their Implications for Breeding

Literature Review

Literature review established that drought is responsible for significant yield losses in maize production in semi-arid areas. Yield losses are large if drought coincides with the reproductive stage, i.e., flowering to grain filling stages. Therefore, improvement of drought tolerance during this period is important. Breeding for drought tolerance has been slow due to the complexity of drought tolerance mechanisms. Furthermore, direct selection for drought tolerance using yield alone is not efficient, thus the use of indirect selection using secondary traits becomes an option. The improvement can be undertaken using recurrent selection procedures. The selection can either be done under optimal conditions, under drought conditions or combination of both strategies.

However, the most common strategy is to use a combination of both strategies and carryout multilocational testing. The knowledge of heterosis and heterotic patterns is important in the breeding of maize hybrids. Various methods of identifying heterotic patterns were discussed. Maize heterotic patterns have been established in the western Kenya but have not been established in the eastern and coastal region. Therefore, this study investigated the heterotic patterns and groups of maize landraces from eastern Kenya using two testers.

Participatory Rural Appraisal

A participatory rural appraisal (PRA) was carried out in two districts in the eastern province of Kenya, Machakos and Makueni districts representing dry mid-altitude (DM) and dry transitional (DT) maize zones, respectively. From the PRA study and secondary data, farmers in this region grew maize as the main crop followed by beans. They grew a wide range of maize varieties but they preferred their local maize varieties to the improved varieties which are already in the market, such as Katumani composite, Pioneer, SC Duma and Pannar hybrids. The most important criteria in order of importance were drought tolerance, early maturity, yield and disease resistance. The constraints to maize production identified in the region in order of importance were drought (low and unreliable rainfall), lack of technical know-how, pest problems, poor/infertile soils, lack of seeds at planting time, disease problems and high prices of farm inputs. The farmers in these semi-arid regions use maize grains from the previous cropping seasons as seed.

Since maize production is the main activity in the region, it follows that the development of improved drought tolerant maize varieties is a major priority. New varieties should also outperform local landraces in most attributes and, more importantly, have good grain qualities. Considering that the farmers prefer recycling seed as a strategy for coping with cash flow constraints, an effort should be made to breed for open-pollinated varieties (OPVs) such as varietal crosses, composites or even improve the landrace populations *per se*. To achieve this it implies that local landraces need to be improved and incorporated into the maize breeding programme in the drylands. Likewise, farmers' views and preferences should be taken into account when developing the new varieties

for this region. This will enhance faster acceptance of these varieties and thus lead to increased food security in the region.

Response to Selection and Genetic Variability

Selection under drought stress increased yield in two local landrace populations KTU, MKS and ZM423 maize populations, whereas there was a decrease in V032 and ZM523 maize populations. This implies that selection improved drought tolerance in KTU, MKS and ZM423 maize populations. This positive linear increase in grain yield in these three populations after two cycles of S_1 recurrent selection implies that with further selection there will be subsequent gains realized. It is envisaged that this rate of progress will be maintained in subsequent selection cycles provided that the same S_1 recurrent selection method is practiced using an effective population size in order to avoid genetic drift. With the two CIMMYT populations V032 and ZM523, any further selection may not lead to any increased performance.

The genetic variability of yield and the secondary traits was reduced after two cycles of selection in some of populations and increased in some populations. Given that selection was only done for two cycles, the trends observed therefore form a basis for further study of these populations.

The observed desired correlation between yield and the secondary traits confirmed the usefulness of these secondary traits as indirect selection for yield in breeding for drought tolerance in maize. Thus, when selecting for drought tolerance in maize these traits should be considered.

Heterotic Classification and Combining Ability

The 19 maize populations were classified into three distinct heterotic groups and that the coastal landrace and CIMMYT maize populations showed a higher heterosis than landrace populations from eastern Kenya with Embu 11. All the landraces from the eastern and coastal areas belong to the Embu 12 heterotic group (P heterotic group), except two populations from the coastal region KWL-KIN-1 and TTA-TVT-2 from Kwale and Taita Taveta districts, respectively and one CIMMYT population ZM523. These

populations showed heterosis with both testers and thus were grouped together into the second heterotic group R. Two populations from the eastern province MKS-YTA and MAK-KIS-2 from Machakos and Makueni districts, respectively, showed low heterosis with both testers and were thus grouped into the third heterotic group Q. The populations in group P were further categorized into two subgroups, eastern and coastal sub-groups, based on their different level of percentage heterosis to Embu 11.

This information on the heterotic patterns of the local landrace populations is useful in that these populations can serve as source germplasm for the development of maize varieties for these regions. These populations can therefore be incorporated into the existing base populations in the maize breeding programme, to increase their genetic variability or used to develop hybrids with Embu 11 given that they were genetically divergent with this population.

Additive gene effects were significant whereas nonadditive gene effects were not significant implying that variation among these crosses was mainly due to additive rather than nonadditive gene effects. Thus, these populations can be improved using recurrent selection methods

5.4 Conclusions and Way Forward

Drought is a major constraint to maize production in the semi-arid eastern Kenya. The breeding of maize for drought tolerance therefore, becomes a priority for this region. However, it is important that, during the development of drought tolerant maize varieties, the farmers' perceptions and preferences should be taken into account. This will increase the chances of the farmers accepting to grow the new variety. Given that selection was only done for two cycles and that the local landrace populations did improve in drought tolerance, further selection and evaluation should be conducted. It is recommended that a further study be done on the eastern and coastal landraces to ascertain whether they are genetically divergent, given that the coastal landraces showed twice as much percentage heterosis, with Embu 11, as the eastern landrace maize populations.