

**COMBINING ABILITY IN ELEVEN MAIZE (*Zea mays* L.) FEW TASSEL BRANCH  
MUTANTS (*fbr*) UNDER OPTIMUM AND DROUGHT STRESS ENVIRONMENTS**

**BY**

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## ABSTRACT

Maize (*Zea mays* L.) is an important cereal crop and primary source of calories in Zimbabwe. Generally two groups of farmers are involved in maize production, the large scale commercial sector (LSC) and the communal farming sector (CFS) categorized based on production systems and scales of operation. Production is dominated by the CFS although yield levels are lower than the LSC. Production in highly stress prone environments with no or limited access to resources to mitigate the stresses has been responsible for the yield gap. Although the tassel is an essential reproductive organ, it often reduces yield either physiologically by competing with the ear or physically by shading effect. The competition effects and shading effects are more pronounced under stress and high density respectively. By reducing the size of the tassel, breeders can reduce the competition effects of tassels especially under drought stress and contribute to higher yields. Eleven CIMMYT few tassel branch (*fbr*) mutants and three testers, CML442 *TAS*, CML442 and CML395 were crossed in a 11 x 3 line x tester design at CIMMYT- Zimbabwe in 2008/09. The testcrosses together with checks were evaluated under one optimum environment and two drought environments in a randomized complete block design with two replications during winter 2009. The objectives of the study were to estimate general and combining ability effects of the eleven *fbr* lines and assess the relationship between grain yield and tassel traits. Seven tassel traits, tassel branch angle, tassel size, total tassel length, central spike length, branch zone length, branch length and tassel weight were recorded. Results revealed significant ( $P < 0.05$ ) differences among hybrids and lines for grain yield across all environments and under the optimum environment but not under drought environments. There were no significant differences among testers for grain yield under all management levels. Significant differences ( $P < 0.05$ ) were also observed among hybrids, lines and testers for all tassel traits across all management levels. L11 showed consistently good GCA for grain yield under both drought and optimum environments, while L2, L6 and L7 showed consistently poor GCA. Hybrids C10-2 and C6-2 showed consistently good SCA for grain yield under both optimum and drought environments while C8-2, C10-3, C3-2, C9-2 and C1-1 showed consistently poor SCA. Lines and testers with good GCA for grain yield showed negative GCA effects for tassel branch angle and anthesis date but positive GCA effects for total tassel length, central spike length, branch zone length, branch length and tassel weight. Similarly hybrids with good combining ability for grain yield showed negative SCA effects for tassel branch angle and anthesis date but positive GCA effects for total tassel length, central spike length, branch zone length, branch length and tassel weight. These hybrids were constituted by parents with an unrelated genetic background. High broad sense heritabilities ranging from 37% (branch zone length) under drought environments to 86% (central spike length) under the optimum environment were found for all tassel traits. Grain yield was negatively correlated with tassel branch angle and anthesis date but positively correlated with total tassel length, central spike length, branch zone length, branch length and tassel weight. Given the high heritability of tassel traits, high correlation with grain yield, easiness and cheapness in measurement they are good candidates for use as secondary traits.

## **DECLARATION**

I, Dean Muungani hereby declare that this thesis represents my own work and that it has not been previously submitted for a degree, diploma or other qualification at this or any other University.

Signature:.....

Date:.....

**APPROVAL**

The University of Zambia approves this thesis of Dean Muungani as fulfilling the requirements for the award of the degree of Master of Science in Plant Breeding and Seed Systems.

Examiner's signature

Date

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## **DEDICATION**

To my wife, Tariro Tatenda and daughter Atipaishe Angela

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## Chapter 1

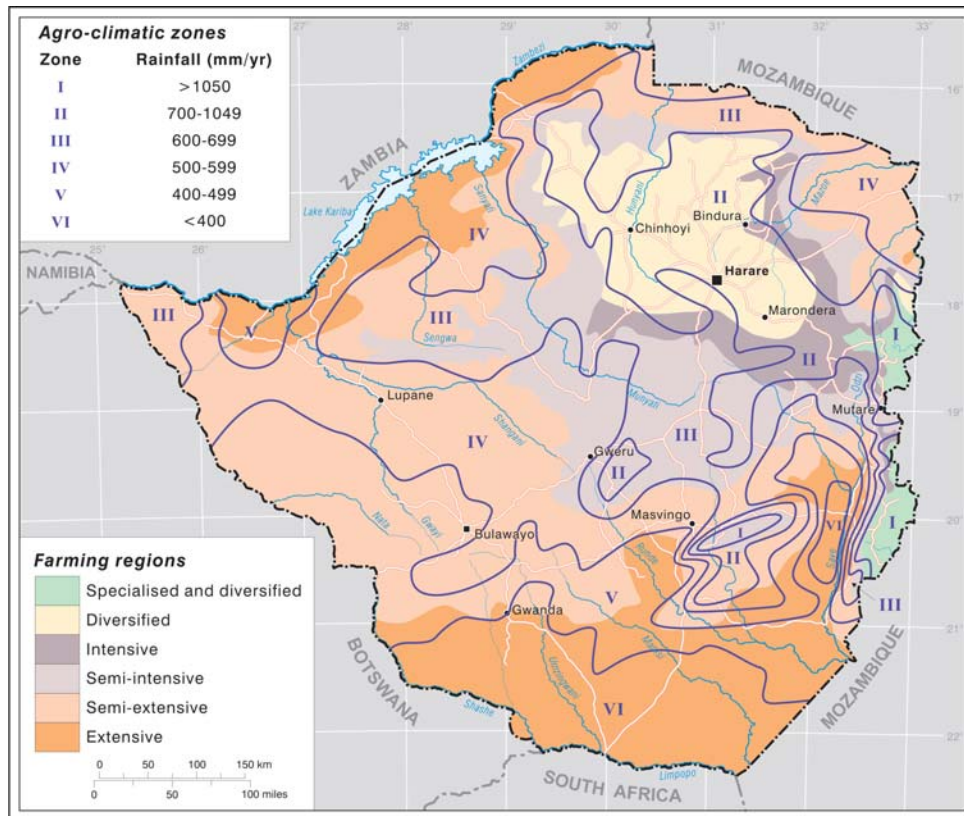
### INTRODUCTION

#### 1.1 Maize production in Zimbabwe

Maize (*Zea mays* L.) is the staple crop and most important source of calories in the diets of many families in Zimbabwe. It has displaced indigenous cereal crops like sorghum (*Sorghum bicolor*), pearl millet (*Pennisetum typhoides*) and finger millet (*Eleusine coracana*). In addition to the wide utilisation options it offers compared to these indigenous cereals, it is also least susceptible to bird damage, more palatable and higher yielding per unit area than the indigenous cereals. For these reasons maize is widely grown in Zimbabwe even in areas where conditions are considered to be unsuitable for production.

Generally there are two groups of farmers involved in the production of maize in the country. These are categorized based on their production systems and scale of operation, namely the large scale commercial farming sector (LSC) and the communal scale farming sector (CFS) (Machida, 1997). The CFS which is largely composed of small scale farmers is characterized by state owned, small farm units (less than 5ha per family), subsistence farming with heavy reliance on animal draft power and family labour and limited access to inputs such as inorganic fertilisers and pesticides (Rohrbach, 1989). In contrast the profit oriented LSC largely composed of commercial farmers with privately owned large units (averaging 2,500ha prior to land reform Rukuni (1992)), relies heavily on machinery, and access to inputs such as inorganic fertilisers, and pesticides. The CFS dominates maize production although average yield levels are lower than in the LSC (Machida, 1997).

Zimbabwe is partitioned into six agricultural production zones commonly referred to as natural regions (NR) I- VI (Figure 1.1) (Chimhowu, 2009). Approximately 91% of the CFS areas fall within natural farming regions III- V, classified as semi-arid regions typical of most post settler colonial states in Southern Africa (Machida, 1997). These areas are characterized by low and erratic rainfall with a high prevalence of mid season dry spells and terminal droughts. In addition these areas have infertile soils with poor water holding capacity (Matauruka, 1995). This implies that maize production in the CFS is done under highly stressful environments of drought and low



**Figure 1.1 Natural farming regions of Zimbabwe. Adapted from Chimhowu (2009).**

soil fertility, exacerbated by disease pressure with limited access to the essential inputs (Bänziger and de Meyer, 2002). Late planting together with inadequate and untimely weed control also exacerbates the effects of drought, low soil fertility and diseases on maize productivity in the CFS. The CFS cannot afford or has limited access to irrigation facilities, and resources to address soil nutrient deficiencies and disease problems.

### **1.2 The importance of drought in Zimbabwe**

Drought is the single most climatic factor limiting maize productivity in Zimbabwe. Past research has shown strong links between rainfall and maize yields in Zimbabwe (Cane *et al*, 1994). Drought is any duration without rainfall which is long enough to reduce plant growth. Practically this occurs when available soil water fails to meet the plant’s transpiration demand for a reasonable period during growth. Drought at any stage of crop development affects production, but maximum damage is inflicted when it occurs around flowering (Cakir, 2004).

Farmers can replant if drought occurs at the seedling stage and obtain reduced yield if drought occurs late in the season, whereas at flowering it can only be mitigated by irrigation which is beyond the reach of many farmers in the CFS (Derera, 2005). Yield losses as much as 67% and 37% were recorded in the CFS and LSC sectors respectively, with mid season drought which often coincides with flowering, being cited as the most common type of drought responsible for the losses even during normal seasons in both sectors (Machida, 1997). Stabilization and improvement of production under these conditions has become an important breeding goal for both the private and public sector breeding programs. The International Maize and Wheat Improvement Centre (CIMMYT) initiated a product oriented breeding project aimed at improving maize yields for the drought prone mid-altitudes of southern Africa (Bänziger *et al*, 2004). An evaluation of 42 hybrids from CIMMYT's stress breeding program with 41 released and pre-released hybrids from private seed companies from the SADC region, showed that hybrids from CIMMYT's stress breeding program showed a consistent advantage over private company hybrid checks at all yield levels (Bänziger *et al*, 2004). Increased stress resistance was the primary cause of increased yielding ability of CIMMYT hybrids. It has been recognized that to enhance these genetic gains, there is need to increase yielding ability by increasing efficiency for grain production in the stress prone environments for example by reducing tassel size.

#### **1.4 Maize tassels and grain yield**

The tassel is an essential reproductive organ, serving as a source of male gametes. However, it often reduces grain yield either physiologically by competing for photosynthates (important energy sink) or physically by shading effect (Gue and Wasson, 1996; Sangoi and Salvador, 1997). It has generally been found that low yielding plants produce large tassels by directing more photosynthates to the tassels (Sofi, 2007). Small tassels would show lower competition for nutrients with the developing ear as well as less shading of the upper leaves (Singh, 2003). Therefore breeding for smaller tassels hypothetically has potential to improve yield for stress prone environments typical of resource poor farmers' operating environments where there is more competition for resources between the tassel and the ear.

The differences between apical (tassel) and axillary (ear) inflorescences in location, timing of differentiation and development may promote competition for resources in the maize plant, especially under stress environments (Sangoi and Salvador, 1997). Apical structures have more

preferential use of the resources available to the plant, more specifically, water, nutrients and photosynthates due to apical dominance resulting in a net developmental priority of the tassel over the ear of the same plant. The ultimate effect of this protandrous behaviour is that under adverse conditions like drought stress, there will be pollen production and distribution at the expense of ear and silk development. Therefore one of the main reasons for reduced yields under drought stress is the potential of lack of synchrony between silk emergence and pollen shed which drastically reduces the rate of fertilization and kernel set (Westgate and Bassetti, 1990; Bolaños and Edmeades, 1996). Since maize has a short and definite period of flowering and pollen viability, any delay in the period between pollen shed and ear pollination (known as anthesis silking interval) increases barrenness resulting in a significant reduction in maize yields (Bolaños and Edmeades, 1993; Beck *et al*, 1996).

Duncan *et al* (1967) found that tassels intercept 4.2 % and 7.5 % incident light at 27,000 plants ha<sup>-1</sup> and 60,500 plants ha<sup>-1</sup>, respectively. These workers further showed through a computer simulation model that shading of the upper leaves by the tassel reduced photosynthesis by 4 % and 19 % at 17,000 plants ha<sup>-1</sup> and 99,000 plants ha<sup>-1</sup>, respectively. Mickelson *et al* (2002) found a significant correlation between tassel branch number and leaf angle and suggested that both play a major role in the penetration of light in the canopy.

Several authors have reported grain yield increases with detasselling. Mashingaidze (2004) reported maize grain yield increases of 11.2 – 12.2 %, with detasselling. Lambert and Johnson (1978) found yield increases over checks of 5% and 2% for complete and partial tassel removal respectively. Detasselling removes apical dominance exerted on axillary buds by the tassel and reduces shading of the upper leaves. It also increases maize yields by allowing more light penetration into the canopy. Detasselling increased radiation interception (RI) by sub-tassel leaves and by the cob leaf by 10 – 28 % and 5 – 27 %, respectively (Mashingaidze, 2004). However, decreasing tassel size rather than completely eliminating the tassel or pollen production may have a positive effect on yield (Schuetz and Mock, 1978).

Tassel size may also be critical in hybrid seed production, where large tassels are required to ensure sufficient and extended pollen availability and in stress environments where pollen production is often drastically reduced (Upadyayula *et al*, 2006). Maize F<sub>1</sub> hybrid seed production requires cross pollination, therefore a viable tassel is required for adequate

pollination. The ideal male parent should have a relatively large tassel that sheds copious amounts of pollen over a long period of time. The ideal female parent should have a relatively large ear that produces a large number of kernels and a small tassel so that more energy is directed towards the production of kernels. By selecting for tassel traits breeders must therefore balance the shading effect of the tassel with the need for adequate pollen in seed production and stress environments.

Clearly breeding programs designed to increase grain yield through reduction of tassel size must know which type of gene action controlling tassel size before initiating a small tassel selection program. Although several studies (Schuetz and Mock, 1978; Upadyayula, 2006) have been done on the genetical analysis of tassel traits, studies of combining ability for tassel traits are rare.

### **1.5 Objectives**

The main objective of the study was to evaluate the performance of few tassel branch (*fbr*) maize mutant lines under optimum conditions and drought stress. The specific study objectives were to:

1. To estimate the general and specific combining abilities among eleven CIMMYT *fbr* mutant lines for grain yield and tassel traits
2. To measure the phenotypic correlation coefficients for grain yield with tassel traits so as to assess the feasibility of using the tassel traits as indirect selection traits for improving yielding efficiency in maize stress prone environments



## **Chapter 2**

### **LITERATURE REVIEW**

#### **2.1 Overview of the maize anatomy**

Maize (*Zea mays* L.) is a monoecious diclinous species where individuals have separate unisexual florets (staminate and pistillate) which produce gametes of both sexes in physically separated parts of the same plant (Sangoi and Salvador, 1998). The male inflorescence is a broad panicle consisting of a central spike and basal lateral branches whereas the un-branched grain-bearing female inflorescence is produced several nodes below the tassel by an axillary bud (Cheng and Pareddy, 1994).

#### **2.2 Physiological Development of Inflorescences**

The underlying organization and development of tassels and ears is remarkably similar until flowers are initiated, therefore it is not surprising that some genes affect both tassels and ears (Upadyayula *et al*, 2006) hence the correlation between their components. Normally the shoot apical meristem (SAM) produces 15 - 26 leaves depending on the genotype and the photoperiodic regime before initiating the tassel. The SAM remains short during the leaf production phase until the complete set of leaves is initiated. It then enters a brief 'transition' phase when it elongates and enlarges rapidly without morphogenetic activity (Irish and Nelson, 1989). Under constant growing conditions, floral transition occurs when about 50% of the total number of leaves is macroscopically visible. This floral transition phase is followed by tassel morphogenesis, which starts by initiation of branch meristems (BM) at the base of the transitional SAM (Irish and Nelson, 1989). Both the tassel and ear inflorescences are derived from the inflorescence meristem (IM) (Figure 2.1) (Upadyayula *et al*, 2006). The shoot apical meristem (SAM) converts into IM, which produces the tassel and approximately at the same time, the axillary meristem (AM) initiates the lateral IM, which gives rise to the ear. The IM then initiates secondary and high order meristems in a progressive manner in both the tassel and the ear (Kaplinsky and Freeling, 2003). Each IM produces an indeterminate number of spikelet pair meristems (SPM) in an acropetal and polystichous manner. Spikelet-pair meristems then form on the central axis and lateral branches of the tassel. Each spikelet-pair meristem will ultimately

give rise to two spikelet meristems (SM) which will each form two floret meristems (FM). The FM will eventually produce floral organs, the palea/ lemma, lodicules, anthers and pistils.

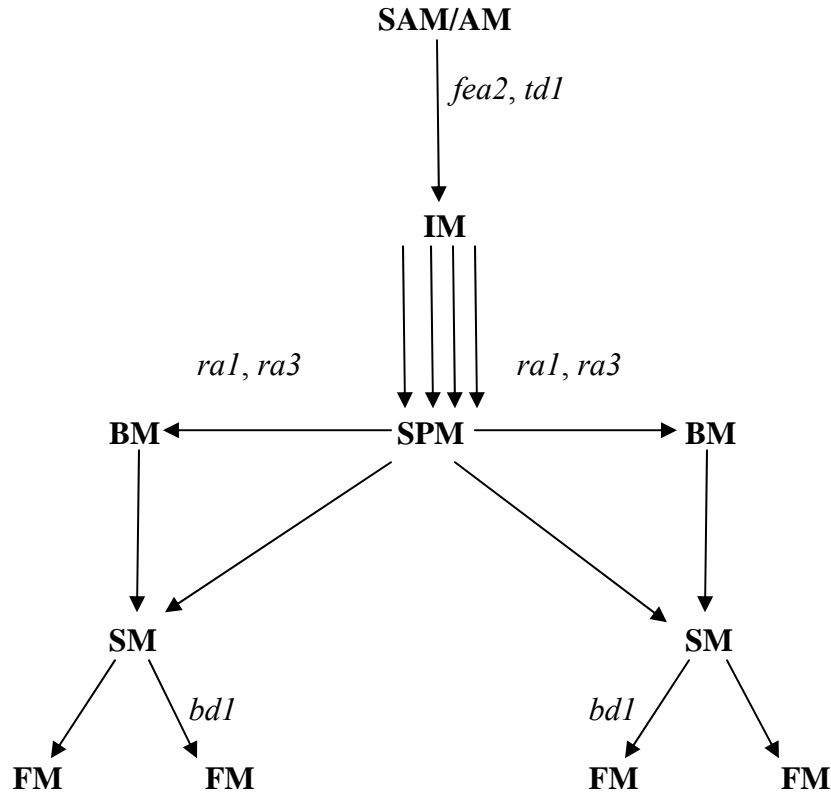


Figure 2.1 Schematic representation of development of tassel and ear inflorescence along with genes likely to affect the various stages of development. **BM** produced only in tassels. **SAM** shoot apical meristem, **AM** axillary meristem, *fea2* fasciated ear2, *td1* thick tassel dwarf1, **IM** inflorescence meristem, *bif2* barren inflorescence2, **SPM** spikelet pair meristems, *ra1* ramosa1, *ra3* ramosa3, **BM** branch meristems, **SM** spikelet meristems, *bd1* branched silkless1, **FM** floret meristems (Adapted from Upadyayula *et al*, 2006)

In the tassel the first few SPM will convert into long branch meristems (BM) whilst in the ear the SPM will convert into a pair of SM to avoid branching (Kaplinsky and Freeling, 2003; Veit *et al*, 1993). SPM are arranged in four rows along the central tassel axis and in only two rows on the lateral branches. The BM and SPM appear initially identical but the BM soon elongate and give rise to lateral axes having indeterminate growth, whereas the SPM do not elongate and give rise to structures (spikelets, florets) with determinate growth. After initiation of the flowers, selective organ abortion in the tassel and ear produces separate unisexual inflorescences (Upadyayula *et*

*al*, 2006). Pistils are aborted in the tassels while anthers are aborted in the ear, allowing the tassel and ear to acquire their respective male and female identities (Veit *et al*, 1993).

### **2.3 Prominent Mutants that affect Tassel Development**

A number of mutations are known to affect the differentiation step from inflorescence meristems (IM) to floral meristems (FM), thus defining distinct genetic steps in the development of the tassel and ear (Upadyayula *et al*, 2006). A few prominent mutations that affect tassel development are, *fbr1*, few tassel branch, fasciated *ear2* (*fea2*), *Thick tassel dwarf* (*td1*), *Barren inflorescence* (*bif2*), *Ramosa1* (*ra1*), *Ramosa2* (*ra2*), *Branched silkless* (*bd1*) and *Tassel seed* (*ts*) (Neuffer *et al*, 1997). Each one affects a separate differentiation stage and has its own unique phenotype which can range in severity.

*Fbr1* is an ethyl methane sulphonate-induced (EMS-induced) dominant mutant whose phenotype is expressed in the tassel only as a reduced number of tassel branches (0-3) (Neuffer *et al*, 1997). This is the mutant that is being manipulated in this study. *Fea2* affects the transition from SAM to IM, resulting in the production of larger IM and thus can lead to more branches (Upadyayula *et al*, 2006). SM and FM may also be fasciated, leading to an increase in spikelet production and irregular rows of seeds (Taguchi- Shiobara *et al*, 2001). *Td1* is similar to *fea2*, but it has a pronounced effect on the tassel resulting in over production of spikelets on the tassel compared to the wild type (Bommert *et al*, 2005). *Bif2* affects the transition from IM to SPM or from SPM to BM resulting in the reduction in the production of ear shoots, branches, spikelets, florets located on the tassel and floral organs (McSteen and Hake, 2001). *ra1* affects the transition from SPM to BM and will result in prolific branching of tassels (Vollbrecht *et al*, 2005). *ra2* has a similar effect with *ra1* except that the pedicellate spikelet is converted to a branch (Upadyayula *et al*, 2006). Both *ra1* and *ra2* have a highly branched and distorted ear, suggesting that *ra1* and *ra2* have a role in BM suppression (Upadyayula *et al*, 2006). In ears of *bd1* mutants, FM are replaced by BM that proliferate SM, suggesting that *bd1* is required for FM identity (Upadyayula *et al*, 2006). Lastly *ts* affects the transition from SM to FM and will cause varying degrees of feminization in tassels. At an early developmental stage, the fate of these two kinds of meristems is apparently not determined. Indeed, in the *tasselseed4* mutant, SPM behave as BM resulting in a highly branched tassel (Irish, 1997), whereas an opposite situation seems to occur in the *unbranched1* (*ubl*) mutant where BM behave as SPM yielding an unbranched tassel.

## **2.5 Inheritance of tassel traits in maize**

The nature of gene action involved in inheritance of tassel traits can help breeders to devise better selection strategies, to seek improvement in these traits in the desired direction. Most studies (Schuetz and Mock, 1978; Gue and Wasson, 1996; Berke and Rocheford, 1999; Wolf and Hallauer, 1997; Hinze and Lamkey, 2003) have revealed that additive gene action is predominant in the inheritance of tassel traits. However, some studies Schuetz and Mock, 1978; Wolf and Hallauer, 1999; Azizi, 2006; Sofi, 2007) found that epistasis to be an integral part of genetic variance for tassel and ear traits. Sofi (2007) revealed that epistasis and its components [I] and [j + I] were significant for tassel and ear traits though the magnitude of non-fixable [j + 1] was greater than the fixable component [I] for tassel branch number and tassel length, whereas the reverse was the case with other traits. He further observed that epistasis and its components interacted significantly with the environment for tassel traits reinforcing the need to conduct experiments involving genetic components across environments to get reliable estimates.

## **2.6 Correlation between grain yield and tassel traits**

Correlation between different traits is usually due to pleiotropy (the same gene affecting different traits in a complementary way) or the presence of linkage/ linkage disequilibrium (Hallauer and Miranda, 1988; Kearsy and Pooni, 1996; McMillan *et al*, 1995). Environment also plays an important role in correlation, affecting traits simultaneously either in the same direction or in different directions. Genetic and environmental causes of correlation combine together to give phenotypic correlation.

Several authors reported significant correlations between different components of tassel architecture, some of which may be useful for selection. Sofi (2007) found a negative correlation between tassel length and tassel weight with ear length which is an important yield attribute. Upadyayula *et al*, (2006) found a negative correlation between tassel branch angle and spikelet pair density which indicates that this trait can be used for indirect selection for yield without compromising on tassel size. Tassels with very upright branches and a cylindrical shape would minimize the amount of shading per unit of biomass. Thus selecting for upright tassel branches may compensate for yield reduction without compromising on tassel size to ensure sufficient pollen availability, especially in hybrid seed production and stress environments. Mickelson *et al*

(2002) reported a significant correlation between tassel branch number and leaf angle and suggested that both traits played a major role in the penetration of light into the canopy. Monneveux *et al* (2008) found negative correlation between tassel weight and grain yield.

## **2.7 Use of tassel traits as secondary traits for grain yield in maize under drought stress**

Given the low heritability of grain yield under drought stress, it is difficult to make genetic progress by selecting for it *per se*. Edmeades *et al* (1997) and Bänziger *et al* (2000) suggested the use of secondary traits which are essentially traits other than grain yield that provide additional information about how the plant performs under a given environment (Lafitte *et al*, 2003). The use of secondary traits improves the selection response by focusing on direct effects of drought and avoiding confounding factors such as additional stresses (such as soil fertility, micronutrient deficiency and diseases) that also determine final grain yield.

To be effective a secondary trait should be easy, cheap and fast to observe or measure non destructive, stable over the measurement period and not associated with yield penalty under unstressed conditions (Edmeades *et al*, 1997, Lafitte *et al*, 2003). Bolaños and Edmeades (1993) and Edmeades *et al* (1999) proposed barrenness, anthesis-silking interval (ASI), leaf senescence and leaf rolling as secondary traits to improve yield in drought prone environments. The heritability of these traits under drought remains high whereas the heritability of yield usually decreases (Bolaños and Edmeades, 1996) and their genetic correlation with grain yield generally increases (Bänziger and Lafitte, 1997).

Several authors published gains under a range of environmental conditions using this approach (Edmeades *et al*, 1999; Chapman and Edmeades, 1999; Monneveux *et al*, 2006). However continued selection for specific secondary traits does not only change their average value, but it also modifies their underlying genetic correlation with yield in improved populations (McMillan *et al*, 1995). Relationships between secondary traits and yield require re-evaluation over time (Edmeades *et al*, 1997). Monneveux *et al* (2008) found no association between grain yield under drought and ASI. This was attributed to the fact that ASI has been a secondary trait with the most utility and use in drought tolerance improvement and hence breeders could have reduced ASI sufficiently in elite germplasm, such that further gains were less likely. Monneveux *et al* (2008) also found weak or non significant correlations between grain yield and senescence or leaf

rolling. This implies that further genetic gains in breeding for drought tolerance can be found by adopting new secondary traits that were not being consciously selected for under drought stress such as reduced tassel sizes or tassel branch numbers.

## **2.7 Combining ability**

Predicting the performance of hybrids from visually assessing or measuring the performance of the component inbred lines is difficult because of the very low correlations between traits in inbred lines and the same traits in the crosses or hybrids especially in traits controlled by polygenes (Hallauer and Miranda, 1988). However it still remains necessary to practice selection during inbred line development. Combining ability is a measure of the value of genotypes based on the performance of their offspring produced in some definite mating system (Allard, 1960). It is an important analysis tool for not only selecting desirable parents but also generating information regarding the nature of and magnitude of gene effects controlling quantitative traits (Basbag *et al*, 2007).

General combining ability (GCA) and specific combining ability (SCA) which identify lines or hybrids with high yield are the most important criteria used to select parental materials in a breeding program (Ceyhan, 2003). Sprague and Tatum (1942) defined general combining ability as the average performance of a genotype in a series of hybrid combinations and specific combining ability as those cases where certain combinations perform relatively better or worse than would be expected on the basis of the average performance. Falconer (1981) observed that GCA is directly related to the breeding value of the parent and is associated with additive genetic effects while SCA is associated with non additive effects such as dominance, epistasis, and genotype x environment interaction effects.

## **2.8 Line x tester design**

Line x tester design is an extension of the top cross method where a broad based genotype is used as a tester to test for line GCA (Singh and Chaudhary, 2004). It is a method used for breeding both self and cross pollinated plants to select favourable parents and crosses, and their GCA and SCA (Ceyhan *et al*, 2008). Line x tester design is analogous to the North Carolina design II (NCII) (Kempthorne, 1957). As with the NCII design, the line x tester is a factorial

experiment that measures the variance of male and female main effects and the male x female interactions, that is line and tester main effects and line x tester interaction effects.

## **2.9 Heritability estimates for tassel traits**

Heritability describes the ratio, expressed in percentage form, of variance due to hereditary differences ( $\sigma^2_g$ ) to the total phenotypic variance ( $\sigma^2_p$ ) Dabholkar (1999). It is a quantitative measure which provides information about the correspondence between genotypic variance and phenotypic variance. The higher the percentage the higher the heritability of the trait. This ratio which is now known as broad sense heritability, is useful if the interest is in relative importance of genotype and environment in the determination of phenotypic values. Its drawback is that it fails to indicate the progress which might be made through selection within a particular population. To counter this drawback, narrow sense heritability was proposed which is the ratio of the additive genetic variance ( $\sigma^2_A$ ) to the phenotypic variance ( $\sigma^2_p$ ) (Dabholkar, 1999). Narrow sense heritability measures the extent of correspondence between breeding values and phenotypic values.

Variable heritability estimates ( $h^2$ ) for tassel traits have been reported by various researchers. (Upadyayula *et al*, 2006) found heritability estimates for tassel traits ranging from 39 % for tassel length to 83 % for tassel weight 26 %. Mock and Schuetz (1974) found heritability estimates ranging from 46 - 89 %. Mickelson *et al* (2002) found heritability estimates of 0.73 for tassel branch angle and 0.81 for tassel branch number.

## **2.10 Heterosis and inbreeding**

Heterosis (hybrid vigour) is defined in quantitative genetics as the superiority of a hybrid over the mean of its parents (mid-parent heterosis) or over the mean of the better parent (better-parent heterosis) (Bernado, 2002). Inbreeding depression which is the loss in vigour due to inbreeding, is the opposite of heterosis (Singh, 2003). Inbreeding is the mating between individuals related by ancestry or descent. Expression of heterosis depends on the differences in the gene frequency of the parental materials that are used to make crosses. The best hybrid vigour or the highest heterotic responses are obtainable when crosses are made between parents originating from genetically different populations (Hallauer and Miranda, 1988).

Inbreeding causes a shift in mean phenotypes in a direction that causes a shift in fitness, on the other hand cross breeding has positive effects on fitness related traits (Lynch, 1991). Heterosis, just like inbreeding depression, depends for its occurrence on dominance, that is, loci without dominance cause neither inbreeding nor heterosis (Falconer, 1981).

Two competing, though not mutually exclusive explanations for heterosis or inbreeding depression are dominance (or partial dominance) and overdominance hypotheses (Singh, 2003; Bernado, 2002, Carr and Dudash, 2003). The dominance hypothesis states that inbreeding depression results from the increased homozygosity of recessive or partly recessive deleterious alleles, the effects of which are masked by dominant alleles in more heterozygous, outbred offspring. The overdominance hypotheses states that heterozygotes at a given locus have an inherent advantage over homozygotes and that the loss of heterozygosity in inbred progeny results in inbreeding depression. Recent marker assisted analyses have repeatedly suggested contributions of over dominant loci and epistasis (Carr and Dudash, 2003).



## Chapter 3

### MATERIALS AND METHODS

#### 3.1 Germplasm

Eleven few tassel branch (*fbr*) inbred lines from CIMMYT were successfully crossed to three testers from CIMMYT- Zimbabwe (Table 3.1) in an 11 x 3 line x tester design. The lines are backcross derivatives of four groups of lines (CML442, CML 395, CML 444 and CML 488). The backcrosses were done with the intention of converting these elite lines into *fbr* lines. The testers represent two heterotic groups used at CIMMYT- Zimbabwe, Heterotic group A (CML 442) and Heterotic group B (CML 395). The crosses were done at the University of Zimbabwe Farm (17.80 S, 31.05 E, 1468 masl) during summer 2008/09 season. There were very limited seed quantities produced from the crosses, which led to the use of single row plots in the evaluation trials.

**Table 3.1 Eleven CIMMYT few tassel branch mutants (*fbr*) and three testers used in the study**

Name	Pedigree	Origin
L1	[CML442/TAS]BC3-2-2-1	CML 442
L2	[CML442/TAS]BC3-2-2-4	CML 442
L3	[[CML395/TAS]BC2/[(CML395/CML444)-B-4-1-3-1-B/CML395//DTPWC8F31-1-1-2-2]-5-1-2-2-B]-12-1-7	CML 395
L4	[CML488/TAS]BC2-6-4-2	CML 488
L5	[[CML395/TAS]BC2/[(CML395/CML444)-B-4-1-3-1-B/CML395//DTPWC8F31-1-1-2-2]-5-1-2-2-B]-10-2-2	CML 395
L6	[CML442/TAS]BC3-2-1-2	CML 442
L7	[CML442/TAS]BC3-2-2-2	CML 442
L8	[[CML395/TAS]BC2/[(CML395/CML444)-B-4-1-3-1-B/CML395//DTPWC8F31-1-1-2-2]-5-1-2-2-B]-10-1-2	CML 395
L9	[[CML395/TAS]BC2/[(CML395/CML444)-B-4-1-3-1-B/CML395//DTPWC8F31-1-1-2-2]-5-1-2-2-B]-8-3-2	CML 395
L10	[CML442/TAS]BC2-2-4-1	CML 442
L11	[[CML444/TAS]BC1/[CML444/CML395//DTPWC8F31-4-2-1-6]-2-1-1-1-B]-11-1-3	CML 444
Tester	Name	
T1	[CML442/TAS]BC3-2-2-1	CML 442
T2	CML395	CML 395
T3	CML442	CML 442

#### 3.2 Evaluation trials

##### 3.1.1 Sites

The thirty- three testcross progenies generated together with four commercial checks SC 633, SC 608, SC 721 and Pan 8M 95 were evaluated under three environments, namely, well-watered,

well-fertilised (optimum) at Muzarabani, and two managed drought stress environments at Chiredzi Research Station (21.02 S, 31.58 E, 433 masl) during winter 2009. The two drought environments were planted in blocks closer to each other with similar soil type separated by a week. All trials were evaluated using a Randomized Complete Block Design (RCBD), with two replications.

The materials were grown in one-row plots at an inter-row spacing of 0.75 m and an intra-row spacing of 0.25 m at all sites. The trials were initially planted at two seeds per hole then later thinned to one plant per station at 3 – 4 weeks after emergence to achieve a plant population of 53,000 plants/ha.

### **3.1.2 Crop Husbandry**

All sites were ploughed or disced and sometimes rolled to break clods to ensure a fine tilth. Rolling was done on sites where the soils appeared very cloddy. Maize fertilizer (N-7, P<sub>2</sub>O<sub>5</sub>-14, K<sub>2</sub>O-7) was applied as a basal fertiliser at 400 kg ha<sup>-1</sup>. All sites received two applications of 200 kg ha<sup>-1</sup> AN (ammonium nitrate) each as top dressing; the first at 4 weeks after crop emergence and the second at 8 weeks after crop emergence.

Carbofuran granules and fipronil insecticide were applied into the planting holes at sowing to control ants, termites and other soil pests. A combination of different types of herbicides (predominantly pre-emergent) and hand weeding were applied at all sites, depending on the weed and soil types, to control weeds. Stalk borer (*Buseola fusca*) were controlled by applying Diptorex 2.5% or Thiodan 1% granules at the rate of 3 kg ha<sup>-1</sup> granules into the funnel of each plant at 3 – 4 weeks and 7 – 8 weeks after crop emergence.

### **3.1.3 Managed drought stress evaluation**

The trial was planted during the off-season (winter 2009) when the chances of receiving rainfall were low. The trial was initially established under irrigation then irrigation was withdrawn three weeks before flowering to target drought stress during flowering and grain filling. A total of only 170 mm of irrigation was applied within the first 35 days after planting. The stress level projected to be achieved in this trial was a yield of about 15 % to 20 % (1 to 2 t ha<sup>-1</sup>) of yields achieved under well-watered conditions at this site (Banziger *et al*, 2000). This stress level

delays silking and causes ear abortion in non-stress tolerant genotypes. Such stress levels achieve an ASI of between four and eight days and about 0.3 to 0.7 ears per plant. If the stress level is not severe enough at flowering, less accurate measures of ASI and ears per plant will be made (Bolanos and Edmeades, 1996).

### **3.2 Data collection**

Data for grain yield, anthesis date, anthesis silking interval and eight tassel traits: total tassel length, central spike length, branch zone length (Figure 3.1), branch length, tassel branch number, tassel branch angle, tassel size and tassel weight was recorded (Table 3.2). TBA and TS were visually scored on 2 - 3 representative tassels for each plot under the optimum environments only. The TBA scores used were an inverse of the scale used by Berke and Rocheford, (1999). After the angle and size estimates were taken, approximately 3 - 4 days after the latest cross finished shedding pollen, four random tassels were harvested from each plot by cutting the tassel one cm below the first tassel branch. These samples were bagged and dried at 40°C. L1, L2, L3, BL, TBN and TW were recorded for each dried sample.

### **3.3 Line x tester analysis**

#### **3.3.1 Analysis of variance**

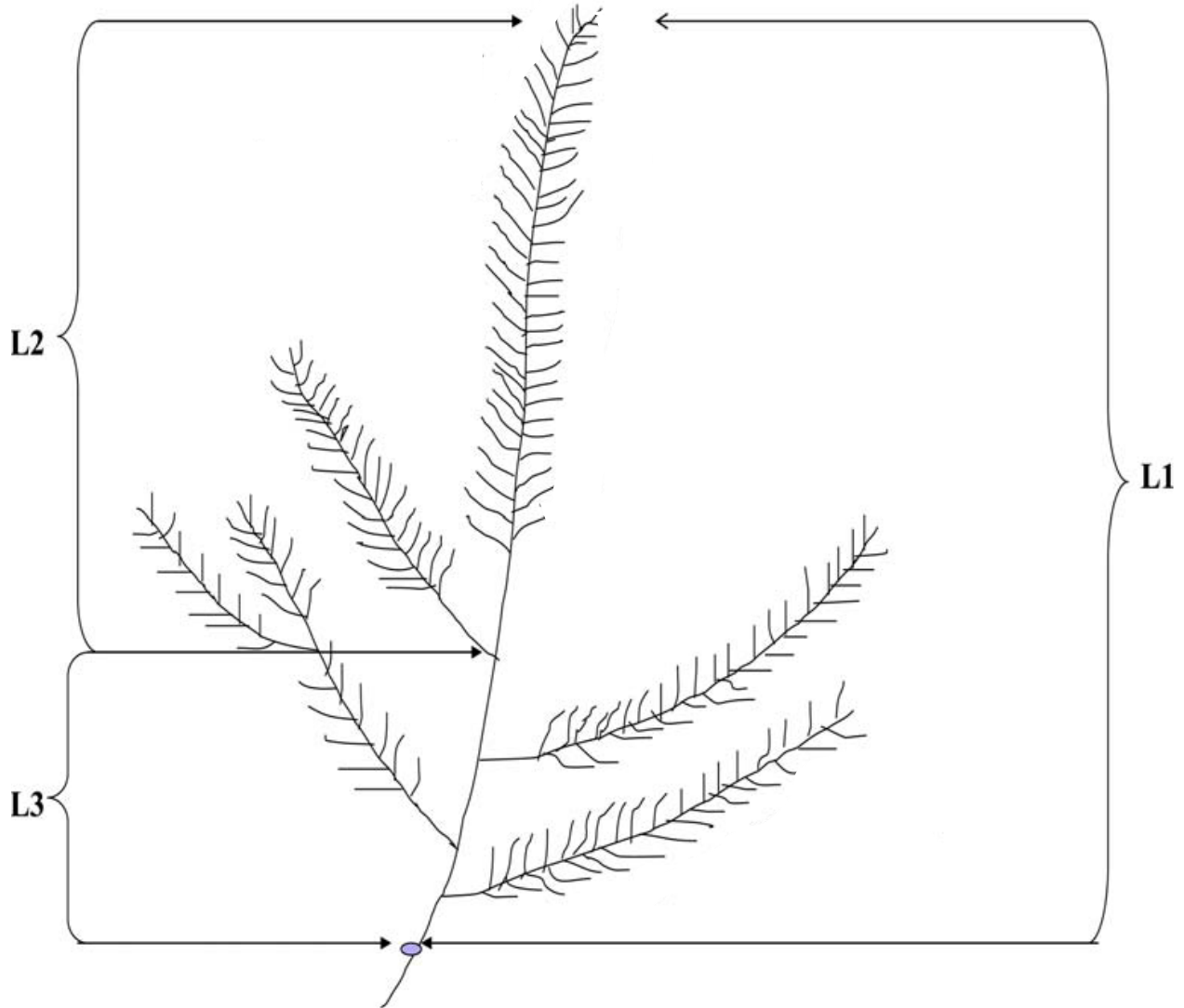
Individual site and across site analyses of variance (ANOVA) were calculated for the testcrosses for each trait measured using the PROC ANOVA procedure of SAS (SAS, 2004). Individual site analysis was done assuming the following model (Dabholkar, 1999):

$$Y_{ijk} = \mu + g_i + g_j + s_{ij} + r_k + e_{ijk}$$

Where  $Y_{ijk}$  is the mean value of a character measured on cross  $i \times j$  in the  $k$ th replication,  $\mu$  is the population mean effect,  $g_i$  is the GCA effect of the  $i$ th tester,  $g_j$  is the GCA effect of the  $j$ th line,  $s_{ij}$  is the SCA effect of the cross between the  $i$ th tester and the  $j$ th line,  $r_k$  is the replication effect and  $e_{ijk}$  is the environmental error associated with each observation.

**Table 3.2 List of traits recorded in the study**

<b>Trait</b>	<b>Abbreviation</b>	<b>How measured/ How calculated</b>
Grain yield	GY	Shelled grain weight per plot adjusted to 12.5% grain moisture and converted to tons per hectare
Tassel Branch Angle	TBA	Recorded using a scale of 1 (= approximately horizontal tassels- 90° from central spike) to 5 (= approximately vertical tassels - < 45° from the central spike)
Tassel size	TS	Recorded using a scale of 1 (= small tassel) to 5 (=large tassel)
Tassel branch number	TBN	measured as the number of primary branches
Total Tassel Length	L1	Measured from the non branching node present below the lowermost primary branch to the tip of central spike
Central spike length	L2	Measured from the top branch to the tip of the central spike
Branch zone length	L3	Calculated as the length from the top branch to the non branching node present below the lower most primary branch
Branch length	BL	Measured as the average length of the top most, lower most and one random middle primary branch
Tassel weight		measured as the mass in g of the entire dried tassel plus 2 cm from the non branching node present below the lowermost primary branch
Anthesis date	AD	Measured as the number of days after planting when 50 % of the plants shed
Anthesis Silking Interval	ASI	Determined as the difference between the number of days after planting when 50% of the plants show silks (SD) and shed pollen (AD): $ASI = SD - AD$ .



**Figure 3.1 Total tassel length (L1), central spike length (L2) and branch zone length (L3)**

A combined analysis of variance was done assuming the following model:

$$Y_{ijl} = \mu + g_i + g_j + s_{ij} + \lambda_k + \lambda_{ik} + \lambda_{jk} + \lambda_{ijk} + e_{ijk}$$

Where  $Y_{ijl}$  is the mean value of a character measured on the  $i \times j$  at the  $l$ th location,  $\mu$  is the general mean,  $g_i$  is the GCA effect of the  $i$ th tester,  $g_j$  is the GCA effect of the  $j$ th line,  $s_{ij}$  is the SCA effect of the cross between  $i$ th tester and the  $j$ th line,  $\lambda_k$  is the effect of site  $k$ ,  $\lambda_{ik}$  is the effect of site  $k$  on tester GCA,  $\lambda_{jk}$  is the effect of site  $k$  on line GCA,  $\lambda_{ijk}$  is the effect of site  $k$  on the SCA of the  $i \times j$  th cross,  $e_{ijk}$  is the error associated with each observation.

### 3.3.2 Estimation of general (GCA) and specific combining ability (SCA) effects

The GCA effects for the lines and testers were generated using the PROC GLM procedure (SAS, 2004) using the procedures by Dabholkar, (1999), Singh and Chaudhary, (2004). The mean values for each trait were generated using the PROC MEANS procedure (SAS, 2004).

$$\text{Line GCA} = \text{Line mean} - \text{Site mean} \quad g_j (\text{lines}) = \frac{Y_{j.}}{rt} - \frac{Y_{..}}{rlt}$$

$$\text{Tester GCA} = \text{Tester mean} - \text{Site mean} \quad g_j (\text{tester}) = \frac{Y_{.j}}{rl} - \frac{Y_{..}}{rlt}$$

Specific combining ability effect for the  $i \times j$ th cross was generated using the PROC GLM procedure (SAS, 2004) using procedures by Dabholkar, (1999), Singh and Chaudhary, (2004).

SCA = Cell mean – line mean – tester mean + site mean

$$s_{ij} = \frac{Y_{ij}}{r} - \frac{Y_{i.}}{rt} - \frac{Y_{.j}}{rl} + \frac{Y_{..}}{rlt}$$

The estimates of the line and tester GCA were tested for their significance using a  $t$ -test (Dabholkar, 1999):

$$tg = \frac{g - 0}{S.E.g}$$

$$S.E.g_i = \left( \frac{MSe}{rt} \right)^{\frac{1}{2}} \quad i = 1, 2, \dots, l$$

$$S.E.g_j = \left( \frac{MSe}{rl} \right)^{\frac{1}{2}} \quad j = 1, 2, \dots, t$$

### 3.3.3 Estimation of genetic components

Magnitudes of additive and dominance variance estimates were estimated from mean squares for testers, lines and line x testers using procedures by Dabholkar (1999).

$$\text{Cov (H.S) testers} = \left( \frac{MS_{\text{testers}} - MS_{\text{line} \times \text{tester}}}{rl} \right)$$

$$\text{Cov (H.S) lines} = \left( \frac{MS_{\text{lines}} - MS_{\text{line} \times \text{tester}}}{rt} \right)$$

$$\sigma^2_A (\text{testers}) = 4 \text{ Cov (H.S) testers}$$

$$\sigma^2_A (\text{lines}) = 4 \text{ Cov (H.S) lines}$$

where both mean squares due to lines and testers were significant an average estimate of the Cov (H.S) was estimated following King *et al* (1961) in (Dabholkar, 1999):

$$\text{Cov (H.S) average} = \frac{Ml + Mt - 2Mlxt}{r(l + t)}$$

Estimates of Cov (F.S) were generated using the following formula (Dabholkar, 1999):

$$\text{Cov (F.S)} = \frac{1}{3r} [MSl + MSt + MSlxt - 3MSe + ry (6 - l - t)]$$

$$\sigma^2_{gca} = \text{Cov (H.S) average}$$

$$\sigma^2_{sca} = \text{Cov (F.S)} - 2\text{Cov (H.S)}$$

### 3.4 Heritability estimates

Broad sense heritability for individual sites and across sites were estimated using PROC GLM procedure (SAS, 2004) using the following formula:

$$h^2 = \sigma_{\text{entry}} / [\sigma_{\text{entry}} + (\sigma_e / r)]$$

where  $\sigma_{\text{entry}}$  is the estimate of genetic variance,  $\sigma_e$  is the error variance, r is the number of replications.

Broad sense heritability for individual sites was estimated using the PROC GLM procedure using the following formula:

$$h^2 = \sigma_{\text{entry}} / (\sigma_{\text{entry}} + (\sigma_{\text{sitentry}} / n_{\text{sites}}) + (\sigma_e / (n_{\text{sites}} * n_r)))$$

where  $\sigma_{\text{entry}}$  is the estimate of genetic variance,  $\sigma_{\text{sitentry}}$  is the estimate of the site x entry variance,  $n_{\text{sites}}$  is the number of locations,  $n_r$  is the number of replications.

## Chapter 4

### RESULTS

#### 4.1 Performance of lines, testers and their hybrids under optimum conditions

The analysis of variance, GCA, SCA variances and broad sense heritability estimates for grain yield and tassel traits under optimum conditions are presented in Table 4.1. Highly significant differences ( $P < 0.001$ ) were observed among hybrids for all traits except anthesis silking interval. Significant differences ( $P < 0.05$ ) were also observed among lines for all traits. There were significant differences among testers ( $P < 0.05$ ) for all traits except grain yield, central spike length and anthesis silking interval. The line by tester (SCA) interaction was highly significant ( $P < 0.05$ ) for all traits except anthesis silking interval. SCA variances were larger than GCA variances for all traits except anthesis silking interval. GCA variance for grain yield was negative and therefore taken to be zero implying the absence of additive gene action in the inheritance of grain yield. Broad sense heritability was highest for grain yield compared to other traits except total tassel length. Mean grain yield for hybrids ranged from  $0.78 \text{ t ha}^{-1}$  (C2-1) to  $12.17 \text{ t ha}^{-1}$  (C11-1) (Appendix A). Generally, early maturing hybrids were higher yielding, had approximately horizontal tassels, larger tassel sizes, longer total tassel lengths, central spike length, branch zone length and branch length and heavier tassels compared to their late maturing counterparts. Mean grain yield ranged from  $4.75 \text{ t ha}^{-1}$  to  $10.18 \text{ t ha}^{-1}$  among lines and  $7.13 \text{ t ha}^{-1}$  to  $7.64 \text{ t ha}^{-1}$  among testers (Appendix C).

#### 4.2 Performance of lines, testers and their hybrids under drought stress

The analysis of variance, GCA, SCA variances and heritability estimates for grain yield and tassel traits across drought environments are presented in Table 4.2. Significantly different ( $P < 0.05$ ) mean values for grain yield and all tassel traits except branch zone length and branch length were found across drought environments. Highly significant differences ( $P < 0.01$ ) were observed among hybrids for all traits except grain yield. Lines significantly differed ( $P < 0.05$ ) for all traits except grain yield. Highly significant differences ( $P < 0.01$ ) were observed among testers for all traits except grain yield, central spike length and anthesis date. Line x tester interaction was significant ( $P < 0.05$ ) for all traits except grain yield and anthesis silking interval. Site x entry and site x line x tester interactions were non-significant for all traits. Site x line interaction was



**Table 4.1 Analysis of variance for grain yield and tassel traits under optimum conditions**

Source	DF	GYG†	TBA	TS	TBN	L1	L2	L3	TW	AD	ASI
HYBRIDS	32	18.75 ***	1.29***	1.07***	46.48***	77.94***	64.07***	33.69***	3.94***	42.44***	12.31
LINE (GCA)	10	26.67***	2.35***	1.01***	87.35***	101.62***	153.41***	37.67***	2.54*	73.58***	20.38*
TESTER (GCA)	2	1.51	1.02*	2.18***	82.20***	67.23**	13.18	29.32*	13.23***	46.77*	17.59
LINE*TESTER (SCA)	20	16.51***	0.78***	0.98***	21.20**	66.61***	22.41***	32.06***	3.70***	26.44**	7.74
Error	32	1.49	0.23	0.23	7.12	8.33	4.65	7.3	0.89	10.15	7.35
$\sigma^2_{gca}$		-0.17	0.06	0.04	4.54	1.27	4.35	0.10	0.30	2.41	0.80
$\sigma^2_{sca}$		7.51	0.28	0.38	7.04	29.13	8.88	12.38	1.41	8.14	0.20
$H^2$		0.85	0.70	0.65	0.73	0.81	0.86	0.64	0.63	0.61	0.25

\*\*\* (P&lt;0.001)

\*\* (P&lt;0.01)

\* (P&lt;0.05)

**Table 4.2 Analysis of variance for grain yield and tassel traits across drought environments**

Source	DF	GYG†	TBN	L1	L2	L3	BL	TW	AD	ASI
SITE	1	6.17	4.40	0.35	41.71	79.9*	26.37*	0.02	16.60	0.01
HYBRIDS	32	4.50	105.61***	195.23***	127.21***	45.08***	119.66***	9.41***	78.70***	13.45**
LINE (GCA)	10	4.62	185.6***	275.86***	287.8***	29.21*	199.31***	7.61***	81.41***	23.25 ***
TESTER (GCA)	2	0.94	269.36***	393.69***	21.33	280.66***	99.81***	36.14***	146.92	50.12 ***
LINE*TESTER (SCA)	20	4.79	49.24***	135.07***	57.5***	29.46*	81.82***	7.63***	70.52***	4.89
SITE*ENTRY	32	1.81	18.45	18.03	13.84	13.61	7.22	0.79	12.12	8.03
SITE*LINE	10	1.31	24.11*	26.60	19.14	15.98	9.55	1.03	9.01	5.73
SITE*TESTER	2	0.99	6.27	21.15	14.25	6.51	19.61*	0.24	3.98	10.64
SITE*LINE*TESTER	20	2.18	16.84	13.42	11.14	13.14	4.82	0.73	14.49	8.94
Error	66	2.93	11.48	19.82	15.49	13.64	5.82	0.82	15.05	5.45
$\sigma^2_{gca}$		-0.14	12.73	14.26	6.93	8.96	4.84	1.02	3.12	2.27
$\sigma^2_{sca}$		0.93	18.88	57.63	21.00	7.91	38.00	3.41	27.73	-0.28
$H^2$		0.19	0.65	0.69	0.65	0.37	0.83	0.72	0.53	0.20

\*\*\* (P&lt;0.001)

\*\* (P&lt;0.01)

\* (P&lt;0.05)

†GYG, grain yield; TBA, tassel branch angle, TS, tassel size, TBN, tassel branch number; L1, total tassel length; L2, central spike length; L3, branch zone length, BL, branch length; TW, tassel weight; AD, anthesis date; ASI, anthesis silking interval

significant ( $P < 0.05$ ) for tassel branch number only whereas that for site x tester was significant ( $P < 0.05$ ) for branch length only. SCA variances were higher than GCA variances for all traits except for anthesis silking interval. The GCA variance for grain yield was negative and was therefore taken as zero. Grain yield had the lowest broad sense heritability estimate compared to all traits, though it was marginally lower than ASI. Mean grain yield for crosses, across drought environments ranged from  $0.15 \text{ t ha}^{-1}$  (C1-1) to  $4.01 \text{ t ha}^{-1}$  (C11-1) (Appendix B). Early maturing hybrids had higher grain yields, longer total tassel lengths, central spike lengths, branch zone lengths, branch lengths and heavier tassels than their late maturing counterparts. For lines, mean grain yield ranged from  $1.00 \text{ t ha}^{-1}$  (L11) to  $2.96 \text{ t ha}^{-1}$  (L5) whereas for testers it ranged from  $1.98 \text{ t ha}^{-1}$  (T2) to  $2.29 \text{ t ha}^{-1}$  (T1) (Appendix D). Similarly early maturing lines had higher grain yields, longer total tassel lengths, central spike lengths, branch zone lengths branch lengths and heavier tassels compared to their late maturing counterparts.

#### **4.3 Performance of lines, testers and their hybrids across environments**

The combined analysis of variance, (GCA), (SCA) variance and heritability estimates for grain yield and tassel traits are presented in Table 4.3. Significantly different ( $P < 0.05$ ) mean values for all traits except tassel branch number were found across environments. Mean values for grain yield, total tassel length, central spike length, branch zone length, branch length and tassel weight under the optimum environment were higher than those under drought environments. Conversely mean values for anthesis dates under the optimum environment were lower than those for drought environments (Appendix D and E). Highly significant ( $P < 0.001$ ) differences were observed among hybrids for grain yield, anthesis date, anthesis silking interval and all tassel traits. Similarly lines differed significantly ( $P < 0.05$ ) for all traits, whereas testers significantly differed ( $P < 0.05$ ) for all traits except grain yield and central spike length. Line x tester interactions were significant ( $P < 0.05$ ) for all traits except anthesis silking interval. Site x line x tester and site x line interactions were non-significant for all traits except grain yield. The site x line interaction was not significant for all traits except grain yield and number of tassel branches. Site x tester interaction was non-significant for all traits except tassel branch angle. SCA variances were larger than GCA variances for all traits except anthesis silking interval. Negative GCA variances estimates were found for grain yield.

**Table 4.3 Combined analysis of variance, GCA, SCA variance, heritability estimates for grain yield and tassel traits**

Source	DF	GYG†	BN	L1	L2	L3	BL	TW	AD	ASI
SITE	2	598.95***	2.62	94.28**	98.57***	42.68*	43.44**	26.6***	16781.19***	24.73*
HYBRIDS	32	13.65***	141.27***	263.26***	179.02***	68.69***	176.81***	12.77***	102.25***	17.92***
LINE (GCA)	10	16.77***	251.62***	370.7***	426.07***	52.83***	310.58***	9.27***	135.14***	33.21***
TESTER (GCA)	2	0.82	347.18***	421.93***	26.71	281.93***	143.65***	50.01***	70.1**	65.69***
LINE*TESTER (SCA)	20	13.37***	65.5***	193.68***	70.73***	55.29***	113.24***	10.8***	89.01***	5.5
SITE*ENTRY	64	5.83***	14.13	12.95	12.23	11.51	5.93	0.63	15.51	7.94
SITE*LINE	20	7.92***	22.72**	16.69	17.14	15.01	5.57	0.96	14.43	8.07
SITE*TESTER	4	1.31	5.32	30.07	11.02	17.28	8.73	0.00	63.79**	6.33
SITE*LINE*TESTER	40	5.21**	10.62	9.28	9.85	9.11	5.84	0.55	11.21	8.04
Error	98	2.39	10.06	16.07	11.95	11.57	5.81	0.84	13.40	6.19
$\sigma^2_{gca}$		-0.33	16.71	14.47	11.12	8.01	8.13	1.35	0.97	3.14
$\sigma^2_{sca}$		5.49	27.72	88.80	29.39	21.86	53.72	4.98	37.81	-0.34
$H^2$		0.35	0.68	0.72	0.70	0.45	0.83	0.71	0.52	0.21

DF: Degrees of Freedom      \*\*\* (P<0.001)      \*\* (P<0.01)      \*(P<0.05)

†GYG, grain yield; TBN, tassel branch number; L1, total tassel length; L2, central spike length; L3, branch zone length, BL, branch length; TW, tassel weight; AD, anthesis date; ASI, anthesis silking interval

#### **4.4 GCA and SCA effects for grain yield and tassel traits**

The general combining ability (GCA) and specific combining ability (SCA) effects for grain yield and tassel traits are shown in Tables 4.4 – 4.7. Positive GCA and SCA effects for grain yield and tassel branch angle imply high grain yield and approximately vertical tassels whereas negative GCA and SCA effects imply low grain yield and approximately horizontal tassels. The smaller the angle between the central spike, the higher the score for tassel branch angle implying that lines with positive GCA effects were desirable for reducing the angle between the central spike length and tassel branches. Lines or testers with negative GCA effects for number of branches, total tassel length, branch zone length, branch length, and tassel weight suggests that they transmitted genes that reduce these traits to their progeny. Similarly negative SCA effects for these traits imply that hybrids had few tassel branches, shorter total tassel lengths, branch lengths, and lighter tassel weights than their counterparts with positive SCA effects.

##### **4.4.1 GCA effects for grain yield under the optimum environment**

The GCA effects for grain yield and tassel traits show that significant positive and negative GCA effects were observed for all traits (Table 4.4). The estimates of GCA effects showed that amongst the lines, the highest positive GCA effect for grain yield was observed for L11 followed by L4, L9 and L8. L11, L4, L9 and L8 were the only lines with significant positive GCA effects for grain yield. In contrast, L6, L7, L1 and L2 had highly significant ( $P < 0.01$ ) negative GCA effects for grain yield. Amongst the lines with significant positive GCA effects for grain yield, L11 showed significant ( $P < 0.01$ ) negative GCA effects for tassel branch angle and anthesis date and highly significant ( $P < 0.01$ ) positive GCA effects for tassel size. L4 showed highly ( $P < 0.01$ ) significant negative GCA effects for tassel branch angle, tassel branch number and total tassel length and positive GCA effects for total tassel length and central spike length. Line 9 exhibited positive GCA effects for grain yield, desirable negative GCA effects for tassel size, tassel branch number, and tassel weight, though it exhibited undesirable significant ( $P < 0.05$ ) positive GCA effects for total tassel length, central spike length, and branch length. Amongst lines with significant negative GCA effects for grain yield, L1 and L2 exhibited highly significant ( $P < 0.01$ ) positive GCA effects for tassel branch angle, branch number and anthesis date but highly significant ( $P < 0.01$ ) negative GCA effects for tassel size, total tassel length, central spike length,

**Table 4.4 GCA effects under optimum environment**

Line	GYG† t ha <sup>-1</sup>	TBA 1-5	TS 1-5	TBN #	L1 cm	L2 cm	L3 cm	BL cm	TW g	AD d
L11	2.64**	-0.69**	0.54**	-1.12	0.86	1.69	-1.22	1.93	0.09	-3.59**
L5	0.79	0.14	-0.29	1.88	4.99**	0.27	4.78**	2.03*	1.04**	-2.76*
L3	0.69	0.81**	-0.46*	-7.08**	3.57**	7.59**	-4.44**	4**	-0.17	-1.42
L4	2.51**	-1.02**	0.21	-2.95**	3.62**	6.62**	-2.94**	3.08**	-0.01	-1.26
L8	1.29**	0.31	0.38	-1.77	2.17	0.42	1.8	1.4	0.12	-1.26
L10	-0.48	0.14	0.04	1.8	-2.71*	-3.19**	0.55	-4.48**	-0.51	-0.59
L9	1.45**	-0.02	-0.46*	-7.45**	2.44*	4.64**	-2.17	4.42**	-1.59**	0.41
L6	-2.74**	0.31	-0.29	2.97**	-4.18**	-4.36**	0.28	-4.78**	-0.38	1.24
<b>&lt;81 AD</b>										
L7	-1.96**	0.64**	-0.46*	1.23	-6.81**	-6.79**	0.05	-6.93**	-0.63	2.74*
L1	-2.67**	0.98**	-0.62**	2.75*	-4.88**	-6.23**	1.4	-6.12**	-0.71	6.08**
L2	-2.79**	0.81**	-0.62**	3.34**	-4.53**	-4.91**	0.43	-4.07**	-0.51	7.41**
<b>&gt;81 AD</b>										
MSe	1.49	0.23	0.23	7.12	8.33	4.65	7.3	5.8	0.89	10
S.E	0.5	0.2	0.2	1.09	1.18	0.88	1.1	0.98	0.39	1.3
<b>Tester</b>										
T2	0.11	-0.02	0.18	1.5**	0.98	-0.06	0.97	0.63	0.6**	-0.95
T3	-0.05	0.39**	-0.36**	-1.7**	0.18	0.39	-0.15	-0.87	-0.7**	0.96
T1	-0.41	0.3**	-0.36**	-2.03**	-2.46**	-1.16*	-1.39*	-2.19**	-0.82**	1.91**
MSe	1.49	0.23	0.23	7.12	8.33	4.65	7.3	5.8	0.89	10
S.E	0.26	0.1	0.1	0.57	0.62	0.46	0.58	0.51	0.2	0.68

\*\*\* (P&lt;0.001)

\*\* (P&lt;0.01)

\* (P&lt;0.05)

†GYG, grain yield; TBA, tassel branch angle; TS, tassel size; TBN, tassel branch number; L1, total tassel length; L2, central spike length; L3, branch zone length, BL, branch length; TW, tassel weight; AD, anthesis date; ASI, anthesis silking interval

branch length and tassel weight. Line L6 showed highly significant (P<0.01) positive GCA effects for tassel branch number but highly significant (P<0.01) negative GCA effects for total tassel length, central spike length, and branch length whereas line L7 exhibited significant (P<0.01) positive GCA effects for tassel branch angle and anthesis date, significant (P<0.05) negative GCA effects for tassel size, total tassel length, central spike length, and branch length. Although L10 showed non-significant negative GCA effects for grain yield it exhibited significant (P<0.05) negative GCA effects for total tassel length, central spike length and branch length. L3 with non-significant positive GCA effects for grain yield, showed significant (P<0.05) negative GCA effects for tassel size, tassel branch number, and branch zone length but highly significant (P<0.01) positive GCA effects for tassel branch angle, total tassel length, central spike length and branch length. The estimates further showed that although there were no significant GCA effects for grain yield amongst testers, T1 exhibited, highly significant (P<0.01)

positive GCA effects for tassel branch angle and anthesis date and significant ( $P < 0.05$ ) negative GCA effects for tassel size, tassel branch number, total tassel length, central spike length, branch zone length, branch length and tassel weight. Similarly, T3 showed highly significant ( $P < 0.01$ ) positive GCA effects for tassel branch angle and highly significant ( $P < 0.01$ ) negative GCA effects for tassel size, tassel branch number and tassel weight whereas T2 showed highly significant ( $P < 0.01$ ) positive GCA effects for tassel branch number and tassel weight.

#### **4.4.2 GCA effects for lines and testers across drought environments**

Significant positive and negative GCA effects were observed for grain yield and tassel traits (Table 4.5). The GCA estimates showed that among lines only five, L11, L5, L6, L2 and L7 showed significant GCA effects for grain yield. L11 and L5 had highly significant ( $P < 0.01$ ) positive GCA effects for grain yield whereas lines L6, L2 and L7 had significant ( $P < 0.05$ ) negative GCA effects. L11 exhibited significant ( $P < 0.05$ ) positive GCA effects for total tassel length, branch length and highly significant ( $P < 0.01$ ) negative GCA effects for anthesis date. L5 had significant ( $P < 0.05$ ) positive GCA effects for tassel branch number, total tassel length, central spike length, branch length and tassel weight. L2 and L7 showed highly significant ( $P < 0.01$ ) negative GCA effects for total tassel length, central spike length, branch length, but highly significant ( $P < 0.01$ ) positive GCA effects for anthesis date. L6 showed significant ( $P < 0.05$ ) negative GCA effects for total tassel length, central spike length, branch length and tassel weight. Although L1 had non-significant GCA effects for grain yield, it showed highly significant ( $P < 0.01$ ) negative GCA effects for total tassel length, central spike length, branch length and tassel weight. L3 and L9 with non-significant positive GCA effects for grain yield, showed significant negative GCA effects for tassel branch number, branch zone length and highly significant ( $P < 0.001$ ) positive GCA effects for central spike length and branch length. The GCA estimates also showed low and non significant GCA effects for grain yield amongst testers. However, T1 showed highly significant GCA effects for tassel branch number, total tassel length, branch zone length, branch length, and tassel weight and highly significant ( $P < 0.01$ ) positive GCA effects for anthesis date. T3 showed highly significant ( $P < 0.01$ ) GCA effects for tassel branch number, total tassel length, branch zone length, tassel weight and anthesis date. T2 with non-significant negative GCA effects for grain yield showed highly significant ( $P < 0.01$ ) positive GCA effects for tassel branch number, total tassel length, branch

**Table 4.5 GCA effects for lines and testers across drought environments**

Line	GY† t ha <sup>-1</sup>	TBN #	L1 cm	L2 cm	L3 cm	BL cm	TW g	AD d
L11	0.83**	0.97	3.32*	2.2	1.11	2.98**	0.27	-3.73**
L4	0.28	2.02	2.13	3.26**	-0.93	3.7**	0.19	-1.56
L10	0.03	0.61	-1.19	-1.14	0.08	-2.67**	-0.48	-1.48
L8	0.14	-5.13**	3.16*	3.41**	0.29	1.6	0.39	-0.31
L5	0.87**	3.37*	4.12**	3.13**	1.51	2.29**	1.29**	-0.06
<b>&lt;107 AD</b>								
L3	0.51	-7.52**	3.00*	4.89**	-2.44*	2.73**	0.02	0.69
L9	0.11	-7.43**	1.89	5.53**	-3.87**	4.06**	-0.36	0.69
L6	-0.78*	1.73	-5.06**	-4.77**	-0.59	-4.04**	-0.67*	1.44
L1	-0.12	1.43	-7.68**	-7.67**	-0.42	-5.93**	-1.13**	3.9**
L2	-0.85**	0.5	-6.99**	-5.68**	-1.69	-4.49**	-1.22**	4.1**
L7	-1.08**	1.02	-7.05**	-5.84**	-1.37	-6.00**	-1.29**	4.6**
<b>&gt;107 AD</b>								
SE	0.32	1.35	1.42	1.2	1.1	0.85	0.28	0.83
T3	0.05	-2.07**	-1.85**	-0.5	-1.4**	-0.57	-0.71**	-1.28**
T1	0.21	-2.31**	-3.37**	-0.78	-2.89**	-2.01**	-0.87**	1.19**
T2	-0.1	2.09**	2.4**	0.54	2.03**	1	0.77**	2.28**
SE	0.12	0.31	0.57	0.46	0.31	0.55	0.06	0.25

\*\*\* (P<0.001)      \*\* (P<0.01)      \* (P<0.05)

†GYG, grain yield; TBN, tassel branch number; L1, total tassel length; L2, central spike length; L3, branch zone length; BL, branch length; TW, tassel weight; AD, anthesis date; ASI, anthesis silking interval

zone length, tassel weight and anthesis date.

#### 4.4.3 SCA effects for grain yield and tassel traits under the optimum environment

Significant positive and negative SCA effects were observed for grain yield and tassel traits (Table 4.6). Significant (P<0.05) positive SCA effects for grain yield were observed for eleven hybrids, C2-2, C7-2, C10-2, C3-3, C11-1, C1-2, C6-2, C5-1, C8-3, C9-1, and C9-3 whereas significant (P<0.05) negative SCA effects for grain yield were observed for ten hybrids C11-3, C5-2, C4-2, C8-2, C10-3, C3-2, C9-2, C7-3, C1-1, and C2-1. The highest positive SCA effects for grain yield were exhibited by C2-2, while SCA effects were lowest in C9-2. C2-2 showed significant (P<0.05) negative SCA effects for tassel branch angle and anthesis date, whereas C9-2 showed significant (P<0.01) negative SCA effects for tassel size, total tassel length, central spike length, branch zone length and branch length. Amongst hybrids with significant positive SCA effects for grain yield, C3-3, C7-2, C1-2 and C9-1 showed significant (P<0.05) negative

**Table 4.6 SCA effects for grain yield and tassel traits under the optimum environment**

Name	GYG† t ha <sup>-1</sup>	TBA 1-5	TS 1-5	TBN #	L1 cm	L2 cm	L3 cm	BL cm	TW g	AD d
C5-3	0.38	-0.55	0.7*	7.04**	3.9	-1.93	5.75**	1.77	1.53*	-3.29
C10-2	3.25**	-0.64	0.82*	2.41	6.7**	1.59	5.16*	4.49*	1.15	-3.55
C3-3	2.49**	-0.72*	0.86*	0.25	4.52*	4.31**	0.61	3.2	0.37	-3.62
C11-2	-0.13	0.19	-0.18	0.48	-0.57	-0.59	0.53	-0.33	-0.44	0.45
C8-1	0.6	-0.63*	0.53	3.02	2.61	-0.58	3.28	1.52	0.94	-4.24
C11-3	-1.92*	-0.72*	-0.14	2.04	-0.87	-0.99	0.5	0.42	0.85	-0.96
C11-1	2.4**	-0.13	0.86*	-0.28	2.73	2.41	-0.46	2.34	0.51	-1.41
C6-2	2.24**	-0.81*	1.15**	3.25	4.47*	2.41	2.08	5.69**	1.53*	-2.88
C3-1	1.29	-0.63	0.86**	5.18**	3.36	-1.79	5.66**	0.52	1.86**	-2.58
C5-2	-1.95*	-0.14	0.15	-0.77	-5.1*	-2.28	-2.72	-4.48*	-0.89	1.62
C4-2	-1.8*	0.52	0.15	-0.99	-0.48	-1.88	1.45	-3.63*	-0.22	0.62
C7-2	3.46**	-1.14**	0.82*	4.33*	8.5**	4.69**	3.91*	6.94**	2.65**	-3.38
C1-2	2.3**	-0.98**	0.99**	2.96	8.12**	3.92**	4.26*	6.92**	1.99**	-6.21**
C4-1	0.65	-0.8*	0.2	4.45*	-1.84	-1.98	0.21	0.54	0.57	-1.74
C4-3	1.49	-0.39	0.2	-1.23	3.62	4.67**	-1.09	5.52**	0.57	-0.79
C5-1	1.91*	0.04	-0.3	-4.03*	2.5	5.02**	-2.46	5.14**	0.27	-0.24
C8-3	2.15*	-0.22	0.53	2.09	4.92*	1.67	3.18	4.00*	1.07	-0.79
C9-1	2.37**	-0.8**	0.86*	2.05	4.75*	4.16**	0.64	3.75*	1.15	-3.41
C9-3	2.51**	-0.39	0.36	1.87	3.4	-0.34	3.7	3.58*	0.91	-2.46
C8-2	-2.4**	0.19	-0.51	-2.87	-6.23**	-0.28	-5.89**	-3.1	-1.1	3.12
<b>&lt;80 AD</b>										
C2-2	4.25**	-0.81*	0.49	2.47	3.47	1.36	2.18	3.22	1.03	-5.05*
C10-3	-2.22**	-0.05	-0.14	-0.63	-4.3*	-1.66	-2.67	-1.57	-0.55	1.04
C3-2	-3.43**	0.69*	-1.18**	-3.2	-6.58**	-1.69	-5.7**	-1.3	-1.3	4.29
C10-1	-0.68	0.04	-0.14	0.45	-1.1	0.89	-1.92	-0.5	0.32	0.59
C7-1	-1.32	0.04	-0.14	-2.13	-4.65*	-2.91	-1.67	-2.25	-0.93	-2.24
C6-3	-1.39	0.28	-0.3	-1.8	0.52	0.96	-0.45	-0.87	0.45	0.71
C6-1	-0.5	-0.13	-0.3	0.78	-3.69	-2.54	-1.06	-2.4	-1.06	0.26
C9-2	-4.53**	0.52	-0.68*	-1.69	-6.85**	-2.99*	-3.77*	-4.91**	-1.14	3.95
C2-3	-0.34	-0.22	0.03	-2.27	-4.63*	-1.69	-3.00	-2.98	-0.93	-1.96
C7-3	-1.79*	0.45	-0.14	0.04	-2.55	-0.96	-1.67	-2.27	-0.8	3.71
<b>80- 87 AD</b>										
C1-3	-0.08	0.11	0.03	-0.98	-3.08	0.22	-3.37	-1.28	-0.22	1.38
C1-1	-1.87*	0.2	-0.47	0.25	-3.74	-3.33*	-0.32	-3.21	-0.85	2.92
C2-1	-3.56**	0.37	0.03	.	.	.	.	.	.	5.09*
<b>&gt;87 AD</b>										
MSe	1.49	0.23	0.23	7.12	8.33	4.65	7.3	5.8	0.89	10.15
S.Esca	0.86	0.34	0.34	1.89	2.04	1.52	1.91	1.7	0.67	2.25

\*\*\* (P<0.001)      \*\* (P<0.01)      \* (P<0.05)

†GYG, grain yield; TBA, tassel branch angle; TS, tassel size; TBN, tassel branch number; L1, total tassel length; L2, central spike length; L3, branch zone length, BL, branch length; TW, tassel weight; AD, anthesis date; ASI, anthesis silking interval



SCA effects for tassel branch angle, significant ( $P < 0.05$ ) positive SCA effects for tassel size, total tassel length and central spike length. In addition C7-2 and C1-2 showed significant ( $P < 0.05$ ) positive SCA effects for branch zone length, branch length, and tassel weight. Both hybrids had negative SCA effects for anthesis date. Amongst hybrids with negative SCA effects for grain yield, C3-2 showed positive SCA effects for tassel branch angle and highly significant ( $P < 0.01$ ) negative SCA effects for tassel size, total tassel length and branch zone length. C8-2 showed highly significant ( $P < 0.01$ ) negative SCA effects for total tassel length and branch zone length. Although C5-3 had non-significant positive SCA effects for grain yield, it showed significant ( $P < 0.05$ ) positive SCA effects for tassel size, tassel branch number, branch zone length and tassel weight. In general hybrids that tasseled after 80 days except C2-2 had negative SCA effects for grain yield, tassel size, branch number, total tassel length, central spike length, branch zone length, branch length, and tassel weight, and positive SCA effects for tassel branch angle.

#### **4.4.4 SCA effects for grain yield and tassel traits across drought environments**

The estimates of SCA effects for all traits varied significantly among the hybrids (Table 4.7). The SCA estimates showed that only seven hybrids C10-2, C6-2, C10-3, C8-2, C1-1, C9-2 and C3-2 showed significant SCA effects for grain yield. C10-2 and C6-2 showed significant ( $P < 0.01$ ) positive SCA effects for grain yield whereas, C10-3, C8-2, C1-1, C9-2 and C3-2 showed significant ( $P < 0.05$ ) negative SCA effects. The highest SCA effects for grain yield were exhibited by C10-2 with the least being exhibited by C1-1. C10-2 showed significant ( $P < 0.05$ ) positive SCA effects for all tassel traits except branch zone length and highly significant ( $P < 0.01$ ) negative SCA effects for anthesis date. On the other hand C1-1 showed significant ( $P < 0.05$ ) negative SCA effects for branch length. Similarly C6-2 had positive SCA effects for all tassel traits but negative SCA effects for anthesis date. In contrast, hybrids, C8-2, C9-2 and C3-2 showed significant ( $P < 0.05$ ) negative SCA effects for tassel branch number, total tassel length, central spike length, branch zone length branch length and tassel weight but positive SCA effects for anthesis date. Although hybrids C1-2 and C7-2 had non-significant SCA effects for grain yield, they showed significant ( $P < 0.05$ ) positive SCA effects for tassel branch number, total tassel length, central spike length, branch length, and tassel weight and significant ( $P < 0.05$ ) negative SCA effects for anthesis date. In contrast, hybrids C1-3 and C2-1 with non-significant

**Table 4.7 SCA effects grain yield and tassel traits across drought environments**

Name	GY† t ha <sup>-1</sup>	TBN #	L1 cm	L2 cm	L3 cm	BL cm	TW g	AD d
C3-3	0.97	2.81	3.89**	2.22	2.18	2.55**	0.69*	-5.3**
C11-3	0.03	2.62	1.72	-0.48	1.83	2.19**	1.00**	-0.88
C8-3	0.29	2.4	3.86**	1.78	2.62	2.77**	0.63	-4.05**
C11-1	0.88	1.48	1.24	1.89	-0.53	1.38	0.41	-2.36
C10-2	1.69**	4.17**	5.41**	3.06*	2.59	5.7**	2.08**	-5.2**
C4-3	-0.63	-3.26*	0.29	2.13	-2.16	1.87*	-0.35	-0.3
C5-3	0.95	5.7**	4.15**	2.26	2.2	2.21**	2.04**	-1.8
C9-1	0.62	2.4	6.6**	5.56**	1.59	5.63**	1.54**	-5.02**
C9-3	0.59	3.34*	2.75	-0.57	3.00*	1.69*	0.94**	-2.3
C3-1	0.03	3.22*	6.31**	1.88	3.52*	4.62**	1.29**	-4.52**
C4-2	0.71	1.95	-0.34	-2.16	1.65	-0.69	0.35	-2.12
C6-2	1.53**	3.52*	6.8**	3.76**	2.79*	5.07**	2.14**	-4.62**
C10-1	-0.26	0.02	-1.25	-1.04	-0.16	-2.77**	-0.59	-0.61
C11-2	-1.07	-1.80	-0.13	-0.68	0.97	-2.00*	-0.61	1.05
<b>&lt;106 AD</b>								
C4-1	-0.23	3.60*	2.88*	0.76	2.78*	0.39	0.81*	0.23
C5-1	-0.42	-4.17**	2.32	2.78*	-0.61	2.7**	-0.11	-1.27
C8-1	0.80	3.51*	6.18**	2.58	3.74**	3.79**	1.54**	-1.02
C6-3	-0.55	-0.82	-0.22	0.33	-0.15	-0.91	-0.43	0.2
C10-3	-1.59**	-1.89	-1.34	-1.29	-0.17	-1.36	-0.68*	3.62*
C1-2	0.79	4.94**	8.79**	4.66**	3.99**	5.49**	1.54**	-5.08**
C2-2	0.46	2.05	9.06**	5.27**	4.09**	6.42**	1.2**	-5.28**
C2-3	-0.33	0.87	-0.19	-0.46	0.38	-1.26	0.31	-1.22
C5-2	-0.68	0.76	-3.65*	-4.31**	0.67	-3.34**	-1.13**	0.88
C7-2	0.55	3.6*	5.54**	4.33**	1.39	5.46**	1.58**	-3.53*
C7-3	-0.06	-1.51	-0.23	0.35	0.08	-1.85*	-0.38	1.03
C6-1	-1.13	-0.41	-3.75**	-3.37**	-0.38	-2.59**	-0.9**	2.23
C8-2	-1.24*	-3.61*	-7.22**	-3.64**	-4.09**	-4.99**	-1.36**	2.88
<b>106- 112 AD</b>								
C1-3	-0.51	-1.84	-4.33**	-3.59**	-1.50	-2.14*	-0.79*	2.74
C1-1	-2.02**	-0.81	-1.64	-0.34	-0.23	-1.77*	0.06	0.60
C7-1	-0.79	0.20	-2.49	-3.95**	0.79	-2.03*	-0.39	0.31
C9-2	-1.36*	-3.45*	-6.52**	-4.26**	-2.33	-5.75**	-1.67**	5.13**
C2-1	-0.77	-0.62	-6.05**	-4.08**	-2.21	-3.59**	-0.70*	4.31**
C3-2	-1.58**	-3.73*	-7.38**	-3.37**	-3.43*	-5.59**	-1.17**	7.63**
<b>&gt;112 AD</b>								
SE	0.57	1.6	1.43	1.3	1.41	0.85	0.33	1.48

\*\*\* (P&lt;0.001)

\*\* (P&lt;0.01)

\* (P&lt;0.05)

†GYG, grain yield; TBN, tassel branch number; L1, total tassel length; L2, central spike length; L3, branch zone length; BL, branch length; TW, tassel weight; AD, anthesis date; ASI, anthesis silking interval

SCA effects for grain yield, showed significant (P<0.05) negative SCA effects for total tassel length, central spike length, branch length and tassel weight.

#### **4.5 Mid-parent heterosis for grain yield and tassel traits**

Mid-parent heterosis (MPH) was estimated for both the optimum and drought environment and the results are presented in Tables 4.8 – 4.9. MPH for grain yield ranged from -86.9% to 46.9% under the drought environment (Table 4.8). All hybrids that flowered before 80 days except C11-3 and C5-2 showed positive heterosis for grain yield and conversely all hybrids that flowered after 80 days except C2-2 showed negative heterosis. The highest MPH for grain yield under the optimum environment was observed for the hybrid C2-2 followed by C10-2 and C11-1 and the lowest was observed for hybrid C2-1 followed by C1-1 and C6-3. Entries C2-2 and C10-2 showed negative heterosis for tassel branch angle, central spike length and anthesis date, and positive heterosis for tassel size, tassel branch number, total tassel length, branch zone length, branch length and tassel weight. Entry C11-1 had negative heterosis for tassel branch angle, tassel branch number, branch zone length, and anthesis date but positive heterosis for tassel size, total tassel length, central spike length, branch length and tassel weight. Entry C2-1 had positive heterosis for tassel branch angle and anthesis date but negative heterosis for tassel size. Entry C1-1 showed positive heterosis for tassel branch angle, tassel branch number and anthesis date but negative heterosis for tassel size, total tassel length, central spike length, branch zone length, branch length and tassel weight.

MPH for grain yield across drought environments ranged from -92.9% to 80.6% (Table 4.9). All hybrids that flowered before 106 days except C4-3 and C10-1 showed positive heterosis for grain yield and conversely all hybrids that flowered after 106 days except C4-1, C5-1, C8-1 and C1-2 showed negative heterosis. The highest MPH for grain yield was observed for the hybrid C10-2 followed by C6-2 and C5-3 and the lowest was observed for the hybrid C1-1 followed by C6-1 and C7-1. Entries C10-2, C6-2 and C5-3 showed positive heterosis for all traits except anthesis date. Conversely C1-1, C6-1 and C7-1 showed negative heterosis for all traits except anthesis date.

**Table 4.8 Mid-parent heterosis for grain yield and tassel traits under the optimum environment**

Name	GYG†	TBA	TS	TBN	L1	L2	L3	BL	TW	AD
C5-3	9.5	-7.6	14.1	59.3	15.7	-6.4	48.3	13.3	37.4	-5.4
C10-2	41.7	-16.3	30.4	29.9	15.4	-0.2	39.1	16.9	27.1	-5.5
C3-3	35.8	-2.9	17.9	-54.9	15.7	29.2	-13.9	25.5	-1.8	-4.9
C11-2	14.0	-5.3	5.5	5.6	0.9	0.9	2.8	5.2	-2.1	-2.4
C8-1	13.1	-8.5	18.2	11.1	6.4	-3.9	23.9	6.7	14.7	-4.9
C11-3	-7.1	-25.8	-1.5	5.9	-0.9	0.2	-1.4	5.4	13.4	-2.9
C11-1	40.6	-9.8	31.3	-17.9	5.1	10.8	-13.5	13.0	3.6	-2.9
C6-2	14.8	-18.2	37.9	38.7	7.7	0.9	18.0	24.0	36.5	-3.5
C3-1	18.6	-1.9	17.9	8.5	9.9	5.1	24.0	7.9	35.1	-2.9
C5-2	-18.8	-2.3	3.4	6.8	-5.1	-8.8	0.9	-17.1	-1.4	-0.3
C4-2	-5.5	0.0	11.1	-15.3	4.4	5.1	3.5	-9.3	1.6	-0.6
C7-2	38.4	-21.7	24.2	42.8	15.6	6.0	29.7	27.1	60.4	-3.1
C1-2	16.3	-12.5	28.0	36.2	16.7	3.7	35.0	29.1	44.6	-4.5
C4-1	19.9	-36.7	4.2	20.7	-3.2	2.8	-16.0	5.6	3.9	-1.8
C4-3	31.0	-22.0	4.2	-37.0	13.6	29.3	-20.5	36.4	5.5	-1.2
C5-1	27.3	6.9	-23.9	-34.6	9.4	19.1	-4.7	29.7	8.5	-0.8
C8-3	33.9	3.3	18.2	3.4	15.2	8.4	26.4	24.5	19.2	-1.2
C9-1	35.9	-18.0	17.9	-37.4	12.2	22.6	-9.0	26.7	-1.7	-2.8
C9-3	38.9	-5.5	-1.8	-36.8	11.7	8.1	19.2	28.4	-7.3	-2.2
<b>&lt;80 AD</b>										
C8-2	-20.7	9.1	-7.3	-25.4	-11.5	-0.4	-28.6	-11.5	-15.6	2.6
C2-2	46.9	-10.6	9.7	34.1	4.6	-5.1	19.1	9.8	24.3	-2.2
C10-3	-34.2	5.6	-10.6	-4.9	-14.8	-13.3	-17.0	-29.4	-30.5	1.5
C3-2	-38.2	27.7	-46.8	-65.5	-10.5	7.4	-58.9	5.2	-23.8	4.0
C10-1	-15.9	6.9	-10.6	2.8	-10.2	-5.8	-16.8	-27.8	-9.3	1.6
C7-1	-39.5	12.7	-21.4	-22.0	-27.2	-33.7	-17.1	-54.2	-45.3	0.1
C6-3	-45.4	16.2	-23.9	-9.3	-4.0	-4.6	-2.7	-25.8	-2.4	2.3
C6-1	-34.8	4.6	-23.9	10.1	-19.7	-24.5	-11.7	-43.1	-43.8	2.3
C9-2	-45.2	14.3	-29.0	-52.0	-12.7	-2.6	-31.7	-12.2	-42.1	4.7
C2-3	-28.7	9.2	-18.8	-11.4	-18.6	-17.8	-19.7	-37.2	-40.5	2.7
<b>80- 87 AD</b>										
C7-3	-42.8	23.8	-21.4	-1.7	-16.5	-19.6	-12.0	-46.7	-39.4	6.9
C1-3	-23.3	18.9	-18.8	-3.7	-14.9	-12.5	-18.3	-35.0	-25.2	5.9
C1-1	-56.8	20.2	-39.1	4.9	-21.1	-33.9	-2.2	-56.8	-44.7	8.3
C2-1	-86.9	22.7	-18.8	.	.	.	.	.	.	11.6
<b>&gt;87 AD</b>										
Mean	-2.03	-0.72	-0.72	-3.40	-0.33	-1.05	-0.81	-2.06	-1.29	-0.05
Min	-86.9	-36.7	-46.8	-65.5	-27.2	-33.9	-58.9	-56.8	-45.3	-5.5
Max	46.9	27.7	37.9	59.3	16.7	29.3	48.3	36.4	60.4	11.6

†GYG, grain yield; TBA, tassel branch angle; TS, tassel size; TBN, tassel branch number; L1, total tassel length; L2, central spike length; L3, branch zone length, BL, branch length; TW, tassel weight; AD, anthesis date; ASI, anthesis silking interval

**Table 4.9 Mid-parent heterosis for grain yield and tassel traits across drought environments**

Name	GY	BN	L1	L2	L3	BL	TW	AD
C3-3	53.0	-27.1	11.8	17.9	2.0	21.6	11.9	-5.3
C11-3	18.5	17.8	6.5	1.6	11.6	20.1	25.8	-3.3
C8-3	17.7	-14.1	11.9	13.5	14.7	20.3	15.2	-4.6
C11-1	54.0	7.0	3.3	11.2	-10.4	11.6	3.8	-3.4
C10-2	80.6	40.9	15.9	12.4	23.3	32.7	65.6	-4.5
C4-3	-20.7	-27.1	1.1	14.7	-24.7	19.9	-20.5	-1.6
C5-3	55.3	49.7	13.7	15.0	15.4	18.6	65.9	-2.3
C9-1	34.8	-33.9	16.0	31.9	-15.9	39.8	35.1	-3.8
C9-3	30.7	-19.1	7.4	7.8	3.1	19.7	15.0	-2.4
C3-1	16.1	-23.5	16.5	16.0	7.1	31.0	30.5	-3.3
C4-2	36.9	28.3	4.9	-1.1	14.5	9.2	22.3	-1.6
C6-2	66.3	38.7	15.2	8.1	22.9	25.1	66.5	-2.5
C10-1	-6.5	-7.4	-10.1	-9.3	-11.8	-38.2	-49.0	-0.7
<b>&lt;106 AD</b>								
C11-2	-28.6	-1.9	6.8	2.9	15.7	-0.1	-2.2	0.3
C4-1	0.6	28.8	6.2	8.4	6.8	7.5	16.1	0.0
C5-1	4.7	-28.7	7.1	16.7	-9.3	18.0	3.0	-0.7
C8-1	43.0	-2.5	16.3	16.4	18.3	23.2	43.2	-0.5
C6-3	-53.2	-8.3	-10.9	-11.6	-8.4	-24.0	-43.9	0.3
C10-3	-73.2	-23.0	-8.0	-9.7	-6.0	-21.1	-48.2	2.1
C1-2	34.2	48.3	17.7	5.8	31.1	22.9	44.4	-1.8
C2-2	-1.1	24.9	19.3	13.6	28.8	33.5	32.2	-1.9
C2-3	-43.8	0.7	-14.0	-18.3	-8.9	-28.8	-28.8	0.2
C5-2	-11.9	23.5	-1.0	-10.2	14.9	-9.7	-2.2	1.8
C7-2	-2.6	37.7	9.2	8.5	11.5	22.4	44.0	-0.1
C7-3	-36.7	-17.5	-14.3	-14.6	-9.9	-41.4	-61.2	2.5
C6-1	-78.7	-5.9	-24.1	-31.1	-16.5	-44.3	-67.3	3.3
C8-2	-58.4	-48.4	-11.1	-6.8	-18.6	-21.7	-20.1	3.6
<b>106- 112 AD</b>								
C1-3	-27.0	-18.3	-27.9	-41.7	-17.6	-43.3	-73.2	3.7
C1-1	-92.9	-10.7	-22.5	-25.0	-14.6	-49.0	-41.7	2.9
C7-1	-74.7	-3.8	-24.0	-37.8	-10.7	-51.7	-67.4	2.9
C9-2	-65.1	-64.6	-11.1	-4.8	-23.7	-17.7	-42.2	6.1
C2-1	-61.9	-13.6	-34.9	-37.9	-36.5	-55.0	-79.2	6.4
C3-2	-60.2	-68.4	-11.7	-2.6	-25.2	-21.2	-21.2	8.4
<b>&gt;112 AD</b>								
Mean	-7.6	-3.7	-0.6	-1.2	-0.8	-2.1	-3.9	0.0
Min	-92.9	-68.4	-34.9	-41.7	-36.5	-55.0	-79.2	-5.3
Max	80.6	49.7	19.3	31.9	31.1	39.8	66.5	8.4

†GYG, grain yield; TBN, tassel branch number; L1, total tassel length; L2, central spike length; L3, branch zone length; BL, branch length; TW, tassel weight; AD, anthesis date; ASI, anthesis silking interval

## **4.6 Relationship between grain yield and tassel traits**

The relationship between grain yield and tassel traits is presented in Tables 4.10- 4.11. It was observed that the smaller the tassel branch angle the higher the score for tassel branches. A positive correlation is desirable between tassel branch angle and grain yield implying that the higher the grain yield the smaller the angle between the central spike length and tassel branches.

### **4.6.1 Relationship between grain yield and tassel traits under the optimum environment**

Under the optimum environment grain yield was strongly and positively correlated to tassel size (0.63\*\*), total tassel length (0.7\*\*\*), central spike length (0.57\*\*\*), branch length, and tassel weight (0.48\*\*) and anthesis date but negatively correlated with tassel branch angle (Table 4.10). There was no association found between grain yield and anthesis silking interval. Anthesis date showed a strong positive correlation with tassel angle, but strong negative correlations with tassel size, total tassel length, central spike length, branch zone length, branch length and tassel weight. There was no association found between anthesis date and number of tassel branches.

### **4.6.2 Relationship between grain yield and tassel traits across drought environments**

Across drought environments grain yield was positively correlated with total tassel length (0.82\*\*\*), central spike length (0.73\*\*\*), branch zone length (0.45\*\*), branch length (0.81\*\*\*), tassel weight (0.72\*\*\*), ear diameter (0.84\*\*\*), and ear weight (0.86\*\*\*), but negatively correlated to anthesis date (-0.075\*\*\*), and ASI (-0.33\*) (Table 4.11). There was no association found between grain yield and number of tassel branches. Tassel branch number was positively correlated with branch zone length (0.78\*\*\*), and tassel weight (0.61\*\*\*). Total tassel length was positively correlated with central spike length (0.85\*\*\*), branch zone length (0.63\*\*\*), branch length (0.93\*\*\*), and tassel weight (0.86\*\*\*), ear diameter (0.81\*\*\*), and ear weight (0.75\*\*\*). Anthesis date was negatively correlated with central spike length (-0.62\*\*\*), branch zone length (-0.34\*), branch length (-0.74\*\*\*), and tassel weight (-0.56\*\*\*). There was no association found between ASI and all tassel traits except central spike length (-0.31\*).

**Table 4.10 Pearson correlation coefficients between grain yield, tassel traits and maturity traits under optimum conditions**

	GY†	TBA	TS	TBN	L1	L2	L3	BL	TW	AD
GY										
TBA	-0.65***									
TS	0.63***	-0.78***								
TBN	-0.09	-0.28	0.44**							
L1	0.7***	-0.5***	0.58***	-0.03						
L2	0.57***	-0.33*	0.25	-0.54***	0.77***					
L3	0.23	-0.28	0.51***	0.72***	0.41**	-0.27				
BL	0.73***	-0.57***	0.56***	-0.18	0.91***	0.85***	0.17			
TW	0.48**	-0.58***	0.76***	0.59***	0.66***	0.26	0.62***	0.58***		
AD	-0.77***	0.69***	-0.74***	-0.05	-0.71***	-0.52***	-0.33*	-0.74***	-0.66***	
ASI	0.13	-0.25	0.44**	0.41**	0.18	-0.16	0.52***	0.05	0.41**	-0.51***
	ns: not significant		*** (P<0.001)		** (P<0.01)		*(P<0.05)			

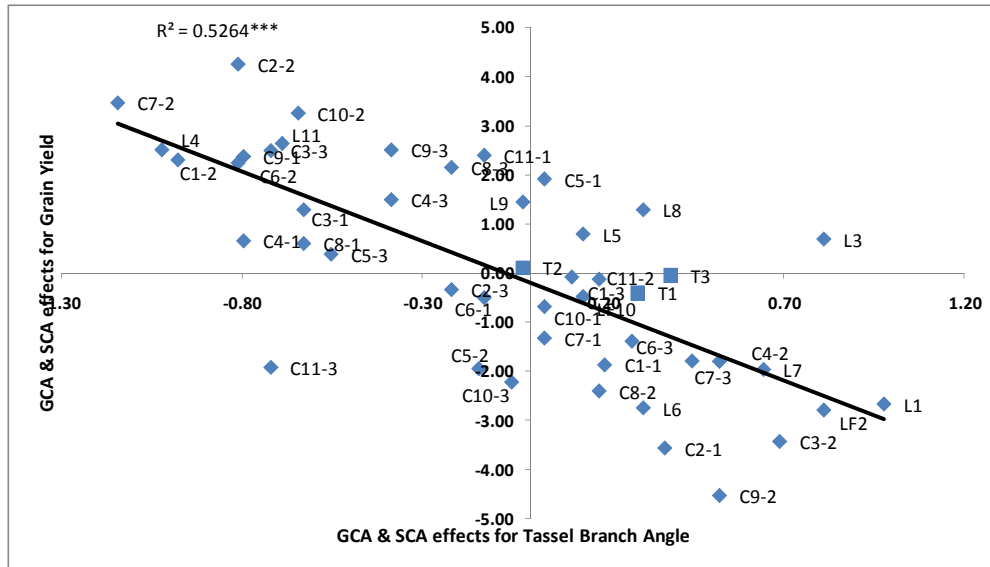
†GYG, grain yield; TBA, tassel branch angle; TS tassel size; TBN, tassel branch number; L1, total tassel length; L2, central spike length; L3, branch zone length, BL, branch length; TW, tassel weight; AD, anthesis date; ASI anthesis silking interval

**Table 4.11 Pearson correlation coefficients between grain yield, tassel traits and agronomic traits under drought environments**

	GY†	TBN	L1	L2	L3	BL	TW	AD	ASI
GY									
TBN	0.28								
L1	0.82***	0.28							
L2	0.73***	-0.16	0.85***						
L3	0.45**	0.78***	0.63***	0.14					
BL	0.81***	0.15	0.93***	0.89***	0.42**				
TW	0.72***	0.61***	0.86***	0.58***	0.77***	0.78***			
AD	-0.75***	-0.23	-0.67***	-0.62***	-0.34*	-0.74***	-0.56***		
ASI	-0.33*	0.27	-0.09	-0.31*	0.29	-0.23	0.08	0.26	
	ns: not significant		*** (P<0.001)		** (P<0.01)		*(P<0.05)		

†GYG, grain yield; TBN, tassel branch number; L1, total tassel length; L2, central spike length; L3, branch zone length, BL, branch length; TW, tassel weight; AD, anthesis date; ASI, anthesis silking interval; ED, ear diameter; EW, ear weight;

Graphical presentations of the relationship between grain yield and tassel traits are shown in Figure 4.1 – 16. Lines with positive GCA effects for grain yield such as L4, L11 and L9 except L8, L5 and L3 showed negative GCA effects for tassel branch angle whereas those with negative GCA effects for grain yield such as L1, L2 and L7 showed positive GCA effects (Figure 4.1). Similarly, hybrids with positive SCA effects for grain yield such as C2-2, C7-2, and C10-2 except C5-1 showed negative SCA effects for tassel branch angle whereas those with negative



**Figure 4.1 Grain yield relative to Tassel Branch Angle under the optimum environment.**  
 \*\*\* ( $P < 0.001$ )

SCA effects for grain yield in entries C9-2, C2-1 and C3-2 except C5-2, C10-3 and C11-3 showed positive SCA effects.

Lines with positive GCA effects for grain yield in entries L11, L4 and L8 except L3 and L5 showed positive GCA effects for tassel size, while those with negative GCA effects such as L1, L2 and L7 except L10 showed negative GCA effects for tassel size (Figure 4.2). Similarly, hybrids with positive SCA effects for grain yield such as C7-2, C10-2 and C6-2 except C5-1 showed positive SCA effects for tassel size whereas those with negative SCA effects for grain yield such as C3-2, C9-2 except C4-2, C5-2 and C2-1 showed negative SCA effects for tassel size.

All lines with positive GCA effects for grain yield under the optimum environment except L5 showed negative GCA effects for tassel branch number. Contrarily all lines with negative GCA effects for grain yield showed positive GCA effects for tassel branch number (Figure 4.3). All hybrids with positive SCA effects for grain yield under the optimum environment showed positive SCA effects for tassel branch number while those with negative SCA effects in entries C9-2, C3-2, C8-2 and C10-3 except C11-3, C1-1, C7-3 showed negative SCA effects. Some of



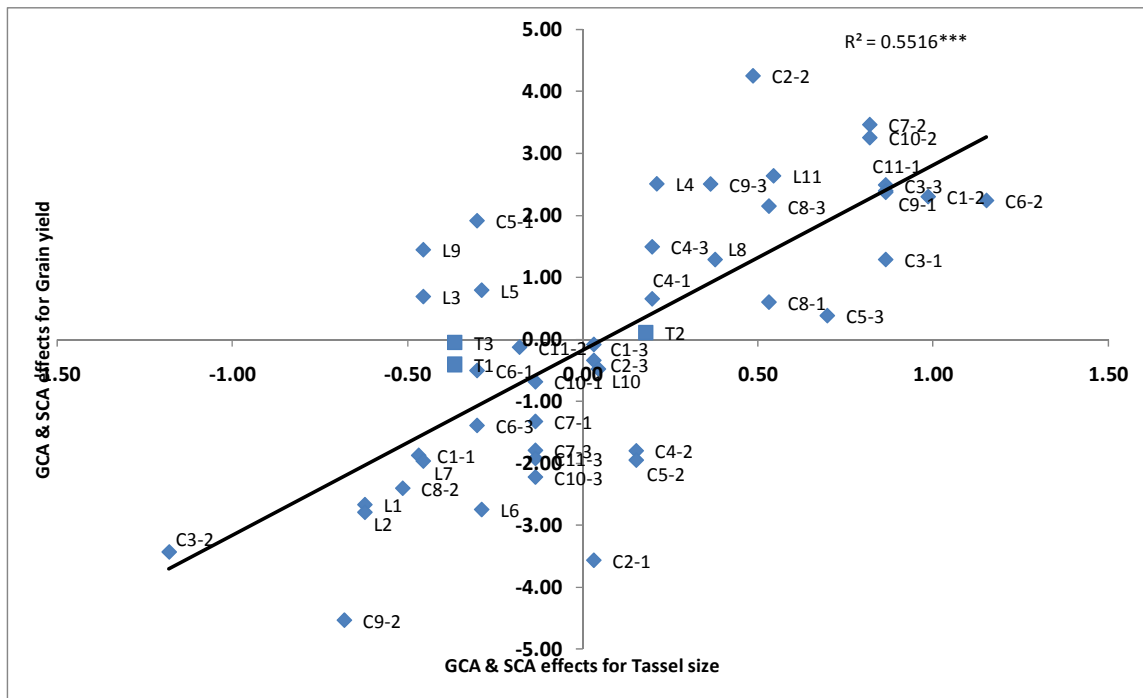


Figure 4.2 Grain yield relative to tassel size under the optimum environment.  
\*\*\* (P<0.001)

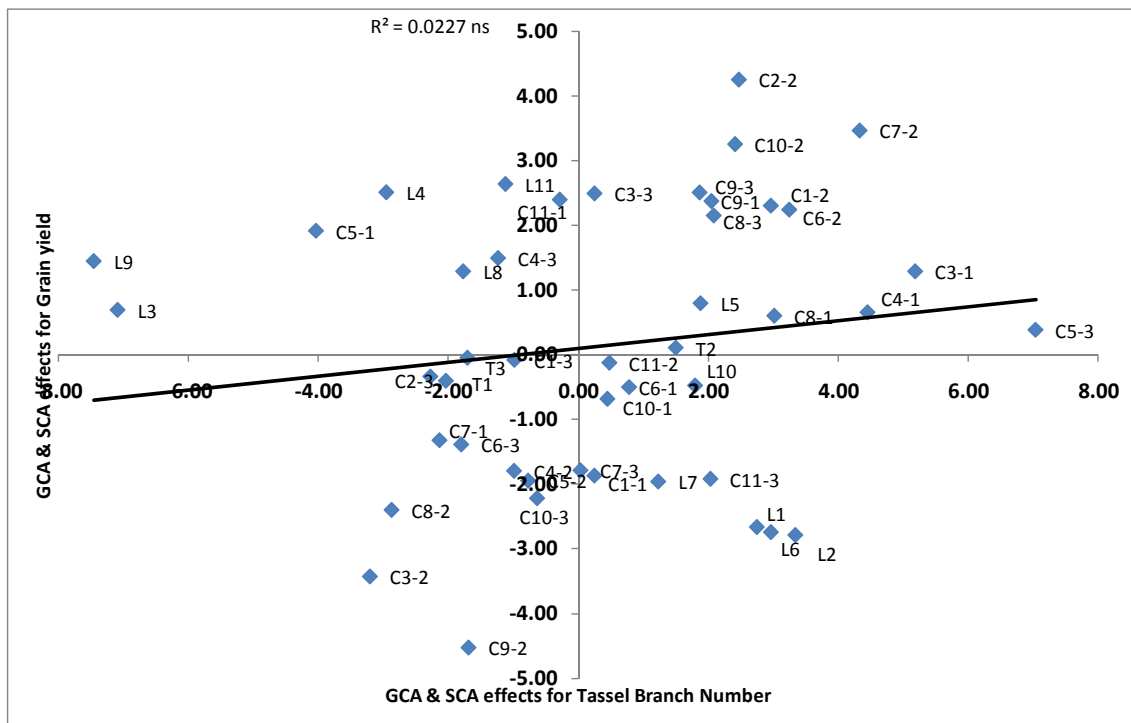


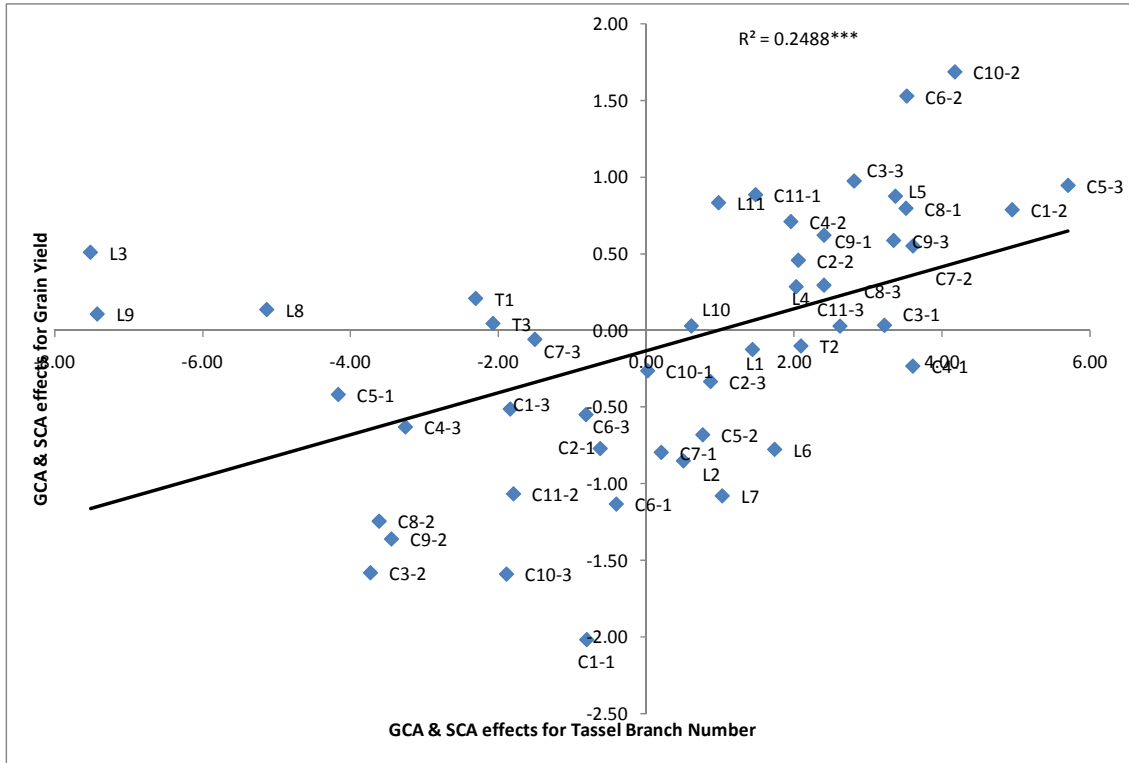
Figure 4.3 Grain yield relative to tassel branch number under the optimum environment.  
ns not significant

the lines with positive GCA effects for grain yield under drought environments such as L3, L9 and L8 showed negative GCA effects for tassel branch number whilst entries L11, L10 and L4 showed positive GCA effects (Figure 4.4).

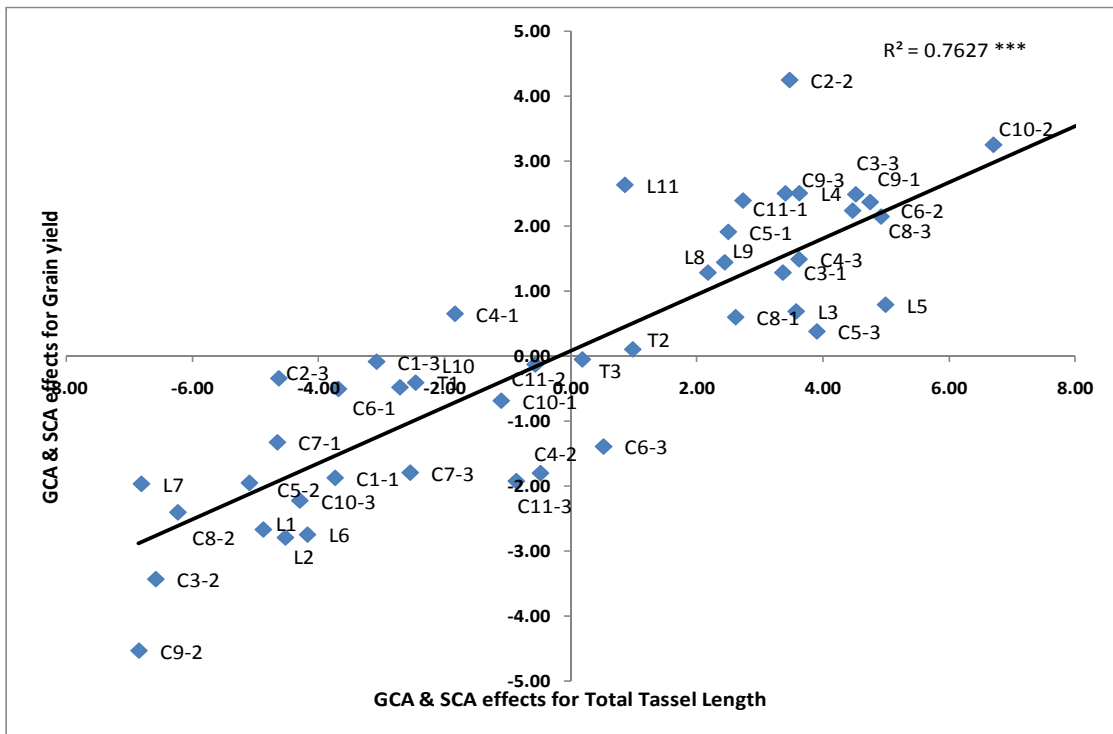
All lines with negative GCA effects for grain yield showed negative GCA effects for tassel branch number. All hybrids with positive SCA effects for grain yield showed positive SCA effects for tassel branch number. Some of the hybrids with negative SCA effects for grain yield such as C1-1, C3-2, C9-2 and C8-2 showed negative SCA effects for tassel branch number whereas entries C7-1, C5-2 and C2-3 showed positive SCA effects. Under the optimum environment, lines and testers with positive GCA effects for grain yield such as L11, L8, L3, L5 and T2 respectively showed positive GCA effects for total tassel length whereas those with negative GCA effects for grain yield such as L7, L1, L6, L2 and T1 respectively showed negative GCA effects for total tassel length (Figure 4.5). Similarly, hybrids with positive SCA effects for total tassel length such as C10-2, C7-2 and C1-2 showed positive SCA effects for total tassel length whereas those with negative SCA effects for grain yield such as C9-2, C3-2 and C10-3 except C6-3 showed negative SCA effects for total tassel length.

Under the drought environment, lines with positive GCA effects for total tassel length such as L11 and L5 except L10 showed positive GCA effects for total tassel length while those with negative GCA effects for grain yield such as L2, L6 and L7 showed negative GCA effects for total tassel length (Figure 4.6). Hybrids with positive SCA effects for grain yield such as C10-2 and C6-2 except C4-2 showed positive SCA effects for total tassel length while those with negative SCA effects for grain yield such as C3-2, C9-2 and C8-2 showed negative SCA effects for total tassel length.

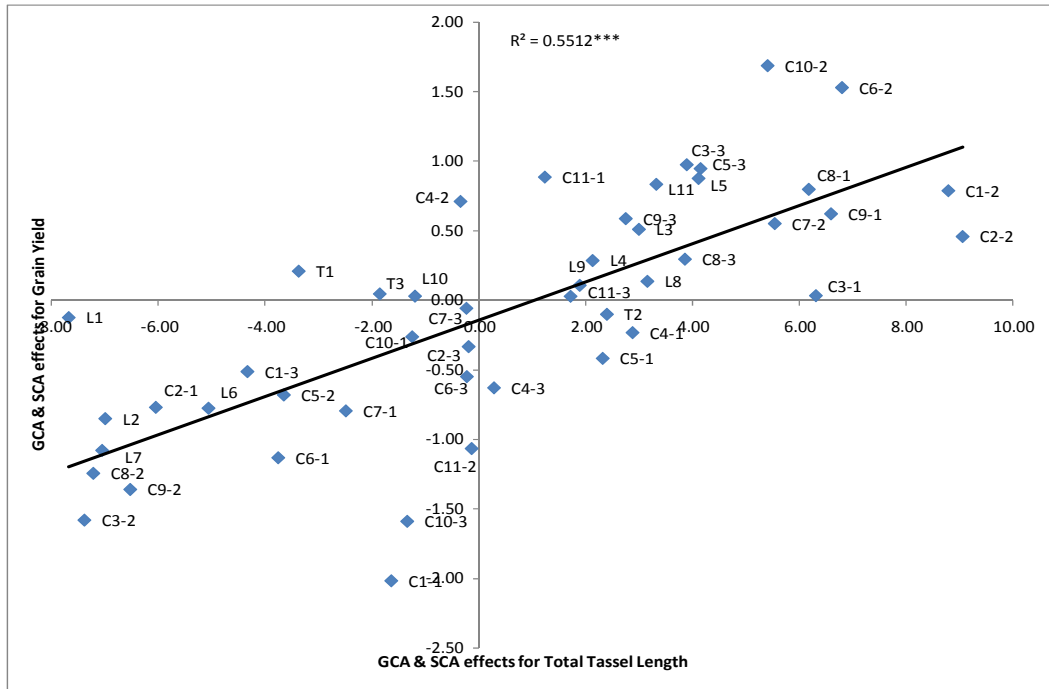
Lines with positive GCA effects for grain yield under the optimum environment such as L9, L3 and L8 showed positive GCA effects for central spike length while those with negative GCA effects such as L7, L6, L1 and L2 showed negative GCA effects for central spike length (Figure 4.7). Hybrids with positive SCA effects for grain yield under the optimum environment such as C7-2, C9-1 and C5-1, except C3-1, C4-1 and C5-3 showed positive SCA effects for central spike length while those with negative SCA effects for grain yield such as C9-2, C3-2 and C8-2 except C10-1 and C6-3 showed negative SCA effects for central spike length.



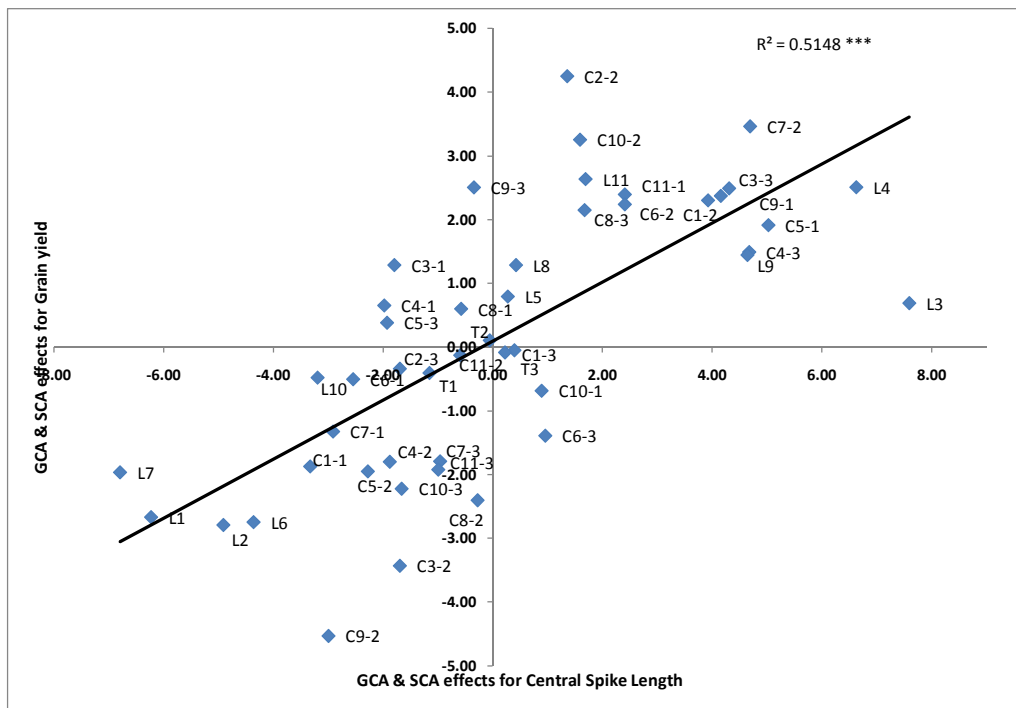
**Figure 4.4 Grain yield relative to tassel branch number across drought environments.**  
 \*\*\* (P<0.001)



**Figure 4.5 Grain yield relative to total tassel length (L1) under the optimum environment.**  
 \*\*\* (P<0.001)



**Figure 4.6 Grain yield relative to total tassel length (L1) across drought environments.**  
 \*\*\* ( $P < 0.001$ )



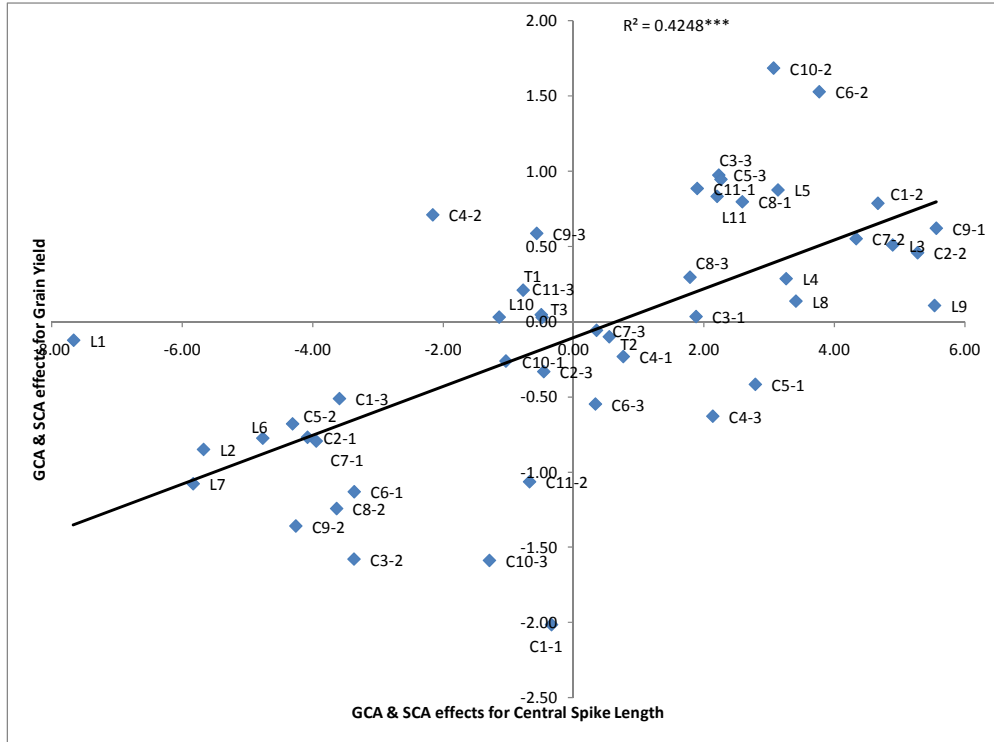
**Figure 4.7 Grain yield relative to central spike length (L2) under the optimum environment.**  
 \*\*\* ( $P < 0.001$ )

Lines with positive GCA effects for grain yield under drought environments such as L5, L11, L4, L8 and L9 except L10 showed positive GCA effects for central spike length while those with negative GCA effects for grain yield such as L2, L6 and L7 showed negative GCA effects for central spike length (Figure 4.8). Hybrids with positive SCA effects for grain yield under drought environments such as C10-2, C6-2, C1-2 except C4-2 and C11-3 had positive SCA effects for central spike length while those that had negative SCA effects for grain yield such as C1-1, C3-2 and C10-3 except C4-1, C5-1, C4-3 and C6-3 had negative SCA effects for central spike length.

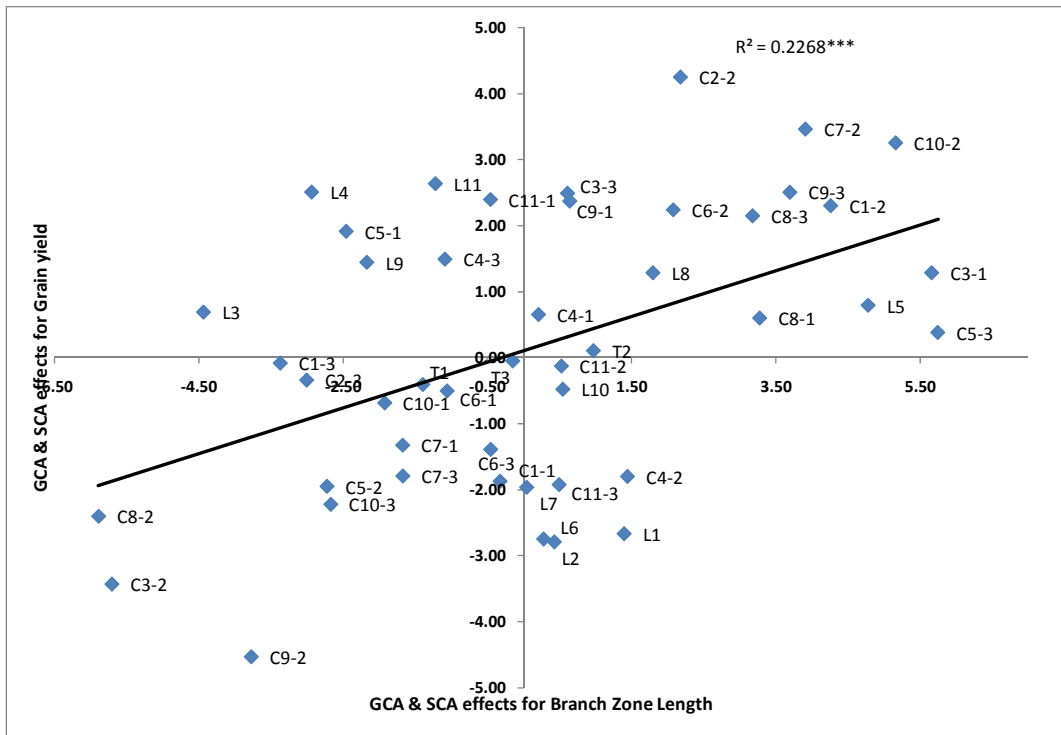
Lines with positive GCA effects for grain yield under the optimum environment such as L3, L4 and L9 except L8 and L5 showed negative GCA effects for branch zone length while those with negative GCA effects for grain yield such as L1, L6, L7 and L2 showed positive GCA effects for branch zone length (Figure 4.9). Hybrids with positive SCA effects for grain yield under the optimum environment such as C7-2, C10-2 and C1-2 except C11-1 and C5-1 had positive SCA effects for branch zone length while those with negative SCA effects for grain yield such as C8-2, C3-2 and C9-2 had negative SCA effects for branch zone length.

Lines with positive GCA effects for grain yield under drought environments such as L11, L5, L8 and L10 except L3, L4 and L9 showed positive GCA effects for branch zone length while those that showed negative GCA effects for grain yield such as L2, L6 and L7 showed negative GCA effects for branch zone length (Figure 4.10). Hybrids with positive SCA effects for grain yield under drought environments such as C10-2, C6-2, C8-1, C1-2 and C2-2 had positive SCA effects for branch zone length while those with negative SCA effects such as C8-2, C3-2 and C1-1, except C2-3, C5-2, C7-1 and C11-2 had negative SCA effects for branch zone length.

Lines with positive GCA effects for grain yield under the optimum environment such as L8, L3, L4 and L11 had positive GCA effects for branch length while those that had negative GCA effects for grain yield such as L1, L2, L6 and L7 showed negative GCA effects for branch length (Figure 4.11). Similarly, hybrids with positive SCA effects for grain yield such as C10-2, C7-2, C1-2 and C6-2 showed positive SCA effects for branch length while those that showed negative SCA effects for grain yield such as C9-2, C3-2 and C8-2 showed negative SCA effects for branch length.



**Figure 4.8 Grain yield relative to central spike length (L2) across drought environments.**  
 \*\*\* ( $P < 0.001$ )



**Figure 4.9 Grain yield relative to branch zone length (L3) under the optimum environment.**  
 \* ( $P < 0.05$ )

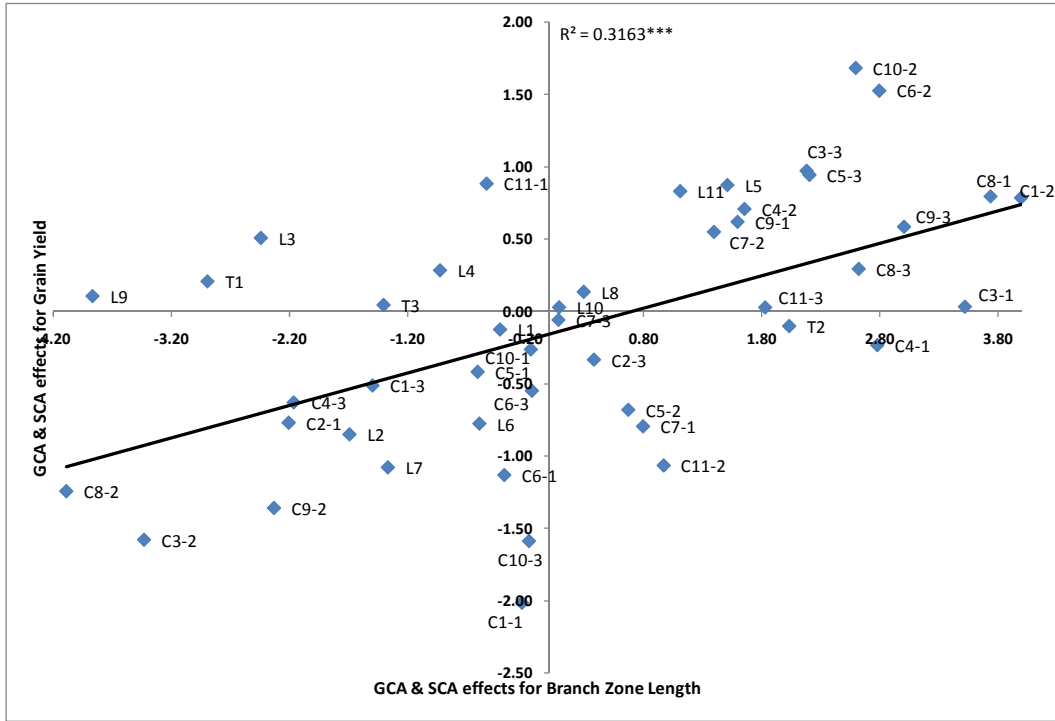


Figure 4.10 Grain yield relative to branch zone length (L3) across drought environments.  
\* (P<0.05)

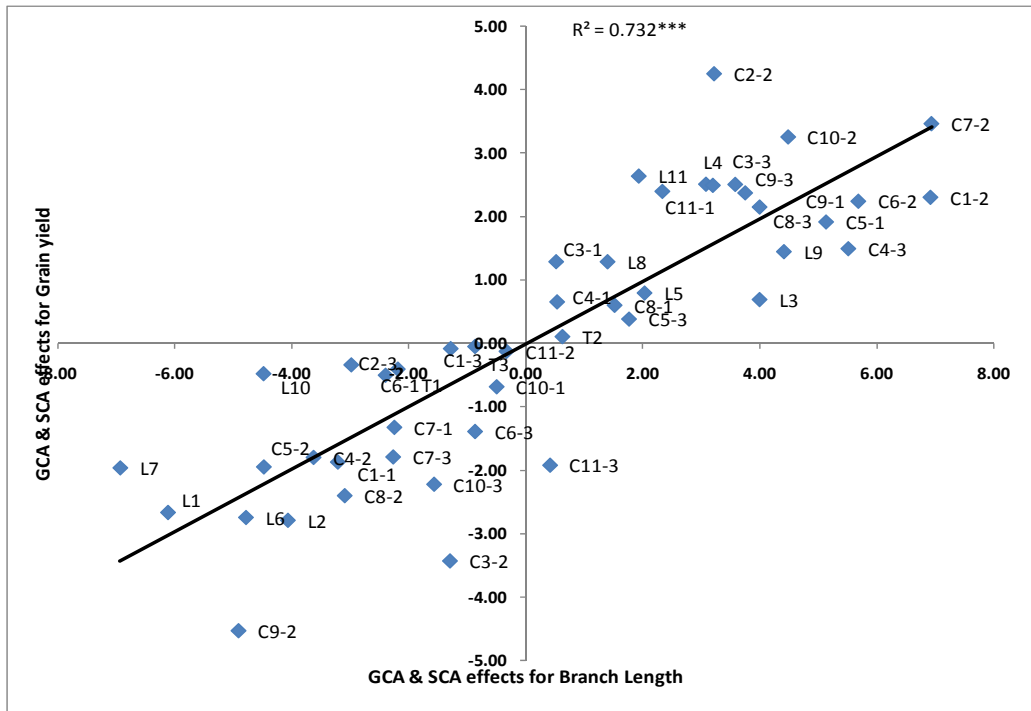


Figure 4.11 Grain yield relative to branch length under the optimum environment.  
\*\*\* (P<0.001)

Lines with positive GCA effects for grain yield under drought environment such as L4, L9, L8 except L10 had positive GCA effects for branch length while those that had negative GCA effects for grain yield such as L7, L6, L2 and L1 had negative GCA effects for branch length (Figure 4.12). All hybrids with positive SCA effects for grain yield had positive SCA effects for branch length while those that had negative SCA effects for grain yield except C4-1, C4-3 and C5-1 had negative SCA effects for branch length.

Lines with positive GCA effects for grain yield under the optimum environment such as L11, L4, L5 and L8 except L9 and L3 had positive GCA effects for tassel weight while those that had negative GCA effects for grain yield such as L2, L6, L7 and L1 had negative GCA effects for tassel weight (Figure 4.13). All hybrids with positive SCA effects for grain yield under the optimum environment had positive SCA effects for tassel weight while those that had negative SCA effects for grain yield except C10-1, C6-3 and C11-3 had negative SCA effects for tassel weight.

Lines with positive GCA effects for grain yield under drought environments such as L11, L3, L4 and L8 except L9 and L10 had positive GCA effects for tassel weight while those that had negative GCA effects for grain yield such as L2, L7, L6 and L1 had negative GCA effects for tassel weight (Figure 4.14). All hybrids with positive SCA effects for grain yield under drought environments had positive SCA effects for tassel weight while those that had negative SCA effects for grain yield except C2-3, C4-1 and C1-1 had negative SCA effects for tassel weight.

Lines with positive GCA effects for grain yield under the optimum environment such as L5, L3, and L8 except L9 had negative GCA effects for anthesis date while those that had negative GCA effects for grain yield such as L6, L1 and L2 had positive GCA effects for anthesis date (Figure 4.15). All hybrids with positive SCA effects for grain yield under the optimum environment had negative SCA effects for anthesis date while those with negative SCA effects for grain yield except C2-3, C7-1 and C11-3 had negative SCA effects for anthesis date.

Lines with positive GCA effects for grain yield under drought environments such as L11, L4, L8 and L10 except L9 and L3 had positive GCA effects for anthesis date while those that had negative GCA effects for grain yield such as L2, L6 and L7 had negative GCA effects for anthesis date (Figure 4.16). All hybrids with positive SCA effects for grain yield such as C10-2,



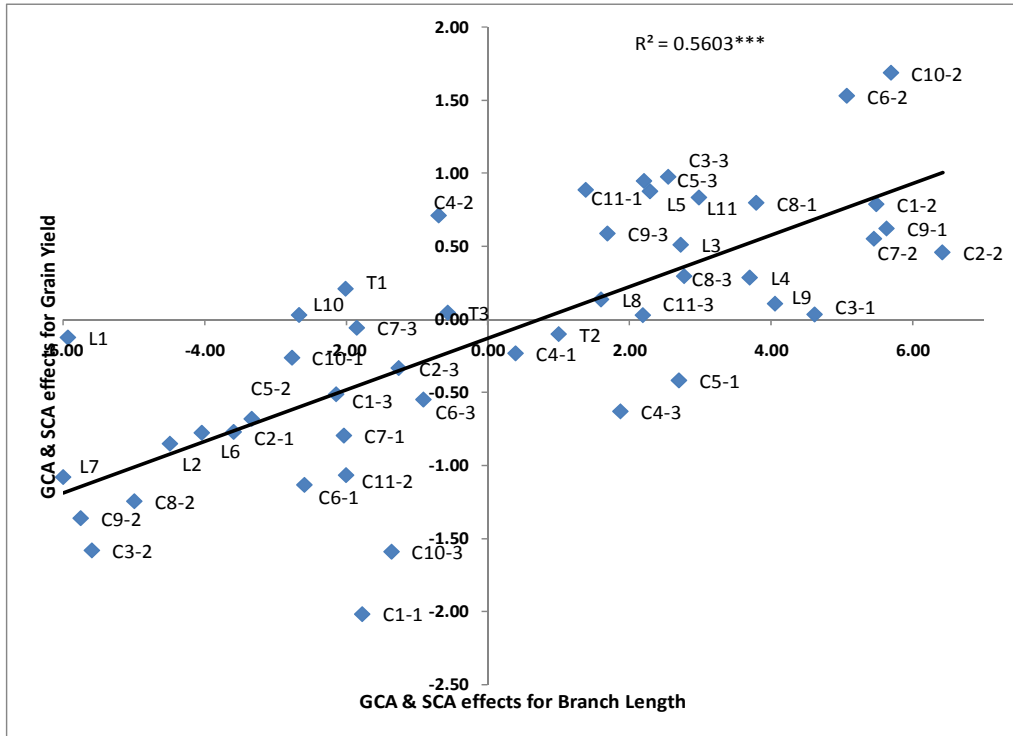


Figure 4.12 Grain yield relative to branch length across drought environments.  
 \*\*\* (P<0.001)

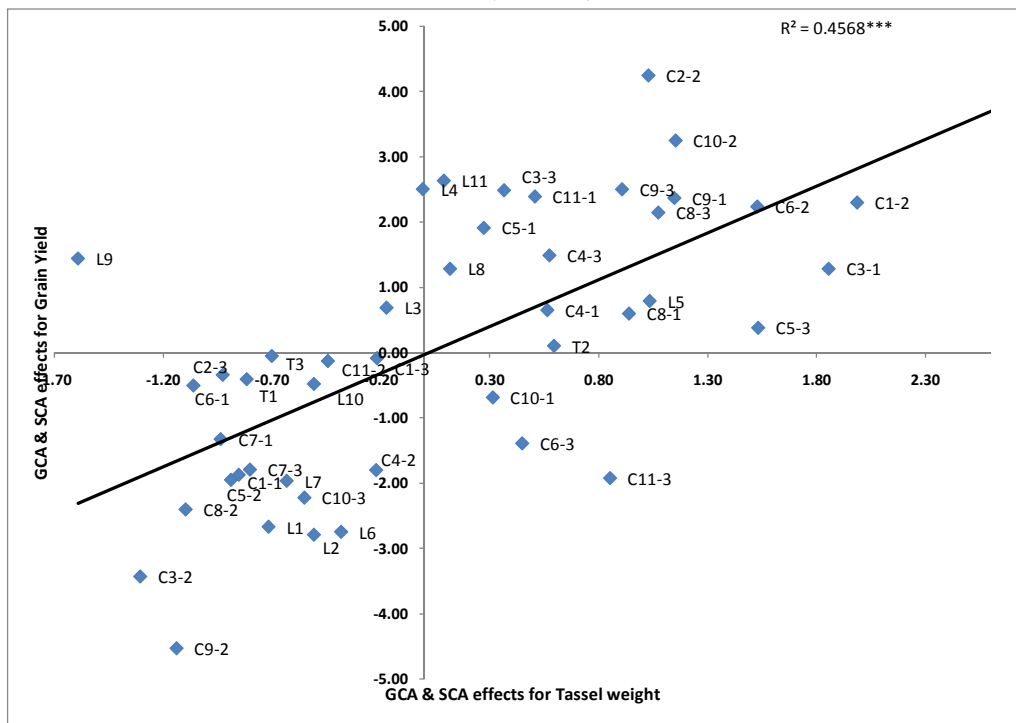


Figure 4.13 Grain yield relative to tassel weight under the optimum environment.  
 \*\*\* (P<0.001)

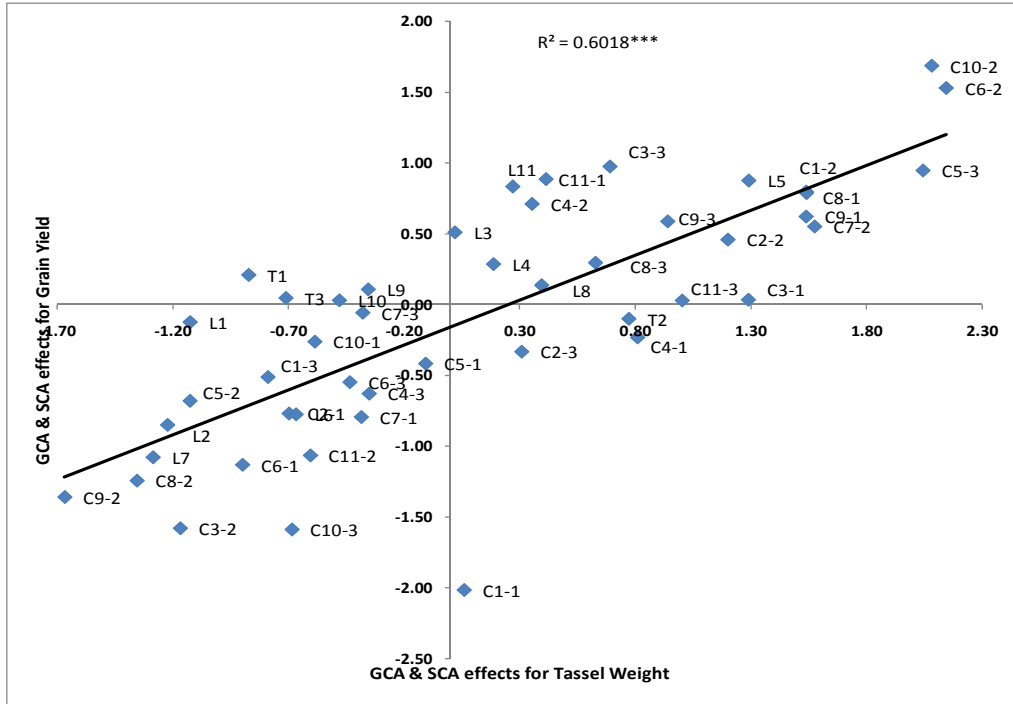


Figure 4.14 Grain yield relative to tassel weight across drought environments.  
 \*\*\* ( $P < 0.001$ )

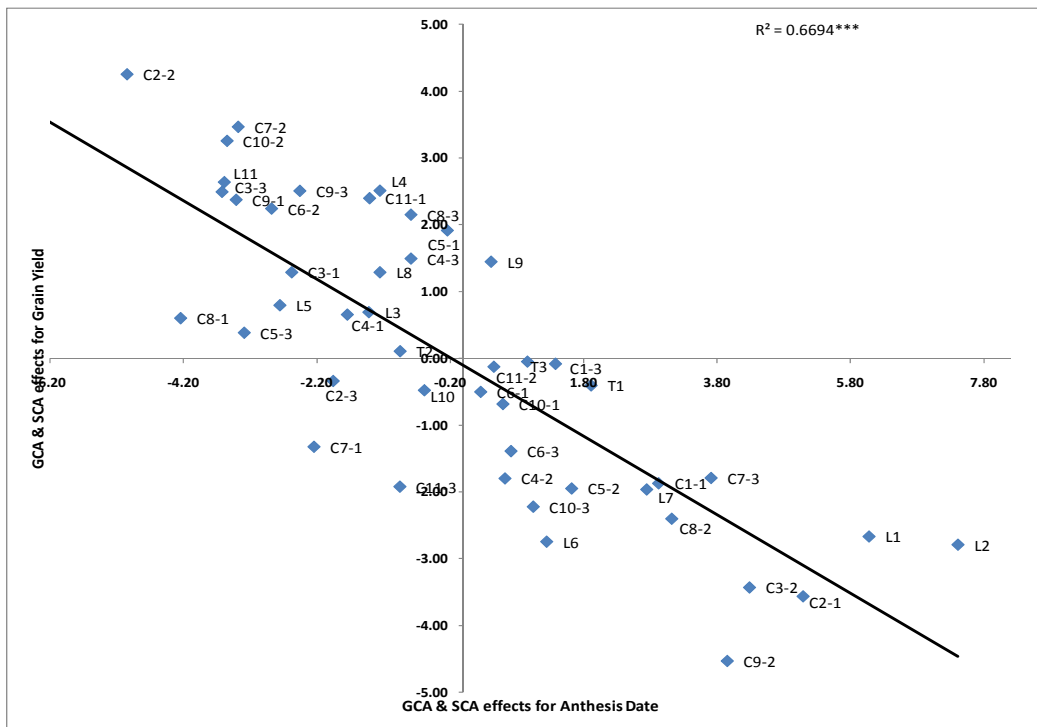
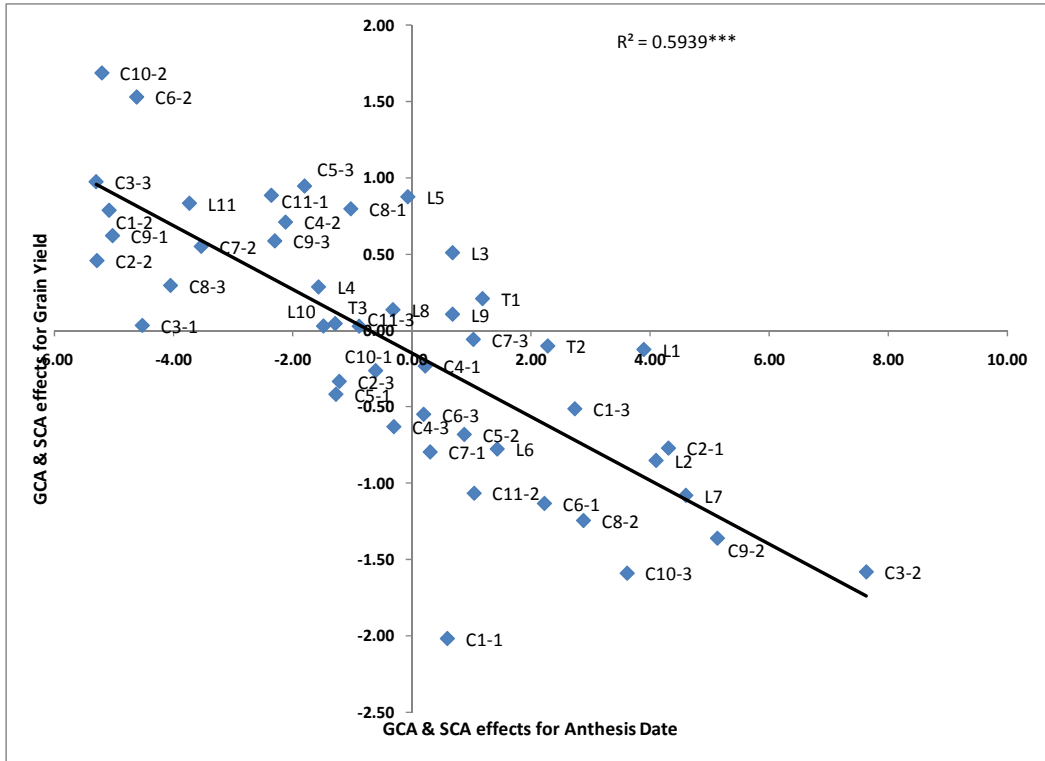


Figure 4.15 Grain yield relative to anthesis date under the optimum environment  
 \*\*\* ( $P < 0.001$ )



**Figure 4.16 Grain yield relative to anthesis date across drought environments  
\*\*\*( $P < 0.001$ )**

C6-2, C3-3 and C1-2 showed negative SCA effects for anthesis date while those that had negative SCA effects for grain yield except C2-3, C5-1 and C10-1 had negative SCA effects for anthesis date.

## Chapter 5

### DISCUSSION

#### 5.1 Performance of lines, testers and their hybrids across environments

Hybrids and lines were significantly different across environments and under the optimum environment but non-significant across drought environments. Grain yields were higher under optimum environment compared to drought environments (Appendix A- D). Similarly line x tester interaction were also significant for grain yield across environments and under the optimum environment but non-significant across drought environments. Makumbi (2005) found significant differences among hybrids, lines and line x tester interactions for grain yield under the optimum environment and across environments but failed to detect differences under drought environments. These results show that genetic variability existed under the optimum environment but was reduced under the drought environments.

In addition to the reduction in genetic variability under drought stress, there was an increase in the coefficient of variation when moving from the optimum to drought environments (Appendix A- D). Experiments conducted under low yielding environments have a higher frequency of producing statistically non-significant differences ( $P > 0.05$ ) for grain yield or having a large coefficient of error variation than those conducted under high yielding conditions and are often discarded (Bänziger and Cooper, 2001). This is because the error variance of grain yield usually does not decrease as much as the genetic variance when moving from high to low yielding conditions (Bänziger *et al*, 1997).

There were no significant differences found amongst testers under all management environments suggesting that testers showed similar performance for grain yield under the different management environments. Site x entry, site x line and site x line x tester interactions were significant for grain yield across environments but non-significant under drought environments. Similar differential responses under different environments in maize have been reported by several researchers (Argillier, 2000; Betran *et al* 2003; Derera, 2005; Narro *et al*, 2003; Kim and Ajala, 1996; Mungoma and Pollak, 1998; Ndhlela, 2007). This suggests that different lines, hybrids and line x tester combinations responded differently to changing environments implying that hybrids, lines and line x tester combinations did not perform consistently for grain yield

across environments. This presents problems for plant breeders in varietal selection as the set of selected hybrids changes in each environment (Cossa *et al*, 1995). These results indicate that in addition to evaluating cultivars under managed drought stress conditions there is also need to evaluate under random stress conditions to estimate the genotype x environment component. These results confirm previous studies that reported significant interaction of GCA and SCA with the environment (Betran *et al*, 2003; Derera, 2005). The non-significance across drought environments suggests that the same information could have been generated from a single drought site thereby reducing costs of testing under two drought environments.

Significantly different mean values were found for all traits except tassel branch number across locations and branch zone length and branch length under drought environments. Mean values were higher under the optimum environment than across drought environments for all tassel traits except tassel branch number and branch length (Appendix A- D). The reduction in mean values when moving from the optimum environment to drought environments can be attributed to negative effects of stress on crop development. It is generally thought that large sizes and high growth rates involve a large demand for environmental resources such that when these are not available a large reduction in growth would occur (Blum, 1997).

Hybrids, lines, testers and line x tester interactions were significantly different for all tassel traits except central spike length under all management environments. This shows that sufficient genetic variability existed among hybrids, lines, testers and line x tester combinations for all tassel traits except central spike length for selection to be conducted. Site x entry and site x line x tester interactions were non-significant for all tassel traits under all management levels. Site x line interactions were only significant for tassel branch number across all environments and across drought environments whereas site x tester interactions were only significant for branch length under drought environments. The non-significance of the interactions shows the absence of genotype x environment interactions in the expression of tassel traits. This suggests that evaluation and selection for tassel traits can be done at one reliable site to reduce costs especially where resources are limiting.

Significantly different mean values were observed for anthesis date across all environments but not across drought environments. Means for anthesis dates for drought environments were longer than those for the optimum environment (Appendix A- D). Makumbi (2005), Vasal *et al*, (1992)

Betran *et al* (2003), Mungoma and Pollack (1988) and Ndhlela (2007) reported significant differences for anthesis dates under different environments. The longer period to anthesis date experienced under drought stress can be attributed to the negative effects of drought stress. Hybrids, lines, testers and line x tester interactions were significantly different for anthesis date across all management levels. This shows the presence of genetic variability amongst hybrids, lines and testers for days to anthesis.

Contrary to the general trend, early maturing lines, hybrids and testers were generally higher yielding compared to their late maturing counterparts across all management levels. This may be due to the priority given to early maturity relative to late maturity in the CIMMYT breeding programme. Early maturing materials are targeted for stress prone environments characterized by a high incidence of terminal droughts. Early maturing materials are preferred as they are able to complete their life cycle before the onset of a terminal drought, a phenomenon known as drought escape (Bänziger *et al*, 2000).

Mean values for anthesis silking interval were significantly different across environments but neither significant under the optimum environment nor across the drought environments. The non-significance of the anthesis silking interval under the drought environments shows that the materials were subjected to similar drought stress levels at the two drought environments. Hybrids, lines and testers were significantly different for anthesis silking interval across environments. This shows that hybrids, lines and testers showed different anthesis silking intervals under the different management levels an indication of differential response to different management levels.

SCA variances were higher than GCA variances for all traits except anthesis silking interval under both optimum and drought environments. This implies that non-additive gene action played a larger role in determining the performance of all traits except anthesis silking interval. Similarly, Bhatnagar *et al* (2004) and Vincente *et al* (1998) reported the predominance of non-additive genetic effects relative to additive genetic effects for grain yield in diallel crosses. In contrast Vasal *et al* (1993), Beck *et al* (1991) and Soengas *et al* (2003) reported the preponderance of additive genetic effects relative to non-additive gene effects in controlling grain yield. The predominance of non-additive gene action implies that breeding gains can be made via inbreeding followed by crossbreeding, thus these traits can be improved by making

selections among recombinants obtained through segregating populations (Ceyhan *et al*, 2008). Selections can be done in later generations (Karademir *et al*, 2007). The best exploitation of this type of gene action would be in F<sub>1</sub> hybrids between different selected parents (Tyagi *et al*, 2005). The type of genetic effects for grain yield is very variable, depending on the type of parents and environments under consideration. The lack of significance of SCA effects for anthesis silking interval across all management levels showed the absence of non-additive gene action in controlling anthesis silking interval. Derera (2005) and Betran *et al* (2003) found that additive gene action was more important in controlling anthesis silking interval. When a trait is controlled by more of additive gene action, the best F<sub>1</sub> may be produced by crossing parents with the highest GCA (Teklewold and Becker, 2005). Contrary to findings of the current study, Schuetz and Mock (1978) reported the predominance of additive gene action relative to non-additive gene action in controlling tassel branch number.

Negative GCA variances were obtained for grain yield under both the optimum and drought environments whereas negative SCA variances were observed for anthesis silking interval under drought. Similar negative variances were also obtained by Akbar *et al* (2009). Negative GCA variances estimates obtained were not theoretically expected since variances are quadratic functions (that is, squares) though such estimates can not be ruled out due to sampling error (Singh and Chaudhary, 2004; Dabholkar, 1999).

Broad sense heritability estimates found in this study were similar or higher than what other researchers have found. Geraldi *et al* (1985) found heritabilities of 36.1 % and 45.8 % for tassel weight and tassel branch number whereas Mock and Schuetz (1974) found heritability estimates of 50% for tassel branch number. Mickelson *et al* (2002) observed heritabilities of 0.73 and 0.81 for tassel branch angle and tassel branch number respectively. Upadyayula *et al* (2006) reported heritability estimates ranging from as low as 39% for total tassel length to 83% for tassel weight. The high heritability estimates for tassel traits suggest that tassel traits are highly heritable and can be used effectively in breeding programs. Heritability estimates for grain yield were higher than for other traits except central spike length under the optimum environment. However, broad sense heritability estimates for grain yield declined from 0.85 under optimum conditions to a low 0.19 under drought environments. Given that heritability of tassel traits remained high as the

heritability of grain yield declined with changing environments, tassel traits are good candidates for use as secondary traits (Bolaños and Edmeades, 1996).

## **5.2 General and specific combining ability effects**

The estimates of GCA effects showed that among lines, L11 showed consistently significant positive GCA effects for grain yield under both optimum and drought environments, whereas lines, L2, L6 and L7 showed consistently significant negative GCA effects. This shows that L11, a CML444 derivative, is a good general combiner for grain yield under both optimum and drought environments whereas L2, L6 and L7, all CML 442 derivatives, are poor general combiners for grain yield.

L4, L8, L9 exhibited significant positive GCA effects for grain yield under the optimum environment while L5 exhibited significant positive GCA effects under the drought environment. This shows the adaptability of the former to well watered, well fertilised environments and the latter to drought prone environments. The GCA estimates also showed that lines derived from CML 395 had larger GCA effects than did lines derived from CML 442. This shows the relative superiority of CML 395 over CML 442 in terms of grain yield performance.

Hybrids C10-2 and C6-2 exhibited significant positive SCA effects for grain yield under both optimum and drought environments whereas hybrids C8-2, C10-3, C3-2, C9-2 and C1-1 showed significant negative SCA effects. This shows that the former hybrids showed good combining ability for grain yield under both environments whilst the latter showed poor combining ability. The good and poor combining ability for grain yield exhibited can be attributed to genetic diversity and relatedness respectively. SCA was positive for crosses involving parents with different genetic background, while it was negative for crosses involving parents with the same genetic background (Betran *et al*, 2003). L10 and L6 are CML442 derived therefore showed high positive heterosis when crossed to T2 (CML395) but negative heterosis when crossed to T1 (CML 442 derived) and T2 (CML 442). Similarly L8, L9 and L3, all CML 395 derived lines showed high heterosis with T1 and T3 but negative heterosis with T2. Some hybrids performed well across management levels indicating that it is possible to combine stress tolerance and yield performance under high input environments. Similar results have been reported by Betran *et al* (2003) with tropical and temperate maize hybrids.



Positive GCA and SCA effects for tassel branch angle implied approximately vertical tassels ( $<45^{\circ}$  from the central spike) while negative GCA and SCA implied approximately horizontal tassels ( $90^{\circ}$  from the central spike). Vertical tassel architecture reduces shading of the flag leaf and upper leaves allowing penetration of more light into the canopy consequently increasing yields (Lambert and Johnson, 1977). However, in the current study, lines with significant positive GCA effects for grain yield (L11 and L4) had significant negative GCA effects for tassel branch angle while those with significant negative GCA effects for grain yield (L7, L1 and L2) had significant positive GCA effects for tassel branch angle. Similarly, testers with negative though non-significant GCA effects for grain yield (T1 and T3) had significant positive GCA effects for tassel branch angle. This shows that lines and testers with good general combining ability for grain yield had approximately horizontal tassels whilst those with poor combining ability had approximately vertical tassels.

The study further revealed that with good combining ability for grain yield had approximately horizontal tassels while those with poor combining ability had approximately vertical tassels. Further analysis revealed that hybrids C2-2, C7-2, C9-1, C1-2, C3-3 and C6-2 were constituted by parents with unrelated backgrounds whereas C3-2 was constituted by parents with a related background. SCA effects were positive for crosses involving parents with the same genetic background, while negative for crosses involving parents with different genetic background (Betran *et al*, 2003). Positive heterosis for grain yield in entries C2-2, C7-2, C9-1, C1-2, C3-3 and C6-2, implied that the hybrids had yield levels above their mid-parents while negative heterosis in entry C3-2 implied that they had lower than the mid-parents. Positive heterosis for tassel branch angle implied that the hybrids had smaller tassel angles (vertical) compared to their mid-parents while negative heterosis meant larger tassel angles (horizontal) compared to their mid-parents.

Crosses between L7, L1 and L2 with significant positive GCA effects (vertical tassels) for tassel branch angle and related testers (T1 and T2) with significant positive GCA effects (vertical tassels) for tassel branch angle showed non-significant positive SCA effects (vertical tassels) for tassel branch angle while those with an unrelated tester (T2) with a non-significant negative GCA effect (horizontal tassel) for tassel branch angle showed significant negative SCA effects (horizontal tassels) for tassel branch angle. This shows that despite T2 having a non-significant

negative GCA effect for tassel branch angle, its hybrids with L7, L1 and L2 had significant negative SCA effects for tassel branch angle. This seems to suggest that genes for smaller tassel branch angles are recessive and are resident on different loci in different genetic backgrounds such that when related parents are crossed there is unmasking of the recessive alleles resulting in vertical tassels. Conversely when unrelated parents are crossed there is masking of the recessive alleles by their dominant counterparts in heterozygous form hence the expression of horizontal tassels. Analysis of crosses of unrelated parents such as C2-2, C10-2 and C7-2 showed no significant differences for grain yield implying that there were no yield gains from reducing the tassel branch angle.

Positive GCA and SCA effects for tassel size implied large tassels while negative effects meant smaller tassels. Small tassels would show lower competition for nutrients with the developing ear as well as less shading of the upper leaves (Singh, 2003). In the current study, lines and testers with good general combining ability for grain yield except L9, L3 and L5 had larger tassels while those with poor combining ability for grain yield had smaller tassels. The study further revealed hybrids with good combining ability for grain yield except C5-1 had larger tassels whereas those with poor combining ability for grain yield except C4-2, C5-2 and C2-1 had smaller tassels. The combination of positive GCA effects for grain yield with negative GCA effects for tassel size shows that it is possible to breed for high yield coupled with tassel reduction.

Crosses between L3 and L9, both with small tassels and testers T1 and T3, with small tassels had significant positive SCA effects for tassel size (large tassels) but those with T2 with a non-significant positive GCA for tassel size had significant SCA effects for tassel size. Crosses between L7, L1 and L2, all with small tassels, and T1 and T3, both with small tassels, had non-significant SCA effects for tassel size but those with T2 had significant positive SCA effects for tassel size. SCA effects were negative for crosses involving parents with the same genetic background, while positive for crosses involving parents with different genetic background (Betran *et al*, 2003). C3-1, C3-3 and C9-1 showed positive heterosis for both grain yield and tassel size whereas C7-1, C7-3, C1-1, C1-3, C2-1 and C2-3 showed negative heterosis for both grain yield and tassel size. Negative heterosis for grain yield implied that hybrids had smaller tassels compared to their mid-parents. This shows that hybrids with related parents had small

tassels while those with unrelated parents had larger tassels. This seems to suggest that genes for smaller tassels are recessive and are resident on different loci in different genetic backgrounds such that when related parents are crossed there is unmasking of the recessive alleles resulting in smaller tassels. Conversely when unrelated parents are crossed there is masking of the recessive alleles by their dominant counterparts in heterozygous form hence the expression of larger tassels. Dominance of large tassel size was also reported by Schuetz and Mock (1978). They also found that to obtain a small-tasseled hybrid, the two parents of a cross must not only be small-tasseled but must possess the same set of alleles for tassel branch number. Analysis of hybrids with unrelated parents showed that C2-2 with a smaller tassel compared to C7-2, C10-2 C6-2 had a higher though non-significant SCA effect for grain yield. This shows that although no significant gains were realized from a smaller tassel, hybrids with relatively smaller tassels had higher though non-significant yields compared relative to their counterparts.

Tassel branch number was found to be negatively associated with grain yield implying that the fewer the number of tassel branches the higher the grain yield (Lambert and Johnson, 1977; Geraldi, 1985; Fischer et al, 1987). Positive GCA and SCA effects for tassel branch number implied more tassel branch numbers whereas negative meant fewer tassel branch numbers. The study revealed that under the optimum environment lines (L9 and L4) with significant positive GCA effects for grain yield had negative GCA effects for tassel branch number while those with significant negative GCA effects for grain yield (L1, L6 and L2) had positive GCA effects for tassel branch number. L9 also showed significant negative GCA effects for tassel branch number although it had a non-significant positive GCA effect for grain yield. Although L3 and L8 had non-significant positive GCA effects for grain yield they showed negative GCA effects for tassel branch number under both drought and optimum environments. T1 and T3 showed positive though non-significant GCA effects for grain yield and significant negative GCA effects for tassel branch number under the drought environments. This shows that lines and testers with good combining ability for grain yield had few tassel branches whereas those that had poor combining ability for grain yield had more tassel branches.

The study also revealed that hybrids with good combining ability for grain yield had more tassel branches whereas those with poor combining ability for grain yield had fewer tassel branches. Crosses of unrelated parents, C3-1, C3-3, C9-1, C9-3, C1-2 and C2-2 had positive though non-

significant SCA effects for tassel branch number under the optimum environment whereas those for related parents C3-2, C9-2, C1-3 and C2-3 had negative though non-significant SCA effects for tassel branch number. Similarly C8-1, C8-3, C3-3, C3-1, C9-1 and C9-3, constituted by unrelated parents, had positive SCA effects whereas C8-2, C3-2 and C9-2, constituted by unrelated parents had significant negative SCA effects for tassel branch number. This shows that crossing lines with few tassel branches will produce hybrids with few tassel branches if they are related but will produce hybrids with more tassel branches if they are not related. This seems to suggest that genes for few tassel branches are recessive and are resident on different loci in different genetic backgrounds such that when related parents are crossed there is unmasking of the recessive alleles resulting in few tassel branches. Conversely when unrelated parents are crossed there is masking of the recessive alleles by their dominant counterparts in heterozygous form hence the expression of more tassel branches. Dominance of more tassel branch number was also reported by Schuetz and Mock (1978). They also found that to obtain a hybrid with few tassel branches, the two parents of a cross must not only have few tassel branches but must possess the same set of alleles for tassel branch number. Analysis of groups of crosses or inbred combinations indicated that there were no significant yield gains among crosses of related and unrelated but significant differences were observed between these two groups.

A longer total tassel length or central spike length competes with the ear for assimilates especially under adverse conditions implying that the longer the tassel length the lower the yield. Longer branch length reduces yields by reducing the amount of light that penetrate into the canopy. The study showed that that under the optimum environment, L4 and L9 with positive GCA effects for grain yield showed significant positive GCA effects for total tassel length, central spike length and branch length whereas L7, L1, L6 and L2 showed negative GCA effects for grain yield, total tassel length, central spike length and branch length under both drought and optimum environments. Although L3 and L5 showed non-significant positive GCA effects for grain yield they also showed significant positive GCA effects for total tassel length and branch length. Conversely L10 showed negative GCA effects for total tassel length, central spike length and branch length. Under drought environments L11 and L5 showed positive GCA effects for grain yield, total tassel length and branch length whereas L6, L2 and L7 showed negative GCA effects. L2, L6 and L7 showed consistently significant GCA effects for grain yield, central spike length and branch length under both drought and optimum environments. Although T1 and T3

showed non-significant positive GCA effects for grain yield they showed significant negative GCA effects for total tassel length and branch length. This implies that lines and testers with good combining ability for grain yield had longer tassel lengths, central spike lengths and branch lengths while those with poor combining ability had shorter tassel lengths, central spike lengths and branch lengths. The study also revealed that under the optimum environment, C7-2, C1-2, C10-2, C3-3, C9-1, C6-2, C8-3 and C9-1 exhibited significant positive SCA effects for grain yield, total tassel length, central spike length and branch length, whereas C5-2 and C9-2 showed negative SCA effects. Under drought C10-2 and C6-2 showed significant positive SCA effects for both grain yield, total tassel length and branch length whereas C8-2, C9-2 and C3-2 showed negative SCA effects. This shows that hybrids with good combining ability for grain yield had longer total tassel lengths, central spike lengths and branch lengths while those with poor combining ability for grain yield had shorter total tassel lengths, central spike lengths and branch lengths.

Under the optimum environment, crosses of unrelated parents, C3-1, C3-3, C9-1, C9-3, C10-2, C6-2, C1-2, C2-2, C7-2 had longer total tassel lengths, central spike lengths and branch lengths while those of related parents, C3-2, C9-2, C6-1, C6-3, C1-1, C1-3, C2-1, C2-3, C7-1 and C7-3 had longer total tassel lengths, central spike lengths and branch lengths. Similarly under the drought environment, crosses of unrelated parents, C5-1, C5-3, C3-1, C3-3, C9-1, C9-3, C1-2 and C2-2 had positive SCA effects for total tassel length while those of related parents C10-1, C10-3, C6-1, C7-1, C7-3, C1-1, C1-3, C2-1 and C2-3 showed negative SCA effects for total tassel length. This shows that crossing lines with shorter total tassel lengths, central spike lengths and branch lengths will produce hybrids with shorter total tassel lengths, central spike lengths and branch lengths if they are related but will produce hybrids with longer total tassel lengths, central spike lengths and branch lengths if they are not related. This seems to suggest that genes for few tassel branches are recessive and are resident on different loci in different genetic backgrounds such that when related parents are crossed there is unmasking of the recessive alleles resulting in shorter total tassel lengths, central spike lengths and branch lengths. Conversely when unrelated parents are crossed there is masking of the recessive alleles by their dominant counterparts in heterozygous form hence the expression of longer total tassel lengths, central spike lengths and branch lengths. Analysis of groups of crosses or inbred combinations

indicated that there were no significant yield gains among crosses of related and unrelated but significant differences were observed between these two groups.

The study revealed that lines with good combining ability for grain yield had longer branch zone lengths while those with poor combining ability for grain yield had shorter branch zone lengths. The study also showed that hybrids with longer branch zone lengths were higher yielding than those with shorter branch zone lengths. Crosses of unrelated parents, C3-1, C3-3, C9-1, C9-3 under both the optimum environment and drought environments, had positive SCA effects for branch zone length whereas those of related parents, C3-2, C9-2, had negative SCA effects for branch zone length. The former hybrids except C9-1 had positive heterosis for grain yield and branch zone length whereas the latter had negative heterosis for both grain yield and branch zone length. This shows that crossing lines with shorter branch zone lengths will produce hybrids with shorter branch zone lengths if they are related but will produce hybrids with longer branch zone lengths if they are not related. This seems to suggest that genes for few tassel branches are recessive and are resident on different loci in different genetic backgrounds such that when related parents are crossed there is unmasking of the recessive alleles resulting in shorter branch zone lengths. Conversely when unrelated parents are crossed there is masking of the recessive alleles by their dominant counterparts in heterozygous form hence the expression of longer branch zone lengths. Analysis of groups of crosses or inbred combinations indicated that there were no significant yield gains among crosses of related and unrelated but significant differences were observed between these two groups.

The study revealed that lines and testers with good combining ability for grain yield were early maturing while those with poor combining ability were late maturing. This shows that hybrids C2-2, C1-2, C4-2, C5-2, C10-3, C1-1, C8-2, C3-2 and C9-2 with good combining ability for grain yield were early maturing while those with poor combining ability for grain yield were late maturing. This may be due to the priority given to early maturity relative to late maturity in the CIMMYT breeding programme. Early maturing materials are targeted for stress prone environments characterized by a high incidence of terminal droughts. Early maturing materials are preferred as they are able to complete their life cycle before the onset of a terminal drought, a phenomenon known as drought escape (Bänziger *et al*, 2000).

An inbred line that expresses negative SCA effects when crossed to a tester implies belongs to the same heterotic group while the reverse is true (Vasal *et al.*, 1992). Line L11 had significant and positive SCA effects with tester T1 and significant and negative SCA effects with tester T3 under optimum environment. This suggests that Line L11 exhibited high heterosis with tester T1 and no heterosis with tester T3. This may suggest that line L11 belongs to the same heterotic group with tester T3 and belongs to an opposite heterotic group with tester T1. Similarly line L8 which had positive GCA effects for grain yield under the optimum environment exhibited positive GCA effects with tester T3, non significant SCA effects with tester T1 and negative SCA effects with tester T2. This suggests that line L8 belongs to the same heterotic group as tester T2 and belongs to an opposite group with tester T3.

The departure of the current study from this phenomenon can be attributed to two factors, lack of response under low plant densities and heterosis or inbreeding. Meyer (1970) as cited in Schuetz and Mock (1978) found no grain yield differences at 44,000 plants ha<sup>-1</sup> but at 89,000 plants ha<sup>-1</sup>. At high population densities there is high competition for light and resources which may not be found at low plant densities such as the 53,000 plants ha<sup>-1</sup> used in the study. SCA effects were also negative for crosses involving parents with the same genetic background, while positive for crosses involving parents with different genetic background (Betran *et al.*, 2003). This shows that heterosis or inbreeding depression accounted for the differences in performance of the parental material.

### **5.3 Relationship between grain yield and tassel traits**

Under both optimum and drought environments grain yield was strongly positively correlated to tassel size, total tassel length, central spike length, branch length, and tassel weight (Table 4.1 – 4.12, Figure 4.1 – 4.8). This implies that the larger the tassel size, the longer the tassel length, the longer the central spike length and the heavier the tassel weight, the wider the tassel angle between the central spike and tassel branches the higher the grain yield under both optimum and drought environments. This is contrary to what other researchers have reported. Lambert and Johnson (1977), Geraldi *et al.*, (1985), Fischer *et al.* (1987) reported that tassel size, tassel weight and tassel branch number are negatively associated with grain yield. The departure can be ascribed to the fact that lines, testers and hybrids with high grain yields had approximately horizontal tassels, larger tassels, longer total tassel lengths, branch lengths, and heavier tassels.

There was a negative correlation between tassel branch angle and grain yield (Table 4.2). This implies that the lower the tassel branch score (approximately horizontal tassels- 90° from central spike) the higher the grain yield, implying that entries with larger tassel branch angle were higher yielding than those with smaller angles. The negative correlation between grain yield and tassel branch angle in the present study was mainly due to the type of scale used in the study. The scale was an inverse of the scale used by Berke and Rocheford, (1999), where a score of 1 referred to an angle less than 45° from the main tassel branch and 5 referred to approximately horizontal tassel branches i.e approximately 90° from the central spike. Duncan *et al* (1967) found that tassels intercept incident light with increasing plant densities and showed through a computer simulation model the reduction in photosynthesis due to shading of the upper leaves by the tassel. This can be attributed to the type of genotypes used in the study. Lines, testers and hybrids with high grain yields had approximately horizontal tassels whereas those with poor grain yields had approximately vertical tassels.

There was no association found between grain yield and tassel branch number. This implies that the number of tassel branches did not account for any variability observed in grain yield that is tassel branch number did not affect grain yield. Similar results were also found by Monneveux *et al* (2008) in a drought tolerant population, LPS, though they found negative correlations with other drought tolerant populations DTP- W and DTP- Y. Geraldi *et al* (1985) also found a high negative correlation between grain yield and tassel branch number. There was a negative correlation between tassel branch number and central spike length implying that the higher the tassel branch number the shorter the central spike length and *vice versa*. Similar results were obtained by Upadyayula *et al*, 2006b). Contrary, Upadyayula *et al* (2006) found a positive correlation between tassel branch number and central spike length. This indicates that the relationship between the number of tassel branches and the central spike length depends on the type of genetic material used in the study.

There was no association between tassel branch number and branch length under both optimum and drought environments. Contrary to this, Upadyayula *et al*, (2006) found a positive correlation between tassel branch number and branch length. The failure to get an association can be attributed to the type of genotypes used in the current study.



There was no association found between grain yield and anthesis silking interval under optimum environment although a low negative correlation was found under drought environments. This implies that the higher the grain yield the lower the anthesis silking interval. Other studies using different germplasm under stress conditions reported similar results (Bolaños and Edmeades, 1993; Lafitte and Edmeades, 1995; Bänziger and Lafitte, 1997; Bänziger et al, 2002; Betran et al, 2003). The protandrous behaviour in maize due to apical dominance over axillary structures gives developmental priority to the tassel relative to the ear especially under adverse conditions. This implies that under drought stress, there will be pollen production and distribution at the expense of ear and silk development. Large anthesis silking intervals associated with low grain yields are an indication of lack of synchrony between silk emergence and pollen shed which drastically reduces the rate of fertilization and kernel set (Westgate and Bassetti, 1990; Bolaños and Edmeades, 1996) consequently increasing barrenness and significant yield reductions (Bolaños and Edmeades, 1993; Beck *et al*, 1996).

Anthesis date showed a strong positive correlation with tassel angle, but strong negative correlations with tassel size, total tassel length, central spike length, branch zone length, branch length and tassel weight under optimum environment. This implies that early maturing lines, testers, or hybrids had approximately horizontal tassels, large tassels, longer total tassel lengths, central spike lengths, branch lengths and tassel weight. There was no association found between anthesis date and number of tassel branches under optimum environment.

Similar to (Bolaños and Edmeades, 1996) the heritability of tassel traits under drought remained high whereas the heritability of grain yield usually decreased. In addition the genetic correlation of tassel traits with grain yield generally increased (Bänziger and Lafitte, 1997). Given the fact that tassel traits are easy, cheap and fast to observe or measure non destructively, stable over the measurement period and their heritability remained high optimum and drought environments they are good candidates for use as secondary traits (Edmeades *et al*, 1997, Lafitte *et al*, 2003).

## Chapter 6

### CONCLUSIONS

The study detected genetic differences among hybrids and lines for grain yield across environments and the optimum environment but failed under drought environments. Failure to detect genetic differences for grain yield across drought environments implied that the same information could have been generated from a single site thereby reducing costs for testing under two drought environments. The study also detected genetic variability among hybrids, lines and testers for anthesis date and all tassel traits across all management levels.

Both additive and non-additive gene action were important in controlling grain yield, anthesis date and all tassel traits, although non-additive gene action was more important in controlling these traits. The best exploitation of this type of gene action would be in F<sub>1</sub> hybrids implying that breeding gains can be made through inbreeding then crossbreeding, with selection being made in later generations. However, the study revealed that anthesis silking interval was controlled by additive gene effects with non-additive gene effects being non-existent. The evidence from the study seems to suggest that genes for few vertical tassel architecture, smaller tassels, fewer tassel branches, shorter total tassel lengths, central spike lengths, branch zone lengths and branch lengths are recessive and are resident on different loci in different genetic backgrounds such that when related parents are crossed there is unmasking of the recessive alleles resulting in full expression of these traits. When unrelated parents are crossed there is masking of these traits through the heterozygous condition and hence expression of horizontal tassel architecture, longer total tassel lengths, central spike lengths, branch zone lengths and branch lengths.

The study identified the inbred L11 as a good combiner for grain yield under both optimum and drought environments. It further identified inbreds L4, L8 and L9 as good combiners for grain yield under the optimum environment reflecting their adaptability to well watered, well fertilised environments and L5 as a good combiner for drought environments reflecting its adaptability to drought prone environments. Inbreds L2, L6 and L7 were identified as poor combiners for grain yield under both optimum and drought environments. Lines derived from CML 395 showed superior performance for grain yield compared to those derived from CML 442. Hybrids C10-2

and C6-2 showed good combining ability for grain yield under both optimum and drought environments reflecting good adaptability to diverse environments whereas C8-2, C10-3, C3-2, C9-2 and C1-1 showed poor combining ability reflecting poor adaptability to both optimum and drought environments. Hybrids with good combining ability for grain yield were constituted by related parents showing heterosis and conversely those with poor combining ability for grain yield were constituted by related parents showing inbreeding depression. Superior performance of hybrids such as C10-2 and C6-2 across all management levels showed that it is possible to combine stress tolerance and superior performance under high input environments.

Inbreds and hybrids with good combining ability for grain yield had horizontal tassel architecture, larger tassel sizes, longer total tassel lengths, central spike lengths, branch zone lengths and branch lengths while their counterparts with poor combining ability for grain yield had vertical tassel architecture, shorter total tassel lengths, central spike lengths, branch zone lengths and branch lengths. In addition lines with good combining ability for grain yield were early maturing while their counterparts were late maturing. Lines with good combining ability for grain yield had lower tassel branch numbers compared to their counterparts with poor combining ability for grain yield.

The study found high broad sense heritability estimates for tassel traits. The estimates ranged from 63% (tassel weight) to 86% (central spike length) under the optimum environment and 37% (branch zone length) to 83% (branch length) under drought environments. This shows that tassel traits are highly heritable. Heritability estimates for grain declined from 0.85 under the optimum environment to 0.19 under drought environments. Instead, the coefficient of variation increased from 16.9% under the optimum environment to 82.2% under drought environments. There were no serious changes in heritability estimates for tassel traits save for branch length. Similarly there were no serious differences between coefficients of variation for tassel traits between optimum and drought environments.

The current study found that grain yield was positively correlated with all tassel traits except tassel branch angle. The negative correlation observed between grain yield and tassel branch angle in the present study showed can be attributed to the inversion of the scale used by other researchers. The positive correlation between grain yield and tassel traits shows that an increase in tassel size, total tassel length, central spike length, branch zone length, tassel weight resulted

in an increase in grain yield. The negative correlation between grain yield and tassel branch angle implied that the higher the angle between the tassel branches and the central spike length the higher the grain yield. The departure of the correlations between grain yield and tassel traits can be attributed to the type of germplasm used in the study. Lines, testers and hybrids with good combining ability for grain yield had poor combining ability effects for tassel traits while those with poor combining ability for grain yield had good combining ability for tassel traits. Hybrids constituted by related parents had poor combining ability for grain yield but good combining ability for tassel traits while those constituted by unrelated parents had good combining ability for grain yield but poor combining ability for tassel traits. Analysis of groups of crosses or inbred combinations indicated that there were no significant yield gains among crosses of related and unrelated but significant differences were observed between these two groups.

Line x tester analysis is a powerful tool that can be used to predict the performance of large numbers of new lines simultaneously generating genetic information required to make informed decisions in plant breeding.

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**Appendix A Grain yield t ha<sup>-1</sup> and tassel traits under the optimum environment**

	GYG†		TBA	TS	TBN	L1	L2	L3	BL	TW
	Rank	t ha <sup>-1</sup>	1-5	1-5	#	cm	cm	cm	cm	g
5x3	15	8.67	3.5	3.0	19	47.9	23.2	24.8	20.1	6.25
10x2	7	10.42	3.0	4.0	18	43.8	22.8	21.1	17.8	5.63
3x3	6	10.67	4.0	3.0	3	47.1	36.7	10.4	23.5	3.88
11x2	9	10.16	3.0	3.5	13	40.1	25.5	14.7	19.4	4.63
8x1	14	9.02	3.5	3.5	11	41.2	23.1	18.1	17.9	4.63
11x3	17	8.21	2.5	3.0	11	39.0	25.5	13.5	18.6	4.63
11x1	1	12.17	3.0	4.0	9	40.0	27.4	11.3	19.2	4.17
6x2	19	7.14	3.0	4.0	20	40.1	22.4	17.7	18.7	6.13
3x1	12	9.11	4.0	3.0	8	43.3	29.1	14.2	19.5	5.25
5x2	21	6.49	3.5	3.0	15	39.7	22.4	17.4	15.3	5.13
4x2	16	8.36	3.0	3.5	10	43.0	29.1	13.9	17.2	4.75
7x2	11	9.15	3.0	3.5	19	41.5	22.3	19.3	17.8	7.00
1x2	18	7.28	3.5	3.5	19	43.1	22.1	21.0	18.6	6.25
4x1	8	10.30	2.0	3.0	11	38.2	27.9	10.3	18.6	4.13
4x3	2	11.49	2.5	3.0	6	46.3	36.1	10.2	24.9	4.25
5x1	10	9.84	4.0	2.0	8	43.9	28.6	15.3	22.1	4.88
8x3	5	10.93	4.0	3.5	11	46.1	26.9	19.2	21.7	4.88
9x1	4	10.95	3.0	3.0	5	43.6	32.1	11.5	23.1	3.13
9x3	3	11.44	3.5	2.5	5	44.9	29.1	15.8	24.3	3.00
8x2	20	6.53	4.0	3.0	9	35.8	24.5	11.3	16.1	4.00
<80 AD		9.41	3.3	3.2	11.4	42.4	26.8	15.5	19.7	4.83
2x2	13	9.11	3.5	3.0	19	38.8	20.8	18.0	16.9	5.50
10x3	24	4.79	4.0	2.5	11	32.0	20.0	12.1	10.2	2.63
3x2	23	4.91	5.0	1.5	3	36.8	30.3	5.2	20.5	3.50
10x1	22	5.97	4.0	2.5	12	32.6	21.0	11.6	10.0	3.38
7x1	29	3.85	4.5	2.0	9	24.9	13.6	11.4	5.8	2.00
6x3	31	3.36	4.5	2.0	11	35.4	21.4	14.1	10.6	3.75
6x1	28	3.89	4.0	2.0	14	28.5	16.4	12.2	7.8	2.13
9x2	26	4.56	4.0	2.0	4	35.4	26.0	9.4	17.3	2.25
2x3	27	4.36	4.5	2.0	11	29.9	18.2	11.7	9.2	2.25
7x3	30	3.74	5.0	2.0	12	29.7	17.1	12.6	7.1	2.25
80- 87 AD		4.85	4.3	2.2	10.7	32.4	20.5	11.8	11.5	2.96
1x3	25	4.74	5.0	2.0	12	31.1	18.8	12.3	8.9	2.75
1x1	32	2.60	5.0	1.5	13	27.8	13.7	14.1	5.6	2.00
2x1	33	0.78	5.0	2.0	.	.	.	.	.	.
> 87 AD		2.71	5.0	1.8	12.5	29.4	16.3	13.2	7.2	2.38
Mean		7.54	3.5	3.0	12	38.8	24.4	14.4	17.1	4.38
MSe		1.49	0.23	0.23	7.12	8.33	4.65	7.3	5.80	0.89
lsd (0.05)		4.99	1.96	1.96	10.90	11.79	8.81	11.03	9.84	3.85
CV		16.19	13.62	16.23	22.36	7.43	8.83	18.80	14.07	21.53

†GYG, grain yield; TBA, tassel branch angle; TS, tassel size; TBN, tassel branch number; L1, total tassel length; L2, central spike length; L3, branch zone length, BL, branch length; TW, tassel weight; AD, anthesis date;

## Appendix B Grain yield (t ha<sup>-1</sup>) and tassel traits across drought environments

Name	Rank	GY t ha <sup>-1</sup>	BN #	L1 cm	L2 cm	L3 cm	BL cm	TW g	AD d	ASI d
C3-3	4	3.61	5	42.4	29.1	13.0	20.4	3.3	101	0.3
C11-3	7	2.99	14	40.5	23.7	16.2	20.3	3.8	101	-0.5
C8-3	14	2.56	7	42.5	27.2	16.1	19.5	3.6	101	1.3
C11-1	1	4.01	12	38.5	25.8	12.3	18.1	3.1	102	-1.5
C10-2	3	3.70	19	43.9	25.0	19.3	19.7	5.6	102	2.3
C4-3	18	1.78	9	37.9	27.4	10.1	20.7	2.4	104	0.0
C5-3	2	3.95	19	43.7	27.4	16.9	19.6	5.9	104	1.0
C9-1	6	3.02	5	42.4	32.8	9.5	23.4	3.6	104	0.3
C9-3	10	2.82	6	40.1	27.0	12.4	20.9	3.1	104	1.8
C3-1	9	2.83	6	43.3	28.5	12.8	21.0	3.7	104	-1.0
C4-2	8	2.98	18	41.5	24.2	17.4	19.7	4.6	105	-2.3
C6-2	12	2.73	19	41.5	22.1	18.9	17.7	5.5	106	2.7
C10-1	17	2.06	10	31.5	19.6	11.7	8.3	1.3	106	2.7
		3.00	11.54	40.74	26.13	14.34	19.17	3.79	103.19	0.53
C11-2	19	1.75	13	42.9	24.6	18.7	17.7	3.7	106	-0.5
C4-1	15	2.34	15	39.0	25.8	13.6	17.8	3.4	107	-0.8
C5-1	11	2.75	9	40.4	27.7	12.6	18.7	3.6	107	-0.8
C8-1	5	3.22	8	43.3	27.7	15.8	19.1	4.3	107	-1.5
C6-3	27	0.80	11	30.2	17.6	12.5	10.2	1.4	107	2.3
C10-3	30	0.57	9	32.9	19.6	13.1	11.1	1.4	108	4.8
C1-2	13	2.64	21	40.8	20.1	20.2	16.3	4.4	108	4.3
C2-2	20	1.59	17	41.8	22.7	19.1	18.6	4.0	108	2.5
C2-3	24	0.94	11	28.3	15.9	11.9	9.4	1.6	108	2.3
C5-2	16	2.18	18	40.2	21.9	18.8	15.7	4.2	110	3.3
C7-2	22	1.45	19	38.2	21.6	16.7	16.2	4.3	110	5.7
C7-3	23	0.99	10	28.2	16.5	11.9	7.3	0.9	111	2.3
C6-1	32	0.38	11	25.1	13.6	10.8	7.1	0.8	112	1.0
C8-2	26	0.87	5	35.7	22.8	12.9	13.3	3.1	112	5.0
		1.61	12.72	36.20	21.27	14.89	14.15	2.93	108.41	2.13
C1-3	21	1.49	10	23.5	10.8	11.3	7.1	0.6	112	1.0
C1-1	33	0.15	10	24.6	13.7	11.1	6.0	1.3	112	0.7
C7-1	31	0.42	11	24.4	12.0	11.2	5.7	0.7	113	2.0
C9-2	28	0.73	3	35.1	24.3	10.5	15.0	2.0	115	2.0
C2-1	29	0.67	10	20.9	12.0	7.8	5.6	0.5	116	0.7
C3-2	25	0.91	3	35.3	24.6	10.8	13.8	2.9	117	2.0
		0.73	7.86	27.30	16.22	10.43	8.85	1.33	114.22	1.39
Mean		2.08	12	37.3	22.5	14.6	15.7	3.3	106.6	1.5
MSe		2.93	11.48	19.82	15.49	13.64	5.82	0.82	15.05	5.45
l.s.d		2.90	5.74	7.54	6.67	6.26	4.09	1.53	6.57	3.95
CV		82.2	27.9	11.9	17.5	25.3	15.4	27.9	3.6	152.9

†GYG, grain yield; TBN, tassel branch number; L1, total tassel length; L2, central spike length; L3, branch zone length; BL, branch length; TW, tassel weight; AD, anthesis date;

### Appendix C Grain yield and tassel traits for lines and testers under the optimum environment

<b>Line</b>	<b>GYG†</b> t ha <sup>-1</sup>	<b>TA</b> 1-5	<b>TS</b> 1-5	<b>BN</b> #	<b>L1</b> cm	<b>L2</b> cm	<b>L3</b> cm	<b>BL</b> cm	<b>TW</b> g	<b>AD</b> d
11	10.18	2.8	3.5	11	39.7	26.1	13.2	19.1	4.47	76
5	8.33	3.7	2.7	14	43.8	24.7	19.2	19.2	5.42	76
3	8.23	4.3	2.5	5	42.4	32.0	9.9	21.1	4.21	78
4	10.05	2.5	3.2	9	42.5	31.0	11.4	20.2	4.38	78
8	8.83	3.8	3.3	10	41.0	24.8	16.2	18.5	4.50	78
10	7.06	3.7	3.0	14	36.1	21.2	14.9	12.6	3.88	79
9	8.98	3.5	2.5	4	41.3	29.1	12.2	21.5	2.79	80
6	4.79	3.8	2.7	15	34.7	20.1	14.7	12.3	4.00	80
	8.31	3.5	2.9	10	40.2	26.1	14.0	18.1	4.20	78
7	5.58	4.2	2.5	13	32.0	17.6	14.4	10.2	3.75	82
1	4.87	4.5	2.3	15	34.0	18.2	15.8	11.0	3.67	85
2	4.75	4.3	2.3	15	34.3	19.5	14.8	13.1	3.88	87
	5.07	4.3	2.4	14	33.4	18.4	15.0	11.4	3.76	85
<b>Tester</b>										
2	7.64	3.5	3.1	13	39.8	24.4	15.3	17.7	4.98	78
3	7.49	3.9	2.6	10	39.0	24.8	14.2	16.3	3.68	80
1	7.13	3.8	2.6	10	36.4	23.3	13.0	14.9	3.57	81
Mean	7.54	3.5	3.0	12	38.8	24.4	14.4	17.1	4.38	79
MSE	1.49	0.23	0.23	7.12	8.33	4.65	7.3	5.80	0.89	10
lsd	4.14	1.63	1.63	9.05	9.79	7.31	9.16	8.17	3.20	10.81
CV	16.19	13.62	16.23	22.36	7.43	8.83	18.80	14.07	21.53	4.03

†GYG, grain yield; TBN, tassel branch number; L1, total tassel length; L2, central spike length; L3, branch zone length; BL, branch length; TW, tassel weight; AD, anthesis date;

### Appendix D Grain yield (t ha<sup>-1</sup>) and tassel traits for lines and testers across drought environments

Line	Rank	GY t ha <sup>-1</sup>	BN #	L1 cm	L2 cm	L3 cm	BL cm	TW g	AD d	ASI d
11	2	2.91	13	40.6	24.7	15.7	18.7	3.5	103	-0.8
4	4	2.37	14	39.4	25.8	13.7	19.4	3.4	105	-1.0
10	7	2.11	13	36.1	21.4	14.7	13.0	2.8	105	3.3
8	5	2.22	7	40.5	25.9	14.9	17.3	3.6	106	0.9
		2.40	12	39.2	24.4	14.8	17.1	3.34	105	0.6
5	1	2.96	16	41.4	25.6	16.1	18.0	4.5	107	1.2
3	3	2.59	5	40.3	27.4	12.2	18.4	3.3	107	0.1
9	6	2.19	5	39.2	28.0	10.8	19.8	2.9	107	1.3
6	9	1.31	14	32.3	17.7	14.0	11.7	2.6	108	2.0
1	8	1.96	14	29.6	14.8	14.2	9.8	2.1	111	2.3
2	10	1.23	13	30.3	16.8	12.9	11.2	2.0	111	1.9
7	11	1.00	13	30.3	16.7	13.3	9.7	2.0	111	3.3
		1.89	11	34.8	21.0	13.4	14.1	2.8	108.8	1.7
Tester										
3		2.13	10	35.5	22.0	13.2	15.1	2.5	105	1.5
1		2.29	10	33.9	21.7	11.7	13.7	2.4	108	0.0
2		1.98	14	39.7	23.1	16.6	16.7	4.0	109	2.2
Mean		2.08	12	37.3	22.5	14.6	15.7	3.3	107	1.5
MSe		2.93	11.48	19.82	15.49	13.64	5.82	0.82	15.05	5.45
l.s.d		2.90	5.74	7.54	6.67	6.26	4.09	1.53	6.57	3.95
CV		82.2	27.9	11.9	17.5	25.3	15.4	27.9	3.6	152.9

†GYG, grain yield; TBN, tassel branch number; L1, total tassel length; L2, central spike length; L3, branch zone length; BL, branch length; TW, tassel weight; AD, anthesis date;