GENETIC VARIABILITY AND INHERITANCE OF DROUGHT AND PLANT DENSITY ADAPTIVE TRAITS IN MAIZE

BY

GEZAHEGN BOGALE GEBRE

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University of the Free State
Faculty of Natural and Agricultural Sciences
Department of Plant Sciences
Plant Breeding
Bloemfontein, South Africa

Major Promoter: Prof. J.B.J. van Rensburg (Ph.D.)

Co-Promoter : Prof. C.S. van Deventer (Ph.D.)

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Dedication

To my parents in memory of my mother, Alaynesh Mekonnen
and my father Bogale Gebre

To my brother Tesfaye Bogale

“The greatest service, which can be rendered to one country, is to add a useful plant to its culture”

T.F. Jefferson, USA President (1801 -09)

Declaration

I hereby declare that this dissertation, prepared for the degree Philosophiae Doctor, which was submitted by me to the University of the Free State, is my own original work and has not previously in its entirety or in part been submitted to any other university. All sources of materials and financial assistance used for the dissertation have been duly acknowledged. I concede that the University of the Free State has the copyright of this dissertation.

Signed on 15th May 2005 at the Free State University, Bloemfontein, South Africa.

Signature
Name: Gezahegn Bogale Gebre

Table of contents

List of tables

List of figures

Abbreviations

AD	Days to 50 % anthesis
ANOVA	Analysis of variance
ASI	Anthesis-silking interval
CIMMYT	Centro Internacional de Mejoramiento de Maiz y Trigo (International Maize and Wheat Improvement Centre)
DSND	Drought stressed normal plant density
DSHD	Drought stressed high plant density
EH	Ear height
EL	Ear length
EPP	Ears per plant
GCA	General combining ability
GCA x E	General combining ability by environment interaction
GEI (G x E)	Genotype by environment interaction
h_b^2	Broad sense heritability
h_n^2	Narrow sense heritability
HD	High plant density
HDB2A	High plant density at Bako in 2002 main season
HDB3A	High plant density at Bako in 2003 main season
HDM2A	High plant density at Melkasa in 2002 main season
HDM3A	High plant density at Melkasa in 2003 main season
HPHD	High parent traits at high plant density
HPND	High parent traits at normal plant density
HPH	High parent heterosis
HSW	Hundred seed weight
MOA	Ministry of Agriculture
MPHD	Mid-parent traits at high plant density
MPND	Mid-parent traits at normal plant density
MPH	Mid-parent heterosis
ND	Normal plant density
NDB2A	Normal plant density at Bako in 2002 main season

NDB3A	Normal plant density at Bako in 2003 main season
NDM2A	Normal plant density at Melkasa in 2002 main season
NDM3A	Normal plant density at Melkasa in 2003 main season
NKE	Number of kernels per ear
NKP	Number of kernels per plant
NTB	Number of tassel branches
OPV	Open pollinated variety
PH	Plant height (cm)
PD	Plant density
r_G	Genetic correlation
r_P	Phenotypic correlation
SD	Days to 50% silking
SCA	Specific combining ability
SEN	Leaf senescence
SCA x E	Specific combining ability by environment interaction
t ha^{-1}	Ton per hectare
σ	Error variance
d_{gxy}	Genotypic covariance of traits x and y
$d^2{}_{gx}$	Genotypic variance of trait x
$d^2{}_{gy}$	Genotypic variance of trait y
σ^2_A	Additive variance
σ^2_D	Dominance variance
σ^2_G	Genotypic variance
σ^2_E	Error or environmental variance
σ^2_{GE}	Genotype by environment interaction variance
WWHD	Well-watered high plant density
WWND	Well-watered normal plant density

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Chapter 1 General introduction

Maize (*Zea mays* L.) ranks as one of the world's three most important cereal crops. It is cultivated in a wider range of environments than wheat and rice because of its greater adaptability (Koutsika-Sotiriou, 1999). Currently, its global production area is about 140 million hectares, of which approximately 96 million hectares are in the developing countries. Although 68% of the world maize area is in developing countries, only 46% of the world's maize production of 602 million tons (FAO, 2003) is produced there. Low average yields in the tropics are responsible for the wide gap between the global share of area and of production (Heisey & Edmeades, 1999; Pingali & Pandey, 2000).

Drought and low N stresses are factors most frequently limiting maize production in the tropics (Edmeades *et al.*, 1997c; Banziger *et al.*, 1999b; Vasal *et al.*, 1997; 1999). The mean annual yield losses in maize due to drought were estimated as approximately 17% per year in the tropics (Edmeades *et al.*, 1992), but losses in individual seasons have approached 60% in regions such as southern Africa (Rosen & Scott, 1992). It is also believed that many of the dry land areas are characterized as highly fragile natural resource bases and mostly associated with low soil fertility (Parr *et al.*, 1990). In addition to these, increased population pressure, high input costs, and extreme poverty force smallholder farmers in the region to implement low input farming systems (Bänziger *et al.*, 1999a). Consequently, maize yields in resource poor farmers' fields average 1 to 2 ton ha^{-1} (CIMMYT, 1994) in contrast to 6 to 9 ton ha^{-1} attained in similar areas with adequate inputs (Loomis, 1997). Under these circumstances, since the smallholder farmers cannot afford additional inputs, it would be desirable to increase the tolerance of the crop to stresses that occur in their fields (Bänziger *et al.*, 1999a).

CIMMYT has implemented a strategy that mainly focuses on improvement of maize tolerance to drought occurring at flowering, while maintaining yield potential under favorable conditions (Bolaños & Edmeades, 1996; Chapman *et al.*, 1997; Edmeades *et al.*, 1997a; Bänziger *et al.*, 1999b). Drought at flowering often results in barrenness and serious yield instability at farm level, since it allows no opportunity for farmers to replant or otherwise compensate for loss of yield. To assist farmers with this problem, CIMMYT has improved drought tolerance of some tropical maize populations and lines. The main sources for these achievements were utilization of drought adaptive traits and especially screening in sites where the timing and severity of water stress can be controlled (Bolaños & Edmeades, 1996; Edmeades *et al.*, 1994; 1997d; 1999). Ears plant^{-1}, kernels plant^{-1} and anthesis-silking intervals are considered as the most important drought adaptive traits, followed by tassel branch number, leaf senescence and plant height (Edmeades *et al.*, 1997d). The basic approach for development of drought tolerant genotypes is to select locally adapted germplasm containing genetic variability for high yield potential and drought adaptive traits (Beck *et al.*, 1997; Vasal *et al.*, 1997). Furthermore, the unpredictable nature of drought dictates that improved genotypes must perform well in both favorable and stressed environments. Thus, combination of stressed and unstressed environments is used in selection of genotypes for drought stressed areas of the tropics.

Many researchers suggested that managed drought stress imposed at flowering is an effective means of increasing tolerance to a number of stresses occurring near flowering (Edmeades & Bänziger, 1997; Bänziger *et al.*, 1999b). Chapman *et al.* (1997) have indicated that selection for tolerance to mid-season drought stress has improved broad adaptation, and specific adaptation to drought environments. In addition, increased grain yield across a range of N stress levels was reported by Lafitte & Bänziger (1997) and Bänziger *et al.* (1999b). These researchers also concluded that another approach for improving yield under low N is the use of controlled drought as a surrogate stress. On the other hand, there is good evidence suggesting that hybrids maintain their advantage over open pollinated varieties in both stress and non-stress environments (Dass *et al.*, 1997; Vasal *et al.*, 1997; Duvick, 1999; Tsaftaris *et al.*, 1999).

CIMMYT's experience suggests that improvement in tolerance to drought and low N can be made in locally adapted maize germplasm, or introduced from CIMMYT sources (Beck *et al.*, 1997; Edmeades & Bänziger, 1997). However, the usefulness of CIMMYT improved genotypes depends on the balance between their tolerance and adaptation to local conditions. This implies the need to test their extent of adaptation, and combining ability of the inbred lines in variable environments under local conditions. It is also suggested to assess genetic variability for drought adaptive traits within elite local populations, especially as an alternative for selection when the improved CIMMYT populations fail to adapt.

In some areas of the tropics, direct selection is difficult due to irregular occurrence of drought or to unpredictable rainfall patterns. To overcome this setback, investigators suggested the use of selection under high plant density (Dow *et al.*, 1984; Reeder, 1997), which is an indicator of tolerance to a number of stresses (Vasal *et al.*, 1997). Plant density in maize is an environmental aspect that can be varied for more effective selection (Troyer & Rosenbrook, 1983), indicating the possibility to increase the number of environments by using different population sizes. Furthermore, there is limited information on the performance of tropical, drought tolerant genotypes under high density, which may indicate general stress tolerance (Beck *et al.*, 1997; Vasal *et al.*, 1997). This is a type of indirect selection by making use of a selection environment that considerably differs from the target environment (Banziger *et al.*, 1997). Thus, testing variability within elite local populations for drought adaptive traits, while evaluating drought tolerant lines and their crosses under stress and non-stress conditions can help to identify their potential for resource constrained farmers. Furthermore, it is important to study the relationship among different environments to determine alternative options for screening drought tolerant germplasm in areas with unpredictable environments.

The objectives of the present study were to assess:

(1) genotypic variability for drought and high plant density adaptive traits in Maize Population A-511

(2) combining ability of CIMMYT's drought tolerant lines in different environments.

(3) extent of heterosis obtained from crosses of drought tolerant lines over different environments.

(4) potential adaptability of drought tolerant genotypes in different environments.

Chapter 2 Literature review

2.1. Effect of drought and high plant density stress on maize

2.1.1. Drought

Stress is defined as a factor that causes, through its presence or its absence, a reduction in plant grain yield (Tollenaar & Wu, 1999). Ashley (1993) termed meteorological drought when precipitation is significantly below expectation for the time of year and location. Drought is a multidimensional stress affecting plants at various levels of their organisation (Yordanov *et al.*, 2000). Drought environments are characterised by wide fluctuations in precipitation, in quantity and distribution within and across seasons (Swindale & Bidinger, 1981). The effect of stress is usually perceived as a decrease in photosynthesis and growth (Yordanov *et al.*, 2000). It is believed that no other environmental factor limits global crop productivity more severely than water deficit (Fischer & Turner, 1978; Boyer, 1982).

In 1998, the total production of grain and silage maize was 604,492,916 tons, of which the United States produced 47%, Asia 27%, South America 9%, Africa 7%, the European Union 6%, and Eastern Europe 4% (Koutsika-Sotiriou, 1999). The average maize yield in the industrialized countries is more than 8 t ha^{-1} while in the developing world it is slightly less than 3 t ha^{-1}. The major factors for this wide gap in maize yield between the developed and developing world are unrelated climatic conditions (tropical versus temperate) and differences in farming technologies (Pingali & Pandey, 2000). Most tropical maize is produced under rain-fed conditions, in areas where drought is widely considered to be the most important abiotic constraint to production (Reeder, 1997; Pingali & Pandey, 2000). Maize grain losses due to drought in the tropics may reach 24-million t year^{-1} (Edmeades *et al.*, 1992). In sub-Saharan Africa, 40% of the maize area experiences occasional drought, whereas 25% of the area is frequently affected (CIMMYT, 1990). Severe drought occurs each year in at least one country within eastern and southern Africa, resulting in frequent crop failures (Waddington *et al.*, 1995). Consequently, the variability of rainfed crop yields in this region is likely of greater socio-economic importance than in any other part of the world (Heisey & Edmeades, 1999).

Moisture deficiency at any growth stage of maize development affects production (Denmead & Shaw; 1960; Vasal *et al*., 1997; Saini & Westgate, 2000). However, the magnitude of the yield reduction depends on the developmental stage of the crop, the severity and duration of the stress, and susceptibility of the genotype to stress (Lorens *et al*., 1987). Accordingly, maximum reduction in productivity is inflicted when it occurs at or around flowering, more so than at any other time in the crop cycle, particularly during the two weeks bracketing flowering (Denmead & Shaw; 1960; Claassen & Shaw, 1970; Grant *et al*., 1989; Schussler & Westgate, 1995; Zinselmeier, 1995; Bolanos & Edmeades, 1993b; 1996; Edmeades & Banziger, 1997). When drought stress is imposed at establishment, it reduces the stand while during the vegetative period it reduces the size of the assimilatory structure (Denmead & Shaw, 1960; Rhoads & Bennet, 1990). During vegetative development, it reduces expansion of leaves, stems, and roots and ultimately affects the development of reproductive organs and potential grain yield (Denmead & Shaw, 1960). The reduced plant size results in a lower assimilation at the time of ear development since production of dry matter is dependent on the size of the assimilatory surface. Herrero & Johnson (1981) reported visible symptoms of midday wilting and of lower leaf senescence due to moisture deficit. Sobrado (1987) also indicated that leaf rolling, which is associated with low leaf water status, reduces the area exposed to radiation. According to Denmead & Shaw (1960), the reduction in grain yield due to moisture stress during the vegetative, silking and ear stages were 25%, 50%, and 21%, respectively.

On the other hand, Grant *et al.* (1989) reported a reduction of two to three times more when drought coincides with flowering, compared with other growth stages. At this period the maize crop responds by abortion of ovaries, kernels and entire ears (Kiniry & Ritchie, 1985; Rhoads & Bennet, 1990; Schussler & Westgate, 1991). In an earlier study, Robins & Domingo (1953) reported that if drought conditions during flowering continue for a week, losses in grain yield might exceed 50%. Drought lasting even one to two days at pollination can reduce grain yield by up to 22% (Fischer *et al*., 1983). It can even be reduced nearly to zero when severe stress occurs during this period (Edmeades *et al*., 1994). The stress just prior to anthesis inhibits ear and silk growth more than tassel growth (Du Plessis & Dijkhuis, 1967; Herrero & Johnson, 1981; Bolaños & Edmeades, 1993b; 1996; Edmeades *et al*., 1993; 1999; Westgate, 1997). The authors indicated that this difference causes increased anthesis-silking interval (ASI) that results in barren or poorly developed ears. Du Plessis & Dijkhuis (1967) found an 82% decline in grain yield as ASI increased from 0 to 28 days. Bolaños & Edmeades (1993b) also reported an almost similar observation on 'Tuxpeño Sequía' that declined in grain yield by 90 % as ASI increased from –0.4 to 10 days. A long ASI is generally equated with drought susceptibility, low harvest index, slow ear growth and barrenness (Edmeades *et al.*, 1997d). Water deficit occurring during anthesis does not affect pollen viability (Herrero & Johnson, 1981; Westgate & Boyer, 1986), but it can cause a decline in silk receptivity if pollination is delayed (Bassetti & Westgate, 1993). Even when gamete and floral development proceed normally, and pollen is not limiting, grain number can be reduced by only a few days of dehydration at flowering (Schoper *et al.*, 1986; Westgate & Boyer, 1986; Westgate, 1997).

Drought at or immediately after flowering is known to accelerate leaf senescence (Bolaños & Edmeades, 1993a), with reduced leaf area, reduced intercepted radiation and photosynthesis that result in a reduction in photo-assimilate flux to the spikelets (Aparicio-Tejo & Boyer, 1983; Westgate & Boyer, 1986; Wolfe *et al.*, 1988a; 1988b; Zinselmeier *et al.*, 1995). Generally, most maize germplasm show increased leaf senescence at flowering, ASI, silk delay, reduced number of ears plant^{-1} (EPP), number of kernels ear^{-1} (NKE) and grain yield. On the contrary, improved maize genotypes obtained through screening under moisture stress at flowering were found to be tolerant to the effect of the stress. Thus to initiate selection for improvement, it is a priority to assess the available variability in elite adapted populations for these traits.

2.1.2. High plant density

Plant density (PD) resulting in interplant competition affects vegetative and reproductive growth (Tetio-Kagho & Gardner, 1988b). An increase in either the number of maize plants per unit area or the number and size of weeds within a maize stand will enhance the competition among plants for resources within the maize canopy (Tollenaar & Wu, 1999). High PD increases stalk breakage, root lodging, barrenness and results in smaller ears and reduced harvest index (El-Lakany & Russell, 1971; Buren *et al.*, 1974; Edmeades & Daynard, 1979; Troyer & Rosenbrook, 1983; Tollenaar *et al.*, 1997). Stalk breakage and ear droppage increase because crowded maize plants have smaller diameter stems and shanks due to mutual shading (Troyer & Rosenbrook, 1983). Unlike other stresses, in densely planted maize many or all plants may be barren but remain green and vigorous in appearance. High PD also causes increased plant and ear heights, fewer EPP, decreased ear length and diameter, less kernel depth, and later anthesis, with silk emergence delayed more than pollen shed (El-Lakany & Russell, 1971). However, Tetio-Kagho & Gardner, (1988a) observed that plant height increases to a maximum and then decreases (parabolically) with increasing PD that probably associates with limitation of assimilate and perhaps minerals and water. The report also indicated that increasing PD increases leaf area index and vegetative dry matter yield but tiller number decreased linearly with increasing PD to no tillers at 3.5 plants m^{-2}. However, a hybrid with tillers and prolificacy at low density was less affected (Andrade *et al.*, 1993).

A hierarchical pattern in reproductive development in which tassel growth dominates ear growth (apical dominance), the main symptom of a limited assimilate supply under high PD is a delay in silking (Edmeades & Daynard, 1979; Edmeades *et al.*, 1993). Intolerant genotypes usually have higher grain yields and larger ears than tolerant hybrids at low populations, whereas the opposite is true at high PD (Buren *et al.*, 1974; Otegui, 1997). Similarly, ASI increased much more with density than days to anthesis (Edmeades & Daynard, 1979; El-Lakany & Russell, 1971) but tolerant genotypes possess shorter ASI and increased EPP than intolerant genotypes (Buren *et al.*, 1974). Drought tolerant genotypes also exhibit reduced ASI under drought conditions but limited information is available about their performance in ASI and other traits under high density.

Kernel row number ear^{-1}, kernel number ear row^{-1}, and KNE were influenced by PD (Tetio-Kagho & Gardner, 1988b). Ear abortion occurs during flowering, whereas kernel abortion can continue up to 20 days after pollination (Tollenaar, 1977). Otegui (1997) observed barrenness (0.5 ears $plant^{-1}$) at 16 plants m^{-2} but spikelet abortion took place in all apical ears after silking at five, eight and 16 plants m^{-2}, except at two plants m^{-2}. These responses are the result of a decrease in photosynthetic rate $plant^{-1}$ (Edmeades & Daynard, 1979) and hence plant growth rates (Tollenaar *et al.*, 1992). Thus, the amount of intercepted radiation at flowering is critical for number of kernel set, which is highly associated with grain yield (Tollenaar, 1977; Kiniry & Ritchie, 1985; Grant *et al*., 1989).

At flowering the total assimilate flux plant^{-1} produces a small increase in NKE by lowering PD from 10 to five plants m^{-2}. At low PD, therefore, maize is inefficient in terms of number of kernels fixed per unit of crop growth rate. However, prolific hybrids are more efficient at low densities (Prior & Russell, 1975; Tollenaar *et al*., 1992). On the other hand, at PD above the optimum, the number of kernels unit area^{-1} is significantly reduced, even though the amount of radiation intercepted by the crop is not affected (Andrade *et al*., 1993). On the contrary, a decrease in PD below the optimum value produces a significant decrease in number of grains set per unit of intercepted photosynthetically active radiation at flowering.

2.1.3. Relationship in effect among some environmental stresses

In both natural and agricultural communities, environmental parameters often fluctuate to levels that are sub-optimal for plant growth. Consequently, the plant is continuously encountering new combinations of environmental stress (Chapin, 1991). In addition, this author indicated that all plants respond to stress of many types in basically the same way (Chapin, 1991). Drought and low N are encountered practically in all production environments where tropical maize is grown (Edmeades *et al.*, 1997c; Bänziger *et al*., 1999b; Vasal *et al*., 1997; 1999). Nitrogen is the nutrient that most often limits maize yields in the lowland tropics (Lafitte & Edmeades, 1994a). In dry land areas, soils are often coarse textured, inherently low in fertility, organic matter, and water holding capacity (Parr *et al.*, 1990). Where farmers know that drought is highly probable, they will usually not risk capital losses by applying fertiliser, even if it is available (McCown *et al*., 1992; Hess, 1997). In addition to drought and low soil fertility, farmers' fields are usually poorly managed in terms of weed control and other agronomic practices (Simmonds, 1991; Bänziger *et al*., 1999b; Pingali & Pandey, 2000). Furthermore, most tropical farmers continue to grow maize to meet their subsistence requirements and have had little need and/or poor access to improved technologies (Bänziger *et al.*, 1997; Loomis, 1997; Pingali & Pandey, 2000). As a result of this, farmers' fields in this region are rarely characterized by only one abiotic stress (Bänziger *et al*., 1997; 1999b), and maize yields in many tropical countries average from 1 to 2 t ha^{-1} (CIMMYT, 1994). Thus it would be desirable to increase the tolerance of crops to several stresses that occur in target environments (Bänziger *et al.*, 1999b). Ceccarelli *et al.* (1992) also emphasized that the objectives of crop breeding programs in developing countries are to combine stress tolerance with yield potential.

As mentioned above, drought stress coinciding with meiosis results in abnormal (sterile) embryo sacs. Saini & Westgate (2000) considered this phenomenon as common to a variety of stresses. Both shading and drought affect grain yield by restricting the supply of photo-assimilates for plant metabolism (Dow *et al.*, 1984; Kiniry & Ritchie, 1985). Features, which enable a plant to channel more of these scarce materials into grain under the one type of stress, may be equally effective under the other (Moss & Stinson, 1961). Drought or shading immediately after flowering have their primary effect on the number of aborting kernels (Kiniry & Ritchie, 1985; Schussler & Westgate, 1991). Increased days to silking, and ASI as symptom of interplant competition (El-Lakany & Russell, 1971; Buren *et al.*, 1974; Edmeades & Daynard, 1979), drought, and low N stress have been reported (Jacobs & Pearson, 1991; Edmeades *et al.*, 1993; Bolaños & Edmeades, 1996). These traits are also considered as indicative of barrenness or intolerance (Bolaños & Edmeades, 1996; Bänziger & Lafitte, 1997). Many authors indicated that the separation of reproductive organs may also account for the crop's unusual susceptibility to stress at flowering (Edmeades *et al.*, 1992; 1993; Edmeades & Bänziger, 1997; Vasal *et al.*, 1997; Westgate, 1997). Silking delayed under conditions of drought or high PD is related to less assimilate being partitioned to growing ears around anthesis, which results in lower ear growth rates, increased ear abortion, and more barren plants (Edmeades *et al.*, 1993). When assimilate supply is limited under stress it is usually preferentially distributed to the stem and tassel at the ear's expense, leading to poor pollination and partial or complete failure in seed set. This occurs with practically all kinds of stress, including drought, low soil N and P, excess moisture, low soil pH, iron deficiency, pre-flowering biotic stress and high PD (Vasal *et al.*, 1997). Considerable evidence indicates that maize plants exposed to any of these stress factors have reduced EPP and kernels plant^{-1} (NKP) (Buren *et al.*, 1974; Edmeades *et al.*, 1993; Bänziger & Lafitte, 1997).

Similarly, accelerated leaf senescence was also reported due to high PPD (Allison, 1969), drought stress (Claassen & Shaw, 1970; Edmeades *et al.*, 1993), and low N stress (Bänziger & Lafitte, 1997). High PD (10.6 m^{-2}) in summer and mild winter drought imposed similar stress levels on the maize crop at flowering, particularly by delaying silking and increasing ASI (Edmeades *et al.*, 1993). Beck *et al.* (1997) also suggested high PD (double of the normal density) as an alternative to obtain greater drought stress. However, the effect of high PD on drought tolerant genotypes, and the relationship in effect of moisture stress and high PD is not yet clear for tropical maize. Both water stress and N stress reduced leaf area, and lengthened the time from emergence to tasseling and silking (Bennett *et al.*, 1989). However, with low N and optimal irrigation, N stress became a limiting factor while N levels had little effect on green leaf area under severe water deficits. Reduced leaf area due to senescence or due to stress during vegetative growth, resulted in reduced biomass accumulation because of lower light interception and photosynthesis. Others reported acceleration of senescence of the lower leaves by drought stress occurring during grain filling (Aparicio-Tejo & Boyer, 1983; Wolfe *et al.*, 1988a) that eliminate future assimilation by those leaves and reduce grain yield (Chapman & Edmeades, 1999). However, in low N situations, grain filling may be enhanced by foliar senescence, which releases leaf N to the grain (Uhart & Andrade, 1995).

2.2. Drought and high plant density adaptive traits

2.2.1. Tolerance to drought at flowering

Stress can be alleviated either by management practices or by modifying the plant so that the impact of the causal factor on plant grain yield is reduced (Tollenaar & Wu, 1999). Plants have evolved a number of adaptive mechanisms that allow the photochemical and biochemical systems to cope with negative changes in environment, including increased water deficit (Yordanov *et al.*, 2000). Like breeding, improved management practices involving more effective uses of naturally occurring supplies of water may close perhaps 15-25% of the gap between realized yields and potential yields (Edmeades & Bänziger, 1997). However, improved genetics can be conveniently packaged in a seed and therefore more easily and completely adopted than improved agronomic practices that depend more heavily on input availability, infrastructure, access to markets, and skills in crop and soil management (Campos *et al.*, 2004). Thus breeding remains the best alternative to many resource poor farmers who cannot afford additional inputs or are simply unable to get access to them (Edmeades & Bänziger, 1997; Vasal *et al.*, 1997; Bänziger *et al.*, 1999b).

The first step towards maximizing yield in drought-prone areas is matching of the phenology of cultivars to the pattern of rainfall in the target environment (Bidinger *et al.*, 1987; Ludlow & Muchow, 1990; Muchow *et al.*, 1994). If the rainy season is reliable but very short, then escape through earliness is a desirable breeding goal (Edmeades *et al.*, 1997c). Edmeades & Bänziger (1997) also pointed out that repeatable terminal drought stress could be managed by using earlier maturing varieties, which can be easily modified by conventional breeding techniques. However, in addition to low yielding ability of early genotypes it is impractical as rainfall is erratic in distribution and can occur at any growth stage of the crop (Fischer *et al.*, 1983; Edmeades & Bänziger, 1997). Besides, farmers in drought prone areas need varieties that have good yields under optimum conditions and still yield relatively better when it is unfavourable (Edmeades & Bänziger, 1997; Edmeades *et al.*, 1997a; Vasal *et al.*, 1997). Furthermore, drought at or around flowering reduces productivity more than drought occurring at other times in the crop cycle (Edmeades *et al.*, 1997d; Vasal *et al.*, 1997). Thus, a more productive strategy would be to develop a high yielding, later maturing variety with tolerance to drought at flowering (Edmeades & Bänziger, 1997; Edmeades *et al.*, 1997c).

According to Ashley (1993), drought tolerance implies the ability not just to survive physiological effects, but also to grow and yield satisfactorily under such conditions. Edmeades *et al.* (1997d) elaborated this term as the ability to produce high grain yields despite showing symptoms of water deficit. However, it should be remembered that the close link between crop production and water use confirms that the gap between well-watered production levels and those obtained under water-limiting conditions will never be closed (Waddington *et al.*, 1995). Accordingly, Rosielle & Hamblin (1981) expressed tolerance to stress as the relative difference in yield between stress and non-stress environments.

Grain yield under stress will remain the primary and most important trait during selection (Edmeades & Bänziger, 1997). However, heritability for grain yield typically reduces under drought conditions because the genetic variance for yield decreases more rapidly than the environmental variance among plots with increasing stress. Under these conditions, secondary traits whose genetic variance increases under stress can increase selection efficiency, provided they have a clear adaptive value under stress, relatively high heritability and are easy to measure (Blum, 1988; Edmeades *et al*., 1989; Ludlow & Muchow, 1990; Bolaños & Edmeades, 1996; Betran *et al*., 1997; Edmeades *et al*., 1997d). For drought at flowering, Edmeades *et al*. (1997d) indicated that emphasis should be planced on traits, which affect ear formation or barrenness. Consequently, traits related to tolerance to drought in combination with grain yield can be used as selection index for identifying superior genotypes (Bolaños & Edmeades, 1996; Edmeades & Bänziger, 1997). Edmeades *et al*. (1997d; 1999) pointed out that an ideal secondary trait should be: (a) genetically variable and genetically associated with grain yield under drought; (b) carry no yield penalty under favorable conditions; (c) moderate to high heritability; (d) cheaper and/or faster to measure than grain yield; (e) stable over the measurement period; (f) able to be observed at or before flowering so that undesirable parents are not crossed; and (g) able to provide an estimate of yield potential before final harvest.

Many studies in CIMMYT, on maize, have shown the importance of ASI as an indicator of barrenness under stress and to identify stress tolerant genotypes at flowering (Bolaños & Edmeades, 1993b; 1996; Chapman & Edmeades, 1999). Du Plessis & Dijkhuis (1967) recorded a correlation coefficient of –0.975 between ASI and the logarithm of the yield per plant. Others found moderately strong associations (r_G = -0.58 and –0.60, respectively) under severe drought stress (Guie & Wassom, 1992; Bolaños & Edmeades, 1996). This indicated that selection for a reduced ASI under drought stress results in higher and more stable grain yield (Bolaños & Edmeades, 1993a; Edmeades *et al*., 1993).

Westgate (1997) suggested selecting against protandry and for high yield across environments. Selecting for silk emergence prior to pollen shed (protogyny) would effectively shift ASI to negative values. A large negative ASI could be advantageous under drought conditions because any delay in emergence would only improve the synchrony between maximum pollen shed and silk emergence and lead to more stable kernel production. Unfortunately, selecting plants for a negative ASI alone will not guarantee high kernel set if drought occurs during the critical pollination period However, both approaches of selection for a minimum ASI at CIMMYT and to select for protogyny and high yield across environments assume that development and fecundity of staminate and pistillate flower types must be synchronised for optimum kernel set (Westgate, 1997). Chapman & Edmeades (1999) pointed out that grain yield, EPP, and NKE were strongly correlated with ASI under drought conditions, but not when water was plentiful. In general, the reduction in florets ear^{-1} with selection for tolerance to drought or low N appears to be an important general mechanism for increasing and stabilizing grain yields under abiotic stress (Lafitte & Edmeades, 1995a).

Bänziger *et al.* (1999b) reported that all drought tolerant selection cycles showed delayed leaf senescence during grain filling, and increased N harvest index, harvest index as well as biomass accumulation at maturity. In contrast, Edmeades *et al.* (1999) indicated that tolerance is also associated with an increased partitioning of biomass to the developing ear under drought conditions, so that harvest index and grain yield are increased but not total biomass. Earlier, Fischer *et al.* (1983) indicated short maize plants as more tolerant to drought at flowering than taller plants. Similarly, selection for reduced tassel size has been shown to increase ear size near flowering (Fischer *et al.*, 1987). These studies suggested that competition for assimilate between competing organs at flowering affects ear growth and grain number in maize (Chapman & Edmeades, 1999). However, Bolaños & Edmeades (1996) reported that genetic correlation between grain yield and leaf rolling, senescence (stay green), leaf angle, canopy temperature, tassel branch number, leaf chlorophyll concentration, and plant height were generally less than |0.20|. Edmeades *et al.* (1997d) rated EPP, NKP and ASI as the most valuable of those factors associated with grain yield under drought conditions. Where resources are scarce, these traits can substitute one for the other. Evidence suggests that focusing on traits which are indicative of partitioning in the plant at flowering (EPP and ASI) will result in increases in harvest index and grain yield in all water regimes (Bolaños & Edmeades, 1996).

At CIMMYT, superior progenies were identified with an index that favored: (a) increased grain yield under drought and non-stress; (b) reduced ASI, barrenness (increased EPP), and reduced leaf senescence and leaf rolling under stress; and (c) reduced tassel size, erect leaves, and resistance to lodging under well watered conditions. Using the index, high attention is given to avoid changes in the time from sowing to 50% anthesis (AD) so that selection would not include early flowering or escapes (Edmeades *et al.*, 1999). However, limited information is available of these traits under high-density conditions, particularly when drought tolerant genotypes are subject to interplant competition.

2.2.2. High plant density tolerance

Many authors pointed out that grain yield improvement of maize hybrids in North America and Europe has been associated with an increased tolerance of high plant density (Troyer & Rosenbrook, 1983; Carlone & Russel, 1987; Tollenaar *et al.*, 1989; Troyer, 1996; Duvick, 1984; 1999). Data on the USA 1980-era hybrids demonstrated that the primary reason for yield gain is the ability of the new hybrids to take advantage of higher plant densities (Carlone & Russel, 1987). In addition, Tollenaar *et al.* (1997) reported that more recently developed hybrids were less influenced by weed interference than the older hybrids in Ontario (Canada). These authors also suggested that progress to increase yields at high densities is likely to be achieved as maize breeders continue to develop and evaluate materials at higher plant densities. Regarding the production of maize hybrid seed, the yield of inbreds is often a limiting factor. So, it seemed appropriate to study the feasibility of increasing the productivity of inbreds through the use of high plant densities. In general, it is important to determine the genotypes that are tolerant to high plant density.

The tolerance of maize grain yields to abiotic stresses is largely determined by events that occur at or shortly after flowering (Lafitte & Edmeades, 1995a). A shortened ASI is indicative of a high relative flow of assimilate to developing ears during early reproductive development under conditions of stress (Dow *et al.*, 1984; Edmeades *et al.*, 1994; 1999). High PD tolerant genotypes possess shorter ASI than intolerant genotypes (Buren *et al.*, 1974). Beck *et al.* (1997) and Vasal *et al.* (1997) also indicated that selection under this stress might improve general stress tolerance as well as specific stress tolerance. Their report indicated that high PD is particularly useful in augmenting selection for drought and low N tolerance. Several commercial maize breeders in North America improved drought resistance by screening under high density (Dow *et al.*, 1984; Beck *et al.*, 1997). This has been advantageous when direct selection for drought tolerance is difficult due to irregular occurrence of drought (Dow *et al.*, 1984). Beck *et al.* (1997) also indicated that the relationship between high PD tolerance, ASI, and drought tolerance seems clear in temperate germplasm but not in tropical materials.

High PD plantings are valuable when selecting for reduced barrenness and lodging as well as shorter ASI (Russel, 1991; Vasal *et al.*, 1997). Reduction in tassel size also tends to reduce barrenness and increase grain yields at high plant densities (Hunter *et al*, 1969). Similarly, Buren *et al.* (1974) reported that reduced ASI, prolificacy, reduced tassel size, and efficient production of grain per unit leaf area would characterize PD tolerant genotypes. On the other hand, optimum plant density for yield increased when recurrent selection for reduced plant height was carried out on tropical maize population, Tuxpeño Crema (Johnson *et al.*, 1986). According to these authors, selection for reduced plant height on this population has reduced the incidence of lodging and barrenness.

2.2.3. Relationship in tolerance to some stresses

Many abiotic stresses manifest a similar set of plant responses, and certain plant characteristics have adaptive value across a range of these stresses (Vasal *et al.*, 1997). Farmers' fields in the tropics are rarely characterized by only one abiotic stress, and the need to increase the tolerance of crops to these constraints has been indicated by Bänziger *et al.* (1999b). The importance of performance in a range of environments is suggested (Rosielle & Hamblin, 1981; Falconer, 1989). In the USA, yield increases have come about principally because of increased stress resistance, particularly the ability to produce under increased stress caused by high PD. The continuing changes in plant architecture and composition conceivably can increase efficiency of grain production under stresses caused by high PD, unfavourable weather, or low soil fertility (Duvick, 1997). Janick (1999) reported that a small part of the yield ability has come about from morphological changes (small tassels, upright leaves) and reduced grain protein.

Differences in stress tolerance between older and more recent hybrids in the USA and Canada were shown for high PD, weed interference, low night temperatures during the grain-filling period, low soil moisture, low soil N, and a number of herbicides (Duvick, 1984; 1997; Tollenaar *et al.*, 1997; Tollenaar & Wu, 1999). According to these reports, yield improvement is the result of more efficient capture of resources (interception of incident solar radiation and uptake of nutrients and water) and more efficient use of these resources. Selection for tolerance to mid-season drought stress appears to increase grain yield across a range of N stress levels and may lead to morphological and physiological changes that are of particular advantage under N stress (Edmeades & Bänziger, 1997; Bänziger *et al.*, 1999b). They concluded that managed drought stress imposed at flowering is an effective means of increasing tolerance to a number of stresses occurring near flowering and which commonly result in barrenness.

The number of florets ear^{-1} and intensity of leaf senescence were reduced with selection for tolerance to drought (Edmeades *et al.*, 1993), and for low N tolerance (Lafitte & Edmeades, 1994b; 1995a). Reduced ear abortion, delayed leaf senescence, increased or unchanged N harvest and harvest index were observed in the drought tolerant versions of Tuxpeño Sequia (Lafitte & Bänziger, 1997; Bänziger *et al.*, 1999b). Edmeades *et al.* (1997c) and Bänziger *et al.* (1999b) also suggested that the use of drought stress at flowering as a selection criterion can simultaneously improve tolerance to drought and low N. These studies concluded that another approach to improving yield under low N is the use of controlled drought as a surrogate stress. The two traits, which are strongly related to yield under stress are ASI and EPP (Vasal *et al.*, 1997). The inter-relationship of EPP and silk delay also suggests an association conducive to stress tolerance (Gevers, 1995). Considerable evidence indicates that genotypes capable of producing grain on more than one ear are tolerant of high PD (Buren *et al.*, 1974), low N (Lafitte & Edmeades, 1995a; Bänziger & Lafitte, 1997), and drought stress (Edmeades *et al.*, 1993; Bolaños & Edmeades, 1996). Edmeades *et al.* (1993) concluded that ASI is a sensitive measure of genotypic tolerance to reduced photo-assimilation plant^{-1} from many causes during the flowering period. Thus, in addition to drought, ASI can be considered as an indicator of tolerance to high PD (Dow *et al.*, 1984) and low N stress (Lafitte & Bänziger, 1995; Bänziger & Lafitte, 1997).

Plant breeders in temperate environments commonly use high PD to improve overall stress tolerance in segregating nurseries (Beck *et al*., 1997; Vasal *et al*., 1997). In an earlier study, Moss & Stinson (1961) reported that hybrids tolerant of thick planting were also tolerant of shade. The evaluation of segregating material for flowering synchrony under high PD is one of the techniques to select for improved drought tolerance (Reeder, 1997). Based on a study in temperate maize varieties, Dow *et al*. (1984) observed that hybrids tolerant of high PD tended to be relatively more resistant to drought stress. The authors also suggested that screening for density tolerance and for early silking relative to anthesis could be beneficial in breeding for drought tolerance in environments where water stress does not occur regularly. However, no adequate information is available on the performance of drought tolerant tropical maize under high PD, and whether selection for drought and high-density tolerance can be done simultaneously. Availability of this kind of information would be beneficial for national breeding programs under irregular rainfall patterns.

2.3. Requirements for development of stress tolerant genotypes

2.3.1. Germplasm with variability to adaptive traits

Genetic potential for high yield without a high level of stress tolerance is an accident waiting to happen. The demands of environmental change also force selection in different directions (Jensen, 1995). However, the maost important factor influencing gains over all environments is the amount of available genetic variation for (1) general adaptation and (2) traits necessary for improved production under specific constraints (Blum, 1988; Ceccarelli, 1989; Vasal *et al.*, 1997). In agreement with them, others indicated that selection cannot create variability but can act on heritable variability already existing in the population (Singh & Chaudhary, 1985; Hallauer & Miranda, 1988). It is considered best to start selection on high performing and agronomically desirable germplasm exhibiting large variation for stress tolerant traits (Vasal *et al*., 1997). The choice of breeding methods for genetic improvement of a crop depends upon the nature and magnitude of genetic variability present (Singh & Chaudhary, 1985; Hallauer & Miranda, 1988). According to Coors (1999) intra population recurrent selection methods based solely on additive genetic variance have been successful in increasing grain yield. Many other researchers reported that genetic variances for grain yield in stress environments are generally lower than in non-stress environments (Buren *et al.*, 1974; Rosielle & Hamblin, 1981; Blum, 1988; Lafitte & Edmeades, 1994c; Bolaños & Edmeades, 1996). Besides, estimated genetic variance refers to a specific population from which the experimental material is a sample for a specific set of environmental conditions (Dudley & Moll, 1969; Hallauer & Miranda, 1988).

Different mating designs that develop progenies for evaluation are used in the estimation of genetic variability and of other components of variance. On the contrary, there is a method without mating design for estimation of genetic variances in a population, that tests the unselected inbred lines themselves (Hallauer & Miranda, 1988). Although no mating is used, variability among inbred lines can be used as an estimation of genetic variability of a reference population. Obilana & Hallauer (1974) estimated genetic variability for many traits within Iowa Stiff Stalk Synthetic (BSSS) by using 224 randomly derived S_6 inbred lines. However, they indicated: (1) the disadvantages of developing six to seven generations to obtain homogeneous lines; and (2) the difficulty of developing a group of unselected lines that adequately represent the base population. Hallauer & Miranda (1988) suggested the use of S_1 lines as a good option for estimation of σ^2_A in maize populations if departures from $p = q = 0.5$ and no dominance are not serious. Others also estimated genetic variance for different traits by using unselected S_1 lines from two sorghum populations (Zavala-Garcia *et al.*, 1992), and from six tropical maize populations (Bolanos & Edmeades, 1996; Banziger *et al.*, 1997). Hallauer & Miranda (1988) reviewed and concluded that in most populations, additive genetic variance for grain yield is usually two to four times larger than dominance variance. Variation for both drought and low N tolerance has been encountered in all types of maize germplasm including open pollinated varieties, hybrids and inbred lines (Balko & Russell, 1980a; Bolaños & Edmeades, 1993a;).

CIMMYT's experience suggests that improvement in tolerance to drought and low N can be made in local maize germplasm and source populations from CIMMYT (Beck *et al.*, 1997; Edmeades & Bänziger, 1997). However, the usefulness of source populations from CIMMYT depends on the balance between their tolerance and adaptation under local conditions. Susceptibility to other abiotic and/or biotic stresses often restricts their usefulness, though this can usually be improved through selection and introgression. Thus emphasis should be given for evaluation of this introduced material under local conditions, and a decision can be made to use the source populations *per se* or to cross them with locally adapted materials (Beck *et al.*, 1997). Shukuan (1997) indicated that maize germplasm that has been grown under drought conditions for a long time presumably has acquired some drought tolerance. Since it seems likely that maize evolved under relatively infertile conditions, crop evolution may have exploited some of the genetic variability for improved performance under low-N (Edmeades *et al.*, 1997a). Based on these notions, the available variability for drought and high PD adaptive traits in elite local genotypes should be tested.

The basic approach for development of drought tolerant varieties is to select locally adapted germplasm containing genetic variability for high yield potential, short ASI and high EPP under drought (Beck *et al.*, 1997; Vasal *et al.*, 1997). Drought at flowering has proven particularly effective in revealing genetic variation for ASI (Bolaños & Edmeades, 1993a; 1996). Almost similar effects of high PD stress have been reported by Buren *et al.* (1974). Considerable genetic variability exists in maize for both the EPP and NKE (Edmeades *et al.*, 1993; Lafitte & Edmeades, 1995a). A study done on two tropical maize populations for drought adaptive traits, indicated that additive genetic variance was more important than dominance variance in controlling the expression of all traits in stress and non stress environments, except for yield under stress (Guei & Wassom, 1992). Similarly, Betran *et al.* (1997) found the presence of dosage effects and the need for drought tolerance in both parental lines to obtain acceptable hybrid performance under drought conditions. In addition, the unreliable nature of drought dictates that those cultivars must perform well in both favorable and stressed environments. These conditions will most likely be met if selection for drought tolerance takes place in elite adapted germplasm exposed periodically to carefully managed conditions of stress during the selection process (Edmeades *et al.*, 1997a). However, no information is available on the genotypic variability of stress adaptive traits in the widely cultivated maize Population A-511 in Ethiopia.

2.3.2. Recurrent selection and intercrossing

Recurrent selection has been effective in gradually improving population performance as well as the performance of the hybrids developed from the succeeding cycles of selection in maize (Vassal *et al*., 1997). Population improvement by recurrent selection is done through increasing the frequency of favorable alleles within the population (Hallauer & Miranda, 1988). Many different recurrent selection procedures have been developed in maize, and each method's effectiveness depend on the population undergoing selection, the selected trait, and the objective and stage of the breeding program (Hallauer & Miranda, 1988; Stojsin & Kannenberg, 1994; Vasal *et al*., 1997). Intra-population improvement methods have been more effective than inter-population methods for improving population means *per se* for all traits (Pandey & Gardner, 1992). They have been also effective for improving the drought tolerance of source populations (Edmeades *et al*., 1997c), and have increased the probability of developing superior drought tolerant inbred lines fom those populations (Edmeades *et al*., 1997b)

Family based recurrent selection methods result in greater gains when traits under selection are complex and of low heritability (Hallauer & Miranda, 1988; Vasal *et al*., 1997). The selfed progeny selection (S_1 or S_2), compared with other recurrent selection procedures, increase genetic variability among families and selects against undesirable recessive genes, thus it is more suitable particularly for low heritability traits (Wright, 1980; Hallauer & Miranda, 1988). Although there is no selection method that is best under all circumstances, selfed progenies are preferred over non-inbred progenies because variability and heritabilities increase with levels of inbreeding (Stojsin & Kannenberg; 1994; Bolaños & Edmeades, 1996; Vasal *et al*., 1997). It significantly improves tolerance to inbreeding over time and generates superior inbred progenies that may be the progenitors of advanced lines (Beck *et al*., 1997; Vasal *et al*., 1997). Thus the type of progenies evaluated affects the rate of improvement and the ability to discriminate among genotypes for stress tolerance (Vasal *et al*., 1997).

According to Edmeades *et al*. (1999), selection improves drought tolerance in tropical maize populations, either by recurrent selection or by intercrossing of known sources of drought tolerance to form a single population. Selection for drought tolerance for three to eight cycles has increased grain yield (GY) under drought at flowering by 30 to 50 % in three lowland tropical maize populations (Chapman & Edmeades, 1999). Besides, recurrent S_1 selection provides 50% greater annual gains than full sib selection, with additional advantages in promoting superior progenies more rapidly to inbred lines in pedigree breeding programs (Edmeades *et al.*, 1999). Bolaños & Edmeades (1996) found higher phenotypic correlations between GY and ASI across S_1s than full-sib progenies reported by Fischer *et al.* (1989). Progenies obtained by this approach can be utilized for development of synthetics, which is one way of concentrating specific traits in one cultivar (Falconer, 1989; Edmeades *et al.*, 1997a). Thus S_1 recurrent selection is the best alternative to assess the variability in traits related to drought and high PD tolerance in elite local populations as well as to improve tolerance to these stresses. Similarly, intercrossing drought tolerant lines with high general combining ability may intensify the degree of tolerance to multiple stresses. However, it takes longer to complete a cycle if there is no off-season facility (Beck *et al.*, 1997; Vasal *et al.*, 1997).

2.3.3. Screening techniques

In crop breeding programs the choice of the optimum selection environment (that maximizes the response for the target environment) is critical, particularly when yield potential of the target environment is low due to climatic stresses and/or low inputs (Atlin & Frey, 1990; Ceccarelli & Grando, 1991; Zavala-Garcia *et al.*, 1992). Due to the complex nature of drought and low N stresses, the decision whether breeding should be done under non-stress, stress or both environments is still being debated (Vasal *et al.*, 1997). Screening of progenies under conditions of abiotic stress is generally associated with an increased level of environmental variability (Blum, 1988; Lafitte & Bänziger, 1995; Vasal *et al.*, 1997). As a result, most crop breeding is conducted under high-yielding conditions where heritability and genotypic variance for grain yield, and therefore potential selection gains, are high (Rosielle & Hamblin, 1981; Simmonds, 1991). In agreement with this notion, Jensen (1995) and Dass *et al.* (1997) indicated that higher yielding genotypes under normal conditions would also be the better yielders under drought and sub-optimal N conditions. On the contrary, Ceccarelli & Grando (1991) indicated that selection for high yield in high yielding environments is an inefficient strategy for improving yield under low yielding conditions. Edmeades *et al.* (1999) also reported that selecting only in unstressed environments does not necessarily increase maize grain yields under water stress conditions. However, the unpredictable nature of drought dictates that those cultivars must perform well in both favourable and stressed environments (Edmeades & Bänziger, 1997; Edmeades *et al.*, 1997a; Vasal *et al.*, 1997). In addition to drought, because of variability within target environments, it is critical to identify either a single optimal environment, or some minimum combination of environments, that will optimise genetic gain both overall and within individual environments (Zavala-Garcia *et al.*, 1992).

Ceccarelli (1987) working with barley, and Byrne *et al.* (1995) working with maize, found little or no gain under drought conditions when these crops were selected under irrigation. It is suggested that breeding progress may be increased if abiotic stress in target environments is included during selection (Atlin & Frey, 1990; Ceccarelli *et al.*, 1992; Guei & Wassom, 1992; Ud-Din *et al.*, 1992; Zavala-Garcia *et al.*, 1992; Bänziger *et al.*, 1997; Chapman & Edmeades, 1999). Earlier, Arboled-Rivera & Compton (1974) suggested that breeding under both optimal and sub-optimal conditions may offer the more attractive option for the breeder. Stability of performance is perhaps more important than yield itself to farmers, especially in semiarid zones (Rosielle & Hamblin, 1981).

In addition to managed levels of those stresses, grain yield and secondary traits, which show increased genetic variance and genetic correlation with yield under stress are suggested to improve genotypes under stress conditions (Blum, 1988; Ludlow & Muchow, 1990; Bänziger & Lafitte, 1997; Edmeades *et al.*, 1997d). The extensive study by Bolaños & Edmeades (1996) endorsed the use of a well-watered environment and one with a severe moisture stress, timed to coincide with flowering. According to them, well-watered conditions expose sufficient genetic variability for yield so that progress for this trait through direct selection can be maintained. Under drought conditions, gains are obtained mainly by selection for ASI and EPP, whose genetic variability increase, and to lesser extent for grain yield itself. Generally, simultaneous selection for yield potential in well-irrigated environments and at least for reduced barrenness and ASI under well managed drought stress at flowering are recommended as a reliable procedure for improving tolerance to mid-season drought and low N environments (Bolaños & Edmeades, 1993a; 1996; Betran *et al.*, 1997;

Lafitte & Bänziger, 1995; Vasal *et al.*, 1997; Bänziger *et al.*, 1999b; Edmeades *et al.*, 1999).

At CIMMYT screening for drought tolerance is carried out at two or three moisture regimes as indicated below (Bolaños & Edmeades, 1993a; 1996; Edmeades *et al.*, 1994; Bänziger *et al.*, 1999b):

(a) Well-watered, irrigated at ten days interval, mainly based on soil texture.

(b) Intermediate or post flowering (grain filling) stress, where irrigation is suspended one to two weeks prior to anthesis.

(c) Severe or pre- and post-flowering stress, where irrigation is suspended three to four weeks prior to anthesis until mid- or late grain filling, when one additional irrigation is provided.

This indicates the need of a rain free season for drought tolerance screening. As to experimental design, especially for screening activities on intra- and inter-population improvement, alpha (0,1) lattice designs are routinely used to adjust for within-block variation caused by soil variation (Bolaños & Edmeades, 1993a; 1996; Edmeades *et al.*, 1994; Bänziger & Lafitte, 1997). The goal in stress management is to expose genetic variability for traits indicative of drought tolerance (Beck *et al.*, 1997). Consequently, the timing and intensity of water deficit is a critical factor in obtaining consistent improvement in drought tolerance (Edmeades *et al.*, 1993; Bolaños & Edmeades, 1993a; 1996). Chapman *et al.* (1997) indicated that selection for drought tolerance under the above conditions has improved broad adaptation, as well as specific adaptation to dry environments. However, it is difficult for some national programs to obtain reliable rain free seasons (Dow *et al.*, 1984), which may be considered as a limitation for drought tolerance screening. In such areas, screening under high PD is suggested as a method to select for improved drought tolerance (Dow *et al.*, 1984) as well as for broad adaptation (Reeder, 1997; Troyer, 1996; Vasal *et al.*, 1997). Nevertheless, a limited attempt has been made to investigate if high PD stress can be used as alternative to managed drought stress, and what the response of drought tolerant genotypes is under high PD.

Plant density in maize is an environmental aspect that can be varied for more effective selection (Troyer & Rosenbrook, 1983). Besides, high PD can easily be incorporated into a breeding program, as neither requires specific testing environments (Vasal *et* *al.*, 1997), which is advantageous especially to programs with difficulty of establishing screening sites for drought tolerance (Dow *et al.*, 1984). Russel (1991) suggested that further gains in hybrids could be achieved by development and evaluation of parental lines at higher PD to identify greater resistance to barrenness. Generally, screening for high PD tolerance could be beneficial in breeding for drought tolerance (Dow *et al.*, 1984), drought and low N tolerance as well as for general stress tolerance (Troyer, 1996; Reeder, 1997; Vasal *et al.*, 1997). Troyer (1996) emphasized that selection at higher PD is survival of the fittest in its purest form, resulting in tougher inbred lines and hybrids.

On the other hand, based on the above justification, indirect selection is suggested as alternative to direct selection in areas with unpredictable rainfall patterns. Indirect selection, that is the use of a selection environment that considerably differs from the target environment, is predicted to be more efficient than direct selection in the target environment itself, provided that $h_r < | r_G h_S |$,

where h_r and h_S are the square roots of the heritabilities of grain yield in the target and selection environments, and r_G is the genetic correlation between grain yields in both environments (Falconer, 1989). It is likely that a selection environment more similar to the target environment would result in larger selection gains (Bänziger *et al.*, 1997). As a result, according to Falconer (1989), Atlin & Frey (1990) and Zavala-Gracia *et al.* (1992) relative efficiency (RE) of indirect selection to direct selection was estimated as:

$$\text{RE} = \frac{\text{Predicted gain from indirect selection}}{\text{Predicted gain from direct selection}} \text{ X } 100$$

Similarly, Bänziger *et al.*, (1997) calculated the efficiency of indirect selection under high N versus direct selection under low N as: $IR_{LowN}/R_{lowN} = r_G h_{High}N/h_{LowN}$, where IR_{LowN} is the predicted response of grain yield under low N to indirect selection under high N, R_{lowN} is predicted response of grain yield under low N to direct selection under low N, r_G genetic correlation between grain yield under low and high N, and $h_{High}N/h_{LowN}$ are the square roots of the heritabilities of grain yield under low and high N. The investigators have suggested that a value of 1.0 for IR_{LowN}/R_{lowN} indicates that indirect and direct selections are equally efficient. Thus when IR_{LowN}/R_{lowN} is less than

1.0, direct selection is regarded to be more efficient than indirect selection. Atlin & Frey (1990) and Ceccarelli *et al.* (1992) suggested that the relative efficiency of indirect versus direct selection is dependent on the magnitude of the heritabilities and the genetic correlation coefficient.

2.4. Combining ability, heterosis, and G x E interaction

2.4.1. Combining ability

Currently there is good evidence suggesting that hybrids maintain their advantage over open pollinated varieties (OPVs) in both stress and non-stress environments (Dass *et al.*, 1997; Vasal *et al.*, 1997; Tsaftaris, 1999). Duvick (1999) has stressed that hybrids facilitate combination of multiple traits into one cultivar. For convenience when incorporating drought and low N tolerant traits, a hybrid breeding methodology will be the simplest approach, since heterosis is associated with stress tolerance (Srinivasan *et al.*, 1997). The importance of genetic diversity of inbred lines used in crosses is generally accepted, and line information indicative of hybrid performance is desirable to reduce hybrid evaluation (Hallauer & Miranda, 1988; Falconer, 1989).

Combining ability has been defined as the performance of a line in hybrid combinations (Kambal & Webster, 1965). Since the final evaluation of inbred lines can be best determined by hybrid performance, it plays an important role in selecting superior parents for hybrid combinations and in studying the nature of genetic variation (Hallauer & Miranda, 1988; Duvick, 1999; Koutsika-Sotiriou, 1999). Sprague & Tatum (1942) introduced the concepts of general combining ability (GCA) and specific combining ability (SCA). The authors defined GCA as the average performance of a line in hybrid combinations, while SCA as those instances in which certain hybrid combinations are either better or poorer than would be expected of the average performance of the parent inbred lines included. For random individuals, GCA is associated with additive effects of the genes, while SCA is related to dominance and epistatic effects (non-additive effects) of the genes. However, Rojas & Sprague (1952) verified that the variance of SCA also contains deviations due to the interaction between genotypes and environments, in addition to those that come from dominance and epistasis. GCA and SCA is an indication of genes having largely additive and non-additive (dominance and epistatic) effects, respectively. Sprague &

Tatum (1942) found that GCA was relatively more important than SCA for unselected inbred lines, whereas SCA was more important than GCA for previously selected lines for influencing yield and stalk lodging. However, studies have indicated that inbred yields predicted GCA more accurately than SCA (Duvick, 1999). GCA effects quantitatively measure the comparative performance of parents and cross combinations in relation to one another.

Diallel mating is a commonly used experimental design for crossing inbred lines in which each line is crossed with every other line (Singh & Paroda, 1984; Falconer, 1989; Sughroue & Hallauer, 1997). Griffing (1956) has developed a range of analytical procedures. In general, diallel analysis have been used primarily to estimate genetic variances (Model II) when parents are either random individuals or inbred lines from a random-mating population in linkage equilibrium, and to estimate general and specific combining ability effects from crosses of fixed lines (Gardner & Eberhart, 1966; Singh & Paroda, 1984; Hallauer & Miranda, 1988; Sughroue & Hallauer; 1997). If the parents of a diallel are selected on performance, then a fixed-effects model (Model I) should be used in the analysis. Since a reference population does not exist under these circumstances, GCA and SCA are valid with Model 1 (Wright, 1985; Hallauer & Mirinda, 1988; Sughroue & Hallauer, 1997). Sughroue & Hallauer (1997) indicated that estimates of variance components from populations can be used to calculate heritabilities, genetic correlations, and predicted gains from selection. In addition, they reported that estimates of additive (σ^2_A) and dominance (σ^2_D) variance from a random sample diallel were significantly different from estimates of σ^2_A and σ^2_D in a fixed sample diallel in their study. They also indicated over estimation of dominance levels for grain yield in a fixed sample compared to a random sample. Thus genetic estimations made in diallel analaysis from fixed lines represent only the lines included in that diallel.

Investigators reported more proportional and significant GCA effects for yield, days to silk and plant height in different groups of broad based CIMMYT maize populations and pools across locations (Beck *et al.*, 1990; Crossa *et al.*, 1990b; Vasal *et al.*, 1992). Mungoma & Pollack (1988) reported similar results of a high proportion of GCA for these traits in a study made between 10 Corn Belt and exotic maize populations. On the other hand, Singh & Asnani (1979) found significant mean squares for GCA and SCA for yield and 100-grain weight, number of kernel rows ear^{-1}, number of kernels row^{-1}, ear length and ear diameter in a 8 x 8 diallel cross of maize inbred lines. These authors concluded that both GCA (additive) and SCA (non-additive) effects play an important role in the inheritance of yield and its components. For a 7 x 7 diallel cross among maize lines in Ethiopia, Shewangizaw *et al.* (1985) also reported significant GCA and SCA for most traits, but predominance of non-additive genetic variance (σ^2_{SCA}) in the case of yield. Furthermore, studies for nitrogen use indicated the greater importance of additive gene action (GCA) as compared to nonadditive (SCA) gene action (Lafitte & Edmeades, 1995b; Below *et al.*, 1997).

Dass *et el.* (1997) reported that the Indian varieties Harsha and Navjot had good GCA for a number of characters, and this likely explains their stable performance across a large number of locations. Estimates of combining abilities across environments have indicated that both GCA and SCA for most characters interacted with environmental change, but GCA was found to be more sensitive to environmental change than SCA. Sprague & Tatum (1942) emphasised that estimates of GCA and SCA are relative to and dependent on the particular set of inbred lines included in the hybrids under testing. Line traits under severe stress were more strongly correlated with top-cross performance under severe drought stress than line traits under normal conditions (Betrán *et al.*, 1997). According to this report, selection for a reduction in ASI, senescence and barrenness in the lines, together with line *per se* yield performance under drought, could be used to select stress tolerant hybrids. In general, the presence of a number of yield limiting constraints on farmers' fields in the tropics (Bänziger *et al.*, 1999b) demand the assessment of drought tolerant lines and their F_1 performance under diverse environments, including high PD. Besides, knowledge about the combining ability of CIMMYT's drought tolerant lines in diverse environments is essential for national research programs that use this germplasm.

2.4.2. Heterosis

Heterosis is the genetic expression of the superiority of a hybrid in relation to its parents (Miranda Filho, 1999). This phenomenon is the opposite of inbreeding depression in that ‘hybrid vigor’ manifests in increased size, or other parameters resulting from the increase in heterozygosity in the F_1 generation of crosses between inbred lines (Sprague, 1983; Duvick, 1999; Miranda Filho, 1999). When dealing with populations, inbreeding depression is an intra-population effect, while heterosis is expressed at the inter-population level. Many authors also pointed out that genetic divergence between parents and non-additive genetic effects are required for heterosis expression (Moll *et al.*, 1965; Sprague, 1983; Hallauer & Miranda, 1988; Miranda Filho, 1999). Although two major theories (dominance and over-dominance) of heterosis have been proposed, mechanisms underlying the phenomena are largely unknown (Hallauer & Miranda, 1988; Coors, 1999; Tsaftaris *et al*., 1999). In general, based on parents used, two major types of estimation of heterosis are reported in literature: 1) Mid-parent or average heterosis (MPH), which is the increased vigor of the F_1 over the mean of two parents; 2) High-parent or better parent heterosis (HPH), which is the increased vigor of the F_1 over the better parent (Sinha & Khana, 1975; Jinks, 1983). For HPH, the term heterobeltiosis has been suggested to describe the increased performance of the hybrid over the better parent (Fonseca & Patterson, 1968).

Maize hybrids typically yield two to three times as much as their parental lines. However, since a cross of two extremely low yielding lines can give a hybrid with high heterosis, a superior hybrid is not necessarily associated with high heterosis (Duvick, 1999). This author suggested that a cross of two high yielding inbreds might exhibit less heterosis but nevertheless produce a high yielding hybrid. Besides, a hybrid is superior not only due to heterosis but also due to other heritable factors that are not influenced by heterosis. Heterosis is also modified by the interaction between genotypes and environment (Duvick, 1999; Chapman *et al.*, 2000). Since inbreds are more sensitive to environmental differences, some traits have been found to be more variable among inbreds than among crossbreds (Falconer, 1989). Similarly, Jinks (1983) indicated that if homozygous and heterozygous genotypes respond differently to environmental change, the magnitude of heterosis would vary with the environment.

Heterosis is dependent not only on the parent combinations but also on the effect of environmental conditions and species as well as the trait under consideration (Knight, 1973; Jinks, 1983; Young & Virmani, 1990; Chapman *et al*., 2000). Young & Virmani (1990), for their particular study, reported that the extent of heterosis in rice was higher in a stress environment than in a favorable environment. For temperate maize, Duvick (1999) pointed out that yield gains in hybrids always were accompanied by improvement in tolerance to biotic and abiotic stresses, and that improvement occurred in parental inbreds as well as in their hybrid progeny. Similarly for tropical maize, Betran *et al.* (2003b) reported extremely high expression of heterosis under stress, especially under severe drought stress because of the poor performance of inbred lines under these conditions. The superior performance of inbreds under high plant density was also observed as superior performance under high densities of hybrids derived from such lines (Troyer & Rosenbrook, 1983; Russel, 1991; Troyer, 1996). It is generally considered that inbred lines with superior yields under drought and low N will result in superior hybrids under these stresses, even though their correlations are relatively weak (Vasal *et al.*, 1997). Since selection for tolerance to mid-season drought appears to increase grain yield across a range of N stress (Bänziger *et al.*, 1999b), tolerance to other abiotic stresses is also expected. However, there is a lack of information about the magnitude of heterosis in hybrids developed from drought tolerant lines when tested under high PD conditions and in different environments.

2.4.3. Genotype x environment interaction (GEI)

Plant breeding aims to improve crop production either within a given macro-environment or in a wide range of growing conditions. These two approaches have important implications on breeding methodologies and strategies (Ceccarelli, 1989). However, a successful cultivar needs to posses high and stable yield potential over a wide range of environmental conditions (Eberhart & Russel, 1969; Wricke & Weber, 1986; Becker & Leon, 1988, Fasoula & Fasoula, 2002). The basic cause for differences between genotypes in their yield stability is a wide occurrence of GEI. The change in rank and the relative differences over a range of locations is defined statistically as GEI, which is a differential genotypic expression across environments (Becker & Leon, 1988; Ceccarelli, 1989; Romagosa & Fox, 1993; Sharma, 1998; Kang, 1998; Janick, 1999). The presence of GEI in any genetic study simply leads to overestimation of genetical and statistical parameters (Sharma, 1998). However, the knowledge of GEI can help to reduce the cost of extensive genotype evaluation by eliminating unnecessary testing sites and by fine-tuning breeding programs. Various biotic and abiotic stresses have been implicated as causes of GEI. It is an inherited trait that can be incorporated into heterotic combinations (Russel & Eberhart, 1968; Eberhart & Russel, 1969). Consequently, improving genotype resistance/tolerance to different stresses to which they would likely be exposed might minimize GEI (Kang, 1998).

Maize yield in resource limited farmers' fields in the tropics average 1 to 2 ton ha^{-1} (CIMMYT, 1994), in contrast to 6 to 9 ton ha^{-1} attained in the same region with adequate water and nutrients, and biotic stress controlled (Loomis, 1997). Abiotic stresses, principally from drought and low soil fertility, and often exacerbated by competition from intercrops and weeds are major reasons for the yield gap (Simmonds, 1991; Bänziger *et al.*, 1997). In addition, increased human population pressure, high input cost and extreme poverty force smallholder farmers in the region to implement low input farming systems (Bänziger *et al.*, 1999a). This indicates that farmers' fields are rarely characterized by only one abiotic stress, and it would be desirable to increase tolerance of crops to several stresses that occur in target environments (Bänziger *et al.*, 1999a; 1999b). Duvick (1999) and Janick (1999) indicated that yield increases in the USA have come about principally because of increased stress resistance, particularly the ability to produce under increased stress of high PD. Furthermore, Tollenaar & Lee (2002) indicated that genetic improvement in maize yield is associated with increased stress tolerance, which is consistent with the improvement in the GEI. Other studies have shown that drought tolerant selections perform well under low N conditions (Bänziger *et al.*, 1999b). Chapman *et al.* (1997) also indicated that selection for drought tolerance has improved broad adaptation, as well as specific adaptation to dry environments. Thus performance in a range of environments, both in favourable and stress environments is what is needed in practice (Rosielle & Hamblin, 1981; Falconer 1989). Earlier, Eberhart & Russel (1966) demonstrated that heterogenous populations (varietal crosses or single crosses) tended to have better yield stability than homogeneous ones (inbreds). Fehr (1987) also indicated that stability of heterozygous individuals seems to be related to their ability to perform better under stress conditions than homozygous plants. These phenomena demand the assessment of drought tolerant lines and their F_1 performance under diverse environments, including high PD, which is an indicator of general stress tolerance.

A number of statistical methods are now known for estimation of phenotypic stability. Finlay & Wilkinson (1963) developed regression coefficients to study the adaptation of barley varieties. Eberhart & Russel (1966) improved this model by including non-linear responses (deviation from regression, S^2di) and the environmental index (Ij) instead of site means. According to these authors a stable genotype is one that shows (i) a high mean yield, (ii) a regression coefficient (bi) approximating unity, and (iii) a mean square deviation from regression (S^2di) near zero. However, Jatasra & Paroda (1980) emphasized the use of deviation from regression alone as a measure of stability whereas linear regression could be treated as a genotype response.

On the other hand, Crossa (1990) and Sharma (1998) noted a number of limitations of the joint regression method. The authors indicated that: (a) the genotype mean is not independent of the marginal means of the environments; (2) errors associated with slopes of genotypes are not statistically independent, because the sum of squares for deviation, with (G-1) (E-1) df, cannot be subdivided orthogonally among the G genotypes; and (3) the assumption of linear relationship between interaction and environmental means can be violated. Furthermore, additive main effects and multiplicative interaction (AMMI) proved distinctly more valuable for description of GEI effects than joint regression (Annicchiarico, 1997). This investigator noted that this model's superiority was not crop specific. Currently AMMI is the model of first choice when main effects and interaction are both important (Zobel *et al.*, 1988). This method integrates analysis of variance and principal component analysis into a united approach. They also indicated that it has no specific experimental design requirements, except for a two-way data structure. The significant feature of this model is that adjustment carried out using information from other locations refines the estimates within a given location. It removes residual or noise variation from GEI (Crossa *et al.*, 1990a).

The main important feature of AMMI analysis is its graphical (biplot) representation; it displays main effect means on the abscissa and scores for the first principal component axis (IPCA1 values) as ordinate of both genotypes and environment simultaneously (Crossa *et al.*, 1990a; 1997; Gauch & Zobel, 1996). In the biplot, genotypes with the same score on the x-axis have similar means and those that fall almost on a horizontal line or with the same y-score have similar interaction (Crossa *et al.*, 1990a; 1997). When a genotype and an environment have the same sign on the PCA axis, positive interaction occurred, but it was negative when one of them had a different sign (Zobel *et al.*, 1988; Crossa *et al.*, 1997). They also indicated that a genotype or environment with a large PCA (positive or negative) score has a large interaction, and a PCA score near zero has small interaction effects. Accordingly, a large genotypic IPCA1 value reflects more specific adaptation to environments with IPCA1 values of the same sign. On the contrary, genotypes with IPCA1 values close to zero show wider adaptation to the tested environments. Thus IPCA scores of a genotype in the AMMI analysis are the key to interpret the pattern of genotype responses across environments (Zobel *et al*, 1988; Gauch & Zobel, 1996; Crossa *et al.*, 1997).

2.5. Heritability and correlation

2.5.1. Heritability

Success of breeders in changing the characteristics of a population depends on the degree of correspondence between phenotypic and genotypic values (Dabholkar, 1992; Singh & Ceccarelli, 1995). A quantitative measure, which provides information about the correspondence between genotypic variance and phenotypic variance, is heritability (Dabholkar, 1992). The term heritability has been further divided into broad sense and narrow sense, depending whether it refers to the genotypic value or breeding value, respectively (Falconer, 1989). The ratio of genetic variance to phenotypic variance (V_G/V_P) is called heritability in the broad sense or genetic determination. It expresses the extent to which individual phenotypes are determined by the genotypes. A large percentage for a character is regarded as highly heritable whereas if it is smaller, some environmental agency is considered responsible for phenotypic manifestation of the character (Dabholkar, 1992). On the other hand, the ratio of additive variance to phenotypic variance (V_A/V_P) is called heritability in the narrow sense. This expresses the extent to which phenotypes are determined by the genes transmitted from the parents. It also expresses the magnitude of genotypic variance in the population, which is mainly responsible for changing the genetic composition of a population through selection (Falconer, 1989; Dabholkar, 1992).

A broad sense heritability estimate based on various components of variance provides information on the relative magnitudes of genetic and environmental variation in the germplasm (Dudley & Moll, 1969). However, the type of gene action involved in the expression of a character has a significant role in determining heritability values. Characters that are controlled largely by genes acting in an additive fashion have higher values of heritability than characters governed by genes with large non-additive effects (Hanson, 1963; Falconer, 1989; Dabholkar, 1992). According to Dabholkar (1992), it is important to note that heritability is a property not only of the character being studied, but also the population being sampled and the environmental circumstances to which individuals have been subjected. More variable environmental conditions also reduce the magnitude of heritability while more uniform conditions increase it (Blum, 1988; Rosielle & Hamblin, 1981). Even the unit used in reporting, influences the magnitude of heritabilities (Hanson, 1963). Furthermore, predicting response to selection, heritability estimates are used to identify optimum environments for selection (Singh & Ceccarelli, 1995). Whether direct or indirect selection is superior depends upon the heritability of the selected trait in stress and non-stress environments and the genetic correlation between stress and non-stress environments (Atlin & Frey, 1990; Ud-Din *et al.*, 1992; Zavala-Garcia *et al.*, 1992). However, many investigators reported a decline in heritability for grain yield under stress (Rosielle & Hamblin, 1981; Blum, 1988).

A large number of studies have been conducted on maize to estimate both broad sense (h_b^2) and narrow sense (h_n^2) heritabilities. According to Hallauer & Miranda (1988), plant and ear height, and oil content had the highest estimates (h^2 >70%). The h^2 value for number of ears, kernel weight, ear length and ear diameter ranged from 30 to 50%, while yield and kernel depth showed less than 30%. A number of reports on heritabilities are available for different traits of maize under drought stress and low N conditions (Edmeades *et al.*, 1993, 1994, 1997d; Bolaños & Edmeades, 1996; Bänziger & Lafitte, 1997). They suggested ASI as a highly heritable trait. Average broad sense heritabilities estimated under low N stress were 0.46 for grain yield, 0.52 for ASI, 0.44 for EPP, 0.35 for leaf chlorophyll concentration, and 0.60 for leaf senescence (Bänziger & Lafitte, 1997). Bänziger *et al.* (1997) found that broad sense heritabilities for grain yield under low N were on average 29% smaller than under high N because of lower genotypic variance under low N. In general, standard errors of heritabilities, genetic correlations, variances, and covariances increase with decreasing heritabilities (Falconer, 1989). Bänziger & Lafitte (1997) concluded that secondary traits are valuable adjuncts in increasing the efficiency of selection for grain yield when broad-sense heritability of grain yield is low. Similarly under three moisture regimes, studies based on S_1 to S_3 progenies in six tropical maize populations indicated increased broad sense heritability with decreased stress for most traits except EPP (Bolaños & Edmeades, 1996). Furthermore, it should be kept in mind that the estimate of heritabilities applies only to environments sampled (Hanson, 1963; Dudley & Moll, 1969; Hallauer & Miranda, 1988; Dabholkar, 1992). Thus, when planning to improve a locally available elite population, in addition to determining variability, priority should be given to estimation of heritabilities of the stress tolerant traits under targeted environmental conditions.

2.5.2. Correlation

Relationships between two metric characters can be positive or negative, and the cause of correlation in crop plants can be genetic or environmental (Hallauer & Miranda, 1988; Falconer, 1989). Two types of correlations, phenotypic and genetic, are commonly discussed in plant breeding. Phenotypic correlation (r_P) involves both genetic and environmental effects. It can be directly observed from measurements of the two characters in a number of individuals in a population (Hallauer & Miranda, 1988). Genetic correlation (r_A) is the association of breeding values (i.e., additive genetic variance) of the two characters (Falconer, 1989). Both measure the extent to which degree the same genes or closely linked genes cause co-variation in two different characters (Hallauer & Miranda, 1988). Estimation of genetic and phenotypic correlations is based on components of variances and covariances that are estimated from analyses of variance and covariance, respectively. However genetic correlations inherently have large errors because of difficulties to avoid the directional effects of confounding factors on additive correlation estimates. A line's performance is correlated with its performance in crosses, to some extent depending on how much of the variance is due to additive genes. Thus evidence to date indicates that improvement in inbreds *per se* will play an increasingly large role in improving the performance of hybrids (Falconer, 1989; Duvick, 1999). According to Gama & Hallauer (1977) the association between traits of inbred lines and their hybrids range from significantly negative to significantly positive. However, other studies on inbred-hybrid yield showed low positive correlation (Duvick, 1999). This author also reported that even low positive correlations may indicate a tendency for high yielding inbreds to produce high yielding hybrids. There is evidence that, under stress conditions imposed through high plant densities, the relationship between line and hybrid performance is somewhat stronger than under non-stress conditions (Beck *et al*., 1997). Balko & Russel (1980b), however, observed a positive but non-significant correlation for efficiency of N use between inbred parents and their hybrids. Lafitte & Edmeades (1995b) also did not find significant association (r = 0.22 ns) between S_2 lines and their top crosses under low N. Others indicated that correlations between inbred line traits and either the same or different traits in their hybrids can be used to determine the effectiveness of selection on hybrid performance (Hallauer & Miranda, 1988).

Genetic correlation in particular determines the degree of association between traits and how they may enhance selection. It is useful if indirect selection gives greater response to selection for traits than direct selection for the same trait. It is suggested that indirect selection would be effective if heritability of the secondary trait is greater than that of the primary trait and genetic correlation between them is substantial (Falconer, 1989). Similarly, Rosielle & Hamblin (1981) also indicated that magnitudes of selection responses and correlated responses will depend on heritabilities and phenotypic standard deviations as well as genetic correlations. Other studies that computed phenotypic correlation found positive correlations between grain yield and yield components, ear height and plant height (Obilana & Hallauer, 1974; Ottaviano & Camuss, 1981). Hallauer & Miranda (1988) summarized available estimates of genetic correlations in literature among 13 traits of maize of different populations under normal environmental conditions. Average genetic correlations with yield were larger for ear traits than for plant and ear height, days to flowering, and tiller number. Plant height and ear height had the highest association (r = 0.81), and some of the ear traits showed moderate correlations. Unlike the results mentioned for groups of populations, days to flowering were negatively correlated (r = -0.52) with yield for Iowa Stiff Stalk Synthetic. Inbreeding that delays flowering has been considered as the main reason for this trend because it was estimated from two sets of unselected inbred progenies.

On the other hand, Cross & Zuber (1973) reported inconsistent interrelationships among plant height, number of leaves and days to flowering due to the effect of different environments. The main criteria for drought tolerant or low N tolerant trait selection is the association of each trait with grain yield under stress conditions (Edmeades et al., 1997d, Bänziger & Lafitte, 1997). Based on evaluation of S_1 to S_3 progenies from six elite tropical maize populations, Bolaños & Edmeades (1996) reported high correlations (r_g= 0.7 to 0.8) between GY and kernels ear^{-1}, ears plant^{-1}, and kernels plant^{-1} under drought and across all moisture regimes. These associations increased when the stress levels intensified. A strong phenotypic association between grain yield and grain number m^{-2} in both water-stressed and well-watered environments (r = 0.96; r = 087) was reported by Chapman & Edmeades (1999). Bolaños & Edmeades (1996) also indicated that variation in grain number has a more pronounced effect on yield rather than grain weight. Similar results were reported in two of these populations by Guei & Wassom (1992), who found high associations between grain yield and days to 50% silking, ASI, and EPP under drought stress. In tropical populations improved for drought tolerance, a strong positive relationship was reported between harvest index and grain yield under drought conditions (Bolaños & Edmeades, 1993a; Edmeades et al., 1993; 1999). Chapman & Edmeades (1999) reported a strong phenotypic association between grain yield and grain number m^{-2} (GNA) in both water-stressed and well-watered environments (r=0.96; r=0.87). They also reported that grain yield, EPP and NKE were strongly correlated with ASI under drought conditions, but not when water was plentiful.

Rosielle & Hamblin (1981) indicated that tolerance and mean productivity show negative genetic correlations when the genetic variance in stress environments is less than the genetic variance in non-stress environments. Under drought and low N stress conditions, yield increases were strongly associated with reduced ASI, reduced barrenness and increased harvest index, but mildly associated with delayed leaf senescence and reduced tassel size (Bänziger & Lafitte, 1997; Edmeades *et al.*, 1997d; 1997c). Similarly, Buren *et al.* (1974) reported strong phenotypic association between yield and ASI for temperate maize under high PD. However, the associations of grain yield with most of these traits under high PD conditions are not well known, especially for drought tolerant tropical genotypes. Thus, it is important to determine if relationships observed under drought conditions hold true under high PD conditions.

Hallauer & Miranda (1988) noted that heritability coefficients, as well as additive genetic correlation, depend on the population under selection and on environmental conditions. This indicates that the advantage of direct and indirect selection must be investigated for each particular situation as demonstrated earlier. Productivity of the plants in the selection environments and /or a high correlation between yield in the test and the target environments have been used to identify the most appropriate selection environments (Zavala-Garcia *et al.*, 1992). Falconer in 1952 (cited by Falconer, 1989) indicated that a trait measured in two different environments is to be regarded not as one trait but as two. If the genetic correlation between the trait in the two environments is high, then performance in two different environments represents very nearly the same trait, determined by very nearly the same set of genes. If it is low, then the traits are to a great extent different, and high performance requires a different set of genes (Falconer, 1989). Similarly, Eisen & Saxon (1983) pointed out that a genetic correlation of close to one implies that genotype by environment (G x E) variance is negligible, while less than one indicates the presence of G x E interaction. Based on this assumption, the genetic correlation between the selection and target environments has been suggested as an alternative method to identify the best selection environment (Falconer, 1989), which was previously discussed under sub-heading 2.3.3. Screening techniques.

Chapter 3 Genotypic variability for drought and high plant density adaptive traits in maize population A-511

3.1. Abstract

In the tropics, drought tolerant maize genotypes are preferable for their performance across variable environments. For development of these genotypes, locally adapted germplasm with adequate variability in drought adaptive traits are suggested for possible genetic gain in selection. In irrigation managed fields, S_1 lines from population A-511 were tested to estimate: (i) available variability for drought and high plant density adaptive traits; (ii) heritability of the traits, and association between grain yield and secondary traits; and (iii) efficiency of high plant density as alternative for drought tolerance screening. The 196 randomly derived S_1 lines from population A-511 were tested at two plant densities in well watered and drought stressed environments. Both plant density and drought stress significantly affected the tested primary and secondary traits of the S_1 lines. More pronounced effects of drought stress as compared to high plant density were observed in reducing grain yield and its components as well as in delaying days to 50% silking. Significant genotypic variability (σ^2_G) existed among the S_1 lines mainly for yield, ears plant^{-1} (EPP), anthesis-silking interval (ASI), kernels ear^{-1}, and kernels plant^{-1}, which are considered as drought and high plant density adaptive traits. The σ^2_G for yield and most of its components reduced with increased stress, while for EPP and ASI it increased in the same direction. Among the stress adaptive traits, the yield components exhibited strong and consistent association with yield in each environment, while ASI showed strong association only under drought stress. However, the association of stress adaptive traits with yield increased with increased stress. Heritability of EPP increased with increased stress while other yield components and grain yield increased with decreasing stress. The indirect and direct selection response estimated in drought stressed normal plant density (DSND) and drought stressed high plant density (DSHD) environments were found to be equally efficient. However, from the observations in the study, DSHD was suggested to be the better alternative to DSND for drought tolerance screening in areas with an unreliable rain-free season. In general there was considerable genotypic variability for yield and stress adaptive traits in population A-511, which can be used for improvement in performance both under drought and non-drought stress conditions.

Key words: Drought adaptive traits, drought stress, plant density.

3.2. Introduction

In sub-Saharan Africa, 40% of the maize (*Zea mays* L.) area experiences occasional drought, whereas 25% of the area is frequently affected (CIMMYT, 1990). In Ethiopia, production of this crop is seriously affected mainly due to recurrent drought occurring in over 66% of the total land area (Fig 3.1; MOA, 1998). For instance, 22.5% of the country's maize yield was reduced due to this stress during the 1997/98 cropping season (FDRE, 1998). Although drought is unpredictable, maize is most susceptible to this stress at flowering (mid-season), which increases the anthesis-silking interval and causes barrenness, resulting in substantial yield losses in the tropics each year (Bolaños & Edmeades, 1996; Edmeades *et al.*, 1997d; Vasal *et al.*, 1997). To assist farmers facing this problem, CIMMYT has improved some tropical maize populations for drought tolerance while maintaining their yield potential under favourable conditions (Fischer *et al.*, 1987; Bolaños & Edmeades, 1996; Edmeades & Bänziger, 1997).

At CIMMYT, both drought stress and well-watered environments, which are managed by irrigation, especially in the rain free season, are used during screening for mid-season drought tolerance (Vasal *et al.*, 1997; Chapman & Edmeades, 1999). This is mainly because of erratic rainfall occurring in the tropic region which needs genotypes that perform well under both stress and non-stress conditions (Edmeades & Bänziger, 1997; Vasal *et al.*, 1997). Besides, resource poor farmers' fields in the tropics are rarely characterized by only one abiotic stress and most farmers practice low input agriculture (Bänziger *et al.*, 1997; 1999a, b). A basic issue to improve productivity for areas with variable environments is choosing the environment to use for selection (Zavala-Garcia *et al.*, 1992). Although not well known, screening under high plant density has been suggested for augmenting selection for drought and other abiotic stress tolerance in areas with unpredictable rainfall patterns (Dow *et al.*, 1984; Reeder, 1997; Vasal *et al.*, 1997), and for wide adaptation (Troyer, 1996).

For drought tolerance improvement, CIMMYT mostly practiced S_1 recurrent selection that mainly used increased grain yield and ears plant^{-1}, and reduced anthesis-silking interval, which are known as the main drought adaptive traits (Edmeades *et al.*, 1997d; Bänziger *et al.*, 1999b). These are also considered as high plant density adaptive traits (El-Lakany & Russel, 1971; Buren *et al.*, 1974; Dow *et al.*, 1984; Tollenaar *et al.*, 1992; Vasal *et al.*, 1997). Studies have shown that mid-season drought tolerant genotypes also perform well under low N conditions (Bänziger *et al.*, 1999b), and have improved broad adaptation (Chapman *et al.*, 1997). Thus, this improvement strategy could increase maize production in countries like Ethiopia if the adapted local genotypes possess variability for the drought adaptive traits. Obilana & Hallauer (1974) determined the amount of genetic variation for various traits in Iowa Stiff Stalk Synthetic by using unselected inbred lines. Similarly, Bolaños & Edmeades (1996) estimated genetic variances for primary and secondary traits in each of the six tropical maize populations across moisture regimes by using S_1 to S_3 lines derived from this population. Others have also suggested testing the unselected inbred lines themselves for estimation of genetic variance in a population and for selection of superior progenies with desired traits simultaneously (Hallauer & Miranda, 1988). They also pointed out that unlike any other level of inbreeding, no handicap is present if randomly derived S_1 lines are used for genetic variance estimation.

A variety grown under drought conditions for a long time may presumably acquires some drought tolerance (Shukuan, 1997). For areas with high environmental variation, Ceccarelli (1996) indicated that genetic gains are possible by using locally adapted germplasm and by selecting in the target environment. Similarly, Edmeades & Bänziger (1997) suggested for national programs to focus on increasing stress tolerance and stability in elite local populations. According to Bänziger *et al.* (1999a) the two strategies that may lead to increased yields in drought prone environments of sub-Saharan Africa are: (1) selection of better adapted materials among drought-tolerant germplasm from CIMMYT, (2) deliberate selection for drought tolerance in materials that are well adapted to sub-Saharan Africa conditions. Although the first option is an ongoing activity in Ethiopia, no one assessed the available variability for drought tolerant traits in elite local maize populations. This study was, therefore, undertaken to assess: (i) genotypic variability for drought and high plant density adaptive traits within maize population A-511; (ii) heritability of the traits, and grain yield association with secondary traits, and (iii) efficiency of high plant density as alternative for drought tolerance screening.

3.3. Material and methods

Experimental materials

Population A-511 is an open pollinated variety, which was developed as an advanced generation of a Kenyan hybrid (H511). It was introduced from Kenya and improved by mass selection and ear-to-row selection methods (IRAT, 1972). Awasa Agricultural Research Station released this population in 1974. It has been widely cultivated in the moisture deficit zone of Ethiopia for more than 29 years. It is intermediate in maturity and farmers in drought stressed zones of the country prefer this variety due to its better performance than other available varieties under favourable rainfall conditions. On November 20, 2001, original seeds of Population A-511obtained from Ethiopian Seed Enterprise were planted in Ethiopia, at Melkasa Research Centre (8°24′N, 39°21′E, 1550 masl) where 400 S_1 lines were randomly produced.

Experimental procedures and design

The study was conducted during the off-season, from October 3, 2002 to February 27, 2003 at Melkasa centre. Out of the randomly selfed progenies, 196 S_1 selections with adequate seed development were evaluated under the following four growing conditions:

1. Well-watered normal plant density (WWND), where about 44 400 plants ha^{-1} were established with a spacing of 30 cm between plants within rows, and irrigated at seven day intervals until maturity.
2. Well-watered high plant density (WWHD), where the plant density in environment "1" was doubled with a spacing of 15 cm between plants (88 800 plants ha^{-1}).
3. Drought stressed normal plant density (DSND), where irrigation was suspended from 15 days prior to 50 % anthesis until 25 days after anthesis when one additional irrigation was made. The plant population was the same as in "1".
4. Drought stressed high plant density (DSHD), similarly drought stressed as in "3" but with plant density increased as in "2".

In the centre where the trial was conducted, a furrow irrigation system was used to apply about 40 mm of water, as estimated by partial flume, every seven days. For the two drought stressed treatments (growing conditions) the same amount of water was applied until watering was suspended. Rain did not interfere with the trial due to drought occurring in most of the country. The soil of the experimental site was classified as a Haplic Andosol (FAO/UNESCO) or Typic Haplustand (USDA), with clay loam to loam texture, with other properties indicated in Table 3.1

The experimental design for each environment was an alpha (0,1) lattice (Patterson & Williams, 1976) with two replications, using an incomplete block size of 14 plots. For each entry, single row plots of 4.2 m length was used, with the spacing between plants as determined for each environment. In addition to the 14 rows in the incomplete block, one border row of A-511 was planted at both ends of the block. The inter-row spacing was 0.75 m for all environments. Plots were established back-to-back in strips 11.25 m wide, with an open alley of 2 m between strips. The four environments were sown in adjacent blocks within the same field, while five free rows between well watered and drought stressed conditions were left to avoid leaching to the stressed treatments. Two seeds hill^{-1} were planted in all trials to ensure uniform stand and then thinned to one plant hill^{-1}. The trial in each environment was handled independently, and plots were kept free of weeds and insects. Except for plant density and moisture level, the same management was applied to each environment. As recommended by the centre, 50 kg P_2O_5 ha^{-1} and 25 kg N ha^{-1} was applied at planting, followed by a side dressing of 25 kg N ha^{-1} 35 days later. Urea and diamonium phosphate (DAP) were used as sources of N and P_2O_5, respectively.

Table 3.1. Soil properties at three depths of the experimental field at Melkasa Agricultural Research Centre, Ethiopia, 2002.

Depth (cm)	% Texture	F.C %	P.W.P %	PH	Available		Total N %
					P^+ (PPM)	K^+(PPM)	
0 –15	CL*	34.85	18.46	5.48	14.40	34.7	0.147
15 – 30	loam	35.67	18.80	5.45	10.80	35.4	0.161
30 – 45	loam	36.13	20.10	5.45	6.40	40.8	0.14

*CL = Clay loam, F.C.= field capacity, P.W.P.= permanent wilting point
Analysed by Ethiopian Agricultural Research Organization, National Soil Laboratory, Addis Ababa

Measurements

The outer plant nearest to the alley in each plot was not used for measurements. Days from planting to anthesis (AD) and silking (SD) were calculated from the date on which 50% of the plants had begun shedding pollen or had silks emerging from the husk. Anthesis-silking interval (ASI) was obtained by subtracting AD from SD. Three weeks after anthesis, plant height from ground level to the point of the flag leaf insertion was measured, and the number of primary tassel branches counted on five randomly selected plants plot^{1}. Visual scores of leaf senescence of lower leaves were taken in each plot on two occasions on February 2 and 9, 2003. Scores were on a scale of 0 (green, 0% dead leaf area) to 10 (dead, 100% dead leaf area).

In all trials, at physiological maturity, lodged plants, numbers of plants and ears were counted per plot bases. At this stage of crop development, ears were harvested excluding border plants. An ear was considered fertile if it had one or more grains on the rachis. Number of kernel rows ear^{-1} and kernels row^{-1} were counted on each fertile ear to determine number of kernels ear^{-1} and kernels plant^{-1}. All harvested ears were shelled and grain mass was recorded per plot in kg, and simultaneously, moisture percentage of the grain was determined by using a Dickey John moisture tester. The grain yield was recorded in ton ha^{-1} after being adjusted to the standard of 15% moisture content. A sample of 100 seeds was taken from each plot and oven dried for 24 hours at 80 ^{o}C to determine 100 seed mass. Repeated scores for each trait were averaged before analysis.

Statistical analysis

Data were first tested for normality, and ASI and LDG were normalized using $\log_e \sqrt{(ASI+10)}$, and arc sine transformation, respectively. As a result, mean squares and CV % for both traits are presented on transformed data. Data were analysed using plant densities and moisture levels (environment) as fixed factors, and genotype, incomplete blocks within replicates, and replicates within environments as random factors. An analysis of variance of each tested trait in each environment was carried out for an alpha (0,1) lattice design by Alpha software (CIMMYT Maize Program, 1999). However, a randomised complete block design (RCBD) was used for covariance estimation, using AGROBASE^{TM} software (Agronomix Software Inc., 1998), since the relative efficiency of the alpha lattice over RCBD was between 0 and 30 % for the tested traits. The genotypic variances (σ^2_G) in each (Singh & Chaudhary, 1985) and across environments were estimated from the variance among S_1 lines derived randomly from the Population A-511, and assuming no dominance effects (p = q = 0.5) (Hallauer & Miranda, 1988).

For each growing condition, σ^2_G and error variances (σ^2_E) were calculated from expected mean squares (Table 3.2.) of the analysis of variance (Singh & Chaudhary, 1985; Hallauer & Miranda, 1988). The error variances (σ^2_E) are equal to mean squares of error (Mse), while σ^2_G was calculated on an environmental basis as:

σ^2_G = (MSg – MSe)/r, where MSg and Mse were the mean squares of genotypes and error respectively, and r was number of replications.

However, it has to be considered that the estimates of components of variance from one environment included a genotype x environment interaction bias. The standard errors of estimates of genetic variance were computed by taking the square root of

$\frac{2}{r^2}\left[\frac{MS^2{}_g}{(n-1)+2}+\frac{MS^2{}_e}{(r-1)(n-1)+2}\right]$, where MS_g and MS_e were mean squares of genotypes and error, and r and n were number of replications and S_1 lines (genotypes), respectively (Hallauer & Miranda, 1988).

Broad sense heritability (h_b^2) for a specific trait in each environment was estimated on a progeny mean basis as $h_b^2 = \sigma^2_G/(\sigma^2_G + \sigma^2_E/r)$, where r was the number of replications, and σ^2_G and σ^2_E were estimates of genotypic and environmental variance, respectively (Hallauer & Miranda, 1988). Since it was not possible to distinguish between additive, dominant, and epistatic effects of the variance components, h_b^2 estimated the extent to which phenotypes were determined by the genotypes (Falconer, 1989).

Table 3.2. Analysis of variance and expected mean squares for S_1 lines in each environment.

Source	d.f.	Mean square (MS)	Expected MS
Replication	r-1		
Genotypes	n-1	MSg	$\sigma^2_E + r\sigma^2_G$
Error	(r-1)(n-1)	MSe	σ^2_E
Total	m-1		

On the other hand, combined analysis across the two plant densities in each moisture regime was conducted with PROC MIXED procedure from SAS (SAS, 1997). This was mainly to separate the value of the S_1 lines by environment interaction variance. Each plant density was considered as an independent environment. From the combined analysis, with similar assumption as indicated above, variance among S_1 lines (σ^2_G)

provides an estimate equivalent to σ^2_A. Direct F-tests and estimates of component of variances made from mean squares are shown in Table 3.3 (Hallauer & Miranda, 1988). Based on the expected mean squares, σ^2_G was estimated as:

$\sigma^2_G = [M3 - (M2 - M1)/r - M1]/re$, where M3, M2, and M1 are the mean squares of S_1 lines, S_1 line x environment interaction (G x E), and experimental error; r and e are the number of replications and environments, respectively. The G x E variance was estimated as σ^2_{GE} = (M2-M1)/r, whereas error variance σ^2 was equal to error mean square (M1). Similarly, for S_1 lines that were evaluated in experiments repeated over environments, h_b^2 for each trait on progeny mean basis was estimated as:

$$h_b^2 = \frac{d_G{}^2}{d^2/(re) + d^2{}_{GE}/e + d^2{}_G}$$

According to Hallauer & Miranda (1988), the standard error (SE) of σ^2_G was obtained from Table 3.3 as the square root of $2/(re)^2 \left[\frac{M^2 3}{n+1} + \frac{M^2 2}{(e-1)(n-1)+2}\right]$

As the combined analysis was done across two plant densities within a moisture regime (drought or well watered), genotypes x environment variances resulting from factors other than plant density were ignored.

Table 3.3. Analysis of variance of S_1 lines repeated over environments.

Source	df	Mean squares	Expected mean squares
Environments, E	e-1$^+$		
Replications / E	e(r-1)		
S_1 lines	n-1	M_3	$\sigma^2 + r\sigma^2_{GE} + re\sigma^2_G$
E x S_1 lines	(e-1) (n-1)	M_2	$\sigma^2 + r\sigma^2_{GE}$
Pooled error	e(r-1)(n-1)	M_1	σ^2

$^+$ e, r, n refer to the number of environments, replications within environments, and inbred lines, respectively.

Genetic and phenotypic correlations between grain yield and secondary traits in each environment were estimated using the formula given by Singh & Chaudhary (1985), and Falconer (1989). Genetic correlation (r_G) between pairs of traits were estimated as:

$r_G = \frac{d_{gxy}}{\sqrt{d^2{}_{gx}.d^2{}_{gy}}}$ where d_{gxy} is the genotypic covariance of traits x and y; $d^2{}_{gx}$ and $d^2{}_{gy}$ are genotypic variances of traits x and y. Similarly, phenotypic correlations (r_P) were estimated as: $r_P = \frac{d_{Pxy}}{\sqrt{d^2_{Px}.d^2_{Py}}}$ where d_{Pxy} is phenotypic covariance of traits x and y; and d^2_{Px} and d^2_{Py} are phenotypic variances of traits x and y, respectively. The significance of the correlation coefficients was determined using the Student t-test (Steel *et al.*, 1997).

The relative efficiency of indirect selection in WWND or WWHD or DSHD in relation to direct selection in drought stressed normal plant density (DSND) was computed in the current study. DSND is the common environment for drought tolerance screening particularly in an area that has a rain free season. This study was designed to assess alternative screening environments to DSND due to lack of a reliable rain free season at Melkasa. The relative efficiency of indirect selection in relation to direct selection in the target environments were estimated using the formula for ratio of correlated response to direct response (Falconer, 1989; Atlin & Frey, 1990; Bänziger *et al.*, 1997):

$CR_{DSND(WWHD)}/R_{DSND} = r_G\, h_{WWHD}/h_{DSND}$

where $CR_{DSND\,(WWHD)}$ is correlated response in DSND to selection in WWHD, R_{DSND}, is predicted response to direct selection in DSND, r_G is the genetic correlation between yield in WWHD and DSND, h_{WWHD} and h_{DSND} are square roots of heritabilities in WWHD and DSND, respectively.

Based on Falconer (1989), genetic correlation (r_G) between grain yield in DSND and in one of the other three environments (e.g. WWHD) was calculated as indicated below.

$r_G = \frac{d_G}{\sqrt{d^2_{G(DSND)}d^2_{G(WWHD)}}}$, where d_G was the estimated genetic covariance of grain yields under DSND and WWHD, and $d^2_{G(WWHD)}$ and $d^2_{G(DSND)}$ were the estimates of genetic variances of grain yield in the respective environments.

Predicted response in each environment was calculated as: $R = h * \sigma_G$

where R is predicted response to selection assuming a standardized selection differential of 1.0; h is the square root of broad sense heritability of grain yield in that environment, and σ_G is the square root of genetic variance of grain yield in the respective environment.

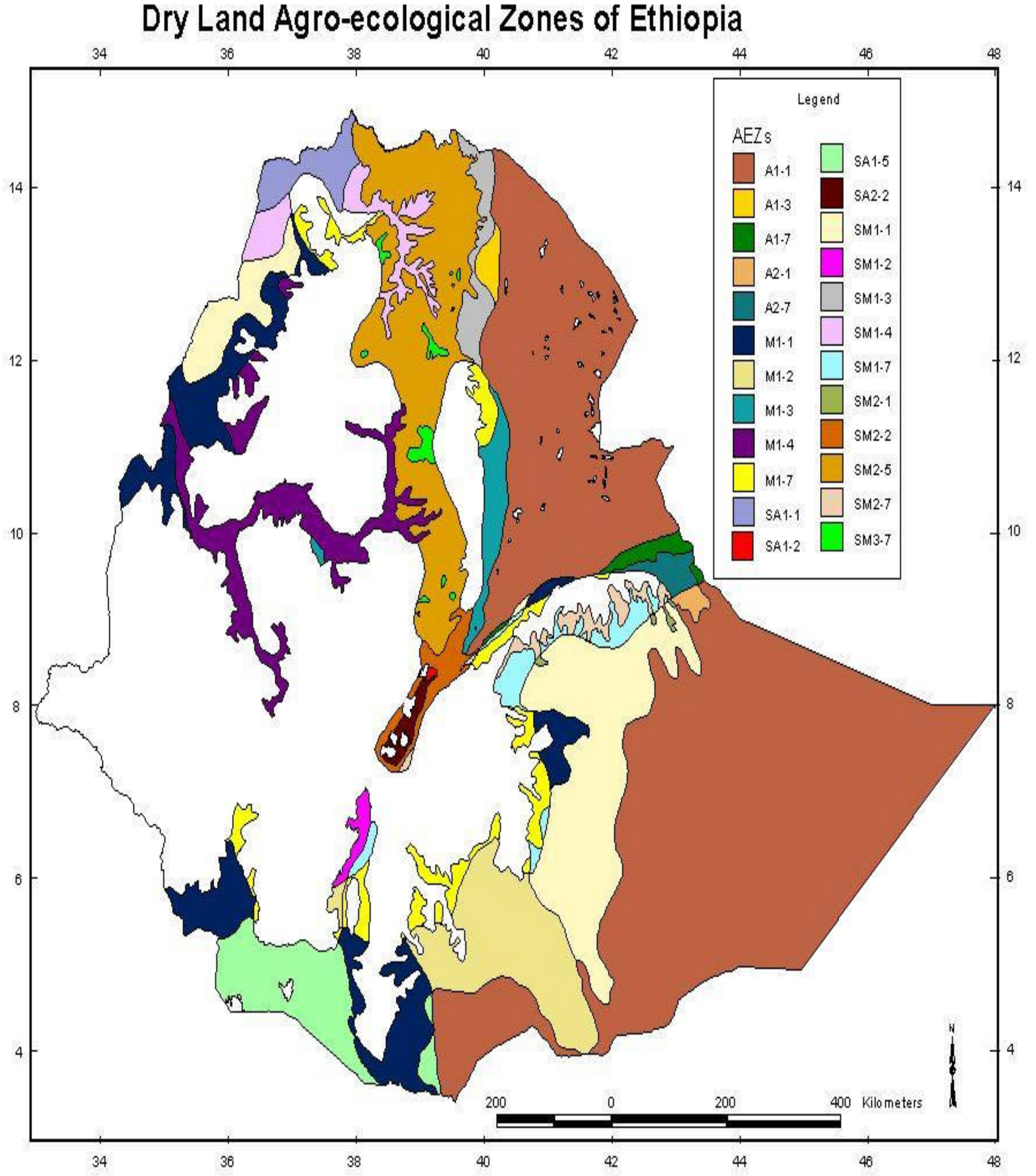

Fig. 3.1. Map of dry land agro-ecological zones of Ethiopia (MOA, 1998).

(Description of the legend in Appendix I)

3.4. Results and discussion

3.4.I. Performances

Grain Yield

The statistical significance, mean and range of performance of the randomly derived 196 S_1 lines when tested for grain yield (GY) in each environment are presented in Table 3.4. The result showed significant variability within population A-511 in yielding ability in each environment. Figure 3.2 demonstrated the adverse effect of each stress on grain yield of these S_1 lines. The progenies were nearly equally distributed about the mean for this trait in which 101, 106, 101 and 104 of them were below the mean in WWND, WWHD, DSND and DSHD growing conditions, respectively. More range and mean values for this trait were observed under well watered (WWND and WWHD) than drought stressed (DSND and DSHD) conditions (Table 3.4). This was indicated by high values of standard deviation, 0.917 in WWND, and 0.772 in WWHD. GY averaged 3.99, 2.86, 1.64 and 0.88 t ha^{-1} in WWND, WWHD, DSND and DSHD environments, respectively. Plant density stress reduced mean grain yield 28.3% under well watered, and 46.2% under drought conditions. The yield was also reduced by 58.9% due to moisture stress, and 77.9% when stresses were combined. Thus the GY reduced considerably due to moisture stress, and the negative impact of high plant density (PD) also increased when combined with drought.

The same trend was reported in each of six tropical maize populations of which S_1 to S_3 lines were tested under three moisture regimes in Mexico (Bolaños & Edmeades, 1996). Similarly, significant variation among full sib progenies within Tuxpeno Sequia (Bolaños & Edmeades, 1993a), and within La Posta Sequia and Pool 26 Sequia (Guei & Wassom, 1992) was noted for the trait across moisture regimes. The depression rate of this trait due to moisture deficit agreed with reported results of Bolaños &Edmeades (1996) who tested 3059 S_1 to S_3 lines derived from six tropical maize populations across moisture regimes in Mexico. According to their report, GY was reduced from well watered (WW) to intermediate drought stress (IS) by about 61.8% while from WW to SS (severe stress) it was reduced about 86%. The IS and SS moisture regimes used for their study were almost similar for this trait in their stress intensity to DSND and DSHD, respectively. Betran *et al.* (1997) also reported a grain yield reduction of about 88 to 90% when S_3 lines derived from Tuxpeño Sequia and La Posta Sequia were evaluated under well-watered and severe stressed conditions. Based on high PD in hybrid maize, Buren *et al.* (1974) indicated that GY decreased progressively as the number of plants increased in a given area, while decreased harvest index with increased PD was reported by Tetio-Kagho & Gardner (1988b). High PD magnified the severity of the stress when combined with intermediate moisture deficit as suggested by Beck *et al.* (1997) and Vasal *et al.* (1997). A more pronounced tendency of non-adaptability under drought conditions was observed as expressed by relatively increased CV% with increased stress (DSND = 28.69%, and DSHD = 50.24%).

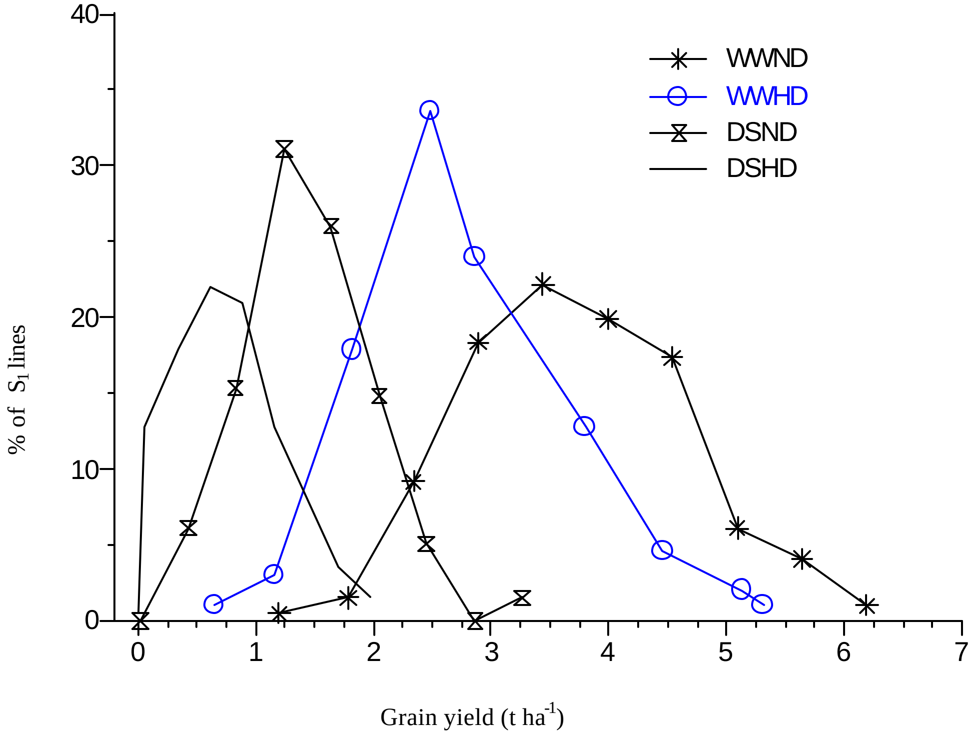

Figure 3.2. Grain yield distribution of 196 randomly derived S_1 lines when evaluated across four environments.

Yield components

Variability among the S_1 progenies for ears per plant (EPP), kernels ear^{-1} (NKE), kernels plant^{-1} (NKP), 100 seeds weight (HSW), and ear length (EL) were highly significant in each environment (Table 3.4). Only a change in moisture regime affected EL while EPP, NKE and NKP were affected by both plant density and moisture level. The HSW was more sensitive to moisture levels than to plant density change. Mean and range of values of the yield components were reduced with increased intensity of stress. For instance, EPP averaged 0.97 under WWND and 0.51 under DSHD conditions, while the corresponding values for NKE were 331.2 and 79.86. Accordingly, the highest and lowest values for all these traits were recorded under WWND and DSHD, respectively. Both plant density and moisture stress affected the performance of these traits but an increased negative effect was observed due to drought, particularly when drought was combined with high density. Relative to well watered normal density (WWND), WWHD, DSND and DSHD reduced mean EPP of the S_1 lines by 13.4%, 23.0% and 47.7%, respectively. Similarly, the corresponding figures for NKE and HSW were 10.96 and 10.72% under WWHD, 65.76 and 28.4% under DSND and 75.9 and 42.2% under DSHD. NKP declined sharply with increasing PD also reported by Tetio-Kagha & Gardner (1988b), and Andrade *et al.* (1993).

The reduction in EPP and NKE under DSND and DSHD was more or less matched with results by Bolaños & Edmeades (1996) who reported 27.37 and 49% reductions under intermediate and 49 and 78% reductions under severe drought stress. However, in the current study the NKE reduction under DSND was higher than their result under intermediate stress. Similarly, with 200 S_3 derived lines from Tuxpeño Sequia (TS) and La Posta Sequia (LPS), Betran *et al.* (1997) found about 53.44% reduction in EPP when tested under severe stress, which was somewhat higher than the result obtained at Melkasa. Under similar conditions, Chapman & Edmeades (1999) reported a reduction rate of 28.43 and 27.62% in EPP, 37.77 and 41.81% in NKE, and 47.96 and 48.44% in seeds weight on the original cycle of TS and LPS, respectively.

On the other hand, in testcrosses of 20 selected lines, El-Lakany & Russell (1971) reported reduced EPP (10%), NKP (33%), 300 seed weight (13.5%) and EL (26%) due to increased PD. However, their reductions were small in magnitude especially for EPP due to relatively reduced PD (60,000 plants ha^{-1}) as compared to the present study. Furthermore, the genotypes were top crossed rather than selfed progenies. Markedly reduced EPP under high PD was also reported by Buren *et al.* (1974) who suggested that density stress tolerant genotypes possess reduced ASI and tassel size as well as increased EPP and GY at high PD. NKP was considered as the most affected by PD among yield components (Tollenaar *et al.*, 1992) as observed in the present study.

Flowering parameters

A highly significant difference among progeny was detected for the three flowering traits in each environment (Tables 3.4). The results showed adequate variability within population A-511 for flowering time as observed among S_1 lines. Mean and range of values for AD of the tested progenies were almost similar across environments with about two days difference in mean values. Thus neither plant density nor moisture level affected days to 50% anthesis significantly. Both SD and ASI increased with increasing stress. Relative to WWND, the mean ASI increased more than double in the other environments, especially in DSHD. Thus both high PD and drought stress in combination or independently had significant effects on SD and ASI. Many investigators confirmed the presence of variability for these traits within tropical maize populations (Bolaños & Edmeades, 1993; 1996; Edmeades *et al.*, 1993; 1999; Betran *et al.*, 1997; Vasal *et al.*, 1997) under different moisture conditions, and among temperate hybrid genotypes under variable PD (El-Lakany & Russell, 1971; Buren *et al.*, 1974; Dow *et al.* 1984; Carlone & Russel, 1987; Tollenaar *et al.*, 1992).

For ASI, based on six selection cycles of Tuxpeño sequia, Bolaños & Edmeades (1993b) reported 1.9 mean days under well-watered conditions that increased to 18.8 days under severe moisture stress. In the original La Posta Sequia and Tuxpeño Sequia, this trait increased by 50.75 and 78.13% respectively, when tested under well watered and drought conditions (Chapman & Edmeades, 1999). They also noted significant changes under drought conditions for AD, which was delayed more than the response observed in Population A-511. El-Lakany & Russell (1971) also indicated delayed AD and SD of test crosses at high PD with more delayed silk emergence than pollen shed, increasing ASI by 14%. Because of hierarchical patterns in reproductive development in which tassel growth dominates ear growth, the main symptom of limited assimilate supply under high PD stress is a delay in silking (Edmeades *et al.*, 1993).

Plant height and number of primary tassel branches

Highly significant variability was observed for plant height (PH) and number of primary tassel branches (NTB) in this population (Tables 3.4). The mean performance for NTB was in the range of 14.4 to 16.69, indicating that NTB was not sensitive to environmental change as compared to PH. Relatively higher means and range of values for PH and NTB were recorded under well-watered (WWND and WWHD) conditions than under drought conditions (Table 3.4). However, NTB showed its highest mean and range of values in WWND and DSHD, respectively, while the corresponding values for PH were obtained with WWHD and DSND. PH decreased by 6.3% due to decreased PD and 32.93% due to drought stress with WWND and DSHD, respectively. The height increased with increasing PD in well-watered environments but was reduced under drought stress, particularly when both stresses were combined. Under drought stress, almost similar effects were reported (21.82%) with Tuxpeño Sequia (Chapman & Edmeades, 1999). Short stature hybrids were reported as more tolerant of high PD or drought at flowering than their taller counterparts (Fischer *et al.*, 1983; Dow *et al.*, 1984). Similarly, Johnson *et al.* (1986) demonstrated that optimum plat density for yield can be increased by selection for reduced plant height. In general, for both traits, the study demonstrated the available variability within population A-511, and a reduced impact of the tested growing conditions on NTB.

Lodging percentage and leaf senescence

Highly significant variability within population A-511 was observed for percentage of plants lodged per plot (LDG) and leaf senescence (SEN) in each environment (Table 3.4). Variability was demonstrated in the range of mean values recorded under each growing condition. The mean and range for percentage lodging and leaf senescence scores increased with increasing stress, particularly under well-watered high PD for LDG and with DSHD for SEN (Table 3.4). Relative to WWND, the mean LDG increased by 34.49% in WWHD, while SEN increased by 59.4% in DSHD. In agreement with the present study, Betran *et al.* (1997) reported 43.75% increased mean senescence due to drought with Laposta Sequia and Tuxpeño Sequia, while a 16.36% increment occurred with Tuxpeño Sequia when compared to well watered conditions (Chapman & Edmeades, 1999). The observed performance indicated that both stresses induced LDG but became more pronounced under well-watered high PD than drought stressed PD. This also implied that either of the two stresses, particularly high PD, could be used for LDG tolerance screening, rather than combining the two.

Table 3.4. Statistical significance and performance of traits of 196 randomly derived S_1 lines when tested across four environments at Melkasa, 2002.

Environment	WWND				WWHD			
Traits	Mean	Range	SS	CV%	Mean	Range	SS	CV%
GY	3.99 ±0.92*	1.4 - 6.29	**	17.34	2.86 ± 0.77	0.89 - 5.35	**	22.67
EPP	0.97 ± 0.11	0.65 -1.18	**	11.93	0.84 ± 0.10	0.53 -1.08	**	11.59
NKE	331.2 ±58.18	178.4- 474.3	**	18.43	294.9 ± 48.04	173.1- 415.5	**	16.44
EL	15.26 ± 1.45	11.4 -20.33	**	9.61	12.6 ± 1.28	8.87 - 16.68	**	11.14
NKP	326.54 ± 53.46	167.54-536.8	**	14.52	224.01 ± 43.06	144.8 - 431.9	**	12. 89
HSW	27.89 ± 2.61	20.06 -34.22	**	7.98	24.9 ± 2.38	18.21 - 29.57	**	9.12
AD	79.87 ± 4.21	71.05 - 88.94	**	3.41	82.1 ± 4.33	71.46 - 94.25	**	3.99
SD	83.45 ± 4.52	72.52 - 93.77	**	3.31	89.05 ± 5.3	74.27 -109.81	**	4.29
ASI	3.77 ± 1.64	0.0 – 7.0	**	3.19	7.03 ± 2.48	0.77 – 20	**	4.54
PH	177.88 ± 16.5	124 .7 - 218.4	**	8.26	189.83 ± 16.98	114.8 – 234.6	**	9.71
NTB	16.69 ± 1.91	11.18 -24.5	**	7.89	15.1 ±2.10	9.71 - 20.08	**	12.61
LDG	12.69 ± 4.71	1.77 -23.43	**	39.62	19.37 ± 8.32	2.13 - 40.81	**	33.67
SEN	3.24 ± 0.69	1.75 -6.13	**	20.9	4.84 ± 0.89	2.96 - 7.85	**	14.22
	DSND				DSHD			
GY	1.64 ± 0.54	0.45 – 3.31	**	28.69	0.88± 0.45	0.07 – 2.1	**	50.24
EPP	0.74 ± 0.15	0.25 – 1.14	**	19.12	0.51 ±0.12	0.19 – 0.8	**	22.9
NKE	113.4 ± 27.53	60.11 – 201.4	**	23.63	79.86 ± 25.62	20.27 –142.3	**	32.81
EL	10.07 ± 1.32	7.08 – 15.76	**	13.99	11.18 ± 1.31	8.07 –15.22	*	13.96
NKP	121.16 ± 32.16	77.61 – 171.1	**	16.03	72.76 ± 21.32	17.35 – 168.4	**	21.26
HSW	19.97 ± 6.32	15.5 – 30.26	**	15.36	16.13 ± 2.69	6.63 – 21.34	**	17.92
AD	80.73 ±3.76	72.48 – 88.06	**	2.94	81.89 ± 3.97	73.11 – 94.19	**	3.73
SD	89.43 ± 5.85	75.46 –99.24	**	4.27	91.35 ±5.82	79.05 –109.7	**	4.98
ASI	8.70 ±4.14	2 – 14.99	**	5.27	9.46 ± 3.26	2.25 –19.3	**	4.95
PH	158.4 ±19.44	84.4 – 211.9	**	10.45	127.31 ±17.69	81.83 – 177.8	**	13.84
NTB	14.43 ± 2.13	9.29 – 18.4	**	10.69	14.4 ± 2.75	8.3 – 23.86	**	17.17
LDG	15.6 ± 6.32	0 – 37.32	**	38.21	17.12 ±6.65	2.35 – 39.22	**	39.71
SEN	6.84 ± 0.75	3.62 - 8.13	**	10.04	7.93 ±0.81	4.92 – 9.34	**	9.82

*Standard deviation for the mean values of each trait estimated during analysis by Alpha software.
GY, grain yield in ton ha^{-1}; AD, days to 50% anthesis; SD, days to 50% silking; ASI, anthesis-silking interval; PH, plant height (cm); EPP, ears per plant; NKE, number of kernels ear^{-1}; EL , ear length in cm; NKP, number of kernels $plant^{-1}$; NTB, number of tassel branches; HSW, hundred seeds weight; LDG, lodging in %; SEN, leaf senescence; SS= statistical significance; *****, ****** significant at P= 0.05 and P = 0.01, respectively, WWND=Well watered + normal density; WWHD=Well watered + high density; DSND =Drought stress +normal density; DSHD= Drought stress +high density.

3.4.2. Genetic variance and heritability

In all environments, the estimated variance components for the tested traits exceeded more than twice their standard errors (Table 3.5). The estimates of genetic variance (s^2_G) in particular were considerably larger than their respective standard errors for all traits. Among the environments, s^2_G and error variance (s^2_E) for grain yield tended to be reduced with increasing relative yield reduction. Similarly, s^2_G for NKE, NKP, EL, HSW and AD were reduced with increasing stress, especially from well watered to drought. These traits showed an almost similar trend, in mean yield (Table 3.4). Many investigators agreed that s^{2}_{G} for yield in stress environments are generally lower than in non-stress environments (Buren *et al.*, 1974; Rosielle & Hamblin, 1981; Blum, 1988; Bolaños & Edmeades, 1996). Based on information in selection experiments, Hallauer & Miranda (1988) pointed out that genetic variability is compressed in stress environments for each of these traits. On the contrary, s^{2}_{G} for EPP, SD, ASI and NTB increased with increasing plant density and moisture stress, with a higher magnitude under drought conditions. PH, LDG and SEN showed no clear trend.

The estimates of the s^{2}_{G} in both moisture regimes, for HSW, NTB, LDG and SEN, were less than their respective $s^{2}_{GE.}$ However, for all traits, the s^{2}_{G} obtained with population A-511 were almost similar to those reported on six tropical lowland maize populations (Bolaños & Edmeades, 1996). According to their data, s^{2}_{G} for GY, NKE and mass kernel^{-1} increased with increasing yield level, while variances for EPP and ASI decreased in the same direction. In contrast to the present results, Guei & Wassom (1992) reported the highest additive variance for SD and ASI within Pool 26 Sequia under non-stress, while for all the traits of La Posta Sequia this occurred under stress conditions. This indicated variability in expression among populations. Except for AD and SD, the order of the s^{2}_{E} for most traits exceeded their respective s^{2}_{G}, especially under drought conditions. Similarly, Hallauer & Miranda (1988) indicated that s^{2}_{E} are inherently large for variance component estimates in stress environments. The changes in magnitude of s^{2}_{G} and s^{2}_{E} with increasing yield were in the same direction and of similar magnitude for all traits that also agreed with the result reported by Bolaños & Edmeades (1996). Under normal conditions, Obilana & Hallauer (1974) reported significant genetic variation among the unselected S_6 lines for all traits of Iowa Stiff Stalk Synthetic. However, they indicated the difficulty of developing a group of unselected homozygous lines that adequately represent the base population. To overcome this setback, Hallauer & Miranda (1988) suggested that no handicap is present if randomly derived S_1 lines are used for s^{2}_{G} estimation. Generally, the results in the present study showed that both stresses (moisture and plant density) independently or in combination influenced the magnitude of variances for each trait. GY, NKE, EL, NKP, HSW and AD, showed higher s_{G}^{2} when well watered while EPP, SD, ASI and NTB obtained their highest corresponding values when drought stressed. Thus, the estimated component of variances for all tested traits showed significant genetic variation in population A-511. Furthermore, high genotypic variability expression of EPP and ASI under high PD and drought stress in contrast to GY confirmed their importance in selection for tolerance improvement. This indicates the importance of high PD for drought tolerance screening in areas that lack a rain free season. The high variability among S_1 lines for flowering times also need high PD to impose stress uniformly. However, since the estimation of genetic variance through S_1 lines alone did not allow to separate additive and non-additive components, further testing with involvement of mating design is crucial.

Broad sense heritability (h_b^2) for GY, NKE, NKP, EL, HSW and PH, increased with decreasing stress or increasing GY level, while for EPP it increased with increasing stress (Table 3.6). Unlike others, ASI was relatively higher under well-watered conditions while similar expression was observed in the rest of the environments. Based on six tropical populations evaluated across moisture regimes, Bolaños & Edmeades (1996) reported the highest h_b^2 for GY, NKP, NKE and kernel mass under well watered conditions while the same applied to LDG and EPP under drought stress. These investigators indicated that the h_b^2 of ASI and EPP either increased or remained fairly constant with increasing moisture stress and declining yield level, which agreed with the estimation obtained for EPP in the present study. AD showed almost similar h_b^2 across PD as well as moisture level, which also agreed with the above investigators who noted decreased effects of environment on this trait. With Pool 26 Sequia, Guei & Wassom (1992) reported larger narrow sense heritability for GY, SD, and ASI under non-stress, and for AD and EPP under stress, but in the other population (La Posta Sequia) the highest heritability estimated for all the traits was under stress conditions. No clear trend was exhibited in NTB, LDG and SEN expression of h_b^2 across environments. This may be due to reduced effects of environmental stress as reported by Bolaños & Edmeades (1996). As expected, except for EPP and NKE, h_b^2 was reduced with increasing stress or decreasing yield level. However, the order of h_b^2 reduction due to PD change was smaller as compared to moisture change. This was due to decreased genotypic variances rather than increased error variances. Accordingly, the highest heritability was obtained with the highest yielding environment. Lower genotypic variances and lower heritabilities for GY under stress conditions have been reported in many other studies (Rosielle & Hamblin, 1981; Blum, 1988; Atlin & Frey, 1990; Ud-Din *et al.*, 1992; Bänziger *et al.*, 1997).

Table 3.5. Estimates of components of variance obtained from the analysis of variance of 196 randomly selected S_1 lines derived from Population A-511 tested in each and across environments at Melkasa, 2002.

Environment	WWND		WWHD		DSND		DSHD	
Trait	σ^2_G	σ^2_E	σ^2_G	σ^2_E	σ^2_G	σ^2_E	σ^2_G	σ^2_E
GY	0.60± 0.089	0.51±0.025	0.49±0.089	0.58±0.029	0.170±0.034	0.279±0.014	0.085±0.026	0.276±0.014
EPP	0.005± 0.001	0.013±0.001	0.006±0.001	0.01±0.001	0.011±0.003	0.024±0.001	0.011±0.002	0.012±0.001
NKE	1438± 444.3	4051±204	1058±296.8	2536±128	415±93.5	830±41.81	357.3±85.59	789. 6±39.78
EL	1.01± 0.249	2.34±0.118	0.57±0.228	2.167±0.11	0.65±0.224	2.421±0.122	0.468±0.285	3.50 ±0.177
NKP	1224± 447.6	4939±249	1196.5±368.1	3254±164	897.7±153.6	1063±53.55	830±159.6	1250±62.96
HSW	4.115±0.742	5.45±0.275	3.055±0.684	5.235±0.26	2.82±0.970	10.5±0.529	2.651±0.919	9.976±0.503
AD	14.05±1.829	7.43±0.374	13.467±2.10	11.43±0.58	11.45±1.453	5.42±0.273	11.60±1.663	8.658±0.436
SD	17.49±2.205	8.03±0.405	18.02±2.808	15.28±0.77	26.90±3.501	14.22±0.716	24.29±3.768	22.7 ±1.143
ASI	3.045±0.377	1.28±0.064	5.129±0.82	4.62±0.233	4.674±0.859	6.434±0.324	6.302±1.21	9.47 ±0.477
PH	167.2±31.47	241.7±12.17	90.47±41.95	410±20.705	162.2±55.26	596± 30.04	99.16±49.74	591.9±29.82
NTB	2.80± 0.381	1.76±0.089	1.986±0.525	4.38± 0.22	3.246±0.471	2.518±0.127	4.217±0.822	6.527±0.329
LDG	9.56± 2.578	25.34±1.277	47.88±7.646	43.06±2.17	22.31±4.745	40.44±2.038	21.61±5.008	45.28±2.281
SEN	0.23± 0.056	0.53±0.027	0.521±0.092	0.59±0.03	0.288±0.062	0.536±0.027	0.313±0.075	0.698±0.035
Environment	Combined WWND + WWHD			Combined DSND + DSHD				
	σ^2_G	σ^2_{GE}	σ^2_E	σ^2_G	σ^2_{GE}	σ^2_E		
GY	0.434±0.065	0.282±0.025	0.540±0.01	0.107±0.020	0.027±0.016	0.277±0.007		
EPP	0.004±0.001	0.004±0.00	0.011±0.00	0.007±0.001	0.004±0.004	0.020±0.001		
NKE	990.295 ±216	1167.37 ±130	3293±82.96	197.44±57.4	112.7±23.34	700.84±17.65		
EL	0.941±0.15	0.361±0.07	2.252±0.06	0.396±0.147	0.217±0.096	2.963±0.075		
NKP	847.1±141	1026.3±66.1	833.7±69.3	283.2±9.5	177.9±41.23	794.77±20.3		
HSW	3.637±0.517	1.267±0.19	5.342±0.14	1.054±0.561	2.241±0.379	10.24±0.258		
AD	11.089±1.39	2.376±0.35	9.930±0.25	7.078±1.043	4.019±0.441	7.27±0.183		
SD	15.868±1.99	4.437±0.50	12.564±0.32	18.32±2.727	9.699±0.960	18.46±0.465		
ASI	2.081±0.38	1.83±0.19	3.232±0.08	3.479±0.720	1.678±0.306	8.453±0.213		
PH	131.3±22.83	78.29±11.5	326.3±8.22	133.01±32	3.16±14.978	594.12±14.81		
NTB	0.424±0.28	3.389±0.22	3.066±0.08	1.111±0.427	3.495±0.295	4.522±0.114		
LDG	15.130±3.35	26.67±1.97	34.2±0.86	3.219±3.099	24.99±2.344	42.86±1.080		
SEN	0.187±0.05	0.389±0.04	0.558±0.01	0.111±0.044	0.253±0.035	0.617±0.016		

See Table 3.4 for abbreviations; σ^2_G, genotypic variance; σ^2_{GE}, genotype by environment interaction variance; σ^2_E, error variance.

Table 3.6. Broad sense heritability estimates of 196 randomly selected S_1 lines derived from Population A-511 in each environment.

Environ-Ment	Estimation in each environment				Across combined environments	
Trait	WWND	WWHD	DSND	DSHD	WWND + WWHD	DSND + DSHD
GY	0.703	0.630	0.549	0.381	0.611	0.564
EPP	0.435	0.545	0.500	0.667	0.457	0.500
NKE	0.415	0.455	0.500	0.475	0.413	0.460
EL	0.462	0.346	0.349	0.211	0.559	0.318
NKP	0.541	0.529	0.481	0.440	0.540	0.496
HSW	0.602	0.539	0.349	0.347	0.649	0.223
AD	0.791	0.702	0.809	0.728	0.751	0.649
SD	0.813	0.702	0.791	0.682	0.748	0.659
ASI	0.826	0.690	0.592	0.571	0.547	0.541
PH	0.580	0.306	0.352	0.251	0.521	0.470
NTB	0.761	0.476	0.720	0.564	0.147	0.279
LDG	0.430	0.690	0.525	0.488	0.409	0.122
SEN	0.463	0.638	0.518	0.470	0.359	0.283

GY, grain yield in ton ha^{-1}; AD, days to 50% anthesis; SD, days to 50% silking; ASI, anthesis-silking interval; PH, plant height (cm); EPP, ears per plant; NKE, number of kernels ear^{-1}; EL , ear length in cm; NKP, number of kernels plant^{-1}; NTB, number of tassel branches; HSW, hundred seeds weight; LDG, lodging in %; SEN, leaf senescence; WWND = Well watered + normal density; WWHD = Well watered + high density; DSND = Drought stress +normal density; DSHD =Drought stress +high density.

In each environment σ^2_G and h_b^2 were considered as over estimated because G x E variance was not assessed, while in the combined environments these estimates were relatively unbiased. In general, the presence of significant genetic variation for all tested traits and high heritabilities estimated in environments where high σ^2_G with reduced σ^2_E were obtained, indicates that selection would be effective in the desired direction for most of these traits.

3.4.3. Grain yield correlation with secondary traits

Genetic (r_G) and phenotypic correlations (r_P) between primary trait (GY) and secondary traits tested in this study are presented in Table 3.7. All the tested yield components and flowering traits showed significant genetic and phenotypic associations with grain yield in each environment. Furthermore, most components obtained their highest corresponding values under drought stressed high PD (DSHD). However, under all conditions, GY associated positively with yield components, and negatively with flowering traits. This observation implies that GY and its components varied in association in the same direction and in the opposite direction with flowering traits.

Among the yield components, EPP, NKE and NKP were consistently strongly correlated (r_G = 0.60- 0.85) in their genetic association with GY in each of the four environments. Other yield components (EL and HSW) showed a tendency of increased relationship with increasing stress or decreasing GY level, but in a smaller magnitude. Results in this study were in agreement with those obtained with 3059 S_1 to S_3 progenies derived from six tropical maize populations that were tested under two to three moisture regimes at Tlaltizapan, Mexico (Bolaños & Edmeades, 1996; Edmeades *et al.*, 1997d). They reported consistently high corresponding values (r_G = 0.60 to 0.90) for EPP, NKP and NKE. The corresponding values for mass kernel^{-1} of the six maize genotypes were small (r_G = 0.22±0.16) and almost similar in magnitude to the trend observed with HSW of A-511 (r_G = 0.25-0.34) at Melkasa. The values obtained in the present study were higher than those reported by Gui & Wassom (1992), who found a strong relationship with EPP under drought stress (r_G = 0.69) and moderate under non-stress (r_G = 0.47) in Pool 26 Sequia. In the present study, r_G of GY with EPP and EL showed significant trends as PD changed under both moisture regimes. Similarly, NKE, EPP and EL showed significant trends as moisture availability changed. Bolaños & Edmeades (1996) and Edmeades *et al.* (1997d) reported significant trends only in EPP as water availability changed, but not in NKP, NKE and mass kernel^{-1}.

The association of flowering traits with the primary trait increased consistently with increasing stress or decreasing yield. As a result, GY showed its highest dependency on these traits ($r_{G\ AD.GY}$ = -0.739, $r_{G\ SD.GY}$ = - 0.78, and $r_{G\ ASI.\ GY}$ = -0.792) under DSHD where drought was combined with high PD. The estimation obtained by other investigators with different genotypes also confirmed their strongest association under drought conditions (Du Plessis & Dijkuis, 1967; Edmeades & Daynard, 1979; Bolaños & Edmeades, 1996). In maize population Pool 26 Sequia, Guei & Wassom (1992) also found stronger relationships of GY with AD, SD and ASI under drought stress (r_G = -0.65, -0.61, and -0.58, respectively) than under non-stress (r_G= 0.37, -0.12, and –0.28, respectively). Bolaños & Edmeades (1996), and Edmeades *et al.* (1997d) indicated that AD and ASI correlated more strongly and more negatively with grain yield as moisture stress intensified and yield levels declined. The consistent negative values estimated for these traits, especially under stress, indicated that earlier flowering S_1 progenies encountered less stress (escaped drought) during flowering or linked with increased GY potential than late flowering progenies. Moreover, studies demonstrated that progenies with reduced ASI and/or synchronized male and female flowering also gained high GY potential under stress (Guei & Wassom, 1992; Edmeades *et al.*, 1997d; Chapman & Edmeades, 1999). Thus Bolaños & Edmeades (1996) suggested that selecting progenies that simply escape moisture stress by flowering early should be avoided in programs that focus on simultaneously increasing yield potential and tolerance.

AD showed non-significant trends as PD changed under well watered conditions ($r_{gGY.AD}$ = -0.301 to –0.338) but showed significant trends within drought conditions ($r_{gGY.AD}$ = -0.531 to –0.723). In contrast, non-significant trends were observed for SD as PD changed under drought stress conditions ($r_{GY.SD}$ = -0. 738 to –0.78). The same applied to ASI ($r_{GY.ASI}$ =-0.741 to –0.792). These phenomena indicated that the effect of PD stress alone could not change the trend in AD but it had adequate impact on SD and ASI. The result demonstrated that both PD and moisture availability, independently or in combination, induced significant effects on the association between flowering traits and GY. However, the magnitude varied across different studies, which need caution in interpretation. Besides, Hallauer & Miranda (1988) pointed out that genetic correlations inherently have large errors. In general, the potential use of the ASI to identify stress tolerant genotypes at flowering is well known, however, since EPP as a measure of barrenness provides similar and perhaps more complete information at final harvest (Chapman & Edmeades, 1999). Thus ASI and EPP are the best drought and high plant density adaptive traits, which are used mainly in drought tolerance improvement.

The other traits, NTB, LDG and SEN were inconsistently associated with GY as well as of small magnitude and variable in sign (Table 3.7). Three of them as well as PH were insignificant in their association with GY under DSND and WWHD. PH was moderately and positively significant in its association with GY only in extremely contrasting environments under WWND and DSHD. No clear explanation can be provided for this phenomenon, but tall plants are known for having a long duration in gaining maturity, which in turn is associated with increased yield when adequate water is available and minimized lodging occurs. In line with this assumption Bolaños &

Edmeades (1996) pointed out that the use of single row plots for evaluation, favoured tall progenies to capture additional radiation when surrounded by shorter neighbours. Even so, they warned that such an advantage would not be expressed in large plots, and this positive r_G may reverse sign under drought conditions. Fortunately, in the present study the exaggerated high positive correlation under WWND reduced due to increased PD under WWHD without the use of increased plot size. Edmeades *et al.* (1997d) noted that PH, NTB and SEN are highly heritable and easily measured, but are not strongly associated with grain yield under stress conditions. However, it should be considered that highly heritable traits can be easily altered by selection (Fischer *et al.*, 1987).

Phenotypic associations (r_P) of GY with its components and with flowering parameters showed almost the same trend and sign but with smaller magnitude than their genetic correlations (r_G) (Table 3.7). Bolaños & Edmeades (1996) and Edmeades *et al.* (1997d) noted that phenotypic correlations were broadly similar in magnitude and sign to genetic correlations of these traits across moisture regimes except for mass kernel^{-1}. Nevertheless, the differences between phenotypic and genotypic associations in the present study were more pronounced as compared to their reports. This implies that environmental correlations for the same traits were probably higher in the present study than in their study at Tlaltizapan. The r_P of EPP, NKE and NKP with GY ranged from 0.46 to 0.70 across growing conditions, which agreed with a study conducted with six tropical maize populations at Tlaltizapan (Bolaños & Edmeades, 1996; Edmeades *et al.*, 1997d). They reported strong r_P of GY with EPP, NKP, and NKE under drought conditions (r_P = 0.77, 0.90 and 0.50, respectively) and when well watered (r_P = 0.49, 0.89, and 0.70, respectively). The GY relationships with EPP and NKE using three tropical maize populations (La Posta Sequia, Pool 26 Sequia and Tuxpeno Sequia) also exhibited similar trends but were higher in magnitude (r_P = 0.79 to 0.94) under stress conditions (Chapman & Edmeades, 1999). With Pool 26 Sequia, Guei & Wassom (1992) found less association of EPP with GY (r_P = 0.43 under stress and 0.36 under non-stress) as compared to other reports. According to Bolaños & Edmeades (1996), the magnitude of association of GY with AD and ASI were -0.28 and -0.35 under well-watered conditions and –0.40 and -0.53 under drought conditions, respectively. Similar to their report, with Pool 26 Sequia , Guei & Wassom (1992) found that associations of GY with AD, SD, and ASI under drought conditions were -0.30, -0.40, and -0.49

respectively, but the result under non-stress conditions varied, between 0.14, -0.07, and -0.27, respectively. However, Chapman & Edmeades (1999) reported highly significant phenotypic associations of GY with AD and ASI under drought conditions (-0.80 and –0.89) but non-significant under well-watered conditions, which exceeded the magnitude estimated under drought conditions in this and other studies mentioned above.

Based on testcrosses of 20 inbred lines, phenotypic correlations of GY with PH, EPP, EL, 300 kernel mass, NKP, AD, SD and ASI under high PD (60,000 plants ha^{-1}) were 0.56, 0.84, 0.72, 0.01, 0.69, 0.14, -0.33, and -0.66, respectively (El-Lakany & Russell, 1971). However, their associations under low PD (31,000) were 0.51, 0.29, 0.38, -0.01, 0.31, 0.29, 0.33, and -0.04, respectively. The estimated values for PH, EPP, NKE, SD, and ASI under high PD and only PH at low PD agreed with the results obtained at Melkasa. However, the positive sign for AD and SD under low PD in their study was not observed in the present study. The corresponding values for mass kernel^{-1} across moisture regimes (Bolaños & Edmeades, 1996), and for 300 kernel mass across plant densities (El-Lakany & Russell, 1971), as well as for 100 seed mass in the present study, showed weak relationships with GY. As stress levels increased, grain yield became increasingly dependent on EPP, NKP, AD and ASI, and less on mass kernel^{-1} (Edmeades *et al.*, 1997a). At a stand of 98,800 plants ha^{-1}, another study with 25 hybrids estimated simple correlation coefficients for GY with SD, ASI, and PH that were –0.58, -0.86 and 0.20 respectively, (Buren *et al.*, 1974). From this study, the value obtained for SD and PH agreed with estimations made with A-511 progenies.

The magnitude of the genetic correlation between GY and EPP across environments was also as function of ASI and EPP (Figure 3.3). The curve fitted to these relationships indicated that $r_{GY.EPP}$ increased to above 0.80 as mean ASI exceeded six days or mean EPP fell below 0.70 with increasing stress (plant density or drought). Bolanos & Edmeades (1996) also observed the same trend across moisture regimes. In earlier studies, this was also observed at high densities (Edmeades & Daynard, 1979). Decline in h_b^2 of GY with increasing drought stress is offset by concomitant increases in the h_b^2 and σ^2_G of ASI and EPP and in the magnitude of the r_G between GY, EPP and ASI under drought stress (Bolaños & Edmeades, 1996). They also concluded that as selection tools, both ASI and EPP increase in utility as stress intensifies and genetic differences become larger.

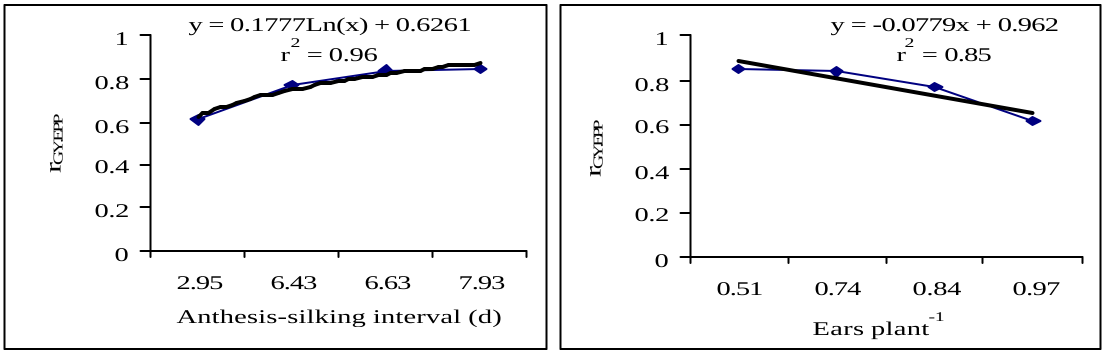

Figure 3.3. Genetic correlation between grain yield and ears plant^{-1} ($r_{GY.EPP}$) plotted against mean anthesis-silking interval and mean ears plant^{-1} for 196 S_1 lines evaluated across four environments at Melkasa, 2002.

Table 3.7. Genetic and phenotypic correlation of 12 traits with grain yield of S_1 lines derived from Population A-511 evaluated in four environments at Melkasa, 2002/03.

Genetic correlation (r_G) with grain yield				
Traits	WWND	WWHD	DSND	DSHD
EPP	0.61**	0.77**	0.84**	0.85**
NKE	0.63**	0.62**	0.78**	0.80**
EL	0.23*	0.37**	0.54**	0.60**
NKP	0.70**	0.68**	0.73**	0.76**
HSW	0.31**	0.25**	0.30**	0.34**
AD	-0.30**	-0.33**	-0.53**	-0.72**
SD	-0.34**	-0.57**	-0.74**	-0.88**
ASI	-0.21*	-0.53**	-0.82**	-0.69**
PH	0.50**	0.13	0.13	0.50**
NTB	-0.03	-0.07	0.11	-0.16
LDG	0.22*	-0.09	0.11	-0.42**
SEN	-0.29**	-0.04	0.03	-0.06
Phenotypic correlation (r_G) with grain yield				
	WWND	WWHD	DSND	DSHD
EPP	0.46**	0.64**	0.65**	0.70**
NKP	0.48**	0.49**	0.62**	0.64**
EL	0.22*	0.32**	0.37**	0.38**
NKP	0.47**	0.51**	0.60**	0.67**
HSW	0.25**	0.21*	0.40**	0.48**
AD	-0.29**	-0.32**	-0.37**	-0.43**
SD	-0.35**	-0.52**	-0.52**	-0.65**
ASI	-0.24**	-0.45**	-0.61**	-0.66**
PH	0.45**	0.19*	0.29**	0.38**
NTB	-0.01	-0.07	0.09	-0.047
LDG	0.07	-0.08	0.06	-0.180
SEN	-0.10	-0.07	-0.10	-0.217*

*, ** Indicates significance at P = 0.05 and P = 0.01, respectively.

Edmeades *et al.* (1997d) considered EPP, NKP and ASI as the most important drought adaptive traits, which are affected by barrenness under drought conditions. Evidence suggests that focusing on EPP and ASI that are indicative of partitioning in the plant at flowering will result in increases in harvest index and grain yield with all water regimes (Bolaños & Edmeades, 1996), as well as in other abiotic stresses, as indicated under high PD.

3.4.4. Efficiency of indirect selection

Efficiency of indirect selection in the other environments as alternative to direct selection in a drought stressed normal plant density environment (DSND) was assessed in this study. The genetic correlation between grain yields under normal PD and high PD within drought environments (DSND and DSHD) was relatively high ($r_G = 0.846$) as compared with other growing conditions (Table 3.9). Correlation with other environments was reduced to below 0.70, which indicated that different physiological mechanisms and genes are responsible for performance in grain yields in each of the tested environments (Falconer, 1989). The relative efficiency of indirect selection under drought stressed high PD (DSHD) to direct selection in DSND was also 0.705 (Table 3.10), which was relatively better than others. However, it was below one, indicating that response to direct selection in DSND was higher than indirect selection in DSHD. As suggested by Atlin & Frey (1990), this was mainly due to a lower magnitude of broad sense heritability of yield in DSHD ($h_b^2 = 0.38$) than in DSND ($h_b^2 = 0.55$). Similarly, indirect selection in WWHD (0.639) was less efficient as compared to direct selection in DSND, but it was better than in WWND.

On the other hand, highest efficiency (1.016) of indirect selection in DSND to direct selection in DSHD was estimated in this study. As suggested by Bänziger *et al.* (1997) a value of 1.0 for $CR_{DSHD\ (DSND)}/R_{DSHD} = r_G\ h_{DSND}/h_{DSHD}$ indicates that indirect and direct selection are equally efficient. However, the observations in this study suggested considerable advantages of drought stressed high PD (DSHD) over DSND especially in intra-population improvement by S_1 recurrent selection. Since the flowering time among the S_1 lines were variable, it was difficult to determine the exact time when to withdraw irrigation to induce drought stress at flowering. Although no rain interfered during the stress period of this trial due to drought occurring in the country, experience has shown a high possibility of interference due to the unpredictable nature of the rainfall pattern at Melkasa. If rainfall interfered when inducing mid-season stress, the induced stress would be less affected in DSHD than in DSND. In this study, it was also realized that WWHD imposed less stress, which was not adequate to differentiate tolerant from non-tolerant genotypes. Thus its efficiency may be improved by reducing the frequency of irrigation applied and by increasing PD. Zavala-Garcia *et al.* (1992) suggested that the relative efficiency estimates might be biased by the standard errors associated with the genetic variance estimates under the assumption of no epistasis and no dominance effects. Variance and broad sense heritability estimated in each environment are considered as over-estimated because G x E variance was not separated. If G x E variances consistently differ between individual environments, this could affect the relative magnitude of genetic variances and heritability, which in turn could affect decisions regarding selection efficiency (Atlin & Frey, 1990; Ud-Din *et al.*, 1992). Thus for areas with an unreliable rain free season, DSHD can be considered as a better alternative to direct screening in DSND than WWHD and WWND. However, intermediate drought stress (where irrigation was suspended one to two weeks prior to anthesis) should be combined with high PD rather than severe drought stress.

If the screening site has a reliable rain-free season as observed in this particular season at Melkasa, screening under managed drought stress at flowering is the best option for drought tolerance screening (Fischer *et al.*, 1983; Bolaños & Edmeades, 1996; Edmeades *et al.*, 1993; 1997d; 1999). For areas that lack a predictable rainfall pattern, a rainout shelter was also suggested to overcome rainfall interference when not needed. Unfortunately, in addition to the expense of constructing the shelter, it is not suitable for tall genotypes, and can not handle large numbers of germplasm for screening. As a result, especially when there is a small chance of having a rain-free site or season, screening for drought tolerance under DSHD can be considered as an alternative for improvement of tolerance. Across environments, genotype variance and error variance for GY tended to decrease with increasing relative yield reduction under PD stress and drought (Table 3.8). However in the present study, positive correlations were observed in all cases, which indicated the possibility of simultaneous selection for a wide range of moisture regimes and plant population sizes.

Table 3.8. Mean grain yield, broad sense heritability (h_b^2), genetic variance (σ^2_G), error variance (σ^2_E), and predicted response (R) estimates for grain yields of S_1 lines in four environments.

Environment	Mean yield ton ha^{-1}	σ^2_G	σ^2_E	h_b^2	R
WWND	3.99	0.598	0.505	0.703	0.648
WWHD	2.86	0.490	0.575	0.630	0.556
DSND	1.641	0.170	0.279	0.549	0.305
DSHD	0.883	0.085	0.276	0.381	0.180

Table 3.9. Estimates of genetic correlations among grain yield of S_1 maize lines in WWND, WWHD, DSND , and DSHD environments

Environment	WWHD	DSND	DSHD
WWND	0.686	0.460	0.619
WWHD		0.596	0.585
DSND			0.846

Table 3.10. Estimates of relative efficiency of indirect selection to direct selection in the target environments.

Indirect	vs.	Direct	Efficiency of indirect selection
WWND		DSND	0.520
WWHD		DSND	0.639
DSHD		DSND	0.705
DSND		DSHD	1.016

WWND = well watered normal plant density; WWHD = well watered high density
DSHD = drought stressed high density; DSND = drought stressed normal density

3.5. Conclusions

Both drought and high plant density stress adversely affected the tested traits of the S_1 lines derived from population A-511. However, the impact of drought was considerably higher than plant density stress. In each environment, highly significant genotypic variability was observed for each tested trait within population A-511. The genetic variance (σ^2_G) and broad sense heritability for ears plant^{-1} increased with increasing stress, while for yield and most other traits it increased with decreasing stress, reflecting their critical importance in selection under contrasting growing conditions. For days to 50% silking and ASI, σ^2_G also increased with increased stress like EPP but their heritability increased under well-watered conditions. However, since the evaluation of S_1 lines alone did not separate additive and non-additive components, further testing with involvement of mating design is crucial to determine each of the genetic variances. Among the traits, the yield components exhibited strong and consistent association with yield in each environment, while ASI showed strong association only under drought stress where susceptible genotypes obtained large values. Most traits showed their corresponding highest magnitude under severe stress, where both (high plant density and drought) stresses were combined. The result indicated that EPP is the best criterion for drought tolerance screening, mainly due to low genetic variance and heritability of yield under drought conditions. In general, adequate genotypic variability for high plant density and drought adaptive traits as well as for other traits was detected within population A-511. Thus, for the drought stressed zone of Ethiopia, it could be improved for promising performance under both drought and non-drought conditions.

Indirect selection in DSHD and direct selection in DSND were predicted to be equally efficient. However, DSHD was suggested to be the better alternative to DSND for drought tolerance screening in areas with an unreliable rain-free season. In intra-population improvement through S_1 recurrent selection, it is difficult to determine the exact time when to induce drought stress at flowering since flowering time of the S_1 lines are mostly variable. Under these conditions, if rainfall interfered when inducing mid-season drought, the induced stress is less affected in DSHD than in DSND because of high PD stress. However, the high PD stress should be combined with intermediate drought stress by suspending irrigation one to two weeks prior to anthesis.

Chapter 4 Combining ability of drought tolerant maize lines in rainfed environments

4.1. Abstract

In the unpredictable environment of the tropics, maize (*Zea mays* L.) genotypes bred for drought tolerance should also perform well under adequate rainfall conditions. The performance and relationship of drought tolerant lines and their crosses in environments with adequate rainfall provides an indication of their capacity to exploit sufficient moisture levels when available. A diallel was produced using eight drought tolerant lines to study: (i) the performance and combining ability of the tested traits, (ii) relationship between lines *per se* and hybrid performance, and (iii) the association of grain yield with secondary traits within lines and hybrids. Parental lines and their hybrids were evaluated separately at two plant densities in four rainfed environments. Across environments, significant differences were observed among genotypes, environments, and the interaction between them (G x E) for most traits. The same held true for general combining ability (GCA) and specific combining ability (SCA), GCA x E and SCA x E interaction except for plant height. High yields were recorded for most genotypes at high population levels suggesting that improvement made for drought tolerance increased their potential to perform well under high plant density. However, the results confirmed greater relative importance of additive (GCA) effects than non-additive (SCA) effects for the expression of all considered traits. The lines CML442 and Mex102 were superior in *per se* performance and GCA effects for yield. In crosses, these lines were also superior in yield and SCA effects as well as for EPP, particularly crosses with Mex102. The observed relationships showed stronger association between yield and its components than with other traits. It also indicated dependence of hybrids on the *per se* performance of lines, reflecting the need of improving *per se* performance of inbred lines. This study demonstrated that drought tolerant lines with high *per se* performance with regard to yield across rainfed environments gave high yielding hybrids under similar conditions. Most of the crosses were superior to local hybrids that confirmed the importance to improve tolerance to drought stress at flowering while maintaining the capability to perform under optimal conditions. Consequently CML442 and Mex102 can be considered as good candidates for direct use in hybrids for resource constrained farmers in rainfed environments.

Key words: Combining ability, drought tolerant, plant density, tropics.

4.2. Introduction

Maize provides for food security especially in most of the tropics. However, most tropical maize is produced under rainfed conditions, in areas where drought is the most important abiotic constraint (Byrne *et al.*, 1995; Bänziger *et al.*, 1999c). The vast majority of tropical maize farmers continue to grow maize to meet their subsistence requirements and are resource constrained (Pingali & Pandey, 2000). Because rainfall in most drought stressed zones is unpredictable in both quantity and distribution, genotypes targeted for these areas should yield well in both the presence and absence of drought (Byrne *et al.*, 1995; Edmeades & Bänziger, 1997). Under these conditions hybrid maize can be considered as the best alternative since it often outperforms their open pollinated counterparts in both favorable and stress environments (Duvick, 1999; Vasal *et al.*, 1997; 1999). However, the area planted to hybrid maize in the tropics does not exceed 19 % of the total maize producing area, except for a few countries (CIMMYT, 1994). The available maize hybrids in the region have also been developed in environments with specific agro-ecological conditions and stress (Vasal *et al.*, 1999). In addition to the prerequisite for new seed every year, there are concerns about the danger of genetic uniformity and high input requirements, which often cause resistance to improved technologies. However, the use of hybrids is becoming more important due to higher and more stable yields obtained in various localities and years (Tsaftaris *et al.*, 1999). In addition, Duvick (1999) pointed out that yield gains in hybrid production always were accompanied by improvement in tolerance to biotic and abiotic stress. Accordingly, prevailing conditions demand the development and identification of drought tolerant hybrids that perform well under both stress and non-stress conditions.

Development of drought tolerant hybrids requires selection for certain traits during inbred line development (Beck *et al.*, 1997; Betran *et al.*, 1997). It is believed that improvements of inbred performance will play an increasingly important role in improving the performance of hybrids (Beck *et al.*, 1997; Vasal *et al.*, 1997; Duvick, 1999). In contrast, some are not convinced that parental performance has any direct relationship to hybrid performance, especially with regard to grain yield (Hallauer & Miranda, 1988; Lamkey & Edwards, 1999). However, specific combinations of inbred lines with good general combining ability will remain an essential requirement for production of superior new hybrids (Hallauer & Miranda, 1988; Duvick, 1999). As a result, CIMMYT has developed several maize lines, which are tolerant to drought and low N under managed conditions (Beck *et al.*, 1997; Vasal *et al.*, 1997; 1999). The maize genotypes bred for mid-season drought tolerance are also reported to be tolerant to N stress (Bänziger *et al.*, 1999b), and have improved broad adaptation (Chapman *et al.*, 1997). Thus, since drought is an unpredictable environmental factor, good performance under non-drought conditions is also expected (Vasal *et al.*, 1997). However, their performance and combining ability, and relationship between hybrid and line performance in different rainfed environments is not well known. Many investigators have also shown that GCA and SCA can interact with environments (Sprague & Tatum, 1942; Matzinger *et al*., 1959; Beck *et al*., 1990; Han *et al*., 1991; Betran *et al*., 2003a,c).

The importance of multi-environment testing and utilization of high plant density stress for selecting inbred lines and for screening widely adapted hybrids have been reported in addition to improved management (Troyer, 1996). This indicated the need of testing combining ability under growing conditions representative of farmers' conditions. Since most reports about drought tolerant lines focused on moisture deficit environments, the gap of information about their performance under adequate rainfall conditions should be investigated. Thus drought tolerant lines and their hybrids that are expected to perform well in moisture deficit areas should be tested for performance under adequate rainfall conditions. This study evaluated the following at two plant densities in various rainfed environments: (i) combining ability and performance of the important traits in lines and their crosses; (ii) association between lines and their crosses in performance; and (iii) correlation of grain yield with secondary traits within lines and hybrids.

4.3. Material and methods

Experimental materials

Eight white-grained maize lines bred for drought tolerance by CIMMYT were used in a diallel study. Details of the parental lines regarding pedigree/source and reaction to drought are provided in Table 4.1. A diallel cross without reciprocals was made during 2001/2002 at the Grain Crops Institute at Potchefstroom, Republic of South Africa. At the same time seed increase of the parents by selfing, and bulking of seeds of five to 10 plants from each parent was done. Evaluation was done in Ethiopia during June to October under rainfed conditions using trial sites at Bako and Melkasa Research Centres. During evaluation, two maize hybrids (BH540 and BH140) from Ethiopia were included as checks to assess the extent of adaptation of the 28 F_1 hybrids in different rainfed environments. Both checks were excluded during diallel analysis. As a result only mean squares and mean performance of the two local hybrids were included in this study.

Field evaluation and experimental design

The trials were conducted for the two years, 2002 and 2003 main seasons, at normal and high plant densities in rainfed fields at Bako and Melkasa Research Centers (Table 4.2). However, each plant density (PD) location^{-1} year^{-1} was considered as one random environment in this study. As a result the genotypes were evaluated in four environments at each PD. Bako Research Center (9^{o}06' N, 35^{o}09' E, 1650 m a.s.l) is located in the hot to warm sub-humid plains of western Ethiopia, and receives an average annual rainfall of 1255 mm in a unimodal pattern. Melkasa (8^{o}24′N, 39^{o}21′E, 1550 m a.s.l) is situated in the hot to warm sub-moist rift valley in the central part of the country, and receives an average annual rainfall of 680 mm in a dimodal pattern. However, due to limitation of rainfall during the 2002 main season at Melkasa, the trials were supplemented once during seed setting by furrow irrigation. The rainfall distribution and amount recorded during the experiments at both localities are presented in Figure 4.1. According to USD and FAO classifications, the soil at Bako was dark reddish brown Altisols while a Haplic Andosol occurred at Melkasa. The result of the laboratory analysis indicated clay loam to loam at Melkasa and from clay loam to clay at Bako, with other properties indicated in Table 4.3.

In each environment, lines and hybrids were evaluated separately in adjacent experiments to eliminate the effects of differences in vigor between inbreds and hybrids. The experimental design was a randomized complete block (RCBD) with four replications. For hybrids, each block was folded to minimize soil variability within block. Each plot consisted of four 4.2 m rows with a spacing of 75 cm between rows. Intra row spacing was 30 cm between hills (for normal PD) and 15 cm (for high PD). The spacing of 30 cm was considered as a normal PD, based on the recommended spacing for the two local hybrids (BH540 and BH140) released by the National Variety Release Committee. A 1.5 m wide alley was left between the blocks within each trial. An additional plot was added at each end of a block, planted to the local hybrid BH140 to avoid border effects. Two seeds hill^{-1} were planted in all trials to ensure uniform stand and thinned to one plant per hill. At Melkasa, for each trial (PD), fertilizer rate was applied at a rate of 50 kg P_2O_5 ha^{-1} and 25 kg N ha^{-1} at planting, followed by a side dressing of 25 kg N ha^{-1} 35 days later. Similarly, at Bako, 75 kg P_2O_5 and 37.5 kg N ha^{-1} was applied at planting, and 37.5 kg N ha^{-1} side dressed 35 days later. Urea and diamonium phosphate (DAP) were used as sources of N and P_2O_5, respectively. Except for the spacing and fertilizer rate, all trials received standard cultural practices to control insects and weeds.

Measurements

All measurements were taken on well-bordered plants in the central two rows by excluding the plant nearest to the alley of each row. Days from planting to anthesis (AD) were calculated from the date on which 50% of the plants had begun pollen shedding. Three weeks after anthesis, plant and ear height were measured as the distance from ground level to the first tassel branch or the base of the uppermost ear using five plants plot^{-1}. At the same time, the number of primary tassel branches was counted on five randomly selected plants plot^{-1}. In all trials, at physiological maturity, the number of plants and ears per plot were counted, and ears were harvested. An ear was considered fertile if it had one or more grains on the rachis. The number of ears plant^{-1} (EPP) was determined by dividing the total number of ears with grain by the total number of plants in the central two rows plot^{-1} excluding a plant nearest the alley of each row. Number of kernel rows ear^{-1} and kernels row^{-1} were counted on each fertile ear to determine number of kernels ear^{-1}. All harvested ears were shelled and grain mass plot^{-1} was recorded. Grain moisture was measured electronically from a representative grain sample. The grain yield plot^{-1} was determined in kg, converted to ton hectare^{-1} (t ha^{-1}) at 15% moisture content. Repeated scores for each trait were averaged before analysis.

Table 4.1. Description of maize parental lines used in an 8 x 8 diallel cross for a study on combining ability in different environments.

CML No. / Name used	Pedigree	Derivation	Source CIMMYT	Reaction to drought	*Grain texture	Maturity group
Mex101	DTPWC8F31-1-1-1-B	TL99B-6640-5B	Mexico	Tolerant	SD	Inter-mediate
Mex102	DTPWC8F266-1-1-1-B	TL99B-6640-2B	Mexico	Tolerant	SD	Early
Mex103	DTPWC8F347-1-3-1-B	TL99B-6640-3B	Mexico	Tolerant	SF	Inter-mediate
CML 440	G16SEQC1F47-2-1-2-1-BBBB	MZ99B-M1	Harare	Tolerant	SD	Early
CML 442	[M37W/ZM607#BF37SR-2-3SR-6-2-X]-8-2-X-1-BBB	HA00A-1121-8	Harare	Tolerant	SF	Inter-mediate
CML 202	ZSR923S4BULK-5-1-BB	HA00A-1124-9	Harare	Intermediate	D	Late
CML 445	[[TUXPSEQ]C1F2/P49SR]F2-45-7-51-BBB	HA00A-1121-4	Harare	Tolerant	SD/SF	Interm-ediate
KEN	[AC8342/IKENE{1}8149 SR/2/PL9A]#B-96-3-4-B-B	KB00B-OOB 38-14	Nairobi	Intermediate	SF	Late

* SD, SF and D indicate semi-dent, semi-flint and dent, respectively; CML No., CIMMYT maize lines number.

Table 4.2. Environments used to evaluate the inbred lines and hybrids.

No.	Location	Year	Season	Plant density	Code
1	Melkasa	2002	Main	Normal	NDM2
2	Bako	2002	Main	Normal	NDB2
3	Melkasa	2002	Main	High	HDM2
4	Bako	2002	Main	High	HDB2
5	Melkasa	2003	Main	Normal	NDM3
6	Bako	2003	Main	Normal	NDB3
7	Melkasa	2003	Main	High	HDM3
8	Bako	2003	Main	High	HDB3

Table 4.3. Soil properties at three depths of the experimental field at Bako and Melkasa Agricultural Research Centres, Ethiopia, 2002.

Depth (cm)	Texture		PH		Available P^+ (PPM)		Available K^+(PPM)		Total N %	
	Bak*	Mel*	Bak	Mel	Bak	Mel	Bak	Mel	Bak	Mel
0 – 15	CL$^+$	CL	5.25	5.45	12.1	14.60	34.7	36.5	0.12	0.147
15 – 30	clay	loam	5.23	5.43	10.5	11.10	35.4	37.1	0.13	0.161
30 – 45	clay	loam	5.22	5.42	2.5	6.70	40.8	42.5	0.07	0.140

- Bak= Bako; Mel = Melkasa; $^+$CL= Clay loam; Analysed by National Soil Laboratory, Ethiopia

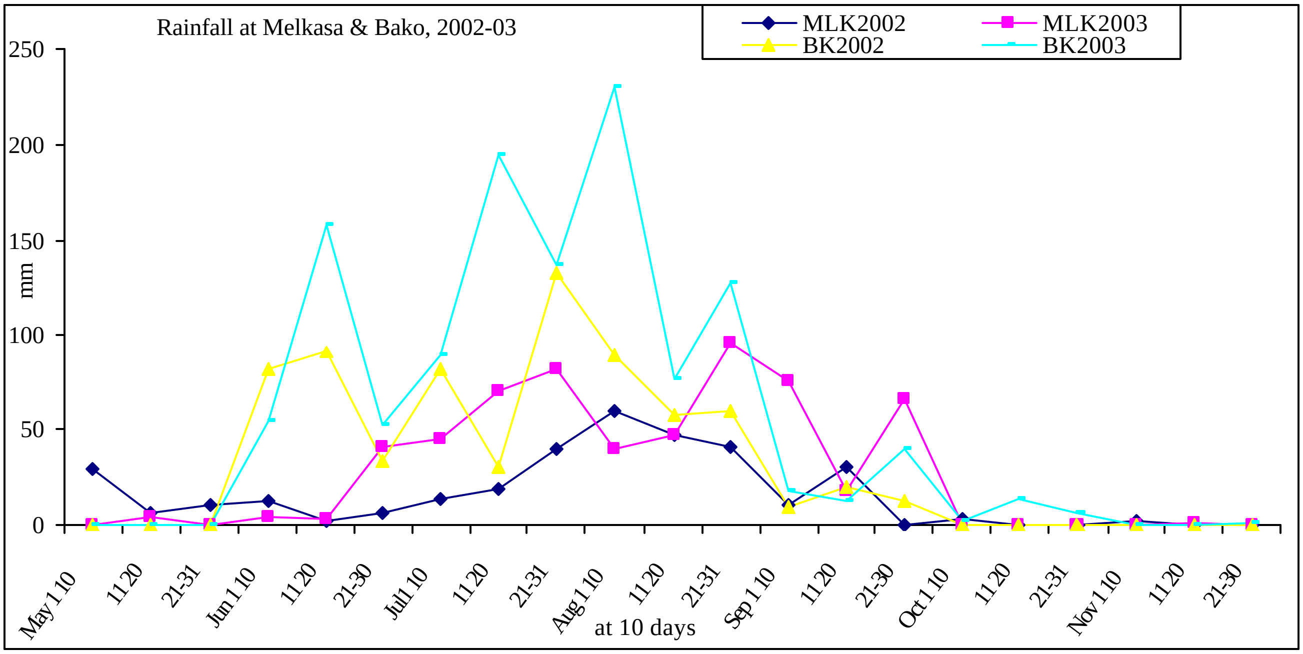

Fig. 4.1. Rainfall distribution and amount (mm) during the experiments at Bako (BK) and Melkasa (MLK) Research Centers, 2002/03.

Statistical analysis

Individual analysis of variance was conducted for each trait in each environment using AGROBASE software (Argonomix Software Inc., 1998). In the ANOVA, genotypes (hybrids or inbreds) and PD were considered as fixed effects, and other environmental factors (location and year) and replications within environments as random effects. The results from individual analyses are not shown but were used to perform analysis across combined environments and for testing combining ability. Combined analyses of variance were also conducted using PROC GLM in SAS (SAS, 1997) for each trait over: (i) four environments planted at normal PD, (ii) four environments planted at high PD, and (iii) all environments.

Each PD location^{-1} year^{-1} was considered as a random environment in the combined analysis of variance as mentioned above. After the detection of significant F-values for genotypes, separate combining ability analyses for each trait across normal PD, high PD, and across all environments were performed using PROC GLM in SAS (1997) and DIALLEL-SAS (Zhang & Kang, 1997). Griffing's Method 4, Model I of the diallel cross analysis was used to estimate GCA of the lines and SCA of the hybrid effects. This was done for each group of environments as well as over all environments (Griffing, 1956). The mean squares for crosses, environments and crosses x environments were tested against the mean squares for crosses x environments, replications within environments, and pooled error, respectively. Significance of GCA and SCA sources of variation were determined using the corresponding interaction with the environments as error terms. Similarly, the significance of GCA × environment (GCA × E), and SCA × environment (SCA × E) interactions were tested against the pooled error.

Heterosis for grain yield was estimated as mid-parent heterosis (MPH) and high-parent heterosis (HPH) for each and across environments, mainly to assess its association with mean hybrid and inbred *per se* performance as well as SCA effects. Mid-parent heterosis was calculated as: $MPH = \frac{(F_1 - MP)}{MP} x100$ where, F_1 is the mean performance of the cross and MP is mean of the two inbred parents. Similarly high parent heterosis was calculated as $HPH = \frac{(F_1 - HP)}{HP} x100$ where HP is the mean of the high yielding parent. The estimated mean values of heterosis were demonstrated across normal and high PD, independently.

Correlations

The genetic correlations (r_G) between grain yield and secondary traits were not estimated in this study, mainly due to the use of fixed parental lines and to small sample size. As a result, only phenotypic correlations (r_p) between grain yield and secondary traits were estimated for the selected improved lines and their crosses across environments. This was mainly done to assess the trend of association in drought tolerant genotypes. The formula provided by Singh & Chaudhary (1985) was used for estimation of the relationship. The variance and covariance combined over environments were used for calculations, which were obtained from analysis by using PROC GLM in SAS.

Phenotypic correlations (r_P between grain yield and other traits were estimated as: $r_P = \frac{d_{Pxy}}{\sqrt{d^2_{Px} . d^2_{Py}}}$ where d_{Pxy} is phenotypic covariance of traits x and y; and d^2_{Px} and d^2_{Py} are phenotypic variances of traits x and y, respectively. The significance of the correlation coefficients was determined using the Student t-test (Steel *et al.*, 1997):

$$t = \frac{r}{\sqrt{1-r^2/n-2}},$$ where r is the correlation coefficient and n is the number of observations. Similarly, Pearson correlation coefficients (r) between inbred line and hybrid performance were estimated by regressing the GCA values on inbred mean performance; and also hybrid yield on all tested parental line traits. In addition, the same estimation was used to calculate association between hybrid yield, SCA, mid-parent heterosis (MPH), high-parent heterosis (HPH), mid parent (MP) and high-parent (HP) *per se* performance using mean environment^{-1} and over environments. NCSS 2000 software (Hintze, 1998) was used in estimating the magnitude and significance of each association.

4.4. Results and discussion

Analysis of variance and mean performance

Significant differences between environments, genotypes, and G x E interactions were observed for most traits tested in each combined ANOVA (Table 4.4). These indicated appreciable variability between environments and within genotypes (lines and hybrids). Although genotypes showed different performances for most traits over environments, hybrids had the same relative performance for yield and EPP across environments at high plant density (PD). The magnitudes of mean squares for all traits were second highest for genotypes after environments, followed by G x E interactions. Analysis of yield across environments showed that environments, genotypes, and G x E accounted for 59, 19 and 21 % of the treatment sums of squares, respectively. When using lines only for the same trait, environments, genotypes and G x E accounted for 62, 28 and 10%, respectively. This was mainly due to topsoil erosion and high frequency of rainfall during the experiment at Bako that reduced performance of the lines (Fig. 4.1). The results for grain yield and most secondary traits were consistent with results obtained with temperate maize testcrosses at three plant densities in the USA (El-Lakany & Russell, 1971), and on relatively similar tropical germplasm across managed environments in Mexico (Betran *et al.*, 2003b).

Across all environments, 23 crosses from drought tolerant lines out yielded the two local hybrids, BH540 and BH140. This indicated that most of the new hybrids showed better performance and adaptation than the conventional hybrids in the rainfed environments. Mean yield of lines were 2.811, 3.735 and 3.273 ton ha^{-1} across normal PD, high PD, and over all, respectively (Table 4.4). In the corresponding environments, hybrid yield averaged 5.442, 6.052 and 5.897 t ha^{-1} (Table 4.5). However, BH540 (check-1) and seven crosses, particularly Mex101 x Mex102 and Mex101 x CML442, performed better under normal than high PD. This indicated that the plant densities used in this study were below optimum for all lines and most hybrids. This observation also suggested that most genotypes increased performance at about 88 800 plants ha^{-1} due to their improvement in stress tolerance through selection for drought tolerance. In agreement with the present result, increased yield and number of ears per unit area due to reduced plant height should be considered as suggested by Johnson *et al.* (1986). However, all hybrids were taller and flowered earlier than their parents in all environments, which was consistent with other studies (Hallauer & Miranda, 1988; Betran *et al.*, 2003a). Although 21 crosses out of 28 showed yield increases under high PD it amounted to only 10.08%, while parental yields increased by 33.21% as compared to normal PD. These differences in tolerance might be due to variation in plant height rather than to genetic effects since hybrid yields were by far higher than their parent yields under all conditions. As a result, relatively reduced heterosis under high PD occurred, mainly due to increased *per se* performance of inbreds at this stand (Table 4.9). Increased yield at high density (59,500 plants ha^{-1}) as compared to lower plant stand was reported on temperate testcrosses (El-Lakany & Russell, 1971).

CML442 and Mex102 consistently provided best *per se* yields at both plant densities, while others showed crossover interaction (Table 4.7). Furthermore, the cross, Mex102 x CMLL442 gave the second highest yield and consistently performed better across environments. Yields were 6.550, 6.543 and 6.547 t ha^{-1} across normal and high PD, and over all, respectively (Table 4.5). Similar trends were also observed with crosses of either of the two lines. Moreover, crosses that involved Mex102 had more EPP as compared to others at both densities. These results indicated that drought tolerant lines with high *per se* yield performance across rainfed environments had the potential to provide promising hybrids for similar conditions. Temperate hybrids have also been reported to be high yielding genotypes under non-stress conditions due to improvement for biotic and abiotic stress (Carlone & Russell, 1987; Duvick, 1997). It should therefore be possible to produce high yielding hybrids for rainfed environments through the combination of drought tolerant lines that perform well under corresponding conditions. With regard to secondary traits, NTB, AD, PH and EH in hybrids increased by 1.35, 1.66, 6.61 and 14.11%, respectively. On the contrary, EPP and NKE were reduced by 26.3 and 41.8%, respectively. This was consistent with other studies, especially those that reported reduced EPP due to drought, low N, and PD stress in both kinds of genotypes (Betran *et al.*, 2003a). However, the yield plot^{-1} was not affected due to an increased number of plants that resulted in an increased number of ears and kernels per plot.

Table 4.4. The analyses of variance for various traits of maize hybrids and lines, planted to different plant densities across environments†.

Genotype	Source	DF	Mean squares						
			GY	AD	PH	EH	EPP	NKE	NTB
	Across normal density environments								
Hybrids	Environment (E)	3	112.31**	8224.91**	58941.88**	28668.3**	0.67	245667.4**	432.43**
	Rep /E	12	12.32**	45.11**	695.03**	154.75	0.211**	17453.9**	9.27**
	Hybrid	29	5.156**	70.88**	3820.74**	2271.65**	0.315**	13963.55*	25.08**
	Hybrid x E	87	2.211**	10.57**	417.61**	195.88**	0.044**	7427.94**	6.37**
	Error	348	0.974	3.999	239.49	108.56	0.017	3665.20	2.453
Lines	Environment (E)	3	23.68**	2880.01**	29978.56**	13527.25**	1.85**	72170.9**	214.9**
	Rep /E	12	0.796**	14.39**	754.53**	244.64	0.113**	33746.01**	10.60**
	Lines	7	4.75**	120.58**	6404.36**	2330.99**	0.217**	15721.8**	12.21**
	Line x E	21	1.33**	7.957	949.59**	517.06**	0.07**	7542.10*	8.78**
	Error	84	0.276	4.78	376.26	143.84	0.021	4125.70	2.26
	Lines mean		2.811	79.547	140.254	59.777	1.055	371.715	11.15
	Across high density environments								
Hybrids	Environment (E)	3	118.82**	5955.43**	4636.56**	34712.8**	0.636**	463794.48**	295.74**
	Rep /E	12	12.18**	29.93**	3479.91**	1587.37**	0.055**	9960.17**	13.50**
	Hybrid	29	2.556**	85.78**	3796.30**	1968.79**	0.030**	8795.17**	24.70**
	Hybrid x E	87	2.113	8.052**	476.49*	279.13**	0.010	3621.64*	4.910**
	Error	348	1.143	5.429	339.58	142.655	0.009	2652.96	2.124
Lines	Environment (E)	3	74.19**	2533.09**	32668.28**	18271.84**	2.080**	10835.25**	199.29**
	Rep /E	12	1.55**	14.27**	1043.09**	434.35**	0.054**	6276.95**	8.91**
	Lines	7	5.37**	138.67**	7603.38**	3548.51**	0.106**	18946.44**	10.29**
	Line x E	21	1.18**	8.57**	1261.94**	470.42**	0.034**	8108.78**	8.52
	Error	84	0.418	2.38	350.17	144.07	0.008	3337.30	3.19
	Lines mean		3.735	79.69	151.461	69.52	0.883	262.039	10.91
	Across all environments								
Hybrids	Environment (E)	7	166.80**	6127.29**	50144.9**	31690.57**	2.587**	153071.85**	313.24**
	Rep /E	24	12.04**	37.52**	2087.47**	871.06**	0.133**	14541.01**	11.38**
	Hybrid	29	6.017**	150.39**	7186.97**	2120.22**	0.239**	19790.91**	45.88**
	Hybrid x E	203	2.218**	8.876**	444.62**	237.51**	0.038**	3296.90**	5.39**
	Error	696	1.117	4.713	289.53	125.61	0.013	2214.03	2.289
Lines	Environment (E)	7	49.75**	2320.10**	27996.97**	14496.56**	1.95**	45553.80**	177.99**
	Rep /E	12	1.19**	14.33**	898.81**	339.49**	0.08**	20011.48**	9.75**
	Lines	7	9.80**	253.91**	13617.98**	5691.08**	0.293**	33015.40**	19.32**
	Line x E	21	1.12**	7.85**	1003.48**	450.12**	0.049**	6943.64**	7.87**
	Error	168	0.347	3.58	363.21	143.96**	0.015	3731.50	2.73
	Lines mean		3.273	79.62	145.86	64.65	0.969	316.877	11.03

† Four environments at each plant density; DF; degrees of freedom; GY, grain yield in ton ha^{-1}; AD, days to 50% anthesis; PH, plant height (cm); EH, ear height (cm); EPP, ears plant^{-1}; NKE, number of kernels ear^{-1}; NTB, number of tassel branches; *, ** Significant at P = 0.05 and P = 0.01, respectively.

Table 4.5. Mean hybrid performances in terms of various traits across environments, planted at normal and high plant densities.

Environments	ND	HD	Across	ND					HD					
Cross / Trait	GY	GY	GY	AD	PH	EH	EPP	NKE	NTB	AD	PH	EH	EPP	NKE	NTB
Mex101xMex102	6.646	6.043	6.345	75.06	195.13	99.38	1.53	534.16	14.37	77.69	205.78	110.61	1.01	373.69	13.61
Mex101xMex103	5.267	5.469	5.368	74.31	189.03	86.64	1.33	501.62	12.08	75.81	200.38	92.56	0.99	330.25	12.44
Mex101xCML440	4.999	5.781	5.390	74.19	173.97	78.34	1.11	501.95	11.90	75.50	188.55	89.99	0.98	352.44	11.98
Mex101xCML442	7.380	6.686	7.033	77.44	195.67	101.97	1.30	580.06	13.50	78.56	212.31	108.95	0.95	370.99	13.59
Mex101xCML202	5.781	5.516	5.649	77.88	206.09	99.53	1.26	532.36	14.19	80.19	206.19	111.62	0.93	368.60	13.71
Mex101x Ken	5.517	5.615	5.566	78.19	213.73	113.97	1.04	524.71	11.64	78.63	217.23	118.23	0.91	358.25	11.75
Mex101xCML445	6.287	6.600	6.443	77.38	198.09	93.09	1.23	520.54	11.98	78.75	222.22	103.59	0.96	353.45	13.46
Mex102xMex103	5.573	6.040	5.807	71.88	175.72	72.36	1.45	513.51	15.04	73.88	205.83	87.82	1.03	363.47	14.50
Mex102xCML440	5.187	5.672	5.429	72.50	162.34	69.31	1.23	505.27	14.23	72.75	183.02	82.31	0.98	373.92	14.06
Mex102xCML442	6.550	6.543	6.547	75.56	186.64	86.48	1.37	552.97	13.12	76.56	183.52	98.76	1.05	371.92	12.91
Mex102xCML202	5.760	6.536	6.148	78.19	187.30	89.81	1.39	508.70	15.71	79.00	196.39	101.08	1.04	402.36	17.05
Mex102xKen	5.748	5.857	5.803	75.19	190.31	91.64	1.25	534.93	13.47	76.06	205.41	112.08	0.94	393.72	13.80
Mex102xCML445	5.848	5.698	5.773	73.44	176.89	81.55	1.37	480.37	13.41	75.94	206.28	95.55	0.96	380.84	13.75
Mex103xCML440	4.331	5.177	4.754	71.38	154.95	61.41	1.11	436.26	12.26	72.63	184.11	80.75	0.97	320.74	12.44
Mex103xCML442	5.699	6.275	5.987	74.56	191.66	76.80	1.28	496.93	14.68	74.75	187.16	95.46	0.93	342.20	14.45
Mex103xCML202	5.842	6.196	6.019	75.00	191.06	87.19	1.30	513.59	15.89	77.56	205.20	103.95	1.00	381.99	16.37
Mex103xKen	5.733	6.113	5.923	74.00	197.47	88.72	1.26	501.23	14.56	73.00	216.23	108.31	0.92	361.48	15.28
Mex103xCML445	5.815	5.866	5.840	72.44	186.86	81.52	1.27	479.48	15.94	74.56	211.64	94.07	0.99	305.88	14.87
CML440xCML442	5.486	6.674	6.080	74.50	170.69	77.98	1.04	479.71	12.74	74.56	198.50	88.07	0.97	361.01	14.43
CML440xCML202	5.502	6.271	5.887	75.00	174.44	81.39	1.11	500.59	14.03	76.56	179.92	89.50	0.93	359.24	15.22
CML440xKen	5.258	5.871	5.564	74.31	175.56	83.97	1.04	508.47	14.16	74.19	190.70	94.72	0.93	374.06	13.98
CML440xCML445	5.272	6.532	5.902	73.25	178.55	79.11	1.03	481.10	14.81	74.44	191.44	88.65	0.93	331.65	14.96
CML442xCML202	5.856	6.431	6.144	77.38	196.84	96.89	1.09	575.44	15.58	78.69	187.97	103.75	0.95	404.27	15.74
CML442xKen	5.577	6.305	5.941	77.00	200.38	97.63	1.08	516.95	13.72	79.06	214.94	114.28	0.90	366.70	13.65
CML442xCML445	5.675	6.047	5.861	78.00	190.58	88.44	1.04	507.67	13.60	78.63	213.95	101.15	0.89	342.08	14.55
CML202xKen	5.777	5.988	5.883	78.25	214.84	108.58	1.21	542.40	14.41	79.75	221.58	122.37	0.91	388.21	15.13
CML202xCML445	6.167	5.987	6.077	77.38	208.47	95.47	1.13	509.53	15.55	78.94	222.19	106.06	0.97	350.82	14.95
KenxCML445	6.251	5.668	5.960	77.00	206.02	100.69	1.06	519.85	14.20	79.00	214.61	114.14	0.89	341.27	13.49
BH540 - check1	5.75	5.38	5.565	76.81	209.06	115.1	1.07	510.5	20	81.75	223.83	125.20	0.86	430.3	15.44
BH140 - check2	5.41	6.02	5.715	75.38	212.80	111.1	1.03	485.6	17.62	81.31	223.98	121.80	0.92	430.9	16.25
Mean	5.442	6.052	5.897	76.96	189.50	88.21	1.21	512.87	13.96	78.38	202.02	100.66	0.96	361.62	14.15
LSD (0.05)	0.575	0.637	0.606	1.08	9.6	6.34	0.089	29.5	1.18	1.3499	10.51	6.82	0.056	27.97	1.02

ND, indicates four environments planted at normal plant density; HD, indicates four environments planted at high plant density; Across indicates over eight environments at both normal and high densities; GY, grain yield in ton ha^{-1}; AD, days to 50% anthesis; PH, plant height (cm); EH, ear height (cm); EPP, ears plant^{-1}; NKE, number of kernels ear^{-1}; NTB, number of tassel branches.

Combining ability

For the tested traits, significant effects for GCA, SCA, and their corresponding interactions with environments were observed at normal PD over four environments, and across all, except

SCA for NKE, and SCA x E for PH (Table 4.6). Similarly, at high PD over four environments, GCA and the GCA x E interaction were highly significant but SCA and the SCA x E interaction were significant only for GY and NTB. The highly significant GCA for all tested traits implied that the inbred lines contributed differently in the crosses in which they were involved. On the other hand, significant SCA indicated that there were hybrid combinations that had a performance different from that expected only on the GCA effects. Furthermore, the results indicated that both additive and non-additive genetic effects controlled the expression of these traits across environments but only additive effects applied to most traits at high PD. The significant interaction showed that the magnitude of differences between the two components of combining ability of genotypes changed with environment. At high plant density, non-significant SCA x E mean squares and significant GCA x E mean squares for AD, PH, EH, EPP and NKE indicated that additive effects were more influenced by the environment than that of non-additive effects for these traits. Thus, the specific hybrid combinations for these traits were stable across high PD environments.

With combined environments, the magnitude of GCA mean squares for all traits were more than twofold in comparison with SCA. The GCA x E interaction mean squares were also higher than the SCA x E interaction for these traits. These results confirmed greater relative importance of GCA than SCA for all considered traits, reflecting more importance of additive genetic effects than non-additive in these traits at two plant densities under rainfed conditions. The GCA and GCA x E interactions were consistent with results reported for managed environments in Mexico (Betran *et al*., 2003a,c). Similarly, except for grain yield, the non-significant SCA x E interaction for most traits observed at high PD across environments was also as reported by the above investigators. However, the previous investigations have shown that both GCA and SCA can interact with environments (Matzinger *et al*., 1959), while others indicated higher stablity of GCA than SCA (Rojas & Sprague, 1952; Kambal & Webster, 1965). Furthermore, the mean squares of GCA, SCA, GCA x E and SCA x E interaction for most traits were higher across combined environments at normal PD as compared to other conditions. The results suggested that genetic expression for these traits increased with a decrease in stress.

Table 4.6. Mean squares of GCA, SCA, GCA x E, and SCA x E for various traits in a diallel of drought tolerant maize lines across environments at two plant densities, 2002/03.

		Mean squares						
Environments		Across normal plant density						
Source	DF	GY	AD	PH	EH	EPP	NKE	NTB
GCA	7	11.75**	248.70**	13498.64**	8197.65**	1.050**	38221.77**	58.06**
SCA	20	2.847**	8.64**	433.48*	197.54*	0.057**	5473.17	13.53**
GCA x E	21	4.063**	15.62**	702.35**	316.54**	0.067**	11575.50**	12.70**
SCA x E	60	1.563**	8.80**	317.95	153.65*	0.036**	5976.30**	4.161**
		Across high plant density						
GCA	7	3.827**	303.50**	13159.90**	7111.94**	0.084**	26984.54**	63.40**
SCA	20	2.111*	9.576*	519.04	168.68	0.012	2428.89	11.15**
GCA x E	21	3.594**	10.94**	928.81**	596.66**	0.014*	6147.00**	7.391**
SCA x E	60	1.594*	7.042	318.18	168.00	0.009	2737.76	4.043**
		Across all						
GCA	7	11.48**	543.46**	25878.43**	7654.80**	0.815**	65230.67**	119.58**
SCA	20	4.105**	12.81**	644.96**	183.11*	0.038**	3887.00*	20.08**
GCA x E	49	3.971**	12.63**	810.51**	456.60**	0.080**	4301.98**	8.879**
SCA x E	140	1.605**	7.561**	316.56	160.82*	0.024**	2945.14*	4.173**

*, ** Significant at P = 0.05 and P = 0.01, respectively; DF, degrees of freedom;
GY, grain yield in ton ha^{-1}; AD, days to 50% anthesis; PH, plant height (cm); EH, ear height (cm); EPP, ears plant^{-1}; NKE, number of kernels ear^{-1}; NTB, number of tassel branches.

General combining ability

The GCA effects and inbred line *per se* performances for traits estimated across environments planted at normal and high plant populations separately, and across all, are presented in Table 4.7. Most parents showed significant GCA effects with different magnitudes and directions, particularly for secondary traits in each combined environment. This suggested the presence of adequate diversity in the genetic constitution of parents for most of the measured traits, and variation among them in sensitivity across different environments. CML202 and CML440 had positive and negative GCA effects respectively, for all tested traits at each plant density over environments. These results demonstrated effective transmission of genes from CML202 to its crosses for most of these traits. Five of the parental lines showed positive GCA effects for grain yield at normal PD, and over all, while only four inbreds expressed similar effects across four environments at high PD. In each of the combined environments, CML442, Mex102, CML445 and CML202 were superior in yield *per se*, and showed consistent positive

GCA effects. This indicated that on average these lines contributed to an increase in yield in crosses at each PD over rainfed environments. Among these parents, the largest GCA effect for yield at both plant densities was contributed by the highest yielding line CML442, followed by Mex102. The crosses of these two, as well as with either CML442 or Mex102 were also superior in environments where they were evaluated. On the contrary, Mex103 and CML440 provided the lowest yield *per se* and GCA effects, and their cross was also the lowest in yield performance (Table 4.5). This indicated a considerable relationship between *per se* performance and GCA effects, which might be considered as the main cause for variability in GCA values among drought tolerant lines. Similar trends in GCA effects for yield were observed among normal maize lines (Debnath & Sarkar, 1990), and among drought tolerant lines under both well watered and stress conditions in Mexico (Betran *et al.*, 2003c). They reported also a consistent relative superiority of lines from La Posta Sequia (LPS) over Tuxpeno Sequia (TS) inbreds across managed environments.

Most lines showed significant, positive GCA effects for AD, PH and EH across environments, indicating additive gene action for increasing these traits. On the contrary Mex102, Mex103 and CML440 had significant negative effects that indicated them as good general combining parents for these traits as they are transmitting genes for early flowering and reduced height. These results were in agreement with similar studies across different managed environments in Mexico, that reported positive GCA effects for plant and ear height in LPS derived lines while TS derived lines showed negative values (Betran *et al.*, 2003a). Similarly, negative corresponding values were also observed with Mex101, CML440 and Ken for NTB, reflecting a small tassel size, which was considered in the study mentioned above as a common character of drought tolerant germplasm. Four lines exhibited consistent, positive GCA effects for EPP and NKE across environments, which was an indicator of promising yield performance. CML202 and Mex102 had high positive GCA effects for EPP and NKE, which consequently appeared as positive GCA effects for yield. The positive GCA effects observed for yield in CML442 appear also to be the consequence of positive GCA effects for NKE only because it had significant, negative GCA values for EPP. Similar studies considered low prolificacy as a major factor limiting grain yield at high plant densities (Buren *et al.*, 1974), as exhibited by Mex102 and its crosses. Although CML442 was the best yielding across rainfed conditions, it may not be superior to Mex102 under stress conditions. Previous studies have proved that positive GCA for EPP is a good indicator of stress tolerance (Bänziger & Lafitte, 1997; Edmeades *et al.*, 1997a; Betran *et al.*, 2003a).

Table 4.7. GCA effects and inbred line *per se* performance (Line) for various traits of maize across environments, and correlation between GCA and lines *per se* for each tested trait

Environment	Normal plant density													
	GY		AD		PH		EH		EPP		NKE		NTB	
Parents	GCA	Line	GCA	Line	GCA	Line	GCA	Line	GCA	Line	GCA	Line	GCA	Line
Mex101	0.280**	2.84	1.130**	78.88	10.33**	148.61	9.243**	69.23	0.053**	1.11	17.55**	362.65	-1.34**	10.17
Mex102	0.186*	3.39	-0.974**	76.06	-8.696**	119.08	-4.49**	48.84	0.187**	1.25	6.637	440.1	0.277	10.49
Mex103	-0.323**	2.16	-2.349**	78.94	-6.626**	126.5	-10.47**	47.11	0.086**	1.04	-24.58**	364.92	0.46**	11.13
CML440	-0.694**	1.99	-2.089**	75.56	-22.67**	113.38	-14.33**	47.84	-0.134**	0.96	-29.46**	364.87	-0.59**	10.32
CML442	0.338**	3.6	1.130**	81.06	3.765*	159.94	1.454	66.64	-0.047**	1.17	19.94**	388.24	-0.127	11.37
CML202	0.082	2.94	1.901**	83.31	8.77**	148.88	6.90**	65.84	0.001	1.06	15.42**	364.39	1.28**	12.66
Ken	-0.056	2.83	1.047**	82.13	11.97**	170.06	11.29**	79.34	-0.089**	0.91	9.740	354.16	-0.257	10.93
CML445	0.186*	2.74	0.203	80.44	3.158*	135.59	0.400	53.36	-0.057**	0.94	-15.26**	334.4	0.300*	12.09
SE (GCA) /LSD	0.0940	0.347	0.191	1.286	1.477	11.406	0.995	7.05	0.0126	0.086	5.780	37.77	1.495	0.885
$r_{(\text{GCA vs. Line})}$	0.87**		0.78*		0.88**		0.91**		0.75*		0.29		0.81*	
High plant density														
Mex101	-0.109	3.94	1.453**	80.13	4.539**	160.13	5.159**	81.28	0.007	0.95	-3.951	264.74	-1.41**	9.69
Mex102	0.004	4.45	-0.755**	76.94	-5.495**	138.64	-2.731*	59.03	0.050**	1.02	21.42**	317.03	0.107	11
Mex103	-0.205*	2.81	-2.370**	78.13	-1.711	140.17	-6.95**	56.14	0.021*	0.89	-20.89**	228.77	0.221	11.67
CML440	-0.065	3.17	-2.630**	74.94	-24.17**	113.67	-15.1**	48.11	-0.003	0.82	-9.719*	263.35	-0.327	10.66
CML442	0.433**	4.48	0.734**	80.94	2.325	167.81	0.970	72.53	-0.011	0.93	4.632	305.85	0.047	10.16
CML202	0.094	3.88	2.380**	83.44	4.638**	151.75	5.622**	76.59	0.004	0.8	20.69**	243.72	1.52**	12.09
Ken	-0.158	3.47	0.547*	83.19	16.91**	187	13.26**	94.14	-0.051**	0.79	8.721	234.16	-0.32*	10.59
CML445	0.005	3.76	0.641**	79.88	2.962	152.52	-0.231	68.36	-0.018*	0.85	-20.9**	216.11	0.166	11.46
SE (GCA) /LSD	0.1021	0.458	0.222	0.907	1.759	11.004	1.140	7.058	0.0089	0.052	4.918	38.701	0.139	1.05
$r_{(\text{GCA vs. Line})}$	0.72*		0.84**		0.94**		0.97**		0.73*		0.56		0.86**	
Across all														
Mex101	0.083	3.39	1.292**	79.50	7.432**	154.37	7.201**	75.26	0.030**	1.03	-0.075	313.7	-1.38**	9.93
Mex102	0.119	3.92	-0.865**	76.50	-7.096**	128.86	-3.61**	53.94	0.119**	1.14	17.94**	378.56	0.192	10.75
Mex103	-0.266**	2.49	-2.359**	78.53	-4.168**	133.34	-8.709**	51.62	0.054**	0.97	-25.34**	296.85	0.34**	11.4
CML440	-0.371**	2.58	-2.359**	75.25	-23.42**	113.52	-14.71**	47.98	-0.069**	0.89	-11.57**	314.11	-0.46**	10.49
CML442	0.393**	4.04	0.932**	81.00	3.045**	163.88	1.212	69.59	-0.029**	1.05	7.026*	347.04	-0.040	10.77
CML202	0.085	3.41	2.141**	83.38	6.706**	150.31	6.261**	71.22	0.0027	0.93	23.05**	304.05	1.40**	12.38
Ken	-0.136	3.15	0.797**	82.66	14.44**	178.53	12.27**	86.74	-0.070**	0.85	12.36**	294.16	-0.29**	10.76
CML445	0.013	3.25	0.060**	80.16	0.437**	144.05	0.084	60.86	-0.005**	0.90	-3.341**	275.26	0.033*	11.77
SE (GCA) /LSD	0.0713	0.286	0.1466	0.783	1.149	7.8804	1.068	4.961	0.0077	0.050	3.176	26.888	0.102	0.684
$r_{(\text{GCA vs Line})}$	0.94**		0.82*		0.93**		0.96**		0.78*		0.39		0.90**	

SE is the standard error of the difference between two GCAs, and LSD is the least significant difference for inbred line *per se* means; *,** Indicates significance of GCA effects estimates at P = 0.05 and P = 0.01, respectively; / *,** significantly different from zero at P = 0.05 and P = 0.01 respectively, for $r_{(\text{GCA vs Line})}$ correlations between GCA and line per se performance ;
GY, grain yield in ton ha^{-1}; AD, days to 50% anthesis; PH, plant height (cm); EH, ear height (cm); EPP, ears $plant^{-1}$;
NKE, number of kernels ear^{-1}; NTB, number of tassel branches.

Specific combining ability

The magnitude and direction of SCA effects varied considerably between the environments within each PD, crosses and traits studied (Table 4.8). Half of the crosses showed negative or positive SCA effects for grain yield across normal or high plant populations as well as across all environments. From each group, 12 of them showed consistent positive SCA effects across combined environments, whereas another 12 also showed consistent negative effects for the trait over combined environments. Only four of the 12 crosses in each group were derived from parents from the same CIMMYT centers, while eight of them were combined from different sources. Most combinations derived from lines from different centers as well as from the same center showed both negative and positive SCA effects. A cross that had a positive SCA effect, mostly implies that the inbred lines in it are genetically divergent among themselves, since they belong to distinct heterotic groups. Thus the source center from where they were introduced did not determine genetic relationships among tested lines. As a result, this study agreed with other studies in that SCA across environments was negative for crosses involving the same genetic background, while it was positive with superior performance for crosses involving inbreds from different genetic backgrounds (Han *et al.*, 1991; Betran *et al.*, 2003b).

In this study, crosses with consistent positive SCA effects ranked 1st to 16th in yield, and also had higher yields in comparison with the grand mean yield (5.897 t ha^{-1}), except for CML440 x Ken (Table 4.5). Over all environments, their SCA effect estimates for the trait ranged from 0.002 t ha^{-1} (CML202 x Ken) to 0.657 t ha^{-1} (Mex101 x CML442). Similarly, those with consistent negative SCA effects ranked 17th to 28th, and had lower yields than the grand mean, except for CML442 x CML202, Mex103 x CML442 and CML442 x Ken. The cross from the two superior parents in *per se* performance, Mex102 x CML442, had consistently higher yields and positive SCA effects in each and across environments. Similarly, crosses in which these lines were involved, were superior in yield and SCA effects as well as for EPP, especially crosses with Mex102. Furthermore, Mex101 x CML442 and Mex103 x CML440 had the highest and second lowest SCA effects for yield, respectively, and were the best and worst in performance at each PD over rainfed environments. Most SCA effects for yield were therefore directly related to performance. Across normal PD environments, SCA effects ranged from 1.019 t ha^{-1} for Mex101 x CML442 to –0.590 t ha^{-1} for CML442 x CML445, while at high density they ranged from 0.651 t ha^{-1} for Mex101 x CML445 to –0.606 t ha^{-1} for Mex103 x CML440. This indicated that the highest positive SCA effects for yield were observed at normal plant populations, while its lowest expression occurred under high PD conditions.

Six and eight crosses showed consistent negative SCA effects for AD and PH respectively, while 10 crosses showed consistent positive effects for each trait across all combined environments. However, all hybrids flowered earlier while plants were taller than their parents (Table 4.5), which was the expected expression in crosses (Hallauer & Miranda, 1988; Betran *et al.*, 2003a). Fourteen and 12 crosses exhibited positive SCA for NKE and EPP across all environments, of which 10 and seven crosses exhibited consistent positive SCA for NKE and EPP, which were also positively corresponding with yield. As a result, these crosses were superior in yield across all environments. On the contrary, seven crosses with poor yield performance showed consistent negative effects for each yield component at two plant densities over all environments. This was to be expected since yield and yield components are highly correlated (Table 4.9), also indicated by another study in Mexico (Bolanos & Edmeades, 1996; Betran *et al.*, 2003a). Furthermore, 12 and nine F_1 hybrids had consistent positive and negative SCA effects, respectively, for NTB across each combined environment. Thus SCA effects in crosses developed from drought tolerant lines related to their performance and showed variability in expression of the corresponding effects for most secondary traits across rainfed environments.

Table 4.8. Estimates of SCA effects for various traits of crosses across environments at two plant densities, and over all, 2002 / 2003.

Environment	High density						Normal density						Across all					
Croses/Trait	GY	AD	PH	EPP	NKE	NTB	GY	AD	PH	EPP	NKE	NTB	GY	AD	PH	EPP	NKE	NTB
Mex101xMex102	0.094	0.3601	8.719*	-0.002	-5.4074	0.7715*	0.437*	-0.473	3.996	0.08**	-2.899	1.48**	0.244	-0.057	6.357*	0.041*	-10.515	1.12**
Mex101xMex103	-0.269	0.0997	-11.1**	0.0065	-6.5300	-0.5135	-0.433*	0.152	-4.169	-0.023	-4.225	-0.99**	-0.348*	0.126	-7.63**	-0.008	-4.604	-0.76**
Mex101xCML440	-0.097	0.0476	0.7840	0.0191	4.4815	-0.4264	-0.330	-0.234	-3.189	-0.023	0.983	-0.123	-0.221	-0.093	-1.203	-0.002	0.069	-0.275
Mex101xCML442	0.310	-0.2545	0.4142	0.0001	8.6825	0.8126**	1.019**	-0.202	8.72**	0.08**	29.70*	1.01**	0.657**	-0.228	4.568	0.042*	13.249	0.91**
Mex101xCML202	-0.52*	-0.2753	-1.8519	-0.035	-9.7601	-0.5512	-0.323	-0.536	-2.411	-0.009	-13.488	0.296	-0.42**	-0.406	-2.131	-0.022	-11.267	-0.128
Mex101xKen	-0.170	-0.0045	-0.2342	-0.004	-8.1412	-0.6561*	-0.449*	0.631	1.941	-0.14**	-15.451	-0.724*	-0.281	0.313	0.853	-0.07**	0.748	-0.69**
Mex101xCML445	0.65**	0.0268	3.2653	0.0162	16.6747	0.5631	0.078	0.662	-4.890	0.024	5.375	-0.94**	0.061	0.057	-0.135	0.003	2.053	-0.032
Mex102xMex103	0.189	0.3705	1.3288	0.0016	1.3149	0.0208	-0.032	-0.182	1.540	-0.036	18.586	0.347	0.055	0.094	1.434	-0.017	8.380	0.184
Mex102xCML440	-0.320	-0.4940	-3.5254	-0.025	0.5883	0.1347	-0.048	0.183	4.206	-0.037	15.216	0.594	-0.217	-0.156	0.341	-0.031	-4.293	0.364
Mex102xCML442	0.054	-0.0461	1.6048	0.050*	-15.7620	-1.395**	0.284	0.027	2.071	0.019	13.525	-0.98**	0.292	-0.010	1.838	0.034*	-10.657	-1.19**
Mex102xCML202	0.386	0.7455	-1.7707	0.0274	-1.3751	1.2737**	-0.250	1.88**	-2.281	-0.007	-26.23*	0.200	0.045	1.31**	-2.026	0.010	8.273	0.74**
Mex102xKen	-0.041	-0.3586	-2.1530	-0.018	1.9533	-0.1312	-0.124	-0.265	-2.460	-0.06*	5.680	-0.509	-0.080	-0.312	-2.307	-0.04*	1.517	-0.320
Mex102xCML445	-0.364	-0.5774	-4.2035	-0.034	18.6880	-0.6745*	-0.267	-1.17**	-7.07*	0.033	-23.878	-1.12**	-0.056	-0.15**	-0.94*	0.000	1.216	-0.15**
Mex103xCML440	-0.61**	0.9955*	-6.0905	-0.009	-10.2721	-1.604**	-0.395	0.433	-5.254	-0.050	-22.576	-1.56**	-0.53**	0.714*	-5.67*	-0.030	-7.109	-1.58**
Mex103xCML442	-0.005	-0.2440	3.8991	-0.04*	-3.1587	0.0400	-0.059	0.402	5.016	0.027	-11.306	0.386	-0.039	0.079	4.458	-0.006	-9.010	0.213
Mex103xCML202	0.255	0.9226	7.6955*	0.0194	20.5725*	0.4818	0.341	0.068	-0.585	-0.001	9.878	0.197	0.301	0.496	3.555	0.009	16.311*	0.339
Mex103xKen	0.424	-1.81**	0.2038	-0.007	12.0273	1.2388**	0.369	-0.077	2.626	0.053	3.194	0.404	0.43**	-0.94**	1.415	0.023	4.322	0.82**
Mex103xCML445	0.013	-0.3378	4.0595	0.0279	-13.9540	0.3361	0.208	-0.796	0.826	0.031	6.450	1.22**	0.019	-0.094	0.407	0.005	-1.382	0.13
CML440xCML442	0.254	-0.1711	0.4512	0.0232	4.4740	0.5596	0.100	0.079	0.089	0.009	-23.64	-0.501	0.221	-0.046	0.270	0.016	-2.301	0.029
CML440xCML202	0.190	0.1830	2.1225	-0.033	-13.3471	-0.1211	0.372	-0.192	-1.169	0.032	1.760	-0.609	0.273	-0.004	0.477	0.000	-4.707	-0.365
CML440xKen	0.041	-0.3586	-0.4316	0.0279	13.4378	0.4821	0.265	-0.025	-3.239	0.055*	15.314	1.05**	0.171	-0.192	-1.835	0.042*	12.650	0.77**
CML440xCML445	0.539*	-0.2024	6.6897	-0.003	0.6376	0.9750**	0.037	-0.244	8.56**	0.014	12.945	1.15**	0.047	-0.037	1.27**	0.001	0.948	0.18
CML442xCML202	-0.147	-1.057*	-6.0754	0.0022	17.3250	0.0186	-0.306	-1.036*	-5.195	-0.07**	27.208*	0.470	-0.234	-1.05**	-5.64*	-0.04*	17.884*	0.244
CML442xKen	-0.022	1.1518*	-2.6920	-0.000	-8.2814	-0.2213	-0.448*	-0.557	-4.859	0.004	-25.60*	0.147	-0.37**	0.298	-3.775	0.002	-10.074	-0.037
CML442xCML445	-0.443*	0.6205	2.3981	-0.036	-3.2794	0.1854	-0.59**	1.29**	-5.846	-0.07*	-9.886	-0.528	-0.51**	0.954**	-1.724	-0.05**	0.910	-0.171
CML202xKen	0.0002	0.1935	8.6981*	-0.004	-2.8220	-0.2145	0.009	-0.077	4.602	0.09**	4.372	-0.570	0.002	0.003	0.33**	0.002*	-0.443	-0.020
CML202xCML445	-0.164	-0.7128	-8.818*	0.0234	-10.5933	-0.887**	0.157	-0.109	7.037*	-0.028	-3.500	0.017	0.000	-0.027	-0.059	0.000	-1.175*	-0.029
Ken x CML445	-0.232	1.1830*	-3.3910	0.0046	-8.1736	-0.4978	0.378	0.371	1.389	-0.007	12.494	0.201	0.007	0.052*	-0.067	0.000	-0.020	-0.010
SE	0.2259	0.4923	3.8936	0.0198	10.8828	0.3079	0.209	0.423	3.270	0.028	12.792	0.331	0.158	0.324	2.542	0.017	7.030	0.226

*. ** Indicates significance of SCA effects estimates at $P = 0.05$ and $P = 0.01$, respectively.

GY, grain yield in ton ha^{-1}; AD, days to 50% anthesis; PH, plant height (cm); EH, ear height (cm); EPP, ears $plant^{-1}$; NKE, number of kernels ear^{-1}; NTB, number of tassel branches.

Correlations

A. GCA effects and line per se performance

For all traits, the correlation between inbred and hybrid performance as regressed GCA values on inbred *per se* performances were highly significant and positive, except for NKE (Table 4.7). Unlike other traits, line *per se* performance for GY and EPP showed relatively better relationships with their corresponding GCA values at normal PD where high GCA values were recorded. Days to 50% anthesis, plant and ear height as well as number of primary tassel branches consistently showed high correlations with GCA under all growing conditions. The strong positive associations in these rainfed environments indicated increased hybrid performance with increased *per se* performance of the lines. Magnitudes of relationships observed in this study were higher, especially for grain yield and days to 50% anthesis, as compared to estimations made under different conditions in Mexico (Betran *et al.*, 2003a,c). However, with grain yield, they found stronger associations under well-watered conditions than in stress environments. Their estimation of other traits was done across all environments but not in each environment, which makes it difficult to relate to results in the present study. Furthermore, in agreement with their suggestion, hybrid performance for most secondary traits across rainfed environments could be well predicted based on parental line performance. These results also indicated the need of improving *per se* performance of lines before testing for combining ability.

B. Hybrid, SCA, heterosis and lines *per se* performance for grain yield

Hybrid grain yield was positively correlated with corresponding SCA and heterosis (MPH and HPH) estimates in each and across combined environments (Table 4.9). SCA effects for yield were also positively and significantly associated with MPH and HPH. This was consistent with a relatively similar study conducted under managed conditions in Mexico (Betran *et al.*, 2003c). Associations between grain yield and SCA were highly significant in each and across environments, which was also the highest across all ($r_{F1.SCA} = 0.69$). This confirms more linkage, especially between hybrid performance and SCA effects than with heterosis expression, which was more affected by parental *per se* performance. It was also consistent with the above study that suggested SCA among lines as a better predictor of hybrid performance than heterosis.

Correlations between hybrid yield and the corresponding heterosis (MPH, HPH) were significant at each PD across environments but not significant when combined across all growing conditions (Table 4.9). This inconsistent association was mainly due to variability in performance of hybrids and their parents in different environments, especially at Bako (Table 4.4). In agreement with the present observation, erratic and inconsistent association between hybrid yield and heterosis was reported in a study across managed environments in Mexico (Betran *et al.*, 2003c). On the other hand, hybrid yield associations with MP and HP were significant across environments but not significant in most individual environments. Furthermore, negative relationships were observed in some environments, especially at Bako. This indicated that high yielding parents transferred their potential to hybrids for combined environments but not for some individual environments. More associations were detected across environments with normal PD than over all and at high PD. The significant positive relationship with parental line yields were reported in seven out of 12 managed environments in Mexico, which agreed with results across combined conditions (Betran *et al.*, 2003c). However, under well-watered conditions at Cotaxtla, the corresponding relationship was 0.08 for the mid-parent and 0.05 for the high parent, corresponding with the results in the present study. Similar results with a negative phenotypic correlation coefficient (-0.12) were also reported in other study on temperate germplasm (Samanci, 1996). Furthermore, this investigator indicated that the high yielding inbreds did not necessarily give rise to high yielding hybrids. However, Kambal & Webster (1965) suggested that those cases in which good parents gave poor hybrids or vice versa could be regarded as due to SCA effects.

Based on estimation at two plant densities over environments, positive associations were observed between hybrid GY and other secondary traits of the lines, except with NTB at high PD (Fig. 4.2). Better association of hybrid grain yield with all traits was obtained with mid-parent than high-parent values. Moreover, line traits showed better relationships with hybrid yield across normal PD than at high populations, except for NKE. The higher correlations of hybrid yield with line NKE across environments at high PD were in agreement with Beck *et al.* (1997), who indicated stronger relationships between line and hybrid performance at high PD. Of all the traits, better associations were detected between hybrid and parent yields in combined environments, while results obtained in Mexico found better association with line AD, followed by yield, under well watered conditions (Betran *et al.*, 1997). In general, the combined results indicated that high yielding drought tolerant lines had the potential to provide high yielding hybrids for rain fed environments. Similarly, in a report that didn't specify environment, Duvick (1999) reported that inbred-hybrid yield correlations were low but positive, indicating a tendency for high yielding inbreds to produce high yielding hybrids. However, the inconsistent, low positive and negative associations observed in individual environments (Table 4.9) suggested the need for evaluation of hybrids rather than depending on parental lines performance. Hallauer & Miranda (1988) pointed out that the ultimate use of inbred lines in crosses must be determined from yield evaluation of crosses.

C. Grain yield and secondary traits

The phenotypic correlations between grain yield and most secondary traits were positive within the fixed inbred lines and their crosses (Table 4.10). PH, EPP and NKE in hybrids had significant phenotypic relationships but none were significant within lines. However, higher phenotypic correlations of GY with secondary traits were estimated in lines than in hybrids for most traits. The relatively strong association, particularly with GY and NKE, indicated the importance of these traits for yield improvement through selection under rainfed conditions. Weak relationships between GY and days to antthesis were observed within lines and hybrids, which is in contrast with the strong association reported by Samanci (1996). The present results were almost similar for most traits, with phenotypic correlations studied in the USA on temperate germplasm (El-Lakany & Russell, 1971), and on tropical germplasm in Mexico (Chapman *et al.*, 1999; Betran *et al.*, 2003a). The same trend in phenotypic correlations was observed for most traits under well-watered conditions in Mexico, in which 3059 S_1 to S_3 lines were drawn from six tropical maize populations (Bolanos & Edmeades, 1996). However, in contrast to the present results, significant negative phenotypic correlations were reported between GY and AD (Bolanos & Edmeades, 1996; Betran *et al.*, 2003a). These investigators found that negative correlations occurred due to intense stress at flowering, which favored early flowering genotypes. In the present study there was adequate rain during flowering as well as before flowering. However, absence of stress in the present study might not be adequate to explain positive associations since Bolanos & Edmeades (1996) reported negative associations ($r_{GY.AD}$ = -0.32±0.22) under well watered conditions. Thus the results in this study should be considered with caution due to the limited number of genotypes of early to intermediate maturity, developed from a limited set of lines.

Table 4.9. Average MPH and HPH, and correlations among F_1 grain yield, SCA, MPH, HPH, and line *per se* performance across each set of plant density and across all density.

Environ-mental	Aveage		Correlation						
Code	MPH	HPH	r(F_1.SCA)	r(F_1.MPH)	r(F_1.HPH)	r(F_1.MP)	r(F_1.HP)	r(SCA.MPH)	r (SCA.HPH)
NDM2	95.855	71.91	0.56**	0.43*	0.55**	0.50**	0.45*	0.52**	0.43*
NDB2	104.57	95.77	0.92**	0.95**	0.96**	-0.13	0.08	0.84**	.86**
NDM3	86.13	71.94	0.67**	0.85**	0.79**	-0.23	-0.17	0.49**	0.48**
NDB3	184.49	154.8	0.61**	0.93**	0.88**	-0.26	-0.30	0.40*	0.39*
Across ND	105.56	84.95	0.64**	0.34	0.52**	0.67**	0.47*	0.68**	0.48**
HDM2	57.73	44.38	0.66**	0.75**	0.68**	0.72**	0.09	0.50**	0.46*
HDB2	115.65	103.53	0.59**	0.89**	0.88**	-0.020	-0.05	0.51**	0.41*
HDM3	51.93	44.08	0.88**	0.81**	0.68**	0.010	0.000	0.73**	0.60**
HDB3	125.21	106.87	0.61**	0.85**	0.70**	-0.16	0.002	0.44*	0.38*
Across HD	62.65	48.71	0.78**	0.42*	0.37*	0.45*	0.45*	0.57**	0.53**
Across all	105.56	66.83	0.69**	0.22	0.26	0.65**	0.54**	0.53**	0.38*

See code in Table 4.2; MPH = mid-parent heterosis; HPH = high parent heterosis; r(F_1.SCA) correlation between F_1 hybrid yield and SCA effects; r(F_1.MPH) correlation between F_1 hybrid yield and MPH; r(F_1.HPH) correlation between F_1 hybrid yield and HPH; r(F_1.MP) correlation between F_1 hybrid yield and mid-parent performance; r(F_1.HP) correlation between F_1 hybrid yield and high parent performance; ND, across four environments planted at normal plant density; HD across four environments planted at high density; *, **, Indicates significance at P = 0.05, and at P = 0.01, respectively.

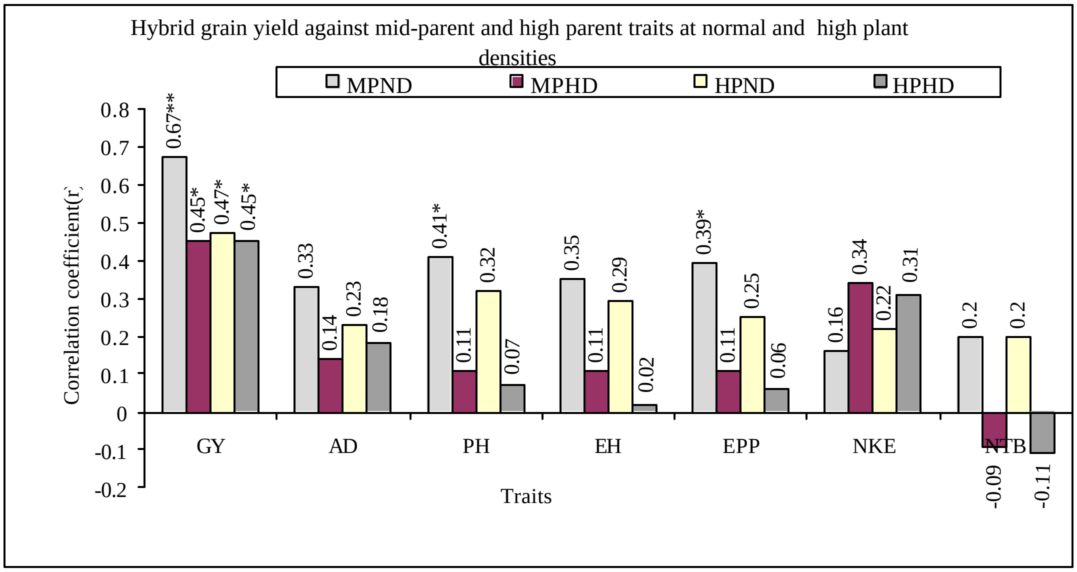

Fig. 4.2. Correlation of hybrid grain yield with mid-parent (MP) and high parent (HP) traits across environments at normal (ND) and high plant density (HD).

*,** Indicates significant correlations at P = 0.05 and P = 0.01, respectively; MPND, Indicates hybrid grain yield correlation with mid-parent traits at normal plant density; MPHD, Indicates hybrid yield correlation with mid-parent traits at high plant density; HPND, Indicates hybrid yield correlation with high-parent traits at normal plant density; HPHD, Indicates hybrid yield correlation with high parent traits at high plant density.

Table 4.10. Phenotypic correlations between grain yield and secondary traits across combined environments.

	Phenotypic correlation (r_p)					
Genotype	Lines			Hybrid		
Environment	Normal density	High density	Across	Normal density	High density	Across
Traits						
AD	0.14	0.03	0.08	0.06	-0.02	0.02
PH	0.51	0.41	0.46	0.41*	0.21	0.30
EH	0.48	0.41	0.44	0.31	0.12	0.28
EPP	0.56	0.25	0.42	0.49**	0.42*	0.45*
NKE	0.46	0.53	0.49	0.42*	0.34	0.26
NTB	0.15	0.12	0.14	0.24	0.31	0.26

*,** Indicates significant correlations at P = 0.05 and P = 0.01, respectively. GY, grain yield in ton ha^{-1}; AD, days to 50% anthesis; PH, plant height (cm); EH, ear height (cm); EPP, ears plant^{-1}; NKE, number of kernels ear^{-1}; NTB, number of tassel branches.

4.5. Conclusions

The results indicated considerable differences in genotype response to variation in environment and within each class of genotype in performance for most traits. Hybrids showed the same relative performance for yield and ears plant^{-1} at high PD across four environments, reflecting more stable performance of hybrids than inbred lines. All lines and most crosses yielded higher at high PD than at normal PD indicating that both population densities were sub-optimal for most short stature, drought tolerant genotypes. Furthermore, the results suggesting that genotype improvement for drought tolerance increased the potential to perform well under high PD stress.

Testing for combining ability indicated that additive genetic effects were more important than non-additive effects for the tested traits in rainfed environments. The cross resulting from the superior parents, Mex102 x CMLL442 was superior in yield across rainfed environments, indicating the importance of parental lines *per se* performance. In addition to the largest positive GCA effects observed with these two parents, their cross as well as other crosses in which they were involved, showed superior SCA effects for yield and its components. A similar trend was observed in most of the other lines and their crosses, indicating a strong relationship between crosses and inbred line performance. Thus improving performance of lines before testing for combining ability is critical to produce superior hybrids for rainfed environments. The stronger associations of grain yield with yield components than with other traits, indicated the need to rely more on these traits during selection for stress and non-stress conditions. SCA effects in this study were considered as reliable predictors of hybrid performance due to their consistent strong association. In general this study demonstrated that drought tolerant lines with high performance in yield across rainfed environments gave high yielding hybrids in corresponding conditions. Most of the crosses were superior to conventional local hybrids that confirmed the importance to improve tolerance to drought stress at flowering while maintaining the capability to perform well under optimal conditions. This is a strategy developed and successfully implemented by CIMMYT. Consequently, CML442 and Mex102 were best in performance and combining ability, and can be considered as good candidates for direct use in hybrids across rainfed environments in countries like Ethiopia.

Chapter 5 Heterosis and combining ability of maize lines in drought stressed and irrigated environments

5.1. Abstract

Maize (*Zea mays* L.) genotypes suitable for tropical areas should ideally perform well in variable environments. Drought tolerant maize lines and their crosses were evaluated in four contrasting environments to estimate: (i) performance, combining ability and heterosis for various traits, (ii) relationship between hybrid grain yield and inbred line *per se* performance for all tested traits, and (iii) correlations among hybrid grain yield, specific combining ability and heterosis. Lines and crosses were evaluated separately in managed trials at two plant densities both in well watered and drought stressed environments. Most of the hybrids and lines increased their yield under well-watered high plant density conditions, mainly due to their short stature and drought tolerance increased their potential to tolerate high-density stress. On the contrary, yield of the inbred lines and their crosses were reduced by 73 and 56% respectively, under drought stressed high plant density conditions. Similarly, heterosis increased with increased stress, which confirmed that stress tolerance was more pronounced in crosses than in inbred lines. A weak association between hybrid grain yield and parental lines *per se*, indicated the importance of hybrid evaluation and combining ability testing in various environments for selection of lines that have superior combining ability. Combining ability testing showed a predominant role of additive (GCA) effects for secondary traits and non-additive (SCA) for yield in each environment. For yield and stress adaptive traits, CML202 and Ken were superior in GCA and *per se* performance across contrasting environments, while Mex101 was superior under severe stress. Similarly, CML440 x Ken, CML440 x CML442 and Mex103 x CML202 consistently showed promising SCA effects and superiority in performance for the same traits. Thus some of the hybrids had combined stress tolerance and yield potential since they performed better in both stress and non-stress environments than conventional hybrids. In general, selected hybrids developed from drought tolerant lines are suggested for resource-poor farmers in variable environments.

Key words: Drought tolerant, resource-poor farmer, variable environments.

5.2. Introduction

In tropical parts of the world, limited and erratic supply of water and nutrients create contrasting environments (Betran *et al.*, 2003b). As a result, drought and low soil nitrogen are the main factors that most frequently limit maize production in this region (Edmeades & Bänziger, 1997; Vasal *et al.*, 1997). Improved genotypes that elevate poor production across diverse environments are crucial for the majority of farmers that practice low input agriculture in the tropics. In general, hybrids that exhibit heterosis are credited for providing large increases in production per unit area and often maintain their advantage over open pollinated varieties, both in favourable and stress environments (Duvick, 1999; Vasal *et al.*, 1997; 1999). CIMMYT has developed stress tolerant maize lines especially for better performance during drought at flowering, while maintaining or increasing production under non-stressed conditions (Edmeades & Bänziger, 1997; Vasal *et al.*, 1997). However, there is limited information on their combining ability and heterosis generated among these lines in variable environments.

The relationship in performance between lines and their crosses is controversial. Some workers reported that *per se* performance of maize lines might not predict yield ability of their hybrids (Hallauer & Miranda, 1988; Samanic, 1996), while others advocated a large role of lines *per se* in improving hybrid performance (Beck *et al.*, 1997; Vasal *et al.*, 1997; Duvick, 1999). It is generally considered that inbred lines with superior yields under drought and low N conditions will provide superior hybrids under stress (Betran *et al.*, 1997; Vasal *et al.*, 1997). The superior performance of inbred lines under high plant density (PD) conditions was also observed at high PD with hybrids derived from such lines (Troyer & Rosenbrook, 1983; Russel, 1991; Troyer, 1996). Many investigators have suggested the use of combining ability tests over different environments for selection of parental lines (Hallauer & Miranda, 1988; Jagadeshwar & Shinde, 1992). Studies on combining abilities have indicated that both general combining ability (GCA) and specific combining ability (SCA) for most characters interacted with environmental change, but GCA was found to be more sensitive to environmental change than SCA (Sprague & Tatum, 1942; Debnath & Sarkar, 1990). On the other hand, mid-season drought tolerant maize genotypes were found to be tolerant to a range of N stresses (Bänziger *et al.*, 1999b) and had improved broad adaptation (Chapman *et al.*, 1997). A recent study in Mexico indicated the need for drought tolerance in both parental lines to provide promising hybrids under severe stress conditions (Betran *et al.*, 2003c). However, there is limited information on the relative relationship and performance of drought tolerant lines and their hybrids in highly variable environments.

The degree of heterosis depends on the relative performance of inbred lines and crosses, as well as on a differential effect of the environment (Knight, 1973; Young & Virmani, 1990; Betran *et al.*, 2003b). Studies have shown that heterosis is greater in stress environments than under favorable conditions (Young & Virmani, 1990; Duvick, 1999), due to higher sensitivity of inbreds to stress than their hybrids (Falconer, 1989; Betran *et al.*, 2003b). This implies that it is more meaningful to characterize a particular combination as showing heterosis for yield at a specific locality or under certain environmental conditions (Chapman *et al.*, 2000).

Diallel analysis plays an important role in the partitioning of total variation of the data into GCA of each genotype and SCA of each cross, and in selecting superior parents for hybrid combinations (Hallauer & Miranda, 1988; Sughroue & Hallauer, 1997; Koutsika-Sotiriou, 1999). According to Griffing (1956) and Hallauer & Miranda (1988), for selected parents, estimation of the effects of each pair of parents for SCA, and GCA for all crosses that include a common parent is appropriate and valid. The objectives of this study were to estimate the following for drought tolerant lines and their crosses under four contrasting, partially managed environments: (i) performance, heterosis and combining ability effects of the tested traits; (ii) relationship between hybrid grain yield and inbred line *per se* performance for all tested traits; and (iii) correlations among hybrid grain yield, specific combining ability and heterosis.

5.3. Material and methods

Experimental materials

A diallel cross excluding reciprocals was made between eight maize lines bred for drought tolerance at CIMMYT. Details of the eight parental lines regarding pedigree/source and reaction to drought are provided under Material and Methods of Chapter 4. During evaluation, two Ethiopian maize hybrids (BH-540 and BH-140) were included as checks to assess the extent of adaptation of the new hybrids over the four environments, which were excluded during diallel analysis. Consequently, only mean squares and mean performances of these two local hybrids are included in this study. At Melkasa Research Centre, a furrow irrigation system was used to apply about 40 mm of water, as estimated by partial flume, every seven days over all growing conditions, until watering was suspended for the two drought stressed environments. Soil texture and other properties at the experimental plots are reported under Materials and Methods of Chapter 4.

Experimental procedures and design

The trials were conducted during the off-season, from September 26, 2002 to February 13, 2003, at Melkassa Agricultural Research Centre ($8^o24'$N, $39^o21'$E, 1550 masl) using four environments as indicated below.

1. Well-watered normal plant density (WWND), where about 44 400 plants ha^{-1} were established with a spacing of 30 cm between plants within rows, and irrigated at seven day intervals until maturity.
2. Well-watered high plant density (WWHD), where the plant density as in environment ‘1’ was doubled with a spacing of 15 cm between plants (88 800 plants ha^{-1}).
3. Drought stressed normal plant density (DSND), where irrigation was suspended 15 days prior to 50 % anthesis until 25 days after anthesis, when one additional irrigation was made. The plant population was as in ‘1’.
4. Drought stressed high plant density (DSHD), similarly drought stressed as in ‘3’ but plant density increased as in ‘2’.

In each environment, the eight inbred lines and 30 hybrids were evaluated separately in experiments planted side by side to eliminate the effects of differences in vigor between inbreds and hybrids. The experimental design was a randomized complete block (RCBD) with four replications. For hybrids, each block was folded to minimize soil variability within block. Each plot consisted of four 4.2 m rows with inter-row spacing of 75 cm. An alley of 1.5 m wide was left between the blocks within each trial. One additional border plot block^{-1} was added at each end of a block, planted to the local hybrid (BH-140) to avoid border effects. All experiments were sown in adjacent blocks of the same field, while five free rows between well watered and drought stressed condition was left to avoid leaching to the stressed treatments. Two seeds hill^{-1} were planted in all trials to ensure uniform stand and thinned to one plant hill^{-1} when the seedlings reached the two-leaf stage. All trials received standard cultural practices to control insects and weeds. For each growing condition, as recommended by the centre, 50 kg P_2O_5 ha^{-1} and 25 kg N ha^{-1} was applied at planting followed by a side dressing of 25 kg N ha^{-1} 35 days later. Urea and diamonium phosphate (DAP) were used as sources of N and P, respectively.

Measurements

All measurements were taken on well-bordered plants in the central two rows by excluding a plant nearest the alley of each row. Days to anthesis (AD) and silking (SD) were determined as days from planting until 50% of the plants had begun shedding pollen or had silks emerged from the husks. Anthesis-silking interval (ASI) was calculated as the difference between silking and anthesis dates or by subtracting AD from SD. Three weeks after anthesis, plant height was measured as the distance from ground level to the first tassel branch, and the number of primary tassel branches was counted on five randomly selected plants per plot. Leaf senescence was visually estimated on a plot basis as the proportion of alive green vs. senesced dried leaves 3-4 weeks after flowering on a 1–10 scale, where 1 = 0 % senesced leaves and 10 = 100 % senesced leaves. At physiological maturity, the numbers of plants and ears were counted. Ears were harvested from each plot. An ear was considered fertile if it had one or more kernels on the rachis. Numbers of ears plant^{-1} (EPP) were determined by dividing the total number of ears with kernels by the total number of plants per plot. Number of kernel rows ear^{-1} and kernels row^{-1} were counted on each fertile ear to determine number of kernels per ear^{-}. All harvested ears were shelled and grain mass was recorded plot^{-1} in kg, and grain moisture was measured electronically from representative grain samples. The grain yield plot^{-1} was adjusted to the standard of 15% moisture content, recorded as ton hectare^{-1} (t ha^{-1}). Repeated scores for each trait were averaged before analysis.

Statistical analysis

Data were first tested for normality, and ASI was normalized using the transformation $\log_e\sqrt{(ASI+10)}$. Data were analyzed with plant densities, moisture regimes, and genotypes (hybrids or inbreds) as fixed effects, and replicates within environment as random effects. An analysis of variance of each tested trait in each and across environments were carried out by using AGROBASE^{TM} software (Argonomix Software Inc., 1998). Mean squares for genotypes were tested against the mean squares of errors for each environment. For combined analysis, mean square for genotypes, environments and genotypes x environments (G x E) were tested against the mean squares for G x E, replications within environments, and the pooled error, respectively. After observation of significant F-values for genotypes, a separate combining ability analysis for each trait in each growing condition was performed, using the same software (Table 5.1). The analyses of combining ability across environments were also computed using PROC GLM in SAS (1997) and DIALLEL-SAS (Zhang & Kang, 1997). Griffing's Method 4, Model I of the diallel cross analysis was used to estimate GCA and SCA effects of lines in each environment and across environments (Griffing, 1956). GCA and SCA effects represent additive and dominant gene effects. For individual trials, significance of GCA and SCA values were determined by t-test, using gi and sij variances, respectively (Griffing, 1956; Singh & Chaudhary, 1985). For trials combined over environments, the significance of GCA and SCA sources of variation were determined using the corresponding interaction with environments as error terms (Zhang & Kang, 1997). The significance of GCA × E and SCA × E interactions was determined using the pooled error. Furthermore, the ratio between GCA and SCA mean squares were also estimated to determine the relative magnitude of mean squares due to GCA and SCA.

Heterosis estimates

Mid-parent heterosis was calculated as: $MPH = \frac{(F_1 - MP)}{MP} x100$ where F_1 is the mean performance of the F_1 hybrid and MP is the mean of the two inbred parents. Similarly, high parent heterosis was calculated as $HPH = \frac{(F_1 - HP)}{HP} x100$ where HP is the mean of the best parent. For grain yield it was estimated in two ways, as mid-parent heterosis (MPH) and high-parent heterosis (HPH) in each and across growing conditions. However, HPH was used only in the estimation of its association with SCA effects, hybrid, mid-parent and high-parent *per se* performance. For other traits, MPH in each environment was estimated but for EPP and NKE results are provided for less stress (WWND), severe stress (DSHD) as well as across the four environments. Similarly, for AD, ASI, PH and NTB only mean MPH environment^{-1} is presented. Significance of MPH values was determined by single degrees of freedom contrasts between F_1 generations and mid-parent values, using the PROC GLM in SAS (SAS, 1997).

Correlation

Pearson correlation coefficients between inbred line *per se* and hybrid performance were estimated by regressing the F_1 grain yield on mid parent values. In addition, the same estimations were calculated between hybrid yield, SCA, MPH and HPH from means environment^{-1} and across environments. The significance of the correlation coefficients was obtained from NCSS 2000 software (Hintze, 1998).

Table 5.1. Analysis for combining ability in Method 4 for Model 1 according to Griffing (1956).

Source of var.	df	MS	EMS Model I
Replications	r-1		
Crossses	[n(n-1)/2]-1	MS_C	$s_e^2 + r d_C^2$
GCA	n-1	MS_{GCA}	$s_e^2 + [r(n-2)/(n-1)] d_{GCA}^2$
SCA	n(n-3)/2	MS_{SCA}	$s_e^2 + [2r/n(n-3)] d_{SCA}^2$
Error	(r-1){[n(n-1)/2]-1}	MS_E	s_e^2
Total	r[n(n-1)/2]-1		

n = number of parents; r = number of replications

5.4. Results and discussion

Analysis of variance and mean performance

Considerable genetic differences were observed among genotypes for most traits at high plant density but only for some traits in other environments (Table 5.2). Across environments, significant differences ($P<0.01$) for all traits were observed for environments and genotypes, while genotype x environment interactions were not significant for most traits. Although substantial environmental and genotypic variability were observed, hybrids showed the same relative performance across environments for most traits. However, the differential response observed for yield and its components agreed with other studies (Han *et al.*, 1991; Hallauer & Miranda, 1988).

Mean yields for hybrids ranged from 2.656 t ha^{-1} under DSHD to 6.976 t ha^{-1} under WWHD (Fig. 5.1 and Table 5.3). Under the same growing conditions, parental lines performed from 0.827 t ha^{-1} to 3.848 t ha^{-1}. Mex102 x CML202 (7.34 t ha^{-1}) and CML440 x CML202 (8.26 t ha^{-1}) were the best performers under WWND and WWHD, respectively, while Mex101 x CML445 (4.5 t ha^{-1}) and Mex101 x Mex103 (4.0 t ha^{-1}) were the best at the same stand under drought stressed conditions. From the parents, Mex102, Mex101 and CML445 showed promising *per se* performance in grain yield in each and across environments (Table 5.5), while Mex103 x CML202, CML440 x CML442, CML440 x Ken and Mex101 x CML442 were relatively better under the same conditions. Furthermore, some of these new hybrids out yielded the local hybrids both in less stress and stress environments, reflecting their adaptation to different growing conditions. However, only seven of them performed better than conventional hybrid (BH540) under WWND, while 11 hybrids yielded more than BH140 under DSHD. BH140 consistently ranked better across environments, which indicated its relatively better performance in variable environments as compared to many new hybrids and BH540. Under WWHD, mean GY of lines and their hybrids increased by 26.3 and 14.89 %, respectively (Fig. 5.1). However, CML442 x Ken and BH540 performed better under WWND than WWHD. Variation in morphology might be the main cause for higher yield gain in lines, since hybrid yields were higher than their parents in all environments. Although the same plant population size reduced GY of unimproved S_1 lines derived from A-511 by 28.3 %

(Chapter 3), this high stand was not above the optimum for most of these short stature genotypes, and their drought tolerance may also have improved their potential under high density stress. Similar trends were reported on temperate testcrosses (El-Lakany & Russell, 1971). Under DSHD, the corresponding values were reduced by 72.8% and 56.3% for parents and hybrids, respectively. This indicated improved drought tolerance in hybrids over inbred lines for the trait. In Mexico, 86% of GY was reduced in S_1 lines due to drought stress (Bolaños & Edmeades, 1996). Under similar conditions in which improved materials were tested, yield of hybrids under severe and intermediate drought stress were 13 and 50% of the yield under well-watered conditions respectively, while their drought tolerant parents provided 5 and 48% (Betran *et al.*, 2003b). Thus a greater reduction was recorded in Mexico than at Melkasa, which may be due to differences in intensity of stress and due to the improvement of the parents.

Hybrid EPP and NKE from WWND to DSHD reduced by 29 and 70%, and for parents by 38 and 79%, respectively. Other studies on 3059 S_1 lines recorded 52 and 57% reductions, respectively (Bolaños & Edmeades, 1996). Recent reports on improved genotypes also indicated that drought, low N, and plant density stress reduced EPP, although hybrids and inbreds had similar numbers of EPP in these environments (Betran *et al.*, 2003a). Hybrids in this study were taller and flowered earlier than parental lines in all environments, in agreement with other reports (Hallauer & Miranda, 1988; Betran *et al.*, 2003a). Leaf senescence scores recorded for crosses and their parents were almost similar, while relatively more NTB was recorded in less stressed environments. On the contrary, the NTB score in Mexico was similar under both stress and non-stress conditions. In general, values for AD, ASI and SEN were higher for parents, but higher GY, EPP, NKE, PH, and NTB were recorded with hybrids in each environment. Furthermore, coefficients of variation (CV%) were higher in drought stressed than in well-watered environments, which was above 30% for GY and NKE, especially for parents in DSHD (Fig. 5.1). This was due to low means and not because of high error variation. In agreement with these, Betran *et al.* (2003c) reported that parental lines were relatively more sensitive to drought as compared to their hybrids. Thus the results indicate better adaptation of hybrids to stress environments.

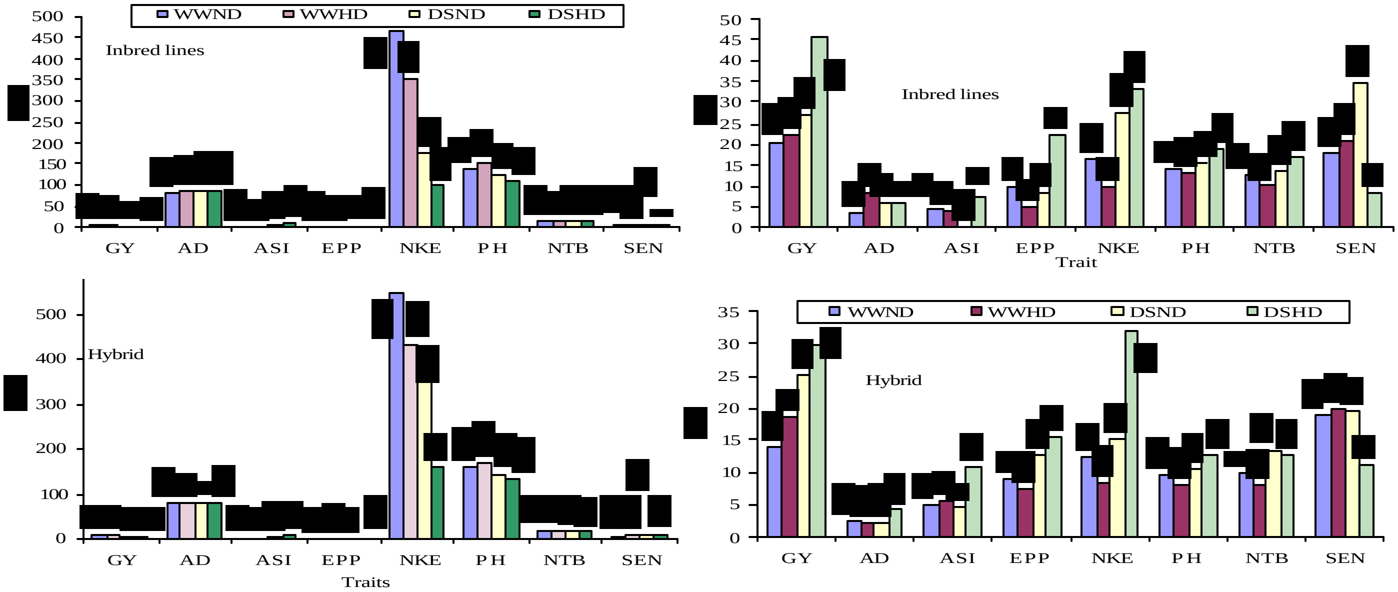

Fig. 5.1. Coefficients of variation (CV%) and means of performances of inbred lines and their crosses for various traits tested in four environments. (See Table 5.3 for abbreviations)

Table 5.2. Mean squares for inbred lines and their crosses for various traits tested in each and across environments, 2002.

Environment		WWND		WWHD		DSND		DSHD	
Trait	Genotype	Parent (7)	Hybrid (27)	Parent	Hybrid	Parent	Hybrid	Parent	Hybrid
GY		1.43*	2.722**	0.906	1.876**	0.439	0.2416	0.559	1.887**
AD		97.50**	24.12**	109.28**	30.41**	117.49**	27.06**	96.55*	41.10**
ASI		0.001*	0.0005	0.002**	0.001	0.002	0.0006	0.009**	0.006
EPP		0.006	0.007	0.007	.022**	0.006	0.067**	0.112**	3.24**
NKE		6133.92	6437.29	12207**	8616.4**	1914.24	550.67*	2327.76	5750.64**
PH		864.27	1137.02**	457.95*	953.97**	462.93	613.66**	464.14	726.53**
NTB		12.346**	12.42**	9.298*	9.191**	12.73**	11.41**	13.87*	10.538**
SEN		0.294	0.238	6.57**	1.969	7.642	1.691	1.375*	1.21
		Parent (7)	F_1 (27)	P CV%	F_1 CV%	F_1 Envt (3)	F_1GxE (81)	†P Envt (3)	P G x E (21)
GY	Combined across all environments	1.113*	2.275**	32.62	21	500.70**	1.673**	68.33**	0.740**
AD		193.69**	104.50**	5.54	0.03	245.19**	2.574	770.78**	75.713**
ASI		0.005**	0.003**	6.01	7.17	0.270**	0.002	0.108**	0.003**
EPP		0.040**	0.077**	14.84	11.14	2.161**	0.019**	1.420**	0.035**
NKE		2042.99**	11582.6**	10.22	14.71	3920697**	4987.09	9635.10**	3513.31
PH		1455.27**	2799.22**	16.65	10.39	4224.06**	210.65	8614.8**	246.09
NTB		40.05**	35.62**	13.6	11.6	34.10**	2.627	11.49*	2.73
SEN		8.86**	1.830**	0.2	16.79	173.82**	1.173	67.28**	2.34*

GY, grain yield in t ha^{-1}; AD, days to 50% anthesis; ASI, anthesis-silking interval in days; PH, plant height in cm; EPP, ears plant^{-1}; NKE, number of kernels ear^{-1}; NTB, number of tassel branches; SEN, leaf senescence; Numbers in parenthesis represent degrees of freedom; *, **, Indicates significance at P = 0.05 and P=0.01, respectively; † Envt, environment; F_1, Hybrid; P, Parent ; G x E, genotype by environment interaction.

Table 5.3. Mean grain yield (t ha^{-1}) and rank in performance in each and across environments.

	Environments and ranks									
Crosses	WWND	Rank	WWHD	Rank	DSND	Rank	DSHD	Rank	Across	Rank
Mex101xMex102	6.35	13	7.13	10	2.50	30	2.75	13	4.68	18
Mex101xMex103	5.09	27	6.52	22	3.25	15	4.00	1	4.71	16
Mex101xCML440	3.50	30	5.83	30	3.50	9	2.75	14	3.89	30
Mex101xCML442	6.27	15	7.42	9.	2.75	25	3.25	6	4.92	9
Mex101xCML202	5.94	21	6.12	27	3.00	19	3.50	4	4.64	20
Mex101xKen	6.01	19	6.45	24	3.50	10	2.75	15	4.68	19
Mex101xCML445	6.53	9	8.01	2	4.50	1	2.25	22	5.32	4
Mex102xMex103	4.83	29	6.06	28	3.00	20	2.50	18	4.10	29
Mex102xCML440	4.90	28	6.49	23	3.75	2	2.50	19	4.41	24
Mex102xCML442	6.38	12	7.07	12	2.75	26	2.00	24	4.55	22
Mex102xCML202	7.34	1	7.89	5	3.00	21	1.75	25	4.99	7
Mex102xKen	6.61	7	6.65	19	2.75	27	3.00	7	4.75	15
Mex102xCML445	5.53	25	6.62	21	3.25	16	3.75	3	4.79	12
Mex103xCML440	6.00	20	7.51	8	3.75	3	1.25	30	4.30	27
Mex103xCML442	6.43	11	7.64	7	3.50	11	2.50	20	5.02	6
Mex103xCML202	7.17	3	7.66	6	3.75	4	3.00	8	5.39	2
Mex103xKen	5.76	23	5.98	29	3.50	12	2.25	23	4.37	26
Mex103xCML445	6.68	6	6.78	16	2.75	28	3.50	5	4.93	8
CML440xCML442	6.33	14	7.97	4	3.25	17	3.00	9	5.14	5
CML440xCML202	6.06	18	8.26	1	3.00	22	4.00	2	5.33	3
CML440xKen	6.87	4	7.99	3	3.75	5	3.00	10	5.40	1
CML440xCML445	5.88	22	6.21	26	3.75	6	1.75	26	4.40	25
CML442xCML202	5.62	24	6.64	20	3.00	23	1.50	29	4.19	28
CML442xKen	7.26	2	6.90	13	3.75	7	1.75	27	4.91	10
CML442xCML445	5.34	26	6.70	18	3.50	13	3.00	11	4.63	21
CML202xKen	6.45	10	7.08	11	3.00	24	2.75	16	4.82	11
CML202xCML445	6.21	17	6.90	14	3.25	18	2.75	17	4.78	13
KEN1xCML445	6.69	5	6.89	15	2.75	29	2.50	21	4.71	17
BH-540 (Check-1)	6.55	8	6.35	25	3.59	8	1.55	28	4.51	23
BH-140 (Check-2)	6.22	16	6.78	17	3.30	14	2.82	12	4.78	14
Mean	6.072		6.976		3.226		2.656		4.750	
LSD (0.05)	1.33		1.15		1.02		0.94		1.11	

GY, grain yield in ton ha^{-1}; AD, days to 50% anthesis; ASI, anthesis-silking interval in days; PH, plant height in cm; EPP, ears plant^{-1}; NKE, number of kernels ear^{-1}; NTB, number of tassel branches; SEN, leaf senescence;

WWND=Well watered + normal density; WWHD=Well watered + high density; DSND =Drought stress + normal density; DSHD= Drought stress + high density.

Combining ability

Significant GCA and SCA mean squares were observed for most traits in less stress and across all environments, but only for yield components under DSHD (Table 5.4). This confirmed that both additive and non-additive gene effects pertained to various environments. Consistent significant GCA effects were detected for NTB and PH in all environments, which indicated that the inbred lines contributed differently in the crosses, and that of additive gene effects played a predominant role in controlling the expression of these traits. Similarly, the importance of non-additive genetic effects in controlling the expression of GY was observed under most growing conditions. The estimates made across environments also showed highly significant effects for GCA, SCA, and GCA x E for most traits. SCA x E was highly significant for GY only, indicating that the specific hybrid combinations for the other traits were stable across environments. The traits that showed significant GCA and GCA x E suggest the need of selecting different parental lines for hybrids to be used in specific environments. Similar studies found significant GCA effects for almost all traits, while SCA was significant for GY, AD, ASI, PH and NTB across 12 environments (Betran *et al*., 2003a, b, c). Many investigators have shown that GCA and SCA can interact with environments (Matzinger *et al*., 1959; Beck *et al*., 1990; Han *et al*., 1991; Betran *et al*., 2003a,c). Recently, Betran *et al*. (2003a, b, c) reported significant GCA × E interactions for all secondary and primary traits, but SCA x E effects were significant only for husk cover. The significant interactions imply that the magnitude of differences among GCA and SCA effects of genotypes change with environment.

The mean squares of GCA and SCA for GY, NKE and PH were reduced with increasing stress, indicating increased importance of additive and non-additive genetic effects under less stress conditions for these traits. On the contrary, an increased importance of additive gene effects was observed under severe stress for AD, ASI, EPP and SEN, as the magnitude of GCA increased with increasing stress. In general, the GCA/SCA ratio over all environments was higher than unity except for GY, indicating the predominant role of additive genetic effects in the inheritance of most of these traits (Baker, 1978), while non-additive effects applied to yield. This was in agreement with a study made with maize lines

Table 5.4. Mean squares of variance for combining ability of various traits of drought tolerant maize lines evaluated in each and across environments at Melkasa, 2002.

Environment	WWND			WWHD			DSND			DSHD			Across all				
Source	GCA (7)	SCA (20)	GCA/ SCA	GCA (7)	SCA (20)	GCA/ SCA	GCA (7)	SCA (20)	GCA/ SCA	GCA (7)	SCA (20)	GCA/ SCA	GCA (7)	SCA (20)	GCA x E (21)	SCAx E (60)	GCA/ SCA
GY	0.804 *	0.634 *	1.268	0.281	0.535 **	0.525	0.154	0.219	0.703	0.276	0.540 **	0.511	0.812	2.786 **	1.748 **	1.646 **	0.291
AD	18.438 **	1.686 *	10.936	26.5 **	1.00 **	26.41	20.976 **	1.79 **	11.72	33.74 **	2.061	16.37	354.77 **	16.90 **	2.678	2.538	20.99
ASI	0.00014	0.0002	0.952	0.00014	0.00002	7.00	0.00014	0.0002	0.952	0.004 **	0.001	4.00	0.0085 **	0.0015	0.003 **	0.0014	5.667
EPP	0.002	0.002	1.0	0.013 **	0.003 *	4.333	0.045 **	0.007	6.429	0.015 **	0.013 **	1.15	0.23 **	0.023 **	0.041 **	0.0111	10.0
NKE	2054.15	1453.6	1.413	6118.46 **	766.57	7.982	2200.5 *	1116.7	1.971	2790.8**	964.1	2.89	26995.3 **	6188.1	9057.9 **	3562.3	4.362
PH	751.132 **	120.85 **	6.216	762.40 **	35.124	21.71	449.83 **	49.671 **	9.056	536.70 **	57.36	9.36	9391.6 **	491.89 **	202.89	213.3	19.09
NTB	8.6 **	1.181 *	7.282	6.008 **	0.999 **	6.014	9.416 **	0.557	16.91	7.92 **	0.785	10.09	117.4 **	6.996 **	3.355	2.372	16.78
SEN	0.065	0.238	0.273	1.225 **	0.236	5.191	0.871 *	0.266	3.274	0.45 *	0.250	1.81	0.56	0.24	0.483	0.194	2.333

GY, grain yield in ton ha^{-1}; AD, days to 50% anthesis; ASI, anthesis-silking interval in days; PH, plant height in cm; EPP, ears plant^{-1}; NKE, number of kernels ear^{-1}; NTB, number of tassel branches; SEN, leaf senescence; WWND=Well watered + normal density; WWHD=Well watered + high density; DSND =Drought stress + normal density; DSHD= Drought stress + high density.

Numbers in parenthesis represent degrees of freedom; *****, ******, Significantly different from zero at P = 0.05 and P = 0.01, respectively.

(Sughroue & Hallauer, 1997), and with populations and pools in Mexico, which indicated greater importance of non-additive effects in controlling yield (Crossa *et al.*, 1990b).

General combining ability effects

The GCA effects and inbred line *per se* performance for traits studied in each and across environments are presented in Table 5.5. The results indicated that GCA effects of the parents for the tested traits under contrasting growing conditions were variable in both magnitude and direction. Many parents showed significant GCA effects for most secondary traits in each and across environments, while only Ken in WWND, and Mex101 in DSHD showed significant positive effects for yield. These results suggested the presence of adequate diversity in the genetic expression of parents for most traits under all growing conditions. However, no parent was a good general combiner for all traits in all environments. Only Ken and Mex101 were good general combiners for grain yield under less and severe stress, respectively. CML202 and CML445 showed consistent positive GCA effects in most environments, with promising *per se* GY, while CML442 and Ken also had positive overall GCA. Furthermore, CML442 showed considerable GCA effects and the best GY *per se* performance under WWHD, but the least in GCA and mean yield under drought stressed conditions. Unlike the rest, Mex102 showed consistent negative GCA effects in all environments but was relatively superior in *per se* GY under most growing conditions. This indicated no positive association between GY GCA effect and *per se* performance of Mex102. Other workers also observed that even lines derived from the same population may have either good or poor GCA (Han *et al.*, 1991; Betran *et al.*, 2003c).

Mex102 and CML202 showed relatively better GCA for EPP and NKE, while Ken was positive for NKE, PH and AD across environments. On the contrary, CML445 showed negative GCA for all the tested yield components, including PH and AD in all environments. Thus Mex102, CML202 and Ken were good general combiners for most yield components across environments, indicating effective transmission of genes for stress adaptive traits from parents to their crosses. Most other lines also showed negative GCA effects for AD and /or ASI under most growing conditions, which are desirable phenomena in drought tolerant lines as they are transmitting genes for early flowering and reduced ASI. Across all, Mex101 and Mex103 were good general combining parents for stressed areas as they showed significant negative GCA effects for ASI. On the contrary, CML442 had significant positive GCA for the trait. This line had relatively the longest ASI *per se* under drought stress, which is not a desirable trait under stress conditions as it showed the least GY *per se* in the same environment. Among these drought tolerant lines, no line had below 0.5 for EPP, even under severe stress, while Mex102 and CML202 were relatively superior and consistent in *per se* performance for the trait in most environments. Although the parents were bred for drought tolerance, their trait expressions were variable in magnitude and direction under most conditions. Most of these observations were consistent with similar studies conducted in Mexico, which found variability among drought tolerant lines (Betran *et al.*, 2003a,c). They found that more lines derived from La Posta Sequia (LP) showed negative GCA effects for flowering traits than other drought tolerant sources. Furthermore, three out of five LP derived lines had positive GCA effects for plant and ear height, while Tuxpeno Sequia inbreds showed negative values.

Significant positive GCA effects for GY, EPP and NKE, and negative effects for SEN and ASI are essential for maize genotypes to sustain production under stressed and non-stressed conditions. CML202 and Ken were relatively better general combiners for yield and most stress adaptive traits, while Mex102 showed stress adaptive yield components, excluding yield, in all environments. Similarly, CML442 had a positive trend for GY in less stress environments, and for some yield components in most growing conditions, whereas CML445 was promising with regard to yield only. Furthermore, consistent negative GCA effects for SEN were showed by Mex102, Mex103, CML202, and Ken under drought stressed conditions. Although Mex101 had the best yield under severe stress conditions, it showed desirable expression for yield components and ASI under most environmental conditions. In general, most parents were good general combiners for some traits under most growing conditions but only few of them responded well in terms of yield and stress adaptive secondary traits across contrasting environments.

Table 5.5. General combining ability effects (GCA) and inbred line *per se* performance (Line) for various traits in four environments.

Environ-ment		WWND		WWHD		DSND		DSHD		Across all			WWND		WWHD		DSND		DSHD		Across all	
Line	Trait	GCA	Line	GCA	Line	GCA	Line	GCA	Line	GCA	Line	Trait	GCA	Line	GCA	Line	GCA	Line	GCA	Line	GCA	Line
Mex101	GY	-0.469	3.390	-0.208	4.220	0.142	0.82	0.414*	0.830	-0.084	2.32	NKE	7.650	421.4	0.967	410.2	-1.175	178.3	20.177	92.60	-4.19	289.13
Mex102		-0.094	3.550	-0.135	4.150	-0.142	1.10	-0.055	1.600	-0.146	2.60		-13.77	492.2	-7.654	534.1	-0.152	196.4	9.22	140.9	3.31	345.89
Mex103		-0.091	2.100	-0.095	3.310	-0.090	0.85	0.074	1.050	-0.027	1.83		-10.11	372.7	-25.39*	385.4	-16.48	177.5	-8.50	118.9	-24.8**	266.75
CML440		-0.494	2.500	0.175	3.200	0.285	1.15	-0.041	0.740	-0.016	1.90		-9.506	420.4	2.407	443.0	19.75	153.7	26.177	110.6	-1.44	280.67
CML442		0.188	2.490	0.272	4.540	0.048	0.99	-0.254	0.320	0.019	2.08		-21.73	481.7	6.58	550.8	4.251	183.7	-18.52	75.95	4.16	319.55
CML202		0.380	3.320	0.305	3.620	-0.077	1.54	0.064	0.630	0.150	2.28		25.328	457.2	24.44*	425.4	-8.482	203.2	-7.792	102.5	19.5**	302.06
Ken		0.523*	3.280	-0.21	3.620	-0.017	1.76	-0.137	0.660	0.081	2.33		28.348	428.9	12.723	410.6	5.640	196.3	-3.127	65.64	23.2**	280.37
CML445		0.057	3.740	-0.101	4.110	-0.149	1.04	0.034	0.790	0.023	2.42		-6.209	413.0	-14.077	415.4	-3.359	140.2	-17.64	89.31	-19.7**	266.99
SED (GCA) / LSD Line		0.237	0.818	-0.208	0.950	0.124	0.609	0.331	0.703	0.089	0.33		16.09	87.29	9.747	54.03	11.22	60.34	31.141	40.42	.96	24.83
		GCA	Line	GCA	Line	GCA	Line	GCA	Line	GCA	Line		GCA	Line	GCA	Line	GCA	Line	GCA	Line	GCA	Line
Mex101	EPP	-0.020	1.190	-0.005	1.140	0.042 *	0.89	0.059	0.89	0.044 **	1.03	PH	4.664	138	6.866 *	168.30	9.378 *	135.5	7.104	108.8	7.0 **	137.0
Mex102		-0.007	1.250	0.018	1.140	0.019	0.85	0.088 *	1.03	0.067 **	1.06		-12.6 **	109.7	-7.144 *	146.90	-10.5 *	111.6	-11.60 **	99.38	-10.5 **	116.9
Mex103		0.011	1.290	0.007	1.050	0.014	0.79	0.024	0.81	0.02 **	0.95		-0.596	129.7	-3.192	141.0	-7.03	128.2	-2.896	107.9	-3.43 *	126.7
CML440		0.013	1.390	-0.032 *	1.180	0.022	0.80	-0.026	0.83	-0.04 **	1.06		-17.2 **	136.4	-21.5 **	155.0	-9.60 *	124.7	-13.0 **	98.88	-15.3 **	123.7
CML442		-0.012	1.330	-0.003	1.140	-0.035 *	0.86	-0.086 *	0.51	-0.05 **	0.93		7.1953 *	155.1	7.297 *	159.40	4.930	144.4	7.917 *	123.2	6.84 **	141.7
CML202		-0.011	1.320	0.041 *	1.170	0.010	0.87	0.066 *	0.94	0.04 **	1.06		12.37 **	149.5	10.74 **	155.20	9.076 *	135.7	5.437	101.9	9.41 **	135.6
Ken		0.034	1.270	-0.019	1.140	-0.042 *	0.89	-0.041	0.63	-0.05 **	0.96		12.46 **	152.2	11.38 **	166.70	7.836 *	143.2	12.08 **	127.8	10.9 **	144.4
CML445		-0.007	1.240	-0.007	1.160	-0.029	0.85	-0.082 *	0.62	-0.06 **	0.97		-6.273	134.2	-4.415	140.40	-4.070	127.1	-5.042	105.8	-4.90 **	126.9
SED (GCA) / LSD Line		0.025	0.166	0.0137	0.068	0.025	0.083	0.061	0.173	0.01	0.05		3.6424	23.36	3.4717	24.35	3.777	24.27	4.30	28.02	1.5	8.92

GY, grain yield in ton ha^{-1}; AD, days to 50% anthesis; ASI, anthesis -silking interval in days; PH, plant height in cm; EPP, ears $plant^{-1}$; NKE, number of kernels ear^{-1}; NTB, number of tassel branches; SEN, leaf senescence; WWND=Well watered + normal density; WWHD=Well watered + high density; DSND =Drought stress + normal density; DSHD= Drought stress + high density; SED = standard error of difference between two GCAs, LSD = the least significant difference for inbred line *per se* means; *,** Indicates significance of GCA effects estimates at P = 0.05 and P = 0.01, respectively.

Table 5.5. Continued.

Environ-ment	Trait	WWND		WWHD		DSND		DSHD		Across all		Trait	WWND		WWHD		Across all	
Line		GCA	Line	GCA	Line	GCA	Line	GCA	Line	GCA	Line		GCA	Line	GCA	Line	GCA	Line
Mex101	AD	1.313*	78.25	1.39**	88.0	1.167*	88.25	1.979*	76.25	1.38**	82.69	NTB	-1.41**	16.06	-0.469	13.81	-0.66**	-2.42
Mex102		-0.479	79.25	-0.188	85.5	-0.583	93.0	-0.979	77.75	-0.49**	83.87		-0.615	12.06	-1.302**	12.25	-1.19**	19.22
Mex103		-0.729	75.75	-1.27**	83.7	-1.30**	90.0	-2.10**	81.75	-1.29**	82.81		0.427	13.94	0.281	15.13	0.01	-45.20
CML440		-2.771**	72.75	-3.23**	80.5	-2.60**	79.0	-3.31**	80.75	-2.91**	78.25		-0.781*	12.88	-0.885*	13.13	-0.84**	-14.27
CML442		-0.146	75.5	0.146	85.5	-0.375	84.25	0.104	83.25	0.003	82.12		0.552	13.38	0.448	13.50	0.59**	6.414
CML202		3.062**	88.75	3.35**	98.0	3.50**	95.75	4.229**	80.25	3.33**	90.69		2.510**	14.88	1.990**	17.13	2.35**	34.39
Ken		0.854*	78.75	1.56**	90.25	1.042*	91.25	0.813	84.75	1.138**	86.13		-0.490	11.5	-0.219	13.19	-0.39*	34.55
CML445		-1.104*	74.25	-1.77**	85.75	-0.792	84.25	-0.729	81.75	-1.133**	81.50		-0.198	16.25	0.1563	14.75	0.13	-32.7
SED (GCA) / LSD Line		0.491	3.469	0.492	4.470	0.673	6.041	0.8342	6.714	0.19	2.0		0.362	2.094	0.5703	1.982	0.17	0.65
													DSND		DSHD		Across all	
Line		GCA	Line	GCA	Line	GCA	Line	GCA	Line	GCA	Line		GCA	Line	GCA	Line	GCA	Line
Mex101	ASI	0.001	-0.50	-0.005	0.00	-0.005	1.75	-0.026	6.50	-0.008*	2.01	SEN	0.34	5.13	0.15	7.75	0.22	4.24
Mex102		0.005	2.0	0.0001	1.75	-0.003	1.50	-0.017	9.0	-0.004	2.65		-0.32	4.25	-0.02	8.50	-0.19	5.57
Mex103		0.005	0.0	-0.004	1.0	0.001	3.75	-0.023	19.0	-0.012**	5.15		-0.16	5.63	-0.02	8.75	-0.11	5.47
CML440		-0.003	1.75	0.003	2.75	-0.004	5.25	-0.014	7.50	-0.003	2.29		0.55*	6.88	0.40*	7.88	0.33*	4.76
CML442		-0.006	1.75	0.006	2.00	-0.002	4.0	0.045**	14.50	0.018**	4.04		0.34	7.0	0.23	8.63	0.15	4.72
CML202		0.002	1.0	-0.003	2.00	0.006	2.0	0.004	10.25	0.001	2.96		-0.49	2.75	-0.52*	7.26	-0.31*	4.05
Ken		-0.003	0.50	-0.006	-0.50	0.007	4.25	0.019	6.75	-0.0002	2.08		-0.32	5.0	-0.06	8.0	-0.10	5.32
CML445		-0.001	0.25	0.011	1.0	0.001	3.25	0.012	5.50	0.000	1.77		0.05	4.75	-0.15	0.81	0.13	2.87
SED (GCA) / LSD Line		0.0048	1.421	0.0054	1.31	0.005	2.87	0.013	5.659	0.004	1.15		0.224	2.19	0.166	7.25	0.147	2.56

Specific combining ability

The estimates of SCA effects for the studied traits varied both in magnitude and direction between environments, and among crosses (Table 5.6). Most crosses showed non-significant SCA effects for each trait under most growing conditions. The number of crosses that had positive and negative SCA effects varied somewhat for each trait in each environment. However, 17 and 19 crosses out of 28 had negative SCA effects for EPP in DSND and DSHD, respectively. Only one cross out of 28 was significantly different from zero in reduced stress environments for NKE, EPP, ASI and PH, and for NKE and AD under drought stressed conditions.

The largest SCA effects for GY was contributed by Mex102 x CML202, Mex101 x CML445, Mex103 x CML440, CML440 x CML202 and CML440 x Ken under WWND, WWHD, DSND, DSHD and across all, respectively. These crosses were also superior in yield in their respective environments (Table 5.3). It is therefore demonstrated that high yielding crosses showed high SCA values, indicating the importance of SCA effects in predicting F_1 hybrid performance for each trait. This observation was consistent with a similar study in Mexico, which suggested that SCA predicts hybrid yield better than heterosis, since it is not affected by parental performance (Betran *et al.*, 2003b). At Melkasa, relatively more crosses showed significant SCA for yield under severe stress (DSHD). Consistent negative SCA effects with poor performance in each and across environments were observed with Mex101 x CML440 and Mex102 x Mex103. On the contrary, Mex101 x CML445, CML440 x CML202, CML440 x Ken, and Mex103 x CML202 were relatively superior in yield and SCA effects in each and across environments. In this study it was difficult to determine genetic relationships between parents based on their source center since most combinations made from different or the same centers showed inconsistent properties. However, it seems to confirm what other studies observed, that cross combination from diverse genetic backgrounds had positive SCA effects with high performance, while the reverse held true for closely related parents. Thus almost the same phenomena were observed as reported in other studies in Mexico (Han *et al.*, 1991; Betran *et al.*, 2003c).

For stress adaptive traits, CML440 x Ken and CML440 x CML442 were superior with regard to NKE and EPP, while Mex101 x Mex102 and CML202 x Ken had high SCA values for EPP across all environments. Moreover, CML440 x Ken, CML442 x CML445, Ken x CML445 and Mex103 x CML440 also had positive SCA values for NKE under most growing conditions. Similarly, consistent negative SCA effects in most environments were observed for ASI in the above crosses, including Mex103 x CML202 and Mex102 x CML445, which were also superior in yield SCA and performance in DSHD. This indicated that high yielding crosses across environments showed desirable expression for drought and high population adaptive traits.

Six crosses for NTB and eight crosses for PH were positive, while another ten crosses for PH and eight for NTB were negative for the corresponding values in the growing conditions indicated in Table 5.6. No clear trend for PH was observed but most crosses with significantly positive and negative SCA effects for NTB showed both poor and good yield respectively, especially under severe stress. Mex101 x Mex102 was the only one that showed positive SCA effects for plant height and tassel size, and was intermediate in yield in most environments. Although all the parental lines were bred for drought tolerance, most of their cross combinations lacked consistent response in different growing conditions for traits considered in this study. However, CML440 x Ken, Mex103 x CML442, and Mex103 x CML202 were relatively promising and performed well in yield and stress adaptive traits across contrasting environments. In general, this study indicated variability in performance among hybrids developed from drought tolerant lines. It indicated also the need for evaluation of these crosses in diverse environments that represent conditions of smallholder farms. As a result, these three hybrids can be recommended for use at various diverse sites.

Table 5.6. Specific combining ability effects of crosses for various traits of maize in each and across environments at Melkasa, 2002.

Environment	WWND	WWHD	DSND	DSHD	Across	WWND	WWHD	DSND	DSHD	Across	WWND	WWHD	DSND	DSHD	Across
Cross / Trait	GY					EPP					NKE				
Mex101xMex102	0.844	0.512	0.242	-0.191	0.175	0.018	0.101**	0.006	0.043	0.100**	33.280	-1.08	7.54	-27.61	10.057
Mex101xMex103	-0.424	-0.133	-0.365	0.916*	0.073	-0.015	0.109**	-0.004	0.057	0.026	30.970	-13.03	-26.72	41.73	-12.659
Mex101xCML440	-1.606**	-1.10*	-0.023	-0.265	-0.77**	-0.019	-0.024	-0.039	0.0245	-0.004	-18.700	-46.37	8.59	-21.75	-1.452
Mex101xCML442	0.483	0.394	0.051	0.474	0.163	0.009	-0.010	0.028	0.0595	0.008	8.200	18.15*	12.92	0.66	10.556
Mex101xCML202	-0.048	-0.938*	0.094	0.15	-0.217	0.032	-0.088*	0.050	-0.0396	-0.029	-7.380	-31.11	-6.31	33.05	11.455
Mex101xKen	-0.115	-0.092	-0.348	-0.159	-0.035	-0.038	-0.052	-0.016	-0.0105	-0.053*	-48.110	-1.54	-64.04*	-23.74	-18.558
Mex101xCML445	0.865	1.357**	0.349	-0.926*	0.615**	0.013	-0.036	-0.026	-0.134*	-0.049*	1.750	74.99	68.03*	-2.34	0.600
Mex102xMex103	-1.06*	-0.673	-0.257	-0.14	-0.470*	-0.023	-0.011	-0.016	-0.009	-0.009	-4.420	-1.28**	-37.06	-15.05	-7.884
Mex102xCML440	-0.588	-0.506	-0.275	-0.043	-0.159	-0.017	-0.048	-0.004	0.016	-0.018	-25.270	-26.63	-31.45	11.56	-9.948
Mex102xCML442	0.219	-0.026	-0.438	-0.296	-0.056	-0.017	-0.021	-0.002	-0.014	-0.041	-56.310	-1.60	-55.34*	-12.52	-36.113**
Mex102xCML202	0.983*	0.762	0.196	-0.855*	0.297	0.019	0.0411	0.0203	-0.048	0.001	42.710	52.22	-6.13	-63.11*	6.239
Mex102xKen	0.113	0.036	0.189	0.38	0.054	-0.021	-0.066	-0.066	-0.014	-0.035	11.730	16.28*	68.95*	60.41	27.267*
Mex102xCML445	-0.51	-0.105	0.343	1.144**	0.158	0.040	0.003	0.062	0.027	0.002	-1.720	-37.93	53.49*	46.33	10.382
Mex103xCML440	0.516	0.472	0.561*	-1.36**	-0.124	-0.037	-0.029	0.094**	-0.101	-0.011	27.580	53.12	32.43	-10.84	18.800
Mex103xCML442	0.256	0.501	0.367	0.049	0.268	0.043	-0.055	0.054	0.005	-0.008	2.000	3.31*	41.61	46.40	10.107
Mex103xCML202	0.813	0.490	0.193	0.273	0.489*	0.006	0.032	-0.026	-0.012	-0.004	-1.350	1.740	23.36	-11.48	6.134
Mex103xKen	-0.744	-0.669	-0.194	-0.342	-0.428*	0.006	-0.042	-0.057	-0.023	-0.012	-48.950	-37.31	0.18	-50.34	-12.897
Mex103xCML445	0.643	0.012	-0.304	0.602	0.192	0.200	-0.004	-0.045	0.083	0.018	-5.820	-6.55	-33.8	-0.43	-1.601
CML440xCML442	0.563	0.568	0.252	0.738*	0.413*	0.004	0.014	0.035	0.010	0.023	51.910	13.18	51.53*	15.96	17.567
CML440xCML202	0.105	0.818*	-0.414	1.152**	0.404*	-0.034	0.063	-0.107**	0.033	-0.015	-63.980*	14.60	-15.66	18.71	-20.601
CML440xKen	0.768	0.567	0.034	0.494	0.630**	0.132**	0.049	0.055	0.065	0.040	47.470	15.46	4.50	53.12	23.026
CML440xCML445	0.242	-0.82*	-0.135	-0.719*	-0.390*	-0.030	-0.025	-0.033	-0.047	-0.015	-19.010	-23.37	-49.94*	-66.75*	-27.392*
CML442xCML202	-1.02*	-0.896*	-0.017	-0.896*	-0.68**	0.007	-0.047	-0.025	-0.047	-0.030	17.360	-8.75	35.08	-21.49	14.212
CML442xKen	0.473	-0.117	-0.152	-0.385	0.087	-0.040	0.094*	-0.054	-0.053	0.021	-39.110	-22.19	-47.40	-41.37	-31.115*
CML442xCML445	-0.973*	-0.425	-0.064	0.316	-0.191	-0.005	0.025	-0.036	0.041	0.027	15.950	-2.10	-38.40	12.35	14.787
CML202xKen	-0.53	0.030	0.305	0.302	-0.106	-0.017	-0.010	0.074*	0.060	0.049*	40.390	2.810	3.430	17.70	-4.194
CML202xCML445	-0.303	-0.266	-0.357	-0.126	-0.182	-0.016	0.009	0.014	0.054	0.028	-27.740	-31.52	-33.77	26.63	-13.246
KENxCML445	0.035	0.245	0.167	0.291	-0.203	-0.023	0.027	0.063	-0.024	-0.010	36.590	26.480	34.39	-15.79	16.470
SE(sca)	0.4773	0.403	0.274	0.331	0.198	0.036	0.035	0.034	0.0609	0.023	28.987	21.572	24.832	31.141	13.184

GY, grain yield in ton ha^{-1}; AD, days to 50% anthesis; ASI, anthesis-silking interval in days; PH, plant height in cm; EPP, ears $plant^{-1}$; NKE, number of kernels ear^{-1}; NTB, number of tassel branches; SEN, leaf senescence; WWND=Well watered + normal density; WWHD=Well watered + high density; DSND =Drought stress + normal density; DSHD= Drought stress + high density; *,** Indicate significance of SCA effects estimates at P = 0.05 and P = 0.01, respectively.

Table 5.6. Continued.

Environment	WWND	WWHD	DSND	DSHD	Across	DSND	DSHD	Across	WWND	WWHD	Across	WWND	WWHD	Across
Cross / Trait			AD				ASI †			PH †			NTB †	
Mex101xMex102	1.256	0.738	1.167	-0.339	0.80	-0.011	0.010	-0.003	14.27*	10.13	8.7**	1.96**	1.298*	0.913*
Mex101xMex103	1.506	0.071	0.167	0.036	0.54	0.005	-0.010	-0.001	-2.15	-0.575	2.334	0.417	-0.786	-0.543
Mex101xCML440	-1.202	-0.72	-1.542	-2.506	-1.4**	0.008	-0.003	0.011	-15.6*	-7.236	-6.160	0.125	0.881	-0.092
Mex101xCML442	-0.577	-1.095	-1.542	-1.673	-1.13**	-0.003	-0.005	-0.011	1.31	1.999	0.774	0.542	0.048	0.621
Mex101xCML202	0.214	0.446	2.833*	3.202*	0.990*	-0.012	-0.033	-0.004	6.13	11.74*	6.015	-2.42**	-1.494*	-1.23**
Mex101xKen	0.173	0.988	-0.208	1.369	0.677	0.032*	-0.001	0.005	-6.7	-8.893	-5.392	-1.67*	-0.036	-0.568
Mex101xCML445	-1.369	-0.429	-0.875	-0.089	-0.490	-0.019	0.042	0.004	2.78	-7.164	-6.269	1.042	0.089	0.897*
Mex102xMex103	0.548	0.155	-0.583	1.244	0.260	0.009	0.009	-0.001	-9.04	-1.627	-4.669	-0.875	-1.202*	-0.501
Mex102xCML440	-0.911	-0.137	-0.042	-0.048	-0.37	0.002	-0.004	-0.004	-9.39	1.399	-3.693	-1.167	-0.786	-0.550
Mex102xCML442	-0.036	-0.262	0.958	0.536	0.219	0.009	-0.009	0.003	6.99	2.822	0.178	-0.500	-0.619	-0.822*
Mex102xCML202	-0.244	0.53	-0.917	-0.339	-0.04	-0.003	0.059	0.017*	6.18	-8.123	-0.035	1.292	2.339**	1.44**
Mex102xKen	-0.536	-0.929	0.292	-0.423	-0.48	0.001	-0.015	0.000	-0.96	-9.383	0.575	0.042	-0.702	-0.136
Mex102xCML445	-0.077	-0.095	-0.875	-0.631	-0.39	-0.007	-0.052	-0.012	-8.05	4.784	-1.053	-0.75	-0.327	-0.342
Mex103xCML440	-1.411	0.446	-0.792	-0.423	-0.63	-0.004	0.032	0.001	-2.87	-2.928	-2.041	0.542	-0.119	0.432
Mex103xCML442	-0.286	-0.179	0.208	0.161	-0.104	0.010	-0.001	-0.003	4.19	7.457	4.977	0.208	0.798	0.176
Mex103xCML202	-0.744	-1.637*	-0.167	-1.964	-0.93*	-0.029*	0.001	-0.019*	10.95	-4.700	3.040	-0.500	-0.244	-0.361
Mex103xKen	-0.036	0.155	0.542	0.952	0.323	-0.013	0.0002	0.016	-1.75	-1.210	-3.382	0.500	0.964	0.486
Mex103xCML445	0.423	0.988	0.625	-0.006	0.531	0.022	-0.031	0.007	0.66	3.582	-0.260	-0.292	0.589	0.311
CML440xCML442	0.006	-0.72	0.00	-0.131	-0.29	-0.039**	0.001	-0.004	-1.54	-5.234	-1.336	0.417	-0.786	0.142
CML440xCML202	3.048**	0.571	1.625*	1.244	1.82**	0.032*	-0.012	0.007	15.22*	2.014	5.906	-0.542	0.673	0.075
CML440xKen	-1.494	-0.637	-1.417	-0.589	-1.12**	0.008	-0.008	-0.004	-0.92	10.50	1.702	0.708	-0.619	0.106
CML440xCML445	1.964*	1.196	2.167*	2.452	1.97**	-0.008	-0.007	-0.008	15.12*	1.482	5.622	-0.083	0.756	-0.113
CML442xCML202	-0.077	1.196	-1.625*	-0.173	0.031	0.013	0.018	0.004	-25.2**	-4.376	-13.6**	0.375	0.339	0.163
CML442xKen1	0.881	-0.012	1.583	0.994	0.781	-0.008	-0.005	0.003	13.52*	-4.949	4.761	-0.875	0.548	-0.115
CML442xCML445	0.089	1.071	0.417	0.286	0.490	0.017	0.001	0.008	0.68	2.28	4.196	-0.167	-0.327	-0.165
CML202xKen	-0.077	1.03	-0.542	-1.131	0.021	-0.008	-0.026	-0.013	-2.66	11.17	1.299	1.417	-0.494	0.364
CML202xCML445	-2.119*	-2.137**	-1.208	-0.839	-1.9**	0.007	-0.007	0.007	-10.68	-7.727	-2.673	0.375	-1.119	-0.452
Ken x CML445	1.089	-0.595	-0.25	-1.173	-0.21	-0.012	0.054	-0.006	-0.51	2.763	0.437	-0.125	0.339	-0.136
SE (SCA)	0.836	0.675	0.77	1.325	0.421	0.013	0.0319	0.008	6.371	5.687	3.318	0.686	0.579	0.380

† Estimates under less stress for ASI, and under drought stress for PH and NTB were omitted from the table.

Heterosis estimates

Negative mid-parent heterosis (MPH) was detected for AD and ASI in most environments, and for EPP with a few crosses under WWND, while the rest of the traits had positive MPH. (Table 5.7 and Fig. 5.2). MPH for GY and its components as well as for PH increased with increasing stress or decreasing yield. Under all conditions, it was almost similar in magnitude for NTB. This was demonstrated for all crosses on an environment basis, e.g. mean MPH for GY under a high yielding environment (WWHD) was 82.57% but 242.44% under low yielding conditions or increasing stress (DSHD) (Fig. 5.2). Similarly, MPH expression of each cross for the trait ranged from 18.97 (Mex101 x CML440) under less stress (WWND) to 464.53% (CML440 x CML442) under severe stress (DSHD). In a similar study in Mexico, high expression of heterosis for GY was recorded under severe drought stress because of the poor performance of inbreds under stress conditions (Betran *et al.*, 2003b). Larger ranges were recorded than in the present study, from 34% in a low N environment to 2225% under severe drought stress at Tlaltizapan (Mexico). Similar to maize, higher heterosis under stress than under favorable conditions was also recorded in rice (Young & Virmani, 1990).

Crosses made in combination with Mex102 were relatively inferior in MPH for GY across environments because of its high *per se* performance (Table 5.5). On the contrary, crosses with Mex103 or CML440 had high MPH in most environments, mainly due to low *per se* performance of these lines. For instance, 142% MPH was observed in Mex101 x CML440, the lowest yielder with 3.89 t ha^{-1} (Table 5.3), whereas Mex101 x Mex102 had a relatively low MPH (109%) but a high yield of 4.68 t ha^{-1}. This confirmed that a high degree of heterosis alone should not be taken as a reliable criterion for selection of inbred lines, but rather its performance in each combination and growing condition. Thus MPH expression of most hybrids was dependent on genetic diversity between parents, parental *per se* performance and environmental conditions. Consistent observations were reported in many other studies (Jinks, 1983; Duvick, 1999; Koutsika-Sotiriou, 1999; Miranda Filho, 1999). Other studies in Mexico showed low heterosis for GY when combinations were made between sister lines, while unrelated lines showed high expression (Han *et al.*, 1991; Betran *et al.*, 2003b). A recent report also indicated that the magnitude of MPH across environments was smaller for La Posta Sequia inbred lines, which had greater *per se* performance for GY than other inbred lines.

The hybrids in this study gave relatively higher yields that ranged from 3.89 to 5.40 t ha^{-1} across environments. CML440 x Ken and CML440 x CML202 were relatively superior under all growing conditions, with high MPH (191 and 207%) and high yields of 5.40 and 5.33 t ha^{-1}, respectively. The other high yielding crosses, Mex102 x Ken (4.75 t ha^{-1}) and Mex102 x CML202 (4.99 t ha^{-1}) showed relatively low MPH (103%). On the other hand, Ken and CML440 were superior in *per se* performance and GCA under well-watered (WWND) and stressed (DSND) conditions, respectively. Their combinations (CML440 x Ken, CML440 x CML442 and CML440 x CML202) were also best yielders and showed high heterosis across all environments. Similarly, Mex101 was superior in GCA and *per se* performance under severe stress (DSHD), while Mex101 x CML442 was also best in performance and heterosis under both WWHD and DSHD, and over all. As observed in other studies, some inbred lines with superior yields under drought conditions or high plant density gave superior hybrids under these stresses (Troyer & Rosenbrook, 1983; Russel, 1991; Troyer, 1996; Betran *et al.*, 1997; Vasal *et al.*, 1997). This confirmed that most of the hybrids developed from drought tolerant lines performed relatively well in both stress and non-stress environments. It was also consistent with an almost similar study that indicated the possibility to combine stress tolerance and yield potential in tropical maize hybrids (Betran *et al.*, 2003b).

The same trend as GY was observed for NKE, EPP and PH, while NTB showed no clear trend. Across all, the top yielding hybrid, CML440 x Ken showed highest MPH (80%) for NKE. A few crosses showed negative heterosis for EPP under WWND, which became positive with increasing stress, except for CML440 x CML445. Moreover, almost all crosses showed negative heterosis for both flowering parameters (AD and ASI), especially under severe stress (Fig. 5.2), reflecting earlier flowering and shorter ASI of hybrids than inbred lines. Consequently, the results obtained on secondary traits also confirmed more stress tolerance in hybrids than their parents. In general, the observed heterosis for yield and its components as well as for flowering traits demonstrated the multiple advantages achieved by hybrids across environments. It also demonstrated the importance of developing hybrids particularly from drought tolerant parents for resource-poor farmers in the tropics.

Table 5.7. Estimates of mean mid-parent heterosis (MPH) for various traits of maize under different growing conditions at Melkasa, 2002.

Environment	WWND	WWHD	DSND	DSHD	Across	WWND	DSHD	Across	WWND	DSHD	Across
Crosses / Trait			GY				NKE			EPP	
Mex101xMex102	83.08**	70.3**	152.7**	130.9*	109.3*	25.08*	53.65	39.2	2.88	12.76	6.10*
Mex101xMex103	85.37**	73.25**	273.1**	331.0**	190.7**	44.24**	77.19*	51.7*	0.43	14.12	15.27**
Mex101xCML440	18.97	57.02**	241.7**	248.7**	141.6**	24.41*	76.32*	61.3**	-1.90	4.65	4.15
Mex101xCML442	113.4**	69.33**	169.2**	456.0**	202.0**	19.22	86.98*	57.3*	2.92	25.00*	8.17**
Mex101xCML202	76.92**	56.08**	153.4**	349.9**	159.1**	29.70**	107.0**	59.1*	1.65	1.37	1.60
Mex101xKen	80.23**	64.44**	175.7**	271.3**	147.9**	25.15*	118.1**	69.7**	1.69	11.84	1.33
Mex101xCML445	83.05**	92.24**	378.5**	167.75*	180.4**	31.21**	72.62*	74.3**	2.89	-9.27	4.48
Mex102xMex103	70.87**	62.35**	201.5**	91.31*	106.5*	19.30	31.01	28.1	2.09	2.72	7.84**
Mex102xCML440	61.84**	76.67**	234.3**	113.6*	121.6**	8.63	48.13	40.9	3.48	-1.08	2.77
Mex102xCML442	111.4**	62.69**	169.0**	101.4*	111.1*	-7.09	47.52	29.7	6.68	7.79	1.96
Mex102xCML202	113.7**	103.1**	133.2**	63.61	103.4*	26.07*	3.90	30.2	4.42	-3.81	6.10*
Mex102xKen	93.68**	71.08**	94.3*	152.3*	102.8*	23.87*	97.80*	55.4*	-2.05	5.42	1.58
Mex102xCML445	51.6**	60.24**	194.2**	216.5**	130.6**	15.45	61.59*	55.0*	2.41	6.06	4.49
Mex103xCML440	161.0**	130.8**	244.2**	45.75	145.4**	39.24**	50.60	61.1**	0.86	-9.76	2.28
Mex103xCML442	179.9**	94.56**	278.8**	253.8**	201.8**	20.41*	69.54*	54.8*	4.24	18.94	8.57**
Mex103xCML202	164.8**	121.0**	190.6**	265.6**	185.5**	34.49**	41.46	51.8*	0.42	5.14	11.82**
Mex103xKen	114.2**	72.63**	164.3**	162.3*	128.3*	28.11*	32.40	47.5	6.44	11.46	5.39*
Mex103xCML445	128.8**	82.61**	200.2**	268.2**	169.9**	32.89**	22.21	40.4	1.89	21.33	9.04**
CML440xCML442	153.7**	106.**	208.3**	464.5**	233.1**	25.24*	81.29*	65.8**	-1.04	10.45	1.52
CML440xCML202	108.4**	142.1**	115.9**	462.9**	207.3**	13.04	67.75*	45.5	4.73	3.39	1.84
CML440xKen	137.7**	134.2**	167.5**	323.1**	190.6**	43.76**	133.9**	80.3**	14.92	15.07	9.26**
CML440xCML445	88.40**	69.97**	210.1**	150.3*	129.7*	22.26*	14.97	38.5	-4.12	-5.17	-5.34*
CML442xCML202	93.49**	62.74**	146.0**	214.1*	129.1*	20.39*	27.39	50.3*	4.67	6.90	0.32
CML442xKen	151.5**	69.13**	171.6**	265.2**	164.3**	12.39	96.50*	65.3**	-2.90	16.23	4.07
CML442xCML445	71.57**	55.01**	255.7**	382.3**	191.1**	18.98	87.38*	66.9**	5.28	26.55*	5.40*
CML202xKen	95.32**	95.60**	82.08*	349.7**	155.7**	44.06**	102.9**	61.7**	-1.65	18.15	5.41*
CML202xCML445	75.82**	78.46**	143.9**	272.6**	142.7**	23.09*	54.13	57.6*	6.85	12.82	4.05
KEN1xCML445	90.53**	78.25**	91.66*	214.0*	118.6*	43.23**	52.38	66.8**	-1.85	11.20	0.95

GY, grain yield in ton ha^{-1}; AD, days to 50% anthesis; ASI, anthesis-silking interval in days; PH, plant height in cm; EPP, ears plant^{-1}; NKE, number of kernels ear^{-1}; NTB, number of tassel branches; SEN, leaf senescence; WWND=Well watered + normal density; WWHD=Well watered + high density; DSND = Drought stress + normal density; DSHD= Drought stress + high density; *, ** Significantly different from zero at P = 0.05 and P = 0.01, respectively; † Across, indicates combined over the four different environments.

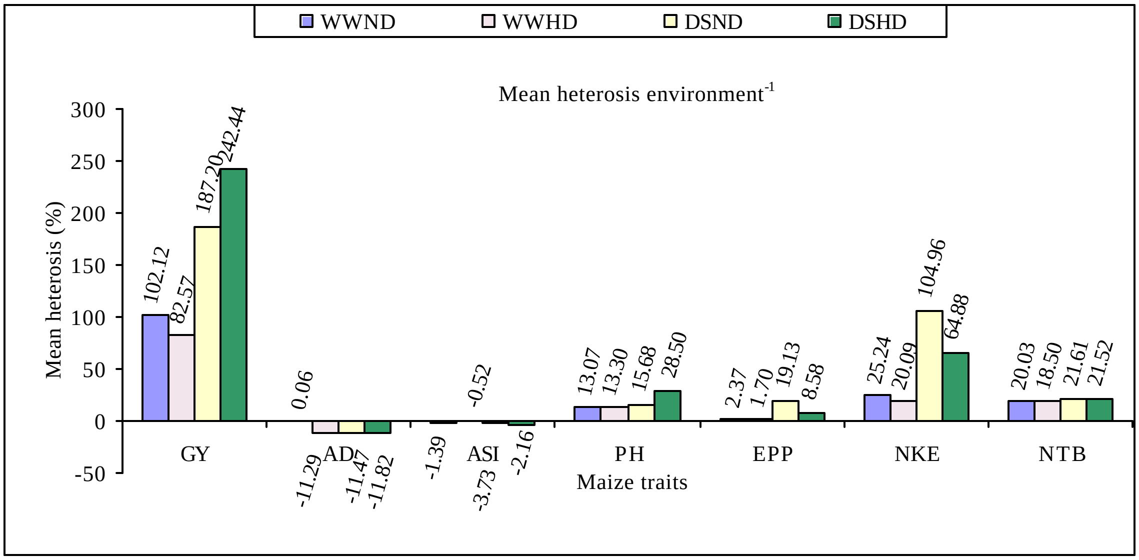

Figure 5.2. Mean mid-parent heterosis (MPH) for seven traits of maize in four environments. (See Table 5.7 for abbreviations)

Correlation

Hybrid grain yield and inbred traits

The correlation between hybrid and mid-parent (MP) grain yields was weakly positive in most environments and weakly negative under well-watered high plant density conditions (Fig. 5.3). As a result, it was difficult to differentiate growing condition effects based on correlation between hybrid and mid-parent grain yields. Similarly, under most conditions except under drought, non-significant positive associations were observed between hybrid yield and most secondary traits of the lines.

In agreement with the present results, Samanci (1996) demonstrated that the high yielding inbreds did not necessarily give rise to high yielding hybrids. However, Duvick (1999) pointed out a tendency for high yielding inbreds to produce high yielding hybrids. Others also suggested that inbreds with superior yields under drought and low N conditions would result in superior hybrids under these stresses, even if these correlations were weak (Vasal *et al.,* 1997). In contrast to the present result, a higher inbred-hybrid correlation was reported under high PD conditions (El-Lakany & Russell, 1971). However, the high PD used at Melkasa was below optimum for most genotypes, since it did not affect yield negatively. The impact of the drought tolerance should also be considered. In a similar study in Mexico, significant positive associations were reported in most environments (Betran *et al.*, 2003b), which contrasted with the present result. They also recorded weak and non-significant associations with low plant populations and with intermediate drought stress at Tlaltizapan. The same applied to well-watered and fertilized conditions at Poza Rica, which had a similar trend to the current results. Thus, the weak associations observed in this study supported the need of evaluation of hybrids rather than depending on *per se* line performance.

The associations of F_1 yield with line AD and ASI were positive and negative under well watered and drought conditions, respectively (Fig. 5.3). Although not strong, it indicated that hybrids derived from late flowering parents gave high yield under well-watered conditions. On the contrary, for drought stress at flowering, a short period to 50% anthesis and synchronization of male/female flowering of parental lines had an advantage in escaping and tolerating of stress by their crosses. Positive associations for AD, ASI and EPP under well watered conditions but negative associations for AD and ASI under drought stressed conditions were consistent with a study of lines and their topcrosses in Mexico (Betran *et al.*, 1997). However, the negative association in this study between parental line EPP and F_1 yield under drought conditions contrasted with their result that indicated significant positive associations. Positive relationships between lines and their crosses were desirable for the trait, particularly for tolerance in high yielding genotypes. This unexpected difference warrants further investigation. Consequently, the inconsistent and weak associations showed by parents and their crosses for pertinent traits in contrasting environments confirm the need to evaluate hybrid performance for selection of parental lines (Hallauer & Miranda, 1988; Beck *et al.*, 1997; Koutsika-Sotiriou, 1999; Vasal *et al.*, 1999).

Hybrid yield, SCA and heterosis

Grain yield of hybrids was significantly and positively correlated with SCA, MPH, and HPH in all environments (Table 5.8). SCA of the crosses for grain yield was also positively and significantly correlated with MPH and HPH in each and across environments. However, the association between F_1 grain yield and SCA was consistently high ($r_{F1.SCA}$ = >0.74) in each and across environments, reflecting more importance of SCA in predicting hybrid performance than the relatively inconsistent heterosis. Similarly, a positive and significant association was reported in most environments while lower and non-significant relationships were also observed under different managed stress conditions at Tlaltizapan in Mexico (Betran *et al*., 2003b). The correlations that involved parent performance (MPH, HPH) were more inconsistent across environments than were the correlations with SCA. This was mainly due to differential response of inbred lines to stress and environmental conditions relative to hybrids. Thus, the present study also confirmed the importance of combining ability testing, especially SCA, in identifying superior combinations.

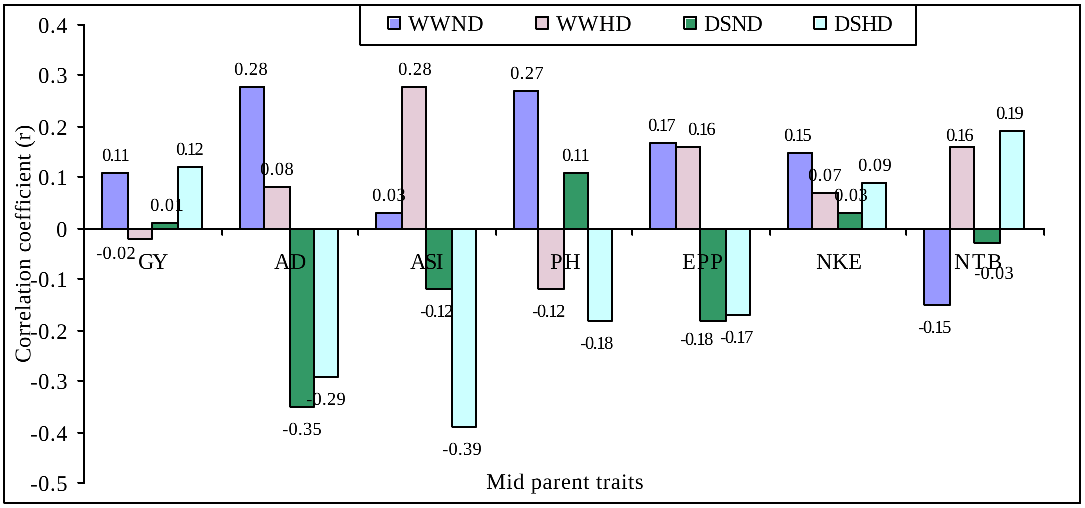

Fig. 5.3. F_1 hybrid grain yield relationship with mid-parent traits in four different environments. (See Table 5.8 for abbreviations).

Table 5.8. Correlation among F_1 grain yield, MPH, HPH, and SCA for the hybrids in each and across environments.

Environment	Correlations				
	r(F_1.SCA) †	r(F_1.MPH)	r(F_1.HPH)	r(SCA.MPH)	r (SCA.HPH)
WWND	0.83**	0.69**	0.71**	0.66**	0.71**
WWHD	0.91**	0.78**	0.76**	0.70**	0.72**
DSND	0.83**	0.54*	0.41*	0.41*	0.30
DSHD	0.90**	0.66**	0.67**	0.71**	0.65**
Across	0.74**	0.54**	0.56**	0.56**	0.55**

GY,grain yield in ton ha^{-1}; AD, days to 50% anthesis; ASI, anthesis-silking interval in days; PH, plant height in cm; EPP, ears plant^{-1}; NKE, number of kernels ear^{-1}; NTB, number of tassel branches; SEN, leaf senescence; †r(F_1.SCA) indicates correlation between hybrid grain yield and SCA effects; *,**, indicate significant correlations at P = 0.05 and P = 0.01, respectively.

5.5. Conclusions

Considerable differences among lines and their crosses were indicated for most tested traits in variable environments. Performance of the inbred lines and most of their crosses, especially for yield, increased at high plant density, indicating that it was not sufficient to impose stress on most of these short stature genotypes. Furthermore, these observations suggested that the improvement made in drought tolerance of parental lines increased their adaptation and potential to perform well under high plant density stress. On the contrary, the 73 and 56% grain yield reduction recorded under severe stress with inbred lines and their crosses respectively, indicated that stress tolerance increased more in crosses as compared to parental lines. Similarly, heterosis increased with increasing stress that confirmed more susceptibility of the lines relative to their crosses. Moreover, performance in grain yield of hybrids was not strongly correlated with those of their parental lines *per se*, which emphasized the importance of crosses evaluation in contrasting environments in order to select lines with superior combining ability.

The results indicated the presence of adequate diversity in parents for important traits, especially for drought adaptive traits under severe stress conditions. As a result, superior *per se* performance of parents in and GCA for yield across contrasting environments were also superior in stress adaptive traits, as exhibited by CML202 and Ken. Similarly, Mex101 was superior under severe stress conditions for yield and yield components, reflecting high yield potential and the possession of drought adaptive traits. However, the predominant role of additive effects for secondary traits was observed in each environment, while non-additive gene effects applied to yield. CML440 x Ken, CML440 x CML442, and Mex103 x CML202 were superior in each and across environments. Furthermore, their better performance than local hybrids both in lower stress and stress environments reflected better adaptation potential to resource poor farmer conditions. The SCA effects of grain yield were considered as a reliable predictor of hybrid performance. In general, some of the hybrids developed from drought tolerant lines performed better in both stress and non-stress environments than the local hybrids. This confirmed that some of the hybrids combined stress tolerance and high yield potential, which should be suitable for resource-constrained farmers in the tropics.

Chapter 6 AMMI analysis of genotype x environment interaction for grain yield in drought tolerant maize (*Zea mays* L.)

6.1. Abstract

Previous studies reported good performance of drought tolerant maize genotypes under a range of soil nitrogen and moisture regimes, which are the main yield limiting factors in the tropics. Based on this suggestion, minimum genotype x environment interaction (GEI) is anticipated when drought tolerant maize is planted under different growing conditions. Eight maize lines bred for drought tolerance, and their 28 crosses with two local hybrids were evaluated separately in 12 environments. The objectives of this study were to estimate the magnitude of GEI: (i) among the drought tolerant inbred lines, (ii) among crosses developed from drought tolerant lines as compared to conventional hybrids; and (iii) relationships between the parental lines and their crosses based on AMMI stability values. An additive main effects and multiplicative interaction (AMMI) model was used to analyze the log-transformed grain yield data of each trial set (lines and hybrids). The first two IPCAs of the AMMI 2 analysis accounted for 81% and 56 % of the GEI sum of squares in trials of the lines and hybrids, respectively. As a result, a large part of the interaction sum of squares was extracted in both multi-environment trials, reflecting efficiency of this model in analyzing the GEI patterns. CML445, CML442, CML440 and Mex103 were superior in yield stability, while the first two lines maintained an above average yield over environments. Considerable differences were observed among crosses in yield and GEI. High yielding hybrids like O, P, S, Z, U, G and BH140 (check-2) showed minimum GEI indicating broad adaptation over environments. The low yielding hybrids Y, I, Q, F and H were also superior in yield stability but can be used only for breeding work, particularly in areas with unpredictable rainfall patterns. In contrast, unstable, high yielding hybrids such as A, D and J, were adapted to unfavorable environments that included drought stressed, and eroded topsoil. As compared to conventional hybrids, 22 and 26 crosses formed from drought tolerant parents were better than BH540 in mean yield and stability, respectively. Although no considerable association in stability was observed between crosses and their parents, increased stability occurred in most of the crosses due to increased stress tolerance.

Key words: Drought tolerance, genotype x environment interaction, yield stability.

6.2. Introduction

In sub-Saharan Africa, crop yield variability under rainfed conditions is likely to be of greater socio-economic importance than in any other part of the world (Heisey & Edmeades, 1999). This is mainly due to drought and low N stresses, which are most frequently limiting maize production in the tropics (Vasal *et al.*, 1997; Betran *et al.*, 2003c). In addition to these, increased population pressure, high input cost and extreme poverty force smallholder farmers in the region to implement low input farming systems (Bänziger *et al.*, 1999a). All these phenomena are common in Ethiopia, where environmental conditions vary considerably (MOA, 1998), and means of modifying the environment are far from adequate. Under these conditions, genotypes that provide high average yields with minimum genotype by environment interaction (GEI) have been gaining importance over increased yields (Rosielle & Hamblin, 1981; Ceccarelli, 1989; Gauch & Zobel, 1997; Kang, 1998). What is wanted in practice is often not good performance in a specific environment but good general performance over a range of environments, both favourable and unfavourable (Rosielle & Hamblin, 1981; Falconer 1989). Previous studies have recommended a combination of stressed and unstressed environments in selection of genotypes that perform well under a wide range of moisture conditions in the tropics (Byrne *et al.*, 1995; Edmeades & Bänziger, 1997; Edmeades *et al.*, 1997a; Vasal *et al.*, 1997).

The dependence of crop performance on the genotype and environment as well as on the interaction between them is well known (Gomez & Gomez, 1984). By exposing a number of genotypes to a set of contrasting environments it is possible to identify genotypes with a high average yield and low GEI (Ceccarelli, 1989). Furthermore, the widespread use of semi-dwarf wheat cultivars is a strong case for the broad adaptation argument (Basford & Cooper, 1998). For this reason, testing selected materials over diverse environments to ensure that forthcoming genotypes have stable performance over a range of environments is a universal practice. However, differential genotypic response to variable environmental conditions associated with GEI may limit accurate yield estimates and identification of high yielding stable genotypes (Crossa *et al.*, 1991; Basford & Cooper, 1998; Kang, 1998). They have also suggested that the larger the relative size of the interaction component, the more complex the problem of identifying broadly adapted genotypes. Various biotic and abiotic stresses have been implicated as causes of GEI. Consequently, improving genotype resistance/tolerance to different stresses to which they would likely be exposed might minimize GEI (Kang, 1998). Selection under managed drought stress at flowering is an effective means of increasing tolerance to a number of stresses occurring near flowering (Edmeades & Bänziger, 1997). Thus mid-season, drought tolerant genotypes that perform well under variable moisture regimes (Chapman *et al.*, 1997) and N levels (Bänziger *et al.*, 1999b) are expected to give better yield with reduced GEI across variable environments as compared to conventionally selected genotypes. However, there is limited information about their GEI across different environments, and relationships between lines and crosses for this trait.

On the other hand, it has to be taken into consideration that data from multilocation trials are imprecise, complex and noisy (Crossa *et al.*, 1997). The conventional method of partitioning total variation into components due to genotype, environment, and genotype x environment interaction (GEI) conveys little information on the individual patterns of response (Kempton, 1984). To increase accuracy, additive main effects and multiplicative interaction (AMMI) is the model of first choice when main effects and interaction are both important (Zobel *et al.*, 1988). This method integrates analysis of variance and principal component analysis into a united approach. The significant feature of this analysis is that adjustment is carried out using information from other locations to refine the estimates within a given location. It removes residual or noise variation from GEI (Crossa *et al.*, 1990a). It has no specific experimental design requirements, except for a two- way data structure (Zobel *et al.*, 1988). AMMI analysis provides a graphical representation (biplot) to summarize information on main effects and interactions of both genotypes and environments simultaneously (Crossa, 1990; Crossa *et al.*, 1990a). The objectives of this study were to estimate the magnitude of GEI: (i) among drought tolerant inbred lines, (ii) among the hybrids developed from drought tolerant lines as compared to conventional local hybrids, and (iii) relationships between parental lines and their crosses based on AMMI stability values.

6.3. Material and methods

A diallel cross excluding reciprocals was made between eight maize lines bred for drought tolerance. Details of the eight parental lines regarding pedigree/source and reaction to drought as well as where the diallel crosses were formed are discussed under Material and Methods of Chapter 4. The eight inbred lines, and their 28 crosses with two Ethiopian local hybrids as checks were evaluated separately under 12 environmental conditions in Ethiopia (Table 6.1). In the text, the hybrids are indicated by alphabetical code (Table 6.4). During two main seasons, eight environments were established for evaluation, which were combinations of location, year and plant density. The other four of the 12 environments used for testing during the off-season were combinations of plant density and moisture regimes. Thus, in analyzing the yield trials a two-way table of genotype by environment was produced. Details of experimental materials, design, field evaluation, and measurements are discussed under Material and Methods of Chapters 4 and 5. Rainfall data for main season trials are presented in Chapter 4.

Statistical analysis

Analysis of variance for each environment was done for grain yield. Homogeneity of error variances was tested for each set of trial using Bartlett's Test (Gomez & Gomez, 1984), which necessitated transformation of data to achieve homogeneity. The data were changed from t ha^{-1} to kg ha^{-1} to make it more suitable (whole numbers) for logarithmic transformation. The transformed data in each environment were again analyzed and confirmed homogeneity of variances through retesting by means of the above procedure. Thus, with the logarithmically transformed data, the AMMI analysis was performed separately for each type of genotype (lines and hybrids) using AGROBASE software (Agronomix Software Inc., 1998). The AMMI model first fits additive effects for the main factors; that is, genotypes (G) and environments (E), using the additive analysis of variance procedure. Subsequently the program fits multiplicative effects for genotype by environment interaction (GEI) by principal component analysis (PCA) (Zobel *et al.*, 1988; Gauch & Zobel, 1996). The statistical significance of analysis of variance, and optimum number of interaction principal component axes (IPCA) to be retained in the model were determined, using the F-test as given by this analytical software. The AMMI model equation according to Gauch & Zobel (1996) is:

$$Y_{ger} = m + a_g + b_e + \Sigma_n l_n g_{gn} d_{en} + r_{ge} + e_{ger}$$

where:

Y_{ger} = the observed yield of gth genotype in eth environment for rth replicate;
m = the grand mean;
a_g = the deviation of mean of the gth genotype from the grand mean m;
be = the deviation of mean of the eth environment from the grand mean m;
l_n = the singular value for the nth interaction principal component axis (PCA);
g_{gn} = the genotype eigenvector for nth (PCA) axis;
d_{en} = the environment eigenvector values for the nth PCA axis;
r_{ge} = the residual effects; and
e_{ger} = the error term.

Furthermore, AMMI's stability value (ASV) was calculated in order to rank genotypes in terms of stability using the formula suggested by Purchase (1997) as shown below.

AMMI stability value (ASV) = $\sqrt{\left[\frac{SSIPCA1}{SSIPCA2}(IPCA1score)\right]^2 + [IPCAscore2]^2}$

where: SS = Sum of squares; IPCA1 = Interaction Principal Component Analysis axis 1
IPCA2 = Interaction Principal Component Analysis axis 2

In general, an absolute AMMI stability value (ASV) was determined using a procedure that combines IPCA1 and IPCA2. By using Pearson correlation coefficients (r) between inbred lines and crosses, the response in GEI (stability) was estimated by regressing F_1 hybrid ASV values on mid parent values. NCSS 2000 software (Hintze, 1998) was used in estimating their association. In addition to these, the AMMI adjusted mean grain yield (ton ha^{-1}) for each line and cross was estimated from untransformed (original) data to demonstrate mean performance.

Table 6.1. Drought stressed and irrigated as well as rainfed environments, where eight drought tolerant lines and 30 hybrids were evaluated, independently.

Environment		Site name	Year/Season	Moisture status/ Plant density
No.	Code			
1.	WN	Melkasa	2002B	WW+ND
2.	DN	Melkasa	2002B	DS+ND
3.	NB2	Bako	2002A	RF+ND
4.	NM2	Melkasa	2002A	RF+ND
5.	NB3	Bako	2003A	RF+ND
6.	NM3	Melkasa	2003A	RF+ND
7.	WH	Melkasa	2002B	WW+HD
8.	DH	Melkasa	2002 B	DS+HD
9.	HB2	Bako	2002A	RF+HD
10.	HM2	Melkasa	2002A	RF+HD
11.	HB3	Bako	2003A	RF+HD
12	HM3	Melkasa.	2003A	RF+HD

B = off-season; A = main season; DS = drought stress during flowering; RF = Rainfed; WW = well-watered; HD = high plant density; ND = normal density;

(1) Off-season trials at Melkasa, WN= well-watered + normal density; DN = drought stress + normal density; WH = well-watered + high density; DH = drought stress + high density.

(2) Rainfed trials, NB2 = normal density at Bako in 2002; NM2 = normal density at Melkasa in 2002; NB3 = normal density at Bako in 2003; NM3 = normal density at Melkasa in 2003; HB2 = high density at Bako in 2002; HM2 = high density at Melkasa in 2002; HB3 = high density at Bako in 2003; HM3 = high density at Melkasa in 2003

6.4. Results and discussion

Analysis of variance

The AMMI analysis for the eight inbred lines and 30 hybrids evaluated separately in 12 environments are presented in Table 6.2. For grain yield of hybrids, this analysis showed that environments (E), genotypes (G), and the genotype x environment interaction (GEI) were highly significant ($P<0.001$) and accounted for 79.96, 3.03 and 17.01% of the treatment combination sum of squares (E+G+GEI SS), respectively. It was also moderate to highly significant ($P<0.05$ and 0.001) for the inbred lines, and distribution of the treatment combination sum of squares for environments, genotypes, and GEI were 84.18, 3.37 and 12.45 %, respectively. The results in both sets of trials indicated that specific and wide adaptations were equally important, as suggested by Gauch & Zobel (1997). In both types of genotypes, although the GEI sum of squares was about four to five times larger than that for genotypes, environmental effects dominated the analysis. Regarding variability within each kind of genotype, more variation in sum of squares was detected among inbred lines than for hybrids. Other studies in multi-environment yield trials (MET) have also reported that sum of squares due to differences among environments ranged from 80 to 90 % (Romagosa & Fox, 1993; Purchase, 1997).

The above information can be obtained through conventional combined analysis of variance. However, beyond detecting the significance of GEI, conventional ANOVA does not contribute to interpret or understand the pattern of genotype response across environments (Zobel *et al.*, 1988; Crossa, 1990). Gauch & Zobel (1996) pointed out that ignoring the interaction is problematic, particularly when GEI is larger than genotype main effects, which was observed in the present study. They also suggested that genotype main effects and GEI are considered as a more relevant source of yield variation, and should be considered simultaneously in cultivar evaluation. In general, it is important to implement AMMI models that estimate accurate genotype response, and remove noise from source of variation through partitioning GEI (Gauch & Zobel, 1996; Crossa *et al.*, 1997).

For both METs, as indicated by the F-test, inclusion of the first two interaction PCA axes was recommended in the model. Although IPCA3 was also highly significant for hybrids it contributed only 14% of the genotype by environment interaction (GEI) sum of squares. As a result, the third IPCA was discarded, considering the difficulty to obtain reliable information due to its relatively small contribution to the interaction. Thus the best fit for both inbred lines and hybrids trials was the AMMI 2 model. The moderate significance observed in the inbred lines' GEI became highly significant when partitioned to IPCA1 and IPCA2. Zobel *et al.* (1988) also reported highly significant IPCA1 when the non-significant GEI was partitioned. For the present drought tolerant lines, the first PCA axis (IPCA1) declared 51 % of the observed line by environment variation sum of squares, while the second axis (IPCA2) declared 30 % of the interaction. The remaining 19 % was regarded as non-interpretable residual and discarded. Similarly, for hybrids IPCA1 and IPCA2 explained 33 and 23 % of the GEI sum of squares respectively, while the residual 44 % was discarded as noise. In general, the first two IPCAs accounted for 81 % and 56 % of the GEI sum of squares in trials of the lines and hybrids respectively, reflecting efficiency of this model in analyzing the interaction pattern as demonstrated by Zobel *et al.* (1988).

Table 6.2. AMMI analysis for grain yield of (A) eight inbred lines, and (B) 30 hybrids evaluated in 12 environments, Ethiopia.

	(A) Inbred lines			(B) Hybrids		
Source	df	Sum of squares	Mean squares	df	Sum of squares	Mean squares
Total	383	49.084		1439	47.057	
Treatment combinations	95	36.215	0.381***	359	34.76	0.097
Environments (E)	11	30.487	2.772***	11	27.793	2.527**
Replicates within E	36	3.046	0.085	36	2.379	0.066
Genotype (G)	7	1.221	0.174***	29	1.053	0.036**
Genotype x Env.	77	4.507	0.059*	319	5.914	0.019***
IPCA1	17	2.309	0.136***	39	1.938	0.05***
IPCA2	15	1.347	0.09**	37	1.372	0.037***
IPCA3	-	-	-	35	0.802	0.023***
IPCA Residual	45	0.85	0.019	208	1.803	0.009
Error	252	9.823	0.039	1044	9.918	0.01
C.V (%)	5.86			2.63		
R^2	79.99			78.92		
Log (mean yield)	3.367			3.709		

The main important feature of AMMI analysis is its graphical (biplot) representation. This displays main effect means on the abscissa and scores for the first axis (IPCA1 values) as ordinate of both genotypes and environments simultaneously (Crossa *et al.*, 1990a; 1997; Gauch & Zobel, 1996). Genotypes or environments with large PCA (positive or negative) scores have large interaction, whereas a PCA score near zero has small interaction effects (Zobel *et al.*, 1988; Crossa *et al.*, 1997). Accordingly, a large genotypic IPCA1 value reflects more specific adaptation to environments with IPCA1 values of the same sign. On the contrary, genotypes with IPCA1 values close to zero show wider adaptation to the tested environments. Thus, IPCA scores of a genotype in the AMMI analysis are the key to interpret the pattern of genotype responses across environments (Zobel *et al.*, 1988; Gauch & Zobel, 1996; Crossa *et al.*, 1997). The following discussion of the lines and hybrids are presented independently, based on their biplots.

Inbred lines

Figure 6.1 provides the AMMI model 2 biplot of the line trials. The environments showed much variability in both main effects and interactions. However, the high potential environments were distributed evenly in quadrants II (NB2, WN, NM2, NM3, HM2, HM3) and III (WH, HB2) with minimum interaction effects, while the lower potential environments were sparsely distributed in quadrants I (DN) and IV (DH, NB3 and HB3) with high IPCA1 values. The lowest yielding environments, DN and DH demonstrated the highest positive and negative interaction IPCA1 scores, respectively. These two environments were characterized by managed drought stress during flowering and grain filling. This biplot also indicated HM3 as the highest yielding environment. On the other hand, as suggested in a study made on rice cultivars (Lafitte & Courtois, 2002), the four environments, HB2, NB2, NM2 and WN were relatively close in the AMMI 2 biplot (Fig. 6.1), indicating a similar discrimination. Similarly, HM2 and WH were grouped together. In general, the interaction PCA1 scores arranged the environments (except DN) in a sequence from positive PCA1 values pertaining to rainfed and irrigated environments to a topsoil eroded, rainfed field at Bako (NB3 and HB3), and drought stressed high plant density at Melkasa (negative PCA1 scores).

The lines showed less variability in mean yield than in interaction scores (Fig. 6.1). From this biplot three groups of lines were identified. Group one includes the late flowering (Chapter 4) lines Mex101, CML202, Ken and CML445 that showed similar main effects (mean yield) to the grand mean. Mex101, CML202 and Ken showed high interaction scores that varied in direction. Mex101 had a high negative interaction score while the other two had a positive direction. Whatever the direction, the greater the IPCA scores the more specifically adapted these lines were to certain environments (Zobel *et al.*, 1988; Crossa *et al.*, 1990a; 1997). Their high interaction with environments was also confirmed by high AMMI stability values (ASV) and rank (Table 6.4), suggesting erratic (unstable) yield across environments. Furthermore, Ken and CML202 performed well in a DN environment where they interacted positively. Similarly, DH, NB3, HB3, HB2 and WH favored Mex101, which interacted with them positively because all their interaction scores had similar signs (Zobel *et al.*, 1988; Crossa *et al.*, 1997). On the contrary, CML445 had an IPCA1 score close to zero and ranked first (least) in ASV value, reflecting minimum GEI or stable yield over the environments.

Group 2 consisted of lines CML442 and Mex102. They were intermediate in growth period, and exhibited the highest mean yield but were unrelated in their interaction scores. Mex102 showed the highest negative interaction score and sixth in ASV value, while CML442 was closer to zero but fourth in ASV value. This indicated that Mex102 was unstable across environments but favored under DH, NB3, HB3, HB2 and WH, which showed a similar sign of interaction scores. CML442 was well adapted across non-drought stressed environments. Group 3 included CML440 and Mex103. They were relatively the shortest and lowest in growth period and mean yield, respectively. Their interaction scores were negative, which allowed them to perform well in environments with negative interaction values (DH, NB3 and HB3). Furthermore, they might escape drought stress at flowering due to their earliness. Although they ranked seventh and eigth in mean yield, they were second and third in ASV values, indicating their relative yield stability.

In the biplot showing mean yield against IPCA1 scores, CML442 appeared to be the best in terms of mean yield as well as in minimum GEI, followed by CML445. However, for the AMMI 2 model IPCA2 scores was considered in interpreting GEI that captured 30 % of the interaction sum of squares as suggested by Gauch & Zobel (1996). Furthermore, when IPCA1 was plotted against IPCA2, Purchase (1997) pointed out that the closer the genotypes score to the center of the biplot (Fig. 6.2), the more stable they are. According to this figure, only CML445 was close to the center, while CML442 had a small interaction score in PCA1, showing the strongest reaction to IPCA2. Mex101, Ken, Mex102 and Mex103 remained in their previous positions, and were unstable in performance, as indicated in both biplots. Thus, based on Fig. 6.2 and ASV ranking as well as in mean yield (Table 6.4), CML445 and CML442 were identified to be superior followed by CML440 in yield stability. Consistent with the present study, Betran *et al.* (2003c) reported that tropical inbreds selected for drought tolerance performed well under both stress and non-stressed conditions.

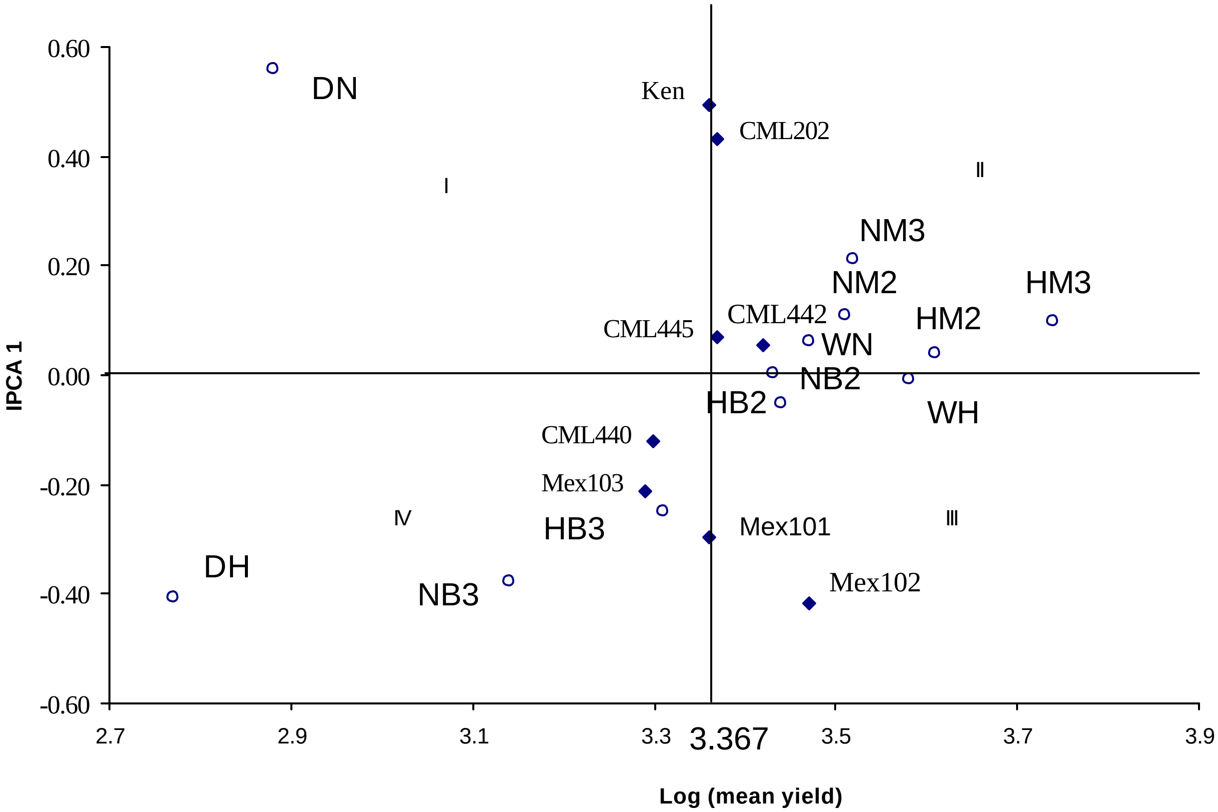

Fig. 6.1. AMMI model 2 biplot for eight inbred lines (◆) evaluated in 12 environments (o). (IPCA1 = interaction principal components analysis axis 1).

(1) Off-season trials at Melkasa, WN= well-watered + normal density; DN = drought stress + normal density; WH = well-watered + high density; DH = drought stress + high density.

(2) Rainfed trials, NB2 = normal density at Bako in 2002; NM2 = normal density at Melkasa in 2002; NB3 = normal density at Bako in 2003; NM3 = normal density at Melkasa in 2003; HB2 = high density at Bako in 2002; HM2 = high density at Melkasa in 2002; HB3 = high density at Bako in 2003; HM3 = high density at Melkasa in 2003

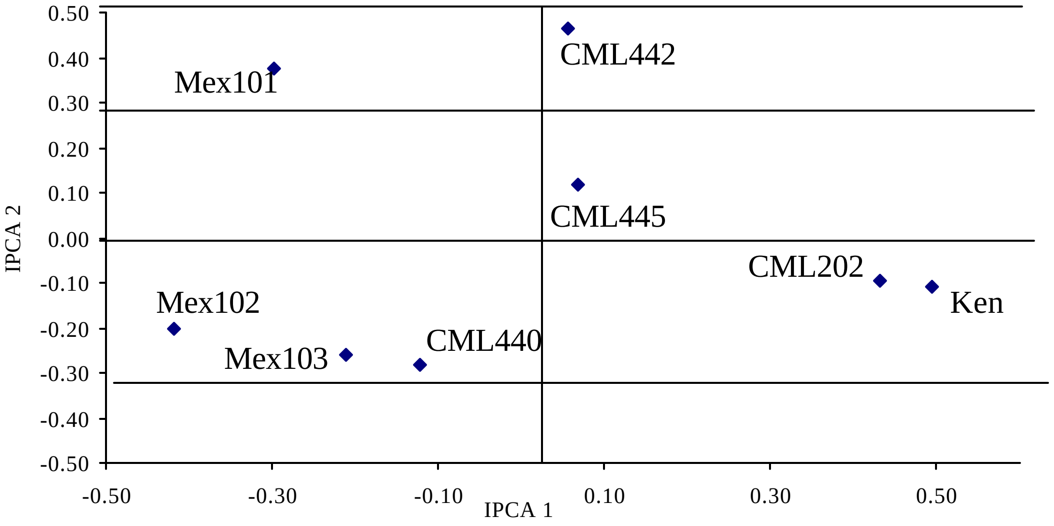

Fig. 6.2. IPCA1 and IPCA2 scores of inbred lines plotted against one another. (IPCA = interaction principal component analysis axis)

Table 6.3. AMMI adjusted mean grain yield (t ha^{-1}) based on untransformed data, AMMI stability values (ASV), and ranking orders of the eight lines tested across 12 environments.

Inbred	Environments code												Mean		ASV	
Names	WN	DN	NB2	NM2	NB3	NM3	WH	DH	HB2	HM2	HB3	HM3	t ha^{-1}	rk*	value	rk
Mex101	3.394	0.820	2.758	3.522	1.866	3.220	4.223	0.825	3.306	4.619	2.357	4.461	2.948	3	0.6343	5
Mex102	3.553	1.097	3.057	3.788	2.900	3.815	4.149	1.603	3.448	5.092	3.294	4.958	3.396	1	0.7449	6
Mex103	2.098	0.847	2.853	2.152	1.410	2.227	3.314	1.045	2.221	2.622	1.991	3.423	2.184	8	0.4458	3
CML440	2.500	1.152	2.103	2.190	1.545	2.113	3.203	0.742	2.619	3.421	1.971	3.658	2.268	7	0.352	2
CML442	2.485	0.987	3.143	4.373	2.214	4.662	4.542	0.323	3.596	4.874	3.049	5.393	3.303	2	0.4724	4
Ken	3.278	1.763	2.584	3.919	0.944	3.881	3.623	0.659	2.638	4.422	1.599	4.203	2.793	6	0.852	8
CML445	3.744	1.042	2.814	3.669	1.160	3.330	4.112	0.792	2.739	4.522	1.942	4.832	2.892	5	0.1652	1
CML202	3.316	1.538	2.757	3.364	0.883	4.743	3.623	0.630	2.751	4.018	1.443	6.294	2.947	4	0.7461	7
Environment mean	3.046	1.156	2.758	3.373	1.615	3.499	3.848	0.827	2.915	4.199	2.206	4.653	2.841			
LSD (0.05)	0.818	1.019	0.540	0.790	0.847	0.659	0.950	0.703	0.506	1.140	0.473	1.347	0.237			

* rk = rank

Hybrids

High variability among environments, both in main and interaction effects, were demonstrated with a distinct pattern as indicated in Fig. 6.3 (biplot). All high potential environments were evenly distributed in the second (WN, NM2, HM2, HM3, WH, HB2) and third quadrants (NB2, NM3), while low yielding environments were sparsely scattered in the fourth (HB3, NB3, DH) and first quadrants (DN). The position of environments in this biplot had an almost similar trend to that of the lines in Fig. 6.1, except for HB2, NM3 and WH that shifted from quadrant II to III or vice versa.

Considerably less variation in mean yield was exhibited among hybrids, as compared to the environments used for evaluation. Based on mean performance (main effects), four groups of hybrids were evident from this biplot. Group one consisted of hybrids with codes W, C_1, X, K, V, Q, H_2, I, F, H, Y, U, L, Z, E and B, which had mean yields closer to the grand mean but varied in interaction (IPCA1) scores. W, C_1, X, K, V, E and B exhibited greater interaction with environments. When IPCA1 was plotted against IPCA2 (Fig. 6.4), their interaction scores remained as high as in Fig. 6.3, and ranked above nineteenth in ASV values (Table 6.4), reflecting erratic (unstable) yield over environments. However, most of them were specifically adapted to environments that have positive interaction scores, while BH540 (check1, coded as C_1) and E adapted to NB3 and HB3 had negative interaction values. Q and Z showed a medium interaction but were well adapted in high yielding environments such as HM3, NM3 and WH (Fig. 6.3), while L favored environments with a negative interaction (NB3 and HB3). H_2, F, H, I, Y and U were close to zero, indicating minimum interaction. When IPCA1 was plotted against IPCA2, Q and Z appeared close to zero. In contrast, intermediate to high interaction scores were recorded for F, L and U (Fig. 6.4). However, H, I, Q, F and L ranked second to fifteenth in ASV values, indicating good yield stability across environments but were found to be unacceptable in most areas due to their poor mean yields. Thus, in this group, only H_2, U and Z were superior both in mean yield and stability across environments.

In group two, O, S, C_2, P, H_1, A, J, T, R and M were included. They were relatively better than group one in mean yield but showed similar trends in their IPCA1 scores. A, J, T, R and M had intermediate to high interaction scores, indicating less stability, while O, S, C_2, P, and H_1 had IPCA1 scores close to zero. However, when the IPCA1 scores were plotted against the IPCA2 scores (Fig. 6.4), only O, P, C_2 and H_1 remained close to zero. The other hybrids like A, J, M, R, S and T reacted more to IPCA2. In addition, their ASV values confirmed the trend observed in Fig. 6.4 but again the previous reaction for hybrid S (Fig 6.3) confirmed being seventh in mean yield and twelfth in ASV value. Thus O, P, S, C_2 and H_1 were high yielding and the most stable in yield over environments. A top cross hybrid BH140 (check2, coded as C_2) demonstrated a similar stability trend that may be due to an improvement made by CIMMYT for reduced plant height in one of its parents (Tuxpeño Sequia C_{18}). Consistent with the current study, Eberhart & Russel (1966) found that heterogenous populations (varietal crosses or single crosses) tended to have better yield stability than homogeneous ones (inbreds). Fehr (1987) also indicated that stability of heterozygous individuals seems to be related to their ability to perform better under stress conditions than homozygous plants. Furthermore, Fischer *et al.* (1983) has indicated short maize plants as being more tolerant of drought at flowering than taller plants. Thus, it is appropriate to consider a top cross hybrid as a non-conventional hybrid.

Group three consisted of the highest yielding (> 6.0 ton ha^{-1}) hybrids G and D, which showed intermediate positive and negative interaction scores, respectively (Fig. 6.3). The same pattern of reaction was observed when IPCA1 was plotted against IPCA2 (Fig. 6.4), and ranked sixteenth and twenty-fourth in ASV values. The cross D was specifically adapted to environments with small positive and negative interactions, while G was superior in environments with positive interaction values. Accordingly, G and D were the best crosses in drought stressed environments DN and DH, respectively. It was suggested that emphasis should be given to specific adaptation to extreme drought stress in semi arid climates (Haussmann *et al.*, 2000) but Rosielle & Hamblin (1981) advocated stability. Thus G and D are preferable in areas with recurrent drought stress, since a reliable minimum grain yield is more important to subsistence farmers than high yields in rarely favorable seasons. In group four, low yielding hybrids C and N are included, which reacted intermediately negative to highly positive, respectively. The cross N was the lowest in mean yield and the most unstable of the tested hybrids.

Although no genotype was superior in all environments, hybrids with codes O, P, C_2, S, H_1, H_2, Z, U and G were relatively superior in descending order, due to a combination of both mean yield and ASV values. Based on two sorghum populations, Zavala-Garcia *et al.* (1992) suggested that a combined index using a stability index and genotype means increased selection efficiency. Hybrids coded as Y, I, Q, F and H were superior only in their ASV (stability) and may not be recommended for direct use in production due to their poor mean yield. However, these five crosses can be used for breeding purposes in areas with unpredictable rainfall patterns. In agreement with the observation in this study, Tollenaar & Lee (2002) pointed out that reduced GEI (increased stability) occurred due to increased stress tolerance. They also suggested that increased stability occurred due to simultaneous evaluation of genotypes under both stress and non-stress conditions. Similarly, high yielding hybrids such as A, D, G and J, were specifically adapted to unfavorable environments that included drought stress and eroded topsoil. These hybrids were relatively poor in high yielding environments but top yielding in the unfavorable environments as mentioned in another study (Haussmann *et al.*, 2000). In contrast, the other high yielding hybrids K and T were narrowly adapted to well-managed conditions but not suitable for resource constrained farmers, particularly in areas with unpredictable rainfall patterns, and eroded topsoil. Of the 30 hybrids, X, W, N, B and C_1 were the most unstable over environments, while N and B were also the poorest in mean yield. BH540 (coded as C_1) was improved for high rainfall areas at Bako Research Center but proved to be one of the most inferior in the present study, both in mean yield and stability. Consequently many crosses from drought tolerant parents were superior in yield stability as compared to the conventionally developed hybrid, BH540. Based on multi-location trials of 12 maize genotypes, Crossa *et al.* (1997) suggested that selection for drought tolerance can combine stability with high yield potential of late maturing genotypes. Betran *et al.* (2003c) also suggested that good performance across stress levels can be achieved in tropical maize hybrids, which are developed from drought tolerant lines.

Relationship between inbreds and crosses in GEI

The attempt made to indicate the relationship between crosses and mid parents based on their ASV values showed no association ($r_{F1ASV.MPASV}$ = -0.004). This indicated that the magnitude of GEI (ASV) of the crosses was not dependent on the parental lines *per se*. Thus, good yield stability in lines may be important for F_1 seed production if it is practiced under low potential environments. As mentioned above and considering ASV values (Table 6.3), CML445, CML440, CML442 and Mex103 appeared to be superior lines over various environments. However, the performance of the crosses developed from stable lines (CML442 x CML445 and Mex103 x CML440) was not impressive (Table 6.4). On the other hand, all the lines except Mex102 were involved in the nine superior crosses (O, P, C_2, S, H_1, H_2, Z, U and G) but non-stable lines were more involved in these crosses than the stable lines. This also confirmed that hybrid stableness was not reflected in their parents *per se* performance.

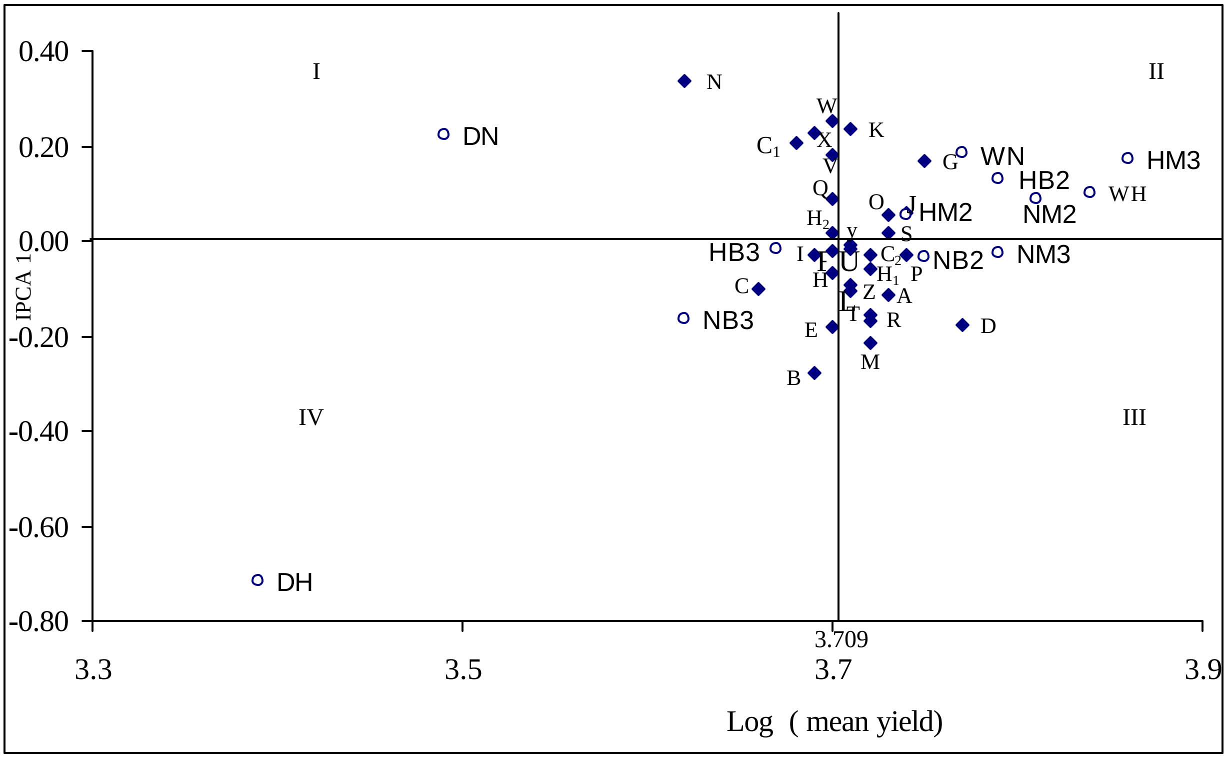

Fig. 6.3. AMMI model 2 biplot of the 30 hybrids (◆) evaluated in 12 environments (o).

WN= well-watered + normal density; DN = drought stress + normal density; WH = well-watered + high density; DH = drought stress + high density. NB2 = normal density at Bako in 2002; NM2 = normal density at Melkasa in 2002; NB3 = normal density at Bako in 2003; NM3 = normal density at Melkasa in 2003; HB2 = high density at Bako in 2002; HM2 = high density at Melkasa in 2002; HB3 = high density at Bako in 2003; HM3 = high density at Melkasa in 2003. (See Table 6.4 for hybrid code descriptions).

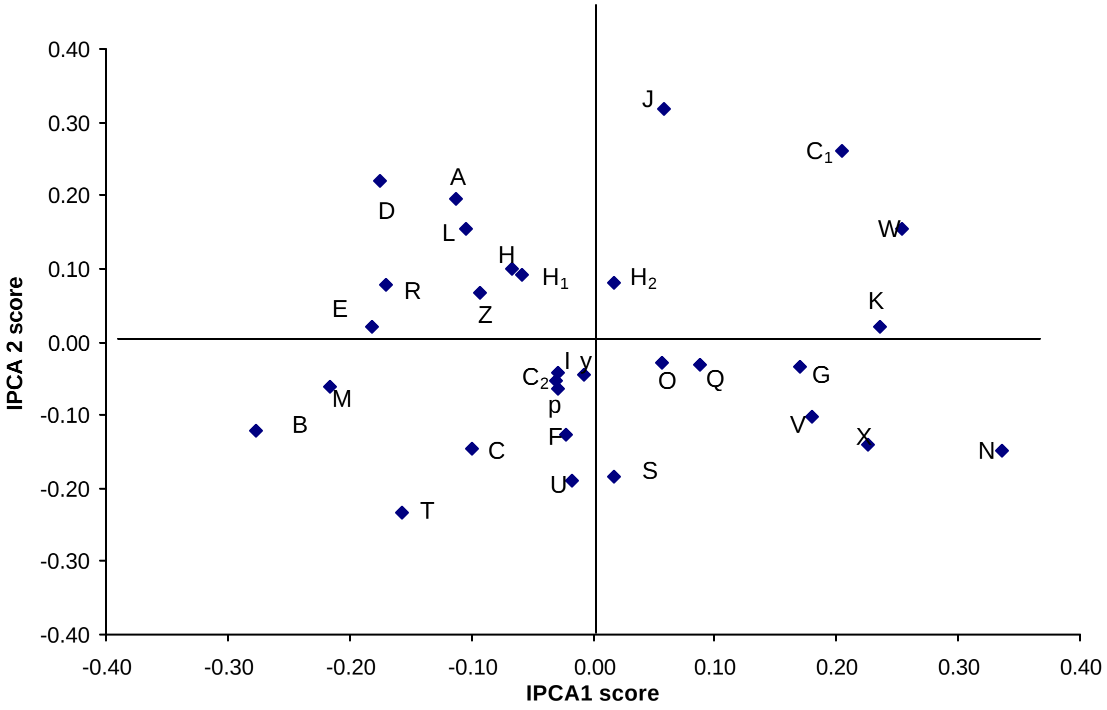

Fig. 6.4. IPCA1 and IPCA2 scores of maize hybrids plotted against one another.

Table 6.4. AMMI adjusted mean grain yield (t ha^{-1}) based on untransformed data, and ASV and ranking orders of the 30 hybrids evaluated across 12 environments.

Hybrid		Environment code												Mean		ASV	
Name	Code	WN	DN	NB2	NM2	NB3	NM3	WH	DH	HB2	HM2	HB3	HM3	ton ha^{-1}	rk*	Value	rk
Mex101xMex102	A	6.246	2.973	6.242	6.828	5.54	7.185	6.812	2.949	5.937	5.539	5.748	7.468	5.79	4	0.251	17
Mex101xMex103	B	5.299	3.045	4.946	7.04	4.095	5.477	6.442	2.333	5.795	5.969	4.644	6.639	5.14	27	0.410	29
Mex101xCML440	C	5.011	2.877	4.603	6.863	3.71	5.081	6.225	2.071	5.61	5.833	4.307	6.366	4.88	29	0.203	14
Mex101xCML442	D	6.206	3.498	6.484	8.312	6.498	7.306	6.973	3.551	6.068	6.612	6.631	7.45	6.30	1	0.331	24
Mex101xCML 202	E	5.514	2.762	5.434	6.877	4.826	6.189	6.349	2.484	5.558	5.586	5.152	6.787	5.29	24	0.258	19
Mex101xKen	F	5.434	3.294	4.997	7.221	4.052	5.47	6.653	2.462	6.046	6.225	4.664	6.791	5.28	25	0.131	9
Mex101xCML445	G	6.157	4.156	5.694	8.145	4.768	6.116	7.449	3.252	6.867	7.153	5.414	7.528	6.06	2	0.242	16
Mex102xMex103	H	5.543	2.674	5.436	6.651	4.735	6.223	6.329	2.412	5.533	5.409	5.058	6.808	5.23	26	0.136	10
Mex102xCML440	I	5.494	2.88	5.088	6.501	3.993	5.723	6.477	2.241	5.808	5.549	4.52	6.808	5.09	28	0.058	2
Mex102xCML442	J	6.215	2.93	6.372	7.075	5.937	7.356	6.734	3.065	5.805	5.607	6.053	7.421	5.88	3	0.328	23
Mex102xCML202	K	6.57	3.738	5.835	6.58	4.092	6.466	7.531	2.857	6.946	6.034	4.771	7.896	5.78	6	0.333	25
Mex102xKen	L	6.291	2.59	6.105	5.778	4.913	7.146	6.697	2.538	5.834	4.765	5.162	7.494	5.44	18	0.213	15
Mex102xCML445	M	5.672	3.052	5.481	7.066	4.746	6.168	6.598	2.623	5.857	5.875	5.152	6.966	5.44	19	0.311	21
Mex103xCML440	N	5.75	2.845	4.737	5.117	2.496	5.328	6.746	1.721	6.244	4.894	3.319	7.095	4.69	30	0.497	30
Mex103x CML442	O	6.291	3.565	5.677	6.713	4.182	6.301	7.273	2.764	6.66	6.014	4.81	7.616	5.66	9	0.084	6
Mex103xCML202	P	6.657	3.443	6.108	6.333	4.512	6.906	7.388	2.872	6.7	5.644	5.033	7.935	5.79	5	0.076	4
Mex103xKen	Q	6.252	3.149	5.638	6.009	3.984	6.385	7.053	2.479	6.398	5.372	4.557	7.544	5.4	21	0.129	8
Mex103xCML445	R	6.492	2.665	6.259	5.668	4.932	7.33	6.849	2.61	5.989	4.729	5.189	7.689	5.53	13	0.252	18
CML440xCML442	S	6.398	4.121	5.474	7.042	3.652	5.88	7.673	2.867	7.212	6.613	4.516	7.788	5.77	7	0.187	12
CML440xCML202	T	6.753	3.779	5.773	6.058	3.556	6.394	7.708	2.711	7.188	5.811	4.352	8.09	5.68	8	0.321	22
CML440xKen	U	6.766	3.45	5.811	5.513	3.49	6.549	7.55	2.524	6.983	5.294	4.223	8.071	5.52	14	0.191	13
CML440xCML445	V	6.317	3.482	5.412	6.006	3.381	6.005	7.319	2.438	6.79	5.651	4.155	7.659	5.38	22	0.275	20
CML442xCML 202	W	6.099	3.214	5.645	6.536	4.352	6.358	6.964	2.622	6.281	5.684	4.867	7.395	5.5	16	0.390	27
CML442xKen	X	5.807	3.851	5.049	7.328	3.646	5.389	7.195	2.647	6.714	6.659	4.463	7.209	5.5	17	0.350	26
CML442xCML445	Y	5.629	3.26	5.311	7.229	4.467	5.886	6.708	2.621	6.038	6.14	4.98	6.956	5.44	20	0.047	1
CML202xKen	Z	6.72	2.823	6.262	5.358	4.529	7.304	7.1	2.576	6.305	4.682	4.901	7.931	5.54	12	0.147	11
CML202xCML445	H_1	6.385	2.872	6.176	6.165	5.027	7.15	6.887	2.733	6.053	5.145	5.315	7.605	5.63	10	0.123	7
Ken x CML 445	H_2	6.604	2.819	6.182	5.507	4.557	7.196	7.028	2.568	6.234	4.771	4.925	7.821	5.52	15	0.084	5
BH540 (Check 1)	C_1	6.315	2.612	5.728	6.224	4.8	6.234	6.478	2.449	5.65	5.086	5.087	7.106	5.31	23	0.390	28
BH140 (Check 2)	C_2	6.361	3.487	5.708	6.449	4.085	6.372	7.281	2.7	6.664	5.818	4.713	7.676	5.61	11	0.068	3
Environment mean		6.094	3.197	5.656	6.540	4.385	6.376	6.949	2.625	6.259	5.672	4.889	7.379	5.502			
LSD (0.05)		1.329	0.954	0.819	1.422	1.324	1.322	1.155	0.940	0.932	1.333	1.458	1.351	0.347			

* rk = rank

6.5. Conclusions

For each set of trials (lines and crosses), AMMI analysis showed that the contribution of the environment to the treatment sum of squares was five to six times more than GEI sum of squares, while GEI contributed four to five times more than genotypes. The results indicated that specific and wide adaptation are equally important in this study. Furthermore, the environments used for evaluation showed more variability in both main effects and interactions than the genotypes. The first two IPCAs of the AMMI 2 analysis accounted for 81% and 56 % of the GEI sum of squares in trials of the lines and hybrids, respectively. As a result, a large part of the interaction sum of squares was extracted in both multi-environment trials, reflecting efficiency of this model in analyzing the GEI patterns.

DH and HM3 were the lowest and highest yielding environments respectively, in each set of trials. NB3 and HB3 were relatively low yielding in rainfed environments due to eroded topsoil. Among the lines, CML445 and CML442 were relatively superior when mean yield and stability were considered in combination, while Mex103 and CML440 were superior only in yield stability. Regarding the hybrids, O, P, S, H_1, H_2, Z, U, G and BH140 (C_2), were superior in both terms. Others like Y, I, Q, F and H were also superior in yield stability but low yielding, and can be used for breeding purposes in areas with unpredictable rainfall patterns. The trend observed with hybrids confirmed the suggestion that increased stability occurred due to increased stress tolerance. Simultaneous evaluation of genotypes under both stress and non-stress conditions can be considered as the main cause for reduced GEI. In contrast, unstable, high yielding hybrids such as A, D and J, were adapted to unfavorable growing conditions. Similarly, high yielding hybrids K and T were narrowly adapted to well managed conditions but were not suitable for resource constrained farmers, particularly in areas with unpredictable rainfall patterns, and eroded topsoil. Unlike all the other hybrids, X, W, N, B and C_1 were the most unstable, and poor in mean yield. As compared to conventionally developed hybrids, 22 and 26 crosses produced from drought tolerant parents outperformed BH540 in mean yield and stability, respectively. The second check, BH140 (C_2) was a top cross (non-conventional hybrid), and one of the nine superior performers, mainly due to improvement made to one of its parents for reduced plant height. In this study, no relationship was observed between lines and their crosses in stability, indicating independence between them for this trait.

Chapter 7 Summary and recommendations

Summary

Drought and low N stresses are factors most frequently limiting maize production in the tropics, where the vast majority of farmers have limited access to improved technology. Previous studies confirmed good performance of the crop under these conditions by improving tolerance to drought occurring at flowering, which is essential for resource constrained farmers in countries like Ethiopia. In addition to screening at sites with rain free seasons, the available genotypic variability for drought adaptive traits within adapted maize populations is crucial for successful improvement of tolerance.

At Melkasa in Ethiopia, 196 randomly derived S_1 lines from Population A-511 were tested for high yield potential, and drought and plant density adaptive traits under two moisture regimes, using two plant densities. Both plant density and drought stress significantly affected the tested primary and secondary traits of the S_1 lines. However, drought effects were more effective in reducing grain yield and its components, as well as in increasing anthesis-silking interval or in delaying days to 50% silking. Significant genotypic variability within Population A-511 was observed for grain yield and most stress (drought and high plant density) adaptive traits.

The association of yield with stress adaptive traits that included ears plant^{-1}, anthesis-silking interval, kernels ear^{-1}, and kernels plant^{-1} increased with increased stress. In contrast, the genotypic variance and heritability of grain yield and its components increased with decreasing stress, except for ears plant^{-1}. Regarding the use of suitable environments for drought tolerance screening in areas with unpredictable rainfall patterns, indirect selection under drought stressed high plant density conditions and direct selection under drought stressed normal density conditions were found to be equally efficient.

CIMMYT drought tolerant lines and their crosses were tested separately at two plant densities under both drought stressed and well watered conditions managed by irrigation, and also in rainfed environments. This was mainly to determine their potential in performance, combining ability and heterosis under both stress and reduced stress environmental conditions. Considerable differences in performance were observed among drought tolerant inbreds, and among their crosses under contrasting growing conditions. However, most crosses from drought tolerant lines provided higher yields than local hybrids, indicating their suitability for the environments in which they were tested.

In rainfed environments, higher yields were recorded for most genotypes at high plant density (≈ 88 800 plants ha^{-1}) than the recommended density (≈ 44 400 plants ha^{-1}) for local hybrids. The opposite held true when unimproved S_1 lines derived from population A-511 were tested in another experiment. This indicated the increased potential in performance and tolerance to high plant density stress, mainly due to improvement made in drought tolerance. CML442, Mex102, CML202 and Mex101 were superior lines in *per se* performance and GCA effects, especially for yield. Crosses in which these lines were involved were also superior in yield and most other traits as well as for the corresponding SCA effects. Both additive (GCA) and non-additive (SCA) effects were important for expression of the tested traits in rainfed environments. However, additive effects were relatively more important than non-additive effects for expression of these traits. Drought tolerant lines with high *per se* performance in yield across rainfed environments gave high yielding hybrids under similar conditions, reflecting an association between crosses and their parental lines.

Similarly, for drought tolerant genotypes evaluated across drought stressed and irrigated environments, the highest grain yield was recorded under well-watered high plant density conditions. On the contrary, under drought stressed high plant density conditions, the yield of lines and their crosses was reduced by 73 and 56%, respectively. Furthermore, the estimated heterosis increased with increased stress. These results confirmed increased tolerance of the improved lines and their crosses to high plant density stress, and increased tolerance of the crosses to drought stress compared to their parental lines. Combining ability tested in contrasting environments showed a predominant role of additive (GCA) effects for secondary traits and non-additive (SCA) effects for yield. For drought adaptive traits and yield, lines CML202 and Ken were superior in GCA and *per se* performance across diverse environments, while Mex101 was superior under drought stress. Among crosses, CML440 x Ken, CML440 x CML442, and Mex103 x CML202 were relatively superior in each and across environments.

Drought tolerant genotypes that perform well in a range of soil N and moisture regimes are expected to give better yields with reduced genotype by environment interaction (GEI) across diverse environments. The AMMI 2 analysis model efficiently estimated the drought tolerant GEI patterns over environments. Crosses developed from drought tolerant lines showed variability in mean yield and GEI across environments. High yielding hybrids such as Mex103 x CML442, Mex103 x CML202, CML440 x CML442, Mex101 x CML445, CM202 x CML445, CML202 x Ken, CML440 x Ken and BH140 showed minimum GEI, indicating their wide adaptation across stress and reduced stress environments. In contrast, the unstable, high yielding hybrids like Mex101 x Mex102, Mex101 x CML442 and Mex102 x CML442 were adapted to unfavourable environments that included drought stress, and eroded topsoil. When compared to conventional hybrids, 22 and 26 crosses produced from drought tolerant parents were better than BH540 in mean yield and stability, respectively. On the contrary, the other local hybrid, BH140 was superior in terms of both parameters, due to one of its parents being improved for reduced plant height by CIMMYT.

Recommendations

Considering the available genetic variability in yield and stress (drought and high plant density) adaptive traits, and their range in mean yields and heritability, A-511 can be improved for both drought stressed and favourable environments. However, further testing with the involvement of mating design is essential, since the estimation of genetic variance through evaluation of S_1 lines cannot separate additive and non-additive components.

Based on observations at Melkasa where rainfall patterns are unpredictable, indirect selection under drought stressed high plant density conditions was suggested as a better alternative to direct selection for drought tolerance improvement. High plant density should be combined with intermediate drought stress by suspending irrigation one to two weeks prior to anthesis.

The increased potential in performance and tolerance to high plant density stress due to improvement made in drought tolerance, indicated tolerance to a number of abiotic stresses. Most of these crosses also gave higher yield than the local hybrids in rainfed, and various stress environments, indicating their suitability in variable environments. As a result, crosses from drought tolerant lines, especially using CML442 and Mex102, could be recommended for smallholder farmer conditions in rainfed environments of Ethiopia. Furthermore, these crosses showed relative yield stability across variable environments due to increased stress tolerance. Thus hybrids from drought tolerant parents with acceptable yield and stability can be recommended for resource limited farmers.

In rainfed environments of Ethiopia, hybrid performance was highly associated with parental trait responses, reflecting the need of improving *per se* performance of inbred lines. This study also confirmed the importance to improve line tolerance to drought occurring at flowering, while maintaining their capability to perform well under favourable conditions. Unlike in rainfed environments, a weak association was observed between crosses and parental lines performance in yield under drought stressed and irrigated conditions, suggesting the importance of combining ability testing in different environments for selection of lines that provide superior hybrids.

The observed increased tolerance and heterosis with increased stress confirmed that stress tolerance was more pronounced in crosses than in inbred lines. Furthermore, the superior hybrids obtained from drought tolerant parents are suggested for smallholder farmers due to their capability to combine stress tolerance and high yield potential.

Hoofstuk 7

Opsomming

Droogte en lae N is stremmingsfaktore wat gereeld mielieproduksie in die trope benadeel, waar die verre meerderheid van produsente beperkte toegang tot gevorderde tegnologie het. Vorige studies het aangetoon dat verbeterde verdraagsaamheid teen droogte tydens die blomstadium tot goeie produksie onder wisselvallige toestande kan lei, wat noodsaaklik is vir hulpbronbehoewende boere in lande soos Ethiopië. Bykomend tot sifting van teelmateriaal in reënvrye omgewings, is genotipiese variasie vir droogteaangepaste eienskappe in omgewingsaangepaste mieliepopulasies noodsaaklik vir suksesvolle teelverbetering.

By Melkasa in Ethiopië is 196 ewekansig verkreë S1 lyne uit Populasie A-511 by twee vogregimes en twee plantdigthede getoets vir opbrengspotensiaal sowel as droogte- en standaangepastheid. Plantdigtheid sowel as droogtestremming het beide die primêre en sekondêre droogteverwante eienskappe beduidend ge-affekteer. Droogte was egter meer effektief as hoë stand om opbrengs en opbrengskomponente te beïnvloed, sowel as om die interval tussen antese en baardverskyning of tyd tot 50% baardverskyning te verleng. Beduidende genotipiese variasie is binne Populasie A-511 vir opbrengs en stremmingsaangepastheidseienskappe gevind.

Die verwantskap tussen opbrengs en stremmingsaangepastheidseienskappe wat koppe plant^{-1}, pitte per kop^{-1}, pitte plant^{-1} en antese-baard interval ingesluit het, het toegeneem met toenemende stremming. Hierteenoor het die genotipiese variasie en erflikheid van opbrengs en opbrengskomponente met die uitsondering van meerkoppigheid, toegeneem met toenemende stremming. Wat die keuse van geskikte omgewings vir seleksie vir droogtegehardheid betref, was indirekte seleksie by hoë plantdigthede onder droogtestremming en direkte seleksie onder stremming by normale digthede ewe effektief.

Droogteverdraagsame lyne vanaf CIMMYT en hulle kruisings is afsonderlik by twee plantdigthede onder beide besproeiing en droogtestremming getoets, sowel as onder droëlandtoestande. Die doel was om hulle potensiaal, kombineervermoë en heterose onder nie-stremming en stremming te bepaal. Aansienlike verskille in prestasie is waargeneem. Meeste van die kruisings afkomstig vanaf droogtegeharde lyne het beter as plaaslike basters presteer, wat hulle geskiktheid vir die teikengebiede bevestig.

Onder droëlandtoestande het die meeste genotipes hoër opbrengste by hoë stand (88 800 plante ha^{-1}) as by die aanbevole stand vir lokale basters (44 400 plante ha^{-1}) gelewer. In ‘n bykomende eksperiment met onverbeterde S1 lyne uit Populasie A-511 het die omgekeerde gebeur. Die resultaat bevestig die verhoogde potensiaal wat droogteweerstand onder hoëstandstremming tot gevolg gehad het. Lyne CML442, Mex102, CML202 en Mex101 was superieur wat algemene prestasie en algemene kombineervermoë betref, veral ten opsigte van opbrengspotensiaal. Kruisings waarin hierdie lyne gebruik was, was ook superieur wat opbrengs en meeste ander eienskappe betref, ook ten opsigte van spesifieke kombineervermoë. Beide additiewe (algemene kombineervermoë) en nie-additiewe (spesifieke kombineervermoë) effekte was belangrik vir die uitdrukking van stremmingsaangepastheidseienskappe onder droëlandtoestande. Droogtegeharde lyne met hoë algemene prestasie onder droëland toestande het as kruisings ook hoë opbrengste onder soortgelyke omstandighede gelewer, wat op 'n prestasieverwantskap tussen kruisings en hulle ouerlyne dui.

Soortgelyk het droogtegeharde genotipes wat onder beide stremming en besproeiing ge-evalueer was, die hoogste opbrengs onder besproeing en hoë stand gelewer. Hierteenoor is die lyne en kruisings se opbrengs onder droogtetoestande en hoë stand met 73 en 56% respektiewelik verlaag. Verder het die beraamde heterose onder stremming toegeneem. Die resultate bevestig dat die verbeterde lyne en hulle kruisings verdraagsaam teenoor hoëstand stremming was en dat kruisings hoër verdraagsaamheid as hulle ouerlyne het. Toetsing van kombineervermoë in kontrasterende omgewings het 'n oorwegende rol van additiewe effekte vir sekondêre eienskappe en nie-additiewe effekte vir opbrengspotensiaal aangetoon. Ten opsigte van droogteaangepastheidseienskappe en opbrengs was die genotypes CML202 en Ken superieur in algemene kombineervermoë en algemene prestasie oor uiteenlopende omgewings, terwyl Mex101 superieur onder droogtestremming was. Van die kruisings was CML440 x Ken, CML440 x CML442 en Mex103 x CML202 relatief superieur in individuele sowel as oor omgewings.

Droogtegeharde genotipes wat onder 'n verskeidenheid van grond N en vogregimes goed presteer, word verwag om in verskillende omgewings beter opbrengste te lewer as gevolg van verminderde genotipe by omgewingsinteraksie (GOI). Die AMMI 2 model is suksesvol gebruik om droogtegeharde GOI patrone oor omgewings te beraam. Kruisings tussen droogtegeharde lyne het variabiliteit in gemiddelde opbrengs en GOI oor omgewings getoon. Hoog produserende basters soos Mex103 x CML442, Mex103 x CML202, CML440 x CML442, Mex101 x CML445, CML202 x CML445, CML202 x Ken, CML440 x Ken en BH140 het die minimum GOI getoon, wat dui op wye aanpassing oor stremmings- en nie-stremmingsomgewings. Hierteenoor was onstabiele hoog produserende basters soos Mex101 x Mex102, Mex101 x CML442 en Mex102 x CML442 beter aangepas by ongunstige omgewings, wat droogtestremming en verweerde bogrond insluit. In vergelyking met konvensionele basters het 22 en 26 kruisings tussen droogtegeharde lyne beter as BH540 gepresteer ten opsigte van opbrengs en stabiliteit respektiewelik. ‘n Ander plaaslike baster, BH140 was in albei opsigte beter aangesien dit ‘n topkruis is waarvan een ouer vir verminderde planthoogte verbeter was.

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Appendix I

Legend descriptions of map the dry land agro-ecological zones of Ethiopia.

A1-1	Hot to warm arid plains
A1-3	Hot to warm arid valleys and escarpments
A1-7	Hot to warm arid mountains
A2-1	Tepid to cool arid plains
A2-7	Tepid to cool arid mountains
M1-1	Hot to warm moist plains
M1-2	Hot to warm moist lakes and rift valleys
M1-3	Hot to warm moist valleys and escarpments
M1-4	Hot to warm moist gorges
M1-7	Hot to warm moist mountains
SA1-1	Hot to warm semi-arid plains
SA1-5	Hot to warm semi-arid mountains and plateau
SA2-2	Tepid to cool semi-arid lakes and rift valleys
SM1-1	Hot to warm sub-moist plains
SM1-2	Hot to warm sub-moist lakes and rift valleys
SM1-3	Hot to warm sub-moist valleys and escarpments
SM1-4	Hot to warm sub-moist river gorges
SM1-7	Hot to warm sub-moist mountains
SM2-1	Tepid to cool sub-moist plains
SM2-2	Tepid to cool sub-moist lakes and rift valleys
SM2-5	Tepid to cool sub-moist plains and mountains and plateau
SM2-7	Tepid to cool sub-moist mountains
SM3-7	Cold to very cold sub-moist mountains